



## Landscape-scale patterns of shrub-species abundance in California chaparral

*The role of topographically mediated resource gradients*

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**Key words:** Digital terrain model, Environmental gradient, Predictive mapping, Resource availability, RHESSys, Vegetation modeling

### Abstract

We examine the degree to which landscape-scale spatial patterns of shrub-species abundance in California chaparral reflect topographically mediated environmental conditions, and evaluate whether these patterns correspond to known ecophysiological plant processes. Regression tree models are developed to predict spatial patterns in the abundance of 12 chaparral shrub and tree species in three watersheds of the Santa Ynez Mountains, California. The species response models are driven by five variables: average annual soil moisture, seasonal variability in soil moisture, average annual photosynthetically active radiation, maximum air temperature over the dry season (May–October), and substrate rockiness. The energy and moisture variables are derived by integrating high resolution (10 m) digital terrain data and daily climate observations with a process-based hydro-ecological model (RHESSys). Field-sampled data on species abundance are spatially integrated with the distributed environmental variables for developing and evaluating the species response models.

The species considered are differentially distributed along topographically-mediated environmental gradients in ways that are consistent with known ecophysiological processes. Spatial patterns in shrub abundance are most strongly associated with annual soil moisture and solar radiation. Substrate rockiness is also closely associated with the establishment of certain species, such as *Adenostoma fasciculatum* and *Arctostaphylos glauca*. In general, species that depend on fire for seedling recruitment (e.g., *Ceanothus megacarpus*) occur at high abundance in xeric environments, whereas species that do not depend on fire (e.g., *Heteromeles arbutifolia*) occur at higher abundance in mesic environments. Model performance varies between species and is related to life history strategies for regeneration. The scale of our analysis may be less effective at capturing the processes that underlie the establishment of species that do not depend on fire for recruitment. Analysis of predication errors in relation to environmental conditions and the abundance of potentially competing species suggest factors not explicitly considered in the species response models.

### Introduction

Comparative and experimental studies on plant resource use (Miller 1981), drought tolerance (Jarbeau et al. 1995; Davis et al. 1999) and seedling establishment (Frazer and Davis 1988; Keeley 1992) have provided much insight into vegetation-environment relationships in chaparral ecosystems. These processes are thought to be of critical importance for driving

spatial and temporal patterns of plant community development (Zedler 1995; Keeley 1998). However, most ecophysiological studies on chaparral have either employed aspatial experimental designs or have been limited to few observations. As a result, little is known about the extent to which ecophysiological processes are expressed in landscape-scale spatial patterns of shrub-species abundance in chaparral. Most studies have either examined chaparral species distributions at

broad scales using climate variables (Westman 1991; Franklin 1998), focused on coastal sage scrub (Westman 1981), or described species distribution in relation to indirect environmental factors, such as aspect and elevation, at widely dispersed plots (Shreve 1927; Steward and Webber 1981).

We hypothesize that landscape-scale spatial patterns of shrub-species abundance reflect topographically mediated environmental conditions in ways that are consistent with ecophysiological processes that influence seedling recruitment and shrub function. In this study, models for predicting spatial patterns in the abundance of individual species are based on spatially distributed fields of soil moisture, solar radiation, air temperature, and substrate rockiness. The energy and moisture variables are derived by integrating high resolution (10 m) digital terrain data and daily climate observations with a process-based hydro-ecological model (RHESSys; Band et al. 1993). Field samples of shrub abundance are spatially integrated with these data in a geographic information system (GIS) for developing and evaluating species response models.

Static equilibrium models that are based only on abiotic environmental conditions cannot explain all variance in species abundance (Franklin et al. 1998). Biotic factors, such as interspecific competition and herbivory also impact demographic patterns. Vegetation dynamics, especially post-fire succession, affect species distributions in space and time (Malanson & O'Leary 1985). Careful examination of errors in vegetation models can help identify additional processes that must be considered for a more complete account of vegetation distribution at a point in time (Davis & Goetz 1990; Brown 1994; O'Brien 1998). We attempt to identify and isolate such factors by controlling for disturbance history, and by examining whether model residuals are related to the abundance of potentially competing species, or to edaphic conditions.

In chaparral, seed dispersal and seedling recruitment processes differ considerably between species depending on life history (Bullock 1978; Keeley 1991). Seeds of some species are dispersed by animals and require moist conditions for germination while the seeds of other species are dispersed locally by the plants themselves and require fire related cues for germination. In the field, we have observed that the distribution of species that do not depend on fire for recruitment is scattered and less coherent relative to spatial patterns of fire-dependent species. Thus, a secondary hypothesis in this study is that the distribution of species that depend on fire for recruitment are

better predicted at our scale of analysis than species that do not require fire for recruitment.

#### *Environmental factors affecting chaparral species recruitment and survival*

It is readily observed that chaparral shrub species are differentially distributed along environmental gradients (Schreve 1927; Mooney & Harrison 1972; Steward & Weber 1981). The mechanisms that underlie these distribution patterns relate primarily to physiological adaptations for the capture and utilization of water and light, the major limiting resources in chaparral (Miller 1981; Vila & Sardans 1999). Although water limitation at xeric sites can reduce productivity in mature chaparral shrubs (Thomas & Davis 1989), the impact of water limitation on shrub distribution may be most critical after fire when recently germinated seedlings with shallow roots must survive four to six months of summer water stress during their first growth year (Kummerow et al. 1985; Frazer & Davis 1988). Recent evidence suggests that the resistance of stem xylem to water stress-induced embolism is the primary mechanism underlying differences in drought tolerance between chaparral shrubs (Jarbeau et al. 1995; Davis et al. 1998, 1999). In terms of light requirements, some species are shade tolerant (e.g., photosynthesis of *Heteromeles arbutifolia* is saturated at less than one-third full sunlight) (Mooney et al. 1975) while other shrubs (e.g., *Ceanothus megacarpus*) exhibit reduced water-use efficiency under low light conditions (Mahall & Schlesinger 1982).

Freezing temperatures can also cause plant mortality (Boorse et al. 1998). *Malosma laurina*, for example, is particularly cold-sensitive, and its distribution may be partially controlled by winter temperature (Misquez 1990). However, cold tolerance is less commonly noted as a factor controlling the spatial distribution of chaparral shrubs.

There are two strategies by which chaparral shrubs regenerate after fire: vegetative sprouting from a root crown (lignotuber) and germination from refractory seeds. Some shrubs such as *C. megacarpus* cannot resprout after fire. These species are referred to as 'obligate seeders' because they require fire cues for seed germination (Keeley 1987, 1991). Obligate seeders also capitalize on the availability of light and nutrients in post-fire environments, but usually must endure xeric conditions (Keeley 1998). Other shrubs, such as *Heteromeles arbutifolia*, can resprout veg-

etatively after fire and are referred to as ‘obligate resprouters’. These species have poorer stomatal control than obligate seeders and tend to develop deep root systems to avoid drought stress (Hellmers et al. 1955; Miller & Poole 1979). Obligate resprouters do not depend on fire for seedling recruitment. Instead, seedlings are established from non-refractory seeds that germinate beneath mature canopies with mesic soils, low light, and ample leaf litter (Keeley 1991). A few species, such as *Adenostoma fasciculatum*, are referred to as ‘facultative seeders’ because they can sprout vegetatively after fire and also establish seedlings from refractory seeds stored in the soil. Unlike obligate resprouters, facultative seeders do not establish seedlings in mature communities, and therefore still depend on fire for seedling recruitment. Spatial patterns of chaparral shrub species are thus governed by the interplay between seed germination requirements, abiotic site conditions (e.g., soil moisture and light), and physiological mechanisms that control water use and drought tolerance.

## Materials and methods

### *The study area*

The Santa Ynez Mountains lie at the western edge of the east-west trending Transverse Ranges in southern California (Figure 1). The dominant vegetation in the Santa Ynez and other coastal mountain ranges in southern California is evergreen sclerophyll forest and shrubland known as chaparral. The Santa Ynez region has a typical Mediterranean-type climate, with a hot dry season from late spring to mid fall and a relatively cool rainy season from late fall through mid spring. Summer fog, common on the coastal flank of the Santa Ynez, occurs when the moist marine layer is trapped between the mountains and the prevalent summertime temperature inversion. The height of the inversion varies (Bailey 1966), but generally occurs at about 400 m (Miller et al. 1977; J. Michaelsen, personal communication). Little research exists on the contribution of summer fog to soil moisture or its impact on temperature and light regimes in chaparral (but see Oberlander 1953; Miller 1979; Campbell 1980).

The Santa Ynez is mostly composed of shales and sandstones deposited as river and marine sediments during the upper Eocene and Oligocene epochs (Page et al. 1955). The topography is highly dissected, with elevation ranging from approximately 275 m in the

foothills to 1215 m at La Cumbre Peak. The major streams drain away from the ridge with tributary streams often tracking shales that are less resistant to weathering than the sandstones (Page et al. 1955).

In this work, we examine landscape-scale variability in chaparral shrub species within three small watersheds in the Santa Ynez Mountains. Mission Canyon and Romero Canyon watersheds are located on the southern flank of the Santa Ynez. Mission Canyon (8.2 km<sup>2</sup>) includes La Cumbre Peak which is the highest point of the Santa Ynez (1215 m). The foot and upper ridge of Mission Canyon are located 6.6 and 9.4 km from the coast, respectively. Romero Canyon (7.1 km<sup>2</sup>) is located 12 km east of Mission Canyon and its foot and upper ridge are 4 and 6.5 km from the coast, respectively. The upper elevation of Romero Canyon is 1067 m. Mission Canyon last burned in 1964 and Romero Canyon in 1971. The third watershed, Devils Canyon (8.5 km<sup>2</sup>), is located on the northern flank with elevation ranging from 367 m to 1177 m. The north-facing position of Devils Canyon results in low solar illumination on many slopes for much of the year and reduced marine exposure allows greater diurnal and seasonal variability in temperature.

### *Species abundance*

Closed-canopy chaparral develops a heavy thicket of understory biomass on steep, and often loose terrain. These conditions impede field access and prevent most researchers from collecting numerous, well-distributed field samples. Moreover, most chaparral studies use small plots with inter- and intraplot variability that may be stochastic, or respond to processes operating at a finer scale than our focus. To reduce data collection costs and allow the acquisition of many well-distributed samples, we sampled species abundance at a hierarchy of spatial units using a high-powered telescope from remote vantage points. The effectiveness of the methods for assessing landscape-scale patterns of shrub composition is fully described in Meentemeyer & Moody (2000).

The sampling strategy was organized around a spatial unit referred to as a *patch*, a stand of vegetation composed of homogeneous shrub composition and constant total cover. Candidate patches, defined in the field, were distributed in order to represent the range of elevations, aspects, and slope positions within the three watersheds. Patch boundaries were delineated where transitions occurred either in composition or in the relative abundance of dominant species. The fol-

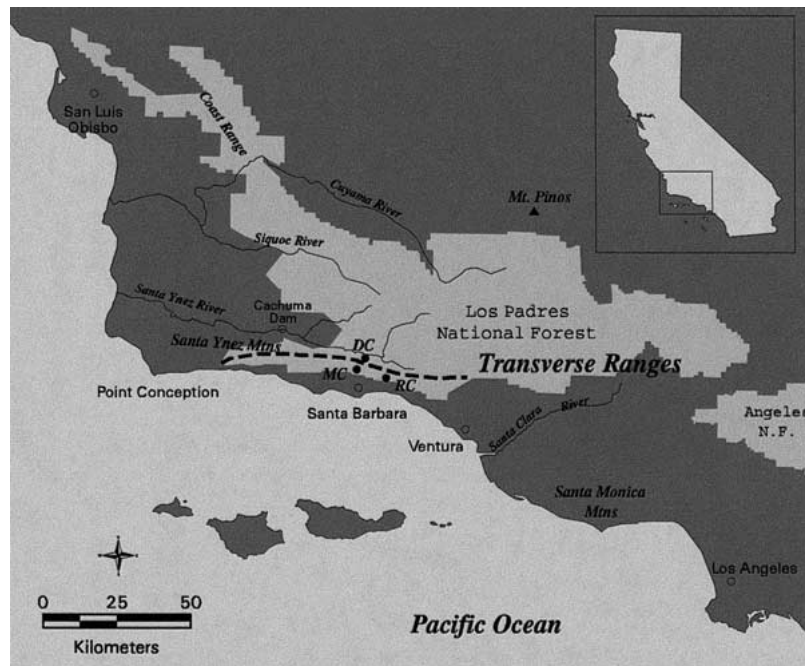


Figure 1. The study region. Mission Canyon (MC) and Romero Canyon (RC) watersheds are located on the southern flank of the Santa Ynez Mountains, California, and Devils Canyon (DC) is located on the northern flank. The dashed line represents the main ridge of the Santa Ynez Range. Daily climate data are compiled from Santa Barbara and Cachuma Dam base stations.

lowing criteria, although not strictly quantified, were used as guidelines to help maintain consistent patch identification. Stands where the relative canopy cover of a single species was greater than or equal to 60% were considered dominant species patches. In these cases, a patch boundary was mapped if a change in the dominant species occurred or if a transition to a mixed species composition occurred. Boundaries were also defined where the cover of any shrub or tree species changed by 20% or more. Finally, boundaries were mapped where absolute cover changed by 20% or more, regardless of species composition.

A candidate patch was only chosen for sampling if it could be mapped onto the high resolution terrain model, and if it fulfilled the following standards. First, patches were required to be within 300 m of the remote viewing location and greater than 10 m from a dirt road or trail. Second, patches had to be visible at an angle greater than  $45^\circ$  between the line of sight and the slope of the terrain. Finally, a minimum patch size of 0.25 ha was established to avoid sampling in the range of patch sizes within which species richness is related to area (Greig-Smith 1983). Analyses of Meentemeyer & Moody (2000) indicate that the internal floristic and environmental variability of patches is low and stable across the sample of patches.

Within each patch, several *sites* were randomly located from a regular array of grid points distributed at 20 m intervals. A zoom telescope ( $15\times$  to  $45\times$ ) was used to sample the cover percentage of shrub and tree species for each site from a remote viewing location. Composition for each site was determined by aggregating species composition within 3 to 4 telescope fields of view (FOV) that were clustered around the site. This process was repeated for each site within a patch. FOVs were constrained to approximately  $100\text{ m}^2$ . Locating and sizing FOVs was accomplished by navigating on a high resolution terrain model overlaid with a 20 m grid in conjunction with clinometer and compass measurements.

For each field of view, we made a list of species present and estimated the percentage cover of each species, percentage cover of exposed bedrock, and total cover. These data were aggregated from the FOV to the site level, and the site-level data were aggregated to provide shrub composition for each patch. A total of 307 patches were sampled, ranging in size from 0.25 ha to 7.5 ha (mean = 1.2 ha).

Species identification was based on leaf and bark color; shrub form and stature; leaf shape, size, and orientation; and bud, flower, and new growth characteristics. The accuracy of species identification has

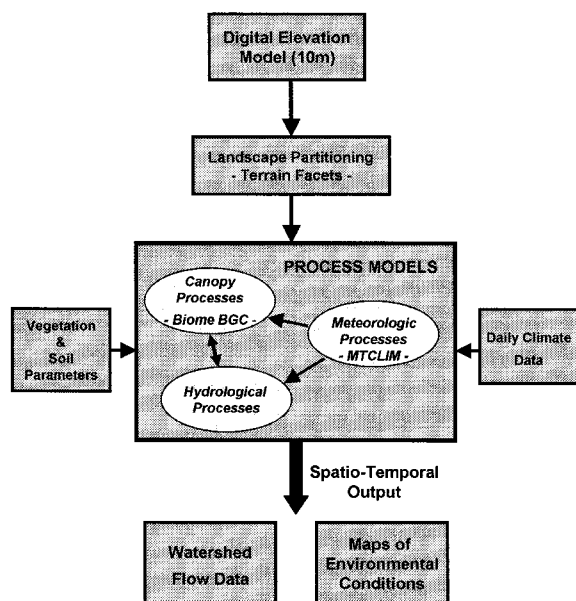


Figure 2. Overview of RHESSys, the Regional Hydro-ecological Simulation System.

been tested for a set of 15 fields of view by comparing *in situ* identification with concurrent remote identification. All shrub species that were included in the *in situ* list were also included in the remote interpreter's list. Individual plant species were correctly identified 90% of the time (Meentemeyer & Moody 2000).

Twelve species were selected for model development and analysis that

- could be identified remotely with confidence;
- were present in at least 60 patches; and
- presented the range of life history strategies in terms of seasonal water status (e.g., Miller 1981; Davis et al. 1999), rooting depth (e.g., Hellmers et al. 1955; Miller 1981), and post-fire regeneration (e.g., Keeley 1986, 1991, 1998; Malanson & O'Leary 1985).

For example, the obligate seeder, *Ceanothus megacarpus*, requires fire for seed germination and is often subjected to low minimum seasonal water potential due to shallow roots (Table 1). In contrast, the obligate resprouter, *Heteromeles arbutifolia*, does not depend on fire and experiences relatively high water potentials due to deep roots. Intermediate between these extremes, some species (e.g., *Ceanothus spinosus*) experience moderate minimum water potentials and have facultative regeneration syndromes (Table 1).

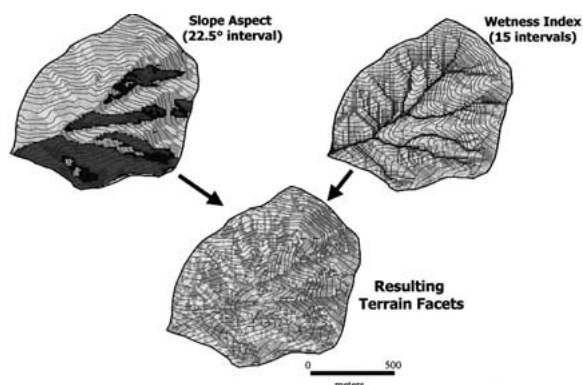


Figure 3. Derivation of terrain facet partitioning for a subcatchment in the Mission Canyon Watershed – an overlay of 15 wetness index intervals and 16 slope-aspect classes.

#### Derivation of environmental predictor variables

Climate data and high resolution (10 m) terrain data were integrated with a hydro-ecological model (RHESSys) to derive variables that are hypothesized to govern shrub distribution. RHESSys combines a set of physically-based process models with a methodology for organizing spatial data in order to compute water, carbon, and nutrient fluxes across watersheds on a daily time step (Band et al. 1993) (Figure 2).

Within RHESSys (Version 4.5), the MT-CLIM submodel (Running et al. 1987) uses digital terrain data and daily climate-station data to estimate solar radiation, minimum and maximum air temperature, and precipitation. Using these estimates, a model of plant canopy processes based on BIOME-BGC (Running & Coughlan 1988; Running & Hunt 1993) is coupled with a distributed hydrologic model, adapted from Wigmosta et al. (1994), in order to model saturated subsurface throughflow and overland flow (Tague et al. 1998; Tague 2000).

We have applied RHESSys such that all processes are computed on terrain facets composed of hydrologically similar 10 m pixels from the digital terrain data (Tague 2000). The facets were derived by overlaying a map of fifteen wetness index intervals (after Beven & Kirkby 1979) with a map of 16 slope aspect classes (Figure 3). These criteria were chosen via trial and error in order to yield a detailed landscape representation, yet allow relatively efficient computation. For Mission Canyon, this procedure reduced the number of processing units from 820 000 10 m grid cells to 36 000 facets, ranging in size from 100 m<sup>2</sup> to 9500 m<sup>2</sup>, with a mean of 1846 m<sup>2</sup>.

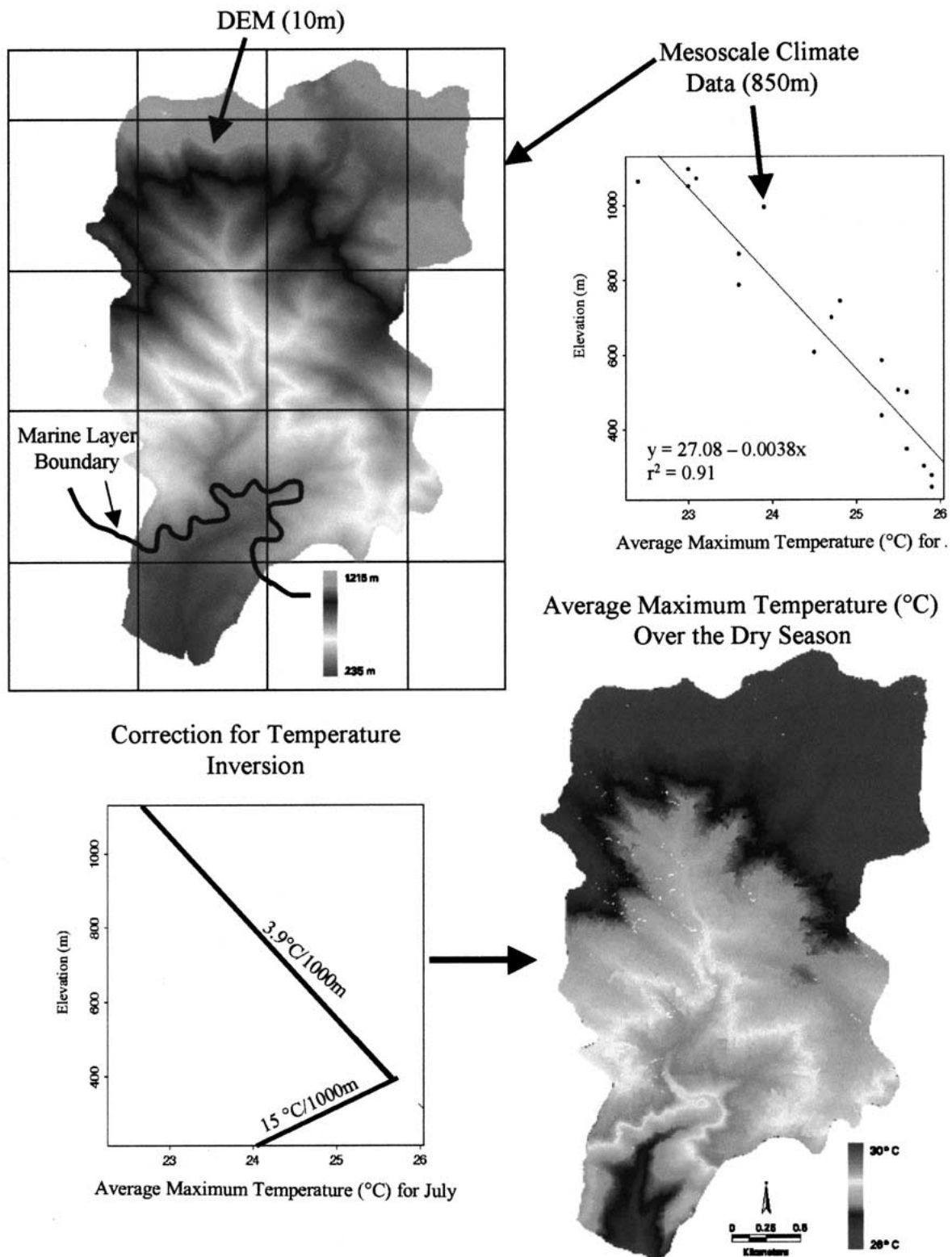


Figure 4. Overview of procedures used to derive elevation lapse rates for air temperature and precipitation.

Table 1. Life history characteristics of 12 common species in the Santa Ynez Mountains, California.

Species	Recruitment mode	Post-fire recovery mode	Dispersal mode	Rooting depth	$\psi$ (MPa)
<i>Arctostaphylos glauca</i>	Dd	Os	Autochory	Shallow	< - 6.5
<i>Ceanothus crassifolius</i>	Dd	Os	Autochory	Shallow	-6.0
<i>Ceanothus megacarpus</i>	Dd	Os	Autochory	Shallow	-8.4
<i>Adenostoma fasciculatum</i>	Dd	Fs	Autochory	Deep	-6.0
<i>Cenathus oliganthus</i>	Dd	Fs	Autochory	Deep	-4.3
<i>Ceanothus spinosus</i>	Dd	Fs	Autochory	Deep	-6.2
<i>Malosma laurina</i>	Dd	Or	Zoochory	Deep	-2.0
<i>Cercocarpus betuloides</i>	Df	Or	Anemochory	Deep	-
<i>Garrya veatchii</i>	Df	Or	Zoochory	Deep	-
<i>Heteromeles arbutifolia</i>	Df	Or	Zoochory	Deep	-4.0
<i>Quercus agrifolia</i>	Df	Or	Zoochory	Deep	-
<i>Umbellularia californica</i>	Df	Or	Zoochory	Deep	-

Species are organized by recruitment mode. These include disturbance-dependent (Dd) and disturbance-free (Df) (Keeley 1998). Post-fire recovery strategies include obligate resprouting (Or), obligate seeding (Os), and facultative seeding (Fs). Zoochory = seeds dispersed by animals; Autochory = seeds dispersed by plant itself; and Anemochory = seeds dispersed by wind (Keeley, 1991). Maximum rooting depths are based on observations of Hellmers et al. 1955 and Miller 1981. Minimum seasonal water potential ( $\psi$ ) is based on measurements by Davis et al. (1999), DeSouza et al. (1986), and Miller (1981).

RHESSys was run over a twenty-one year period (1970–1991) after initializing conditions from 1960–1970. Daily climate data from Cachuma Dam (34.58° N 119.98° W; elevation = 237 m) and Santa Barbara (34.43° N 119.83° W; elevation = 3 m) (Figure 1) were used to extrapolate daily precipitation and minimum/maximum air temperature to the partitioned terrain facets of the northern and southern flank watersheds, respectively. Lapse rates – required to estimate precipitation and air temperature – were derived from mesoscale fields (850 m resolution) of average monthly air temperature and annual precipitation (J. Michaelsen, unpublished data) (Figure 4). These mesoscale field were interpolated from climate station data using spatial coordinates, elevation, and a topographic barrier index to capture rainshadow effects. The mesoscale data were regressed against elevation (degraded to 850 m resolution) within each watershed (average  $r^2 = 0.83$ ) (Figure 4). For each variable, resulting lapse rates were averaged over the three watersheds, yielding an air temperature lapse rate of 3.9 °C/1000 m and a precipitation lapse rate of 285 mm/1000 m (Meentemeyer & Moody 2000).

Over the dry season (May–October), we modified the air temperature lapse rates for the southern flank watersheds to account for the temperature inversion that generally occurs from sea level up to elevations of approximately 300–450 m (J. Michaelsen, personal communication). Coastal air temperature data from

south of Los Angeles (Miller et al. 1977) suggest a similar inversion height; annual average maximum air temperatures rapidly increase with elevation up to 400 m at a rate of about 15 °C/1000 m and then decrease above 400 m. We implemented a temperature inversion in RHESSys with a 400 m ceiling during the dry season to account for this effect. Air temperatures are extrapolated such that maximum air temperatures below 400 m increase with elevation at a rate of 15 °C/1000 m, but then decrease with elevation at our derived rate of 3.9 °C/1000 m above 400 m (Figure 4). The precipitation lapse rate is used for all watersheds over the entire year.

RHESSys can be run by specifying vegetation (e.g., leaf area index) and soil characteristics (e.g., hydraulic conductivity) that are allowed to vary spatially. We parameterized the model using uniform soil characteristics because soils data are not available at a sufficient resolution for modeling topographically-distributed soil water in this environment. Uniform vegetation is assumed for simplification. Vegetation parameters, such as leaf conductance and rooting depth, were based on averaged species characteristics reported in ecophysiological studies of Miller (1981). The model was calibrated for a sub-catchment of Mission Canyon (shown in Figure 3) by iteratively varying saturated hydraulic conductivity and its decay with soil depth until modeled monthly transpiration rates

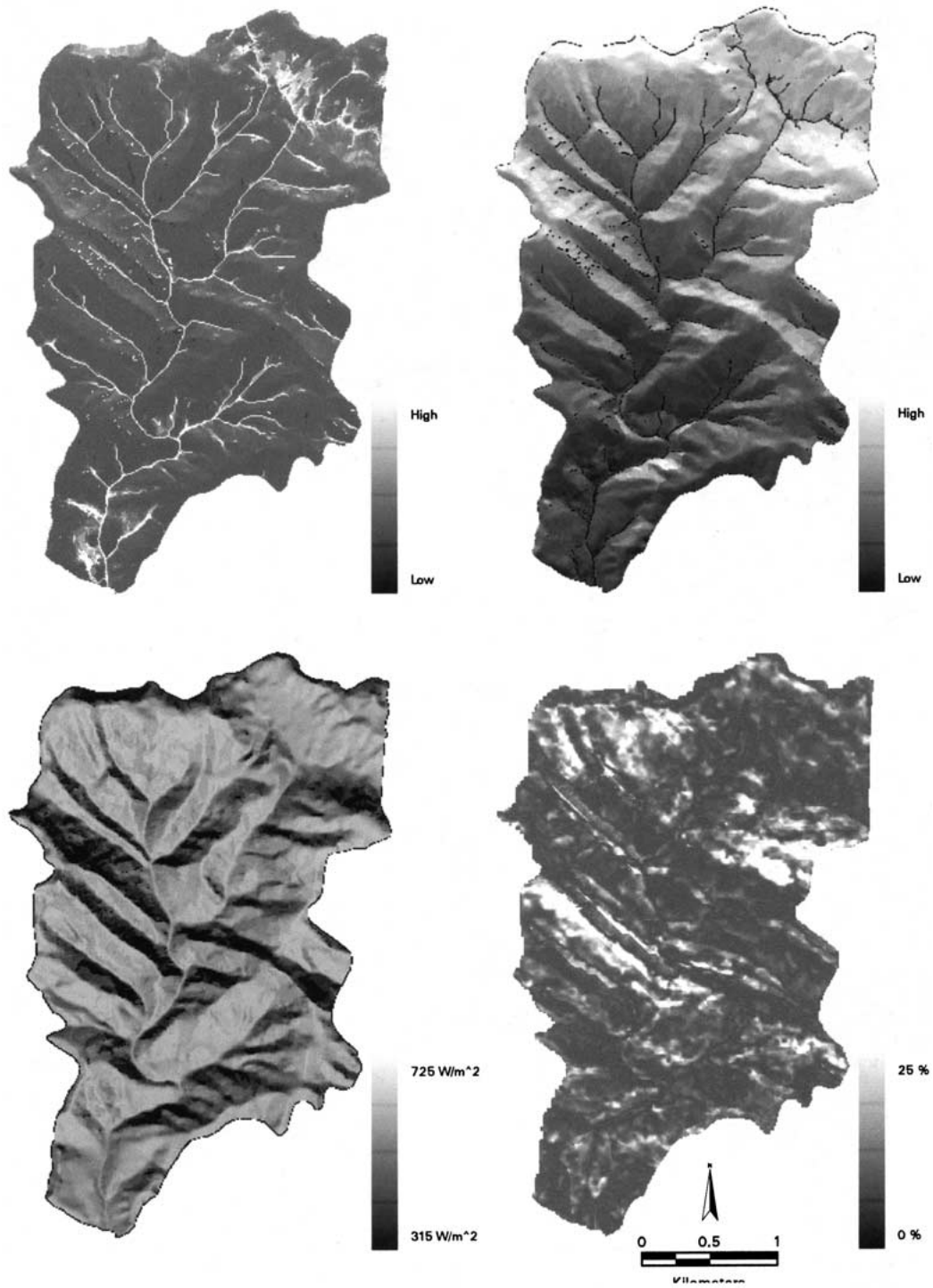


Figure 5. Environmental variables used to drive the species abundance models in the Mission Canyon watershed: (a) Average annual soil moisture availability (SMI), (b) Seasonal variability in soil moisture (SCI), (c) Average annual photosynthetically active radiation (PAR), and (d) Exposed bedrock percentage (RCK).

Table 2. Variables used to model species abundance. SMI and SVI are scaled 0 to 1 from RHESys estimates of saturation deficit. Lithologic rock types include shale (Sh), sandstone (Ss), and Quaternary deposits (Qd). The study watersheds are Mission Canyon (MC), Romero Canyon (RC), and Devils Canyon (DC).

Variable	Description	Range			
		Units	Min	Max	Mean
SMI	Average annual soil moisture	unitless	0.015	1.000	0.15
SVI	Seasonal variability in soil moisture	unitless	0.040	1.000	0.37
PAR	Average annual solar radiation	W.m <sup>2</sup>	316	715	579
TMAX	Avg. maximum daily temperature (May-Oct)	C	26.3	30.0	28.5
RCK	Exposed bedrock cover	%	0.0	41.0	2.0
LITH	Lithologic type	Sh, Ss, Qd	–	–	–
WSHED	Watershed	MC, RC, DC	–	–	–

roughly corresponded with measurements in Miller (1981).

For vegetation modeling, the daily results were aggregated on a monthly basis and averaged over the twenty-one year period to produce long-term monthly averages of energy and moisture across the watersheds. The variables selected for use in the species response models are summarized in Table 2. For each variable, data were produced by averaging 10 m cells that lie within the digitized vegetation patches that were delineated in the field.

Principal components analysis of the time series of monthly soil moisture fields (calculated in RHESys as saturation deficit) revealed that much of the spatio-temporal variation in soil moisture is captured by the first two components (91% and 8%, respectively). The first component captured variability associated with spatial patterns of soil moisture averaged over the year. The second component captured temporal variability associated with differences in average soil moisture between the wet and dry seasons. Based on this information, we selected average annual soil moisture (SMI) and the difference in soil moisture between the wettest (January) and driest months (September) (SVI) as variables to explain species distribution. SMI is scaled from zero to one (wet to dry) as an index of soil moisture availability (Figure 5a). SVI is scaled from zero to one as an index of variability in soil moisture. High SVI values typically occur on sites with sheltered slopes, toeslopes, and/or drainages at high elevations with cool air temperatures (Figure 5b). Sites with low SVI typically occur on exposed, south-facing slopes at lower elevations and exposed topographic positions with little upslope contributing area, such as ridges.

Monthly estimates of photosynthetically active radiation (PAR) were also aggregated to produce average annual estimates (Figure 5c). Monthly maximum air temperature (TMAX) was averaged over the dry season (May–October). Although minimum air temperature may also be a factor in controlling chaparral species distribution (Boorse et al. 1998), it was not included due to high collinearity with TMAX ( $r = 0.84$ ).

Twenty-two lithologic formations, mapped by Dibblee (1986a–c), were aggregated to shale, sandstone, and quaternary deposit types. We also derived a substrate rockiness variable (Rock) based on telescope estimates of exposed rock cover percentage within each vegetation sample. In order to provide spatially distributed estimates of rock cover, we developed a regression model based on two terrain variables (slope angle and solar exposure), a vegetation index derived from Landsat Thematic Mapper data, rock type (Dibblee 1986), and mapped outcrops (Dibblee 1986) and applied it across the study area (Figure 5d). Twenty-five percent of the rock cover samples ( $n = 77$ ) were held aside to validate predictive accuracy. The model explains 65% and 39% of the variability in the training data and test data, respectively. Unexplained variability was not an issue in the development of the species response models as we used the original rock cover samples. However, unexplained variability at unsampled, extrapolated areas will influence the predictive power of vegetation models.

## Analysis methods

### Relative differences between species

Boxplots and one-way analysis of variance were used to assess whether species are differentially distributed along energy and moisture gradients as measured by SMI, SVI, PAR, and TMAX. Relationships were examined using two measures of species abundance. First, we examined environmental conditions that are associated with species presence. In order to identify environmental regimes that are most suitable for establishment, relationships were also examined between environmental conditions and observations that are greater than or equal to the average cover value of each species ('commonness'). For these analyses, samples were omitted where species were absent.

### Model development

Regression tree models were used to model relationships between species abundance and environmental conditions for the 12 chaparral species (Table 1). Twenty-five percent of the observations were withheld from model development and used for model evaluation. In order to represent the range of cover values, the test data were drawn by sorting the data on percent cover and extracting every fourth sample. Predictive maps of species abundance were generated by applying the models to the spatially distributed fields of environmental variables.

Regression tree models were used as an alternative to generalized linear models (GLM) due to their ability to characterize hierarchical and nonlinear relationships and expose interactions among predictor variables (Michaelsen et al. 1994). GLMs were also developed but had approximately 30% lower model fit and 5% lower predictive accuracy and will not be discussed further. While the literature recommends comparisons between methods (e.g., Austin et al. 1995; Franklin 1998), that is not the objective of this paper.

The tree models were fit by recursively partitioning a response variable into increasingly homogeneous subsets based on critical thresholds in continuous or categorical predictor variables. The tree-based models can be graphically displayed so that a progression of binary splits on the independent variables leads to a prediction at an end node (e.g., see Figure 7). The predicted value at each end node is the mean value of all observations that flow through the tree to that node.

To avoid over-fitting the tree models, the training dataset was repeatedly divided into random subgroups for model testing and model development (Davis et al.

1990). The cross-validated performance increased up to a critical tree size beyond which model performance dropped as a tree 'grew' in response to peculiarities in the development data, but failed to account for variance in the test data. The critical tree size suggested the appropriate number of terminal nodes for tree development.

### Assessing model performance

Evaluation of regression tree model performance for the twelve species was based primarily on the fit between observed and predicted species cover. In order to identify under- vs. over-predictions of canopy cover, predictive accuracy was also evaluated based on the mean error (MER):

$$\text{MER} = 1/n \sum_{i=1}^N (P_i - O_i),$$

where  $n$  is the number of samples,  $P_i$  is predicted cover, and  $O_i$  is observed cover. Positive and negative MER values indicate over- and under-estimation, respectively.

We evaluated whether prediction errors ( $P_i - O_i$ ) were related to factors not directly accounted for in the vegetation models. Correlations were examined between prediction errors and the continuous environmental variables (SMI, SVI, PAR, TMAX, and Rock) in order to identify environmental conditions that were associated with over- vs. under-prediction.  $T$ -tests were used to assess whether prediction errors were associated with watershed or substrate. In order to explore biotic factors that inhibit shrub abundance, prediction errors were also examined in relation to the percent cover of potentially competing species. Tests were based only on observations where both species were present.

## Results

### Exploratory analyses

Correlations between the environmental variables are relatively weak. However, seasonal variation in soil moisture (SVI) is moderately correlated with solar radiation (PAR) ( $r = -0.44$ ) and average maximum temperature (TMAX) ( $r = -0.56$ ). Analysis of variance indicates that there are no significant differences in soil moisture availability (SMI), soil moisture variability (SVI), solar radiation, or air temperature between the two south-flank watersheds. However, air

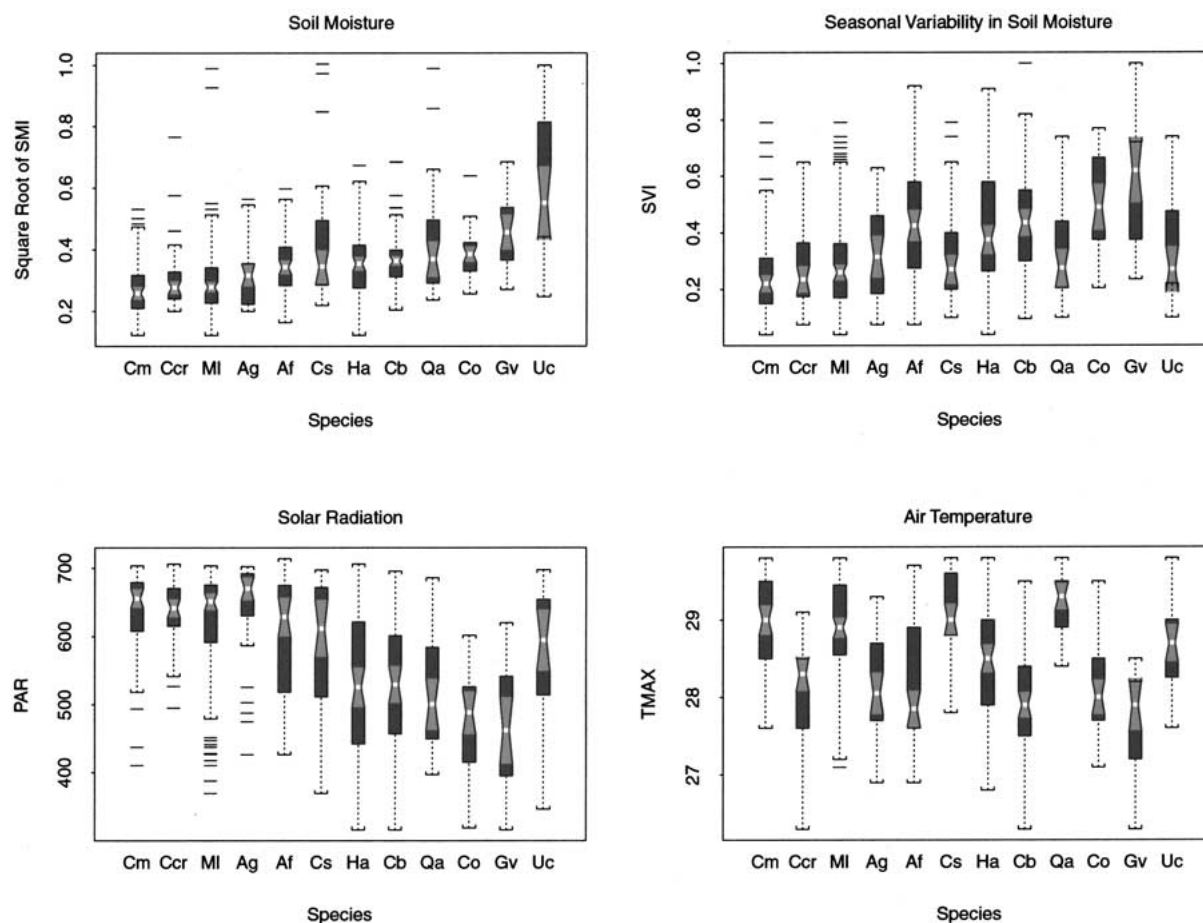


Figure 6. Environmental differences between the 12 species at optimum abundance: (a) Average annual soil moisture availability (SMI), (b) Seasonal variability in soil moisture (SVI), (c) Average annual photosynthetically active radiation (PAR), and (d) Exposed bedrock percentage (RCK). Cm = *Ceanothus megacarpus*, Ccr = *C. crassifolius*, MI = *Malosma laurina*, Ag = *Arctostaphylos glauca*, Af = *Adenostoma fasciculatum*, Cs = *Ceanothus spinosus*, Ha = *Heteromoles arbutifolia*, Cb = *Cercocarpus betuloides*, Qa = *Quercus agrifolia*, Gv = *Garrya veatchii*, Uc = *Umbellularia californica*.

temperature and solar radiation are significantly lower on the north side of the range ( $P < 0.05$ ). This is due to the predominance of sheltered, north-facing slopes on the north side.

#### Environmental differences between species

Analysis of variance indicates that the species considered are differentially distributed within the study area according to environmental conditions. For example, *Ceanothus megacarpus* and *C. crassifolius* are associated with lower soil moisture than *Umbellularia californica*, *Garrya veatchii*, and *Quercus agrifolia* (Figure 6a). Similar patterns also occur along the gradient of variability in soil moisture, with the exception of *C. spinosus*, *Q. agrifolia* and *U. californica* (Figure 6b). Most species associated with dry sites are

also associated with high solar radiation (Figure 6d). However, species that are associated with low air temperatures are not necessarily associated with mesic conditions. For example, the distributions of *Ceanothus crassifolius* and *A. fasciculatum* correspond to xeric sites with high solar radiation, but relatively low air temperatures. Environmental differences between species are more significant based on observations where species are common than where they are merely present (Table 3). The environmental variability and the median environmental condition (correspond to boxplot notches in Figure 6) associated with each species is shown in Table 4.

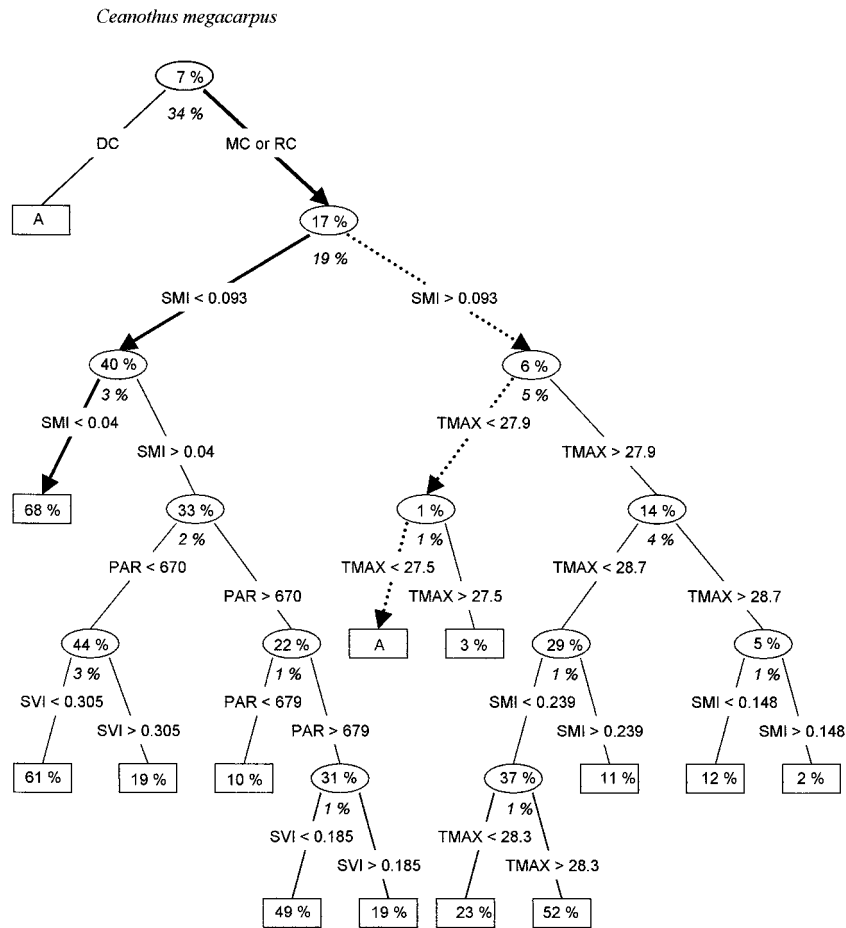


Figure 7. Regression tree model for *Ceanothus megacarpus* canopy cover. Ovals and squares represent non-terminal and terminal nodes, respectively. The values inside the ovals and squares are the predictions (means) of species percent cover. The values beneath the predictions indicate the proportion of the total deviance that each split explains. Critical thresholds are displayed between the node connections, splits that provide the basis for calculating predictions. The variable abbreviations are: SMI = Average annual soil moisture, SVI = Seasonal variability in soil moisture, PAR = Average annual photosynthetically active radiation, TMAX = Average maximum temperature over the dry season (May–October), and WSHEd = watershed location. The dark solid arrows indicate the combination of environmental conditions associated with maximum canopy cover. The intermittent arrow indicates the combination of environmental conditions associated with lowest abundance or absence (A).

*Species response models*

*Species-environment relationships*

When evaluated with the data used to train the regression tree models, correlations between the observed and predicted values range from 0.68 to 0.88 (mean = 0.79) (Table 5). Predictive accuracy is lower when evaluated with the test data. For the test data, correlations from the regression trees range from 0.42 to 0.76 (mean = 0.58). The tree models produce over- and under-prediction ranging from -0.4 to 4.1 (Table 5).

Solar radiation, on average, explains the most variance (14.1%) in species abundance, followed by soil moisture (12.7%), air temperature (12.3%), watershed

(10.4%), rock cover (6.6%), and soil moisture variability (5.6%) (Table 6). Most of the inter-watershed variability in abundance exists between the north and south flanks of the range. The lithology variable, which was rarely important after accounting for rock cover, was not used in the final models. Along the soil moisture gradient (SMI), 7 species increase in abundance with increasing soil moisture and 5 species decrease (Table 6). Species with a positive response to soil moisture generally show a negative response to solar radiation (PAR), and vice versa. However, *Ceanothus spinosus* tends to increase abundance at sites with increasing solar radiation and the response

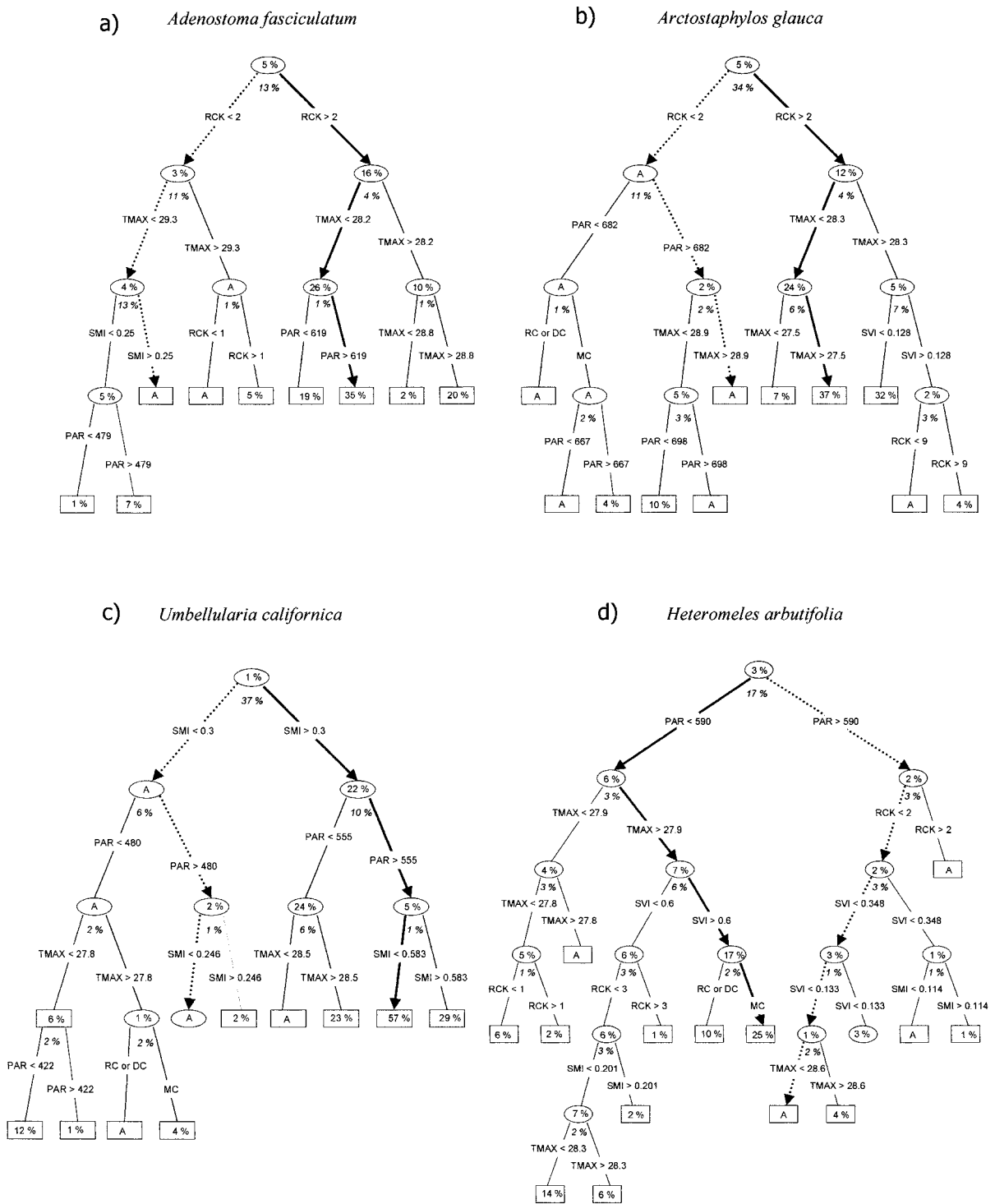


Figure 8. Regression tree models for (a) *Adenostoma fasciculatum*, (b) *Arctostaphylos glauca*, (c) *Umbellularia californica*, and (d) *Heteromeles arbutifolia*. See caption of Figure 7 for explanation of this figure.

Table 3. Analysis of variance results. SMI = Average annual soil moisture; SVI = Seasonal variability in soil moisture; PAR = Average annual photosynthetically active radiation; TMAX = Average maximum temperature over the dry season (May–October).

Variable	Source	Present		Common	
		MS	F	MS	F
SMI	Between	0.1242	3.12	0.2283	12.35
	Within	0.0398		0.0184	
SVI	Between	0.1383	3.45	0.2586	6.82
	Within	0.0401		0.0379	
PAR	Between	64306.29	6.41	119445.4	11.83
	Within	10031.23		10094.5	
TMAX	Between	30.16	51.77	45.15	85.32
	Within	0.58		0.53	

of *Umbellularia californica* to solar radiation depends on soil moisture availability (Figure 8c). Of the five species that increase abundance at dry sites, only *Ceanothus megacarpus* and *Malosma laurina* exhibit a positive response to air temperature (TMAX). Along the rock cover gradient, four species consistently decrease abundance with increasing rock (e.g., Figure 8d) and two species show a clear positive response to rockiness (Table 6).

Model results are presented in greater detail for *Ceanothus megacarpus*, *Adenostoma fasciculatum*, *Arctostaphylos glauca*, *Heteromeles arbutifolia*, and *Umbellularia californica*. These species are representative of the range of life history strategies (Keeley 2000) and environmental settings in the study area and, with the exception of *U. californica*, are well understood physiologically.

*C. megacarpus* dominates (>60% canopy cover) on many of the most xeric slopes in the study area, but is absent both in the northern watershed and at upper elevations on the south side of the range (Figures 7 and 9a). Soil moisture availability (SMI) explains most of the variability in abundance on the south slide (Table 6). Sites with soil moisture less than 0.093 have considerably higher cover (40%) than sites above 0.093 (6%) (Figure 7). *C. megacarpus* is most abundant (68% cover) at sites with very low soil moisture (SMI < 0.04). These conditions are characteristic of mid- to low elevation, south-facing slopes and dry ridges with high solar exposure and high summer air temperature (Figure 5). At sites where soil moisture is

greater than 0.093, *C. megacarpus* abundance varies along a temperature gradient, decreasing from 14% cover (TMAX > 27.9 °C) to 1%. It is absent at cooler sites (TMAX < 27.5 °C). *C. megacarpus* cover is low (2%) at sites within its optimal temperature zone (TMAX > 28.7°C) (Figure 7), but where soil moisture is high (SMI > 0;148). These conditions are characteristic of ephemeral and perennial drainages, gentle toeslopes, and slopes with low solar exposure (Figure 5). *C. megacarpus* is predicted to be both present and common across a greater proportion of the southern watersheds than any other species – 85% and 31%, respectively (Table 7).

The distributions of *Adenostoma fasciculatum* and *Arctostaphylos glauca* are strongly associated with the presence of exposed rock (Figures 8a and 8b). However, the two species respond differently to other environmental conditions. *A. fasciculatum* (Figure 8a) peaks (35% cover) at rocky sites with moderately low summer temperature (<28.5 °C) and high solar radiation (>619 W m<sup>-2</sup>). It is absent at moister sites (SMI > 0.25) without rock cover (Rock < 2%). Under low light conditions (<479 W m<sup>-2</sup>), *A. fasciculatum* only reaches 1% cover even when soil moisture is suitably low (<0.25). The model predicts that *A. fasciculatum* is present across a larger portion of the entire study area (87%) than any other species (Table 7; Figure 9b).

*A. glauca* is most abundant (37% cover) on rocky slopes within a narrow temperature range (27.5°–28.3 °C), and on the small proportion of slopes with very low moisture variability (SVI < 0.128) (Fig-

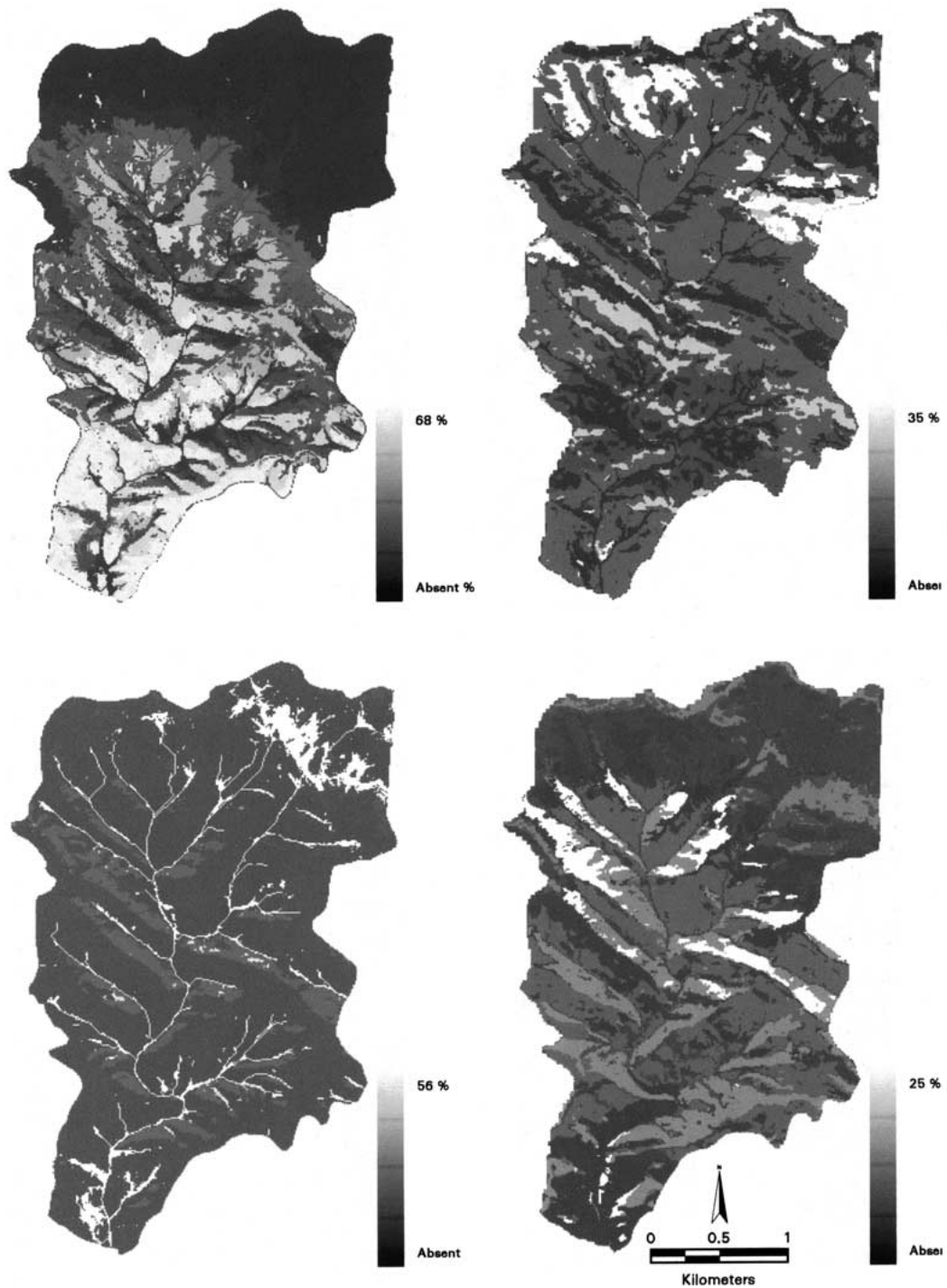


Figure 9. Regression tree predictions of shrub abundance across the Mission Canyon watershed: (a) *Ceanothus megacarpus*, (b) *Adenostoma fasciculatum*, (c) *Umbellularia californica*, and (d) *Heteromeles arbutifolia*. Model performances are given in table 5. The variable abbreviations are: SMI = Average annual soil moisture, SVI = Seasonal variability in soil moisture, PAR = Average annual photosynthetically active radiation, TMAX = Average maximum temperature over the dry season (May – Oct), RCK = Exposed rock percentage, and WSHED = watershed location.

Table 4. Mean (M) values and variance ( $S^2$ ) of environmental conditions for locations where species are common. See Table 3 for definitions of variables.

Species	Common cover (%)	SMI		SVI		PAR		$T_{MAX}$	
		M	$S^2$	M	$S^2$	M	$S^2$	M	$S^2$
<i>Ceanothus. megacarpus</i>	39	0.07	0.003	0.26	0.025	637	3818.2	29.0	0.392
<i>Ceanothus crassifolius</i>	27	0.09	0.009	0.29	0.025	634	2828.7	28.1	0.442
<i>Malosma laurina</i>	6	0.09	0.004	0.29	0.036	638	4758.2	28.8	0.396
<i>Arctostaphylos glauca</i>	17	0.10	0.005	0.33	0.027	639	5387.7	28.2	0.407
<i>Adenostoma fasciculatum</i>	19	0.12	0.005	0.43	0.040	598	7159.5	28.1	0.485
<i>Ceanothus spinosus</i>	19	0.12	0.042	0.32	0.035	584	10963.1	29.0	0.298
<i>Heteromeles arbutifolia</i>	7	0.13	0.006	0.41	0.038	530	10514.8	28.5	0.530
<i>Cercocarpus betuloides</i>	11	0.13	0.007	0.45	0.032	528	8696.0	27.9	0.425
<i>Quercus agrifolia</i>	35	0.14	0.039	0.33	0.025	520	7270.3	29.2	0.146
<i>Ceanothus oliganthus</i>	7	0.15	0.004	0.51	0.027	470	6315.0	28.2	0.379
<i>Garrya veatchii</i>	6	0.21	0.015	0.56	0.050	467	8853.5	21.7	0.398
<i>Umbellularia californica</i>	19	0.30	0.081	0.35	0.038	566	11001.0	28.6	0.372

ure 8b). *A. glauca* is distributed across 12.5% of the entire study area, about 5% of the northern watershed, and is common (17% cover) across only 2.5% of the entire study area (Table 7).

*Umbellularia californica* and *Heteromeles arbutifolia* (Figures 8c and 8 d) are associated with more mesic conditions than the other species described in detail. *U. californica* is most abundant (57% cover) along ephemeral and perennial drainages ( $0.3 < SMI < 0.583$ ) with moderate solar exposure ( $PAR > 555 \text{ W m}^{-2}$ ), but it is also relatively abundant (23% cover) on sheltered slopes ( $PAR < 555 \text{ W m}^2$ ) with moist soils ( $SMI > 0.3$ ) and warm temperatures ( $TMAX > 28.5 \text{ }^\circ\text{C}$ ). *U. californica* is predicted to occupy only 12.6% of the study area (Table 7; Figure 10c).

*H. arbutifolia* (Figure 8d) occupies a wide range of environmental conditions and is distributed across almost 86% of the study area (Table 7; Figure 9d). Suitable conditions for *H. arbutifolia* range from mesic ( $PAR < 590 \text{ W m}^{-2}$ ;  $SVI > 0.6$ ) to xeric ( $PAR > 590 \text{ W m}^{-2}$ ;  $SVI < 0.133$ ) (Figure 8d). *H. arbutifolia* decreases where exposed rock is present and it is absent on exposed slopes ( $PAR > 590 \text{ W m}^{-2}$ ) with rock cover over 2%.

#### Prediction errors

The vegetation models tend to slightly over-estimate abundance (positive MER) of every species except *Ceanothus spinosus* (Table 5). Significant correlations between prediction errors and environmental

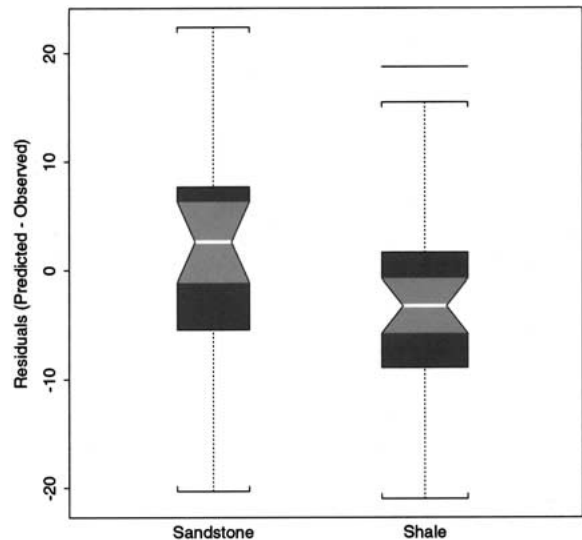


Figure 10. Boxplot of *Heteromeles arbutifolia* prediction residuals on sandstone vs. shale substrate. Abundance is generally over-predicted on sandstone and under-predicted on shale ( $P = 0.016$ ).

conditions exist for five species (Table 8). The negative relationship between *Adenostoma fasciculatum* and SMI, for example, shows that the cover of this species is increasingly over-estimated with decreasing soil moisture at sites where soil moisture is less than 0.10, but under-estimated at sites where soil moisture exceeds 0.10. *Ceanothus oliganthus*, and *Heteromeles arbutifolia* are over-predicted on sandstone substrate (Table 8) (Figure 10). Prediction errors

Table 5. Explanatory power (based only on training data) and predictive accuracy (based on independent test data) of the models. Positive and negative mean error (MER) values are given.  $n$  Pres = number of positive occurrences out of 307 samples.

Species	$n$ Pres	Explanatory power $r$	Predictive accuracy	
			$r$	MER
<i>Adenostoma fasciculatum</i>	181	0.68	0.56	3.0
<i>Artostaphylos glauca</i>	94	0.82	0.57	2.0
<i>Ceanothus crassifolius</i>	102	0.88	0.71	2.0
<i>C. megacarpus</i>	135	0.86	0.72	4.1
<i>C. oliganthus</i>	79	0.71	0.42	0.9
<i>C. spinosus</i>	110	0.83	0.76	-0.4
<i>Cercocarpus betoides</i>	192	0.75	0.51	1.5
<i>Garrya veatchii</i>	68	0.78	0.42	0.5
<i>Heteromeles arbutifolia</i>	227	0.71	0.42	1.2
<i>Malosma laurina</i>	113	0.84	0.67	0.1
<i>Quercus agrifolia</i>	69	0.80	0.61	2.5
<i>Umbellularia californica</i>	73	0.82	0.47	1.7
Average		0.79	0.58	

are also correlated with the abundance of other species in three cases (Table 8). For example, *Artostaphylos glauca* is increasingly over-predicted with increasing *A. fasciculatum* abundance at sites where *A. fasciculatum* is greater than 20%. At sites where *A. glauca* exceeds 39% cover, *C. crassifolius* is increasingly over-predicted. *C. megacarpus* is increasingly over-predicted with increasing *Malosma laurina* abundance at sites where *M. laurina* is greater than 6%.

## Discussion

### *Species-environment relationships*

In this environment, landscape-scale spatial patterns of shrub abundance correspond to topographically-regulated gradients of soil moisture, solar radiation, air temperature, and substrate rockiness. Moreover, species are differentially distributed in ways that are consistent with ecophysiological processes that are known to operate at fine scales. Based on these findings, we hypothesize that the landscape patterns of shrub abundance reflect species-specific differences in seed germination requirements, susceptibility to water stress, shade tolerance, and root depth.

The common occurrence of resprouters on sheltered, north-facing slopes (e.g. Figure 5c) reflects their dependence on moist, cool soil conditions for seed germination (Keeley 1991, 1992). The sensitivity of

their seed viability to drought and high soil temperatures (Keeley 1991) may also contribute to the lower abundance of resprouters on hot slopes and ridges with high solar exposure. In contrast, the refractory seeds of most disturbance-dependent shrubs can remain dormant at hot, dry sites for several decades until the first growing season after fire (Keeley 1991).

A complementary factor underlying these patterns may relate to the effect of regeneration niche conditions on seedling survival during summer drought (Davis 1989, 1991; Keeley 1998). Resprouters generally have poorer stomatal control (Miller 1981) and are vulnerable to water stress-induced xylem embolism (Jarbeau et al. 1995; Davis et al. 1998; Keeley 1998). While the deep root systems of mature resprouters can prevent water stress (Poole et al. 1981; Davis & Mooney 1986), shallow rooted seedlings must persevere months of water stress (Thomas & Davis 1989). Thus, the establishment of resprouters is further limited to sites that not only provide germination conditions, but also remain sufficiently moist through the first post-germination dry season.

*Malosma laurina*, a broad-leaved resprouter that occurs on xeric slopes, is an exception to this pattern despite its relatively high minimum water potentials (Table 1) and its vulnerability to water stress (Poole & Miller 1975; DeSouza et al. 1986; Davis et al. 1998). This may relate to observations of Frazer & Davis (1988) that *M. laurina* seedlings often survive on xeric

Table 6. The proportion of the total deviance that each variable explains in the tree models of species cover. The direction of the relationship is indicated by (+) or (-). RCK = rock cover, and WSHED = watershed location. Other variables are defined in Table 2.

Species	SMI	SVI	PAR	$T_{MAX}$	RCK	WSHED
<i>Adenostoma fasciculatum</i>	4.5 (-)	-	5.4 (+)	11.0 (-)	13.7 (+)	-
<i>Arctostaphylos glauca</i>	-	7.7 (-)	6.2 (+)	16.3 (-)	34.7 (+)	1.0
<i>Ceanothus crassifolius</i>	2.3 (-)	9.2 ( $\pm$ )	38.9 (+)	10.8 (-)	-	16.3
<i>C. megacarpus</i>	23.0 (-)	3.6 (-)	2.8 (+)	10.9 (+)	-	34.1
<i>C. oliganthus</i>	8.2 (+)	-	33.0 (-)	7.1 (-)	4.3 (-)	-
<i>C. spinosus</i>	5.9 (+)	2.7 (+)	4.0 (+)	28.3 (+)	8.1 (-)	19.9
<i>Cercocarpus betuloides</i>	6.2 (+)	12.3 (+)	5.1 (-)	7.7 (-)	7.5 (-)	18.1
<i>Garrya veatchii</i>	16.1 (+)	19.6 (+)	13.6 (-)	9.3 (-)	-	2.4
<i>Heteromeles arbutifolia</i>	3.7 (+)	9.0 ( $\pm$ )	17.1 (-)	10.3 (+)	7.2 (-)	1.7
<i>Malosma laurina</i>	31.5 (-)	2.1 (-)	1.0 (+)	2.8 (+)	1.1 (+)	30.4
<i>Quercus agrifolia</i>	11.8 (+)	1.2 (+)	24.0 (-)	24.3 (+)	3.1 ( $\pm$ )	-
<i>Umbellularia californica</i>	39.5 (+)	-	18.0 ( $\pm$ )	8.2 ( $\pm$ )	-	2.0
Average	12.7%	5.6%	14.1%	12.3%	6.6%	10.4%

slopes at mesic microsites with partial shading, site factors that operate at a finer scale than this work.

While the seedlings of resprouters are susceptible to water stress, disturbance-dependent shrubs typically establish on xeric topographic positions. Moreover, most of the disturbance-dependent species increase in abundance with decreasing soil moisture and increasing solar radiation. These patterns probably relate to their resistance to embolism (Davis et al. 1998) and greater stomatal control at extremely low water potentials (Miller 1981). Certain species, such as *C. megacarpus*, tolerate extremely water-limited sites. The model and predictive map of *C. megacarpus* illustrate its dominance at xeric sites relative to other drought tolerating shrubs, such as *A. fasciculatum* and *A. glauca*. These patterns are consistent with Davis et al. (1999) who observed that *C. megacarpus* resists water stress-induced xylem embolism, despite very low water potentials. The *Ceanothus* species of the subgenus *Euceanothus* (*C. oliganthus* and *C. spinosus*) occur at more mesic sites than species of subgenus *Cerastes* (*C. megacarpus*, *C. crassifolius*). It has been argued by Wells (1969) and others that the anatomical and physiological mechanisms of species in subgenus *Euceanothus* are not as well adapted as subgenus *Cerastes* to persistent summer drought and periodic fire in southern California (Axelrod 1989; Stine 1994).

The scarcity of some drought-tolerant species, such as *C. megacarpus*, *C. crassifolius*, and *A. glauca*,

on mesic, north-facing slopes may also relate to light requirements. While most of the broad-leaf shrubs (e.g., *H. arbutifolia*) are productive in low-light environments (Mooney et al. 1975), optimal photosynthesis of some *Ceanothus* and *Arctostaphylos* species requires high illumination (Oechel and Lawrence 1981). *C. megacarpus*, for example, has marked drops in water-use efficiency at shaded sites (Mahall & Schlesinger 1982) and *C. crassifolius* has been shown to have smaller stature, experience greater mortality, and produce fewer seeds on a mesic, north-facing slope compared to a drier, south-facing slope (Keeley 1986).

The dominance of *A. fasciculatum* and *A. glauca* rather than *C. megacarpus* on dry, shallow rocky soils and ridges was also observed by Schlesinger et al. (1982). During summer drought, water is more available deep in fissures and cavities of weathered bedrock than in overlying soils (Jones & Graham 1993; Sternberg et al. 1996). However, we did not parameterize RHESSys with a map of hydraulic conductivity, and as a result, ridge locations and rocky sites probably experience drier conditions near the surface (<1.5 m) than our models suggest. For *A. fasciculatum*, a combination of drought tolerance and moderately deep roots (Hellmers et al. 1955) may allow it to survive at sites with little soil. The absence of *C. megacarpus* at dry, rocky sites could be due to an inability of its shallow root system to reach deeply stored water, and/or the lack of near-surface soil moisture that it requires

Table 7. Proportion of area that each species is predicted to occupy across the three study watersheds. Proportion of area is tabulated for two abundance classes on the southern flank (Mission and Romero Canyons are aggregated) and northern flank of the Santa Ynez. The two abundance classes include the percent area for which a species is predicted to be present and the percent area for which a species is predicted to be common.

Species	Common (%)	Present (%)			Common (%)		
		South	North	Overall	South	North	Overall
<i>Adenostom afasciculatum</i>	19	81.5	92.3	86.9	11.3	13.7	12.5
<i>Arctostaphylos glauca</i>	17	19.1	5.4	12.5	3.9	1.1	2.5
<i>Ceanothus crassifolius</i>	27	26.9	74.4	50.6	0.0	29.6	14.8
<i>C. megacarpus</i>	39	84.8	0.0	42.4	30.8	0.0	15.4
<i>C. oliganthus</i>	7	21.0	48.6	34.8	3.0	8.5	5.8
<i>C. spinosus</i>	19	45.5	2.6	24.0	11.2	0.0	5.6
<i>Cercocarpus betuloides</i>	11	40.8	98.9	79.8	10.8	47.8	29.3
<i>Garrya veatchii</i>	6	20.6	44.7	32.6	4.8	3.3	4.1
<i>Heteromeles arbutifolia</i>	7	81.7	86.1	85.0	9.4	7.9	8.7
<i>Malosma laurina</i>	6	49.2	0.0	24.6	0.0	0.0	0.0
<i>Quercus agrifolia</i>	35	32.2	66.4	44.3	4.8	8.7	6.8
<i>Umbellularia californica</i>	19	13.5	11.7	12.6	6.5	2.6	4.6

for rapid growth following fire (Schlesinger & Gill 1980). Alternatively, Quick (1935) suggests that obligate seeders such as *C. megacarpus* less frequently recruit seedlings at rocky sites because their seeds do not survive fires unless they are insulated by a litter layer and topsoil. Although the common occurrence of *A. glauca* (also an obligate seeder) on rocky substrate contradicts this explanation, its hard, thick seed coats (Hickman 1993) provide greater seed protection than the relatively delicate seeds of *C. megacarpus*.

#### Factors not accounted for in the models

Over- and under-prediction of shrub abundance may be related to biotic factors that are not directly accounted for in the species response models (Table 8). For example, over-prediction may occur in some cases where interspecific competition inhibits certain shrubs. The connection between *A. fasciculatum* abundance and the over-prediction of *A. glauca* suggests that *A. glauca* is negatively affected by an increase in the presence of *A. fasciculatum*. A possible explanation for this relationship is the frequently suggested allelopathic effect of *A. fasciculatum* on other plants, although this has not been firmly established (Keeley & Keeley 1989).

Similarly, *C. megacarpus* and *C. crassifolius* are negatively associated with an increase in the abundance of *M. laurina* and *A. glauca*, respectively. The former pattern may be associated with the success of

*M. laurina* in mesic microsites with relatively low illumination (Frazer & Davis 1988). *C. megacarpus* may not be as competitive at such sites due to reduced water-use efficiency (Mahall & Schlesinger 1982).

Prediction error also varied with environmental conditions for several species. For example, the negative relationship between *A. fasciculatum* prediction error and soil moisture availability (SMI) suggests that additional factors (e.g., other soil characteristics) need to be explored in order to explain what is inhibiting success of *A. fasciculatum* at dry sites (over-prediction) while promoting success at mesic sites (under-prediction). In such cases, prediction errors may relate to locations where the distributed fields of environmental conditions are of insufficient resolution to capture all the factors governing shrub abundance.

Over-prediction of *C. oliganthus*, *G. veatchii*, and *H. arbutifolia*, on sandstone suggests that substrate influences the abundance of these species (Table 8; Figure 10). These three species all exhibit a preference for mesic conditions (Figure 6), and are expected to function and recruit seedlings more effectively on the weathered, deep shale substrates than the shallower soils associated with rocky sandstone substrates. Additionally, the resistant sandstones often form ridges (Page et al. 1951) that are sometimes below the resolution of the digital terrain data, and are therefore probably drier than the modeled fields of soil moisture indicate.

Table 8. Prediction error residuals in relation to environmental and biotic factors (percent cover of other species). Only significant relationships are presented ( $P < 0.05$ ). Thresholds that separate over- and under-prediction are given for the independent variables. Variables are defined in Table 2.

Test	Model residuals	Independent variable	$n$	$r$	Thresholds
Environmental	<i>Adenostoma fasciculatum</i>	SMI	45	-0.31	0.10
	<i>Adenostoma fasciculatum</i>	SVI	45	-0.26	0.35
	<i>Ceanothus oliganthus</i>	SMI	19	-0.46	0.19
	<i>Garrya veatchii</i>	SMI	17	-0.65	0.11
	<i>Quercus agrifolia</i>	SVI	17	0.51	0.20
	<i>Malosma laurina</i>	SVI	28	-0.59	0.21
	<i>Malosma laurina</i>	PAR	28	0.44	660 W m <sup>-2</sup>
	<i>Malosma laurina</i>	TMAX	28	0.52	29.2 °C
Substrate	<i>C. oliganthus</i>	Lithology	19	$P = 0.000$	
	<i>G. veatchii</i>	Lithology	17	$P = 0.018$	
	<i>Heteromeles arbutifolia</i>	Lithology	57	$P = 0.016$	
Biotic	<i>Arctostaphylos glauca</i>	<i>A. fasciculatum</i>	17	0.51	20%
	<i>Ceanothus crassifolius</i>	<i>A. glauca</i>	13	0.50	39%
	<i>C. megacarpus</i>	<i>Malosma laurina</i>	34	0.37	6%

Predictive accuracy is higher for disturbance-dependent species (average  $r = 0.64$ ) than for disturbance-free species (average  $r = 0.49$ ). The scale of our analysis may be less effective at capturing the processes that underlie the establishment of disturbance-free species. Bullock (1978) showed that chaparral species with fleshy fruits – such as most disturbance-free species – are often randomly and sparsely distributed. These are interstitial species that recruit seedlings at mesic microsites in small canopy openings where seeds happen to be deposited by birds and mammals (Bullock 1978; Keeley 1991, 1992). Furthermore, the germination of their short-lived seeds must coincide with the timing of specific moisture and temperature conditions, unlike disturbance-dependent species which produce large, dormant seed banks and dense cohorts of seedlings after fire (Keeley 1991, 1998). The less organized pattern and patchiness of the predicted distribution of *H. arbutifolia* (Figure 9d) relative to the more systematic and extensive patches of *C. megacarpus* (Figure 9a) illustrate this difference on the predicted distribution maps for these two species.

The species response models developed in this work can also be used to predict landscape-scale redistribution of vegetation due to climate change (reviewed in Franklin 1995). However, the impact of climate change on demographic patterns in chaparral is complicated by an inadequate understanding of how

fire frequency might change as well. An important research priority is to investigate how differences in the severity and frequency of summer drought – in combination with variable fire frequencies – alter landscape patterns of plant community development in chaparral. Assuming modern fire frequencies (20–150 years), it could be expected that a wetter summer climate would enable many resprouters to establish seedlings at sites that, under the present climate, are too dry for these species. Before the onset of the modern Mediterranean climate in this study region, the distribution of many resprouters was more extensive (Axelrod 1989). Under the current climatic regime, there are still suitable sites for establishment by resprouters, but their distribution has contracted (Keeley 1998). Drier conditions would likely lead to an increase in the abundance of disturbance-dependent species at higher elevations. However, many disturbance-dependent species could not expand onto topographically sheltered slopes due to their need for direct sunlight. According to fossil evidence presented by Axelrod (1989), vegetation patterns and climate have been relatively stable in southern California chaparral for at least 4000 years.

## Conclusions

Chaparral species are typically thought to establish only under certain environmental regimes due to specialized traits for reproduction, dispersal, and growth (Zedler 1995; Keeley 1998). Our results are consistent with this model, and suggest that shrub responses shown in ecophysiological literature also operate at landscape scales. In particular, landscape patterns of shrub establishment appear to reflect species-specific differences in seed germination requirements, vulnerability to water stress, light requirements, and rooting depth.

Similarity in many of the ecological relationships, as illustrated by the species response models, suggests that the shrub species can be grouped according to their seedling recruitment strategies. In general, disturbance-dependent shrubs commonly occur in xeric, high light environments (e.g., south-facing slopes and ridges), whereas disturbance-free shrubs are more common at higher elevations and topographically sheltered settings. The scale of our analysis is less effective at capturing the processes that underlie the establishment of disturbance-free species because these shrubs tend to have interstitial distributions in response to micro-scale processes that are below the scale of this work.

From our results, it appears that shrub-species abundance in California chaparral is strongly related to physiology and life-history strategies for recruitment and post-fire regeneration. Our results not only complement well-established concepts determined in the lab or for small plots, but also illustrate that ecophysiological processes, known to impact plant growth and survival at fine scales, are strongly expressed in landscape-scale spatial patterns of plant species composition.

## Acknowledgements

We gratefully acknowledge the logistic and field support of D. Johnson, S. Johnson, and C. Moody. Our work benefited from conversations with L. Band, M. Borchert, and J. Michaelsen. We also thank L. Band and C. Tague for guidance using RHESys, J. Michaelsen (Professor, University of California at Santa Barbara) for providing climate data and M. Moritz (Professor, California Polytechnic Institute) for providing fire history data. This research was partially supported under NASA grant NAG5-6583.

## References

- Austin, M. P., Meyers, J. A., Belbin, L. & Doherty, M. D. 1995. Modelling of landscape patterns and processes using biological data: Sub-project 5, Simulated data case study. Division of Wildlife and Ecology, Commonwealth Scientific and Industrial Research Organization, Canberra.
- Austin, M. P., Nicholls, A. O. & Margules, C. R. 1990. Measurement of the realized qualitative niche: environmental niches of live Eucalyptus species. *Ecol. Monogr.* 60: 161–77.
- Axelrod, D. I. 1989. Age and origin of chaparral. In: S. C. Keeley (ed), *The California chaparral: paradigms reexamined*. Natural History Museum of Los Angeles County.
- Bailey, H. P. 1966. *Weather of Southern California*. University of California Press, Berkeley and Los Angeles.
- Band, L. E., Patterson, P., Nemani, R. & Running, S. W. 1993. Forest ecosystem processes at the watershed scale: incorporating hillslope hydrology. *Agric. For. Meteorol.* 63: 93–126.
- 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.
- Brown, D. B. 1994. Predicting vegetation types at treeline using topography and biophysical disturbance variables. *J. Vegetation Sci.* 5: 641–656.
- Bullock, S. H. 1978. Plant abundance and distribution in relation to types of seed dispersal in chaparral. *Madrono* 25: 104–105.
- Campbell, B. 1980. Some mixed hardwood forest communities of the coastal ranges of southern California. *Phytocoenologia* 8: 297–320.
- Davis, F. W. and Goetz, 1990. Modeling vegetation pattern using digital terrain data. *Land. Ecol.* 4: 69–80.
- Davis, F. W., Michaelsen, J., Dubayah, R. & Dozier, J. 1990. Optimal terrain stratification for integrating ground data from FIFE. *Proceeding of the American Meteorological Society, Symposium on FIFE Boston, MA*, pp. 11–15.
- Davis, S. D. 1991. Lack of niche differentiation in adult shrubs implicates the importance of the regeneration niche. *Trends Ecol. Evol.* 9: 272–274.
- 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.
- Davis, S. D., Kolb, K. J. & Barton, K. P. 1998. Ecophysiological processes and demographic patterns in the structuring of California chaparral. In: P. W. Rundel, G. Montenegro & F. M. Jaksic (eds), *Landscape disturbance and biodiversity in mediterranean-type ecosystems*. Springer-Verlag, Berlin.
- Davis, S. D. & Mooney, H. A. 1986. Water use patterns of four co-occurring chaparral shrubs. *Oecologia* 70: 172–177.
- DeSouza, J., Silka, P. A. & Davis, S. D. 1986. Comparative physiology of burned and unburned *Rhus laurina* after chaparral wildfire. *Oecologia* 71: 63–68.
- Dibblee, T. W. 1986a. Geologic map of the Santa Barbara Quadrangle. Thomas Dibblee, Jr Geological Foundation.
- Dibblee, T. W. 1986b. Geologic map of the Carpinteria quadrangle. Thomas Dibblee, Jr. Geological Foundation.
- Dibblee, T. W. 1986c. Geologic map of the Little Pine quadrangle. Thomas Dibblee, Jr. Geological Foundation.
- Franklin, J. 1995. Predictive vegetation mapping: geographic modeling of biospatial patterns in relation to environmental gradients. *Prog. Phys. Geogr.* 19: 474–499.

- Franklin, J. 1998. Predicting the distributions of shrub species in California chaparral and coastal sage communities from climate and terrain-derived variables. *J. Veg. Sci.* 9: 733–748.
- Franklin, J., McCullough, P. and Gray, C. 1998. Terrain variables used for predictive mapping of vegetation communities in Southern California. In: Wilson, J.P. & Gallant, J. C. (eds) *Terrain Analysis*. GeoInformation International, Cambridge.
- Frazer, J. M. & Davis, S. D. 1988. Differential survival of chaparral seedlings during the first summer drought after wildfire. *Oecologia* 76: 215–221.
- Greig-Smith, P. 1983. *Quantitative plant ecology*, 3rd edition. University of California Press, Berkeley, CA.
- Hanes, T. L. 1977. Chaparral. Pp. 417–469. In: Barbour, M. G. & Major, J. (eds), *Terrestrial vegetation of California*. John Wiley & Sons, New York.
- Hastie, T. J. 1993. Generalized additive models. In: Chambers, J. M. & Hastie, T. J. (eds), *Statistical models*. Chapman & Hall, Inc., London.
- Hellmers, H. Horton, J. S., Juhren, G. & O'Keefe, J. 1955. Root systems of some chaparral plants in southern California. *Ecology* 36: 667–678.
- Jarbeau, J. A., Ewers, F. W. & Davis, S. D. 1995. The mechanism of water stress-induced embolism in two species of chaparral shrubs. *Plant Cell Environ.* 19: 189–196.
- Jones, D.P. & Graham, R. C. 1993. Water-holding characteristics of weathered granitic rock in chaparral and forest ecosystems. *Soil Sci. Soc. Am. J.* 57: 256–261.
- Keeley, J. E. 1986. Resilience of mediterranean shrub communities to fires. In: Dell, B., Hopkins, A. J. M. & Lamont, B. B. (eds), *Resilience in mediterranean-type ecosystems*.
- 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. *Botan. Rev.* 57: 81–116.
- Keeley, J. E. 1992. Recruitment of seedlings and vegetative sprouts in unburned chaparral. *Ecology* 73: 1194–1208.
- Keeley, J. E. 1998. Coupling demography, physiology and evolution in chaparral shrubs. In: Rundel, P.W., Montenegro, G. & Jaksic, F.M. (ed.), *Landscape disturbance and biodiversity in mediterranean-type ecosystems*. Springer-Verlag, Berlin.
- Keeley, J. E. 2000. Chaparral. In: Barbour, M. G. and Billings, W. D. (eds) *North American terrestrial vegetation*, 2nd edition. Cambridge University Press, Cambridge.
- Keeley, J. E. & Keeley, S. C. 1989. Allelopathy and the fire induced herb cycle. In: Keeley S. C. (ed), *The California chaparral: paradigms reexamined*. Natural History Museum of Los Angeles County.
- Kummerow, J., Ellis, B. A. & Mills, J. N. 1985. Post-fire seedling establishment of *Adenostoma fasciculatum* and *Ceanothus greggii* in southern California chaparral. *Madrono* 32: 148–157.
- Mahall, B. E. & Schlesinger, W. H. 1982. Effects of irradiance on growth, photosynthesis and water use efficiency of seedlings of the chaparral shrub *Ceanothus megacarpus*. *Oecologia* 54: 291–299.
- 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 California coastal sage scrub. *Oecol. Plant.* 6: 169–181.
- Meentemeyer, R. K. & Moody, A. 2000. Rapid sampling of plant species composition for assessing vegetation patterns in rugged terrain. *Land. Ecol.* 15: 697–711.
- McPherson, J. K. & Muller, C. H. 1969. Allelopathic effects of *Adenostoma fasciculatum*, 'chamise', in the California chaparral. *Ecol. Monogr.* 39: 177–198.
- Michaelsen, J., Schimel, D., Friedl, M., Davis, F. W. & Dubayah, R. C. 1994. Regression tree analysis of satellite and terrain data to guide vegetation sampling and surveys. *J. Veg. Sci.* 5: 673–686.
- Miller, P. C. 1979. Quantitative plant ecology, Pp. 179–231. In: Horn, D., Stairs, G. R. & Mitchell, R. D. (eds), *Analysis of ecosystems*. Ohio State University Press, Columbus.
- Miller, P. C. (ed.). 1981. *Resource use by chaparral and matorral: a comparison of vegetation function in two mediterranean type ecosystems*. Springer-Verlag, New York.
- Miller, P. C., Bradbury, D. E., Hajek, E., La Marche, V. & Thrower, N. J. W. 1977. Past and present environment. In: Mooney, H. A. (ed), *Convergent evolution in Chile and California mediterranean climate ecosystems*. Dowden, Hutchinson and Ross, Stroudsburg, PA.
- Miller, P. C., Hajek, E. & Miller, P. M. 1983. The influence of annual precipitation, topography and vegetation cover on soil moisture and summer drought in southern California. *Oecologia* 56: 385–391.
- Misquezu, E. 1990. Frost sensitivity and distribution of *Malosma laurina*. Master's thesis, University of California, Riverside.
- Mooney, H. A. & Harrison, A. T. 1972. The vegetational gradient on the lower slopes of the Sierra San Pedro Martir in northwest Baja California. *Madrono* 21: 439–445.
- Mooney, H. A., Harrison, A. T. & Morrow, P. A. 1975. Environmental limitation of photosynthesis on a California evergreen shrub. *Oecologia* 19: 293–301.
- Oberlander, G. T. 1953. The taxonomy and ecology of the flora of the San Francisco watershed reserve. Ph.D. Dissertation, Stanford University, Stanford, CA.
- O'Brien, E. M. 1998. Water-energy dynamics, climate, and prediction of woody plant species richness: an interim general model. *J. Biogeogr.* 25: 379–398.
- Oechel, C. & Lawrence, W. 1981. Carbon Allocation and Utilization. In: Miller, P. C. (ed), *Resource Use by chaparral and matorral: a comparison of vegetation function in two mediterranean type ecosystems*. Springer-Verlag, New York.
- Page, B. M., Marks, J. G. & Walker, G. W. 1955. Stratigraphy and structure of the mountains northeast of Santa Barbara, California. *Bull. Amer. Assoc. Petrol. Geol.* 35: 1727–1780.
- Poole, D. K. & Miller, P. C. 1975. Water relations of selected species of chaparral and coastal sage communities. *Ecology* 56: 1118–1128.
- Quick, C. R. 1935. Notes on the germination of *Ceanothus* seeds. *Madrono* 3: 135–139.
- Running, S. W. & Coughlan, J. C. 1988. A general model of forest ecosystem processes for regional applications. I. Hydrologic balance, canopy gas exchange and primary production processes. *Ecol. Model.* 42: 125–154.
- Running, S. W. and Hunt, R. E. 1993. Generalization of a forest ecosystem process model for other biomes, BIOME-BGC, and an application for global-scale models, Pp. 141–158. In: Ehleringer, J. D. & Field, C. D. (eds), *Scaling physiologic processes: leaf to globe*. Academic Press, San Diego, CA.
- Running, S. W., Nemani, R. R. & Hungerford, R. D. 1987. Extrapolation of synoptic meteorological data in mountainous terrain and its use for simulating forest evapotranspiration and photosynthesis. *Can. J. For. Res.* 17: 472–483.
- Schlesinger, W. H. & Gill, D. S. 1978. Demographic studies of the chaparral shrub, *Ceanothus megacarpus*, in the Santa Ynez Mountains, California. *Ecology* 59: 1256–1263.
- Schlesinger, W. H. & Gill, D. S. 1980. Biomass, production, and changes in the availability of light, water, and nutrients during the development of pure stands of the chaparral shrub, *Ceanothus megacarpus*, after fire. *Ecology* 61: 781–789.

- 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.
- Shreve, F. 1927. The vegetation of a coastal mountain range. *Ecology* 8: 37–40.
- Steward, D. and Webber, P. J. 1981. The plant communities and their environment. In: Miller, P. C. (ed), *Resource use by chaparral and matorral: a comparison of vegetation function in two mediterranean type ecosystems*. Springer-Verlag, New York.
- Tague, C. L. 2000. Modeling seasonal hydrologic response to forest harvesting and road construction: the role of drainage organization. Ph.D. Dissertation, University of Toronto.
- Tague, C. L., Fernandes, R. & Band, L. E. 1998. RHESSys 4.5: User Manual.
- Thomas, C. M. & Davis, S. D. 1989. Recovery patterns of three chaparral shrub species after wildfire. *Oecologia* 80: 309–320.
- Vila, M. & Sardans, J. 1999. Plant competition in mediterranean-type vegetation. *J. Veg. Sci.* 10: 281–294.
- Westman, W. E. 1981. Factors influencing the distribution of species of California coastal sage scrub. *Ecology* 62: 439–455.
- Westman, W. E. 1991. Measuring realized niche spaces: climatic response of chaparral and coastal sage scrub. *Ecology* 72: 1678–1684.
- Wigmosta, M., Vail, L. & Lettenmaier, D. 1994. Distributed-hydrology-vegetation model for complex terrain. *Water Res. Res.* 30: 1665–1679.
- Zedler, P. A. 1995. Plant life history and dynamic specialization in the chaparral/coastal sage shrub flora in southern California, Pp. 89–115. In: Arroyo, M. T. K., Zedler, P. H. & Fox, M. D. (eds), *Ecology and Biogeography of Mediterranean Ecosystems in Chile, California, and Australia*. Springer-Verlag, New York.