2005

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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 Biscui5w ( )Tj3bath

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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 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):

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 ESIMATES (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

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, R

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, 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 rich-

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