MARITIME CHAPARRAL COMMUNITY TRANSITION IN THE ABSENCE OF FIRE

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ABSTRACT

Maritime chaparral stands on California's central coast are dominated by a number of endemic *Arctostaphylos* species and are the habitat for several other species of concern. Although chaparral is a fire-adapted vegetation type, maritime chaparral occurs in densely populated regions where fire suppression prevents most stands from burning. In 2000, we re-sampled vegetation at six locations in north Monterey County's Prunedale sandhills that were sampled in 1975-6 by Griffin (1978); this allowed us to document changes in community composition, canopy cover, and seedling abundance over a 25-year interval after more than 70 years of fire exclusion. Although species richness in the tree and shrub layers changed little between 1975-6 and 2000, combined tree and shrub cover increased from 86 to 99%. Cover of *Arctostaphylos pajaroensis* increased from 58 to 82%. Cover of *Quercus agrifolia* and *Heteromeles arbutifolia* also increased significantly, whereas percent cover for most shrub species decreased, often dramatically. Species richness in the herb layer was markedly lower in the 2000 survey. Seedlings were rare under the dense canopy, although seedling abundance for *Q. agrifolia* and

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Mimulus aurantiacus increased. These results suggest that the long absence of fire in maritime chaparral stands may lead to dominance by one or two species and a gradual transition from chaparral to oak woodland. Land managers should consider the reintroduction of wildfire, or practices that mimic the effects of fire, to assure the long-term survival of maritime chaparral vegetation communities.

KEYWORDS

Arctostaphylos, fire, maritime chaparral, succession, vegetation community dynamics

INTRODUCTION

Large areas of California's central coast are reported to have been covered with dense chaparral at the end of the nineteenth century (Cooper 1922). Today, only small, isolated fragments of northern and central maritime chaparral can be found growing in well-drained sandy soils along ridgelines and on coastal terraces between Sonoma and Santa Barbara counties (Holland 1986). Each of these stands is dominated by one or more *Arctostaphylos* species, including about 20 that are narrowly distributed endemics (Hickman 1993).

Although chaparral is widely reported to be dependent on periodic burning for renewal (e.g. Wells 1962; Hanes 1988), the cool and foggy central coast has one of the lowest rates of lightning-caused fire in California (Greenlee and Langenheim 1990). Estimates of historic fire return intervals for the Monterey Bay area range from as short as 10 to as long as 100 years or more (Greenlee and Langenheim 1990; Moritz 1997), but none of these estimates are presented with much confidence. Modern fire suppression practices have greatly reduced the size and frequency of wildfires in these heavily populated areas (Greenlee and Langenheim 1990).

Deviation from the natural fire frequency may alter the relative proportions of shrubs in the chaparral canopy by favoring obligate seeding *Arctostaphylos* species over crown sprouters (Keeley and Zedler 1978) and taller, longer-lived *Arctostaphylos* over *Ceanothus*, *Adenostoma*, or *Salvia* (Davis 1972; Davis et al. 1988). The long absence of fire may eventually favor crown sprouting species such as *Quercus* and *Heteromeles* over obligate seeders (Keeley 1992b; Zammit and Zedler 1993). Fire frequency also affects the composition of the chaparral understory, both through the direct effects of heat, smoke, and ash, and indirect effects such as reduced competition and herbivory (Sweeney 1956; Christensen and Muller 1975a; Keeley and Keeley 1987; Tyler 1996).

Chaparral remnants in the coastal sandhills of north Monterey County between the communities of Pajaro and Prunedale are dominated by *Arctostaphylos pajaroensis* and include several other uncommon species (Table 1). These stands continue to be fragmented and degraded by agricultural conversion and residential development, and their preservation is considered a high priority by Monterey County and by conservation organizations (Monterey County Planning Department 1981; Elkhorn Slough Foundation 1999). Unfortunately, little is known about the long-term effects of changing disturbance regimes on this unusual vegetation community.

The objective of this study was to identify changes in community composition, canopy cover, and seedling abundance that occur in maritime chaparral stands during long periods of fire suppression and habitat fragmentation. The existence of field data from a 25-year old survey of maritime chaparral in the Monterey Bay region (Griffin 1978) provided a unique opportunity to compare historical vegetation data with current conditions. Most previous studies of chaparral dynamics in the absence of fire have relied on a chronosequence of sites (e.g. Zammit and Zedler 1988; Keeley 1992a, b) that may vary along abiotic or biotic gradients.

STUDY AREA

Griffin (1978) surveyed maritime chaparral stands in the Monterey Bay region between October 1975 and March 1977 using the Braun-Blanquet minimal-area relevé method (Mueller-Dombois and Ellenberg 1974). Between five and ten plots were sampled in the least disturbed portions of each of these stands. Seven stands were within the range of *Arctostaphylos pajaroensis* in the Prunedale sandhills.

In spring and summer 2000, we re-surveyed the seven Prunedale area stands (Fig. 1; Table 2). Griffin's field data and sketch maps for five of the stands, along with historic aerial photographs, allowed us to re-locate 50 plots to within a few meters of the original. Of these, 21 no longer contained maritime chaparral due to development. In the two stands where there was insufficient information to permit exact re-location, we selected 18 plots with slope, aspect, and substrate matching the original. Plots were identified on topographic maps to avoid selection bias and adjusted in the field only as necessary to avoid edge effects from roads or other human disturbance.

Davis (1972) estimated that approximately 50 years had elapsed since the last major fire in the Prunedale hills region by counting annual growth rings in mature *A. pajaroensis*. We verified that none of our study plots have burned during the past 70 years by examining historic vertical aerial photographs of each stand taken at intervals between 5 and 12 years beginning in May 1931.

Maritime chaparral stands in the Prunedale hills occur within a matrix of oak woodland and coastal sage scrub. The chaparral comprises two distinct plant associations. The 1932 Vegetation Type Map survey (US Forest Service 1932) distinguished a shorter "dwarfed chamise type" and a taller "chaparral type". Exposed plateaus, ridges, and sandstone outcrops support a patchy chaparral that rarely exceeds one meter in height and where *A. hookeri* ssp. *hookeri* and *Adenostoma fasciculatum* are dominant. On slopes and in depressions below the ridgelines, a tall, dense *A. pajaroensis* canopy predominates. Boundaries between these two chaparral types are typically quite abrupt. The majority of plots sampled for this study are composed of the *A. pajaroensis* dominated association.

Soils at the Prunedale hills are Arnold-Santa Ynez complex, a mixture of deep, excessively drained, slightly acid loamy sand derived from old marine dunes and soft, weathered sandstone outcrops (US Department of Agriculture 1978). Slopes vary from flat on plateaus and ridges up to 40 percent. Elevation ranges from 50 to 150 m. The distance to Monterey Bay is between 7 and 11 km. Mean precipitation is 50 cm, falling mainly during the winter months (Monterey County Water Resources Agency). Summers are dry, moderated by frequent fog.

METHODS

We employed Griffin's (1978) sampling techniques to facilitate comparison. Forty-seven 10 × 10 m square plots were delineated and all vascular plant species identified. Three height strata were distinguished: tree layer (rising above the shrub canopy), shrub layer (the chaparral canopy), and herb layer (the understory). At every plot, we recorded an estimate of the average canopy height and the percentage of vegetation cover for all three layers. We ranked every species in each layer according to the Braun-Blanquet cover-abundance scale: "r" = 1 individual, "+" = few individuals, "1"

= 1-5% cover, “2” = 5-25% cover, “3” = 25-50% cover, “4” = 50-75% cover, “5” = 75-100% cover (Mueller-Dombois and Ellenberg 1974). A single species might occupy more than one layer. Adult *Quercus*, for example, contribute to the tree layer, saplings contribute to the shrub layer, and seedlings to the herb layer. In both surveys, all species of annual and perennial grass were combined into two categories. Additional species observed nearby but outside the plots were recorded separately; these species are included in Appendix 1, but not in quantitative analyses. Nomenclature is according to *The Jepson Manual* (Hickman 1993).

We calculated a “coefficient of community similarity” according to Jaccard (Mueller-Dombois and Ellenberg 1974) to compare species present in the tree and shrub layers among the plots of each survey and between the 1975-6 and 2000 surveys at individual plots. We also calculated differences in mean percent cover for the combined tree and shrub layers and for individual tree and shrub species between the plots of the two surveys. Because a Braun-Blanquet scale value represents a range of percentages, we used the median of each class (e.g. 62.5% for rank “4”, which represents 50-75% cover). The two lowest Braun-Blanquet scale values represent number of individuals rather than cover; we chose cover percentages of 0.1% for rank “r” and 0.5% for “+”. We applied paired *t*-tests to arcsine-transformed percentages to determine the significance of each change in tree and shrub cover (Sokal and Rohlf 1995). As an index for comparing community similarity based on percent cover, we calculated “percent similarity” (Wolda 1981) between the plots of each survey and between the two surveys. We calculated changes in the herb layer using Braun-Blanquet scale ranks rather than estimates of percent cover because converting abundance to cover for the two lowest classes could be misleading where overall percentages are low.

For the 2000 data, we tested whether the number of species present at each stand was dependent on average canopy height or mean percent cover using linear regression. The 1975-6 data did not include canopy height, so comparison between the two surveys was not possible. Nearly all plots tend to south facing, although their slopes vary considerably. We used linear regression to test whether changes in species composition or canopy cover were dependent on slope or aspect. Variations in soil type, relative elevation, and distance inland were minimal between plots, so the effects of these variables were not tested.

RESULTS

A total of 20 plant species were present in the tree and shrub layers of all plots in the 1975-6 survey; 19 species were present in 2000. All species encountered both in and near the sample plots are listed in Appendix 1. Three shrub species that were uncommon in the earlier survey, *Ceanothus dentatus*, *C. thyrsiflorus*, and *Ericameria ericoides*, were absent from the 2000 survey. The shrub *Vaccinium ovatum* and the introduced tree *Pinus radiata* were not encountered in 1975-6 and were rarely present in 2000. The average number of species per plot was nearly unchanged, increasing from 6.2 to 6.4. The Jaccard index, which compares the number of species in common, showed greater similarity for plots between the two surveys (0.81) than among the 1975-6 plots (0.65) or among the 2000 plots (0.69). Jaccard indices were lowest at the two stands where re-location was approximate, suggesting that these locations were somewhat mismatched.

Mean percent cover of the combined tree and shrub layers increased from 86 to 99% during the 25-year period ($t = 6.5$, $P < 0.0001$). This increase in canopy cover was chiefly due to a growing dominance by *Arctostaphylos pajaroensis* in nearly every plot. Mean cover of *A. pajaroensis* increased from 58 to 82% ($t = 7.34$, $P < 0.0001$; Fig. 2).

Large increases in percent cover were also recorded for *Quercus agrifolia*, *Heteromeles arbutifolia*, *Rhamnus californica*, and *Garrya elliptica*, but the total contribution of these oak woodland-associated sclerophylls remained small. Percent cover for all other shrubs decreased. Leading this decline was *Salvia mellifera*, which dropped from 6.0 to <0.5% ($t = 4.48$, $P < 0.0001$). The percent similarity index confirmed a dramatic increase in homogeneity among the plots, from 0.61 in 1975-6 to 0.92 in 2000.

In the herb layer, overall species richness decreased from 27 species in 1975-6 to 18 in 2000, and the average number of species per plot decreased from 2.8 to 1.7 ($t = 2.54$, $P = 0.015$; Table 3). All five tree and shrub species that had seedlings present in the earlier survey also had seedlings present in 2000, and three of these, *Mimulus aurantiacus*, *Q. agrifolia*, and *Toxicodendron diversilobum*, were more numerous and widespread (Table 4).

The Braun-Blanquet cover-abundance rankings for most subshrubs, herbs, and grasses decreased, as did the number of plots where they were found ($\chi^2 = 6.1$, $P = 0.047$ for all species; Table 4). The fern *Pteridium aquilinum* var. *pubescens* showed the largest decline, from up to 15 percent cover in each of 12 plots down to just a few individuals in four plots. More than half of the annual and perennial herbs counted in 1975-6 were no longer present in 2000.

The number of species present in a plot was inversely related to canopy height ($F = 8.87$, $R^2 = 0.16$, $P = 0.005$) and to percent cover ($F = 9.14$, $R^2 = 0.17$, $P = 0.004$). Regression revealed no significant relationship between number of species or percent cover and slope or aspect.

Non-native species were not major constituents of intact maritime chaparral in the Prunedale hills. Introduced annual grasses such as *Bromus* spp. were occasionally present in plots in the earlier study, as they were in 2000. No exotic trees, shrubs, or herbs were counted in 1975-6, although Griffin (1978) noted that *Carpobrotus edulis*, *Cortaderia jubata*, and *Genista monspessulana* were invading nearby disturbed areas. In 2000, *C. jubata* was widespread near all of the sampling locations, although only one individual appeared within the study plots. Introduced *Pinus radiata* grew near three of the sites, and a single sapling was present in one plot. Large numbers of *Eucalyptus globulus* saplings were present in chaparral near three of the stands in 2000.

DISCUSSION

Maritime chaparral stands in the Prunedale hills have undergone significant changes in community composition, canopy cover, and seedling abundance between 1975-6 and 2000, a period during which fire has been excluded. In the 1970s, the vegetation was patchy. Trees large enough to rise above the shrub layer were uncommon. *Arctostaphylos pajaroensis* competed with several other shrubs for dominance. A variety of grasses and forbs contributed to a sparse but widespread herb layer under the broken canopy. Today, the tree and shrub layers approach 100 percent cover forming a dense, closed canopy. *A. pajaroensis* is now the overwhelming dominant, although *Quercus agrifolia* cover has also increased significantly. The understory is generally bare except for occasional *Q. agrifolia* and *Mimulus aurantiacus* seedlings. Most herb layer species are restricted to the few remaining canopy gaps. All three of these trends, increased dominance by *A. pajaroensis*, loss of species diversity, and invasion by *Q. agrifolia*, may be attributed to the long absence of fire in the Prunedale hills.

Arctostaphylos pajaroensis *dominance*. The dramatic increase in *A. pajaroensis* cover, and similarly dramatic decreases for several other shrubs, likely result from the greater relative height of this long-lived species when freed from periodic destruction by wildfire. Davis (1972) noted that, with sufficient time and in the absence of fire, the stature of *A. pajaroensis* exceeds that of all other associated species except *Q. agrifolia*. This competitive advantage is largely due to the adaptation of "bark striping", where the amount of living tissue on stems in the lower, shaded portions of the shrub is minimized while providing structure to support the growth of new leaves and branches in full sunlight above (Davis 1973). We encountered a tangle of dead *Salvia*, *Adenostoma*, *Ceanothus*, and other shrubs in plots wherever the canopy exceeded two meters in height, suggesting the fate of these shorter species as they become overtopped and shaded by *A. pajaroensis*. McPherson and Muller (1967) described a similar competition for light in mature coastal chaparral in which shorter *Salvia* were progressively killed by taller shrubs. The dominant in this case was *Ceanothus cuneatus*, a species that also exhibits the bark striping strategy (Keeley 1975). Interestingly, in the Prunedale hills *C. cuneatus* var. *rigidus* is one of the species that is overtopped and killed by taller *A. pajaroensis*.

Herb layer composition. Declining species richness and abundance in the understory are probably consequences of greater canopy height and density, and the resulting shade and litter accumulation, rather than differences in precipitation. Griffin (1978) suggested that the herb layer did not develop fully in 1975-6, a drought year, yet he recorded a wider diversity of species growing under and among the trees and shrubs than we encountered in 2000, a normal rainfall year (Monterey County Water Resources Agency).

Many studies have commented on the absence of herbs and shrub seedlings under mature, undisturbed chaparral (e.g. Sampson 1944; Christensen and Muller 1975b; Hanes 1988). Competition for light, moisture, and nutrients and high levels of herbivory are common explanations (e.g. McPherson and Muller 1969; Schlesinger and Gill 1980; Swank and Oechel 1991; Tyler 1996; Keeley 2000). *Arctostaphylos* may also be a source of allelopathic substances, inhibiting the establishment of seedlings under the chaparral canopy (Muller et al. 1968; Chou and Muller 1972). The only herbaceous species that showed a significant increase in the shade under dense *A. pajaroensis* was *Marah fabaceus*, a vine that resprouts annually from a large underground tuber and can quickly reach sunlight in the shrub canopy (Schlising 1969).

Two annual herbs, *Chorizanthe pungens* var. *pungens* and *Navarretia hamata*, and three perennial shrubs or subshrubs, *Eriophyllum confertiflorum*, *Helianthemum scoparium*, and *Lotus scoparius*, were restricted to openings in the canopy in 2000. Canopy gaps are important for seed germination and seedling establishment and for maintaining the seed banks of many chaparral species (Davis et al. 1989; Zammit and Zedler 1994; Odion and Davis 2000). As tree and shrub layer cover has increased, gaps have grown increasingly rare.

Quercus agrifolia *invasion*. An increase in *Q. agrifolia* canopy cover and seedling abundance in Prunedale hills maritime chaparral stands is consistent with Keeley's (1992a, b) conclusion that species like *Q. agrifolia* that are capable of regeneration from root crowns will only produce seedlings after a long fire-free period, and only under a dense canopy in a heavy accumulation of leaf litter. Callaway and D'Antonio (1991) found that shrubs frequently serve as "nurse plants", providing microhabitat conditions that facilitate the establishment of *Q. agrifolia* seedlings that will eventually overtop and kill their hosts. We frequently encountered mature *Arctostaphylos* skeletons in the shaded understory of oak woodland immediately adjacent to chaparral stands, an observation also reported by Davis (1972).

Boundaries between chaparral, coastal sage scrub, and oak woodland communities are dynamic and highly dependent on fire frequency (Gray 1983; Callaway and Davis 1993). Live oak woodland is widely characterized as the successional climax for maritime chaparral stands in the absence of fire (e.g. Wells 1962; Davis 1972; McBride and Stone 1976; Griffin 1978). Several studies suggest that a gradual transition to oak woodland is underway at various locations on the central coast as *Q. agrifolia* invades long unburned areas (Davis et al. 1988; Callaway and Davis 1993; Mensing 1998; White 1999). Various studies have also proposed that the segregation of maritime chaparral and oak woodland communities is at least partially due to edaphic differences (e.g. Wells 1962; Cole 1980; Davis et al. 1988). Davis (1972) and Griffin (1978) both conclude that *Q. agrifolia* is successional to the more mesic *A. pajaroensis* association in the absence of fire, while conversion from chaparral to oak woodland will progress more slowly, and perhaps even be arrested, in the more xeric *A. hookeri* association. Even on the harshest sandstone ridges, *Q. agrifolia* is occasionally present, but only as seedlings and shrub-sized individuals.

Long-term vegetation changes in the absence of fire. As was the case in 1975-6, no recruitment of obligate seeding *Arctostaphylos* or *Ceanothus* species was observed in any of our study plots in 2000. The only seedlings of these taxa that we encountered anywhere during this survey were a few dozen young *A. pajaroensis* and *C. dentatus* that had established near one of the plots in a small area that had burned two years previously. These results are not surprising as seeds of several species in these two genera are reported to require heating or exposure to smoke or charate to stimulate germination (Keeley 1987; Keeley and Keeley 1987; Keeley and Fotheringham 1998).

The effect of long fire-free periods on chaparral is a topic of considerable discussion. Keeley (1992a) has persuasively argued that pejorative terms such as decadent and senescent that are often applied to long-unburned chaparral stands (e.g. Sampson 1944; Hanes 1988) are inappropriate for describing a gradual successional shift from obligate seeding *Arctostaphylos* and *Ceanothus* species to crown sprouting *Quercus* and *Heteromeles*.

Keeley (1992a) also notes the importance of variable fire regimes to maintain equilibrium in species composition. The long absence of fire may lead to local extinction of certain species if soil seed banks become exhausted. The length of time that seeds remain viable is unknown for most maritime chaparral species (Tyler and Odion 1996). Further study of seed bank longevity is needed to understand the risk to species of concern such as *C. cuneatus* var. *rigidus*, *Chorizanthe pungens* var. *pungens*, *Ericameria fasciculata*, and *Piperia yadonii*.

Because the majority of Prunedale hills maritime chaparral has not burned for at least 70 years, we feel that concern for the future of *A. pajaroensis*, *C. cuneatus* var. *rigidus*, and the other plants that characterize this unusual vegetation community is warranted. Neither they nor their seeds can survive forever. If wildfire continues to be excluded, the composition of these stands will undoubtedly be very different in the future.

Management implications. Griffin (1978) concluded with this warning: “Pressures for development are so great around Monterey Bay that maritime chaparral stands need legal protection to survive. No adequate sample of chaparral near Prunedale has formal protection now.” Since this writing, several important Prunedale hills stands have received protection as conservation lands. At the same time, additional chaparral acreage is lost every year and development pressures continue to grow. Of the seven original 1975-6 sampling areas, three are highly modified with only fragments of undisturbed chaparral remaining, two had remained relatively intact but currently have subdivision plans underway, and two are within the boundaries of Manzanita County Park where sports facility expansion is proposed.

Areas dominated by the low *A. hookeri* chaparral association are generally unsuited for agriculture because of their shallow soils and remain as fragments along ridgelines throughout the Prunedale hills. Monterey County land use policies discourage development on ridges and encourage the dedication of scenic and conservation easements on unbuildable portions of subdivisions that contain these maritime chaparral fragments (Monterey County Planning Department 1981). Stands of the taller *A. pajaroensis* association, because they occur on the gentler south-facing slopes and deeper soils favored for cultivation, have been lost to agricultural conversion over a period of many decades. In recent years, a shortage of land suitable for residential development in north Monterey County has accelerated the destruction of this chaparral type. Alternative management strategies are needed for these two different chaparral types.

Loss of species diversity caused by shading is associated with canopy height, thus with the *A. pajaroensis* dominated chaparral type. Invasion by *Q. agrifolia* is also rapid in these more mesic sites. For these areas, the introduction of prescribed burning, or perhaps mechanical disturbance with smoke or charate treatment, may be necessary to open the canopy, facilitate seedling establishment, and slow the advance of oaks. Enhancement of the seed bank with stockpiled chaparral soil, in conjunction with burning, could be necessary in degraded areas (Odion 1995). Unfortunately, non-native species often follow disturbance in chaparral (Zedler and Scheid 1988; D’Antonio et al.

1993; Tyler and Odion 1996; Holl et al. 2000), so a control program would likely be required. In the low *A. hookeri* chaparral type, where gaps are frequent and *Quercus* grow slowly, prevention of any kind of disturbance might be the more appropriate management strategy.

Land protection is the essential first step toward conserving increasingly rare maritime chaparral communities. Conservation efforts should focus on stands that include both chaparral associations. Active land stewardship will also be necessary in order to conserve the full complement of native plant species. Management strategies should attempt to maximize diversity by maintaining a variety of successional stages and canopy heights including bare rock and soil, patchy mixed chaparral, closed *Arctostaphylos* canopy, and mixed chaparral/oak woodland. The effects of a modified disturbance cycle in the Prunedale hills will need to be understood in order to ensure the survival of this unusual vegetation and to minimize the loss of endemic species.

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TABLE 1. UNCOMMON PLANTS OF PRUNEDALE HILLS MARITIME CHAPARRAL.

Species	Rarity[1]
Arctostaphylos hookeri ssp. *hookeri*	CNPS List 1B (rare, threatened, or endangered)
Arctostaphylos pajaroensis	CNPS List 1B
Ceanothus cuneatus var. *rigidus*	CNPS List 4 (watch list)
Chorizanthe pungens var. *pungens*	Fed. threatened; CNPS List 1B
Ericameria fasciculata	CNPS List 1B
Piperia yadonii	Fed. endangered; CNPS List 1B

[1] California Department of Fish and Game 2001; Skinner and Pavlik 1994

TABLE 2. PRUNEDALE HILLS MARITIME CHAPARRAL SAMPLING LOCATIONS.

Stand	Description	Number of plots	
		1975-6	2000
1	McGuffie Road	10	6 original plots; 4 plots lost to development
2	Vierra Canyon	10	3 original plots; 7 plots lost to development
3	Castroville Boulevard	7	10 approximate plot locations
4	Manzanita Circle	10	10 original plots
5	Prunedale	10	10 original plots
6	Lewis Road	10	10 plots lost to development
7	Hidden Valley	5	8 approximate plot locations

TABLE 3. HERB LAYER: TOTAL NUMBER OF SPECIES AND MEAN NUMBER OF SPECIES PER PLOT. * = $P < 0.05$; *** = $P < 0.001$ from paired *t*-test. ±1 standard error in parentheses. For species included in each category see Appendix 1.

Category	Total species			Species per plot	
	1975-6	2000	common	1975-6	2000
Tree and shrub seedlings	5	5	5	0.27 (0.09)	0.73 (0.13) *
Perennial subshrubs, herbs, and grasses	18	11	8	2.37 (0.31)	0.94 (0.18) ***
Annual herbs and grasses	4	2	1	0.15 (0.07)	0.04 (0.04)
All species	27	18	14	2.78 (0.39)	1.7 (0.24) *

TABLE 4. HERB LAYER: NUMBER OF PLOTS IN EACH BRAUN-BLANQUET COVER-ABUNDANCE CLASS. For additional species included in each category see Appendix 1.

Category and selected species	1975-6			2000		
	"r"	"+"	"1"-"2"	"r"	"+"	"1"-"2"
Tree and shrub seedlings	7	4	0	10	25	0
Baccharis pilularis	2	2	0	2	0	0
Mimulus aurantiacus	1	0	0	4	7	0
Quercus agrifolia	3	0	0	2	13	0
Rhamnus californica	1	0	0	1	0	0
Toxicodendron diversilobum	0	2	0	1	5	0
Perennial subshrubs, herbs, and grasses	23	66	8	15	30	0
Gnaphalium spp.	6	6	0	2	0	0
Helianthemum scoparium	0	5	0	0	0	0
Lotus scoparius	3	9	0	2	3	0
Marah fabaceus	0	0	0	3	6	0
Pteridium aquilinum	0	4	8	0	4	0
Annual herbs and grasses	0	6	0	0	2	0
All species	30	76	8	25	57	0

APPENDIX 1. SPECIES ENCOUNTERED AT PRUNEDALE HILLS MARITIME CHAPARRAL SAMPLING LOCATIONS.

[1] = present in plots 1975-6, [2] = present in plots 2000, [3] = present in plots both surveys. Species without numbers in brackets were observed near but never in plots.

Trees:

Eucalyptus globulus (non-native)
Pinus radiata (introduced) [2]
Quercus agrifolia [3]
Quercus wislizenii

Shrubs:

Adenostoma fasciculatum [3]
Arctostaphylos hookeri ssp. *hookeri* [3]
Arctostaphylos pajaroensis [3]
Arctostaphylos tomentosa ssp. *crustacea* [3]
Artemisia californica
Baccharis pilularis ssp. *consanguinea* [3]
Ceanothus cuneatus var. *rigidus* [3]
Ceanothus dentatus [1]
Ceanothus thyrsiflorus [1]
Chrysolepis chrysophylla
Dendromecon rigida [3]
Ericameria ericoides [1]
Ericameria fasciculata [3]

Eriophyllum confertiflorum [3]

Garrya elliptica [3]

Genista monspessulana (non-native)

Heteromeles arbutifolia [3]

Lepechinia calycina

Mimulus aurantiacus [3]

Pickeringia montana [3]

Rhamnus californica [3]

Salvia mellifera [3]

Solanum umbelliferum

Symphoricarpos mollis

Toxicodendron diversilobum [3]

Vaccinium ovatum [2]

Perennial subshrubs, herbs, and grasses:

Achillea millefolium [1]

Calochortus albus

Cardionema ramosissimum

Carex spp. [1]

Carpobrotus edulis (non-native)

Castilleja foliolosa

Chlorogalum pomeridianum

Cortaderia jubata (non-native) [2]

Dichelostemma capitatum

Dudleya lanceolata [3]

Eriogonum nudum

Galium californicum [1]

Gnaphalium spp. [3]

Helianthemum scoparium [1]

Horkelia cuneata [1]

Iris douglasiana

Lessingia filaginifolia

Lomatium sp. [1]

Lotus scoparius [3]

Lupinus spp.

Marah fabaceus [2]

Oxalis albicans ssp. *pilosa*

Pedicularis densiflora [3]

Pellaea mucronata [1]

Pentagramma triangularis [3]

perennial grass [3]

Piperia yadonii

Polygala californica [3]

Pteridium aquilinum var. *pubescens* [3]

Rosa gymnocarpa [2]

Rubus ursinus [1]

Rupertia physodes

Scrophularia californica [1]

Scutellaria tuberosa

Sisyrinchium bellum

Solidago sp. [1]

Zigadenus fremontii var. *fremontii*

Annual herbs and grasses:

annual grass [1]

Camissonia spp.

Chorizanthe pungens var. *pungens* [2]

Cryptantha sp.

Hemizonia sp. [1]

Linaria canadensis

Lupinus spp.

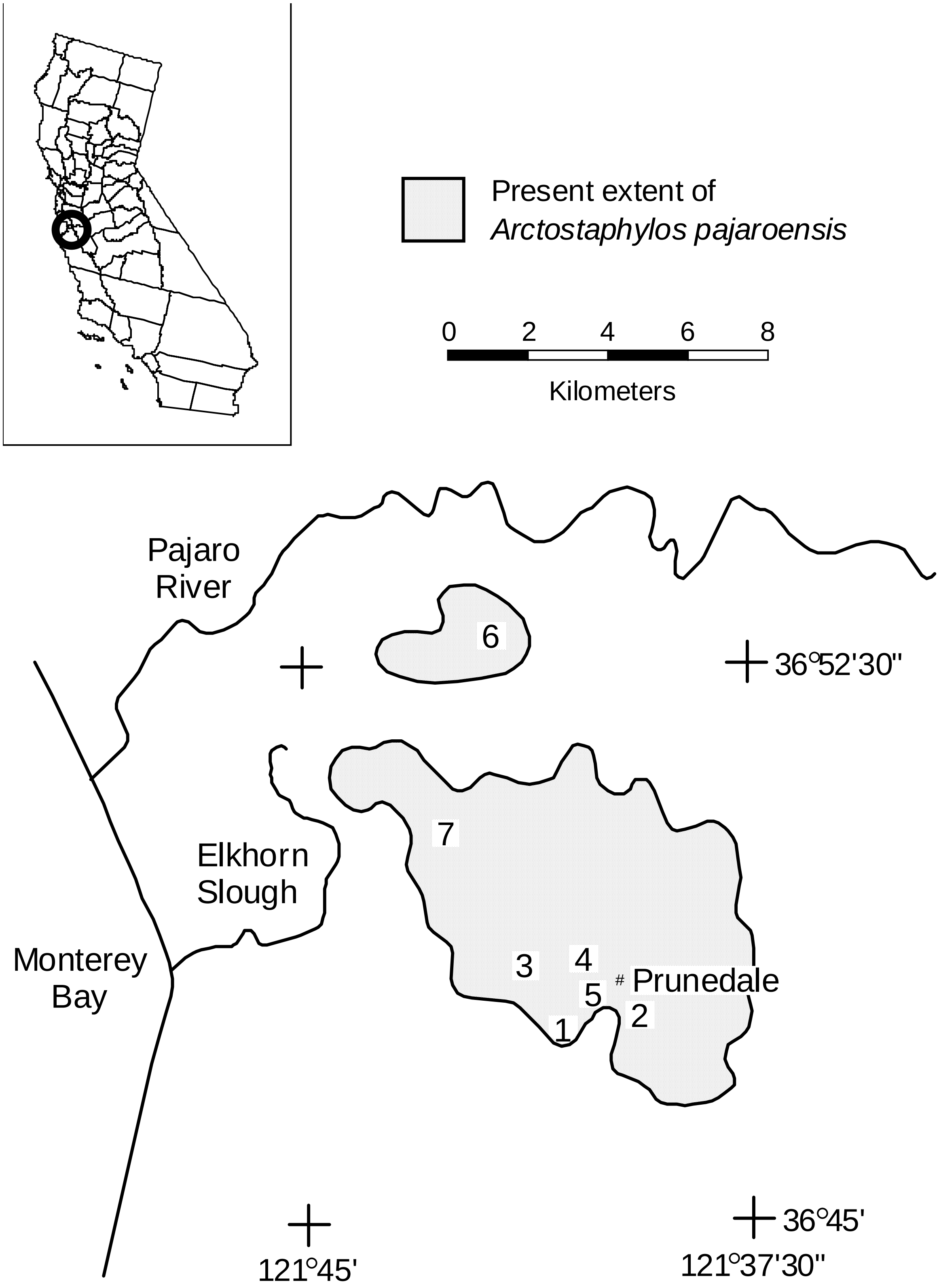
Madia sp. [1]

Navarretia hamata [3]

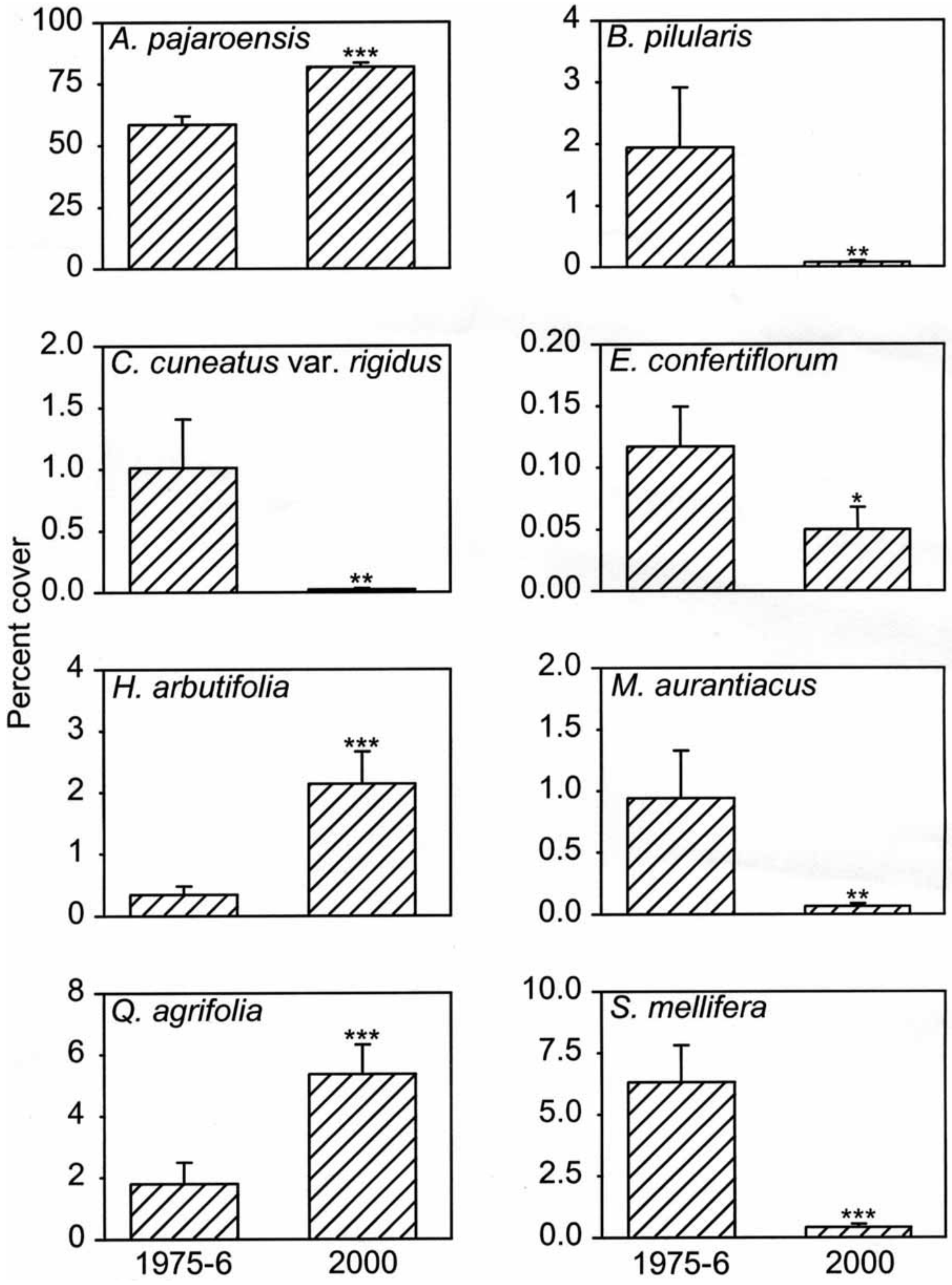
FIGURE CAPTIONS

FIG. 1. Location of stands surveyed and present extent of *Arctostaphylos pajaroensis*. For descriptions of numbered stands see Table 2.

FIG. 2. Change in mean percent cover between 1975-6 and 2000 for selected species. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$ from paired *t*-test on arcsine-transformed percentages. Error bars indicate ±1 standard error. Note different y-axis scales.


Present extent of
Arctostaphylos pajaroensis
0
2
4
6
8
Kilometers
Pajaro River
6
36°52'30"
Elkhorn Slough
7
Monterey Bay
3
4
5
Prunedale
2
1
36°45'
121°45'
121°37'30"

(Figure 1)


Percent cover
A. pajaroensis
***
100
75
50
25
0
B. pilularis
**
4
3
2
1
0
C. cuneatus var. rigidus
**
2.0
1.5
1.0
0.5
0.0
E. confertiflorum
*
0.20
0.15
0.10
0.05
0.00
H. arbutifolia
***
4
3
2
1
0
M. aurantiacus
**
2.0
1.5
1.0
0.5
0.0
Q. agrifolia
***
8
6
4
2
0
S. mellifera
***
10.0
7.5
5.0
2.5
0.0
1975-6
2000
1975-6
2000

(Figure 2)