DEMOGRAPHIC PATTERNS OF POSTFIRE REGENERATION IN MEDITERRANEAN-CLIMATE SHRUBLANDS OF CALIFORNIA

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Abstract. This study uses detailed demographic data to determine the extent to which functional groupings, based on seedling recruitment and resprouting response to fire, capture the dynamics of postfire responses and early successional change in fire-prone ecosystems. Following massive wildfires in southern California, USA, we sampled chaparral and sage scrub vegetation in nested 0.1-ha plots from 90 sites for five postfire years. Prefire density of woody skeletons and cover and density of all postfire species were recorded.

Functional types of postfire obligate seeder, facultative seeder, and obligate resprouter are broadly useful but fail to capture much of the dynamics of postfire succession in these shrublands. For the woody flora, stratifying these three regeneration modes by life-form captures important differences. Postfire obligate-seeding shrubs exhibit a single postfire seedling cohort whereas the faster growing suffrutescent species reach reproductive maturity by the second year and produce multiple seedling cohorts. Postfire obligate-resprouting shrubs reach reproductive maturity early but have very limited seedling recruitment in the early postfire years, whereas obligate-resprouting subshrubs flower the first year from resprouts and have seedling recruitment pulses in the second and subsequent postfire years.

For the rich herbaceous flora, further subdivisions are needed to capture the range of variation. Herbaceous perennials are nearly all postfire obligate resprouters, and there are important demographic differences during early succession in different growth forms such as geophytes and rhizomatous grasses. Annuals lack resprouting ability and are postfire obligate seeders. Some exhibit extreme life-history specialization and are present only in the immediate postfire year(s). Others are highly specialized on fire but persist during early succession, and still others are opportunistic species widely distributed on open sites but can expand their populations during early succession.

Key words: California (USA) shrublands; chaparral; facultative seeders; fire endemics; functional types; obligate resprouters; obligate seeders; postfire regeneration; sage scrub; seedling survivorship.

Introduction

Understanding community responses to disturbance and subsequent successional pathways requires knowledge of both patterns and processes, which can be viewed as comprising changes in biodiversity and ecological function. The former focuses on species whereas the latter views the biota as suites of species that play equivalent ecosystem roles. These suites are commonly referred to as "functional groups," and it is believed that understanding the dynamics of these groups will provide a broad-brush view of ecosystem functioning (Chapin 1993). One of the limitations to the functional-type approach is that when species are grouped with respect to a particular variable, they often re-assemble into different groups when another variable is considered (Noble and Gitay 1996). Indeed, the independent variation of traits strongly supports the need for a species approach (Eviner 2004), and

emphasizes the importance of biodiversity patterns in understanding ecosystem function. This in fact has led to a consideration of covariance patterns in trait distribution and the recognition of functional strategies that are fundamentally species-specific approaches (Reich et al. 2003, Ackerly 2004).

Functional-type approaches have been widely utilized to predict plant community responses to disturbances such as fire (Noble and Gitay 1996, Lavorel et al. 1997, Bradstock and Kenny 2003). However, critical to understanding life-history responses to fire is recognition of how various fire regimes select for different suites of traits. For example, in western North America many coniferous forests have historically burned frequently with fires that predominantly consumed surface fuels and left large patches of intact forest. Life-history responses to fire have been very different in these surface-fire regimes than for the adjacent shrublands that always burn in crown fires, which kill all above-ground vegetation (Keeley and Zedler 1998). Colonization, for example, may be an important part of forest recovery in ecosystems with surface fire, or mixed fire

PLATE 1. Burned skeletons of chaparral shrubs and regrowth in the first postfire growing season from shrub resprouts and annuals germinating from dormant seed banks. Photo credit: C. J. Fotheringham.

regimes (Turner et al. 1998), whereas it represents a minor part of biomass recovery in crown-fire regimes such as California chaparral (Keeley et al. 2005a).

Postfire recovery in shrubland crown-fire ecosystems (see Plate 1) largely involves residual species present at the time of fire, and regeneration is initiated by germination of dormant seed banks or resprouting from lignotubers or other vegetative structures (Keeley 1981, Trabaud 1987, Whelan 1995, Bond and van Wilgen 1996, Lamont and Wiens 2003, Pausas et al. 2004). Species are commonly divided into (1) *obligate seeders*, which are ones incapable of vegetative regeneration and are present in the first postfire year as seedlings from fire-stimulated germination of dormant seed banks, (2) *facultative seeders*, which have postfire germination of dormant seed banks coupled with resprouting, and (3) *obligate resprouters*, which lack a dormant seed bank but regenerate vegetatively. While obligate- and facultative-seeding species are known to recruit heavily following fire, there are few quantitative data on how this recruitment pulse compares to recruitment in subsequent years, or the range of variability in early successional recruitment for these two postfire regeneration types. Obligate resprouters are recognized by their lack of reproduction in the immediate postfire environment, but they do recruit during the fire-free interval (Keeley 1998a). Based on apparent differences in postfire

recovery of seeders and sprouters, it is expected that they exhibit very different competitive relationships during early postfire succession (Tyler and D'Antonio 1995).

These different postfire regeneration modes may lead to demographic patterns that play important roles in community reassembly. Although community-assembly theory has long been ruled by models based on stability and equilibrial processes—in particular, competition—it is increasingly apparent that in fire-prone communities other models that invoke less deterministic factors may be more appropriate (Chesson and Case 1986). In particular, large pulses of seedling recruitment are considered to be a potentially powerful force behind species coexistence in communities (Warner and Chesson 1985). This is very applicable to fire-prone mediterranean-climate ecosystems that experience pulse recruitment in the first postfire year (Laurie and Cowling 1994, Lamont and Witkowski 1995, Bond and van Wilgen 1996).

Characteristic of many fire-prone plant communities is a marked dominance hierarchy illustrated by a geometric dominance diversity distribution (Keeley and Fotheringham 2003), and thus it is not too surprising that postfire regeneration studies have largely focused on the woody dominants. Consequently relatively little study has been directed at regeneration

modes in other life-forms, which represent an important knowledge gap since many of the subordinate species in communities may play critical roles in community development and ecosystem functioning (Walker et al. 1999).

It is apparent that there is need for a better understanding of the mechanisms controlling the postfire demographic patterns of entire communities. Our present study investigates the extent to which regeneration types exhibit modal differences following wildfire in fire-prone shrublands, and the extent to which they can be of predictive value in understanding early-successional dynamics. We investigate species-specific responses and evaluate whether or not regeneration modes of obligate-seeding, facultative-seeding, and obligate-resprouting respond in a functionally similar manner across all life-forms. We also use these detailed demographic data to address questions about community structure and function. We studied these reponses during the first five years following wildfires in southern California, USA, shrublands. These included evergreen chaparral and the lower stature, semi-deciduous, sage-scrub communities. Because of marked landscape-scale variation in community structure (Keeley et al. 2005), we have included wildfires that burned over a large portion of the region at approximately the same time.

METHODS

Ninety study sites were selected from 16 fires that burned over 80 000 ha across an area of more than 10 000 km^2 in southern California (USA) in late October and early November 1993 (further details in Keeley et al. 2005a). The number of sites in each burn was based on fire size, diversity of vegetation types, fire severity, and accessibility. Selection criteria included absence of other disturbances, proximity to roads for easy access, roughly comparable numbers of low- and high-severity fires, and comparable numbers of evergreen chaparral and semi-deciduous sage-scrub sites in the final study. Sample plots were 0.1-ha rectangles that were laid down parallel to the elevational contour. We expected that this orientation would capture the greatest range of variation since drainage patterns parallel to the slope appeared to be the primary determinant of community patterns. Plots comprised burned shrublands with an apparently homogenous distribution of shrub skeletons of similar stature, species composition, and spacing.

Sampling began in the first spring after fire and continued for a total of five growing seasons (two sites were lost to development after the second year). For analysis, both chaparral and sage-scrub sites were stratified by landscape position: coastal if within 10 km of the coast, and interior if >20 km from the coast. Thus, our initial analysis was with four plant associations, coastal chaparral, coastal sage scrub, interior chaparral, and interior sage scrub. Where we found no significant differences between coast and interior populations, our analysis was restricted to comparison of

TABLE 1. First postfire year distribution of regeneration modes among all life-forms and within woody (shrubs, subshrubs, and suffrutescents) and herbaceous perennial life-forms.

| Life-form | Number of species | | |
	Obligate seeders	Facultative seeders	Obligate resprouters
All life-forms			
Coastal chaparral	94	24	57
Coastal sage scrub	89	22	55
Interior chaparral	170	36	72
Interior sage scrub	155	32	78
Woody species			
Coastal chaparral	5	13	6
Coastal sage scrub	3	12	8
Interior chaparral	8	18	15
Interior sage scrub	3	13	7
Herbaceous-perennial species			
Coastal chaparral	1	3	42
Coastal sage scrub	1	2	35
Interior chaparral	2	4	46
Interior sage scrub	2	5	61

Note: Obligate seeders lack vegetative regeneration and are present solely as seedlings; facultative seeders also recruit seedlings after fire but can regenerate vegetatively as well; and obligate resprouters have seedling recruitment restricted to fire-free intervals and are present after fire entirely from vegetative regeneration (Keeley 1998a).

the two vegetation types, chaparral and sage scrub. Nomenclature was according to Hickman (1993).

Vegetation was sampled in 20 × 50 m (0.1-ha) sites with nested subplots, and to this extent had much in common with the widely cited "Whittaker plot" method (Keeley and Fotheringham 2005). However, the highly clumped distribution of subplots in the Whittaker design is only appropriate for sites where the vegetation is homogenous at the 0.1-ha scale, and this did not hold for our sites (Keeley 2004). We used a design with greater dispersion of nested subplots across the tenth hectare (Keeley et al. 2005a). Briefly, the 0.1-ha sites were subdivided into 10 non-overlapping 100-m^2 square plots, each containing two 1-m^2 subplots in opposite corners (interior subplots were offset 1 m from the center to reduce contagion effects with the adjacent plot). Within each 1-m^2 subplot, cover was visually estimated for each species, and density of individual genets was precisely determined for all perennial species, and for annuals with densities less than ~25 plants/m^2, but higher densities of annuals were estimated. Within the 100-m^2 plots a list was made of additional species not recorded from the 1-m^2 subplots. A few species produced both seedlings and root suckers that could be confused. Sufficient excavations (outside the plots), and examination of morphological characteristics were done to be certain we correctly identified seedlings from these resprouts.

Prefire woody-plant density was based on a census of skeletal remains of shrubs and subshrubs (and occasional trees) in each 100-m^2 plot. All skeletons were recorded by species, which were identifiable based on
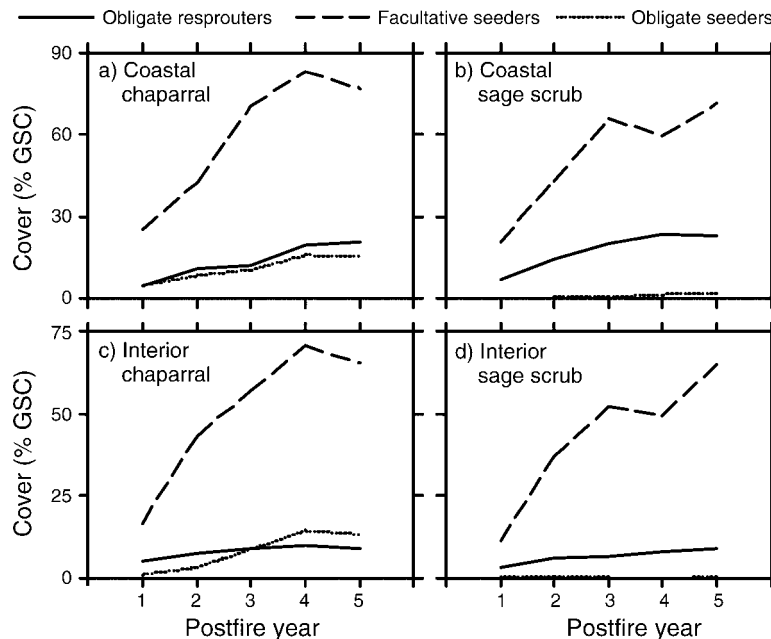
FIG. 1. Cover changes (percentage of ground surface covered [GSC]) for woody (shrub, subshrub, and suffrutescent) postfire regeneration types in coastal and interior chaparral and sage scrub, in the first five years after fire.

form, branching pattern, and bark. On some sites skeletons were burned to ground level but there still persisted characteristics of root-crown shape that allowed us, in most cases, to assign a species name. In a small percentage of cases (<1%) skeletal remains were unidentifiable to species. Skeletons in the first postfire year were used to estimate prefire populations. In these communities skeletons can be identified to species based on branching pattern and bark characteristics (Keeley et al. 2005a). We inferred that these skeleton populations represented the prefire shrub population density, however, we lack a measure of the amount of error associated with this method. In general, skeletons at densities and spacing similar to that observed in unburned stands were observed, and so we assumed that they represented an acceptable estimate of the prefire population of living shrubs. It seems likely that this estimate comprises mostly living shrubs prior to the fire as dead shrubs would be more likely to be completely consumed by fire and not leave a recognizable skeleton.

Precipitation data were obtained from the Climatological Annual Summary, published by the National Oceanic and Atmospheric Administration (Ashville, North Carolina, USA). Totals for the period (September–August, which encompasses a single growing season) during the five-year study were averaged from several climate stations distributed within the range of coastal and interior sites. The first, third, and fourth years were ~80%, the second year was 175%, and the fifth year was 250%, of the long-term average.

Data were analyzed initially by plant association (coastal chaparral, coastal sage scrub, interior chaparral, or interior sage scrub). Where significant differences were detected these were presented. Otherwise data were summarized by vegetation type (chaparral or sage scrub) or by species. Data were analyzed and graphically displayed with SYSTAT 10.0 (SPSS 2000). Effect of time since disturbance and plant association on cover and density of regeneration modes was tested with a fixed-effects two-way ANOVA. Relationships between variables were tested for significance by regression analysis, and significant relationships were fitted with least-squares regression lines. Where bivariate data did not fit an arithmetic relationship, semi-log and log-log transformations were compared and the one giving the highest adjusted r^2 value was presented. Between-treatment comparisons used two-tailed t tests.

RESULTS

Life-form distribution

In the first postfire year fire regeneration types included obligate seeders, facultative seeders, and obligate resprouters (Table 1). The preponderance of obligate-seeder species is driven by the high number of annuals, which were particularly abundant in interior associations. Resprouting of course is not an option for annuals, and when considering only perennials (woody and herbaceous) we see that obligate-seeder species were relatively few in number (Table 1). The majority of woody species were facultative seeders, whereas herbaceous perennials had very few seeder species, and nearly all were obligate resprouters. These patterns were

TABLE 2. Results of two-way fixed-effects ANOVA, showing the effect of time since disturbance and plant association on woody-plant cover or density of the different regeneration modes.

Source of variation	df	F	P
Cover			
Obligate seeder			
Year	4	4.795	<0.001
Plant association	3	21.005	<0.001
Year × association	12	1.517	0.12
Error	430		
Facultative seeder			
Year	4	37.045	<0.001
Plant association	3	4.761	0.003
Year × association	12	0.740	0.71
Error	430		
Obligate resprouter			
Year	4	1.195	0.31
Plant association	3	4.723	0.003
Year × association	12	1.458	0.14
Error	430		
Density			
Obligate seeder			
Year	4	4.524	<0.001
Plant association	3	4.122	0.007
Year × association	12	1.517	0.092
Error	430		
Facultative seeder			
Year	4	4.000	0.003
Plant association	3	4.078	0.007
Year × association	12	1.362	0.18
Error	430		
Obligate resprouter			
Year	4	1.969	0.098
Plant association	3	4.346	0.005
Year × association	12	0.940	0.51
Error	430		

Note: Woody plants include shrub, subshrub, and suffrutescent species; $n = 440$ (88 sites over five years).

remarkably similar between the four plant associations, coastal and interior chaparral and coastal and interior sage scrub.

Woody species

The general patterns of postfire change in cover for the dominant woody vegetation (Fig. 1) illustrate broad similarities between vegetation types with facultative-seeding woody plants (i.e., shrubs, subshrubs, and suffrutescents) dominating. All four plant associations had a moderate component of obligate resprouters that increased gradually over time, but only chaparral associations (Fig. 1a, c) had any significant obligate-seeding component.

For this woody flora, cover of both obligate and facultative seeders increased markedly through the first five postfire years, and this was evident in highly significant effects due to postfire year (Table 2). Obligate resprouters on the other hand grew rapidly in the first postfire year, but over the five years of study there was no significant effect due to year. Density of all seeders (obligate and facultative) declined over time and this was evident in a significant effect due to year. Not surprisingly, obligate-resprouter density changed very little. Cover and density for all three regeneration modes varied between vegetation types, and these differences were consistent from year to year as suggested by the lack of a significant interaction term (Table 2).

Seedling recruitment patterns for species comprising the three woody fire-response functional types are shown for individual species in Appendix A and representative species are illustrated in Fig. 2. Species are presented by vegetation type and it is clear that there were relatively few species not found in both chaparral and sage scrub (Appendix A). Obligate seeders were only represented by four genera, whereas facultative seeding was a widely distributed mode, being found in 5 times as many genera. Obligate resprouting was also widely distributed among many genera.

All obligate-seeding shrubs had seedling recruitment essentially restricted to the first postfire year (Appendix A, Fig. 2a). As a consequence these populations largely comprised even-aged cohorts throughout succession, and very few of these shrubs reached reproductive maturity during the course of this five-year study. The only obligate-seeding subshrub followed a similar pattern (Fig. 2b), except these plants became reproductive in the second or third postfire year. The relatively short-lived suffrutescent species reached reproductive maturity in the second year and had a low level of seedling recruitment in subsequent years (Appendix A, Fig. 2c).

Facultative seeders varied in the timing of seedling recruitment, with some species exhibiting synchronized postfire recruitment and other species having multiple recruitment events (Appendix A). Those with seedling recruitment concentrated in the first year were mostly shrubs such as *Adenostoma fasciculatum* (Fig. 2d), *Ceanothus spinosus*, *Malosma laurina*, and *Rhus ovata*. While very few of the postfire seedling recruits reached reproductive maturity during the first five years, the resprouting individuals of most shrub species were reproductive and dispersing seeds by the second postfire year. However, despite their capacity for seed production early in succession, these species exhibited very limited seedling recruitment in subsequent years (Appendix A). Only one shrub, *Rhus integrifolia*, exhibited substantial seedling recruitment after the first year, in the high-rainfall years 2 and 5; however, total seedling recruitment was 1–2 orders of magnitude less than other facultative-seeding shrubs.

Facultative-seeding subshrubs and suffrutescents were quite different from facultative-seeding shrubs in that recruitment was not restricted to the first postfire year; rather, all of them exhibited substantial seedling recruitment in subsequent years (Appendix A, Fig. 2e and f). Resprouts in many of these species were reproductive in the first growing season, and seedlings of these species commonly were reproductive by the third year. One
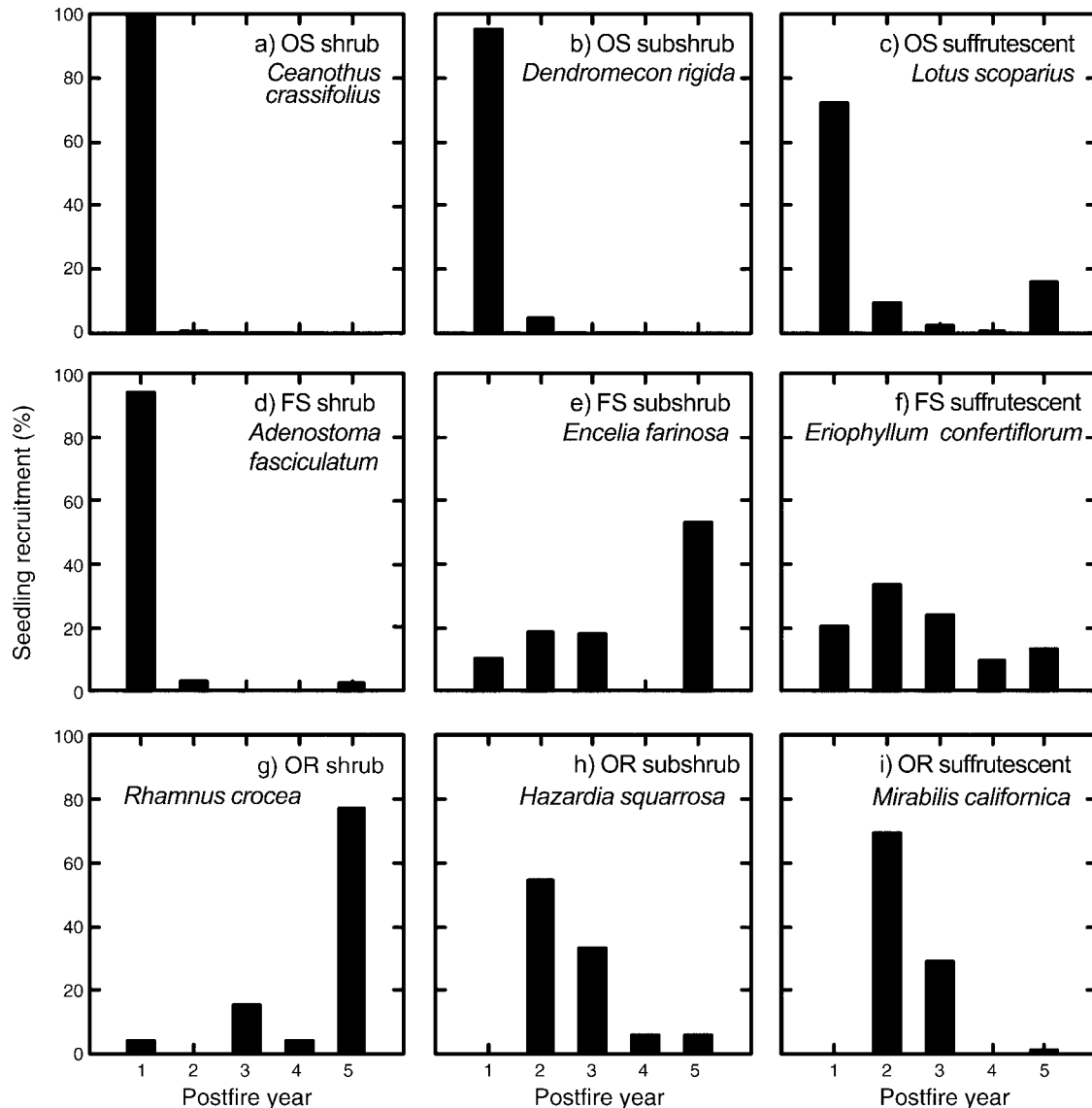
Fig. 2. Postfire demographic changes in seedling recruitment for representative examples of (a, b, c) obligate-seeding (OS), (d, e, f) facultative-seeding (FS), and (g, h, i) obligate-resprouting (OR) species, with examples for the three woody life-forms: (a, d, g) shrubs, (b, e, h) subshrubs, and (c, f, i) suffrutescents.

exception to this pattern was *Malachothamnus fasciculatus*, which exhibited a pattern more similar to the facultative-seeding shrubs (Appendix A). This plant could be classified as a shrub due its stature, but here it was considered a subshrub due to its relatively short life span.

Obligate resprouters by definition largely failed to recruit seedlings in the first growing season and recruitment in subsequent years largely varied with life-form (Appendix A). Obligate-resprouting shrubs had very little recruitment in subsequent postfire years, with *Rhamnus crocea* (sensu *lato*) being the most widespread and averaging the highest density of seedlings, with a peak in year 5 (Fig. 2g). However, even for this species the total five-year seedling recruitment was orders of

magnitude less than that of seeders, which recruited in the first postfire year.

Obligate-resprouting subshrubs and suffrutescents were quite unlike their shrub counterparts (Appendix A). All resprouted and flowered the first year, and most exhibited massive seedling recruitment in the second postfire year. Obligate resprouters with a second year peak in seedling recruitment included species of *Encelia, Eriogonum, Galium, Hazardia* (Fig. 2h), *Lessingia*, and *Mirabilis* (Fig. 2i).

Useful to understanding recruitment strategies is the seedling-to-prefire parent ratio (Table 3). Species exhibited very limited differences when comparing chaparral vs. sage scrub populations, but often there were substantial differences between coastal vs. interior

TABLE 3. First-year postfire resprouting success and seedling/parent ratios (parents based on census of shrub skeletons) for woody species, by regeneration mode and life-forms (data are means ± SE, with number of species in parentheses).

Species	Percentage resprouting†		Seedling/parent ratio‡	
	Coast	Interior	Coast	Interior
Obligate seeders: shrubs				
Ceanothus crassifolius				74 ± 22 (9)
C. greggii				208 ± 142 (3)
C. megacarpus			101 ± 49 (9)	
Facultative seeders: shrubs				
Adenostoma fasciculatum	74 ± 3 (7)	73 ± 4 (27)	66 ± 40 (3)	64 ± 10 (22)
Ceanothus spinosus	40 ± 11 (5)		108 ± 59 (4)	116 (1)
Malachothamnus facsciculatus	7 ± 3 (7)		546 ± 341 (6)	
Malosma laurina	92 ± 5 (10)	97 ± 2 (5)	240 ± 81 (9)	90 ± 44 (4)
Rhus integrifolia	74 ± 7 (9)		8 ± 6 (3)	
R. ovata	81 (1)		86 ± 26 (5)	70 ± 25 (3)
Ribes aureum, malvaceaum, and *R. speciosum*	100 (1)	92 ± 8 (2)	25 ± 13 (4)	1341 ± 1205 (4)
Facultative seeders: subshrubs and suffrutescents				
Artemisia californica	18 ± 8 (11)	20 ± 6 (19)	15 ± 0 (2)	33 ± 10 (23)
Encelia farinose		20 ± 6 (3)		7 ± 6 (3)
Eriodictyon crassifolium and *E. trichocalyx*		87 ± 9 (4)		
Eriogonum fasciculatum	9 ± 4 (27)	10 ± 7 (9) 7	136 ± 64 (3)	34 ± 17 (17)
Mimulus aurantiacus	36 ± 12 (8)	56 ± 44 (2)	1 ± 1 (8)	25 ± 14 (5)
Salvia apiana		63 ± 6 (9)		2 ± 1 (6)
S. leucophylla	50 ± 15 (4)	87 ± 4 (2)	5 (1)	1 (1)
S. mellifera	5 ± 2 (13)	14 ± 6 (15)	76 ± 40 (4)	97 ± 24 (15)
Obligate resprouters: shrubs				
Cercocarpus betuloides	95 ± 5 (2)	100 (1)	0	0
Heteromeles arbutifolia	87 ± 4 (2)		0	0
Keckiella antirrhinoides		96 ± 4 (2)	0	0
Prunus ilicifolia	100 (1)		0	0
Quercus berberidifolia		98 ± 1 (6)	0	0
Rhamnus crocea/ilicifolia	100 ± 1 (2)	100 (1)	<0.1	0
Toxicodendron diversilobum	100 ± 1 (3)	100 (1)	<0.1	<0.1
Xylococcus bicolor	100 (1)		0	0
Obligate resprouters: subshrubs and suffrutescents				
Encelia californica	83 ± 8 (8)		0	0
Eriogonum cinereum	74 ± 4 (8)		0	<0.1
Galium angustifolium	100 (1)		0	0
Hazardia squarrosa	99 ± 1 (8)	100 ± 0 (8)	<0.1	<0.1
Yucca whipplei	81 ± 8 (4)	86 (1)	0	0

Notes: Most species occurred in both chaparral and sage scrub and were sometimes more abundant in one vegetation type or the other (Appendix A), but regeneration patterns did not differ greatly between them. However, there often were differences in resprouting success between coastal and interior populations. Other common woody species not represented in the prefire community or lacking skeletons that survived the fire included the obligate seeders *Ceanothus oliganthus, Dendromecon rigida, Helianthemum scoparium,* and *Lotus scoparius*; the facultative seeders *Calystegia macrostegia, Eriophyllum confertiflorum, Galium nuttallii, Keckiella cordifolia, Porophyllum gracile, Solanum parishii, S. umbelliferum, S. xantii,* and *Venagasia carpesioides*; and the obligate resprouters *Lessingia filaginifolia, Lonicera* spp., and *Mirabilis californica*. Data are means ± SE, with number of sites in parentheses.

† Resprouting percentages are presented only for those sites with >30 skeletons sampled.

‡ Seedling ratios are presented only for sites with >5000 seedlings/ha.

populations. For shrubs, there was relatively little difference in this ratio for obligate vs. facultative seeders, which very roughly could be placed at about 100 seedlings per prefire adult, with notable exceptions (Table 3).

Resprouting success varied between facultative-seeding and obligate-resprouter species (Table 3). In general, a greater proportion of the prefire obligate-resprouter population resprouted than was the case with facultative seeders. Indeed, the size of many obligate-resprouting shrub populations remained unchanged due to 95–100% resprouting.

For shrubs and subshrubs (but not suffrutescents) with woody skeletons it was possible to evaluate the change in proportional representation from the prefire community to the first postfire year population comprising seedlings and resprouts (Fig. 3). For the three dominant obligate-seeding shrubs, only *Ceanothus megacarpus* (Fig. 3g) approximates a proportional replacement of prefire populations with seedling populations. The other two species, *C. crassifolius* (Fig. 3a) and *C. greggii* (Fig. 3d), had abundant postfire seedling recruitment in excess of their proportional representation in the prefire community.
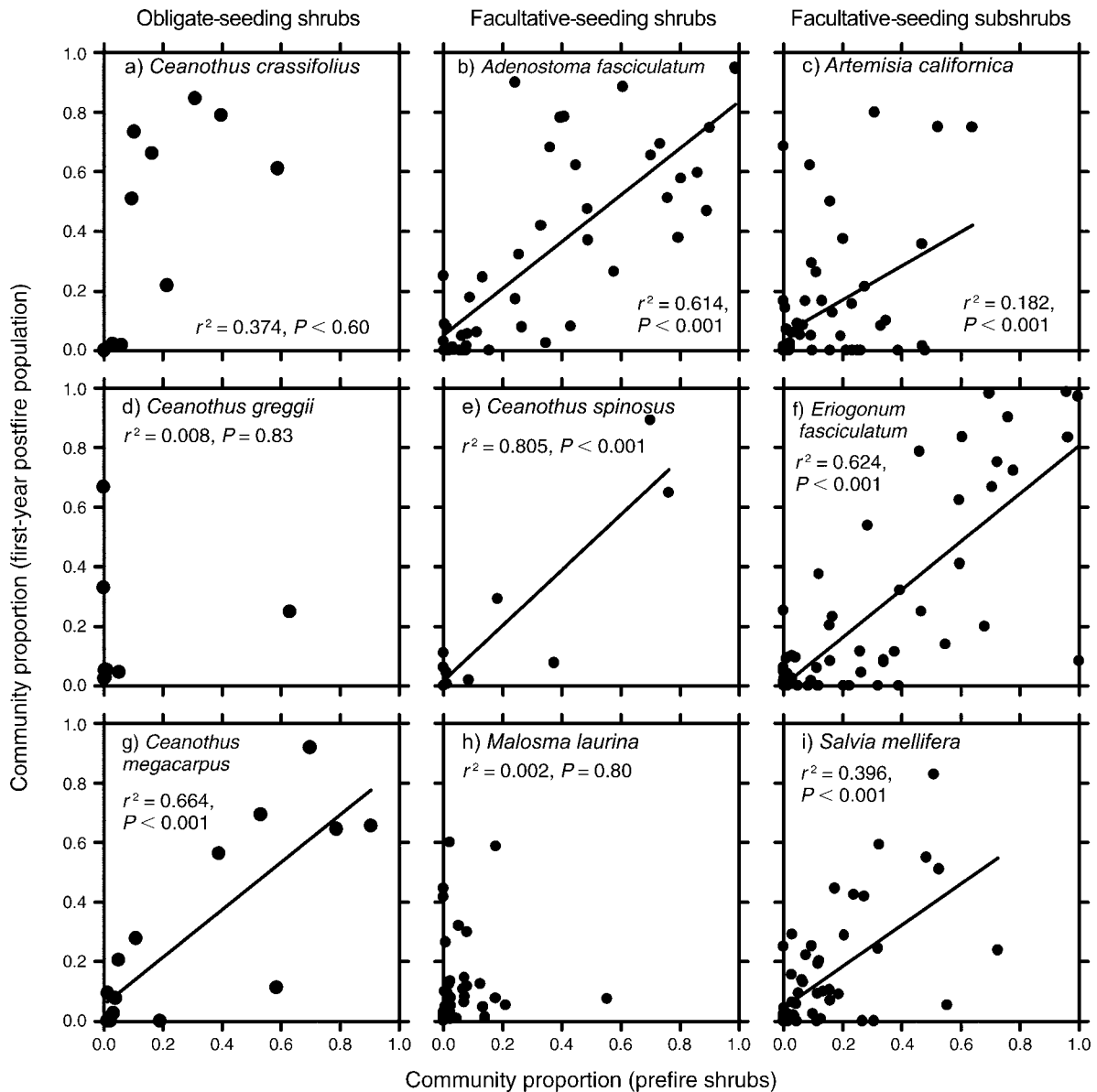
FIG. 3. Proportional density of first-year postfire populations vs. prefire populations for the most common obligate-seeding shrubs (a, d, g), facultative-seeding subshrubs (b, e, h), and shrubs (c, f, i), for seedlings and resprouts. Each panel shows the species proportional contribution to the community both before and after fire.

Facultative-seeding shrubs *Adenostoma fasciculatum* (Fig. 3c) and *Ceanothus spinosus* (Fig. 3f) and the subshrubs *Artemisia californica, Eriogonum fasciculatum,* and *Salvia mellifera* (Fig. 3b, e, and h) showed significant relationships between their proportion of the prefire population and the postfire population, which included both resprouts and seedlings. Also, these species comprised roughly the same proportion of the community before and after the fire.

During the first postfire year, separating out the influence of seedlings vs. resprouts for the facultative seeders is of interest (Table 4). For the widespread *Adenostoma fasciculatum*, seedlings alone exhibited a significant relationship between prefire and postfire populations, and adding in resprouts did not greatly alter that relationship. The postfire *Ceanothus spinosus* populations on the other hand approximated the prefire composition only when both resprouts and seedlings were included. The widespread *Malachothamnus fasciculatus* produced a slope much greater than 1, indicating that this species comprised a much greater proportion of the postfire community than the prefire community. This is largely due to the fact that it is a relatively short-lived plant, and thus on most sites there were few living plants prior to the fire. Another very widespread species, *Mimulus aurantiacus*, had a slope that was much less

TABLE 4. Relationship of prefire populations vs. first-year postfire populations for seedlings or seedlings plus resprouts for woody species present at ≥7 sites, based on proportion of community by density.

Species	No. sites	Seedlings			Resprouts + seedlings		
		r^2	P	Slope	r^2	P	Slope
Obligate seeders: shrubs							
Ceanothus crassifolius	10	0.327	0.060				
C. greggii	8	0.004	0.83				
C. megacarpus	14	0.608	<0.001	0.869			
Facultative seeders: shrubs							
Adenostoma fasciculatum	46	0.568	<0.001	0.767	0.614	<0.001	0.782
Ceanothus spinosus	10	0.279	0.12		0.805	<0.001	0.780
Melachothamnus fasciculatus	43	0.117	0.025	4.269	0.092	0.048	3.193
Malosma laurina	42	0.018	0.41		0.002	0.80	
Rhus integrifolia	21	0.027	0.47		0.211	0.036	1.184
R. ovata	22	0.131	0.098		0.098	0.16	
Facultative seeders: subshrubs and suffrutescents							
Artemisia californica	55	0.093	0.024	0.522	0.182	0.001	0.570
Encelia farinose	7	0.862	0.003	0.950	0.836	0.004	0.803
Eriodictyon crassifolium and E. trichocalyx	9	0.027	0.67		0.864	<0.001	0.562
Eriogonum fasciculatum	59	0.606	<0.001	0.836	0.624	<0.001	0.803
Mimulus aurantiacus	31	0.021	0.44		0.517	<0.001	0.280
Salvia apiana	18	0.572	<0.001	0.361	0.636	<0.001	0.467
S. leucophylla	14	0.701	<0.001	1.386	0.761	<0.001	1.103
S. mellifera	54	0.275	<0.001	0.667	0.396	<0.001	0.690
Obligate resprouters: shrubs							
Cercocarpus betuloides	15				0.040	0.48	
Heteromeles arbutifolia	21				0.084	0.20	
Keckiella antirrhinoides	12				0.809	<0.001	1.255
Prunus ilicifolia	8				0.213	0.25	
Quercus berberidifolia	21				0.688	<0.001	0.183
Rhamnus crocea/ilicifolia	57				0.013	0.40	
Obligate resprouters: subshrubs and suffrutescents							
Encelia californica	13				0.804	<0.001	0.851
Eriogonum cinereum	10				0.909	<0.001	1.140
Hazardia squarrosa	36				0.481	<0.001	0.481
Yucca whipplei	29				0.571	<0.001	0.568

Note: For seedlings, blank cells indicate that no regression was done for that variable; for slopes, blank cells indicate the slope was insignificant.

than 1, indicating the postfire population was far below replacing the prefire population (Table 4). The reasons for this were the relatively low level of resprouting (Table 3), and the fact that seedling recruitment was mostly in the second postfire year (Appendix A), apparently from seeds produced by resprouts in the first year.

Several obligate resprouters exhibited a very similar community proportion between prefire and postfire from just resprouts (Table 4). *Quercus berberidifolia* had a very shallow slope, indicating postfire populations comprised a much lower proportion of the community than prefire populations. The absolute population size of this species did not change since nearly 100% of the population resprouted, however, proportionately it comprises far less of the postfire density, which is largely dominated by seeding species.

Seedling survivorship curves for obligate-seeding shrubs all exhibited a marked first-year decline followed by a more gradual decline in subsequent years (Fig. 4a, c, and e). Some facultative seeders such as *Ceanothus spinosus* (Fig. 4d) were quite similar to the obligate-seeding *Ceanothus* species. However, two of the most widespread

facultative seeders, *Adenostoma fasciculatum* (Fig. 4b) and *Malosma laurina* (Fig. 4f), had very step declines in survivorship and, for both of them, seedling survivorship declined much more rapidly in coastal populations.

Considering the subshrubs and suffrutescents, the seedling thinning rates were generally similar between obligate-seeding (Fig. 5a, c, and e) and facultative-seeding (Fig. 5b, d, and f) species. Although *Helianthemum scoparium* (Fig. 5c) exhibited a much steeper thinning curve on coastal sites than on interior sites, most species exhibited remarkably similar curves for these different populations.

By the fifth postfire year the density of most seeding populations of shrubs, both obligate seeders (Fig. 6a, d, and g) and facultative seeders (Figs. 6c, f, and i, and 7a, d, and g) had returned close to their prefire composition. The same was true of the seeding subshrubs as well (Fig. 6b, e, and h). However, some of the obligate-resprouting shrubs still had not returned to their prefire proportions (Fig. 7c and f). One exception was *Quercus berberidifolia* (Fig. 7i), which by the fifth year had returned to near its prefire proportion of total community density, due not
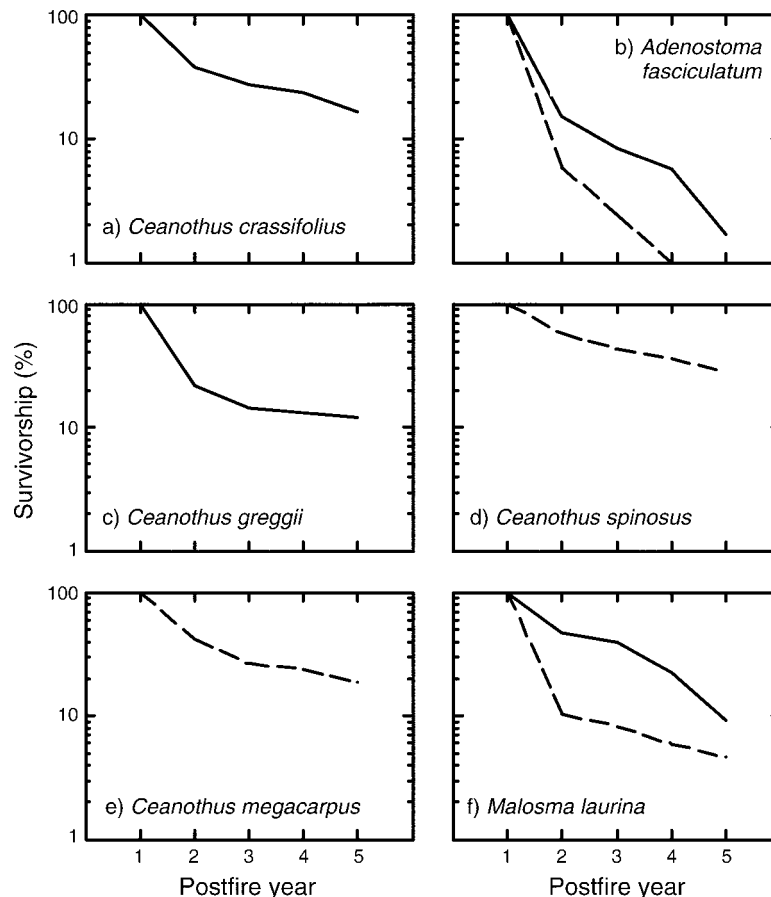
FIG. 4. Survivorship curves for the first-year cohort of seedlings for the dominant obligate-seeding shrubs (a, c, e) and facultative-seeding shrubs (b, d, f) during the first five postfire years for coastal (dashed lines) and interior (solid lines) populations. Note the *y*-axis logarithmic scale.

to any significant seedling recruitment (Appendix A), but likely due to the thinning of seeder populations. Obligate-resprouting subshrubs on the other hand, due in part to the copious seed and seedling production in the second year (Appendix A), had largely recovered to their prefire composition (Fig. 7b, e, and h).

Herbaceous species

Although most herbaceous perennials were re-sprouters (Table 1), some obligate seeders and facultative seeders were recorded (Appendix B, Fig. 8). As observed with the woody flora, the majority of herbaceous perennials were found in both chaparral and sage scrub. However, unlike woody species (Appendix A), the perennial herbs were far more restricted in their distribution, with only five being found at >20 or more sites, in contrast to three times that many woody species being found at >20 sites.

Dicentra chrysantha and *D. ochroleuca* were the only herbaceous perennials with seedling recruitment limited to the first postfire year, and these were only found on chaparral sites (Fig. 9a). These species also differed from typical herbaceous perennials because they were short-

lived, surviving only two years on some sites, and perenniating buds were aboveground, and in this respect were more like suffrutescent species. Most seeders had recruitment in all years, but the second and fifth years were peaks for many (Fig. 9b–f, Appendix B).

Obligate resprouters dominated the herbaceous-perennial flora and even facultative seeders were largely represented by resprouts in the first postfire year, as evident by the low seedling/resprout ratios (Appendix B). Obligate-resprouting herbaceous perennials re-cruited almost no seedlings in the first postfire year, but exhibited variable recruitment in subsequent postfire years (Fig. 9g–i, Appendix B). Recruitment peaked generally in one of the two high rainfall years, either the second or fifth years.

Although largely resprouters, these herbaceous perennials exhibit some important demographic differences that are associated with growth form. Geophytes peaked in abundance in the first postfire year, grasses generally peaked in the second year, and forbs as a group were more evenly distributed (Appendix C).

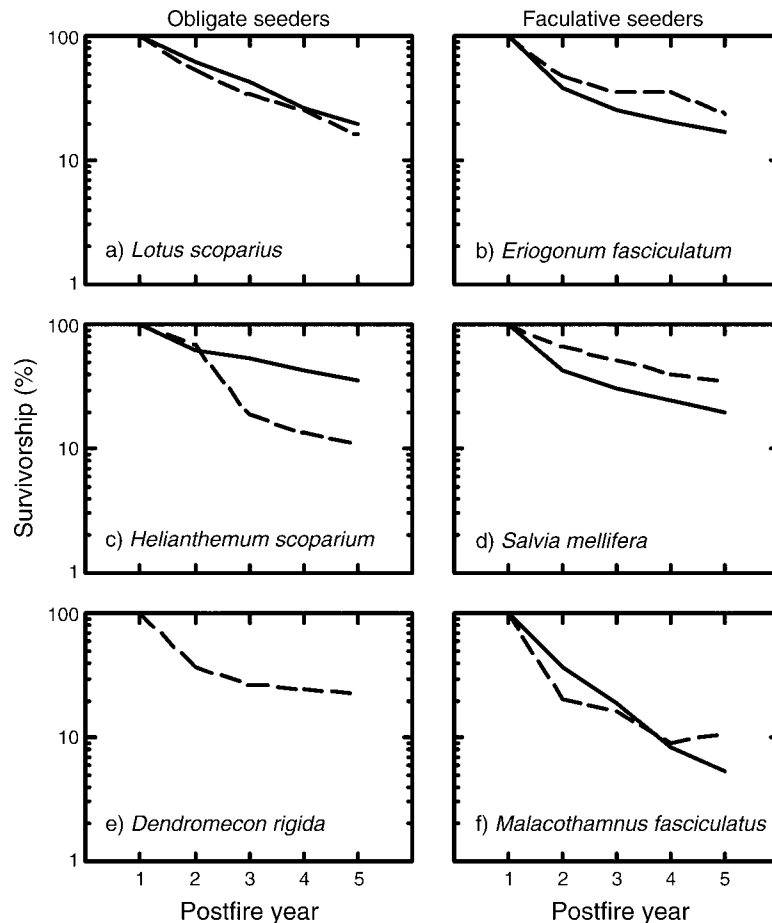A sizable number of annuals were alien species and are not covered here (but see Keeley et al. 2005c). Most

FIG. 5. Survivorship curves for the first-year cohort of seedlings for the dominant obligate-seeding suffretescents (a, c) and subshrub (e), and for facultative-seeding subshrubs (b, d, f) during the first five postfire years for coastal (solid lines) and interior (dashed lines) populations. Dominants such as *Artemesia californica* are not included because of multiple seedling cohorts during the first five years (see Table 3). Note the *y*-axis logarithmic scale.

native annual species, like the other life-forms, exhibited very little specificity for either chaparral or sage scrub (Appendix D). With respect to distribution, annuals resembled woody plants in that a large portion of the flora was found at >20 sites—more than half of the annual species shown in Appendix D.

All annuals by definition are obligate seeders, having no capacity for resprouting. However, they exhibited some important demographic patterns that are best represented by their timing of abundance during early succession. In this study 18 species were considered postfire endemics, almost entirely restricted to the first and second postfire years (Fig. 10a–c, Appendix D). A great many other species specialized on fire and exhibited their highest densities in the first two years after fire, but still retained some presence during later years (Fig. 10d–f). Other species, here referred to as "opportunists," were weakly represented in the first postfire year but their populations grew in the subsequent years (Fig. 10g–i). A few species were categorized as late successional (Fig. 10j–l). Regardless of the

postfire demographic patterns, only a very small fraction of all species were not present on one or more burned sites in the first postfire year.

DISCUSSION

Predicting ecosystem responses to disturbance is potentially simplified by focusing on functional groupings of species with similar responses and impacts on system processes (Lavorel et al. 1997). In mediterranean-climate shrublands exposed to stand-replacing crown fires, functional types are often approached from the perspective of regeneration modes, in particular postfire seeding from dormant seed banks and resprouting from vegetative structures (Zammit and Westoby 1987, Bond 1997, Lamont et al. 1999, Lloret and Vilà 2003, Pausas and Lavorel 2003). Others have advocated that plant life-forms are a useful means of grouping functionally equivalent species in such ecosystems (McIntyre et al. 1995).

It is widely believed that for fire-prone mediterranean-climate shrublands, much of the dynamics of postfire
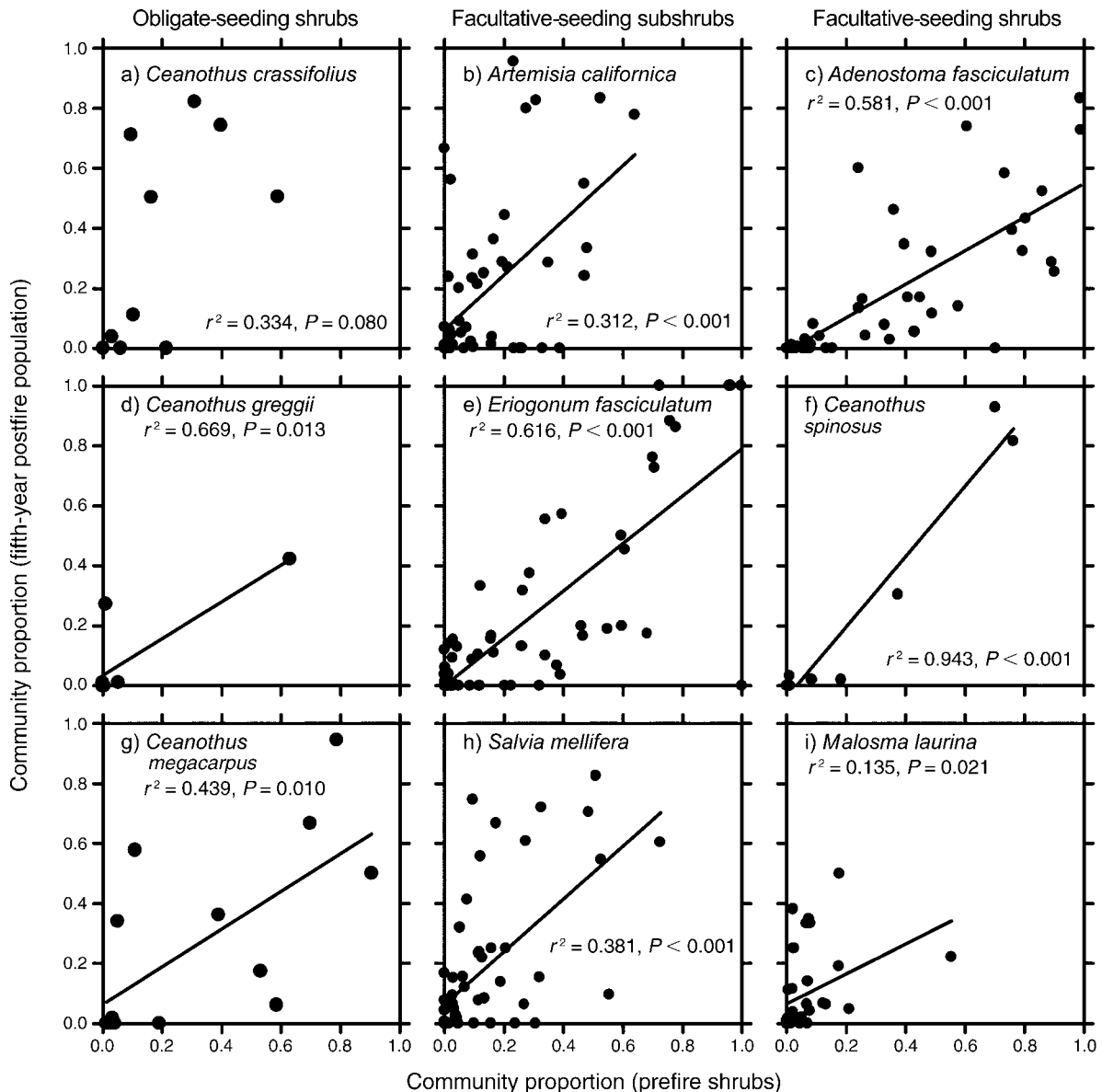
Fig. 6. Proportional density of fifth-year postfire populations vs. prefire populations for the most common obligate-seeding shrubs (a, d, g), facultative-seeding subshrubs (b, e, h), and shrubs (e, f, i), for seedlings and resprouts.

recovery can be captured by focusing on the relative importance of just three functional types—obligate seeders, facultative seeders, and obligate resprouters. One of the limitations to the functional-type approach is that when species are grouped with respect to a particular variable, they often reassemble into different groups when another variable is considered. Based on the present study, this would seem to be a major limitation to the use of these regeneration modes in predicting community responses to fire. While these regeneration modes are a useful means of focusing study of postfire regeneration, they are of limited predictive value without consideration of the diversity of species-specific responses frequently encountered in these

communities. Within each regeneration mode there are uniquely different seedling-recruitment patterns that affect successional changes in community structure and diversity. This is true both for the Californian shrublands studied here as well as other mediterranean-type shrublands (Lamont et al. 1999, Groom et al. 2001). Resprouting regeneration modes likewise exhibit sufficient variations to defy simple generalizations about postfire demography and successional development, at least without a more detailed and complicated functional classification.

Here we discuss the unique characteristics found within each of these regeneration modes in California shrublands. Then we address the question, To what
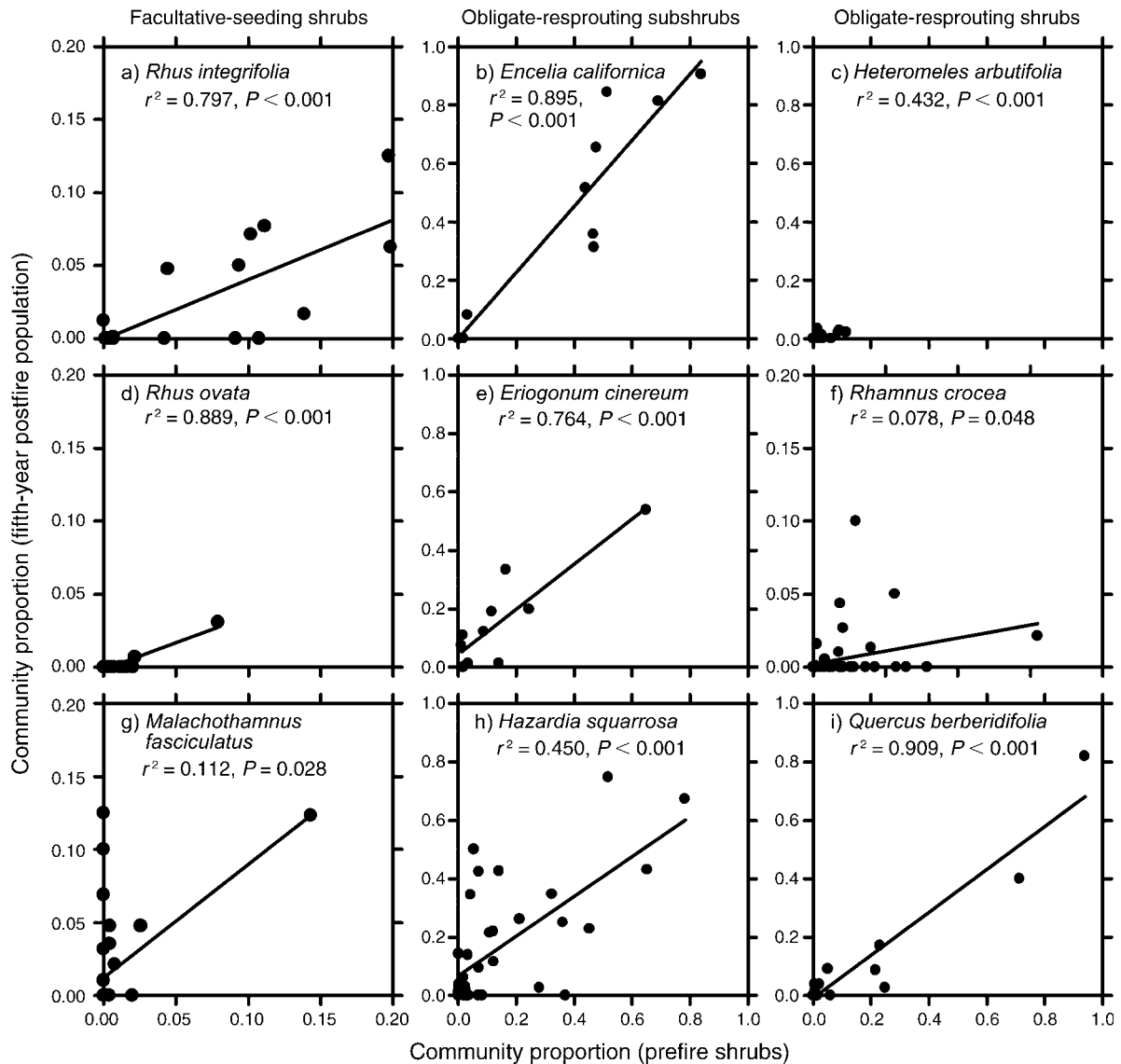
FIG. 7.   Proportional density of fifth-year postfire populations vs. prefire populations for the more common facultative shrubs (a, d, g), obligate-resprouting subshrubs (b, e, h), and shrubs (c, f, i).

extent do these differences affect our understanding of postfire processes?

Obligate-seeding mode

The "obligate-seeding mode" refers to species that lack the capacity for vegetative regeneration and whose presence following disturbance is entirely from seedling recruitment in the first postfire year. It is normally applied to perennial species, although technically all annuals are obligate seeders as well. In California shrublands, obligate seeders are residual species present before the fire, and they recruit from dormant soil-stored seed banks (Keeley 1977, Parker and Kelly 1989, Zedler 1995). There is good reason to believe that on the sites studied here, first-year seedling recruitment was the

result of fire-triggered germination of dormant seed banks rather than dispersal from outside the burned area. Almost none of the species present in the first year have specialized propagule structures for long-distance dispersal (Keeley 1991), which would be necessary since many of the fires were on the order of 1000–10 000 ha in size. Further, these species disperse seeds in the spring or summer, and fires occurred in the fall, thus it is highly unlikely that postfire recruitment is the result of a postfire 'seed rain' from outside the site.

If the interval between fires is sufficiently long, obligate-seeding populations may die out above-ground and persist strictly as a dormant seed bank, as appears to have been the case in the present study with *Ceanothus greggii* (Fig. 3d). Longevity of the parent
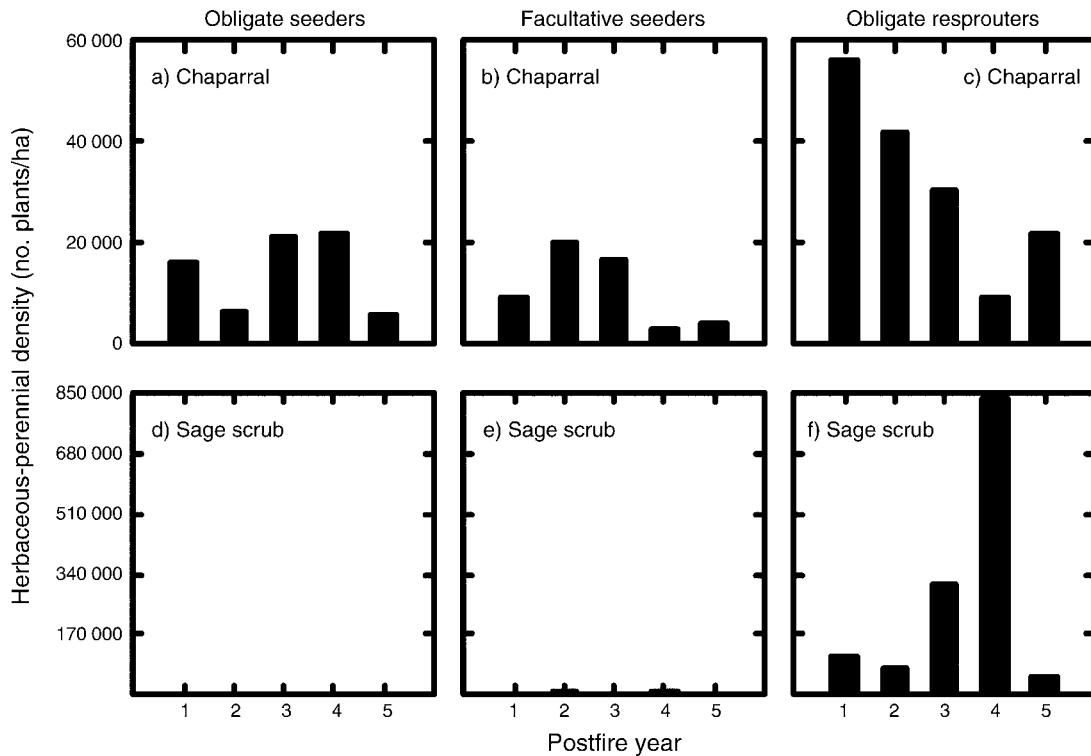
Fig. 8. Postfire changes in herbaceous-perennial density for (a, d) obligate seeders, (b, e) facultative seeders, and (c, f) obligate resprouters, for (a, b, c) chaparral and (d, e, f) sage scrub.

population is critical to the long-term sustainability of these obligate-seeding shrub populations because seed banks experience attrition over time, and once seed input has ceased, the seed bank has a finite life span (Zammit and Zedler 1988, 1992). Predicting longevity for the functional-type obligate-seeder mode requires a species-specific approach since longevity is typically 1–2 decades for *Dendromecon rigida*, mostly less than a century for *Ceanothus* species, but more than a century for many species of *Arctostaphylos* (Keeley 2000). Longevity of seeds in the soil also likely varies with species, but relatively little is known about the upper limits other than circumstantial evidence suggests it is on the order of a century or more (Keeley 1991, Zedler 1995, Keeley et al. 2005*d*). A factor of particular importance in longevity is landscape position, and in this respect living plants of obligate-seeding species respond roughly similarly in that they are shaded out more quickly on mesic slopes than on drier more exposed sites (Keeley 1992*a*).

Another way obligate seeders reassemble into different groups is with respect to lifetime recruitment patterns. Many *Ceanothus* species produce a single age cohort after fire (Appendix A), and thus form even-aged populations, whereas others, e.g., *Lotus scoparius* (Fig. 2c), produce multiple cohorts and an uneven age structure. Life-form plays a significant role in producing these different recruitment patterns. *Ceanothus* shrubs

generally do not reach reproductive maturity until the shrub canopy has closed in and produced unsuitable conditions for seedling recruitment; thus there has been strong selection for deep seed dormancy triggered by fire (Keeley 1991). However, the less woody suffrutescent *Lotus scoparius* is capable of rapid growth and reproductive maturity by the second postfire year. This species produces a mixed seed pool, some with deep dormancy and others with little or no dormancy (Keeley 1991). The facts that during the first five years after fire, stands are somewhat open and recruitment sites still available, may be the factors that have selected for mixed seed banks and the capacity for multiple cohorts.

Annuals by their very nature are all obligate seeders. As with woody species, they too have species-specific patterns of recruitment. As with obligate-seeding *Ceanothus*, a very important component of the native postfire flora are species we term "postfire endemics," because their seedling recruitment (and presence) is almost entirely confined to the immediate postfire year or two (Appendix D). These species have deeply dormant seed banks, which germinate only in response to fire cues of either chemicals from charred wood or smoke, or heat shock (Keeley and Fotheringham 2000). For any single fire cycle they have only one or two generations, and then remain as a dormant seed bank until the next fire. However, many annuals are more opportunistic and form a continuum of specialization on
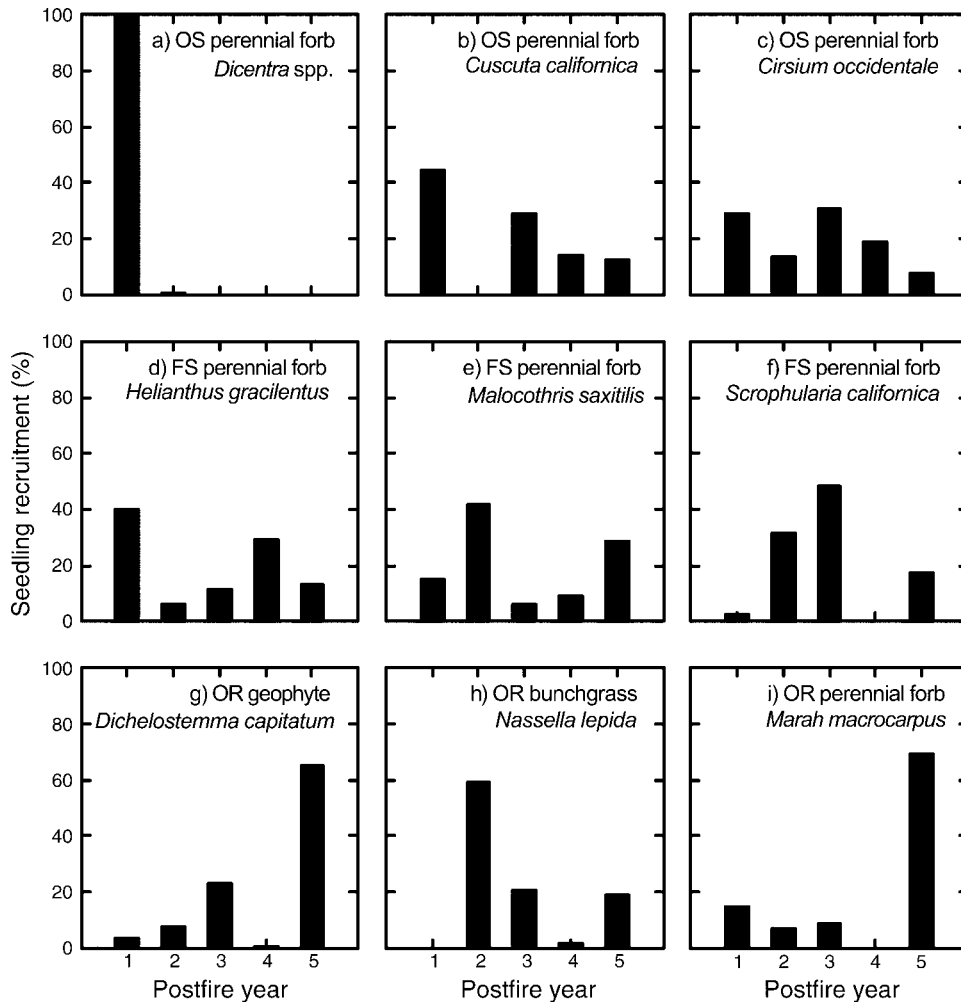
FIG. 9.   Postfire changes in herbaceous-perennial seedling recruitment, by regeneration functional type: (a, b, c) obligate seeders (OS); (d, e, f) facultative seeders (FS); and (g, h, i) obligate resprouters (OR).

fire, many of which have multiple generations during early succession (Appendix D). In these species, fire triggers germination of the seed bank, but they appear to produce a polymorphic seed pool in which a portion is triggered to germinate by other environmental cues such as high precipitation.

Facultative-seeding mode

Facultative-seeding species are those present after fire as both seedlings and resprouts, and comprise the dominant cover in all four plant associations (Fig. 1). Some of these, such as *Adenostoma fasciculatum* and species of *Arctostaphylos* and *Ceanothus*, resprout from specialized basal lignotubers that are a normal developmental feature present in young saplings (Keeley 1981). Facultative-seeding shrubs mostly have strict postfire recruitment, and populations comprise a single cohort of seedlings, although resprouting plants have overlapping generations (Stohlgren et al.1984). These shrubs, such as *Adenostoma fasciculatum, Ceanothus*

spinosus, and *Malosma laurina,* often co-occur with facultative seeders of other life-forms. Less woody subshrubs and suffrutescents vary from ones with strict postfire seedling recruitment to ones with multiple recruitment events and overlapping generations (Appendix A).

Seedling recruitment, expressed as offspring/parent ratios, are not generally much different between obligate-seeding and facultative-seeding shrubs in these California shrublands. However, these ratios are substantially higher than typically observed for postfire obligate-seeding shrubs in other mediterranean-climate shrublands such as South African fynbos (Bond et al. 1995) or Australian shrublands (Lamont et al. 1999). One likely factor is that these Southern Hemisphere shrubs mostly have aerial seed storage in serotinous fruits, whereas all of the California shrubs have soil stored seeds. In contrast, California facultative-seeding subshrubs had relatively low recruitment in the first postfire year.
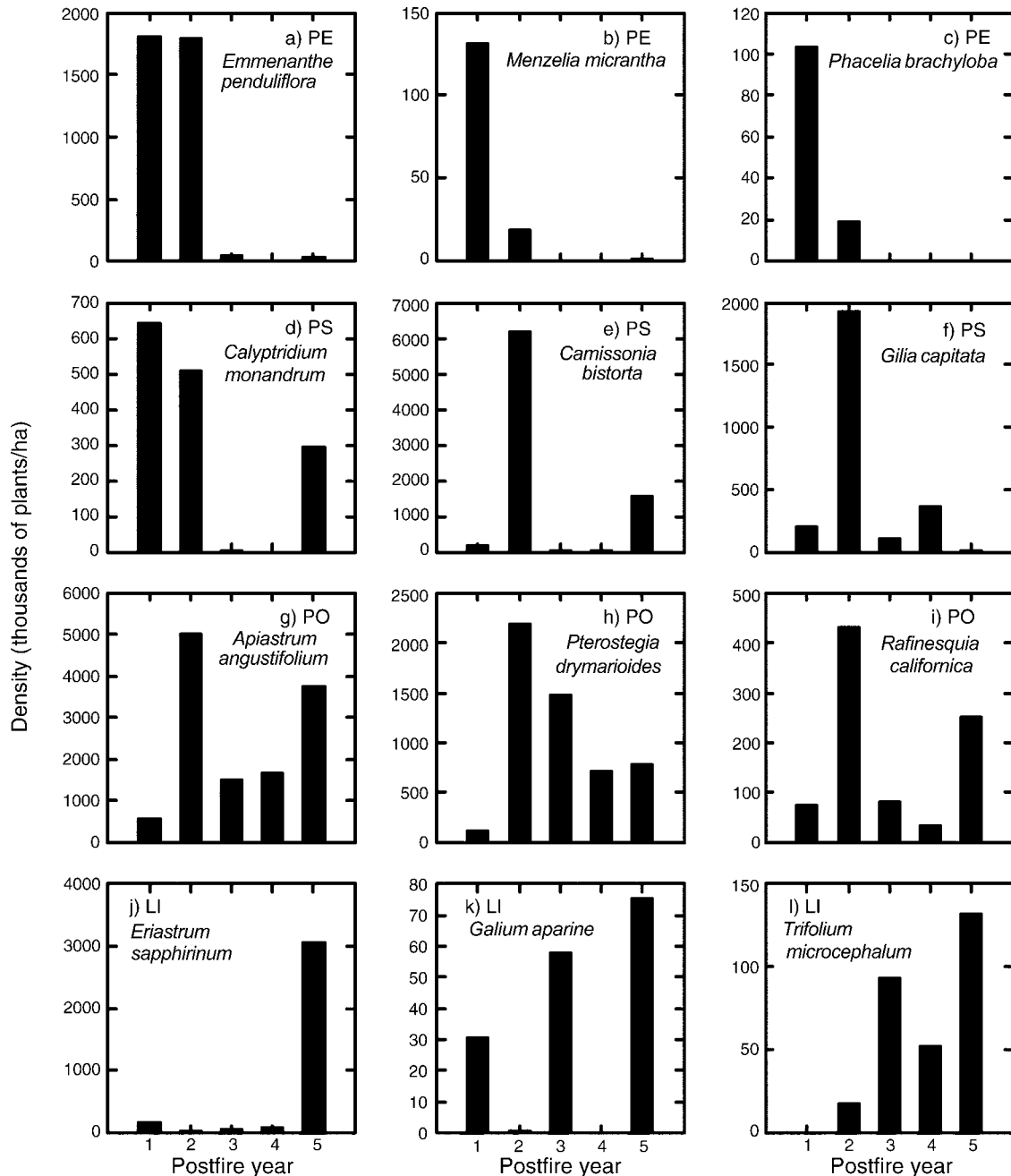
FIG. 10. Postfire demographic changes for representative examples of annual (a, b, c) postfire endemics (PE); (d, e, f) postfire specialists (PS); (g, h, i) postfire opportunists (PO); and (j, k, l) later-successional increasers (LI).

Survivorship curves for first-year seedling cohorts are remarkably similar among obligate-seeding species (Figs. 4a, c, and e, and 5a, c, and e), but rather variable among facultative seeders. By the fifth postfire year most obligate seeders have a substantially higher proportion of seedlings surviving than some of the common facultative seeders such as *Adenostoma fasciculatum* (Fig. 4b), *Malosma laurina* (Fig. 4f), or *Malacothamnus fasciculatus* (Fig. 5f). With respect to the facultative

seeders, life-form does not explain the variation since high survivorship is observed in both shrubs (Fig. 4d) and subshrubs (Fig. 5b and d).

Very few herbaceous perennials couple resprouting and immediate postfire seedling recruitment (Appendix B). For the few that do have limited seedling recruitment, this is a minor part of their immediate postfire regeneration. All herbaceous perennials have multiple recruitment events during the early postfire years and

thus populations comprise multiple cohorts. Most of the interesting demography of this life-form is left to discussion of obligate resprouters.

Obligate-resprouting mode

Obligate-resprouting species are present in postfire environments entirely from vegetative resprouts (Table 3). Most have very high resprouting success (Table 3) and thus genets appear to have great longevity, likely surviving many fire cycles, and in this sense represent an extreme case of the "storage effect" (Warner and Chesson 1985).

Shrubs and subshrubs differ markedly in seedling recruitment strategies. Shrubs such as *Cercocarpus betuloides, Heteromeles arbutifolia, Prunus ilicifolia, Quercus berberidifolia,* and *Rhamnus* spp. exhibit almost no recruitment during the first five years after fire (Appendix A). These species are more drought sensitive than most seeding shrub species (Keeley 2000), and they endure summer drought by maintaining deep root systems that evade water stress. While such a strategy works well for mature shrubs it is not an option for seedlings, thus seedling recruitment in these summer-drought climates is precarious on burned sites (Keeley 1998). Considering the drought sensitivity of these seedlings one might expect that recruitment spread over multiple years would be enhanced in high-rainfall years, and there is some evidence for that here (Appendix A). However, non-climatic factors such as stand development, in particular closing in of the canopy and development of a thick duff layer, both of which ameliorate the summer drought, appear critical to successful seedling recruitment (Lloret and Zedler 1991, Keeley 1992a).

Obligate-resprouting subshrubs exhibit a very different recruitment strategy. Many of these, such as *Encelia californica, Eriogonum cinereum, Hazardia squarrosa*, and *Mirabilis californica*, resprout vigorously after fire and flower in the first postfire year. This is not fire-induced flowering, as these species regularly flower between fires. Postfire flowering, however, is significant because this flowering event is coupled with widespread suitable habitat for seedling recruitment. Copious seed production by these resprouts results in a large pulse of seedling recruitment in the second postfire year (Fig. 2 h and i, Appendix A; see also Keeley and Keeley [1984]). Thus, here we see a fundamentally different role for fire in the regeneration of obligate resprouters with different life-forms; for shrubs, reproduction is restricted to long fire-free periods, whereas subshrubs have a substantial proportion of lifetime seedling recruitments restricted to early postfire years. Since flowering continues during their lifetime, and most if not all of the seed pool lacks innate dormancy (Keeley 1991), these subshrubs are also capable of taking advantage of other disturbances during the fire-free period and actively recruit into adjacent grasslands between fires as well (DeSimone and Zedler 1999).

Bond and Midgley (2003) contend that species resprouting following disturbance commonly share the trait of low seedling recruitment rates, and slower sapling growth rates. While this may be widely applicable in other ecosystems, it does not apply to chaparral and sage scrub shrublands. In these systems, total seedling recruitment by facultative-seeding shrubs ranged from 10^3 to 10^5 seedlings per hectare, which is within the range observed for obligate-seeding species (Appendix A). Their argument holds only for the very limited case of obligate-resprouting species, and then only during the immediate postfire years. These obligate resprouters do recruit in the absence of disturbance, and their total seedling recruitment during extended fire-free periods (Keeley 1992b) is well within the range observed for obligate seeders that have a single postfire pulse of recruitment. Thus, the widely used term "seeder" in the fire-ecology literature needs to be qualified as "postfire seeder," because even postfire obligate resprouters are seeders during other parts of their life cycle. It is also important to recognize that sprouting is a characteristic that is manifested throughout the life span of resprouting shrubs (Malanson and Westman 1985, Keeley 1992a), thus, it would be clearest if we specified "postfire resprouting."

These patterns call into question the generalizations about relative allocation to resprouting vs. seeding in woody plants as proposed by Bellingham and Sparrow (2000), for which there is some support in Australian shrublands (Lamont and Wiens 2003). Nearly all resprouting species in California shrublands recruit seedlings at some point in their life cycle. Direct comparisons of reproductive allocation in postfire obligate-seeding and resprouting facultative seeders have failed to demonstrate substantial differences in reproductive allocation patterns (Keeley 1977, Keeley and Keeley 1988), although some subtle changes in internal allocation patterns are evident (Schwilk and Ackerly 2005). As demonstrated in our present study there is relatively little difference in the seedling/parent ratios between obligate-seeder and facultative-seeder shrubs. While the postfire obligate resprouters fail to recruit seedlings immediately after fire, they do recruit seedlings, and, as discussed above, the timing is dependent on life-form. While comparative studies of reproductive allocation have not been done between postfire obligate seeders and postfire obligate resprouters, the latter do produce sizable seed crops, annually in some species or periodic mast crops in others (Keeley 2000). Thus, in California shrublands, generalizations about the relative seedling recruitment of postfire seeders vs. resprouters breaks down when one considers the entire fire cycle rather than just the immediate postfire seedling recruitment.

The vast majority of dominant herbaceous perennials are obligate resprouters following fire, however, this is likely a preadaptation to seasonality since this life-form typically dies back during the summer drought and

resprouts during the winter-spring growing season. That is not to say that these species do not exhibit responses keyed to fire, since some, but not all species, may remain dormant as bulbs or corms for long periods of time in the absence of fire (Stone 1951, Tylor and Borcher 2002). Seedling recruitment is nil in the first postfire year due to the lack of a dormant seed bank (Keeley 1991) but is abundant in early succession, but with much species-specific variation in timing that involves precipitation and other environmental cues (Appendix B; see also Borchert [1989]).

Demographic patterns and community structure and process

The complexities of postfire demographic patterns are not merely interesting variations on a functional-type theme, but rather play important roles that need to be made clear if we are to fully comprehend the functioning of these fire-prone systems. A few examples will suffice to illustrate the importance of such demographic data.

Plant community succession models abound, but one characteristic that many share is the sequential replacement of species (Glenn-Lewin et al. 1992). Postfire succession in chaparral has been considered something of an exception to this pattern in that early succession is dominated by residual species present prior to the fire (Keeley et al. 2005a), a phenomenon captured in Hanes (1965) auto-succession model. In addition, in the first postfire year many of the dominant species immediately regain their prefire proportional representation in the community (Fig. 3). However, successional changes are evident in obligate resprouters that require longer periods before returning to their prefire proportional abundance in the community (Fig. 7), a process largely driven by intense thinning of associated seeding shrub species (Schlesinger et al. 1982). Herbaceous species illustrate a diversity of patterns that could be explained by various successional models.

Plant community ecology depends upon recognizing specific communities that are distinguished from other such communities by their unique assemblage of species, and presumably their own set of community processes. In the case of chaparral and sage scrub, these are typically recognized by the dominance of either shrubs in the former or subshrubs in the latter vegetation type. It is commonly presumed that they comprise unique collections of species that are fundamental to the community relationships. However, in this study, sites were categorized as either chaparral or sage scrub based on the dominant life-form, yet nearly all of the several hundred species encountered in this study (woody and herbaceous species) occurred, often with equal frequency, in both vegetation types (Appendices A, B, and D). Thus, the uniqueness of these two community types is perhaps more apparent than real, and has much to do with the physiognomy of a few dominants and less to do with the composition of these communities. This suggests that top-down classification schemes that

attempt to base plant associations on a couple of dominant species (e.g., Sawyer and Keeler-Wolf 1995) is of limited value in understanding ecological communities (see also Zedler 1997), although it may have useful management applications.

In a recent study of succession in these communities (Keeley et al. 2005a) it was found that over 90% of the plant cover in year 5 was from residual species present in year 1, but ~40–50% of the species present in year 5 were not present at that site in the first postfire year. This suggests that colonization, while not a big part of community structure, is an important process in determining patterns of species diversity in postfire succession. Commonly when one considers colonization of burned sites one is envisioning the movement of species from unburned to burned sites. One value of the present demographic data set is that it provides a means of examining that assumption. Detailed demographic data (Appendices A, B, and D) suggest that what is referred to as "colonization" in Keeley et al. (2005a) is perhaps better described as "mass effects" (Shmida and Wilson 1985). All of the perennial species, and 95% of the annuals present in the fifth year, occurred on one or more burned sites in the first year. This, coupled with the large size of these fires (most were thousands of hectares), suggests that these colonists were not the result of long-distance movement of new species into burned sites, but rather of residual species present early on in adjacent burned areas that underwent population expansion during early succession and expanded into our sites.

In another study of these same sites it was found that community diversity reached a peak in the first or second postfire year and then began a decline (Keeley et al. 2005b). This of course is not surprising since other studies of these shrubland ecosystems have likewise noted similar patterns (Sampson 1944, Horton and Kraebel 1955, Westman 1981). What was surprising about the diversity studies at these sites is that in the fifth postfire year the communities exhibited a sharp rise in diversity that was nearly comparable to the first-year levels. Without detailed demographic data such as are in Appendices A, B, and D, one might conclude that these diversity peaks were driven by similar processes. However, that is clearly not the case as evident by the fact that 18 of the most common annual species in the first year are "postfire endemics," which largely disappear from all sites after the second year and another dozen or so are "postfire specialists" that disappeared from many sites by the fourth postfire year (Appendix D). Taking their place are more "opportunistic" species that expand their populations during early succession, particularly following winters with high rainfall. Thus, the second peak in diversity in year 5 comprises a very different flora than the early diversity peak. The first peak is due to life-history specialization on fires (Keeley and Fotheringham 2000), but the fifth-year peak appears to be driven by "colonization" of new species.

As discussed above, this is likely the result of rather localized metapopulation dynamics, due to species in the surrounding burned landscape that expand their populations into the 0.1-ha plots, and may be considered evidence of a "mass effect" where individuals flow from core areas of high success into less favorable areas (Shmida and Wilson 1985).

Conclusions

Functional groups based on regeneration responses to postfire disturbance capture some of the dynamics of mediterranean-climate shrublands. As with many other functional classifications, when we focus on other system attributes such as demographic patterns in early succession we find that often-used categories of obligate seeder, facultative seeder, and obligate resprouter fail to sufficiently capture the important processes.

However, if we stratify our regeneration functional groups by life-form, we can come closer to capturing both postfire responses and early successional dynamics. For example, by separating obligate-seeding shrubs from the more diminutive obligate-seeding suffrutescents, we separate out species with a single even-aged postfire cohort from those with multiple cohorts and an uneven age structure early in succession. At the other extreme, with obligate resprouters, we see that shrubs and smaller woody life-forms respond the same to the immediate postfire environment, but have very different demographic patterns during early succession. Shrubs have weak or no seedling recruitment during early succession, whereas faster growing subshrubs and suffrutescents capitalize on postfire resources by massive seedling-recruitment events in the second year, and production of more cohorts in subsequent postfire years.

Previously, these functional groupings have been widely applied to the dominant woody plants, but the postfire responses of herbaceous species have generally been ignored. However, in most mediterranean-climate shrublands, herbs comprise the bulk of the postfire diversity, and are likely critical elements of ecosystem functioning. Herbaceous perennials in these systems are mostly all postfire obligate resprouters, which flower in the first postfire year and have seedling recruitment pulses in subsequent postfire years. However, within this life-form further diversity is evident when examined by growth form (Fig. 9, Appendix C). For example, geophytes peak in abundance the first postfire year and then enter varying periods of dormancy for one or more years. Bunchgrasses on the other hand persist as long as site conditions are suitable. Rhizomatous grasses use the early successional years for expanding their populations with both seedling recruitment and vegetative spread.

Annual plants likewise exhibit important demographic differences, despite all being postfire obligate seeders. Some have specialized life histories that restrict recruitment to the immediate postfire environment, rarely establishing after the second year. Thus, these species normally spend more than 95% of their life cycle as a dormant seed bank. Other annual plants exhibit varying degrees of specialization on postfire conditions, but many apparently utilize these environments as opportunities for population expansion and movement into new habitats.

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APPENDIX A

A table showing woody species seedling recruitment during the first five years after fire in chaparral and sage scrub (*Ecological Archives* M076-009-A1).

APPENDIX B

A table showing herbaceous-perennial species seedling recruitment during the first five years after fire in chaparral and sage scrub (*Ecological Archives* M076-009-A2).

APPENDIX C

A figure showing postfire changes in herbaceous-perennial density, by growth form (*Ecological Archives* M076-009-A3).

APPENDIX D

A table showing annual species population density during the first five years after fire in chaparral and sage scrub (*Ecological Archives* M076-009-A4).

Ecological Archives M076-009-A1

Jon E. Keeley, C. J. Fotheringham, and Melanie Baer-Keeley. 2006. Demographic patterns of postfire regeneration in Mediterranean-climate shrublands of California. *Ecological Monographs* 76:235–255.

Appendix A (Table A1). Woody species seedling recruitment during the first five years after fire in chaparral and sage scrub. Total five-year seedling recruitment presented for chaparral and sage scrub but not for coast vs. interior to simplify presentation. Percentage distribution did not vary greatly between vegetation types and therefore is presented collectively for all sites where the species occurred. Dominant species here were selected because they were abundant at two or more sites. Total suffrutescent, subshrub, and shrub species were 12, 29, and 32, respectively, for chaparral, and 11, 30, and 21 for sage scrub.

| Species | Life form[†] | Total seedling recruitment for all 5 years (no./ha) | | | | | | Percentage by year | | | | |
| | | Chaparral | | Sage scrub | | | | | | | | |
		No. sites	Mean ± SE	No. sites	Mean ± SE	1	2	3	4	5
Obligate-Seeders										
Ceanothus crassifolius	s	10	62,100 ± 17,800	3	1,500 ± 800	99	1	0	0	0
C. cuneatus	s	1	14,000	2	9,800 ± 9,800	97	3	0	0	0
C. greggii	s	8	18,500 ± 18,500	1	1,000	100	0	0	0	0
C. megacarpus	s	9	55,700 ± 24,200	2	11,000 ± 7,000	96	4	0	0	0
C. oliganthus	s	6	103,900 ± 95,500	0	-	100	0	0	0	0
C. tomentosus	s	2	56,300 ± 700	0	-	99	1	0	0	0
Dendromecon rigida	ss	1	53,000	0	-	95	5	0	0	0
Helianthemum scoparium	su	12	33,500 ± 17,500	3	109,200 ± 75,200	73	13	7	0	7
Lotus scoparius	su	39	46,100 ± 8,400	43	77,600 ± 33,900	72	9	2	1	16
Facultative Seeders										
Adenostoma fasciculatum	s	31	104,500 ± 22,800	11	23,700 ± 12,700	94	3	0	0	3
Artemisia californica	ss	12	11,600 ± 4,800	41	31,500 ± 10,600	41	42	13	1	4
Calystegia macrostegia	su	25	49,700 ± 12,100	34	38,630 ± 7,200	92	5	2	0	1

Ceanothus spinosus	s	9	36,600 ± 25,100	1	2,000	92	3	0	0	5
Encelia farinosa	ss	0		8	21,100 ± 8,500	10	19	18	0	53
Eriodictyon crassifolium and E. trichocalyx	ss	4	3,100 ± 800	1	1,000	52	24	10	12	2
Eriophyllum confertiflorum	su	25	168,700 ± 42,900	30	24,000 ± 8,500	20	33	24	10	13
Eriogonum fasciculatum	ss	24	8,600 ± 2,900	32	24, 500 ± 7,200	71	21	5	0	3
Galium nuttallii	su	16	12,300 ± 4,200	27	27,700 ± 14,300	3	32	21	12	32
Keckiella cordifolia	su	14	10,600 ± 4,300	2	8,500 ±8,500	17	24	16	0	43
Malachothamnus fasciculatus	ss	19	21,200 ± 9,400	25	54,400 ± 31,700	93	1	5	1	0
Malosma laurina	s	25	9,400 ± 4,600	27	3,900 ± 1,100	90	8	1	1	0
Mimulus aurantiacus	ss	13	59,000 ± 27,600	24	142,800 ± 76,400	4	60	16	4	16
Porophyllum gracile	su	1	62,500	4	10,800 ± 9,400	12	25	4	21	38
Rhus integrifolia	s	4	500 ± 500	13	800 ± 600	50	20	0	0	30
Rhus ovata	s	13	2,400 ± 800	4	1,000 ± 700	90	2	8	0	0
Ribes aureum, malvaceaum, and R. speciosum	ss	19	1,200 ± 300	11	20,100 + 11,200	85	6	4	0	5
Salvia apiana	ss	2	500 ± 0	14	22,900 ± 14,400	23	23	42	10	2
S. leucophylla	ss	2	800 ± 300	10	10,000 ± 4,500	46	12	31	1	10
S. mellifera	ss	27	41,900 ± 16,100	25	15,900 ± 5,500	73	12	3	3	9
Solanum parishii, S. umbelliferum and S. xantii	su	28	5,000 + 1,400	23	4,400 ± 3,600	40	21	20	4	15
Venagasia carpesioides	ss	8	12,300 + 9,700	4	5,300 ± 3,300	30	37	26	0	7
Obligate Resprouters										
Cercocarpus betuloides	s	8	200 + 100	3	0	0	33	0	33	34
Encelia californica	ss	2	497,300 ± 487,800	11	172,100 ± 96,100	0	67	15	0	18
Eriogonum cinereum	ss	3	22,700 ± 12,900	8	93,400 ±78,200	0	55	22	23	0
Galium angustifolium	su	15	4,000 ± 1,700	23	40,600 ± 33,300	4	55	10	17	14

Hazardia squarrosa	ss	13	37,700 ± 17,300	22	49,500 ± 23,100	0	54	34	6	6
Heteromeles arbutifolia	s	10	100 ± 100	1	0	0	100	0	0	0
Keckiella antirrhinoides	ss	1	0	8	7,900 ± 6,900	0	83	14	3	0
Lessingia filaginifolia	su	4	1,800 ± 1,100	10	47,400 ± 30,100	0	41	18	12	29
Lonicera interrupta and L. subspicata	su	8	300 ± 200	2	7,800 ± 7,800	0	0	44	11	45
Mirabilis californica	su	3	6,200 ± 5,700	19	1,900 ± 700	0	70	29	0	1
Prunus ilicifolia	s	3	300 ± 200	0	-	0	50	0	0	50
Quercus berberidifolia	s	11	100 ± 100	2	0	0	50	0	50	0
Rhamnus crocea and R. ilicifolia	s	21	400 ± 100	14	300 ± 100	4	0	15	4	77
Toxicodendron diversilobum	ss	3	200 ± 200	10	300 ± 300	0	0	0	0	100
Xylococcus bicolor	s	2	0	0	-	-	-	-	-	-
Yucca whipplei	ss	13	0	7	0	-	-	-	-	-

† s = shrub, large stature, typically > 2 m, hard wood and long-lived, ss = subshrub, smaller stature, light wood and much shorter lived, su = suffrutescent, barely woody at base with substantial annual die-back of stems.

‡ Total seedlings recruited per prefire shrub or for those in italics, per postfire resprout; dash indicates no prefire adults present.

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Ecological Archives **M076-009-A2**

Jon E. Keeley, C. J. Fotheringham, and Melanie Baer-Keeley. 2006. Demographic patterns of postfire regeneration in Mediterranean-climate shrublands of California. *Ecological Monographs* **76:235–255.**

Appendix B (Table B1). Herbaceous perennial species seedling recruitment during the first five years after fire in chaparral and sage scrub. Dominant species here were selected because they were abundant at two or more sites; total herbaceous perennial species were 66 in chaparral and 74 in sage scrub.

Species	Growth form[†]	Total seedling recruitment years 1-5 (no./ha)				Percentage by year					First year seedling/resprout ratio	
		Chaparral		Sage scrub								
		No. sites	Mean ± SE	No. sites	Mean ± SE	1	2	3	4	5	Chaparral	Sage scrub
Obligate-Seeder												
Cirsium occidentale	f	5	50,900 + 49,800	9	4,300 + 2,100	29	13	31	19	8	-[‡]	-
Cuscuta californica	f	4	3,300 + 1,500	4	3,600 + 2,800	44	0	29	14	13	-	-
Dicentra chrysantha and D. ochroleuca	f	6	50,400 + 19,500	0	-	100	0	0	0	0	-	-
Gnaphalium bicolor	f	14	35,000 + 20,600	14	2,300 + 1,100	4	13	21	1	61	-	-
Plagiobothrys nothofulvus	f	2	2,500 + 2,000	4	13,400 + 6,100	50	0	17	0	33	-	-
Facultative Seeders												
Bromus carinatus	b	5	26,700 + 25,000	6	15,500 + 13,300	15	53	1	31	0	-	-
Chamaesyce polycarpa	f	4	18,400 + 6,700	8	8,800 + 2,800	3	45	10	10	32	0.8	0.7
Gnaphalium canescens	f	12	12,000 + 7,400	13	3,800 + 2,100	4	38	31	19	8	0.0	8.0
Helianthus gracilentus	f	4	5,400 + 1,800	1	1,500	40	6	11	29	14	2.0	0.0
Maolcothrix saxatilis	f	25	19,100 + 9,000	35	10,500 + 2,200	15	42	6	9	28	0.7	2.4
Erigeron foliosus	f	5	14,000	11	5,300 +	13	41	19	14	13	0.0	0.2

Species												
			+ 7,600		2,900							
Scrophularia californica	f	2	36,800 + 19,300	2	22,000 +21,500	3	31	48	0	18	17.8	-
Stachys ajugoides	f	0	-	6	6,600 + 800	7	10	0	0	76	0.0	0.2
Obligate Resprouters												
Acourtia microcephala	f	3	500 + 0	4	800 + 100	29	36	21	0	14	0.2	0.0
Agrostis exarta, A. hallii, A. hooveri, and A. pallens	r	4	79,100 + 31,000	11	2,704,300 + 1,736,200	2	25	26	36	11	<0.1	<0.1
Bloomeria crocea	g	0		2	1,200 + 750	0	0	50	50	0	0.0	0.0
Calochortus catalinae, C. clavatus, C. concolor, C. plameri, C. plummerae, C. splendens, and C. weedii	g	6		7	3,400 + 1,600	8	12	43	6	31	<0.1	0.0
Castilleja affinis	f	0		4	1,600 + 1,000	0	24	48	25	3	0.0	0.0
Chlorogalum parviflorum and C. pomeridianum	g	3		3	3,700 + 3,200	16	29	34	0	21	0.0	<0.1
Delphinium cardinale, D. parishii, and D. patens	f	2		4	27,400 + 15,100	1	0	29	0	80	0.0	<0.1
Dichelostemma capitatum	g	11		16	7,100 + 2,200	4	8	23	0	65	0.0	<0.1
Geranium carolinianum	f	3		6	3,500 + 1,700	0	9	17	24	50	0.0	0.0
Gnaphalium leucocephalum	f	8		0	-	0	27	0	0	73	-	-
Jepsonia parryi	f	1		1	1,500	17	33	0	0	50	0.0	<0.1
Leymus condensatus	r	4		4	800 + 100	0	41	9	0	50	0.0	0.0
Lomatium lucidum	r	1		1	1,000	0	100	0	0	0	0.0	0.0
Marah macrocarpus	f	13		4	750 + 100	15	7	8	0	70	<0.1	<0.1
Melic imperfecta	b	7		7	18,300 +16,600	14	38	31	15	2	<0.1	<0.1
Nasella lepida	b	9		20	192,000 + 84,600	0	59	21	2	18	0.0	0.0
N. pulchra	b	1		4	1,750 + 500	0	88	0	12	0	0.0	0.0
Oxalis albicans	f	0		6	5,700 + 3,400	17	40	32	1	10	0.0	<0.1
Sanicula crassicaulis	f	6		12	12,000 +	0	19	47	3	31	0.0	0.0

					6,800							
Scutellaria tuberosa	f	2		1	500	0	33	0	0	67	0.0	0.0
Silene laciniata	f	5		3	500 + 0	12	39	13	12	34	0.0	0.1
Sysrinchium bellum	f	1		4	6,900 + 3,600	0	37	23	20	20	0.0	<0.1
Tauchsia arguta	f	2		0	-	0	50	0	50	0	0.0	-
Zigadenaus fremontii	g	3		2	0	-	-	-	-	-	0.0	0.0

† f = forb, g = geophyte (bulb), b = bunchgrass, c = rhizomatous grass.

‡ dash indicates no resprouts present.

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Ecological Archives **M076-009-A3**

Jon E. Keeley, C. J. Fotheringham, and Melanie Baer-Keeley. 2006. Demographic patterns of postfire regeneration in Mediterranean-climate shrublands of California. *Ecological Monographs* **76:235–255.**

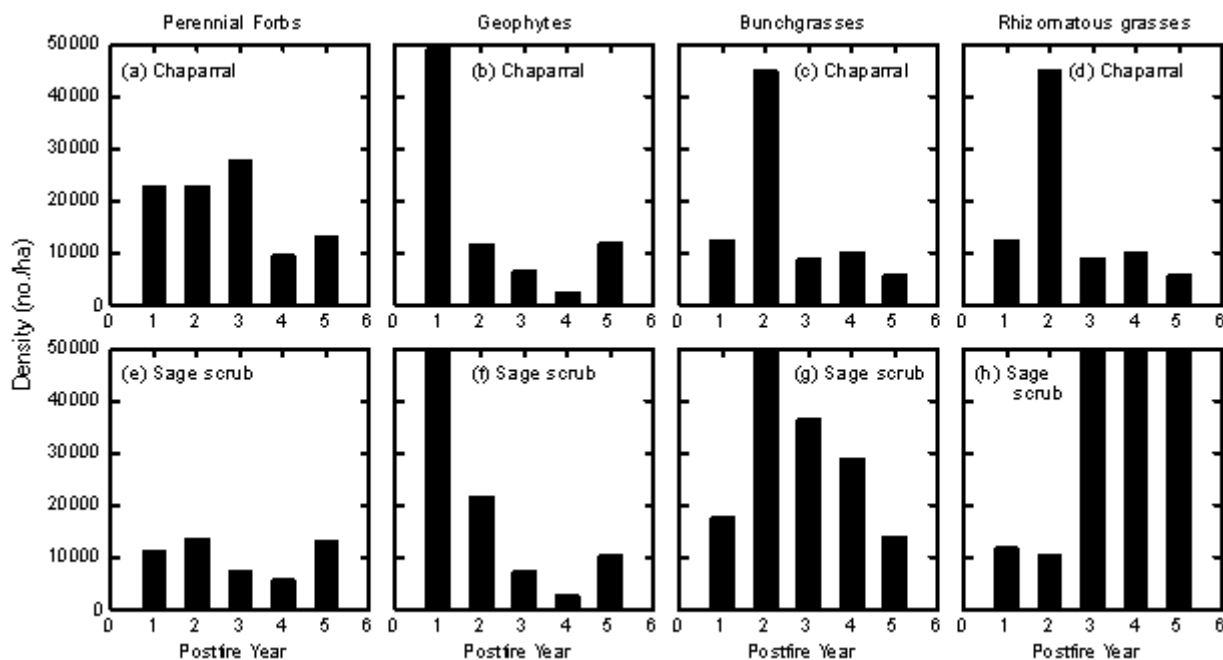Appendix C. A figure showing postfire changes in herbaceous-perennial density by growth form.

   FIG. C1. Postfire changes in herbaceous-perennial density by growth form: (a, e) perennial forbs, (b, f) geophytes, and (c, g) caespitose grasses, and (d, h) rhizomatous grasses for (a, b, c, d) chaparral and (e, f, h) sage scrub.

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Ecological Archives M076-009-A4

Jon E. Keeley, C. J. Fotheringham, and Melanie Baer-Keeley. 2006. Demographic patterns of postfire regeneration in Mediterranean-climate shrublands of California. *Ecological Monographs* **76:235–255.**

Appendix D (Table D1). Annual species population density during the first five years after fire in chaparral and sage scrub. Dominant species here were selected because they were abundant at two or more sites: total number of native annual species 175 in chaparral and 164 in sage scrub. A substantial number of alien annual species are not considered here and are treated in Keeley et al. (2005).

| | Total density over years 1–5 (no./ha) | | | | | | | | |
| | Chaparral | | Sage scrub | | Percentage by year | | | | |
Species	No. sites	Mean ± SE	No. sites	Mean ± SE	1	2	3	4	5
Native postfire endemics									
Allophyllum gilioides	8	10,800 ± 6,400	4	5,500 ± 3,500	50	47	1	0	2
A. glutinosum	9	15,500 + 12,400	4	2,100 + 1,500	9	87	4	0	0
Calandrinia ciliata	2	1,300 + 700	2	7,600 + 7,100	35	64	1	0	0
Camissonia micrantha	3	51,600 + 42,800	7	14,300 + 7,100	25	74	0	1	0
Caulanthus heterophyllus	6	700 + 300	14	10,600 + 3,100	56	37	4	0	3
Descurainia pinnata	5	33,600 + 32,500	2	1,600 + 900	2	96	2	0	0
Emmenanthe penduliflora	31	81,600 + 23,100	31	36,900 + 18,900	49	49	1	0	1
Guillenia lasiophylla	5	31,600 + 30,000	0	-	98	1	0	0	1
Lotus salsuginosus	15	45,700 + 19,900	15	51,000 + 27,200	65	24	9	0	2
Lupinus succulentus	5	1,300 + 500	19	8,500 + 3,600	70	21	2	2	5
Menzelia micrantha	6	1,100 + 600	14	10,300 + 5,300	87	12	0	0	1
Nicotiana attenuate and N. quadrivalvis	8	2,100 + 700	4	200 + 100	99	1	0	0	0
Papaver californicum	10	19,200 + 13,400	1	100	37	63	0	0	0
Phacelia brachyloba	6	20,500 + 13,700	2	100 + 100	84	16	0	0	0
P. grandiflora	11	15,100 + 9,800	3	300 + 200	17	82	1	0	0

P. parryi	6	71,400 + 42,900	17	19,700 + 12,600	53	38	6	3	0
Silene multinervia	4	20,100 + 15,500	3	900 + 600	43	56	1	0	0
Native postfire specialists									
Antirrhinum coulterianum	6	3,400 + 2,900	17	7,400 + 3,500	18	66	5	10	1
Blenosperma nanum	6	283,400 + 167,300	11	8,200 + 5,100	8	52	7	24	9
Calandrinia breweri	7	8,000 + 4,200	8	2,500 + 1,600	23	29	46	0	2
Calyptridium monandrum	14	87,900 + 63,500	15	14,300 + 5,600	44	35	0	0	21
Camissonia bistorta	18	383,700 + 305,300	20	52,000 + 19,300	2	77	0	1	20
C. californica	23	22,900 + 8,900	18	6,900 + 2,800	38	41	6	3	12
C. hirtella	19	96,800 + 65,800	18	17,800 + 7,100	7	85	1	0	7
Chaenactis artemisiifolia	16	82,100 + 35,800	16	93,200 + 65,400	6	75	8	9	2
Chorizanthe fimbriata	1	700	1	122,900	1	44	22	30	3
C. staticoides	6	95,700 + 78,100	4	1,600 + 900	1	14	66	19	0
Cryptantha microstachys	13	95,100 + 66,300	4	26,800 + 16,200	4	81	10	2	3
C. micromeres	2	136,900 + 134,000	6	56,100 + 17,100	7	82	9	0	2
Eremocarpus setigerus	4	300 + 200	13	7,700 + 5,100	35	35	30	0	1
Eucrypta chrysanthemifolia	28	95,300 + 33,200	36	108,700 + 58,100	60	22	4	5	10
Gilia angelensis	15	327,500 + 133,500	23	234,300 + 92,400	6	84	2	4	4
G. capitata	3	404,900 + 403,200	11	126,600 + 56,500	8	74	4	14	0
Linaria canadensis	10	78,400 + 32,300	16	26,500 + 14,600	15	54	3	1	27
L. strigosus	25	60,600 + 16,800	34	93,300 + 23,400	28	24	6	26	16
Lupinus bicolor	7	1,200 + 500	17	5,600 + 2,600	11	48	10	19	12
L. hirsutissimus	9	2,500 + 1,200	15	4,700 + 2,300	66	21	4	5	4
L. sparsiflorus	2	500 + 500	16	1,500 + 500	20	26	54	0	0
Malocothrix clevelandii	12	14,700 + 7,700	6	6,400 + 4,800	7	88	3	0	2

Mimulus brevipes	14	20,100 + 10,900	14	37,900 + 16,500	9	55	9	2	25
Navarretia atractyloides	7	301,500 + 194,500	7	42,100 + 40,400	4	67	15	10	4
Nemacladus ramosissimus	13	20,900 + 11,700	15	6,900 + 5,000	35	57	1	0	7
Phacelia cicutaria	26	21,300 + 10,500	29	29,200 + 14,300	59	21	6	8	6
P. minor	19	47,000 + 22,600	22	86,500 + 35,000	19	53	3	13	12
P. distans	15	14,000 + 7,700	24	3,600 + 1,900	2	55	28	10	5
Salvia columbariae	12	43,100 + 27,900	15	95,000 + 27,400	1	55	12	19	13
Senecio californicus	40	1,500 + 900	50	2,600 + 1,200	13	36	19	9	23
Silene antirrhinia	6	4,000 + 2,300	20	71,600 + 44,900	1	54	40	1	4
Trifolium gracilentum	5	149,800 + 148,600	9	64,700 + 46,700	15	69	5	9	2
T. wildenovii	8	60,200 + 59,700	14	22,000 + 16,400	12	41	36	10	1
Vulpia microstachys	7	215,400 + 156,300	6	38,000 + 24,500	8	32	60	0	0
Native postfire opportunists									
Amsinckia menziessi	6	4,200 + 3,900	14	10,400 + 4,500	6	18	32	10	34
Antirrhinum kelloggii	16	33,300 + 17,400	16	6,900 + 5,300	7	32	20	2	39
A. nuttallianum	13	23,400 + 12,800	17	2,800 + 1,600	49	28	12	3	8
Apiastrum angustifolium	21	247,700 + 79,900	38	191,400 + 132,200	5	40	12	13	30
Conyza bonariensis	35	81,600 + 32,400	50	52,900 + 14,000	1	44	45	1	9
Cryptantha clevelandii	25	96,700 + 32,400	16	86,800 + 41,200	3	62	10	6	19
C. muricata	31	231,700 + 128,400	37	258,300 + 72,200	5	64	11	14	6
Daucus pusillus	23	130,600 + 60,200	37	126,700 + 63,900	1	51	31	10	7
Filago californica	30	776,200 + 324,400	29	390,100 + 133,100	0	34	14	47	5

Githopsis diffussa	6	12,100 + 7,400	7	18,700 + 12,500	1	50	7	16	26
Gnaphalium californicum	37	84,700 + 47,800	44	8,500 + 2,500	2	5	73	10	10
G. stramineum	14	10,600 + 4,700	16	38,600 + 24,700	1	0	83	5	11
Hemizonia fasciculata	10	34,400 + 21,900	31	237,100 + 147,100	2	19	15	42	22
Lepidium nitidum	5	12,700 + 10,900	6	19,000 + 10,800	25	48	9	2	16
L. virginicum	2	105,500 + 105,500	10	96,500 + 43,100	22	13	13	36	16
Lotus hamatus	20	9,800 + 4,000	26	45,500 + 20,800	13	54	19	5	9
Lupinus concinnus	5	1,100 + 500	20	10,200 + 3,500	4	33	15	28	20
L. truncatus	3	800 + 400	9	7,400 + 1,800	2	11	8	27	52
Plagiobothrys collinus	3	48,500 + 32,500	0	-	0	79	1	0	20
Pterostegia drymarioides	23	88,500 + 36,400	27	120,500 + 52,700	2	41	28	14	15
Rafinesquia californica	37	9,700 + 1,800	48	10,700 + 4,300	9	49	9	4	29
Stephanomeria virgata	35	10,700 + 3,800	46	13,600 + 3,000	3	34	49	12	2
Trifolium ciliatum	0	-	13	6,300 + 4,400	6	15	8	71	0
Triodanus biflora and T. perfoliata	3	39,600 + 18,300	3	2,000 + 1,500	2	6	79	0	13
Uropappus lindleyi	20	5,100 + 1,800	28	53,200 + 28,200	1	67	10	7	15
Vulpia octoflora	1	43,600	3	392,700 +301,800	1	23	17	22	37
Native late successional increasers									
Bowlesia incana	1	40,500	1	25,000	0	0	0	0	100
Claytonia perfoliata	22	301,000 + 114,700	13	141,700 + 61,900	9	17	5	24	45
Collinsia parryi	4	13,600 + 4,400	7	7,300 + 4,700	1	42	0	1	57
Crassula connata	18	214,200 + 787,200	28	690,500 + 237,300	7	9	9	9	66
Eriastrum sapphirhinum	18	164,600 + 51,400	18	21,600 + 6,000	5	1	2	2	91
Galium aparine	12	7,200 + 3,500	14	5,500 + 2,000	18	1	35	0	46

Pectocarya linearis	6	800 + 600	13	25,800 + 11,600	19	5	13	0	63
Plagiobothrys canescens	1	217,500	1	600	0	80	0	0	20
Trifolium microcephalum	4	326,400 + 325,900	8	205,900 + 136,000	0	6	31	18	45

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Keeley, J. E., M. Baer-Keeley, and C. J. Fotheringham. 2005. Alien plant dynamics following fire in Mediterranean-climate California shrublands. Ecological Applications **15**:2109–2125.

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