

# Comparison of post-fire seedling establishment between scrub communities in mediterranean and non-mediterranean climate ecosystems

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## Summary

**1** Both fire regimes and the conditions under which fires occur vary widely. Abiotic conditions (such as climate) in combination with fire season, frequency and intensity could influence vegetation responses to fire. A variety of adaptations facilitate post-fire recruitment in mediterranean climate ecosystems, but responses of other communities are less well known. We evaluated the importance of climate by comparing sites with mediterranean and subtropical climates.

**2** We used paired burned and mature sites in chamise chaparral, mixed chaparral and coastal sage scrub (California), and rosemary scrub, sand pine scrub and sandhill (Florida), to test whether (i) patterns of pre-fire and post-fire seedling recruitment are more similar between communities within a region than between regions, and (ii) post-fire stimulation of seedling establishment is greater in regions with marked fire-induced contrasts in abiotic site characteristics.

**3** Post-fire seedling densities were more similar among sites within climatic regions than between regions. Both seedling densities and proportions of species represented by seedlings after fires were generally higher in California.

**4** The only site characteristic showing a pre-fire–post-fire contrast was percentage open canopy, and the effect was greater in California than in Florida. Soil properties were unaffected by fire.

**5** Mediterranean climate ecosystems in other regions have nutrient-poor soils similar to our subtropical Florida sites, but show post-fire seedling recruitment patterns more similar to the nutrient-rich sites in California. Climate therefore appears to play a more major role than soil characteristics.

*Key-words:* California chaparral, fire ecology, Florida scrub, mediterranean climate ecosystems, seedling recruitment

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## Introduction

Although natural fires occur in virtually all terrestrial ecosystems (Whelan 1995), variations in predictability, frequency and intensity of fire lead to quite different community responses (Bond & van Wilgen 1996). Environments with unpredictable, infrequent fires that function as catastrophic disturbances (e.g. tropical rainforests; Mueller-Dombois

& Goldammer 1990) contrast with landscapes with more frequent and predictable fires, where fire has played a selective role in the evolution of life-history characteristics, as seen in mediterranean climate ecosystems (Christensen 1985; Keeley 1986).

Natural fires are essential for maintaining species diversity in those mediterranean climate scrub communities in which a large percentage of plant species (at least 70%) have seedlings that establish after fires (Vogl & Schorr 1972; van Wilgen & Forsyth 1992). Many such species are fire-dependent, and seedling recruitment, which is nil in the absence of fire, is triggered by immediate post-fire conditions as a result of stimulation of germination of a persistent

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soil seed bank by heat, smoke or charred wood (Keeley *et al.* 1985; Bond & van Wilgen 1996; Keeley & Fotheringham 1998). It is generally assumed that this is an evolutionary response to improved conditions for survival after fire, such as the creation of large light gaps for recruitment (Keeley 1986). Similarity in post-fire response among mediterranean climate ecosystems is commonly cited as an example of evolutionary convergence between these climatically similar regions (Cody & Mooney 1978; Naveh & Whittaker 1979; Shmida 1981), although the degree of climatically driven convergence has been questioned (Barbour & Minnich 1990).

Non-mediterranean communities such as Florida scrub can be used to assess the importance of climate. Although Florida scrub is physiognomically similar to mediterranean-type vegetation, this scrub persists under a summer rain/winter drought (rather than winter rain/summer drought) climate. Florida scrub is subjected to fires of varying frequency (Myers 1990; Brenner 1991), with Florida having the highest frequency of lightning-ignited fires in the United States (Komarek 1964).

This study evaluated the role of fire in altering vegetation structure in three plant communities in inland peninsular Florida, and compared these patterns with three mediterranean communities in southern California. We tested two predictions: (i) that patterns of pre-fire and post-fire seedling recruitment are more similar between communities within a region than between regions; and (ii) that post-fire seedling establishment is more prevalent in regions with larger fire-induced contrasts in abiotic site characteristics (e.g. canopy cover, soil nutrients). We determined pre-fire and post-fire seedling densities and species richness by sampling paired burned and unburned sites. We also assessed site characteristics and used canonical analysis to relate site variables to seedling establishment patterns, to suggest processes underlying the observed patterns.

## Methods

### STUDY SITES

Florida and California differ markedly in climate and seasonal distribution of wildfires. In Florida, 65% of the *c.* 1400 mm annual precipitation occurs during the summer (Chen & Gerber 1990) and peak months for lightning-ignited wildfires are April–June (Komarek 1964; Myers 1990). In contrast, in southern California less than 5% of the 400–700 mm precipitation occurs in summer (Keeley 1992) and the peak fire season is June–October (Keeley 1982). These regions also differ in soil characteristics, with nutrient-poor entisols in upland Florida sites (Brown *et al.* 1990) and relatively nutrient-rich xeralfs in southern California (Foth 1978).

The six communities studied were sandhill, sand pine scrub and rosemary scrub in Florida, and chamise chaparral, mixed chaparral and coastal sage scrub in California. For each community, we sampled five paired burned and adjacent or nearby unburned sites.

### FLORIDA SITES

Sites were located in Ocala National Forest in Marion County, Withlacoochee State Forest in Sumter and Citrus Counties, Tiger Creek and Saddleblanket Lake preserves in Polk County, and Lake Apthorpe Preserve and Archbold Biological Station in Highlands County (Fig. 1). Sites in all community types are topographically flat and occur on well-drained, low-nutrient soils classified as quartzipsamments (i.e. well-drained, quartz-dominated sandy soils; Foth 1978; Buol *et al.* 1989). Natural fires in most burned sites occurred between March and August, although one sandhill site burned during February. Fires in all burned sites had occurred 3 months to 1 year before data collection (nine sites burned in 1993, and the remaining six in 1994). Nomenclature for Florida species follows Wunderlin (1982).

Although the three Florida community types have relatively similar climate and soils, they differ in physiognomy, species composition and fire frequency and intensity. Rosemary scrub is dominated by Florida rosemary (*Ceratiola ericoides*), a needle-leaved, obligately seeding shrub that may occur as a monoculture or with other shrubs such as oak (*Quercus* spp.) and *Sabal etonia*. Sand pine (*Pinus clausa*), the only tree species, is sparse if present, herbaceous species are usually sparse in mature sites, and large openings with bare soil may occur between shrubs. Fires are intense but infrequent, with return intervals usually at least 30–40 years (Myers 1990).

In contrast, sand pine scrub typically has a high density of both shrubs and small trees, with an often dense overstorey of sand pines. The understorey consists largely of several oak species that are capable of resprouting after fires, and herbaceous species are again sparse. Intense fires occur every 10–100 years, killing adult sand pines and triggering seed release from cones (Myers 1990).

Sandhill communities typically have a diverse understorey of herbaceous species, including many grasses, and an overstorey of widely spaced, fire-resistant longleaf pine (*Pinus palustris*). Ground cover and litter are often abundant, and the shrub layer of resprouting oaks is usually sparse. Low-intensity ground fires occur every 2–10 years (Myers 1990).

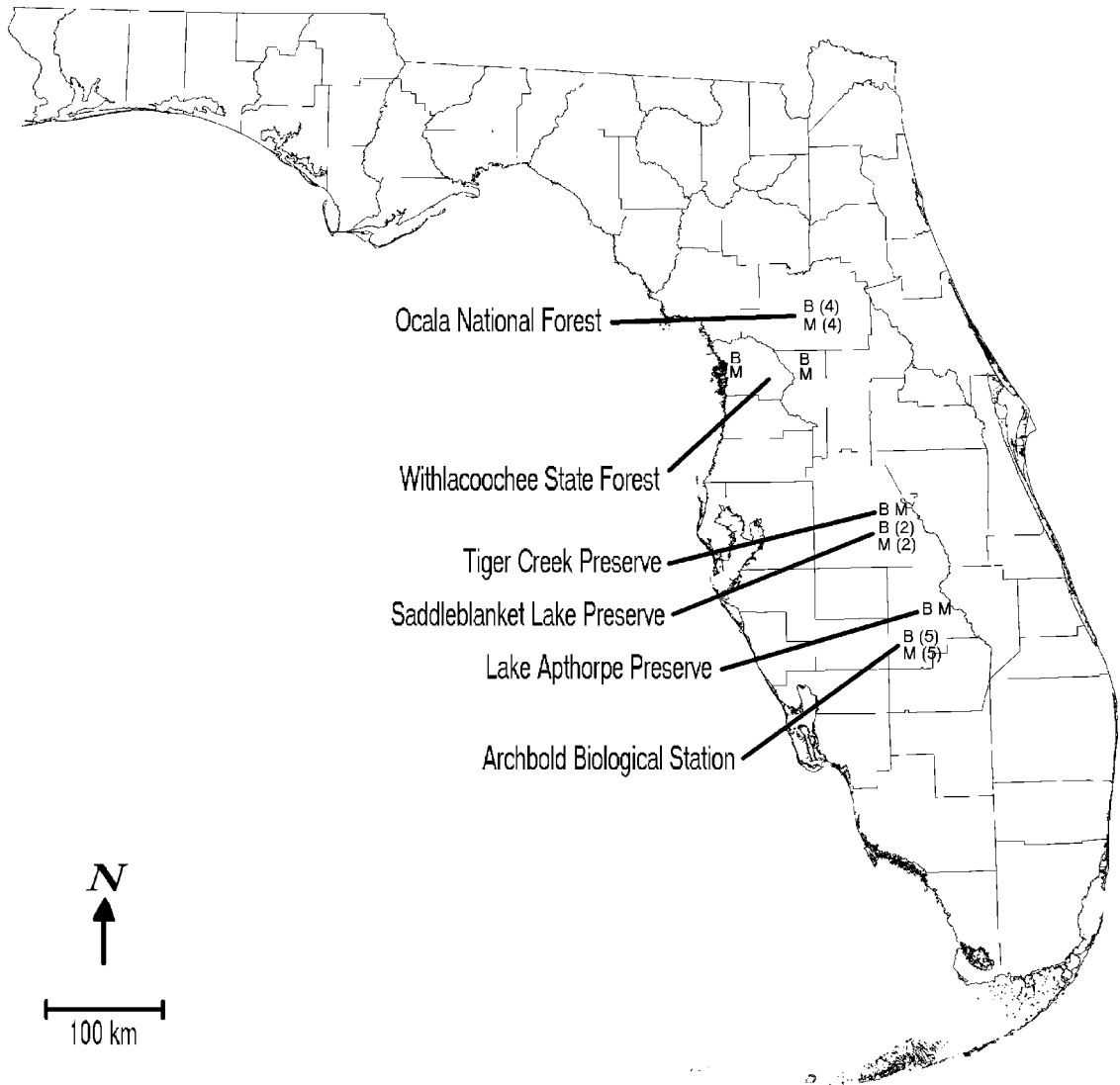


Fig. 1 Map of study sites in recently burned (B) and mature (M) communities in Florida.

#### CALIFORNIA SITES

Sites were located between 100 and 600 m elevation in the Santa Monica Mountains in Los Angeles and Ventura Counties, California (Fig. 2). Topography is rugged, with 15–25% slopes. Soils are largely xerorthents (i.e. xeric, loamy or clayey, undifferentiated soils), with some xeralfs (i.e. xeric soils with high base saturation and an argillic, or clay, horizon) occurring in the region (Foth 1978; Buol *et al.* 1989). Fires occurred in all burned sites during October and November 1993.

Chamise and mixed (i.e. *Ceanothus*- and *Quercus*-dominated) chaparral are relatively similar in physiognomy and fire regime, but differ in site characteristics and species composition. Evergreen, sclerophyllous-leaved shrubs 1–6 m tall are dominant in California chaparral, with their intertwining branches typically forming impenetrable thickets.

Intense fires during the summer dry season occur approximately every 10–40 years (Hanes 1981). Nomenclature for California species follows Hickman (1993).

Although the predominant chamise chaparral can occur under most site conditions in the Santa Monica Mountains, it is most often on relatively xeric south- and west-facing slopes. The community is dominated by chamise (*Adenostoma fasciculatum*), a needle-leaved shrub capable of both resprouting and establishing seedlings after fires (Keeley 1992). Other shrub species such as *Salvia mellifera* and *Eriogonum fasciculatum* may co-occur with chamise, but no understorey exists and litter is sparse in mature sites (Hanes 1981).

Mixed chaparral tends to occur on relatively mesic north- and east-facing slopes in the study area, and the dominant species differ in life-history characteristics. The most common species include

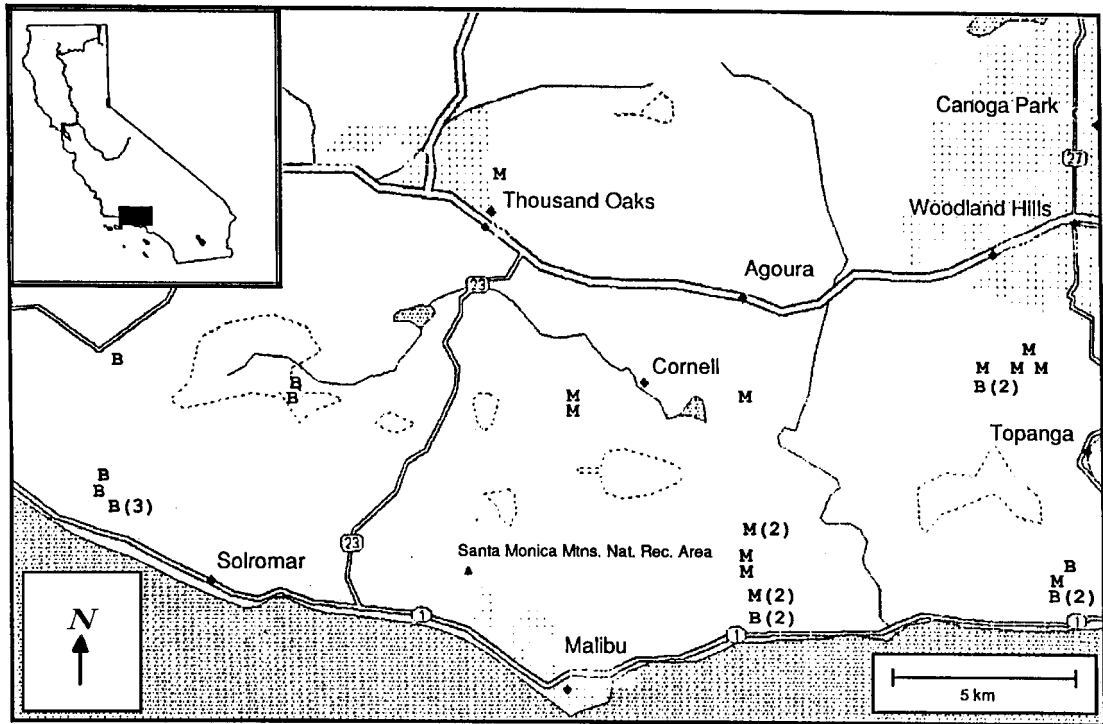


Fig. 2 Map of study sites in recently burned (B) and mature (M) communities in the Santa Monica Mountains, California.

the obligately seeding *Ceanothus megacarpus*, *Ceanothus spinosus*, which is capable of both resprouting and establishing seedlings after fires, and *Quercus dumosa*, which resprouts but does not establish seedlings after fires (Keeley 1992). *Cercocarpus betuloides*, *Heteromeles arbutifolia*, *Rhus ovata* and *Adenostoma fasciculatum* are less frequent (Hanes 1981), and the understorey is sparse in mature sites.

Coastal sage scrub usually occurs on drier sites at lower elevations than chaparral, and is characterized by summer-deciduous shrubs 1–3 m tall. Mature coastal sage scrub is often more open than mature chaparral and herbaceous understorey species are more numerous. Most of the shrub species are capable of resprouting after fires, and include *Artemisia californica*, *Eriogonum fasciculatum*, *Hazardia squarrosus* and *Salvia leucophylla* (Hanes 1981). Fires in coastal sage scrub are often more frequent than in chaparral, and may occur as often as every 5–10 years (Keeley & Keeley 1988).

#### SAMPLING METHODS

Data for Florida sites were collected from December 1993 to August 1994, except for one sand pine scrub site that was studied during July 1995. Paired burned and mature sites within the same community type were less than 1 km apart and data collection dates within site pairs differed by 6 days

or less, except for two pairs at Archbold Biological Station (one sand pine scrub, one rosemary scrub) where dates differed by 151 days.

At each site, density and species of seedlings and adult plant species composition were quantified within six randomly located plots, each 8 × 1 m. Percentage open canopy was quantified with a spherical densiometer (Lemmon 1957) placed on the ground at the midpoints of four randomly selected plots, and a sample of soil was collected to a depth of 5 cm at the midpoints of three randomly selected plots.

For California sites, data were collected from February to June 1994. Sites within community types were paired by aspect, with distances between pairs ranging from 0.5 to 33 km and the median time between collection dates being 18 days (range = 1–40 days). Data were collected from mature sites as in the Florida sites, with the six plots orientated parallel to slope contour. In burned sites, however, data were collected within a 50 × 20-m area orientated with the long axis parallel to the slope contour, and subdivided into 10 × 10-m squares. Seedling density, seedling species and adult plant species composition were quantified within 20 plots, each 1 × 1 m; two plots were located at opposite corners within each of the 10 squares. Percentage open canopy was quantified by placing a spherical densiometer on the ground at four random points within the 50 × 20-m area. Three soil samples were taken at

random locations along the outside perimeter of the area; each sample was collected to a depth of 5 cm.

#### SOIL ANALYSIS

Percentage total nitrogen, total phosphorus, sand and clay and pH were quantified for each soil sample. Total nitrogen was determined by flash combustion using a Carlo Erba Combustion Analyser. Percentage phosphorus was quantified by digestion with 60% perchloric acid after first digesting the samples with nitric acid to oxidize organic matter (Olsen & Sommers 1982). Percentage sand and clay in samples were determined using the hydrometer method for California samples (Cox 1985) and the pipet method for Florida soils (Gee & Bauder 1986). Analysis of four California samples using both methods indicated no difference between the methods.

#### DATA ANALYSIS

For each site, seedling density  $m^{-2}$  was averaged over all plots (i.e.  $n = 8$  for all Florida sites and California mature sites, and  $n = 20$  for California burned sites). The proportion of species establishing seedlings was calculated by dividing the number of seedling species in each plot by the total number of species (including seedling species) in the plot; proportions were then averaged for each site. Means for percentage open canopy and soil phosphorus, nitrogen, sand and clay and pH were also calculated for each site.

Initial statistical analyses were conducted to detect differences in seedling density between Florida and California mature sites, and to detect differences in seedling density and site characteristics between all paired burned and mature sites. Differences in seedling density among the mature sites (five sites in each of six communities) were analysed using a Kruskal–Wallis test. Differences between paired sites in seedling density, canopy openness and soil total phosphorus, nitrogen and pH were analysed separately for each variable in each community using paired *t*-tests (SAS Institute Inc. 1988).

The remaining analyses were conducted on data from burned sites. First, differences between Florida

and California sites in seedling and site variables were analysed. Differences in seedling density and in the proportion of species represented by seedlings were tested using a Kruskal–Wallis test and an analysis of variance, respectively ( $n = 30$  sites for each test). Stepwise discriminant analysis was used to identify site variables that best discriminated between Florida and California sites (SAS Institute Inc. 1988).

Second, ordinations based on site variables were conducted using canonical discriminant analyses (SAS Institute Inc. 1988), and relationships between seedling and site variables were analysed using canonical correlations (SAS Institute Inc. 1988). Canonical discriminant analyses and canonical correlations were conducted separately for Florida and California sites. For each of the two canonical correlations, seedling density and proportion of species represented by seedlings were designated as criterion variables, and percentage open canopy and soil phosphorus, nitrogen, sand, clay and pH were designated as predictor variables (Dillon & Goldstein 1984).

#### Results

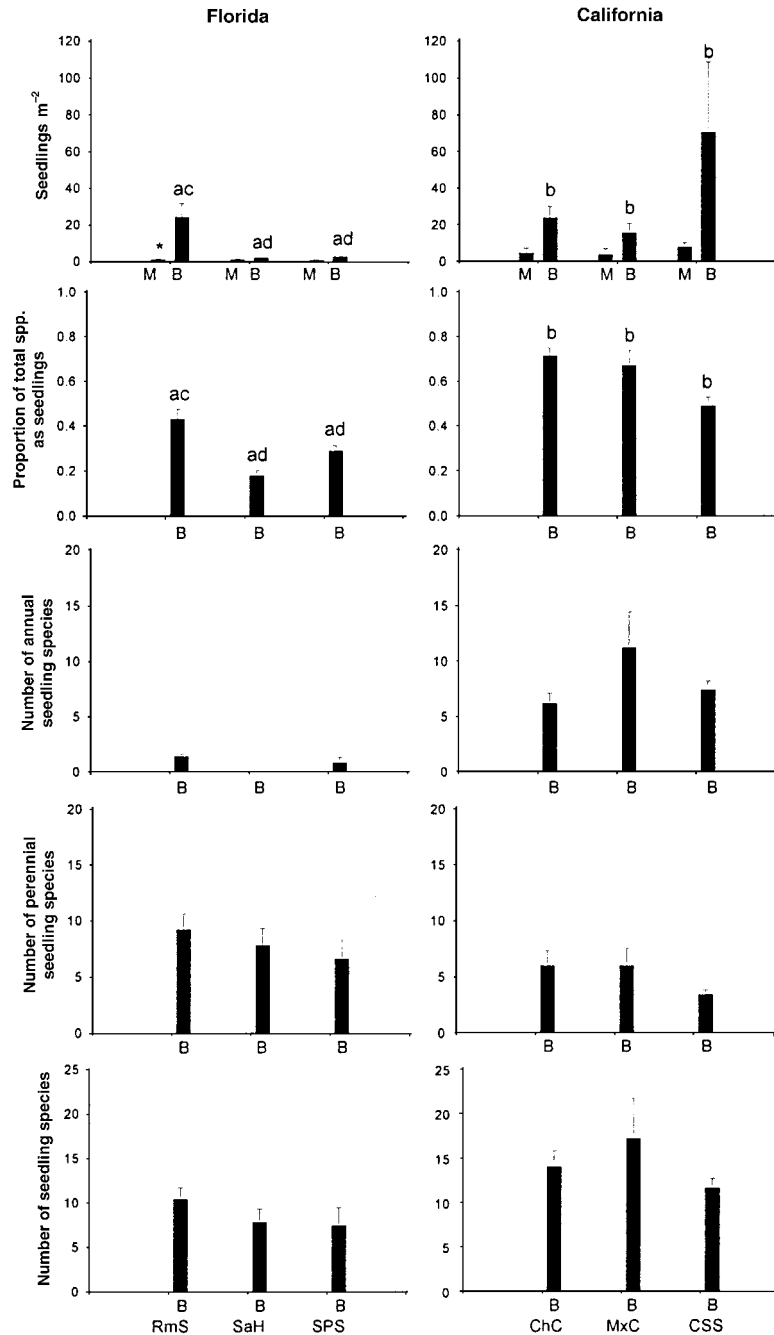
Seedling densities in mature sites did not differ between Florida and California, although densities tended to be higher in California (Fig. 3). Among recently burned sites, seedling densities were lowest in Florida sandhill and highest in California coastal sage scrub, and, overall, were higher in California communities (planned comparison test,  $P < 0.001$ ; Fig. 3). Recently burned sites tended to have higher numbers of seedling species in California, even though species were quantified there over a smaller area per site (Table 1 and Fig. 3). Annuals comprised large proportions of the seedling species in California, but were virtually absent in Florida communities (Fig. 3).

Total species richness (i.e. including adult plants) varied from  $21.2 \pm 3.1$  (mean and standard error; Florida sand pine scrub) to  $38.8 \pm 6.3$  (Florida sandhill). Mean percentage of total species represented by seedlings varied from  $18.0 \pm 2.1\%$  in Florida sandhill to  $71.4 \pm 3.4\%$  in California chamise chaparral, and was higher in California com-

**Table 1** Mean proportions of species represented by seedlings, total numbers of seedling species and numbers of these species thought to be dependent on fire for recruitment in recently burned sites in southern California and Florida

Location ( $n = 15$ sites)	Proportion of species represented by seedlings (mean $\pm$ standard error)	Total number of seedling species	Number of species dependent on fire for recruitment*
California	$0.62 \pm 0.04$	74	25
Florida	$0.30 \pm 0.03$	25	7

\*From Keeley (1991), Menges & Kohfeldt (1995) and Carrington (1997).



**Fig. 3** Seedling density in mature (M) and recently burned (B) sites in Florida and southern California, and proportion of species represented by seedlings, number of species of seedlings of annuals and perennials, and total number of seedling species. Sites consisted of rosemary scrub (RmS), sand pine scrub (SPS) and sandhill (SaH) in Florida; and chamise chaparral (ChC), mixed chaparral (MxC) and coastal sage scrub (CSS) in California. Bars represent means and standard errors from five sites of each community type. Letters above bars show results of planned contrasts among recently burned sites after a Kruskal–Wallis test (for seedling densities) and an analysis of variance (for proportions of species represented by seedlings). Different letters denote significant differences ( $P < 0.05$ ). Asterisk shows a difference between mature and recently burned sites ( $P < 0.05$  for RmS only). Seedling species numbers were not counted over the same area at all sites, and differences in means were therefore not tested statistically.

communities ( $F_{1,24} = 70.8$ ,  $P < 0.001$ ; Table 1 and Fig. 3).

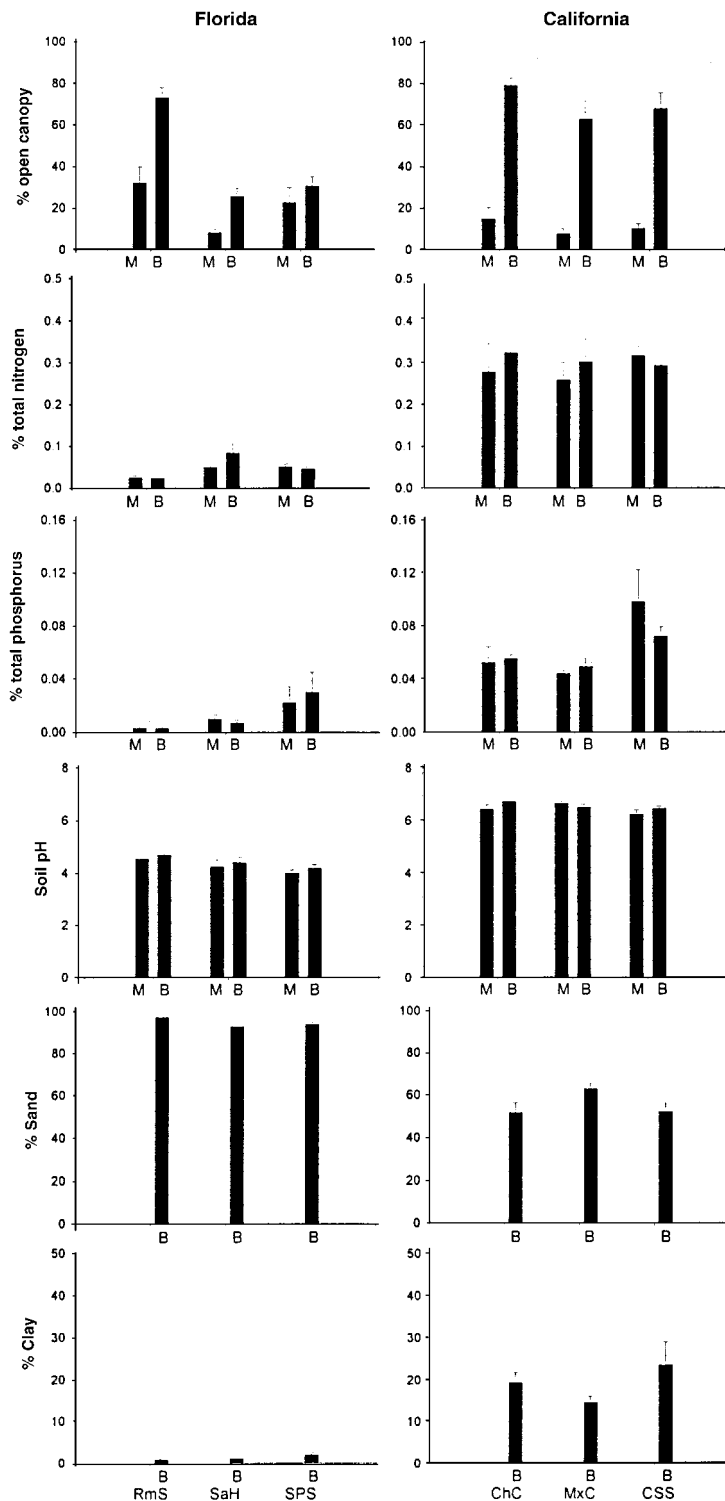
California and Florida sites were very different with respect to most of the site variables quantified.

California soils had higher percentage total nitrogen, percentage clay and pH, while Florida soils had higher percentage sand (stepwise discriminant analysis,  $P < 0.05$  for nitrogen, clay and pH; Fig. 4).

DIFFERENCES BETWEEN BURNED AND MATURE SITES

Among Florida community types, only rosemary scrub had higher percentage open canopy, seedling

density or soil pH in burned areas (Figs. 3 and 4). An unusually long time (151 days) between collection dates within a pair of sites did not affect the contrasts. Although seedling densities did not differ



**Fig. 4** Means and standard errors for percentage open canopy and percentage total soil nitrogen, percentage total soil phosphorus, soil pH and percentage soil sand and clay in burned and mature sites in Florida and California (abbreviations as in Fig. 3).  $n = 5$  for each community type.

within site pairs in sand pine scrub and sandhill, seedling species composition did vary. Coefficients of community similarity between paired sites (Mueller-Dombois & Ellenberg 1974) were 0 and 0.23 for sand pine scrub and sandhill, respectively (data not shown). Burning did not affect soil phosphorus or soil nitrogen at any Florida sites (Fig. 4).

Percentage open canopy alone differed between paired California sites, with burned sites having greater values (Fig. 4). Seedling species were more similar between burned and mature sites in mixed chaparral and coastal sage scrub than they were in chamise chaparral or in any of the communities in Florida. Coastal sage scrub had the highest coefficient of community similarity (0.37), although almost half of the species shared by burned and mature sites were exotics.

PATTERNS OF SEEDLING AND SITE VARIABLES IN BURNED SITES

Florida sites

The canonical discriminant analysis comparing Florida community types yielded one significant axis that accounted for 80% of the variability in the data. Rosemary scrub sites, with more open canopies and sandier, higher-pH, lower-nitrogen soils, were clearly separated from sand pine scrub and

sandhill sites along this axis. Sand pine scrub and sandhill were less clearly separated from each other, but the former tended to have less open canopies, higher soil nitrogen and lower pH (Fig. 5).

Although seedling densities and proportions of species represented by seedlings were higher in rosemary scrub sites (Fig. 3), canonical correlation did not demonstrate a significant relationship between these seedling variables and site variables. Neither of the canonical variates was significant (Table 2), and both site canonical variates combined explained only 41% of the variance in seedling density and proportion of species represented by seedlings.

California sites

One significant axis accounted for 71% of the variability in the data and defined a gradient from less open sites with relatively sandy low-pH soils to more open sites with less sandy higher-pH soils (loadings shown in Table 3). Although sites intergraded somewhat, the general order of community types along the gradient was mixed chaparral, coastal sage scrub and chamise chaparral (Fig. 5).

Although neither seedling densities nor proportions of species represented by seedlings differed between community types (Fig. 3), canonical correla-

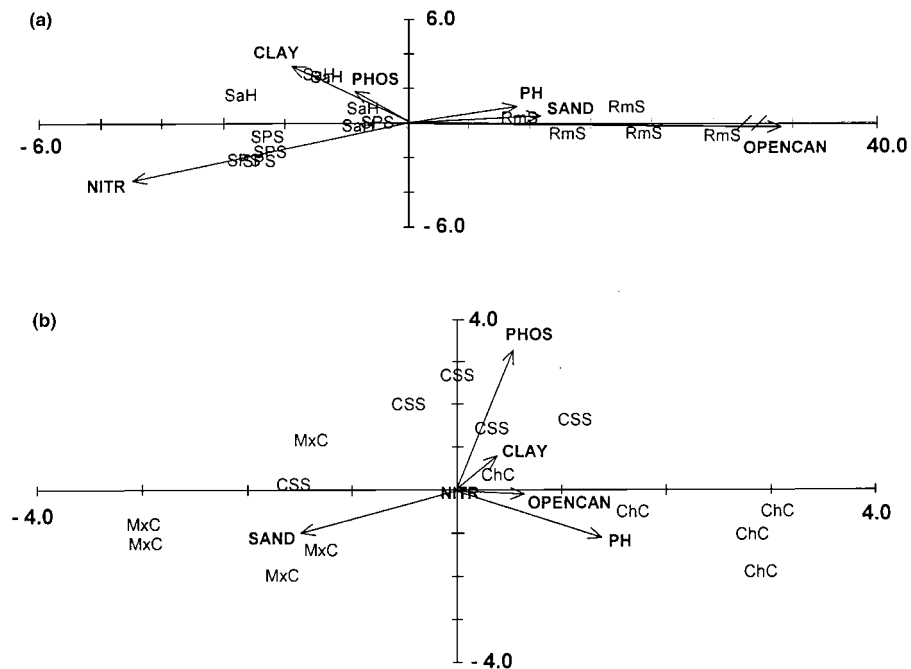


Fig. 5 The first and second canonical axes from canonical discriminant analyses of recently burned sites in (a) Florida and (b) California (abbreviations as in Fig. 3). Coordinates of vectors represent direction and strength of loading on canonical axes for six site variables (see Table 3), and axis lengths are proportional to the amount of variation in site variables that is explained. The first canonical axes explain 80% and 71% of the variation in site variables in Florida and California, respectively (see Table 2 for significance levels).



**Table 2** Significance tests of variation in site characteristics explained by canonical axes, and of variation among seedling-related variables (i.e. seedling density, proportion of species represented by seedlings) and site-related variables (i.e. percentage open canopy and soil phosphorus, nitrogen, sand, clay and pH) explained by canonical variates in recently burned sites in Florida and southern California

Canonical axis or variate	Likelihood ratio	Approximate <i>F</i>	Numerator d.f.	Denominator d.f.	<i>P</i>
Florida sites					
Variation in site characteristics					
1	0.043	4.47	12	14	0.005
2	0.358	2.86	5	8	0.090
Variation among seedling and site variables					
1	0.274	1.06	12	14	0.453
2	0.608	1.03	5	8	0.459
California sites					
Variation in site characteristics					
1	0.083	2.89	12	14	0.031
2	0.393	2.47	5	8	0.123
Variation among seedling and site variables					
1	0.044	4.42	12	14	0.005
2	0.323	3.35	5	8	0.063

tion suggested a relationship between seedling-related characteristics of sites (i.e. seedling density, proportion of species represented by seedlings) and site-related characteristics (i.e. percentage open canopy and soil phosphorus, nitrogen, sand, clay and pH). The canonical correlation produced two canonical variates, with the first variate significant (Table 2); the second, although only barely significant, nevertheless substantially improved the corre-

lation. The two site canonical variates combined explained 78% of the variance in seedling density and proportion of species represented by seedlings.

Seedling density and the proportion of species represented by seedlings were not correlated with each other ( $r = -0.17$ ,  $P > 0.05$ ), and were correlated with different canonical variates. The first statistically significant variate was associated with high values for proportion of species represented by seedlings, and with high soil pH and low phosphorus, while the second was associated with high seedling densities, high soil clay contents and low soil sand and canopy openness values (Table 3).

**Table 3** Loadings of seedling and site variables from recently burned sites in three southern California communities on canonical variates, and canonical correlations. Seedling-related variables are seedling density (DENSITY) and proportion of species represented by seedlings (PROPSPP); site-related variables are percentage open canopy (OPENCAN), percentage total soil phosphorus (PHOS), percentage total soil nitrogen (NITR), percentage soil sand (SAND), percentage soil clay (CLAY) and soil pH (PH)

Variables	Canonical variate	
	1	2
Seedling		
DENSITY	-0.259	0.966
PROPSPP	0.996	0.095
Site		
OPENCAN	-0.182	-0.488
PHOS	-0.526	0.292
NITR	-0.021	-0.016
SAND	0.057	-0.493
CLAY	-0.174	0.803
PH	0.767	0.417
Canonical correlations	0.898	0.789
% variance of seedling variables explained	46	32

## Discussion

Although numerous comparisons of post-fire responses between mediterranean-type ecosystems exist (Cody & Mooney 1978; Naveh & Whittaker 1979; Barbour & Minnich 1990), this study is the first to compare responses with other scrub communities (but see Whelan 1985). We predicted that because of differences in climate between California (mediterranean) and Florida (subtropical), seedling establishment patterns would be more similar within regions than between regions. This prediction was borne out for recently burned sites, in which both post-fire seedling densities and proportions of species represented by seedlings were higher in California than in Florida.

In contrast, most previous comparisons among communities have quantified post-fire seedling species richness and/or relative cover of species recruiting by seed (Naveh & Whittaker 1979; Shmida 1981; Barbour & Minnich 1990). Our two parameters gauge the response of the community to fire, because together they approximate a measure analo-

gous to the species' importance values (Spurr & Barnes 1973) used in other community-level studies. Different processes may operate at different spatial and temporal scales: values for seedling density suggested that they reflected immediate post-fire conditions for germination and establishment, whereas the proportion of species represented by seedlings largely resulted from longer-term evolution of species' characteristics in response to particular disturbance regimes and climates. Both parameters contribute to the characteristic post-fire 'flush' of recruitment (e.g. Barbour & Minnich 1990).

Seedling densities in mature sites may reflect recruitment between fires and so help to characterize communities in different regions. Although means were not statistically different, values were slightly higher and had much higher variances in California than in Florida. This difference suggests that establishment conditions between fires were occasionally favourable in California, but only rarely so in Florida.

Among recently burned sites, California sites had higher seedling densities and proportions of species represented by seedlings than Florida sites, and also had more species dependent upon fire for seedling recruitment (Table 1 and Fig. 3). Florida densities were similar to previous reports (Johnson 1982; Hawkes & Menges 1995; Carrington 1996) but those for chaparral were modest. For example, 90 post-fire sites (including chaparral and coastal sage scrub) averaged 68 seedlings  $m^{-2}$  (Keeley 1997), and higher densities are not uncommon (Keeley 1998).

Greater post-fire recruitment in California communities and Florida rosemary scrub was associated with greater canopy openness, supporting the suggestion that fire-recruiting species are gap-dependent (Keeley & Zedler 1978; Christensen 1985; Malanson & O'Leary 1985). We hypothesize that the observed change in canopy coverage may be the cause of post-fire seedling establishment: the closed canopy in mature chaparral may inhibit recruitment *via* limited levels of light, water and nutrients, as well as biotic factors such as increased predation and allelopathy (Keeley & Keeley 1989). Post-fire recruitment capitalizes on improved biotic and abiotic conditions, and in California is particularly marked in sites with relatively mesic conditions (e.g. high soil clay contents, higher percentage canopy cover).

Two factors lead to the diminished importance of post-fire seedling recruitment in Florida: gaps in mature vegetation are larger, allowing some inter-fire recruitment (Menges & Kimmich 1996), and rapid resprouting limits the opportunities for seedling establishment, even in burned sites. Rosemary scrub, the only Florida community with seedling densities comparable to chaparral, had, as would be expected from this analysis, the largest fire-induced contrast in percentage open canopy (Fig. 4). Its see-

ingly harsh, xeric conditions for seedling establishment (i.e. sandy, low-nutrient soil) may, however, reduce competition by slowing regrowth of competitively superior adult plants (Menges & Kohfeldt 1995). The physiognomic and floristic differences between Florida sand pine scrub and sandhill, which have similar soil conditions and low seedling densities, are probably due to different fire regimes (Kalisz & Stone 1984; Myers 1985).

Sorting out selective factors responsible for seedling establishment patterns in California and Florida communities requires careful analysis, because climate, soils and fire histories differ between the two regions. In California, summer drought may limit post-fire cover by reducing survivorship of resprouting species and by delaying resprouting until winter rains, whereas summer rains in Florida may enhance survivorship. Greater canopy coverage in mature chaparral results in more intense fires and thus reduced survivorship (Borchert & Odion 1995), whereas in Florida the more open canopy results in lower fire intensity and increased survival (Hawkes & Menges 1995; Menges & Kimmich 1996).

Florida and California are similar in that most seedling establishment occurs in spring (Carrington 1996; Lambert & Menges 1996; Keeley 1998). In Florida, however, natural fires typically occur in spring and early summer, and seedling establishment is thus delayed until 9–10 months post-fire. Summer rains following the fire season allow resprouts to grow for a full season before seedlings can establish. In California, fires typically occur in autumn and resprout growth is limited initially by drought and later by winter temperatures. Seedlings and resprouts thus start growth at roughly the same time, and opportunities for successful recruitment are therefore greater in chaparral.

Fire season was consistent for all sites within each region, and therefore should not have contributed to differences in seedling recruitment patterns. Fire histories, however, undoubtedly varied among sites, especially in Florida where fire suppression has been practised for most of the last six decades. The extremely long fire return interval, particularly in sand pine scrub sites, probably contributed to low post-fire seedling recruitment (Abrahamson & Abrahamson 1996).

Despite very marked differences in soil texture and fertility (Fig. 4) and in fire history, we believe that seedling recruitment patterns in California and Florida are largely determined by climate. Two other mediterranean climate ecosystems, South African fynbos and Western Australian kwongan, occur on sandy infertile soils comparable to the subtropical Florida scrub sites, but their post-fire seedling recruitment (Kruger *et al.* 1983) matches that observed at our California sites.

Climatic processes may influence seedling recruitment patterns in California and Florida by differentially modifying levels of competition and/or allelopathy from adult plants (Williamson *et al.* 1992). Because this study only identified patterns in seedling recruitment and site characteristics that suggest underlying processes, experimental studies are needed to determine causal mechanisms. Empirical field research is particularly needed on the effects of competition and allelopathy on post-fire seedling establishment, and on the influence of fire regime on characteristics of species- and community-level post-fire recruitment. Research in these areas will elucidate further between-region differences in community responses to fire.

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