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RESEARCH

The effects of fire, local environment and time on ant assemblages in fens and forests

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ABSTRACT

We investigated the effects of the abiotic environment, plant community composition and disturbance by fire on ant assemblages in two distinct habitat types in the Siskiyou Mountains in northern California and southern Oregon, USA. Sampling over 2 years in burned and unburned *Darlingtonia* fens and their adjacent upland forests, we found that the effects of disturbance by fire depended on habitat type. In forests, fire intensity predicted richness in ant assemblages in both years after the fire, and plant community composition predicted richness 2 years after the fire. No factors were associated with richness in the species-poor fen ant assemblages. Species-specific responses to both habitat type and disturbance by fire were idiosyncratic. Assemblage composition depended on habitat type, but not disturbance by fire, and the composition of each assemblage between years was more dissimilar in burned than unburned sites.

Keywords

Ants, community similarity, community structure, *Darlingtonia*, fire, habitat complexity, Intermediate Disturbance Hypothesis, vegetation structure.

INTRODUCTION

A central focus of community ecology has been to understand why relative abundance and species richness vary among local assemblages in both space and time (Ricklefs & Schluter, 1993; Weiher & Keddy, 1999; Hubbell, 2001). Multiple factors can interact to shape assemblage structure. For example, the influence of a particular abiotic variable, such as temperature, may depend on habitat structure (Pringle *et al*., 2003). Similarly, the effect of disturbance on local assemblages may depend on habitat type and mediate the effects of other important factors (Lambrinos, 2002). In this study, we examined interactions between habitat type and disturbance by fire and measured their effects on species richness and relative abundance in a ground-foraging ant assemblage.

Because of their near ubiquity and dominance in terrestrial ecosystems, ants are an ideal taxon for examining factors that govern assemblage structure. Several recent studies have examined how environmental factors influence the number of species in local assemblages (e.g. Kaspari *et al*., 2000; Gotelli & Ellison, 2002; Kaspari *et al*., 2003, 2004), the effects of disturbance by fire (Andersen & Yen, 1985; Andersen, 1991a; Farji-Brener *et al*., 2002; Izhaki *et al*., 2003; Parr *et al*., 2004; Sanders, 2004) and how habitat characteristics shape assemblages (e.g. Gotelli & Arnett, 2000; Yanoviak & Kaspari, 2000; Gotelli & Ellison, 2002). Few studies, however, have examined the combined or interactive effects of governing environmental factors and disturbance on ant assemblages, or how these factors depend on habitat type. For example, Farji-Brener *et al*. (2002) showed that the effect of fire history on ant assemblages can depend on habitat type. Studies such as Farji-Brener *et al*.'s (2002) suggest that the environmental factors and disturbance agents may interact to determine the relative abundance and number of species in local assemblage, and their effects might vary across habitats.

To examine how habitat type may mediate the interactive effects of abiotic factors and disturbance by fire on ant assemblages, we sampled ants in two distinct habitat types, *Darlingtonia* fens and adjacent forests, for 2 years following a major wildfire in the Siskiyou Mountains in southern Oregon and northern California. Our study addresses three interrelated questions:

(1) Does the relative abundance, richness or composition of ant assemblages depend on the interaction between disturbance by fire and habitat type?

(2) What environmental factors are correlated with ant species richness, and how does the relative importance of those factors depend on habitat type and disturbance history?

(3) How does disturbance by fire affect assemblage composition through time, and does that effect depend on habitat type?

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METHODS

Study sites

We studied ants in *Darlingtonia* fens and adjacent forests in the Siskiyou Mountains near the Oregon–California border during June–August 2003 and again in July–August 2004. The climate of the study area is Mediterranean, with cool winters (mean January minimum temperature = 0 °C) and warm dry summers (mean July maximum temperature = 31.7 °C; mean annual precipitation = 154 cm, with only 4 cm falling between June and August). The Siskiyou Mountains are known for their high plant diversity with many rare and endemic species and vegetation types (Whittaker, 1954, 1960; DellaSala *et al.*, 1999). *Darlingtonia* fens are one of these vegetation types. These fens are dominated by the carnivorous plant, *Darlingtonia californica*, and are distinct from the surrounding upland forests where *D. californica* is absent (Fig. 1). Though the plant communities are well known in the Siskiyou Mountains, little is known about the ant assemblages.

Study design

From July to September 2002, a major forest fire, the Biscuit Fire, burned approximately 202,000 ha of the Siskiyou Mountains (Anonymous, 2004). We sampled 16 pairs of fen and forest plots beginning in the summer of 2003. Eight of the pairs were in areas that burned during the fire, and eight were not. Therefore, we sampled four plot types: burned fens, unburned fens, burned forests and unburned forests. The plots were undisturbed by recent human activity other than the burn and were large enough to contain an 8 × 8 m sampling plot (see below). Forest plots were located at least 50 m away from the fen boundary in a direction that placed the plot at approximately the same elevation, slope and aspect as the fen plot. If more than one direction from the fen fit these criteria, then we randomly chose the direction for the placement of the forest plot.

(a) Upland forest site

(b) Fen site

Figure 1 An example of a typical upland forest (a) (Photo credit: Erik Jules) and *Darlingtonia* fen (b) (Photo credit: Jaime Ratchford) in the Siskiyou Mountains, northern California.

Ant sampling

In each plot, we placed an 8 × 8 m sampling grid and sampled ants using a standardized protocol that included observing 25 bait stations (arranged in a 5 × 5 grid with 2-m spacing) nine times throughout the day. Each bait station consisted of two laminated 7.6 × 12.7 cm index cards. We baited one card with approximately 5.5 g of tuna and the other with a cotton ball soaked in honey water. These baits represent protein and carbohydrate food resources. There is some evidence that ant species differ in their preference for protein baits or carbohydrate baits (Stein *et al.*, 1990; Yanoviak & Kaspari, 2000). Therefore, using different bait types should have sampled a potentially wider spectrum of species. We stocked the bait stations each morning at approximately 08:00 and replenished them with tuna and water (to moisten the cotton balls and tuna) as necessary throughout the day and evening.

At each of the 32 plots, we observed ants during three observation blocks throughout 1 day: one in the morning beginning at approximately 08:30, one in the afternoon beginning at 13:00 and one in the evening beginning at 18:30. During each of the three observation blocks, we visited the bait stations three times, once every 30 min and observed each bait station for approximately 20 s during each visit. Thus, each bait station was visited a total of nine times (three observations in three blocks) in both 2003 and 2004. For one site in 2004 (Lone Mt. 1), we conducted only one complete observation in both plots during the evening block because of heavy rains. Neither mean July maximum temperature nor precipitation in 2003 and 2004 differed significantly from their long-term average values.

Baits tend to undersample trophic specialists and subordinate or single-foraging species because baits are often dominated by mass-recruiting species. We used several baits in an area and made multiple observations throughout the day to minimize these problems (Bestelmeyer *et al.*, 2000). In 2003 (but not 2004) we supplemented the bait station data by hand-searching the plots, but only one ant species, *Lasius flavus*, was found only by general collecting. Our sampling strategy captured the potential changes in the activity of foraging ants over the course of the day. We did not use pitfall traps in this study because the water table in the fens is generally at the surface, so pitfall traps flood, and because the soil in the forest sites was so rocky that installing pitfall traps would have required a jackhammer.

Table 1 A summary of site attributes for each of the 32 plots. Burn intensity values are unburned (0), low intensity (1), moderate intensity (2), high intensity (3) and extreme intensity (4); see text for further details. Latitude and longitude are given as degrees, and temperature refers to the mean soil surface temperature at each site

Site name	Habitat type	Burn intensity	Elevation (m)	Latitude (dd)	Longitude (dd)	Aspect (°)	Temperature (°C)	Open canopy (%)
Aimee's	Fen	4	568	42.07	124.12	170	24.97	80.50
	Forest	3	466	42.07	124.11	230	37.64	78.00
Cedar Root	Fen	3	466	42.18	123.97	200	24.16	85.75
	Forest	3	797	42.19	123.98	149	35.65	91.00
Diamond Creek	Fen	3	792	42.10	124.07	110	24.08	77.50
	Forest	3	513	42.10	124.06	170	35.09	69.75
Dragonfly	Fen	0	498	42.09	124.06	340	22.20	88.50
	Forest	0	536	42.10	124.05	60	32.47	53.75
Greg's	Fen	2	540	42.13	124.19	260	27.78	67.00
	Forest	1	567	42.13	124.20	260	35.02	60.25
Happy	Fen	0	569	42.21	123.78	40	20.59	94.25
	Forest	0	477	42.20	123.79	45	22.77	19.50
L.E. Horten	Fen	3	475	42.00	124.08	60	25.09	90.25
	Forest	3	478	42.01	124.08	150	36.44	67.50
Lone Mountain 1	Fen	0	522	42.07	123.92	65	24.38	92.00
	Forest	0	542	42.08	123.92	120	33.66	82.50
Lone Mountain 2	Fen	0	522	42.15	123.85	150	23.94	95.75
	Forest	0	447	42.15	123.85	60	32.97	83.50
O23	Fen	2	448	42.44	123.89	20	29.96	90.75
	Forest	2	565	42.45	123.90	20	32.15	86.50
Scrap	Fen	0	427	42.48	123.80	170	25.92	94.25
	Forest	0	427	42.49	123.82	130	38.30	66.50
Sh*t	Fen	4	685	42.17	124.00	260	30.27	60.75
	Forest	3	689	42.17	124.01	30	38.85	91.25
South side	Fen	0	424	42.49	123.79	140	25.38	93.75
	Forest	0	432	42.49	123.78	292	37.41	29.25
Star Flat	Fen	0	392	42.47	123.87	150	28.12	93.00
	Forest	0	375	42.48	123.88	200	35.07	3.75
Upper Day's Gulch	Fen	1	510	42.41	123.91	90	28.46	93.25
	Forest	2	510	42.23	123.71	140	40.30	75.25
Whiskey Creek	Fen	0	524	42.12	123.87	340	29.38	88.00
	Forest	0	540	42.13	123.88	67	38.62	89.75

For each observation at a bait station, we recorded the number and identity of each species. Individual workers were collected at the end of the observation period if they could not be readily identified in the field. Phil Ward at the University of California, Davis confirmed the species identifications. Voucher specimens are deposited at the University of Tennessee in Knoxville. Nomenclature follows Bolton (1994, 2003).

Independent variables

We measured average surface temperature, canopy cover and burn intensity and examined their relationships with ant species richness. During each observation at a bait station, we measured the soil surface temperature to the nearest 0.1 °C using a Raytek® Raynger ST20 XB hand-held infrared thermometer (Santa Cruz, CA, USA). To examine light availability (as an estimate of energy availability), we estimated the percentage of open canopy for each plot using a spherical densiometer (Forestry Suppliers, Jackson, MS, USA). To estimate burn intensity, in the summer of 2003 we classified each plot into one of five categories: 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). Table 1 summarizes characteristics of each of the 32 plots.

Because other recent studies (Morrison, 1998; Gotelli & Ellison, 2002) have shown that ant communities respond to differences in plant community composition, we also examined that relationship here. To examine how differences in plant species richness and composition influence ant species richness and composition, we sampled the plant communities at each of the 16 pairs of plots in both 2003 and 2004 by centreing a 0.25-m^2 quadrat on each of the 25 bait stations within each plot. Each quadrat was divided into 100 individual units of 5 × 5 cm such that each unit represented 1% of the total area of the quadrat. In each quadrat the identity and percent cover of all herbaceous plant species were recorded. For each of the 32 plots, we used principal components analysis (PCA) to quantify the vegetation composition of each plot. We used the percent cover of plant species in each plot to derive plant species loadings for fen and forest habitats. We excluded from the analysis plant species that did not occur in at least three sites. Analyses were conducted using PC-ORD version 4.01 (McCune & Mefford, 1999).

Statistical analysis

We examined how species richness (the total number of ant species occurring in a plot) depended on habitat type, burn history (burned or unburned), year and the environmental variables associated with each plot. Counts of observed species may reflect total species richness, but they are also sensitive to total abundance and the number of individuals collected in the sample (Gotelli & Colwell, 2001). For these reasons, the response variable in our analyses was the estimated asymptotic number of ant species. We estimated asymptotic species richness using the Chao2 estimator (Colwell & Coddington, 1994):

$$S_{\mathrm{Chao2}} = S_{\mathrm{Obs}} + Q_1^2/2Q_2$$

where S_{Obs} is the number of species that occurred in the sample, Q_1 is the number of species that occur in only one sample (uniques) and Q_2 is the number of species that occur in two samples (Colwell & Coddington, 1994; Magurran, 2004). The Chao2 index uses data on the rare species collected in the samples (Q_1 and Q_2) to estimate the number of additional species that are present in the habitat, but were not recorded in the samples. As in other biodiversity studies of this kind (Colwell, 2005), we treated each bait station as a sample, so each of the 32 plots has 25 samples. Each species was counted only once at a bait station regardless of the number of times it was detected during the nine observations throughout the day. Because estimators such as the Chao2 are sensitive to sample size (Colwell & Coddington, 1994), we used Colwell's ESTIMATES (Colwell, 2005) to construct 50 randomized accumulation curves for each site to calculate the standard deviation of the estimated species richness. For almost every site in both years, the asymptotic richness estimator was very similar to the observed total species richness ($r^2 = 0.96$ across all sites), suggesting that our sampling methods recorded most of the species present within the sample grid. Nevertheless, we used the Chao2 estimator for all of our analyses, which we will refer to as 'species richness'.

To examine how ant species richness depended on habitat type, burn history, year and their interactions, we used a three-way fixed-factor ANOVA. We did not use a repeated-measures ANOVA because the response variables between years were independent of one another. We determined the ability of the abiotic variables (temperature, percentage of open canopy, plant community composition [the PCA scores of the plant community analysis] and burn intensity) to predict ant species richness using least squares linear regressions, polynomial regressions and stepwise multiple regressions. For cases in which both linear and polynomial regressions explained a significant amount of the variation in the relationship between the predictor variable and ant species richness, we report the adjusted r^2 for the model that explained more of the variation in ant species richness. The adjusted r^2 penalizes models with more parameters in them, because models with more parameters inevitably explain more variation in the response variable. Burn intensity values were treated as continuous rather than categorical variables because of insufficient within-treatment replication required for standard ANOVA. Prior to analysis, percentage of open canopy and species richness were log-transformed, and the burn intensity values (+0.5) were square root-transformed. We performed the analyses on the fen and forest plots and each year separately. In the stepwise regression analyses, the criterion for inclusion of a variable into the model was $P < 0.15$.

We constructed rank abundance curves for both forests and fens in 2003 and 2004 to assess how relative abundance and evenness depended on habitat type and year. To test whether the abundances of the four most common species (i.e. those detected in at least 40% of the sites) differed among plot types and years, we used a three-way fixed-factor ANOVA to analyse the effects of habitat type, burn history, year and their interactions. We estimated the abundance of each ant species in each plot as the total number of bait stations at which it occurred out of 25. Because sociality can result in extreme clumping of individual ants, the frequency of occurrence is often a more accurate measurement of ant abundance than is the total number of individuals collected (Andersen, 1991b; Longino *et al.*, 2002). To improve normality, these occurrence values were square root-transformed for all analyses.

We used non-metric multidimensional scaling (NMDS) in PC-ORD version 4.0 (McCune & Mefford, 1999) with the Bray–Curtis distance measure to examine how ant assemblage composition varied among the four plot types. NMDS is well suited for non-normal data and does not assume linear relationships among variables (McCune & Grace, 2002). Species that did not occur in at least three of the plots were excluded from the data analyses.

We used the Bray–Curtis similarity index to examine similarity in species composition among the four site types (burned fen, burned forest; unburned fen, unburned forest). The effect of habitat type, burn history and their interaction on the Bray–Curtis similarity indices were examined using a two-factor ANOVA. All analyses, except NMDS, were conducted with NCSS 2001 (Kaysville, UT, USA).

RESULTS

In total, we observed 125,280 ants representing 26 species in 14 genera across all sites in 2003 and 2004 (Table 2). In 2003, 24 ant species in 12 genera were observed; 13 species were found in fens and 23 were found in forests. In 2004, 22 species in 13 genera were observed; 12 and 19 species were found in fens and forests, respectively. In both years, we found only one rare species, *Leptothorax* sp. A, only in fens (Table 2). Plot types differed in

Table 2 A list of ant species observed at bait stations and the presence or absence of each species in each plot type and in each year. Numbers represent the presence (1) or absence (0) of the species in the habitat type and year

	2003				2004			
	Fen		Forest		Fen		Forest	
Species	Burned	Unburned	Burned	Unburned	Burned	Unburned	Burned	Unburned
Aphaenogaster occidentalis	1	1	1	1	1	1	1	1
Brachymyrmex depilis	0	0	1	1	0	0	1	1
Camponotus essigi	0	0	0	1	0	0	0	1
Camponotus laevigatus	0	0	0	1	0	0	0	1
Camponotus vicinus	1	1	1	1	0	1	1	1
Formica accreta	0	0	1	0	1	0	1	1
Formica argentea	0	0	0	1	0	0	0	0
Formica lasiodes	0	0	1	1	1	0	1	1
Formica moki	0	1	1	1	1	0	0	1
Formica neogates	0	0	0	1	0	0	0	0
Formica subelongata	1	0	1	1	0	0	1	1
Formica subpolita	1	0	1	1	0	0	0	1
Lasius pallitarsis	1	0	1	1	0	1	0	0
Leptothorax (muscorum) sp. A	1	1	0	0	1	1	0	0
Liometopum occidentale	0	0	0	1	0	0	0	0
Prenolepis impairis	1	0	1	1	0	0	0	1
Solenopsis molesta	1	0	1	0	0	0	0	1
Temnothorax nevadensis	1	0	1	1	1	1	1	1
Temnothorax nitens	0	0	1	1	0	0	1	1
Temnothorax rudis	1	1	1	1	0	1	1	1
Temnothorax rugatulus	0	0	0	1	0	0	0	1
Temnothorax sp. Ca-03	0	0	0	1	0	0	0	0
Crematogaster coarctata	1	0	1	1	1	0	1	1
Myrmica incompleta	0	0	0	0	0	1	0	0
Pheidole californica	0	0	0	0	0	0	1	0
Tapinoma sessile	1	1	1	1	1	1	1	1

mean (± SE) temperature (unburned fen = 25.0 ± 1.0; unburned forest = 33.9 ± 1.8; burned fen = 26.8 ± 0.9; burned forest = 36.4 ± 0.9) and percent open canopy (unburned fen = 92.4 ± 1.0; unburned forest = 53.6 ± 11.5; burned fen = 80.7 ± 4.2; burned forest = 77.4 ± 4.0).

Forest plots (mean richness = 7.0 ± 0.5 [SE]) had more than twice as many ant species as did fen plots (2.5 ± 0.3; $F = 74.49$, d.f. = 1, 56, $P < 0.0001$; Fig. 2). There was also a significant interaction between habitat type and burn history ($F = 5.41$, d.f. = 1, 56, $P = 0.02$) on ant species richness: in fens, species richness was higher in burned plots (3.0 ± 0.4) than in unburned plots (2.0 ± 0.3), but in forests, species richness was higher in unburned plots (8.2 ± 0.6) than in burned plots (5.7 ± 0.6) (Fig. 2). Ant species richness did not differ between years ($F = 2.34$, d.f. = 1, 56, $P = 0.13$), and there was no main effect of burn history ($F = 0.72$, d.f. = 1, 56, $P = 0.40$).

In fens, the stepwise regression analyses indicated that none of the four measured environmental variables were significantly associated with species richness in either year. In contrast, ant species richness in forests was highest at intermediate burn intensities in 2003 (adjusted $r^2 = 0.40$, $P = 0.04$; Fig. 3), but lowest at intermediate burn intensities in 2004 (adjusted $r^2 = 0.43$, $P < 0.0001$; Fig. 3). The polynomial regression relating burn intensity to ant species richness in forests in 2004 explained 17% more of the variation in ant species richness than the linear regression. In the forest plots, the stepwise multiple regression model indicated that PCA-1 and PCA-2 scores for plant community composition together predicted 50% of the variation in ant species richness (adjusted $r^2 = 0.50$, $P = 0.01$).

The rank abundance curve for the fen plots was very steep (Fig. 4) for both years and across burned and unburned sites, because one species, *Tapinoma sessile*, was abundant, while other species were rare. The rank abundance curve for the forest plots was much shallower (Fig. 4), because the relative abundance of species in forest ant assemblages was more evenly distributed than in fens.

The abundance of the four most common species, *Tapinoma sessile*, *Aphaenogaster occidentalis*, *Camponotus vicinus* and *Temnothorax nevadensis*, responded idiosyncratically to fire history and habitat variables. The abundance (i.e. number of bait occurrences out of 25) of *Tapinoma sessile* was greater in fen plots (21.6 ± 0.7) than in the forest plots (8.9 ± 1.1) ($F = 91.1$, d.f. = 1, 56,

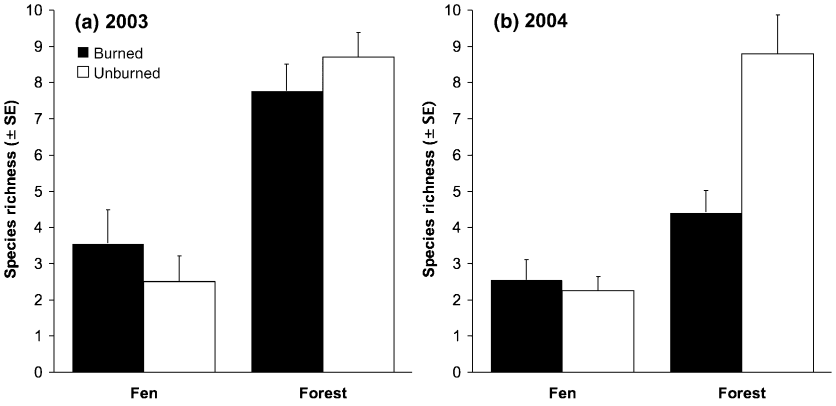

Figure 2 The effects of habitat type, burn history and year on the mean (± SE) estimated ant species richness.

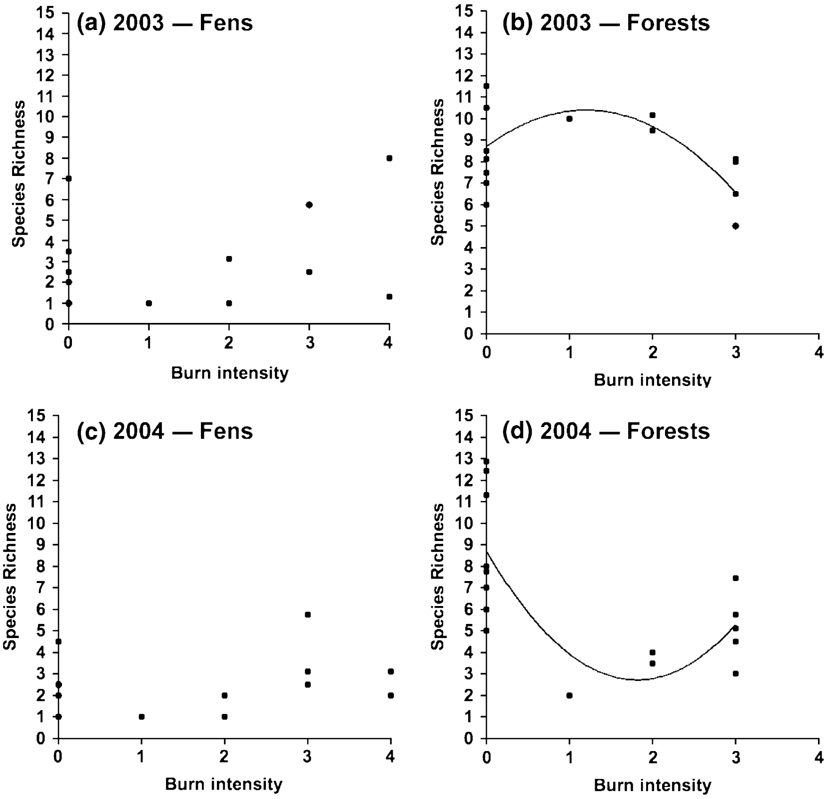

Figure 3 The relationship between burn intensity and estimated ant species richness in fen and forest plots. The relationship was not statistically significant in fen plots in either year.

$P < 0.0001$) and in unburned plots (17.6 ± 1.5) than in burned plots (4.2 ± 1.2) for both fens and forests and in both years ($F = 10.7$, d.f. = 1, 56, $P = 0.002$).

Aphaenogaster occidentalis was more abundant in forests (9.6 ± 1.2) than in fens (1.5 ± 0.5) ($F = 59.5$, d.f. = 1, 56, $P < 0.0001$). There was no overall effect of fire history on the abundance of *A. occidentalis* ($F = 0.14$, d.f. = 1, 56, $P = 0.70$), but there was an interaction between habitat and fire ($F = 12.13$, d.f. = 1, 56, $P = 0.001$). In fens, the abundance of *A. occidentalis* was higher in burned plots (2.9 ± 0.9) than unburned plots (0.06 ± 0.06). However, in forests, its abundance was lower in burned plots (8.1 ± 1.9) than unburned plots (11.2 ± 1.5). In 2004, the abundance of *A. occidentalis* was lower (4.0 ± 0.9) than in 2003 (7.1 ± 1.3) for all plot types ($F = 6.82$, d.f. = 1, 56, $P = 0.01$).

Camponotus vicinus was more abundant in forests (4.8 ± 1.1) than in fens (0.1 ± 0.08) ($F = 35.01$, d.f. = 1, 56, $P < 0.0001$), and less abundant in burned sites (1.4 ± 0.7) than in unburned sites (3.6 ± 1.0) ($F = 8.71$, d.f. = 1, 56, $P = 0.005$). The effect of fire on the abundance of *C. vicinus* was greater in forests than in fens ($F = 6.25$, d.f. = 1, 56, $P = 0.015$). The abundance of *C. vicinus* was lower in 2004 (1.2 ± 0.6) than in 2003 (3.8 ± 1.1) ($F = 10.41$, d.f. = 1, 56, $P = 0.002$) especially in forest plots ($F = 9.68$, d.f. = 1, 56, $P = 0.003$).

Temnothorax nevadensis was more abundant in forest plots (8.7 ± 1.1) than in fen plots (0.3 ± 0.2) ($F = 53.37$, d.f. = 1, 56, $P < 0.0001$), but there was no effect of year or burn history on its abundance.

NMDS ordinations of all the plot types (burned fens, unburned fens, burned forests and unburned forests) yielded a

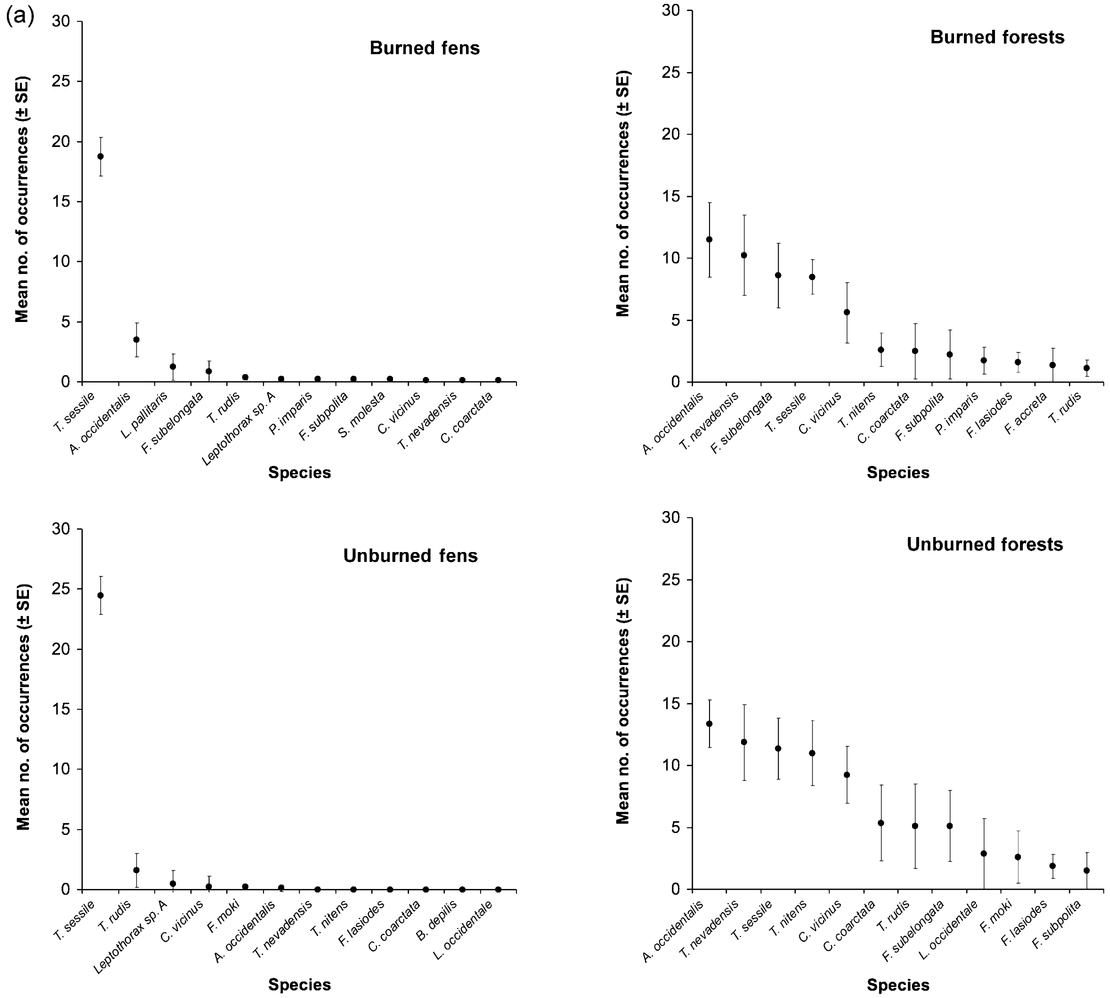

Figure 4 The rank abundance curves for fen and forest plots in 2003 (a) and 2004 (b). Symbols indicate the mean (± SE) number of occurrences of each species.

two-dimensional solution that accounted for 89% of the variation in ant assemblage composition in 2003 (Fig. 5). Fen and forest plots separated strongly. Burned and unburned forest plots did not separate, but burned and unburned fens did. For the 2004 data, NMDS ordinations yielded a three-dimensional solution accounting for 93% of the variation in ant assemblage composition (Fig. 5). There was considerable separation between fens and forests, and between unburned and burned fens, but again no separation between assemblages in burned and unburned forests.

The similarity in ant assemblage composition between years, as indicated by the Bray–Curtis similarity index, depended on habitat type and fire history. Fen plots (0.66 ± 0.04) were more similar between years than forest plots (0.49 ± 0.05) ($F = 8.78$, d.f. = 1, 28, $P = 0.006$). Unburned plots (0.68 ± 0.05) were more similar between years than burned plots (0.46 ± 0.04) for both fens and forests ($F = 14.09$, d.f. = 1, 28, $P < 0.001$).

DISCUSSION

Species richness, relative abundance and composition of ground-foraging ant assemblages in *Darlingtonia* fens and nearby uplands in the Siskiyou Mountains depended on habitat type, the habitat type × fire interaction and the year × fire interaction. Furthermore, environmental variables of importance for ant species richness varied between both habitat types and sampling year.

Ant species richness was generally higher in forests than in adjacent fens. Because fens are saturated wetlands, they likely lack suitable nest sites for most ant species. Adjacent forest sites, in contrast, may provide suitable nest sites under rocks, in rotting logs or in unsaturated soils. Furthermore, fens tend to be both cooler (Table 1) and more nutrient-poor (Ratchford, 2005) than the adjacent forests. Both of these factors may limit both the activity of workers and nest site selection of queens (Hölldobler & Wilson, 1990). Interestingly, while fens are a rare vegetation type, the ant assemblages in them are dominated by an extremely widespread ant species, highlighting that patterns of rarity of ants and plants need not be concordant.

The effects of fire on ant assemblages are idiosyncratic. Several studies have found that species richness is higher in burned areas than unburned areas (Andersen & Yen, 1985; Donnelly & Giliomee, 1985; Andersen, 1991a; York, 1994), while others have found no

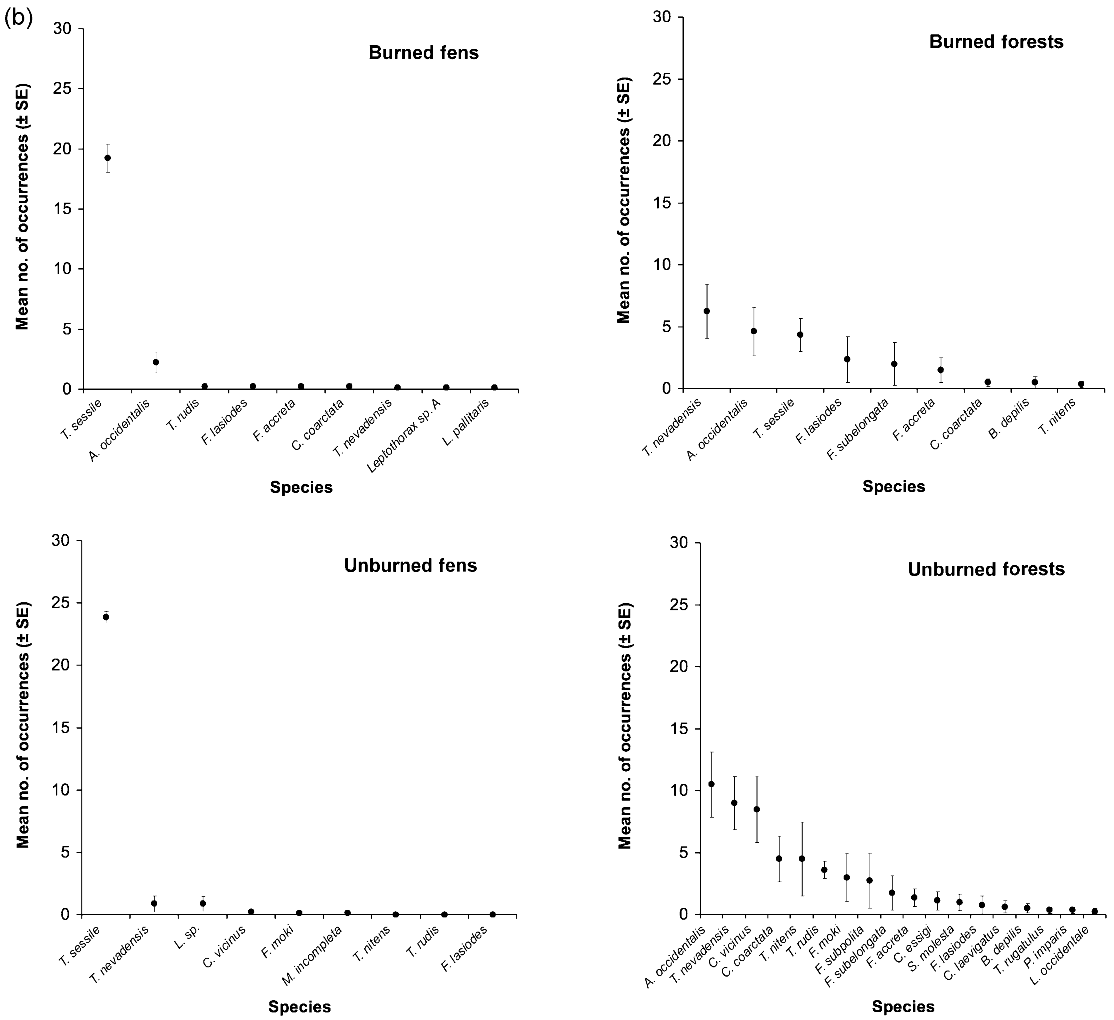

Figure 4 *Continued*

effect of fire on ant species richness (Hoffmann, 2003; Parr *et al.*, 2004). Here, as in other studies (e.g. Farji-Brener *et al.*, 2002; Hoffmann, 2003; Parr *et al.*, 2004), the effect of the fire depended on habitat type: in fens, species richness was higher in burned sites than in unburned sites, but in forests, species richness was lower in burned sites than unburned sites. The characteristics of different habitats may determine the extent of the changes induced by disturbance (Farji-Brener *et al.*, 2002; Hoffmann & Andersen, 2003; Parr *et al.*, 2004). In steppe areas in northwest Patagonia, richness did not depend on whether a site burned or not (Farji-Brener *et al.*, 2002). But fire significantly reduced richness in nearby scrublands. Farji-Brener *et al.* (2002) and others (e.g. Hoffmann, 2003; Parr *et al.*, 2004) have suggested that the effects of fire on ant assemblages is indirect, usually altering the habitat or food supply. For example, in areas with sparse vegetation (e.g. steppes, deserts, fens), plant communities and the habitat they provide may recover quickly. But in sites with more complex vegetation (e.g. scrublands and forests), plant communities and the habitats they provide may take longer to recover. In our study system, fens likely became drier after the Biscuit Fire in 2002, which may have allowed more ant species to forage or nest in the fens. Another related explanation for the habitat-specific effects of fire on the ant communities might be that the effect of the disturbance depends on the structural complexity of the habitat. For example, because forests are more structurally complex than fens, the differences in complexity before and after the fire are likely greater than in the fens. Thus, the ants that occupy the forests experience greater change in the habitat complexity to which they might be pre-adapted, but ants in fens experience much less change.

In forests, burn intensity was an important predictor of ant species richness in both 2003 and 2004, but the relationship differed between years. This result suggests that the effect of a disturbance on ant species richness may depend not only on disturbance intensity, but also on the time since disturbance, as has been shown in other non-ant systems (e.g. Airoldi, 1998). We note, however, that this reversal in the relation between ant species richness and burn intensity between years results from richness changing at only three sites and thus the pattern we observed may have been unrelated to burn intensity.

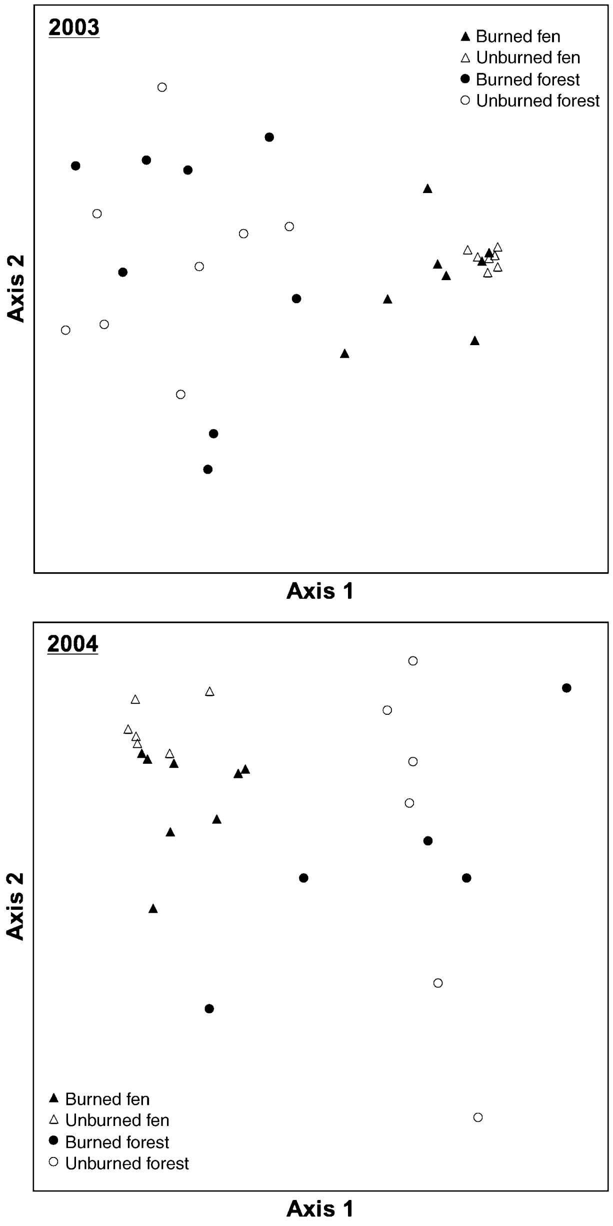

Figure 5 Non-metric multidimensional scaling of ant assemblage composition in 2003 and 2004. Each point is a two-dimensional (axis 1 and axis 2) representation of ant species composition in each plot type (e.g. unburned fens, burned fens, unburned forests and burned forests). Points that are close together have ant assemblages that are more similar in composition compared to points that are far apart.

When we considered all of the environmental variables in a multiple regression model, burn intensity was the most important variable in predicting ant species richness in forests one year after fire (in 2003). Two years after the fire, however, vegetation composition (PCA-1 and PCA-2) predicted more of the variation in ant species richness than did burn intensity. Previous studies (e.g. Morrison, 1998; Ellison *et al.*, 2002; Gotelli & Ellison, 2002) have shown that ant assemblages often respond to temporal vegetation dynamics at small spatial scales. Other studies have shown that disturbance affects ant assemblages by altering shade regimes (King *et al.*, 1998; Hoffmann *et al.*, 2000) and temperature (Andersen, 1991a; MacKay *et al.*, 1991), vegetation structure (Greenslade & Greenslade, 1977) and plant species richness (Hoffmann *et al.*, 2000). In our system, shade regimes, surface temperatures and vegetation structure (Table 1; Jules *et al.* unpublished data) were all altered by the fire. As a result, burned fens and forests were, on average, about 2 °C hotter than unburned sites (Table 1). Abundance of particular taxa also depended on habitat type and its interaction with fire. *Tapinoma sessile* was much more abundant in the fens than any other ant species. It was also the only ant species that was more abundant in the fen plots than in the forest plots. At least two explanations for the abundance of *T. sessile* in fens are worth considering. First, most *T. sessile* nests may occur in the forests adjacent to the fens while workers forage in the fens, at even the baits near the centres of the fen plots. Most other species that occurred in the fens were detected at baits near the edges of the fens, suggesting that either workers did not venture into the fen because of the wet habitat or because workers usually do not forage more than a few meters from the entrance of their nests, which are located outside of the fens. A second explanation for the abundance of *T. sessile* in fens might be that *T. sessile* workers can tolerate the generally wet environment in the fens and their nest structure allows it to escape flooding. In two years of searching, the only species we saw nesting in the fens was *T. sessile.*

Fire also affected the abundance of the other common ant species, *Aphaenogaster occidentalis*, *Camponotus vicinus* and *Temnothorax nevadensis*. Fire-induced changes in habitat structure or resource availability may have altered the dynamics of competitive interactions among species. However, it is unclear what mechanisms contributed to the higher abundance of some ant species in the fens but not in the forests after the fire.

Given that the abundance of particular species depended on habitat type, disturbance history and year, it is not surprising that assemblage composition varied among plots. Interestingly, assemblages in sites that did not burn were more similar between years than those that did burn, and fen ant assemblages were more similar between years than were forest ant assemblages. A similar study on butterflies in the Great Basin (Fleishman, 2000) demonstrated that there was no effect of burning on assemblage similarity, and she suggested that the baseline temporal variability in butterfly assemblage composition swamped any effect of disturbance by fire. In contrast, the ant assemblages we studied were affected by fire, and they changed rapidly following disturbance, suggesting that ants may serve as useful bioindicators of habitat disturbance and restoration (Kaspari & Majer, 2000; Andersen & Majer, 2004).

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