

Environmental factors influencing spatial patterns of shrub diversity in chaparral, Santa Ynez Mountains, California

Moody, Aaron* & Meentemeyer, Ross K.

Department of Geography, University of North Carolina, Chapel Hill, NC 27599-3220, USA;

*Fax +19199621537; E-mail aaronm@email.unc.edu

Abstract. We examined patterns of shrub species diversity relative to landscape-scale variability in environmental factors within two watersheds on the coastal flank of the Santa Ynez Mountains, California. Shrub species richness and dominance was sampled at a hierarchy of spatial units using a high-powered telescope from remote vantage points. Explanatory variables included field estimates of total canopy cover and percentage rock cover, and modeled distributions of slope, elevation, photosynthetically active radiation, topographic moisture index, and local topographic variability. Correlation, multiple regression, and regression tree analyses showed consistent relationships between field-based measurements of species richness and dominance, and topographically-mediated environmental variables. In general, higher richness and lower dominance occurred where environmental conditions indicated greater levels of resource limitation with respect to soil moisture and substrate availability. Maximum richness in shrub species occurred on high elevation sites with low topographic moisture index, rocky substrate, and steep slopes. Maximum dominance occurred at low elevation sites with low topographic variability, high potential solar insolation, and high total shrub canopy cover. The observed patterns are evaluated with respect to studies on species-environment relations, resource use, and regeneration of shrubs in chaparral and coastal sage scrub. The results are discussed in the context of existing species-diversity hypotheses that hinge on reduced competitive dominance and increased resource heterogeneity under conditions of resource limitation.

Keywords: Coastal sage scrub; Digital terrain model; Environmental gradient; Regression tree; Resource limitation; Species diversity.

Abbreviations: DEM = Digital Elevation Model; FOV = Field of View; PAR = Photosynthetically Active Radiation; PC = standard deviation of Profile Curvature; PSI = Potential Solar insolation; TMI = Topographic Moisture Index.

Nomenclature: Hickman (1993).

Introduction

In many communities maximum diversity occurs under conditions of moderate resource limitation (Rosenzweig 1971; Tilman 1982; Margules et al. 1988; Braakhekke & Hooftman 1999). This scenario may be viewed with reference to the *competition hypothesis* (Menge & Sutherland 1976), or the *spatial competition hypothesis* (Tilman 1994), in which niche diversity is maintained by inter- and intraspecific competition for limited resources. These hypotheses presume that resource limitation reduces competitive dominance by individual species, and creates increased local habitat diversity, thus facilitating recruitment of different species with variable resource constraints (Grime 1979).

In chaparral and coastal sage scrub, several studies have shown that certain species and species-assemblages are distributed in accordance with gradients in environmental conditions (Shreve 1927; Mooney & Harrison 1972; Kirkpatrick & Hutchinson 1980; Steward & Webber 1981; Westman 1981a; Franklin 1998). However, variability in chaparral *diversity* along environmental gradients has received little attention. Exceptions either approach the issue of diversity in a post-disturbance scenario (Davis et al. 1988; O'Leary 1990), focus on coastal sage scrub communities (Westman 1981b; O'Leary 1990), focus primarily on microsite effects (Shmida & Whittaker 1981), or treat specific cases, such as diversity on serpentine soils (Harrison 1997).

In general, water and light appear to be the primary resources for which plants compete in chaparral and other Mediterranean-type vegetation communities (Vilà & Sardans 1999). Soil moisture permitting, sites with high photosynthetically active radiation (PAR) often support nearly monospecific, closed canopy stands of large-stature shrub species (Schlesinger et al. 1982). However, on exposed sites where moisture is limiting, percentage shrub cover is often reduced in chaparral (Bauer 1936; Miller & Poole 1979; Ng & Miller 1980). The resulting open vegetation structure permits greater spatial heterogeneity of light, temperature, nutrients and

moisture conditions. According to some perspectives on environment-diversity relationships (Pielou 1975; Grime 1979; Tilman 1982, 1994; Stone & Roberts 1991), as well as observed patterns in chaparral (Shmida & Whittaker 1981), these conditions facilitate greater species richness. In particular, where chaparral canopy closure is prohibited due to insufficient soil moisture, coastal sage scrub species exploit canopy openings due to their superior drought tolerance (Kirkpatrick & Hutchinson 1980; Shmida & Whittaker 1981; Schlesinger et al. 1982). Conversely, where light is limited by closed canopy chaparral, coastal sage scrub and herbaceous species are almost entirely precluded from the subcanopy environment (McPherson & Muller 1967; Swank & Oechel 1991).

We present a landscape-scale study of relationships between spatial patterns in the diversity of common chaparral shrub species and abiotic environmental factors in the Santa Ynez Mountains, California. Our general hypothesis is that shrub diversity is increased under conditions of moderate resource limitation. This hypothesis is based on two presumptions. First, there are certain combinations of environmental conditions that – through their control on light regime, soil moisture, percent shrub cover, and recruitment opportunities – will control habitat heterogeneity, and thus govern spatial patterns of species diversity. Second, resource limitation leads to reduced competitive dominance, and produces greater habitat heterogeneity by prohibiting canopy closure. We ignore herbaceous species and natural disturbance in our analysis of this ecosystem, but will return to these points in the discussion.

Study sites

The coastal zone of southern California has a mediterranean climate with variable precipitation from mid-fall to mid-spring and a drought period from late spring through early fall. Soils are very dry in summer with obvious impacts on plant productivity (Thomas & Davis 1989). Summer fog is common, occurring when the moist marine layer, trapped between the mountains and the frequent summertime temperature inversion, cools in the early morning (Bailey 1966).

The Santa Ynez Range runs east-west along the coast between Point Conception and Ventura (Fig. 1), and occupies portions of Santa Barbara and Ventura Counties, California. It forms the western end of the Transverse Ranges. The range is composed of marine sediment, alluvial deposits and accretionary materials sequentially added into the coastal margin during interactions between the Pacific and North American plates (Page et al. 1955). The mountains are highly dissected into steep slopes and deeply cut canyons.

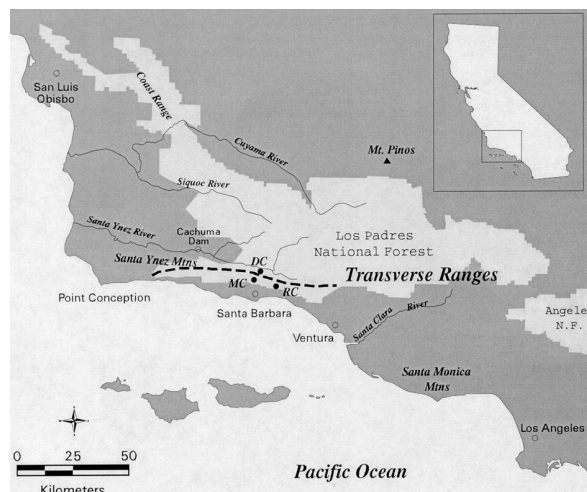


Fig. 1. Study area. The dashed line represents the main ridge of the Santa Ynez Mountain Range. The abbreviations MC and RC indicate the approximate locations of Mission Canyon and Romero Canyon.

Chaparral vegetation is dominated by drought-tolerant or drought-adapted, evergreen sclerophyllous trees and shrubs (Hanes 1977). Chaparral is extensively distributed in California, dominating the flanks of the southern coastal mountain ranges deep into Baja, and extending north into southern Oregon. It can occupy sites from coastal bluffs to high montane environments, and it is a common lower elevation community in the mountains surrounding the California central valley (Hanes 1977).

On the south flank of the Santa Ynez Range, as elsewhere in the southern California chaparral, lower elevations and dry mid-elevation sites support aromatic, drought-deciduous, herbaceous perennials characteristic of the coastal sage scrub community (e.g. *Salvia* spp., *Eriogonum fasciculatum*, *Artemisia californica*) (Smith 1998). With increasing elevation, lower chaparral shrubs such as *Ceanothus megacarpus*, *C. spinosus* and *Adenostema fasciculatum* begin to dominate (Schlesinger et al. 1982). An upper chaparral community is typified by the emergence of *Arctostaphylos* spp., *Ceanothus crassifolius*, and shrub forms of *Quercus* spp. (Smith 1998). Occasional conifer stands (e.g. *Pinus coulteri* and *Pseudotsuga macrocarpa*), often with an understory shrub layer, are found at uppermost elevations in the Santa Ynez (Smith 1998).

The geology of the Santa Ynez expresses strong elevational zonation with distinct contacts between formations. Within our two study sites, these zones form a sequence of alternating sandstones and shales, primarily of marine origin (Dibblee 1986a, b).

The study sites are two small watersheds on the coastal flank of the Santa Ynez Mountains directly

north of Santa Barbara, California (Fig. 1). Mission Canyon is an 8.2 km² watershed that includes La Cumbre Peak which, at 1215 m, is the highest point in the Santa Ynez. The foot and upper ridge of Mission Canyon are located 6.6 and 9.4 km from the coast, respectively. Sampling in Mission Canyon began above the residential zone (within the boundary of the Los Padres National Forest) at an elevation of 274 m. Mission Canyon was last burned in 1964.

Romero Canyon is a 7.1-km² watershed located 12.5 km east of Mission Canyon, with an upper elevation of 1067 m. The foot and upper ridge are 4.0 and 6.5 km from the coast, respectively. Sampling in Romero Canyon began above the residential zone at an elevation of 244 m. Romero Canyon was last burned in 1971. While no fog climatology exists for the Santa Ynez, our observations suggest that Romero Canyon is influenced by a more persistent summer fog regime than Mission Canyon.

Methods

Field sampling

Chaparral commonly forms a closed canopy and develops a heavy thicket of understory biomass on steep, and often unconsolidated terrain. These conditions have prevented most researchers from collecting large numbers of well-distributed field samples. In addition, most studies have used small plots (e.g. 100 m²) with inter- and intraplot variability that may be stochastic, or respond to processes that operate at a finer scale than our focus. To resolve these issues, we sampled shrub composition at a hierarchy of spatial units using a high-powered telescope from remote vantage points. This approach reduced the cost of data collection and permitted acquisition of a large number of field samples distributed throughout the study sites. An evaluation of the method by Meentemeyer & Moody (2000) indicates that the sampling approach provided vegetation data at an appropriate scale for modeling landscape-level patterns of shrub composition as driven by topographically-mediated environmental conditions.

The field sampling was organized around a spatial unit referred to as a *patch* (Fig. 2). A patch is a continuous stand of vegetation that is homogeneous in terms of shrub composition and total cover. Candidate patches, delineated in the field from remote vantage points, were distributed in order to represent the range of elevations, slope positions, and aspects available within the two watersheds. The delineation of patch boundaries was based on a set of thresholds relating to shrub composition, the relative abundance of dominant species, and total

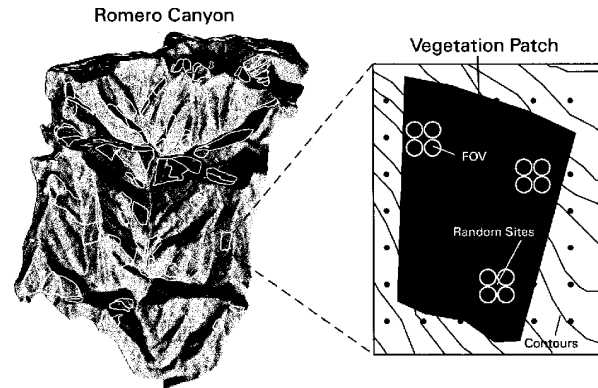


Fig. 2. Field sampling strategy illustrated for the Romero Canyon Watershed. The right panel is an expanded view of a single patch. Three random sites are chosen from the regular, 20-m grid of points. Around each point, four telescope fields of view (FOV) are sampled for shrub species composition. The contour lines represent 10-m elevation intervals. The base map, used for illustrative purposes, is the Potential Solar Insolation data layer, modeled using the Atmospheric and Topographic Model (Dozier & Frew 1990; Dubayah 1992) described in the text. The field-sampled vegetation patches for Romero Canyon are overlaid on this data layer.

cover. These characteristics, estimated by surveying candidate patches from remote vantage points, were used as guiding parameters to help maintain consistency in patch definition. For candidate patches where the relative canopy cover of a single species was greater than 60%, patch boundaries were mapped where a change in the dominant species occurred, or where a transition to a mixed species composition occurred. For candidate patches with mixed species composition, boundaries were determined where the abundance of any shrub species changed by 20% or more. Patch boundaries were also defined where absolute cover changed by 20% or more.

A candidate patch was selected for sampling if it could be reliably mapped on the high resolution terrain model, and if it met the following additional criteria. First, a minimum patch size of 0.25 ha was used to filter out fine scale floristic variability and to avoid sampling in the range of patch sizes over which richness and area are fundamentally related (Greig-Smith 1983). Second, a patch had to be completely visible from an accessible remote viewing location at an angle greater than 45° between the terrain facet and the line of site. Finally, a patch had to be within 300 m of the vantage point, and greater than 10 m from a dirt road or trail.

Within each patch, two to a maximum of five *sites* were randomly located from a regular array of grid points distributed at 20 m intervals (Fig. 2). Sites that were either less than 10 m from a patch boundary, or

adjacent to an already selected site within the patch were rejected. This guideline was relaxed in the case of small patches where adjacent sites were used to ensure that at least two sites were sampled within the patch. A zoom telescope (15× to 45×) was used to sample shrub and tree composition for each site from a remote viewing location. Composition for each site was determined by aggregating species composition within four non-overlapping telescope fields of view (FOV) surrounding the site (Fig. 2). If one of the four FOVs surrounding a site was excessively close to the patch boundary the FOV was dropped and only three FOVs were used to characterize the site. The location and sizing of FOVs was achieved by navigation on a high resolution (10 m) terrain model overlaid with a 20 m grid, and supported with clinometer and compass measurements. Each FOV was restricted to ca. 100 m² using the navigation information and the zoom capability of the telescope.

For each FOV we determined the shrub species present, the percentage of each species, percentage of exposed bedrock, and total canopy cover. Species identification was based on leaf and bark color; shrub form and stature; bud, flower, and new growth characteristics; and leaf shape, size, and orientation. The FOV data were aggregated from the FOVs to the site level, and the site data were aggregated to produce shrub composition data for each patch. For each site, species richness was determined by tabulating all species found within the three to four surrounding FOVs. Species abundance was determined by averaging the percent cover of each species within the surrounding FOVs. Total cover was also determined by averaging. Aggregation from the site level to the patch level was accomplished analogously.

The patches were mapped onto the digital elevation model (DEM) used to derive terrain-based environmental characteristics. After excluding samples from riparian areas and upper elevation conifer woodland, a total of 175 patch samples remained for Mission Canyon (106) and Romero Canyon (69). The patches ranged in size from 0.25 ha to nearly 7.5 ha. 36 chaparral and coastal sage scrub species were identified in this set of samples (Table 1). Non-woody species, vines, fungi, lichens, and parasitic plants were omitted from the analysis because of concerns regarding the reliability with which we could detect, identify, and estimate percentages for these types.

From the remaining data set, we derived within-patch shrub species richness and dominance as measures of shrub species diversity. Richness is the number of shrub species present within the patch. To characterize species dominance, each patch was ranked from 1 to 16 depending on the relative percentage of the most abundant species. A value of 1 was given if the most

abundant species composed less than 24 % of the patch. A value of 2 was given if the most abundant species composed between 25 % and 29 %. A 3 was given if the most abundant species composed between 30 % and 35 %, and so on. If the most abundant species composed 95 % or greater a dominance value of 16 was assigned.

The sampling method involved sacrificing a degree of site-level data accuracy in order to achieve sufficient sampling frequency and distribution. As a result, there were several potential sources of error. First, plant species were occasionally misidentified within a given FOV. Second, within an FOV some species may have been missed, particularly if individual plants were masked by others. Either of these cases could result in

Table 1. Richness and Dominance indicator status and general elevation strata for shrub and tree species in this study. Richness and Dominance indicator status (X) corresponds to *T*-test results where significant at $P < 0.01$. Only species marked with an asterisk were tested for association with Richness and Dominance. General elevation zones are low to moderate (L/M), moderate to high (M/H), high (H), and low to high (L/H). The symbol § indicates species found in the field sampling validation plots.

Species	Richness		Dominance		Elevation
	High	High	Low	High	
Chaparral:					
<i>Adenostoma fasciculatum</i> *§	X				L/H
<i>Arbutus menziesii</i>					H
<i>Arctostaphylos glandulosa</i> *§	X		X		M/H
<i>A. glauca</i> *§					M/H
<i>Cercocarpus betuloides</i> *§	X				L/H
<i>Ceanothus crassifolius</i> *	X		X		H
<i>Ceanothus megacarpus</i> *§		X			L/M
<i>Ceanothus oliganthus</i> *	X		X		M/H
<i>Ceanothus spinosus</i> *§		X			L/H
<i>Dendromecon rigida</i>					M/H
<i>Fraxinus dipetala</i> §					M/H
<i>Garrya veatchii</i>					H
<i>Heteromeles arbutifolia</i> *§					L/H
<i>Lithocarpus densiflora</i>					H
<i>Malosma laurina</i> *§	X				L/H
<i>Pickeringia montana</i>					M/H
<i>Prunus ilicifolia</i> *§	X				L/H
<i>Quercus agrifolia</i> *					L/M
<i>Quercus berberidifolia</i>					M/H
<i>Quercus chrysolepis</i> *	X		X		M/H
<i>Quercus wislizenii</i>					M/H
<i>Rhamnus californica</i>					M/H
<i>R. ilicifolia</i>					H
<i>Rhus ovata</i> *	X		X		H
<i>Sambucus mexicana</i>					L/M
<i>Toxicodendron diversilobum</i> §					L/H
<i>Umbellularia californica</i> §					L/H
<i>Yucca whipplei</i> *	X				M/H
Coastal Sage Scrub:					
<i>Artemisia californica</i>					L/M
<i>Erodium crassifolium</i> *	X		X		M/H
<i>Eriogonum fasciculatum</i>					L/H
<i>Eriophyllum confertiflorum</i>					L/H
<i>Mimulus longiflora</i> *	X		X		L/H
<i>Ribes californicum</i>					L/M
<i>Salvia apiana</i>					L/H
<i>Salvia mellifera</i> *§	X				L/H

errors in richness values. The accuracy of shrub species identification and cataloguing was evaluated for a set of 15 FOVs by comparing *in situ* identification with simultaneous remote identification. Based on the *in situ* sampling, a total of 13 shrub species were present within this set of FOVs (species are identified in Table 1), with an average of five species in each FOV. Individual shrubs within the FOVs were correctly identified from the remote vantage point 91 % of the time (Meentemeyer & Moody 2000).

We attempted to minimize the effect of detection and identification error by repeat sampling and data aggregation from the FOV up to the level of the patch. Because patch-level data were aggregated from numerous FOVs, most shrub species that were present in the patch should have been tabulated as present. In the complete set of 15 FOVs used for validation of the field data, all 13 shrub species that were found *in situ* were also identified as present by the remote interpreter. Moreover, only those species that were actually present were included in the remote interpreter's list for each FOV. Nevertheless, there were undoubtedly some errors of commission and omission in the patch-level shrub composition data. We do not know the relative rates of these two types of error, nor whether errors were biased toward certain species. However, our field validation results suggest that patch-level species richness data are within one or two species of the correct values (Meentemeyer & Moody 2000).

Finally, the variability in patch sizes and, more importantly, the variability in the number of fields of view within each patch, was a potential source of bias in patch-level richness estimates. However, there was no relationship between shrub species richness and patch area ($r = 0.13$; $P > r = 0.09$) nor between richness and the number of FOVs sampled within patches ($r = 0.11$; $P > r = 0.32$). This suggests first that, within the range of patch sizes, richness was independent of the area over which the FOVs were distributed, and second, that richness was independent of the actual area sampled within the patches, i.e. the number of FOVs within a patch.

Environmental variables

High resolution (10 m) digital elevation models (DEMs) were derived for each watershed by digitizing and rasterizing elevation contours from 1 : 24 000 USGS topographic quadrangles. Five explanatory environmental variables were derived from the DEMs. These include elevation (m); topographic moisture index (*TMI*; m^2); potential average clear-sky wintertime surface irradiance (*PSI*; $0.4 - 0.7 \mu m$; W/m^2); slope gradient (degrees); and the standard deviation of profile curvature (*PC*; $1/l$), a measure of within-patch topographic

Table 2. List of variables and associated summary statistics.

Variable	Abbr.	Units	Min	Max	Mean
Potential Solar Insolation	PSI	W/m^2	8	266	163
Elevation	ELEV	m	92	1155	722
Slope	SLP	unitless	19	74	59
Topographic Moisture Index	TMI	m^2	0.0	6.8	1.2
Standard dev. Profile curvature	PC	m^{-1}	0.6	17.0	5.9
Rock presence	RCK	unitless	0	80	3
Total % cover	TTL	%	20	100	69
Richness	R	species	2	14	7.5
Dominance	D	rank	1	16	8.1

roughness (Table 2). Exposed rock percentage and total canopy cover, which were also used as explanatory variables, were determined in the field. Preliminary analysis suggested that it was the presence or absence, rather than the amount of exposed bedrock that was important for shrub species richness. The regression trees presented here were thus produced using presence/absence of exposed bedrock to represent rockiness.

Potential surface solar irradiance (*PSI*) was estimated for each grid cell in the DEM using the Atmospheric and Topographic Model of distributed solar radiation (Dozier & Frew 1990; Dubayah 1992). This model calculates both direct and diffuse radiation components for photosynthetically active radiation (PAR; 0.4 to $0.7 \mu m$). It has been validated for calculating surface energy budgets (Dubayah 1992) and has been applied in other vegetation models (Davis & Goetz 1990; Franklin 1998). For our purposes, relative energy inputs were calculated assuming clear-sky conditions and spatially uniform surface albedo to produce spatial fields of average, clear-sky, wintertime surface irradiance. Other chaparral studies have shown strongest correlations between vegetation patterns and winter insolation (Davis & Goetz 1990; Franklin 1998). This is probably due to increased illumination differences between north- and south-facing slopes during the winter (Franklin 1998).

The topographic moisture index (*TMI*) (Beven & Kirkby 1979) was calculated to characterize topographic effects on potential soil moisture distribution. *TMI* is the natural log of the ratio between upslope drainage area, a (m^2) and the slope gradient for a given grid cell, b (Moore et al. 1991):

$$TMI = \ln \left[\frac{a}{\tan b} \right] \quad (1)$$

The equation in this form assumes uniform soil transmissivity across the watershed. Although *TMI* is typically used as a relative index, it has units of m^2 . Locations with small upslope drainage areas (e.g. ridges) have lower *TMI* values than locations with large upslope areas (e.g. slope bottoms and drainages). Given constant

upslope area, steep slopes have lower *TMI* values than gentle slopes.

Profile curvature is calculated on a cell-by-cell basis by iteratively fitting a quadratic polynomial to a 3×3 moving window across the DEM (Moore et al. 1991). The second derivative of this surface represents the convexity or concavity of the topographic surface at each grid cell. A positive curvature value indicates that the surface is upwardly convex at the cell, and a negative curvature indicates concavity. Curvature is in units $1/l$ (per length) and represents the rate of change of slope surrounding a cell. The standard deviation of curvature (*PC*) was used in our analysis to represent the variability of profile curvature within a patch, or within-patch topographic roughness.

Analysis

Box plots and *t*-tests were used to evaluate whether presence of exposed bedrock, or the presence of particular species, were associated with shrub diversity. Correlations and linear regressions were used to identify relationships between the explanatory and dependent variables. However, relationships between diversity and environmental factors may be non-monotonic or involve complex interactions. As an alternative to linear models, regression tree models are useful for capturing non-linear relationships and exposing interactions among predictors (Chambers & Hastie 1992).

Regression trees are developed by recursively partitioning a dependent variable into increasingly homogeneous subsets by splitting the data set on critical thresholds in a set of categorical or continuous explanatory variables. At each iteration, the data set is partitioned on the explanatory variable which, upon splitting at some break point, produces the greatest reduction in the error sum of squares for the dependent variable. Tree-based models are graphically structured from the top node (*root*), through a series of binary splits on the explanatory variables (*branches*), to an end node (*leaf*) (e.g. Fig. 4). The estimate for all observations that follow the same path from the root to a given leaf is the mean value of the dependent variable for that set of observations (Chambers & Hastie 1992).

In our analysis, tree sizes were determined using an iterative cross-validation procedure that identifies an optimal tree size beyond which validation performance drops as additional branches are produced in response to nuances in the development data, but fail to account for variance in the test data. The point at which this occurs suggests a conservative number of terminal nodes for developing a tree from the entire data set (Chambers & Hastie 1992; Davis et al. 1990). Regression trees for richness and dominance were restricted to have no more

than five levels beyond the root node, and no greater than 16 end nodes.

Results

There were no significant differences in shrub richness or dominance either between the two watersheds, or by basic geologic substrate type (i.e. sandstones vs. shales) (Table 3). When exposed bedrock was present, however, richness was significantly higher than when bedrock was absent ($t = 3.87$; $P > t = 0.00$) (Table 3). Dominance appeared to be lower when bedrock was present, although this difference was of marginal significance ($t = 1.90$; $P > t = 0.06$) (Table 3).

Correlations between the explanatory variables and shrub species richness (Table 4) suggest that richness decreased with topographic moisture index, and increased with slope, elevation, total canopy cover, and local topographic roughness. Dominance increased with total canopy cover and potential solar insolation, and decreased with elevation and topographic roughness.

Multiple regression models of shrub richness and dominance based on the environmental variables exhibit poor explanatory power, although the regression coefficients, which indicate the marginal influence of each independent variable on richness or dominance, are all significant (Table 5). The signs of the coefficients correspond to the signs of the individual correlations in Table 4. Correlations between actual and predicted values of richness and dominance are 0.46 and 0.56, respectively. The regression tree structures for richness and dominance (Figs. 3 and 5) correspond with the coefficients from the correlation and multiple regression results (Table 4 and Table 5). However, the tree models provide a much greater strength of fit than the multiple regression models. Correlations between actual and tree-predicted values of richness and dominance are 0.68 and 0.76, respectively.

Changes in shrub richness along axes of environmental characteristics are illustrated in a four-variable partition plot (Fig. 4). The partitions for each variable in Fig. 4 correspond to the split values in the associated regression tree (Fig. 3). Richness increases on the higher side of each elevation partition (from left to right), on the lower side of each *TMI* partition (top to bottom), on the rocky side of each rock partition (upper left to lower right), and on the steeper side of each slope partition (from lower left to upper right). That is, shrub richness was greatest at high, dry, steep, rocky sites (Figs. 3 and 4).

The initial split on *TMI* (at 1.2) generally distinguishes lower from upper hill slopes in this environment, and indicates that richness was greater on the drier upper slopes. The *TMI* split at 3.7 separates ephemeral

drainages from hill slopes, and the split at 0.66 distinguishes dry ridges, where richness was slightly lower than on the upslope positions below the ridges.

The direction of the effect of each variable on richness is the same at all levels of the tree (Fig. 3). For example, higher richness was associated with higher elevation regardless of whether the site had a high or low topographic moisture index. The only exception to this directional consistency was for *TMI* at the end of the tree (indicated by an asterisk in Figs. 3 and 4). This branch represents sites with *TMI* < 1.2; elevation > 531 m; presence of exposed rock; and slope > 66°. These sites had a high average shrub species richness (10.5). This set of sites was then split into two groups at a *TMI* value of 0.66. Sites

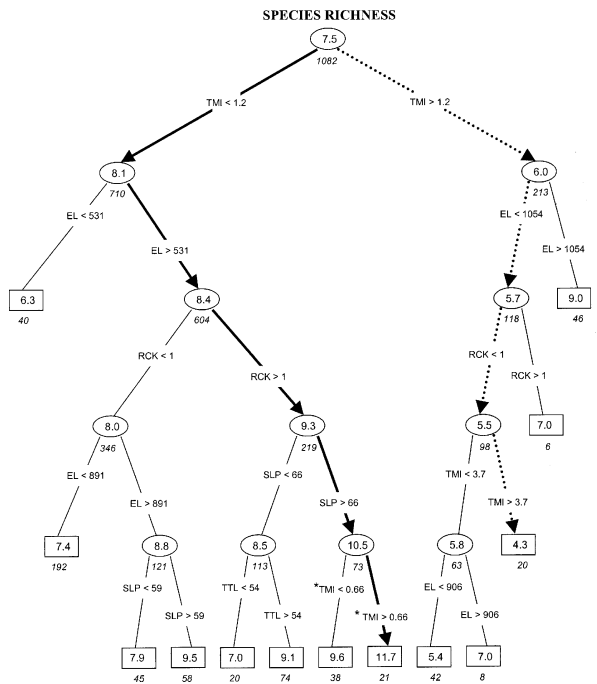


Fig. 3. Regression tree structure for shrub species richness. Ellipses and rectangles represent non-terminal and terminal nodes, respectively. Within each oval or rectangle is the estimate (mean richness value) of all samples that flow through the tree to that particular node. The ellipse at the root (top) node contains the overall average richness. The values beneath each ellipse or rectangle are the root-mean-squared errors associated with using the mean as the estimate for all samples that flow through that node. Values along the inter-node connections represent critical thresholds of given variables which provide the basis for the previous split. The variable abbreviations are: *TMI* = Topographic Moisture Index, *EL* = Elevation, *RCK* = Rock, *SLP* = Slope. The solid arrow represents the pathway through the tree for greatest richness (*TMI* < 1.2; *EL* > 531 m; *RCK* present; *SLP* > 66°; *TMI* > 0.66). The dotted arrow represents the pathway through the tree for lowest richness (*TMI* > 1.2; *EL* < 1054 m; *RCK* absent; *TMI* > 3.7).

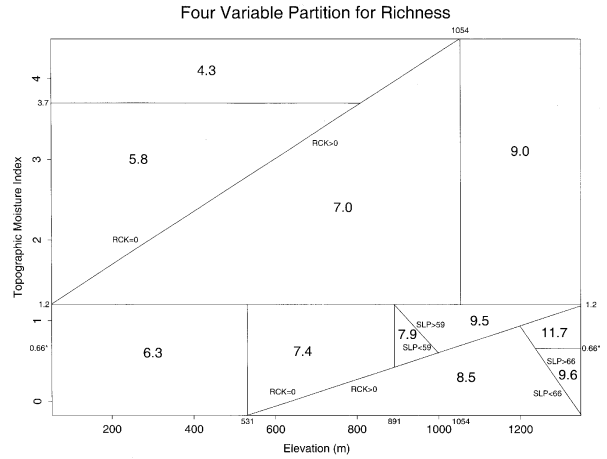


Fig. 4. Four-variable partition plot for the Richness regression tree. The variable abbreviations are: *RCK* = Rock (present or absent); *SLP* = Slope. Each partition on the plot represents a split threshold on the regression tree in Fig. 3. The large numbers in each region represent the predicted values from the tree. For example, a vegetation patch at an elevation above 891 m, with a *TMI* below 1.2, with no exposed rock, and a slope gradient below 59° is predicted to have a richness value of 7.9.

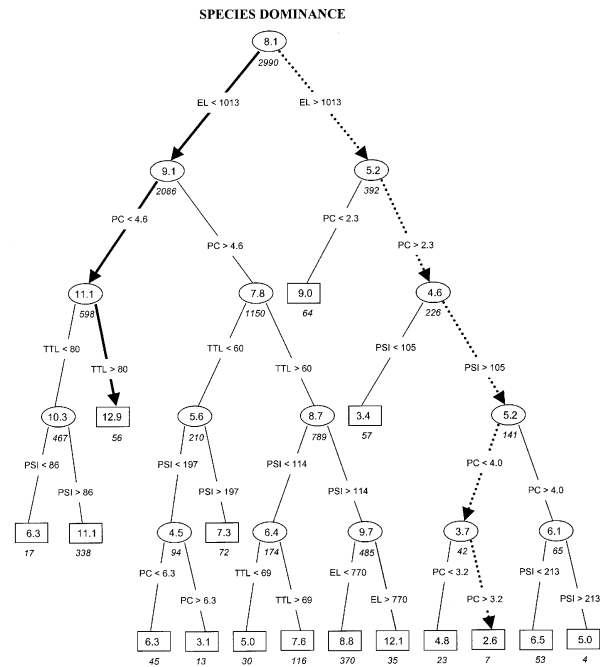


Fig. 5. Regression tree for Dominance. See caption for Fig. 3. The variable abbreviations are: *EL* = Elevation; *PC* = Standard Deviation of Profile Curvature; *TTL* = Total Percentage Shrub Cover; *PSI* = Potential Solar Insolation. The solid arrow represents the pathway through the tree for greatest dominance (*EL* > 1013 m; *PC* < 4.6; *TTL* > 80%). The dotted arrow represents the pathway through the tree for lowest dominance (*EL* > 1013 m; *PC* > 2.3; *PSI* > 105; *PC* < 4.0; *PC* > 3.2).

Table 5. Linear regression summaries for richness and dominance. Richness model $R^2_{adj} = 0.21$. Dominance Model $R^2_{adj} = 0.31$. ELEV = Elevation; PC = Standard Deviation of Profile Curvature; PSI = Potential Solar Insolation; TMI = Topographic Moisture Index; TTL = Total Canopy Cover.

	Coefficient	Standard error	<i>t</i> -value	$P > t $
Richness model:				
β_0	7.78	1.44	5.39	0.00
ELEV	0.001	0.0003	3.213	0.002
TMI	-0.394	0.162	-2.434	0.02
TTL	-0.036	0.014	-2.573	0.01
Dominance model:				
β_0	4.54	2.2741	1.996	0.048
TTL	0.095	0.022	4.388	0.00
ELEV	-0.002	0.0004	-4.055	0.00
PC	-0.217	0.088	-2.457	0.015
PSI	0.013	0.003	3.742	0.00

One mechanism underlying the observed patterns may be reduced competitive dominance by species such as *Ceanothus megacarpus* and *C. spinosus* on especially xeric or rocky sites. Several other chaparral studies have illustrated that, under closed canopy conditions, light limitation excludes most coastal sage scrub and herbaceous species from the subcanopy environment (McPherson & Muller 1967; Swank & Oechel 1991). These species types, thus, cannot contribute to local richness. However, on xeric sites, where moisture limitation prohibits canopy closure by dominants such as *C. megacarpus*, the increased light in canopy openings enables establishment by coastal sage scrub species whose adaptations for drought tolerance allow survival in dry conditions (Kirkpatrick & Hutchinson 1980; Steward & Webber 1981; Schlesinger et al. 1982; Keeley 1986).

If competitive dominance is an important factor governing shrub species richness in this environment, then it is most likely related to the dominance status of *C. megacarpus*, the most typical dominant in our study watersheds. We found that dominance increased with PAR, and then decreased at locations with the highest PAR values (over 213 W/m²), which correspond to exposed ridges that are probably also moisture limited (Fig. 5). The increase in dominance with PAR may relate to the importance of abundant light for supporting *C. megacarpus*, which frequently grows in nearly monospecific, closed-canopy stands on highly illuminated slopes in the Santa Ynez Range (Mahall & Schlesinger 1982; Schlesinger et al. 1982). The most xeric sites, however, are probably too dry for *C. megacarpus* to dominate and are thus likely to permit colonization by coastal sage scrub species (Steward & Webber 1981).

In addition to reduced competitive dominance, the reduction in total cover under resource limited conditions may result in a more spatially heterogeneous habitat mosaic with respect to PAR, soil moisture, leaf litter,

and soil nutrients. The resulting microhabitat heterogeneity may, in turn, facilitate the recruitment of a more diverse assemblage of species with variable resource requirements and stress tolerances (Grime 1979). This corresponds to the suggestion by Shmida & Whittaker (1981) that microsites differ in ways that give different species different relative advantages. In the case of this study, coastal sage scrub species are able to take advantage of abundant light in the canopy openings on particularly xeric sites.

Greater shrub diversity may also occur as a result of species overlap at upper elevations where numerous species emerge, but few species that are common at lower elevations drop out. The most notable absences at high elevations are *C. megacarpus* and *C. spinosus*, which often dominate and are indicators of low diversity at lower elevations (Table 1). These changes in community composition at high elevations may result from factors such as lower winter temperatures, which provide cold-stratification periods for regeneration of some shrubs (e.g. *C. crassifolius*) (Quick & Quick 1961), but cause leaf damage and mortality in others (e.g. *Malosma laurina*) (Boorse et al. 1998).

The absence of *C. megacarpus* and *C. spinosus* at upper elevations may also relate to the reduced fog regime or to historical fire and subsequent recruitment patterns. At higher elevations in the Santa Ynez, *C. crassifolius*, *C. oliganthus* and shrub forms of *Quercus* spp. emerge in closed canopies, possibly outcompeting *C. megacarpus* and *C. spinosus* for light (Schlesinger et al. 1982; Keeley 1992). *C. crassifolius* and *C. oliganthus* do not typically dominate at upper elevations on the south flank of the Santa Ynez. Rather, *Q. chrysolepis* and/or *Q. wislizenii* are the most likely dominants. However, these species are associated with higher species richness than the *Ceanothus*-dominated stands at lower elevations (Table 1).

There are alternative, although not necessarily con-

tradictory, perspectives on factors governing species diversity. For example, both Connell (1978) and Huston (1979) have proposed that diversity is a function of frequent, small-scale disturbances that create a mosaic of local habitats, each occupied by a different successional stage of community development. Others have proposed that local diversity depends on the size of the regional species pool (Grime 1979; Pärtel et al. 1996). According to this hypothesis, species in the regional pool are 'filtered' through dispersal, disturbance, and the environmental conditions at the local scale. Although these alternative mechanisms may be important for structuring patterns of species diversity in our watersheds, this study was not designed to quantify, or test the strength of these effects. Nevertheless, future work may show these to be more powerful explanations of diversity patterns, or to combine with the mechanisms that we hypothesize in critical ways.

In the work presented here, we have ignored several components of the floristic community, including vines, herbs, and grasses. It is frequently suggested that the subcanopy environment beneath dense chaparral is largely devoid of vegetation (McPherson & Muller 1967; Swank & Oechel 1991). Although not always the case, we find this to be generally true in our study area. Nevertheless, there are some species that we observed within our closed-canopy samples, but did not include because of uncertainty that we could consistently spot and identify them from remote vantage points. Most notable among these were climbing vines and shrubs such as *Marah macrocarpus*, *Clematis lasiantha*, *Lonicera subspicata*, *Toxicodendron diversiloba*, and a few others. In open locations, we often observed numerous perennial or annual species such as *Phacelia* spp., *Lotus scoparius*, *Eriogonum* spp., *Eriophyllum confertiflorum*, *Gnaphalium* spp., and several others.

By ignoring these species, we clearly under-represent richness within our sample patches. Based on our observations and the findings reported in other chaparral research (Kirkpatrick & Hutchinson 1980; Shmida & Whittaker 1981), we believe that the degree of under-representation is much greater in open sites where coastal sage scrub occurs, than in closed canopy chaparral sites. If so, the strength of the relationships found in our analysis would increase if all shrubs, trees, vines, and woody and herbaceous annuals and perennials were included in our estimates of richness.

We have also ignored the influence of fire (as well as other disturbances) on shrub diversity. The time since fire in our sample watersheds is sufficient so that annuals that only occur in the first few years after fire are no longer present, and so that a fully mature chaparral canopy structure has evolved. However, fire has not been absent for long enough to permit major community

changes such as diminishing populations of refractory seeders (e.g. *Ceanothus* spp.) in the long-term absence of fire. Nevertheless, spatial patterns of fire and fire characteristics may be important in structuring patterns in shrub community composition. For example, Odion & Davis (2000) found that spatial variability in the physical and chemical properties of the chaparral canopy creates variability in the heat and type of combustion that occurs during fire. These patterns in fire characteristics in turn influence seed-bank survival and resprout success. Such processes may have played a significant role in producing the patterns in species distribution and species diversity observed in our study area.

Much research on chaparral and coastal sage scrub has focused on seed germination requirements (Keeley 1991); dispersal mechanisms (Bullock 1978); species interactions (McPherson & Muller 1967; Davis 1989), resource use (Miller 1981; Mahall & Schlesinger 1982); drought adaptations (Ehleringer & Comstock 1989; Davis et al. 1999); and post-disturbance recruitment patterns (Hanes 1971; Zedler et al. 1983; Malanson & O'Leary 1985; Keeley 1987; Davis et al. 1989; O'Leary 1990; Odion & Davis 2000). These factors are of critical importance for driving spatio-temporal patterns of species distributions and, hence, patterns of species diversity. They operate in combination with the competition and resource driven patterns that we suggest are at play in the results presented here. Research that synthesizes factors such as life-history syndromes, physiological constraints, species interactions and disturbance patterns, with empirical results such as those presented here can provide further insight into the spatio-temporal patterns of species diversity in chaparral and other communities.

Acknowledgements. We gratefully acknowledge the logistic and field support of Don Johnson, Sheila Johnson and Carl Moody. Our work benefited from input by Larry Band, Mark Borchert, Janet Franklin, and Joel Michaelsen. Valuable comments on the manuscript were provided by Rebecca Vidra, Peter White, and three anonymous reviewers. This research was partially supported by a grant from the National Aeronautics and Space Administration.

References

- Bailey, H.P. 1966. *Weather of Southern California*. University of California Press, Berkeley, CA.
- Bauer, H.L. 1936. Moisture relations in the chaparral of the Santa Monica Mountains, California. *Ecol. Monogr.* 6: 409-454.
- Beven, K.J. & Kirkby, M.J. 1979. A physically based, variable contributing area model of basin hydrology. *Hydrol. Sci. Bull.* 24: 43-69.
- Boorse, G.C., Ewers, F.W. & Davis, S.D. 1998. Response of chaparral shrubs to below-freezing temperatures: Acclimation, ecotypes, seedlings vs. adults. *Am. J. Bot.* 85: 1224-1230.
- Braakhekke, W.G. & Hooftman, D.A.P. 1999. The resource balance hypothesis of plant species diversity in grassland. *J. Veg. Sci.* 10: 187-200.
- Bullock, S.H. 1978. Plant abundance and distribution in relation to types of seed dispersal in chaparral. *Madrono* 25: 104-105.
- Chambers, J.M. & Hastie, T.J. 1992. *Statistical models in S*. Wadsworth & Brooks/Cole, Pacific Grove, CA.
- Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1301-1310.
- Davis, F.W. & Goetz, S. 1990. Modeling vegetation pattern using digital terrain data. *Landscape Ecol.* 4: 69-80.
- Davis, F.W., Borchert, M.I. & Odion, D.C. 1989. Establishment of microscale vegetation pattern in maritime chaparral after fire. *Vegetatio* 85: 53-67.
- Davis, F.W., Hickson, D.E. & Odion, D.C. 1988. Composition of maritime chaparral related to fire history and soil, Burton Mesa, Santa Barbara County, California. *Madroño* 35: 169-195.
- Davis, F.W., Michaelsen, J., Dubayah, R. & Dozier, J. 1990. *Optimal terrain stratification for integrating ground data from FIFE*. Proceedings of the American Meteorological Society, Symposium on FIFE, pp. 11-15. Boston, MA.
- Davis, S.D. 1989. Patterns in mixed chaparral stands: differential water status and seedling survival during summer drought. In: S.C. Keeley (Ed.) *The California chaparral: paradigms reexamined*. No. 34 Science Series. Natural History Museum of Los Angeles County, Los Angeles, CA.
- Davis, S.D., Ewers, F.W., Wood, J., Reeves, J.J. & Kolb, K.J. 1999. Differential susceptibility to xylem cavitation among three pairs of *Ceanothus* species in the transverse mountain ranges of southern California. *Ecoscience* 6: 180-186.
- Dibblee, T.W. 1986a. *Geologic map of the Carpinteria Quadrangle*. Thomas Dibblee, Jr. Geological Foundation, Santa Barbara, CA.
- Dibblee, T.W. 1986b. *Geologic map of the Santa Barbara Quadrangle*. Thomas Dibblee, Jr. Geological Foundation, Santa Barbara, CA.
- Dozier, J. & Frew, J. 1990. Rapid calculation of terrain parameters for radiation modeling from digital elevation data. *IEEE Trans. Geoscience Remote Sens.* 28: 963-969.
- Dubayah, R. 1992. Estimating net solar radiation using Landsat Thematic Mapper and digital elevation data. *Water Resour. Res.* 28: 2469-2484.
- Ehleringer, J.R. & Comstock, J.P. 1989. Stress tolerance and adaptive variation in leaf absorptance and leaf angle. In: Keeley, S.C. (ed.) *The California chaparral: Paradigms re-examined*. No. 34 Science Series. Natural History Museum of Los Angeles County, Los Angeles, CA.
- Franklin, J. 1998. Predicting the distributions of shrub species in California from climate and terrain-derived variables. *J. Veg. Sci.* 9: 733-748.
- Greig-Smith, P. 1983. *Quantitative plant ecology*. 3rd ed. University of California Press, Berkeley, CA.
- Grime, P.J. 1979. *Plant strategies and vegetation processes*. John Wiley & Sons, New York, NY.
- Hanes, T.L. 1971. Succession after fire in the chaparral of southern California. *Ecol. Monogr.* 41: 27-52.
- Hanes, T.L. 1977. California chaparral. In: Barbour, M.G. & Major, J. (eds.) *Terrestrial vegetation of California*, pp. 417-470. John Wiley, New York, NY.
- Harrison, S. 1997. How natural habitat patchiness affects the distribution of diversity in Californian serpentine chaparral. *Ecology* 78: 1898-1906.
- Huston, M. 1979. A general hypothesis of species diversity. *Am. Nat.* 113: 81-101.
- Keeley, J.E. 1986. Resilience of Mediterranean shrub communities to fire. In: Dell, B., Hopkins, A.J.M. & Lamont, B.B. (eds.) *Resilience in mediterranean-type ecosystems*, pp. 95-112. Junk, Dordrecht.
- Keeley, J.E. 1987. Role of fire in seed germination of woody taxa in California chaparral. *Ecology* 68: 434-443.
- Keeley, J.E. 1991. Seed germination and life history syndromes in the California chaparral. *Bot. Rev.* 57: 81-116.
- Keeley, J.E. 1992. Demographic structure of California chaparral in the long-term absence of fire. *J. Veg. Sci.* 3: 79-90.
- Kirkpatrick, J.B. & Hutchinson, C.F. 1980. The environmental relationships of Californian coastal sage scrub and some of its component communities and species. *J. Biogeogr.* 7: 23-38.
- Mahall, B.E. & Schlesinger, W.H. 1982. Effects of irradiance on growth, photosynthesis, and water use efficiency of seedlings in the chaparral shrub *Ceanothus megacarpus*. *Oecologia (Berl.)* 60: 267-270.
- Malanson, G.P. & O'Leary, J.F. 1985. Effects of fire and habitat on post-fire regeneration in Mediterranean-type ecosystems: *Ceanothus spinosus* chaparral and Californian coastal sage scrub. *Oecol. Plant.* 6: 169-181.
- Margules, C.R., Nicholls, A.O. & Austin, M.P. 1988. Diversity of *Eucalyptus* species predicted by a multivariable environmental gradient. *Oecologia (Berl.)* 71: 229-232.
- McPherson, J.K. & Muller, C.H. 1967. Light competition between *Ceanothus* and *Salvia* shrubs. *Bull. Torr. Bot. Club* 94: 41-55.
- Meentemeyer, R.K. & Moody, A. In press. Rapid sampling of plant species composition for assessing vegetation patterns in rugged terrain. *Landscape Ecol.*
- Menge, B.A. & Sutherland, J.P. 1976. Species diversity gradients: Synthesis of the roles of predation, competition, and temporal heterogeneity. *Am. Nat.* 110: 351-369.
- Miller, P.C. 1981. (ed.) *Resource use by chaparral and matorral: A comparison of vegetation function in two mediterranean-type ecosystems*. Springer, Berlin.

- Miller, P.C. & Poole, D.K. 1979. Patterns of water use by shrubs in southern California. *For. Sci.* 25: 84-98.
- Mooney, H.A. & Harrison, A.T. 1972. The vegetational gradient on the lower slopes of the Sierra San Pedro Martir in northwest Baja California. *Madroño* 21: 439-445.
- Moore, I.D., Grayson, R.B. & Ladson, A.R. 1991. Digital terrain modelling: A review of hydrological, geomorphological, and biological applications. *Hydrol. Proc.* 5: 3-30.
- Ng, E. & Miller, P.C. 1980. Soil moisture relations in the southern California chaparral. *Ecology* 61: 98-107.
- Odion, D.C. & Davis, F.W. 2000. Fire, soil heating, and the formation of vegetation patterns in chaparral. *Ecol. Monogr.* 70: 149-169.
- O'Leary, J.F. 1990. Post-fire patterns in two subassociations of Californian coastal sage scrub. *J. Veg. Sci.* 1: 173-180.
- Page, B.M., Marks, J.G. & Walker, G.W. 1955. Stratigraphy and structure of the mountains northeast of Santa Barbara, California. *Bull. Am. Assoc. Petrol. Geol.* 35: 1727-1780.
- Pärtel, M., Zobel, M., Zobel, K. & van der Maarel, E. 1996. The species pool and its relation to species richness: Evidence from Estonian plant communities. *Oikos* 75: 111-117.
- Pielou, E.C. 1975. *Ecological diversity*. John Wiley & Sons, New York, NY.
- Quick, C.R. & Quick, A.S. 1961. Germination of *Ceanothus* seeds. *Madroño* 3: 135-140.
- Rosenzweig, M. 1971. Paradox of enrichment: Destabilization of exploitation ecosystems in ecological time. *Science* 171: 385-387.
- Schlesinger, W.H., Gray, J.T., Gill, D.S. & Mahall, B.E. 1982. *Ceanothus megacarpus* chaparral: A synthesis of ecosystem processes during development and annual growth. *Bot. Rev.* 48: 71-117.
- Shmida, A. & Whittaker, R.H. 1981. Pattern and biological microsite effects in two shrub communities, southern California. *Ecology* 62: 234-251.
- Shreve, F. 1927. The vegetation of a coastal mountain range. *Ecology* 8: 27-44.
- Smith, C.F. 1998. *A Flora of the Santa Barbara Region, California*. 2nd ed. Santa Barbara Botanic Garden & Capra Press, Santa Barbara, CA.
- Steward, D. & Webber, P.J. 1981. The plant communities and their environments. in: Miller, P.C. (ed.) *Resource use by matorral and chaparral: A comparison of vegetation function in two mediterranean type ecosystems*, pp. 43-68. Springer-Verlag, New York, NY.
- Stone, L. & Roberts, A. 1991. Conditions for a species to gain advantage from the presence of competitors. *Ecology* 72: 1964-1972.
- Swank, S.E. & Oechel, W.C. 1991. Interactions among the effects of herbivory, competition and resource limitation on chaparral herbs. *Ecology* 72: 104-115.
- Thomas, C.M. & Davis, S.D. 1989. Recovery patterns of tree chaparral shrub species after wildfire. *Oecologia (Berl.)* 80: 309-320.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, NJ.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75: 2-16.
- Vilà, M. & Sardans, J. 1999. Plant competition in Mediterranean-type vegetation. *J. Veg. Sci.* 10: 281-294.
- Westman, W.E. 1981a. Factors influencing the distribution of species of Californian coastal sage scrub. *Ecology* 62: 439-455.
- Westman, W.E. 1981b. Diversity relations and succession in Californian coastal sage scrub. *Ecology* 62: 170-184.
- Zedler, P.H., Gautier, C.R. & McMaster, G.S. 1983. Vegetation change in response to extreme events: The effect of a short interval between fires in California chaparral and coastal scrub. *Ecology* 64: 809-818.

Received 23 June 1999;

Revision received 12 June 2000;

Accepted 23 June 2000.

Coordinating Editor: P.S. White.