

**INFLUENCE OF FIRE ON A RARE SERPENTINE PLANT
 ASSEMBLAGE: A 5-YEAR STUDY OF *DARLINGTONIA* FENS¹**

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- *Premise of the study:* Serpentine soils have attracted the attention of evolutionary biologists for decades because of their high number of rare and endemic taxa, though less is known about the ecological factors that govern the diversity and composition of serpentine communities. Theory suggests that vegetation on these low-productivity soils will be relatively resilient to fire, the most common natural disturbance in serpentine systems.
- *Methods:* We studied the recovery of vegetation in *Darlingtonia* fens, a unique habitat dominated by herbaceous perennials, from a major fire that burned ~202,000 ha in California and Oregon's Klamath Mountains in 2002. We established permanent plots in eight unburned and eight burned fens in 2003 and recorded percent cover of vascular plant species. We re-sampled plots each year through 2007.
- *Key results:* Burned fens had less plant cover than unburned fens for 2 yr after the fire. Average species density was ~10% lower in burned fens 1 yr after the fire but ~4–8% higher for the next 4 yr. Burned fens exhibited greater evenness but not until 4 yr after the fire. Differences in community composition were detected between the two fen types, but species ranks were similar, and species neither were added to nor removed from the burned assemblages.
- *Conclusions:* Burning of *Darlingtonia* fens has detectable, albeit modest, effects on serpentine communities. Because fens have little or no canopy cover, fire has little influence on light availability in this system. This relatively small resource change, combined with high soil moisture and well-developed underground organs of fen plants, produces a highly resilient assemblage.

Key words: Biscuit Fire; *Darlingtonia californica*; *Darlingtonia* fens; edaphic ecology; fire ecology; Klamath Mountains province; plant diversity; rarity; serpentine; ultramafics.

Serpentine soils harbor some of the Earth's most unique and unusual vegetation (Whittaker, 1954; Brooks, 1987; Kruckeberg, 2002). Found on every continent, serpentine soils are derived from ultramafic parent material and are notable for their lack of essential nutrients; high concentrations of potentially toxic heavy metals such as nickel, chromium, and cadmium; and low Ca²⁺/Mg²⁺ ratios (Kruckeberg, 1984; Alexander et al., 2006). These characteristics generally result in vegetation with physiognomies that are strikingly different from those of surrounding soil types. For example, serpentine vegetation often comprises xeromorphic taxa that exhibit relatively slow growth and a

stunted appearance (Roberts and Proctor, 1992). In addition, high levels of plant species diversity and endemism are found on many serpentine formations (Brooks, 1987; Harrison et al., 2006). For instance, although serpentine habitat occupies only 1.5% of California, it harbors 12.5% of the state's endemic plants (Harrison, 1997; Safford et al., 2005). Given their unique edaphic conditions and flora, it is not surprising that serpentine regions have long fostered interests in speciation and ecotypic differentiation among taxonomists and evolutionary biologists (Kruckeberg, 1967; Antonovics et al., 1971; Shaw, 1990; Harrison and Rajakaruna, 2011). In contrast, work on basic ecological processes on serpentine soils has begun to gain increased attention only more recently (Boyd et al., 2009). The work we present here focuses on the role of disturbance, in particular, fire, in shaping serpentine plant assemblages. Our work explores the suggestion that serpentine assemblages tend to be relatively stable compared with those on more productive sites, a result of low biomass and comparatively small changes in aboveground competition (Harrison et al., 2003; Safford and Harrison, 2004; Eugenio and Lloret, 2006).

Large expanses of serpentine substrate include, for example, those of New Caledonia, Cuba, Mediterranean Europe, central Brazil, and western North America (Brooks, 1987). Of the western North American serpentine complexes, the largest contiguous areas of serpentine are found in the Klamath Mountains of northern California and southwestern Oregon (Coleman and Kruckeberg, 1999). This region is well known for its diverse and heterogeneous vegetation (Whittaker, 1960; Irwin, 1966;

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DellaSala et al., 1999; Sawyer, 2007). Within the xeric serpentine landscapes of the Klamath Mountains are discrete, isolated wetlands that are dominated by *Darlingtonia californica* Torrey (California pitcher plant; Sarraceniaceae), an insectivorous plant restricted to southwestern Oregon and northern California (Schnell, 1976). Fed by perennial sources of cool water, these serpentine wetlands, or “*Darlingtonia* fens,” remain moist during summer, a time when upland vegetation experiences a prolonged dry season of approximately 5 mo. The constant moisture in fens results in continually saturated soils that allow for little aerobic decomposition, leading to accumulations of decomposed organic matter (peat or muck) with limited available nutrient content (Tolman, 2007; Sawyer et al., 2008; Franklin, 2009). Besides providing habitat for *D. californica*, fens support small, isolated populations of several rare and regionally uncommon mesophytic plant species, such as *Gentiana setigera* A. Gray (Mendocino gentian), *Hastingsia bracteosa* var. *bracteosa* Watson (large-flowered rush-lily), and *Viola lanceolata* subsp. *occidentalis* (A. Gray) Russell (western bog violet) (Frost and Jules, 2007).

Fire is by far the most important source of disturbance for serpentine plant communities in northern California and southwestern Oregon (Atzet and Martin, 1992; Fry and Stephens, 2006; Skinner et al., 2006). Before contemporary fire-suppression efforts, upland serpentine areas experienced median fire return intervals from 8 to 42 yr (Skinner, 2003a; Taylor and Skinner, 2003), and *Darlingtonia* fens experienced median fire return intervals of 18 to 42 yr (Skinner, 2003b; Skinner et al., 2006). Although fire is a potentially important and historically frequent agent of disturbance, few studies have assessed the effects of fire on upland serpentine vegetation (Tyndall, 1994; McCoy et al., 1999; Harrison et al., 2003; Safford and Harrison, 2004), and only one study to date has assessed the role of fire in *Darlingtonia* fens specifically (Cramer, 2005; see also Borgias and Biegel, 1998, for a qualitative study). Cramer (2005) attempted to survey all vascular plant species in 24 *Darlingtonia* fens and found that fire significantly reduced tree and shrub canopy cover but had no effect on the total percent cover of herbaceous and graminoid species.

The effects of fire on vegetation have received considerable attention from ecologists in more common, nonserpentine ecosystems (e.g., Agee, 1993; Whelan, 1995; Bond and van Wilgen, 1996; Keeley et al., 2005; Webster and Halpern, 2010). Because of the rapid accumulation of fuel in highly productive sites, these locales may experience relatively dramatic vegetation changes due to fire, where intense aboveground competition is temporarily reduced, and factors that control recruitment and growth become more important (Bond and van Wilgen, 1996). Conversely, the impact of fire on low-productivity sites may be less pronounced, as these are often open habitats in which light is not a limiting resource (e.g., Safford and Harrison, 2004; Eugenio and Lloret, 2006). For example, Safford and Harrison (2004) suggested that serpentine floras may be less influenced by fire than other, more productive chaparral on nearby sandstone substrates (see also Harrison et al., 2003). *Darlingtonia* fens have several features that similarly may lead to dampened fire effects on vegetation, including their nutrient-poor serpentine parent material and low productivity. Fen soils in our study area contain exceptionally low concentrations of nitrogen (Franklin, 2009; see also Tolman, 2007), and they support generally open (or absent) canopies (Cramer, 2005). In addition, fens are dominated by rhizomatous perennial species (Frost et al., 2004; Cramer, 2005) that may quickly regenerate

aboveground biomass after fire. The relatively small number of studies regarding the effects of fire on serpentine vegetation, however, limit any generalizations that can be made for how *Darlingtonia* fen vegetation will respond to wildfire.

Our study assessed the impact of fire on *Darlingtonia* fen plant assemblages by taking advantage of the 2002 Biscuit Fire, a lightning-ignited fire that burned ~202,000 ha in northern California and southwestern Oregon (USDA Forest Service and BLM, 2004). Because the fire burned across many different vegetation types, including numerous *Darlingtonia* fens, it provided an unparalleled opportunity to study the effects of fire on various taxonomic groups and ecosystem processes (Ratchford et al., 2005; Donato et al., 2006; Sanders et al., 2007; Thompson et al., 2007; Fontaine et al., 2009; Wittman et al., 2010). In the study presented here, we used a set of eight unburned and eight burned fens to examine the effects of burning on plant cover, species density and diversity, evenness, and community composition. Although the unpredictable timing of the Biscuit Fire did not allow for preburn data to be collected, our study analyzes data from fixed plots for vascular plants over the course of 5 yr (2003–2007) after the fire. We predicted that the life histories of plants in *Darlingtonia* fens (i.e., perennials with well-developed underground storage organs) coupled with low site productivity and high summertime moisture would minimize species losses and changes in community structure and composition resulting from fire.

MATERIALS AND METHODS

Study sites—We studied the vegetation in unburned and burned *Darlingtonia* fens on the serpentine soils straddling the border of northern California and southwestern Oregon (see also Ratchford et al., 2005; Sanders et al., 2007; Wittman, 2010). The area is characterized by a Mediterranean climate with warm, dry summers and mild, wet winters (Whittaker, 1960). On average, the region experiences ~154 cm precipitation annually, though only ~4 cm falls between June and August. Common serpentine plant associations in the Klamath Mountains include Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) savanna, knobcone pine (*P. attenuata* Lemmon) forest, mixed conifer forest, and serpentine meadows and barrens (Whittaker, 1960). Within our study area, *Darlingtonia* fens are found across an elevational range of 200–1300 m, though the majority of fens occur between 350 m and 600 m (Frost et al., 2004). In addition to the dominant *D. californica*, the distinct vegetation of *Darlingtonia* fens is composed mainly of perennials such as *Narthecium californicum* Baker (California bog asphodel), *Sanguisorba officinalis* L. (great burnet), *Rudbeckia californica* A. Gray (California coneflower), and other hydrophytic forbs and graminoids (Frost et al., 2004). Several trees and shrubs, including *Chamaecyparis lawsoniana* A. Murray (Port Orford cedar), *P. jeffreyi*, *Rhododendron occidentale* Torrey & A. Gray (western azalea), and *Ledum glandulosum* Nutt. (Labrador tea), grow in *Darlingtonia* fens.

In the summer of 2003, 1 yr after the Biscuit Fire, we established a permanent 8 × 8 m plot in each of 16 fens (eight unburned and eight burned) within or immediately adjacent to the fire boundary. We chose fens that had no apparent human disturbance and were large enough to contain an 8 × 8 m plot. Plots were positioned in randomly selected locations within fens, though we excluded areas that were encroached by large trees that reduced the cover of the dominant fen vegetation (i.e., herbaceous perennials). Nine fens were within the Rogue River–Siskiyou National Forest, six sites were in the Six Rivers National Forest, and one was on land administered by the Bureau of Land Management.

Data collection—Within each 8 × 8 m plot, we established 25 subplots 0.5 m × 0.5 m (0.25 m²), with each subplot separated from the others by 2 m in a 5 × 5 grid. Measurements in each subplot were done by using a quadrat divided into 100 separate cells; each cell represented 1% of the quadrat. In a few cases, subplot locations included large trees (usually dead snags), in which case subplots were relocated a short distance away in one of the four cardinal directions to avoid shading and tree roots. Between late June and early August in each summer from 2003 through 2007, we recorded percent cover (as the fraction of the 100 grid cells in a subplot) of all vascular plant species in each of the subplots

at each of the 16 sites. Because of the remote locations of many of our sites, we were able to visit each fen only once each year. Although unburned and burned fens did not differ significantly in elevation (Table 1), we attempted to sample the lowest sites first to minimize phenological differences among sites.

At each fen, we recorded location and elevation using a handheld Garmin GPS 12 XL (Garmin International, Olathe, Kansas, USA). Several site characteristics also were recorded at each fen. Fen slope was recorded with a clinometer (Suunto, Vantaa, Finland), and percent open canopy was recorded with a spherical densiometer (Forest Densimeters, Arlington, Virginia, USA). Aspect was recorded with a standard compass. We used a geographic information system (GIS) to determine latitude, longitude, and the nearest distance to the Pacific Ocean for each fen. Lastly, to estimate burn intensity, in the summer of 2003 we classified each plot into one of five categories by visually assessing trees near our plots: unburned, low-intensity burn (<10% canopy mortality), moderate-intensity burn (>10 to <80% canopy mortality), high-intensity burn (>80% canopy mortality with dead needles on trees), and extreme-intensity burn (>80% mortality with no needles on trees).

Species identification—Because we visited fens only once per year, we could not identify every plant to the species level; some plants were grouped together at the genus level. For the graminoids overall, although at least 15 species have been identified within *Darlingtonia* fens, we included only five distinguishable taxa: *Danthonia californica* Bolander (California oat grass), *Eriophorum criniger* (A. Gray) Beetle (cotton grass), *Calamagrostis* spp. (reedgrasses), *Carex* spp (sedges), and all other graminoids (“unknown graminoids”). In addition, three potential *Epilobium* (fireweed) species are within fens, though we grouped them together in a single genus. Lastly, all pine seedlings were lumped into one group (*Pinus* spp.), though there are potentially four pine species: *P. attenuata*, *P. contorta* subsp. *contorta* Loudon (lodgepole pine), *P. jeffreyi*, and *P. monticola* Douglas (western white pine). Nomenclature follows Hickman (1993).

Data analysis—We used repeated measures analysis of covariance (ANCOVA) to examine differences in percent total plant cover between unburned and burned *Darlingtonia* fens over the 5 yr of our study. To control for differences among the sites in factors other than whether they burned, we included a covariate that accounted for variation in the suite of geographic variables and site characteristics we measured (Table 1). Because of a high degree of collinearity among some of the site measures, we used principal components analysis (PCA) to reduce the seven characteristics (Table 1). We used the PCA score for each site as the covariate in the ANCOVA. This principal axis accounted for 58% of the variance in the data and reflected the influence of all site variables except aspect (Table 2). In three additional tests, we used repeated measures ANCOVA to assess the effects of fire on species density (species per 25 plots × 0.25 m² = 6.25 m²), Jost’s true diversity, and evenness. Species density, the number of species per unit area (sensu Gotelli and Colwell, 2001) is the number of species in a defined area. Jost’s true diversity (Jost, 2007) is defined as exp(*H*), where *H* is the Shannon index (*H*):

$$H = -\sum_{i=1}^S p_i \ln p_i$$

To estimate evenness, we used Hurlbert’s (1971) probability of an interspecific encounter (PIE):

$$PIE = \frac{N}{(N-1)} \left(1 - \sum_{i=1}^S p_i^2 \right)$$

where *N* is the total cover of individual species sampled, *S* is the number of species, and *p_i* is the proportion of the sample comprising species *i*. PIE is an estimate of the probability that two randomly sampled individuals (or points of coverage) represent two different species. PIE is equivalent to the slope of an individual-based rarefaction curve measured at its base (Olszewski, 2004). To understand the potential impact of fire on individual taxa, we used separate repeated measures ANCOVAs for each of the seven dominant plant species. Rather than adjust the critical level (alpha) for rejection of the null hypothesis because of multiple tests, we simply report actual *P* values (cf. Gotelli and Ellison, 2004). Here again, the first principal component was used as a site covariate. We also constructed rank abundance curves for each of the 5 yr to visually assess differences in richness and evenness between the two fen types. Differences in species abundance between plots in unburned and burned fens were compared for each of the 5 yr with Kendall’s tau (τ). The Kendall’s rank tests and ANCOVAs were performed with SPSS 16.0 (Levesque, 2007), and the PCA was performed with the princomp function in R version 2.9 (R Development Core Team, 2007).

We used nonmetric multidimensional scaling (NMDS) ordination and multiresponse permutation procedure (MRPP) performed in PC-ORD version 5.1 (McCune and Mefford, 2006) to examine whether community composition differed between unburned and burned fens across and during each of 5 yr. Before this analysis, we removed species that were present in fewer than 5% of plots (9 of 49 taxa) to reduce noise from infrequent taxa that provide little community information. For the NMDS ordination, we used PC-ORD’s “slow and thorough” mode, which uses a random starting configuration and Sørensen distances to express the community similarities. Fifty runs with real data and 250 runs with randomized data for a Monte Carlo test of significance were used. We used MRPP as a test for significant differences in community composition between unburned and burned fens for each of the 5 yr of the study.

To detect differences in temporal trends in species assemblages between unburned and burned *Darlingtonia* fens, we used an index of temporal change developed by Gotelli et al. (2010). We first calculated the slope *b_i* of a simple linear regression of percent cover (*Y*) vs. year (*X*) for each species *i* = 1 to *S* in the assemblage, fitting the model to the 5 consecutive years of census data:

$$Y = a_i + b_i X$$

Next, we created two indices to summarize community change in each plot, average trend (*AvgTrend*) and temporal change (*TC*). *AvgTrend* is the mean of the slope estimates for a single plot, and *TC* is the sample variance. A large

TABLE 1. Summary of study site attributes for 16 *Darlingtonia* fens. Burn intensity values are unburned (0), low intensity (1), moderate intensity (2), high intensity (3), and extreme intensity (4); see text for details. Latitude and longitude are given as decimal degrees (dd).

Site name	Burned?	Burn intensity	Latitude (dd)	Longitude (dd)	Distance to coast (km)	Elevation (m)	Aspect (°)	Open canopy (%)
Dragonfly	No	0	42.09	124.06	16.447	498	340	88.5
Happy	No	0	42.21	123.78	36.317	569	40	94.25
Lone Mtn 1	No	0	42.07	123.92	38.968	522	65	92
Lone Mtn 2	No	0	42.15	123.85	36.171	522	150	95.75
Scrap	No	0	42.48	123.8	52.574	427	170	94.25
Southside	No	0	42.49	123.79	52.654	424	140	93.75
Star Flat	No	0	42.47	123.87	53.72	392	150	93
Whiskey Creek	No	0	42.12	123.87	35.949	524	340	88
Greg’s	Yes	2	42.13	124.19	21.141	540	260	67
L.E. Horton	Yes	3	42.00	124.08	16.447	475	60	90.25
Shoot	Yes	4	42.17	124	27.251	685	260	60.75
Upper Days Gulch	Yes	1	42.41	123.91	48.392	510	90	93.25
O23	Yes	2	42.44	123.89	50.49	448	20	90.75
Aimee’s	Yes	4	42.07	124.12	26.839	568	170	80.5
Cedar Root	Yes	3	42.18	123.97	20.971	466	200	85.75
Diamond Creek	Yes	3	42.1	124.07	28.305	792	110	77.5

TABLE 2. Factor loadings describing the contribution of fen characteristics to six principal component (PC) axes.

Site factor	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
Burn intensity	0.374	0.458	0.177	0.399	0.572	0.29
Latitude (decimal degrees)	-0.394	0.154	0.574	0.219	-0.095	0.258
Longitude (decimal degrees)	0.438	-0.011	-0.050	0.416	-0.731	0.306
Distance to coast (km)	-0.436	0.223	0.373	-0.115	-0.255	0.093
Elevation (m)	0.343	0.331	0.099	-0.773	-0.106	0.362
Aspect (°)	0.197	-0.776	0.423	-0.093	0.199	0.331
Open canopy (%)	-0.409	-0.074	-0.555	0.030	0.111	0.711
Variance explained	57.7%	15.8%	12.3%	9.1%	2.8%	1.4%

value of *AvgTrend* means the slopes of temporal change for most species in the assemblage are large. A large value of *TC* means the variance is high, so some species are increasing steeply, whereas others are remaining constant in abundance or declining. Differences in *AvgTrend* and *TC* indices between burned and unburned fens were assessed with ANCOVA, with the first principal component score as our covariate describing site variation. Temporal change was log-transformed before analysis.

RESULTS

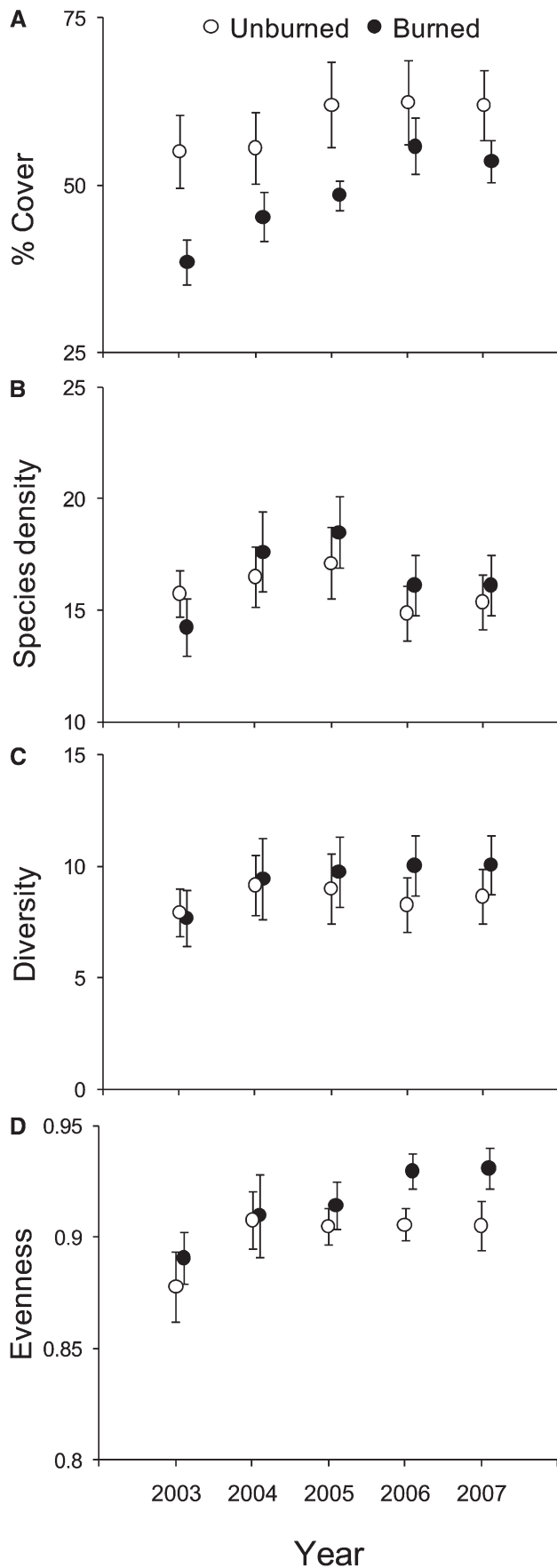
We recorded 44 species and five taxon groups that included multiple species (e.g., *Calamagrostis* spp.; see *Species identification* section in Materials and Methods) in the *Darlingtonia* fen plots during the 5-yr study. A total of 38 taxa were found in the eight unburned fens, and 46 taxa were found in the eight burned fens (Appendix S1; see Supplemental Data with the online version of this article). Only three tree taxa occurred in the plots, all of which were seedlings or saplings: *Pseudotsuga menziesii* (Mirbel) Franco (Douglas fir), *C. lawsoniana*, and *Pinus* spp. In total, we detected seven shrub species, 34 forbs, and five graminoids. All the species we identified were perennials except for *Hypericum anagalloides* Cham. & Schldl. (tinker's penny), which is known to be either annual or perennial (Hickman, 1993). Although we could not identify every plant to the species level, the genera in which these unidentified plants are found include only perennials known from *Darlingtonia* fens. We detected one rare plant species (*Epilobium oregonum* E. Greene, Oregon willow-herb) in three unburned and three burned fens. *Epilobium oregonum* is listed as a species of concern by the U.S. Fish and Wildlife Service and as a sensitive species by the U.S. Forest Service and BLM (Frost and Jules, 2007). In the sites in which *E. oregonum* was detected, cover was always <1%. No nonnative species were detected in any of the fens. The complete lack of nonnatives and annuals (except *H. anagalloides*) in our sites is in agreement with past studies of *Darlingtonia* fens (Cramer, 2005; Tolman, 2007).

Percent plant cover did not differ significantly between unburned and burned *Darlingtonia* fens ($F_{1, 312.3} = 0.481$, $P = 0.5$), though unburned fens tended to have higher cover, and the differences were most pronounced 1 yr after the fire (Fig. 1). Among individual fens, cover ranged from 23.8% (in a burned fen the year after the fire, 2002) to 89.2% (in an unburned fen in 2006). Cover increased over the course of the study ($F_{4, 424.6} = 8.633$, $P < 0.001$), especially in the first 3 yr (Fig. 1). However, the rate of change in cover did not differ between unburned and burned fens ($F_{4, 38.1} = 0.775$, $P = 0.546$). Species density ranged from 24 taxa per = 6.25 m² in a burned fen 3 yr after the fire to nine taxa in two fens, including a burned fen the year after the fire and an unburned fen 4 yr after the fire. On average, species density was 5–8% greater in burned fens in all years except for

the first year after the fire (Fig. 1). During the first year after the fire, burned fens had, on average, 10% fewer species recorded. Overall differences in species density between fen type were marginally significant ($F_{1, 137.4} = 3.79$, $P = 0.074$). Species density varied significantly over the 5 yr ($F_{4, 21.9} = 13.21$, $P < 0.001$), with average species density peaking 3 yr after the fire for both unburned and burned fens (Fig. 1). Site characteristics, as described by the first principal component, were strongly related to species density ($F_{1, 510.3} = 14.05$, $P = 0.002$).

True diversity did not differ between unburned and burned fens ($F_{1, 0.81} = 0.077$, $P = 0.785$; Fig. 1). Diversity increased significantly over the 5 yr of the study ($F_{4, 7.16} = 8.399$, $P < 0.001$), though unburned and burned fens changed similarly through time ($F_{4, 0.518} = 0.607$, $P = 0.659$). Site characteristics had a marginally significant impact on diversity ($F_{1, 36.56} = 3.51$, $P = 0.084$). Interestingly, sampling in only 1 yr would have led to differing results: sampling in 2006 or 2007 would have yielded marginally higher diversity in burned fens (2006: $t = 1.82$, $df = 14$, $P = 0.090$; 2007: $t = 1.76$, $df = 14$, $P = 0.109$). Evenness was greater in burned fens, though the differences were marginally significant ($F_{1, 0.01} = 3.017$, $P = 0.106$). Differences in evenness between unburned and burned fens were greatest in the last 2 yr of the study (Fig. 1). Evenness varied significantly among the 5 yr of the study ($F_{4, 0.003} = 6.367$, $P < 0.001$), though interannual differences were similar among unburned and burned fens ($F_{4, 0.001} = 0.395$, $P = 0.811$). Evenness was lowest for both unburned and burned fens in the first year after the fire (Fig. 1). As with species diversity, sampling evenness would have yielded significant differences only in the last 2 yr of the study (2006: $t = 2.29$, $df = 14$, $P = 0.038$; 2007: $t = 1.85$, $df = 14$, $P = 0.085$).

A high level of concordance existed in the ranks of species between unburned and burned fens in all 5 yr (for all years $\tau \geq 0.6$, $P < 0.001$). That is, common species in burned fens tended to be common in unburned fens also. However, the order of dominance differed for several of the most abundant species between unburned and burned fens, and differences between unburned and burned fens were variable among species (Figs. 2, 3). For instance, *S. officinalis* remained the dominant species in both fen types, and its abundance did not differ significantly between fen types ($F_{1, 47.0} = 0.44$, $P = 0.517$). Similarly, the abundances of *N. californicum* and *R. californica* did not differ between fen types ($F_{1, 175.1} = 18.88$, $P = 0.370$; $F_{1, 62.8} = 0.452$, $P = 0.513$; respectively). *Rudbeckia californica*, usually the fourth most dominant plant in unburned fens, was reduced to the tenth most abundant plant in burned fens, though this is likely to be an artifact of one unburned fen that had 3–5× more *R. californica* cover than other unburned fens, depending on the year. *Darlingtonia californica* was always one of the four most abundant plants, regardless of fen type, but we detected at best a marginally significant difference between unburned and burned



fens ($F_{1,119.4} = 3.44, P = 0.087$); approximately half the cover of *D. californica* occurred in burned fens as compared with unburned fens. In contrast, the cover of *E. criniger* was significantly higher in burned fens ($F_{1,294.7} = 6.17, P = 0.027$). Its cover was 1.7× higher in burned fens the year after the fire, and at the end of our study *E. criniger* was 2.2× higher in burned fens. Lastly, *Ledum glandulosum* was one of the top four ranked plants in burned fens but was ranked no higher than ninth in unburned fens. Differences in *L. glandulosum* did not differ significantly between fen types ($F_{1,5.4} = 0.129, P = 0.725$).

Nonmetric multidimensional scaling ordination resulted in a 3-dimensional configuration that described 87% of the variation in the species matrix with a final stress of 13.15. The MRPP result shows that variation in composition is greater between fen types (burned vs. unburned) than among fens of the same type (Fig. 4) in all years except 2004 (2003: $T = -1.91, P = 0.045$; 2004: $T = -0.87, P = 0.185$; 2005: $T = -1.90, P = 0.045$; 2006: $T = -1.86, P = 0.047$; 2007: $T = -2.09, P = 0.032$). The ordination suggests that, on average, burned fens tended to be more similar from year to year than were unburned fens (Fig. 4). *AvgTrend* was similar in unburned and burned fens ($F_{1,0.004} = 0.13, P = 0.6$; Fig. 5), indicating comparable rates of average temporal change for species in each assemblage. The *TC* values were similar in burned and unburned fens ($F_{1,0.649} = 1.12, P = 0.309$; Fig. 5), meaning that temporal trajectories among species exhibited similar amounts of variance. However, *TC* values were significantly more variable for unburned fens (Levene's test: $F = 7.511, df = 1, P = 0.016$); the range of *TC* in unburned fens was ~3.5× that found in burned fens (Fig. 5). Site characteristics as described by the first principal component were related, though weakly, with *TC* ($F_{1,2.04} = 3.51, P = 0.083$).

DISCUSSION

Our expectations were that communities would reassemble after the fire on a trajectory to become more similar to prefire conditions, and that at least initially some dramatic changes in composition would occur in burned fens, regardless of the generally dampening effects predicted on serpentine. However, the changes resulting from fire we observed were modest and often not immediate, nor did they include any apparent colonization or extinction events. Overall, burning led to increases in species density of approximately 0.8 to 1.4 species per plot (6.25 m²) and to slight increases in species diversity and evenness. Increases in diversity and evenness, however, were not apparent until 4 yr after the fire. Most of the dominant fen species showed no detectable responses to fire, whereas *D. californica* showed modest decreases, and *E. criniger* showed only a modest increase (Fig. 2). In total, changes in species densities and abundances resulted in significant differences in community composition (as indicated by MRPP) for 4 of the 5 yr of this study. Interestingly, ordination indicated that burned fens changed less during the course of our study than did unburned fens: the average ordination solution for unburned fens showed more than twice the year-to-year variation as did burned fens (Fig. 4). Similarly, the *TC* index showed that burned fens exhibited less disparity

Fig. 1. Average percent cover (A), species density (number of species per 6.25 m²) (B), Jost's diversity ($\exp[H]$) (C), and evenness (Hurlbert's PIE) (D) for plots in unburned (n = 8) and burned (n = 8) *Darlingtonia* fens. Error bars show ±1.0 SE. Data are jittered to avoid overlap.

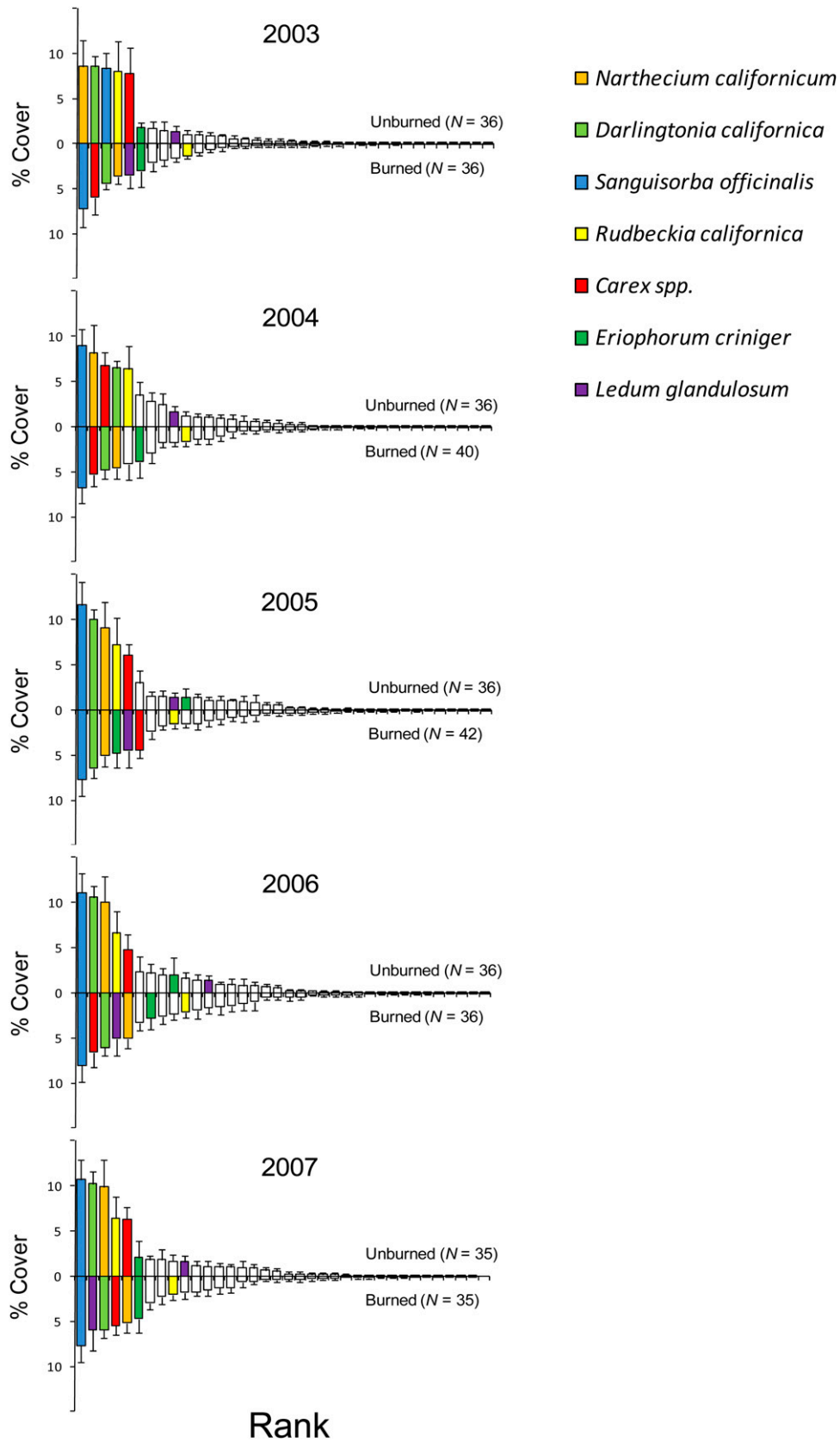


Fig. 2. Rank abundance curves for vegetation in unburned ($n = 8$) and burned ($n = 8$) *Darlingtonia* fens for the years 2003–2007. Bars indicate mean cover found in the eight fens of each type, and error bars indicate ± 1.0 SEM. Colors indicate individual species and are intended to highlight both temporal changes and differences among fen type for seven dominant species.

in the amount of variance in species responses over the 5 yr (Fig. 5). In other words, the amount of change that occurred was quite similar in burned fens assemblages, whereas unburned fens showed more variable temporal patterns of change among fens. This indicates that the fire homogenized these plant assemblages and, perhaps more importantly, restricted their trajectories within relatively narrow bounds.

Cover in burned *Darlingtonia* fens was, on average, 39% the year after the Biscuit Fire, whereas cover in unburned fens was approximately 55% (Fig. 1). The difference in cover between fen types gradually diminished during the course of our study, and by 2007, 5 yr after the fire, burned fens had 54% cover and unburned fens had 62% cover (Fig. 1). Importantly, differences between cover in unburned and burned fens were not signifi-

cant. However, had we conducted our study during only a single year, we would have detected differences in cover between burned and unburned fens only in 2003 and 2005. Interestingly, another study of *Darlingtonia* fens burned during the Biscuit Fire (Cramer, 2005), conducted 2 yr after the fire in 2004, did not detect differences in herbaceous cover. It is possible that differences were largely diminished by 2004 in Cramer's (2005) study fens, of which only three of their 24 were used in our study. In addition, Cramer's (2005) use of broad cover values (i.e., a modified Daubenmire scale) may have reduced her ability to detect differences. Given the results of our work, it appears that the influence of fire on cover of these unique perennial herbaceous plant communities is immediate and temporary, and it can persist for approximately 3 yr.

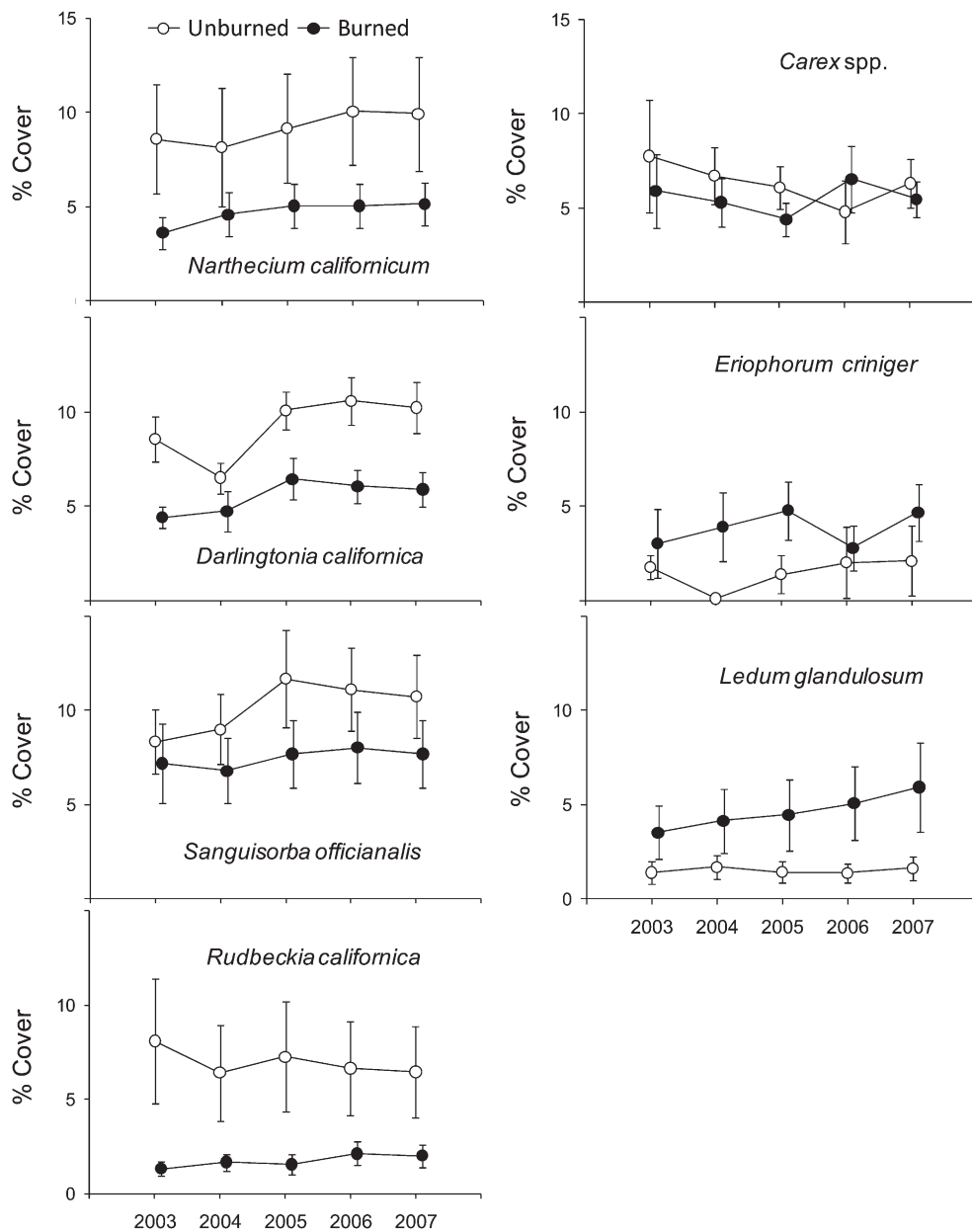


Fig. 3. Average percent cover of seven dominant species in unburned (n = 8) and burned (n = 8) *Darlingtonia* fens. Error bars show ± 1.0 SE. Data are jittered to avoid overlap.

It is also worth noting that cover increased not only for burned fens but also for unburned fens during the 3 yr after the fire (Fig. 1). We consider two plausible explanations of the similar pattern seen in both habitat types. First, the dense smoke that covered much of the region from late July 2002 until well into the autumn could have temporarily reduced cover in the unburned fens. Smoke has been shown to have significant effects on plant productivity, even in areas outside of the immediate fire (Davies and Unam, 1999; Calder et al., 2010). Second, 2001–2003 included notably dry summers in the study region as measured by the Palmer Drought Severity Index (PDSI), an index of soil moisture, temperature, precipitation, and evapotranspiration, where higher PDSI indices indicate low moisture stress (Palmer, 1965). The summertime PDSI value (June–August) for the previous 10 yr (1991–2000) was always positive and averaged 2.36. In contrast, the indices for the years 2001, 2002, and 2003 were -2.56 , -1.89 , and -1.21 , respectively. It is possible that throughout our study, all the fens were recovering from smoke or drought regardless of whether they had burned.

It is difficult to compare our results with those of other studies concerning the effects of fire on vegetation. The majority of fire-effects studies focus solely on dominant species (e.g., trees, shrubs), or they combine all species into large taxonomic groups such as graminoids, herbs, and shrubs (e.g., Menges et al., 1993; Albrecht & McCarthy, 2006; Blankenship and Arthur, 2006). Few studies take the approach that we did with *Darlingtonia* fens, in which changes in entire plant communities or metrics such as species density, diversity, and evenness were measured. In addition, many fire studies, quite appropriately, assess the effects of varying frequencies of fire (e.g., Collins, 1992; Mehlman, 1992; Glitzenstein et al., 2003) rather than make simple comparisons of unburned vs. burned sites. Nonetheless, those studies that do assess full suites of community metrics sometimes demonstrate dramatic increases in species richness. For example, fire can double plant richness in productive forest systems (e.g., Brockway and Lewis, 1997; Webster and Halpern, 2010). Less dramatic increases are frequently observed (Uys et al., 2004; Hutchinson et al., 2005; Collins et al., 2007; Schwilk et al., 2009), though these results may reflect the limited length of the studies (Webster and Halpern, 2010). Far fewer studies have been conducted in wetlands as compared with other, more xeric habitats. Moreover, wetland fire studies are difficult to compare directly with our own because they usually assess effects on only dominant species or broad taxonomic categories, or they assess individual species separately rather than use any conglomerate metrics like diversity or evenness (Timmins, 1992; Gabrey et al., 1999; Main and Barry, 2002; Hinman and Brewer, 2007). Nonetheless, it is clear that fire exhibits variable effects on wetland vegetation. For example, fire can double species richness in peatlands of New Zealand (Norton and de Lange, 2003) but have no effect on richness of Carolina bay wetlands in the southeastern United States (Kirkman and Sharitz, 1994).

No other study to date has assessed the factors that govern richness, diversity, or evenness of plant assemblages in *Darlingtonia* fens (but for ants, see Ratchford et al., 2005). Cramer (2005) measured cover of all vascular plant species in unburned and burned fens but did not measure any of the standard community metrics. In upland serpentine habitats, however, work by Harrison et al. (2003) and Safford and Harrison (2004) closely mirrors our own. In that work, a total of 33% more species were found in burned serpentine than in unburned serpentine. That increase was observed among twenty 250-m² plots in each habitat type. At a smaller scale, they noted an average of

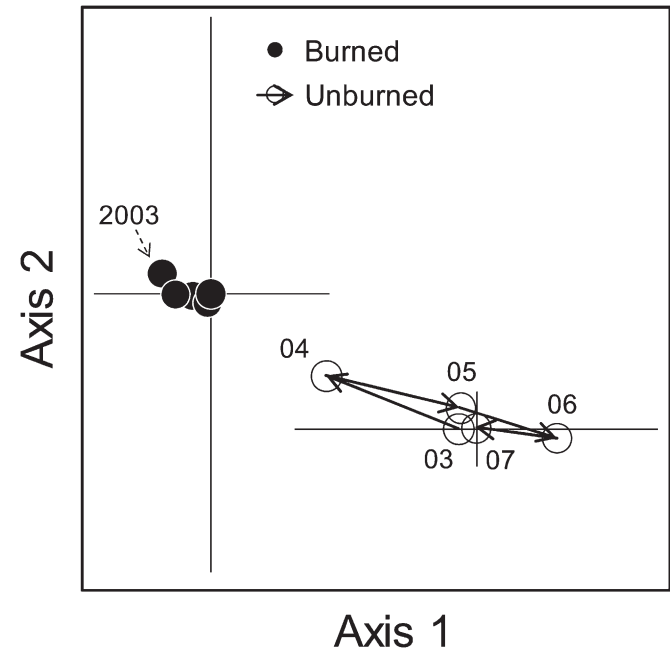


Fig. 4. Nonmetric multidimensional scaling of vegetation in unburned ($n = 8$) and burned ($n = 8$) *Darlingtonia* fens. Error bars (± 1.0 SE) describe the variation among plots in unburned and burned plots and are shown for the year 2007 only. Lines show the sequence of years for unburned plots but are not included for burned plots.

1.9 more species per 5 m² in burned serpentine habitat than in unburned serpentine habitat (Harrison et al., 2003), which is in agreement with the differences we found in *Darlingtonia* fens. Our work supports the prediction made by Safford and Harrison (2004) that fire would have relatively modest effects on serpentine floras. Taken together, the previous work on serpentine habitat and our own suggest that burning has relatively small yet positive influences on the number of species in local serpentine plant assemblages.

Safford and Harrison (2004) suggested that modest effects of fire on serpentine vegetation vs. adjacent sandstone vegetation were due to lower fertility of serpentine soils and the resulting open structure of serpentine vegetation. Because space and light are less likely to be limiting resources on serpentine than on sandstone soils, fire does not produce dramatic increases in the availability of these resources on serpentine. In our study, in which canopy cover is low and many species have well-developed rhizomatous networks, most species were able to quickly regenerate aboveground foliage after the fire. Extensive rhizomatous networks were visible in our burned fens in which fire had consumed much of the surrounding matrix of peat. Nitrogen availability had been assessed in nine of our 16 *Darlingtonia* fens and surrounding upland soils in a previous study (Franklin, 2009). That work, which was done 5 yr after the Biscuit Fire, found exceptionally low levels of available nitrogen ($0.01\text{--}0.025$ $\text{NH}_4^+\text{-N mg}\cdot\text{g}^{-1}$ and $\text{NO}_3\text{-N mg}\cdot\text{g}^{-1}$). Differences in nitrogen between unburned and burned sites were not detected, nor were differences detected between fen and upland soils (Franklin, 2009). Although ephemeral changes due to burning may have been missed in that study, it is clear that *Darlingtonia* fens and their surrounding matrix are nutrient limiting. We suggest that vegetation in fens seems to be resilient to fire because of high

moisture content, low productivity (and the resulting low fire intensity), as well as the dominance of perennials with large rhizomatous networks. Lastly, the lack of recruitment from seed banks may explain the small turnover of serpentine species (see also Safford and Harrison, 2004). Although little is known about seed banks in *Darlingtonia* fens, high soil moisture and the resulting low fire intensity may reduce postfire germination. Interestingly, *H. anagalloides*, the only plant we found that was not a perennial (i.e., it can be an annual or biennial) was found in six unburned fens but only one burned fen. Because it is short lived, *H. anagalloides* would be expected to have a well-developed seed bank, but it was either not present or was not stimulated by the fire.

Our study results indicate that few species show significant changes in abundance as a result of fire. Of the seven dominant plants, only *D. californica* appeared to have been significantly negatively affected, and this effect was still visible 5 yr after the fire (Fig. 3). In contrast, *E. criniger* showed strong positive effects of burning (Fig. 3). The effects on *D. californica* and *E. criniger* that we observed are in agreement with the findings of Cramer (2005). Both species have rhizomes, and it is unknown what factors control the differential responses to fire. Cramer (2005) found that *Danthonia californica* (California oatgrass) was less common in burned fens and suggested that belowground parts may be sensitive to fire. None of our burned fens contained *Danthonia californica*, though it was found in low abundance (average cover $\sim 0.08\%$) in 2–4 unburned fens, depending on the year. *Rhododendron occidentale* showed a similar response; we found this shrub in five unburned fens (average cover $\sim 0.9\%$) and in only two burned fens (average cover $\sim 0.2\%$). Lastly, *Calamagrostis* spp. were found in 2–3 unburned fens (average cover $\sim 0.2\%$) and in 6 burned fens (average cover $\sim 1.6\%$). Our findings for *R. occidentale* and *Calamagrostis* spp. are in agreement with Cramer's (2005).

Several caveats should be taken into consideration when interpreting our results or using them to inform any management issues. First, because fires vary in their effects on vegetation, primarily on the basis of differences in their intensity, frequency, and size (Agee, 1993), little doubt exists that the burning that occurred in our 16 fens varied considerably. Although we tried to capture some of these differences by using a coarse measure of intensity and incorporating that into our site characterization, we were unable to predict how burn intensity influenced the response of fen vegetation. Second, because the study region has been an area of active fire suppression since the early to mid 1900s (Skinner, 2003a; Taylor and Skinner, 2003), *Darlingtonia* fens and their surrounding uplands may have accumulated unusually large amounts of fuel. Thus, the Biscuit Fire may not be representative of historical fire intensities. Last, because we designed our study to estimate changes in the dominant, open canopy vegetation of fens, we cannot assess how burning may influence the encroachment of woody plants into fens. Encroachment is generally most apparent along edges of *Darlingtonia* fens or in very small fens, and it is considered one of the most pressing management concerns (Frost and Jules, 2007). Because Cramer (2005) used a different sampling regime (i.e., fen-wide sampling), that study is more useful than ours for documenting changes in shrub and tree cover, both of which appeared to be reduced by burning. For instance, Cramer (2005) documented a 80% reduction in tree cover and a 94% reduction in shrub cover. Given the minimal effects of fire we observed in relatively open vegetation, a strong focus on the potential effects of encroachment by woody plants in future work is warranted (see also Tolman, 2007).

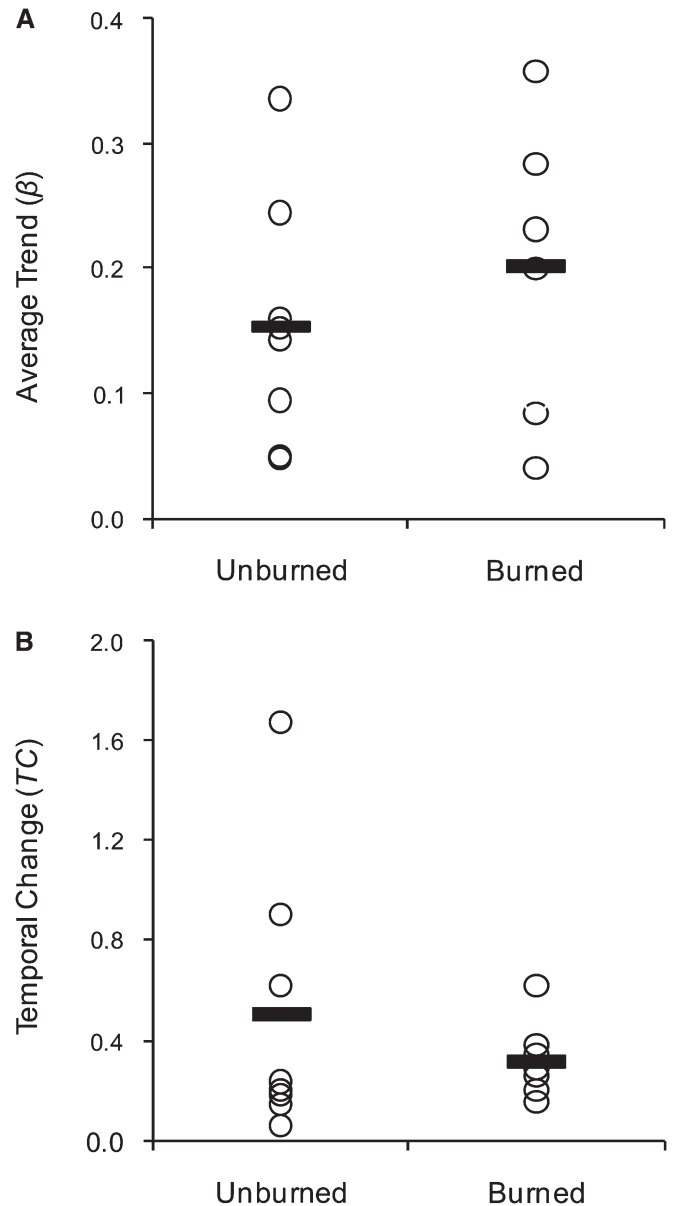


Fig. 5. Average trend (AvgTrend; β) (A) and temporal change trend index (TC) (B) for plots in unburned ($n = 8$) and burned ($n = 8$) *Darlingtonia* fens. AvgTrend is the mean of the slope estimates of species cover over 5 yr for a single plot, and TC is the sample variance (see text for details). Solid bars indicate average values.

Our results suggest that the effects of fire on plant assemblages in *Darlingtonia* fens were both slight and subtle. Importantly, some of these effects only manifested themselves several years after the fire. A single year of study would not have detected most of the differences we found between unburned and burned fens, supporting the great value of studies that use multiple years of observation for assessing vegetation responses to fire (e.g., Menges et al., 1993; Hutchinson et al., 2005; Webster and Halpern, 2010). The relatively high soil moisture levels coupled with the lack of an effect of fire on light availability and the well-developed underground rhizome of many plant species in *Darlingtonia* fens suggest these assemblages are moderately resilient to fire. More generally,

our work is part of a small but growing body of research suggesting that, though subtle effects might appear, serpentine systems are resilient to fire.

LITERATURE CITED

- AGEE, J. K. 1993. *Fire ecology of Pacific Northwest forests*. Island Press, Washington, DC, USA.
- ALBRECHT, M. A., AND B. C. MCCARTHY. 2006. Effects of prescribed fire and thinning on tree recruitment patterns in central hardwood forests. *Forest Ecology and Management* 226: 88–103.
- ALEXANDER, E. B., R. G. COLEMAN, T. KEELER-WOLF, AND S. P. HARRISON. 2006. Serpentine geocology of western North America: Geology, soils, and vegetation. Oxford University Press, New York, New York, USA.
- ANTONOVICS, J., A. D. BRADSHAW, AND R. G. TURNER. 1971. Heavy metal tolerance in plants. *Advances in Ecological Research* 7: 1–85.
- ATZET, T., AND R. E. MARTIN. 1992. Natural disturbance regimes in the Klamath Province. In H. M. Kerner [ed.], *Proceedings of the Symposium on Biodiversity of Northwestern California*, October 28–30, 1992, 40–48, Santa Rosa, California, USA. Wildland Resources Center Report 29, Berkeley, California, USA.
- BLANKENSHIP, B. A., AND M. A. ARTHUR. 2006. Stand structure over 9 years in burned and fire-excluded oak stands on the Cumberland Plateau, Kentucky. *Forest Ecology and Management* 225: 134–145.
- BOND, W. J., AND B. W. VAN WILGEN. 1996. *Fire and plants*. Chapman and Hall, London, UK.
- BORGAS, D., AND J. BIEGEL. 1998. Cedar Log Flat Research Natural Area prescribed fire effects monitoring. Second year report: Preburn vegetation data summaries, and fire and weather observations. Report submitted to the Siskiyou National Forest, Grants Pass, Oregon, USA.
- BOYD, R. S., A. R. KRUCKEBERG, AND N. RAJAKARUNA. 2009. Biology of ultramafic rocks and soils: research goals for the future. *Northeastern Naturalist* 16: 422–440.
- BROCKWAY, D. G., AND C. E. LEWIS. 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure, and productivity in a longleaf pine wiregrass eco-system. *Forest Ecology and Management* 96: 167–183.
- BROOKS, R. R. 1987. *Serpentine and its vegetation: A multidisciplinary approach*. Dioscorides Press, Portland, Oregon, USA.
- CALDER, W. J., G. LIFFERTH, M. A. MORITZ, AND S. B. ST. CLAIR. 2010. Physiological effects of smoke exposure on deciduous and conifer tree species. *International Journal of Forestry Research* 2010: 1–7.
- COLLINS, B. M., J. J. MOGHADDAS, AND S. L. STEPHENS. 2007. Initial changes in forest structure and understory plant community following fuel reduction activities in a Sierra Nevada mixed conifer forest. *Forest Ecology and Management* 239: 102–111.
- COLLINS, S. L. 1992. Fire frequency and community heterogeneity in tall-grass prairie vegetation. *Ecology* 73: 2001–2006.
- COLEMAN, R. G., AND A. R. KRUCKEBERG. 1999. Geology and plant life of the Klamath-Siskiyou Mountain region. *Natural Areas Journal* 19: 320–340.
- CRAMER, J. 2005. The Biscuit Fire and the flora of serpentine fens: Differences in species composition between burned and unburned fens. Master's thesis, University of Vermont, Burlington, Vermont, USA.
- DAVIES, S. J., AND L. UNAM. 1999. Smoke-haze from the 1997 Indonesian forest fires: Effects on pollution levels, local climate, atmospheric CO₂ concentrations, and tree photosynthesis. *Forest Ecology and Management* 124: 137–144.
- DELLASALA, D. A., S. T. REID, T. J. FREST, J. R. STRITTHOLT, AND D. M. OLSON. 1999. A global perspective on the biodiversity of the Klamath-Siskiyou ecoregion. *Natural Areas Journal* 19: 300–319.
- DONATO, D. C., J. B. FONTAINE, J. L. CAMPBELL, W. D. ROBINSON, J. B. KAUFFMAN, AND B. E. LAW. 2006. Post-wildfire logging hinders regeneration and increases fire risk. *Science* 311: 352.
- EUGENIO, M., AND F. LLORET. 2006. Effects of repeated burning on Mediterranean communities of the northeastern Iberian Peninsula. *Journal of Vegetation Science* 17: 755–764.
- FONTAINE, J. B., D. C. DONATO, W. D. ROBINSON, B. E. LAW, AND J. B. KAUFFMAN. 2009. Bird communities following high severity fire: Response to single and repeat fires in a mixed-evergreen forest, Oregon, USA. *Forest Ecology and Management* 257: 1496–1504.
- FRANKLIN, D. 2009. A comparative analysis of four methods for detecting nitrogen in a heterogeneous serpentine landscape: The potential influence of fire and habitat. Master's thesis, Humboldt State University, Arcata, California, USA.
- FROST, E. J., AND E. S. JULES. 2007. Draft conservation strategy for Oregon fireweed (*Epilobium oregonum*), Mendocino gentian (*Gentiana setigera*), large-flowered rush-lily (*Hastingsia bracteosa* var. *bracteosa*), purple-flowered rush lily (*H. bracteosa* var. *atropurpurea*), western bog violet (*Viola lanceolata* ssp. *occidentalis*) in serpentine *Darlingtonia* wetlands of southwest Oregon and northwest California. Report for the Bureau of Land Management and the United States Forest Service, Medford, Oregon, USA.
- FROST, E. J., R. J. SWEENEY, AND W. L. BIGG. 2004. Distribution and environmental/habitat relations of five endemic plants associated with serpentine fens in southwestern Oregon and northwestern California. Report to the Six Rivers and Siskiyou National Forests, Eureka, California and Grants Pass, Oregon, USA.
- FRY, D. L., AND S. L. STEPHENS. 2006. Influence of humans and climate on the fire history of a ponderosa pine-mixed conifer forest in the Southeastern Klamath Mountains, California. *Forest Ecology and Management* 223: 428–438.
- GABREY, S. W., A. D. AFTON, AND B. C. WILSON. 1999. Effects of winter burning and structural marsh management on vegetation and winter bird abundance in the Gulf Coast Chenier Plain, USA. *Wetlands* 19: 594–606.
- GLITZENSTEIN, J. S., D. R. STRENG, AND D. D. WADE. 2003. Fire frequency effects on longleaf pine (*Pinus palustris* P. Miller) vegetation in South Carolina and northeast Florida, USA. *Natural Areas Journal* 23: 22–37.
- GOTELLI, N. J., AND R. K. COLWELL. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4: 379–391.
- GOTELLI, N. J., R. M. DORAZIO, A. M. ELLISON, AND G. D. GROSSMAN. 2010. Detecting temporal trends in species assemblages with randomization procedures and hierarchical models. *Philosophical Transactions of the Royal Society* 365: 3621–3631.
- GOTELLI, N. J., AND A. M. ELLISON. 2004. A primer of ecological statistics. Sinauer, Sunderland, Massachusetts, USA.
- HARRISON, S. 1997. How natural habitat patchiness affects the distribution of diversity in Californian serpentine chaparral. *Ecology* 78: 1898–1906.
- HARRISON, S., B. D. INOUE, AND H. D. SAFFORD. 2003. Ecological heterogeneity in the effects of grazing and fire on grassland diversity. *Conservation Biology* 17: 837–845.
- HARRISON, S., AND N. RAJAKARUNA. 2011. Serpentine: The evolution and ecology of a model system. University of California Press, Berkeley, California, USA.
- HARRISON, S., H. D. SAFFORD, J. B. GRACE, J. H. VIERS, AND K. F. DAVIES. 2006. Regional and local species richness in an insular environment: Serpentine plants in California. *Ecological Monographs* 76: 41–56.
- HICKMAN, J. C. 1993. *The Jepson manual*. University of California Press, Berkeley, California, USA.
- HINMAN, S. E., AND J. S. BREWER. 2007. Responses of two frequently-burned wet pine savannas to an extended period without fire. *Journal of the Torrey Botanical Society* 134: 512–526.
- HURLBERT, S. H. 1971. The nonconcept of species diversity: A critique and alternative parameters. *Ecology* 52: 577–586.
- HUTCHINSON, T. F., R. E. J. BOERNER, S. SUTHERLAND, E. K. SUTHERLAND, M. ORTT, AND L. R. IVERSON. 2005. Prescribed fire effects on the herbaceous layer of mixed-oak forests. *Canadian Journal of Forest Research* 35: 877–890.
- IRWIN, W. P. 1966. Geology of the Klamath Mountains province. In E. H. Bailey [ed.], *Geology of Northern California*. *California Division of Mines and Geology Bulletin* 190: 19–38.

- JOST, L. 2007. Partitioning diversity into independent alpha and beta components. *Ecology* 88: 2427–2439.
- KEELEY, J. E., C. J. FOTHERINGHAM, AND M. BAER-KEELEY. 2005. Factors affecting plant diversity during postfire recovery and succession of Mediterranean-climate shrublands in California, USA. *Diversity & Distributions* 11: 535–537.
- KIRKMAN, L. K., AND R. R. SHARITZ. 1994. Vegetation disturbance and maintenance of diversity in intermittently flooded Carolina bays in South Carolina. *Ecological Applications* 4: 177–188.
- KRUCKEBERG, A. R. 1967. Ecotype response to ultramafic soils by some plant species of the southwestern United States. *Brittonia* 19: 133–151.
- KRUCKEBERG, A. R. 1984. California serpentines: Flora, vegetation, geology, soils, and management problems. University of California Press, Berkeley, California, USA.
- KRUCKEBERG, A. R. 2002. Geology and plant life: The effects of land forms and rock types on plants. University of Washington Press, Seattle, Washington, USA.
- LEVESQUE, R. 2007. Programming and data management: A guide for SPSS and SAS users, 4th ed. SPSS Inc., Chicago, Illinois, USA.
- MAIN, M. B., AND M. J. BARRY. 2002. Influence of season of fire on flowering of wet prairie grasses in South Florida, USA. *Wetlands* 22: 430–434.
- MCCOY, S., T. JAFFRE, F. RIGAUULT, AND J. E. ASH. 1999. Fire and succession in the ultramafic maquis of New Caledonia. *Journal of Biogeography* 26: 579–594.
- MCCUNE, B., AND M. J. MEFFORD. 2006. PC-ORD. Multivariate analysis of ecological data, version 5.10. MjM Software, Glenden Beach, Oregon, USA.
- MEHLMAN, D. W. 1992. Effects of fire on plant community composition of North Florida second growth pineland. *Bulletin of the Torrey Botanical Club* 119: 376–383.
- MENGES, E. S., W. G. ABRAHAMSON, K. T. GIVENS, N. P. GALLO, AND J. N. LAYNE. 1993. Twenty years of vegetation change in five long-unburned Florida plant communities. *Journal of Vegetation Science* 4: 375–386.
- NORTON, D. A., AND P. J. DE LANGE. 2003. Fire and vegetation in a temperate peat bog: Implications for the management of threatened species. *Conservation Biology* 17: 138–148.
- OLSZEWSKI, T. D. 2004. A unified mathematical framework for the measurement of richness and evenness within and among communities. *Oikos* 104: 377–387.
- PALMER, W. C. 1965. Meteorologic drought. Research paper no. 45. U.S. Weather Bureau, Washington, D.C., USA.
- R DEVELOPMENT CORE TEAM. 2007. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- RATCHFORD, J. S., S. E. WITTMAN, E. S. JULES, A. M. ELLISON, N. J. GOTELLI, AND N. J. SANDERS. 2005. The effects of fire, local environment, and time on ant assemblages in fens and forests. *Diversity and Distributions* 11: 487–497.
- ROBERTS, B. A., AND J. PROCTOR. 1992. The ecology of areas with serpentinized rocks: A world view. Kluwer, Dordrecht, Netherlands.
- SAFFORD, H. D., AND S. HARRISON. 2004. Fire effects on plant diversity in serpentine vs. sandstone chaparral. *Ecology* 85: 539–548.
- SAFFORD, H. D., H. VIERS, AND S. P. HARRISON. 2005. Serpentine endemism in the California flora: A database of serpentine affinity. *Madrono* 52: 222–257.
- SANDERS, N. J., N. J. GOTELLI, J. S. WITTMAN, J. S. RATCHFORD, A. M. ELLISON, AND E. S. JULES. 2007. Assembly rules of ground-foraging ant assemblages are contingent on disturbance, habitat and spatial scale. *Journal of Biogeography* 34: 1632–1641.
- SAWYER, J. O. 2007. Why are the Klamath Mountains and adjacent North Coast floristically diverse? *Fremontia* 35: 3–11.
- SAWYER, J. O., T. KEELER-WOLF, AND J. M. EVENS. 2008. A manual of California vegetation, 2nd ed. California Native Plant Society, Sacramento, California, USA.
- SCHNELL, D. E. 1976. Carnivorous plants of the U.S. and Canada. John F. Blair, Winston-Salem, North Carolina, USA.
- SCHWILK, D. W., J. E. KEELEY, E. E. KNAPP, J. MCIVER, J. D. BAILEY, C. J. FETTIG, C. E. FIEDLER, ET AL. 2009. The national Fire and Fire Surrogate study: Effects of fuel reduction methods on forest vegetation structure and fuels. *Ecological Applications* 19: 285–304.
- SHAW, A. J. 1990. Heavy metal tolerance in plants: Evolutionary aspects. CRC Press, Boca Raton, Florida, USA.
- SKINNER, C. N. 2003a. Fire regimes of upper montane and subalpine glacial basins in the Klamath Mountains of northern California. *Tall Timbers Research Station Miscellaneous Publication* 13: 145–151.
- SKINNER, C. N. 2003b. A tree-ring based fire history of riparian reserves in the Klamath Mountains. In P. M. Faber [ed.], California riparian systems: Processes and floodplains management, ecology, and restoration. Proceedings of Riparian Habitat and Floodplains Conference, March 12–15, 2001, 116–119. Riparian Habitat Joint Venture, Sacramento, California, USA.
- SKINNER, C. N., A. H. TAYLOR, AND J. K. AGE. 2006. Klamath Mountains bioregion. In N. G. Sugihara, J. W. van Wagtenonk, J. Fites-Kaufman, K. E. Shaffer, A. E. Thode [eds.], Fire in California's ecosystems, 170–194. University of California Press, Berkeley, California, USA.
- TAYLOR, A. H., AND C. N. SKINNER. 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. *Ecological Applications* 13: 704–719.
- THOMPSON, J. R., T. A. SPIES, AND L. M. GANIO. 2007. Reburn severity in managed and unmanaged vegetation in a large wildfire. *Proceedings of the National Academy of Sciences, USA* 104: 10743–10748.
- TIMMINS, S. M. 1992. Wetland vegetation recovery after fire: Eweburn Bog, Te Anau, New Zealand. *New Zealand Journal of Botany* 30: 383–399.
- TOLMAN, D. A. 2007. Soil patterns in three *Darlingtonia* fens of Southwestern Oregon. *Natural Areas Journal* 27: 374–384.
- TYNDALL, R. W. 1994. Conifer clearing and prescribed burning effects to herbaceous layer vegetation on a Maryland serpentine “barren.” *Castanea* 59: 255–273.
- UYS, R. G., BOND W. J., AND T. M. EVERSON. 2004. The effect of different fire regimes on plant diversity in southern African grasslands. *Biological Conservation* 118: 489–499.
- USDA FOREST SERVICE AND BLM. 2004. Biscuit Fire recovery project final environmental impact statement. USDA Forest Service and BLM, Medford, Oregon. Website <http://www.fs.fed.us/r6/rogue-siskiyou/biscuit-fire/feis.shtml> [accessed February 2009].
- WEBSTER, K., AND C. B. HALPERN. 2010. Long-term vegetation responses to reintroduction and repeated use of fire in mixed-conifer forests of the Sierra Nevada. *Ecosphere* 1: art9 10.1890/ES10-00018.1.
- WHELAN, R. J. 1995. The ecology of fire. Cambridge University Press, Cambridge, UK.
- WHITTAKER, R. H. 1954. The ecology of serpentine soils. *Ecology* 35: 258–288.
- WHITTAKER, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30: 279–338.
- WITTMAN, S. E., N. J. SANDERS, A. M. ELLISON, E. S. JULES, J. S. RATCHFORD, AND N. J. GOTELLI. 2010. Species interactions and thermal constraints on ant community structure. *Oikos* 119: 551–559.