

## A STRUCTURAL EQUATION MODEL ANALYSIS OF POSTFIRE PLANT DIVERSITY IN CALIFORNIA SHRUBLANDS

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*Abstract.* This study investigates patterns of plant diversity following wildfires in fire-prone shrublands of California, seeks to understand those patterns in terms of both local and landscape factors, and considers the implications for fire management. Ninety study sites were established following extensive wildfires in 1993, and 1000-m<sup>2</sup> plots were used to sample a variety of parameters. Data on community responses were collected for five years following fire. Structural equation modeling (SEM) was used to relate plant species richness to plant abundance, fire severity, abiotic conditions, within-plot heterogeneity, stand age, and position in the landscape. Temporal dynamics of average richness response was also modeled. Richness was highest in the first year following fire, indicating postfire enhancement of diversity. A general decline in richness over time was detected, with year-to-year variation attributable to annual variations in precipitation. Peak richness in the landscape was found where (1) plant abundance was moderately high, (2) within-plot heterogeneity was high, (3) soils were moderately low in nitrogen, high in sand content, and with high rock cover, (4) fire severity was low, and (5) stands were young prior to fire. Many of these characteristics were correlated with position in the landscape and associated conditions. We infer from the SEM results that postfire richness in this system is strongly influenced by local conditions and that these conditions are, in turn, predictably related to landscape-level conditions. For example, we observed that older stands of shrubs were characterized by more severe fires, which were associated with a low recovery of plant cover and low richness. These results may have implications for the use of prescribed fire in this system if these findings extrapolate to prescribed burns as we would expect.

*Key words:* colonization; diversity; fire; heterogeneity; landscape; niche partitioning; prescribed burning; productivity; resource availability; species richness; structural equation modeling (SEM).

### INTRODUCTION

There exists a large number of theories about individual mechanisms that can potentially influence species diversity (see reviews in Huston 1994, Palmer 1994, Rosenzweig 1995). Involved in these mechanisms are factors such as (1) resource availability and community productivity, (2) competition and facilitation, (3) spatial heterogeneity and dispersal, (4) disturbance and succession, (5) the influences of regional and local species pools, and (6) the role of stochastic factors. The challenge that now faces ecologists is to ascertain how these various forces work together in natural systems to regulate patterns and dynamics in diversity.

It is often unappreciated how limited conventional analytical approaches are when it comes to addressing questions about multiple controlling factors. Because of the intercorrelations among factors, piecewise analysis of systems using univariate procedures (those that

consider one response variable at a time) are helpful for describing overall patterns, but leave unresolved many questions that relate to networks of interactions. Alternative approaches, such as structural equation modeling (Shipley 2000, Pugsek et al. 2003, Grace 2006), are designed for the study of multivariate hypotheses and apply more directly to understanding interacting systems. Structural equation modeling (SEM) involves the use of a multiequational framework to develop and test theoretically based models in order to understand responses controlled by multiple factors (Bollen 1989). Through the use of a simultaneous analysis procedure, SEM derives results that seek to account for the roles of multiple factors in a single analysis.

Commonly, SEM provides quite a different perspective by partitioning direct from indirect effects and thereby revealing a variety of mechanisms behind the overall patterns. When SEM is used in the study of natural systems, it is frequently shown that reliance on conventional univariate relationships can lead to misleading impressions. For example, Johnson et al. (1991) found that the addition of the herbicide atrazine to

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replicate experimental ponds had no consistent effect on phytoplankton despite the fact that atrazine is known to be toxic to algae. Using SEM, they were able to ascertain the roles played by aquatic macrophytes and fish, enhancing both their understanding of the system and the specific effects of atrazine on phytoplankton. Similarly, Grace and Jutila (1999) found no overall effect of grazing on plant diversity in coastal grasslands. However, SEM revealed that behind this pattern was an offsetting pair of processes: (1) grazing promoted diversity indirectly by reducing community biomass and competition, and (2) grazing resulted in the direct elimination of some species. Representing a somewhat different example, Gough and Grace (1999) found that fertilization effects on plant diversity could be partitioned into three separate processes: (1) a loss of species through enhanced productivity, (2) promotion of diversity by allowing for more rapid recovery from disturbance, and (3) reduced diversity associated with changes in canopy architecture and greater shading. In general, enhancements in our understanding of natural systems as illustrated by these examples have been found to be typical of the use of SEM (Grace 2006).

In this study, we investigate patterns of plant diversity following wildfires in fire-prone shrublands of California and the conditions associated with those patterns using SEM. During a two-week period in the fall of 1993, 16 major fires burned through southern California, representing a major, though not unprecedented, disturbance to the natural systems of the region (Keeley et al. 2005a). The areas affected included regions characterized by both chaparral and sagebrush communities in coastal and inland regions. These systems are of interest in part because they are known to be "hot spots" of biodiversity (Mooney et al. 2001, Myers 2001) and also because they represent a unique component of the North American flora. Much of what is known about diversity in this region concerns patterns of diversity rather than underlying processes (Bond 1983, Specht 1988, Fox 1995, Cowling et al. 1996, Keeley and Fotheringham 2003). Far less is known about the precise conditions that contribute to the maintenance of high species richness, the temporal dynamics of recovery, or the associated processes (Shmida and Wilson 1985, Lavorel 1999).

In this paper we began with a conceptual model of expected multivariate relationships based on studies in other ecosystems and then adapted this model to the particulars of the landscape investigated and the data collected. The structural equation model subsequently developed was then used to address specific questions about the importance of local conditions (such as local site favorability, abiotic conditions, and small-scale spatial heterogeneity), as well as landscape factors, in explaining richness patterns. Additional analyses were used to examine the temporal dynamics of richness over a five-year period and how this relates to successional trends as well as to year-to-year variations in rainfall.

Finally, we consider the implications of our results for management of shrublands in this region, especially the role of prescribed burning as a means of reducing the risk of wildfires.

*A priori model relating habitat conditions to patterns of diversity*

The modeling process in SEM is guided by the investigator's a priori and theoretical knowledge and begins with a consideration of expected relationships based on mechanisms thought to operate in the system. In this study, we relied on previous work relating patterns of richness within a landscape to local conditions and to landscape features (summarized in Grace 1999). Studies of wetlands, prairies, and meadows have suggested that richness is commonly related to (1) degree of disturbance, (2) favorableness of abiotic conditions, (3) total plant cover or biomass, and (4) spatial heterogeneity. These four factors represent ones most frequently given importance in general theories of community structure (cf. Grime 1973, Tilman 1988, Taylor et al. 1990, Huston 1994). Landscape features are also believed to influence patterns of diversity at a broad scale (Currie et al. 1999, Francis and Currie 2003, Ricklefs 2004), and such patterns often represent historical influences whose effects are still seen in today's species distributions (Grace and Guntenspergen 1999, Harrison 1999, Keeley and Fotheringham 2003, Harrison et al. 2006).

In the particular case of this study, where the landscape of southern California experienced widespread fire, we first sought to understand initial postfire patterns of richness. In particular, we related spatial variations in richness to four kinds of local factors: (1) fire severity, (2) the recovery of plant abundance, (3) local abiotic conditions, and (4) within-plot spatial heterogeneity (Fig. 1). These four factors characterized conditions within the sample plots and correspond to some degree with the influences of disturbance, resources, abiotic filters, and niche complementarity. We also sought to understand how local conditions related to landscape characteristics. In particular, we wished to see whether landscape position, community type (coastal sage vs. chaparral), and stand age related to patterns of richness and whether such relationships could be explained by the local conditions associated with particular circumstances. Several specific questions of interest relate to the model in Fig. 1.

1) Does richness increase with increasing plant cover? Is there an optimum level of cover beyond which richness declines?

2) Are there significant relationships between local abiotic conditions and richness? Are these relationships explained by associated variations in plant cover or are there unique influences of abiotic conditions on richness as have been reported in some other systems?

3) Is richness greater where within-plot heterogeneity is greater?

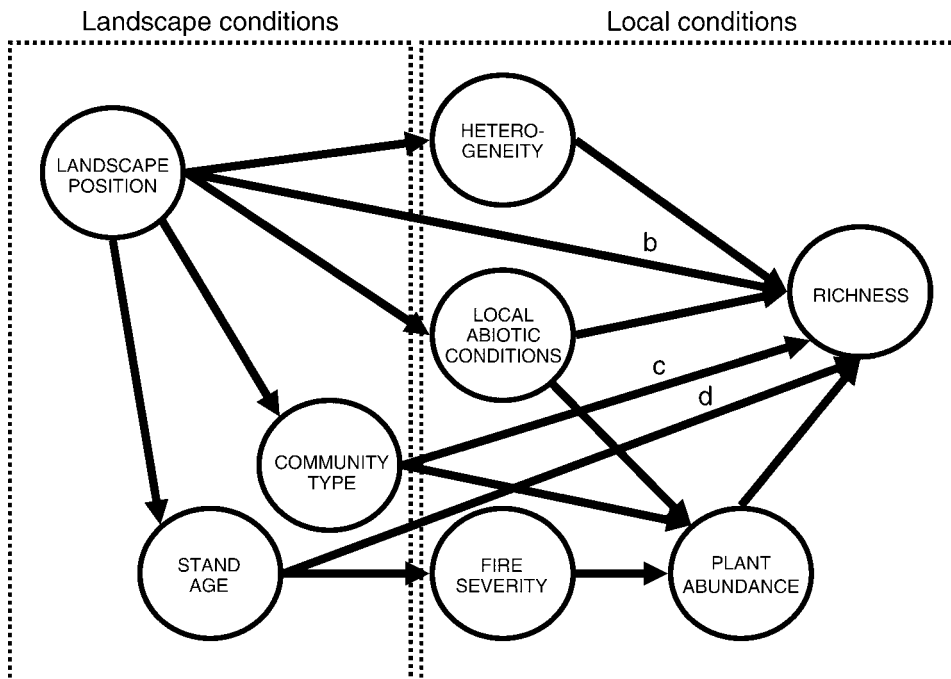


FIG. 1. Conceptual model representing hypothesized relationships between local and landscape factors and species richness. Model structure was based on earlier studies. Four competing models are represented by this figure. Model A contains all paths not labeled with a letter. Model B represents the case where path b (representing additional effects of landscape position) is included along with the paths in Model A. Model C includes path c and considers whether community type has effects on richness independent from those resulting from differences in plant abundance among communities. Finally, Model D includes path d and considers whether there are important effects of stand age unrelated to associated variations in fire severity and plant abundance (such as a loss of species from the system during long fire-free periods).

4) Does a relationship exist between richness and fire severity and, if so, can it be explained by accompanying variations in plant cover?

5) Does richness vary conspicuously with major gradients in the landscape? Can such correlations be explained by changes in local conditions within the landscape or are there unique associations with landscape position indicating the importance of other factors (i.e., should the model include path b)?

6) Do major community types vary with gradients in the landscape? Do such variations explain some of the variations in richness (i.e., should the model include path c)?

7) Does the age of the stand prior to burning have any relationship to fire severity or to richness (i.e., should the model include path d)?

8) What are the relative strengths of different relationships? Do local conditions strongly predict richness patterns or are there strong, unique associations with landscape conditions?

#### METHODS

Ninety sites were located in the areas burned by the 16 fires that occurred during a two-week period in the fall of 1993 in southern California, USA (Keeley et al. 2005a). The number of study sites in each burn was

based on fire size, diversity of vegetation types, fire severity, and accessibility. Sampling began in spring of the first postfire year and continued for four more years (two sites were lost to development after the second year). Precipitation totals (annual climatological summary, available from National Oceanic and Atmospheric Administration, Asheville, North Carolina, USA)<sup>5</sup> for the growing season (September–August) during the five-year study were averaged from several climate stations distributed within the range of coastal sites and interior sites. The first, third, and fourth years were ~80% of normal, the second year was 175% of normal, and the fifth year was an El Niño year of more than 250% of normal (Keeley et al. 2005a).

At each site, vegetation was sampled in 20 × 50 m (0.1 ha) sites with nested subplots. Briefly, the 0.1-ha sites were subdivided into 10 nonoverlapping 100-m<sup>2</sup> plots, each containing two 1-m<sup>2</sup> subplots in opposite corners (interior subplots were offset 1 m from the center to reduce contagion effects with the adjacent plots). Within each 1-m<sup>2</sup> subplot, density and cover were estimated for each species, and within the 100-m<sup>2</sup> plots a list was made of additional species. In this analysis, only diversity at the level of the whole plot (0.1 ha) was evaluated since

<sup>5</sup> (<http://www.ncdc.noaa.gov/oa/ncdc.html>)

this is the level at which the majority of habitat characteristics were measured.

Litter and soil samples from the top 6 cm of the profile were collected, texture and pH were analyzed (Cox 1995), and total N, P, and K were measured. Prefire stand age was determined from ring counts of stem samples. Fire severity estimates were based on two indexes derived from the skeletal remains of shrubs following fire. Index 1 was based on the diameters of the smallest twigs remaining and Index 2 was based on the height of the remaining shrub skeleton. Plant association type (sage vs. chaparral) was noted for each site. Site factors that were measured included distance from the coast, elevation, slope aspect, slope inclination, and calculated annual solar insolation (Frank and Lee 1966).

A measure of within-plot spatial heterogeneity in species composition was used in this study (Collins 1992). This measure was the mean dissimilarity in species composition among samples within a site, where percentage dissimilarity (PD) is defined as summation of individual dissimilarities among subplots within the whole plot using the following formula:

$$PD = 1 - \left(1 - 0.5 \sum |p_a - p_b|\right)$$

where dissimilarity in cover-weighted species composition between all pairwise comparisons of 1-m<sup>2</sup> subplots at a site was calculated. To convince ourselves that this index, even though it is derived from species composition, is statistically independent of richness, we created and analyzed artificial data. For this exercise, we selected random samples from simulated populations that differed only in richness. We found that this index does not suffer from autocorrelation with species richness and, therefore, represents an independent measure of spatial heterogeneity.

#### *Structural equation modeling (SEM)*

*Development of the specific structural equation model.*—Following the development of a conceptual model to guide the modeling process, the next step in the SEM process relates observed variables to the relevant constructs (the term “construct” refers to the conceptual units in structural equation models) in order to form the complete structural equation model. The complete structural equation model represents a specific architecture that can include latent variables (which represent hypothesized but unmeasured factors), observed variables, and sometimes composite variables (which represent combinations of variables). Observed variables that serve as measures of concepts are referred to as “indicators.” For example, the number of species in a 1000-m<sup>2</sup> whole plot represents the sole indicator of the latent variable “richness” in this study. In this case, we used the data for 1994 as the indicator for richness because the number of species per plot generally peaks in this system in the first year following fire and subsequently declines over time (which was found in

our time course analysis). Total stem density and total plant cover were both considered as potential indicators for the latent variable “plant abundance.” However, because stem density was found to be unrelated to species richness, only total cover was used as a measure of plant abundance in our analyses. Fire index 1 was found to be a more consistent measure of fire severity in terms of community responses than was fire index 2, so this index was used as the sole indicator. An examination of bivariate relations, along with stepwise regression, was used to devise an index of optimum abiotic conditions. This index served as the sole indicator for the latent variable “local abiotic conditions.” The vegetation heterogeneity index of Collins (1992) served as the indicator for the latent variable “heterogeneity,” while the maximum age of plants in a stand was used to indicate “stand age.” Subshrub : shrub cover ratio largely distinguishes between the two major community types, chaparral and sage scrub, and served to indicate “community type” in the model. Finally, examination of patterns of variation in richness within the landscape revealed that richness was conspicuously related to distance from the coast of California. This then served as the indicator for “landscape position.”

*Model estimation and evaluation.*—Prior to SEM analyses, all variables were examined for distributional properties and the linearity of relationships. Certain relationships suggested the need for nonlinear specification, either prior to the SEM analysis or as part of the formal model. The relationship between distance from the coast and other measured variables was found to be unimodal; thus distance from the coast was transformed using polynomial regression to create a linear transform. Plant cover was also found to be unimodally related to richness. To accommodate this relationship while still allowing other variables to relate linearly with plant cover, an explicit nonlinear relationship between plant cover and richness was built into the model by including a second-order term, cover squared. All other relationships were observed to be linear.

Structural equation modeling permits the incorporation of estimates of measurement error for individual indicators of latent variables, thus allowing for reduced bias in path coefficients (Bollen 1989). An assessment was made of the reliability of individual indicators selected for inclusion in the model. Based on our knowledge of the methods used, we judged that a number of concepts were represented by indicators with little measurement error, specifically landscape position, stand age, and community type. Further, we also judged that including estimates of measurement error for the indicator of plant cover would have adverse impacts on our ability to model its nonlinear relationship with plant diversity (by inflating the correlation between plant cover and plant cover squared), thus measurement error was not assigned for cover. For two of the remaining variables, fire severity and within-plot heterogeneity,

conservative estimates of reliability were made and incorporated into the analysis. Since local abiotic conditions were estimated using a linear combination of other variables, we have no experience from which to estimate the reliability (repeatability) of this index. Therefore, the latent variable was fixed to the value of the indicator.

Model estimation was based on maximum likelihood. Robust estimation methods (Muthén and Muthén 2003: Appendix 4) were used to reduce effects of any deviations from multivariate normality on chi-square estimates and standard errors. The adequacy of model fit was evaluated using the model chi-square and its associated  $P$  values, as well as through the examination of deviations between observed and expected covariances. Other fit indexes examined (e.g., AIC, BIC, GFI) were found to be consistent with the chi-square test results. Individual path coefficients were also evaluated using  $z$  tests (equivalent to  $t$  tests) and by testing the consequences for model chi-square of omitting them from the model. Results presented are based on models found to have no significant difference between expected and observed covariances based on a critical  $P$  value of 0.05. Analyses were guided by the four models represented in Fig. 1, with Model A referring to the model containing all paths other than those indicated with letters, Model B additionally including path b, and so forth. Ultimately, results and interpretations presented in this paper are based on the model judged to be the best representation of the data, judged from comparisons among models and objective measures of model fit.

*Time course modeling.*—Temporal changes in richness over time (from the first to the fifth year) were evaluated separately from the comparison of models of spatial relationships. The purpose of this evaluation was to examine the joint hypothesis that (1) following fire, species richness declines over time, and (2) richness levels in any year were positively influenced by the amount of precipitation in that year. To evaluate this hypothesis, a form of SEM referred to as “latent growth curve modeling” (McArdle 1986) was performed using the software Mplus (Muthén and Muthén 2003: Chapter 22). The model evaluated was of the following form:

$$y_{it} = \eta_{0i} + \eta_{1i}x_t + \beta_p x_t + \varepsilon_{it}$$

where  $y_{it}$  refers to diversity in plot  $i$  at year  $t$ ,  $\eta_{0i}$  refers to initial postfire diversity in each plot,  $\eta_{1i}$  is the rate of decline for each plot,  $x_t$  is year number,  $\beta_p$  is a coefficient relating precipitation to diversity for the whole population of samples, and  $\varepsilon_{it}$  is the random error for each plot in each year. Latent growth curve modeling has the advantages that it accounts for interdependence over time (i.e., it is a form of repeated-measures analysis that examines the trajectories of individual plots) and allows for independent errors for each time period (thus relaxing the assumption of homogeneity of variance

across times). Robust estimation methods were again used to address possible deviations from multivariate normality.

## RESULTS

### *Bivariate relationships*

Richness in 1000-m<sup>2</sup> plots was found to correlate significantly with all local and landscape predictors except for community type. Not only was community type (sage vs. chaparral) not found to correlate with richness ( $P = 0.52$ ), it was also not found to correlate with any other variable. As a result, the construct “community type” was omitted from subsequent models (note that “construct” refers to a latent variable and its indicators). Scatter plots showing the bivariate relationships of variables with richness are shown in Fig. 2. Regression analysis confirmed that cover had a nonlinear relationship to richness, and a second-order polynomial model provided the most parsimonious fit of the relationship. The strength of the nonlinear correlation was  $r = 0.40$ . Several local abiotic variables were found to correlate with richness. Soil nitrogen was found to have a curvilinear negative relation, while sand content and rock cover had positive relationships with richness (Fig. 3). Stepwise regression was used to create an index of optimum abiotic conditions. This process yielded a predictor possessing an  $r$  value of 0.51 with richness. By examining the correlations between the multivariate predictor and individual abiotic variables, we determined that the greatest richness was associated with conditions of moderately low nitrogen ( $r = -0.39$ ), soils of high sand content ( $r = 0.26$ ), and high rock cover ( $r = 0.24$ ).

Richness was greater where the vegetation was more heterogeneous ( $r = 0.46$ ). Also, richness was lower where fire severity was greater ( $r = -0.37$ ) and where the preburn stand age was greater ( $r = -0.30$ ). Finally, richness generally increased with increasing distance from the California coast, peaking at a distance of ~60 km and declining somewhat at greater distances.

### *SEM results*

Community type was unrelated to any other variables in the model. This lack of association was confirmed within the context of the structural equation model, thus the community type construct was dropped from further consideration. Model evaluation proceeded as indicated by Fig. 1. Model A included only direct paths to richness from optimum cover, local abiotic conditions, and heterogeneity. It was found that plant cover did not depend on local abiotic conditions, therefore this path was dropped. It was also found that while the univariate relationship of richness to cover was unimodal, within the context of the SEM, only a positive linear relationship was detected. With adjustments for these non-significant relations, the resulting model yielded a chi-square of 22.45 with 12 df ( $P = 0.0328$ ), still suggesting a

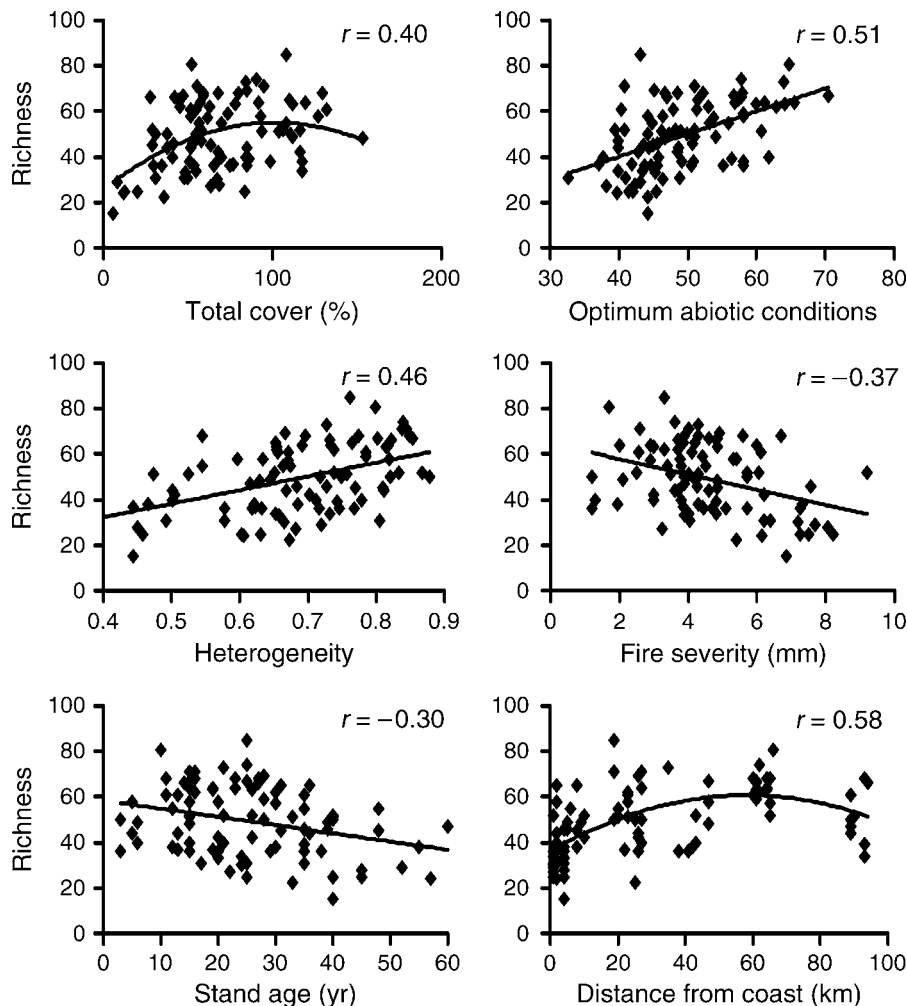


FIG. 2. Bivariate relationships. Richness refers to the number of species in 0.1-ha plots. Optimum abiotic conditions is a dimensionless scalar. Heterogeneity is in units of dissimilarity (see *Methods*). Fire severity is a measure of the diameters (in mm) of remaining twigs.

remaining discrepancy between model and data (note that in SEM, a nonsignificant  $P$  value means there are no major discrepancies between model and data). The inclusion of a path from landscape position to richness (path b in Fig. 1) resulted in a chi-square of 13.30 with 11 df ( $P = 0.2740$ ), indicating a substantial improvement in model fit. Both single degree of freedom chi-square tests ( $\Delta$  chi-square = 9.15) and tests of the significance of the path coefficient confirmed that the added pathway was justified. Since community type was dropped from the SEM analysis, results from Model C are not presented. The evaluation of Model D tested whether a direct path from stand age to richness led to a significant improvement in model fit. Model chi-square did not change significantly (13.30 vs. 12.11; note that a chi-square difference of 3.81 is required to indicate significant model improvement) and the coefficient associated with this added path was not significant ( $P$

= 0.25). Therefore, we rejected Model D in favor of Model B.

The results from the accepted model are shown in Fig. 4. Presented are a number of parameters, including (1) the proportion of variance in richness explained ( $R^2 = 0.53$ ), (2) loadings of indicators on latent variables (either 1.0 or 0.95), and (3) path coefficients (numbers associated with paths between latent variables). Two kinds of path coefficients (both are standardized based on the standard deviations) are presented in Fig. 4. For response variables with multiple predictors (in this case richness is the only one that meets this criterion), the incoming paths are represented by partial regression coefficients followed by semipartial coefficients. Partial coefficients, which are what is normally presented, represent the change expected if a predictor is varied (in standard deviation units). Thus, partial coefficients measure the predicted sensitivity of  $y$  to  $x$ . Semipartial coefficients (which follow the slash when presented)

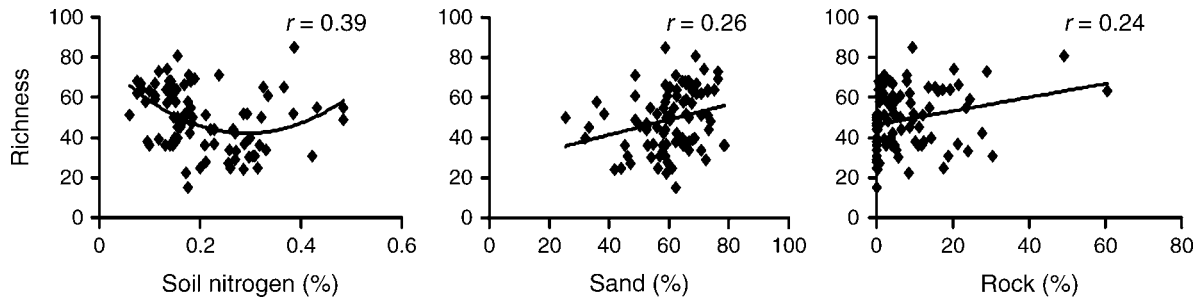


FIG. 3. Additional bivariate relationships involving species richness and specific abiotic predictors.

represent the square root of the unique variance explanation by  $x$  on  $y$ . Thus, semipartial coefficients represent unique explanatory information that can be attributed to a variable and that is uncorrelated with any other variable.

Overall, the model results (Fig. 4) reveal that (1) richness was positively and linearly related to plant cover, (2) plant cover was lower where fire severity was

high, (3) fire severity was greater where stand age was greater, (4) the correlations of stand age and fire severity to richness can be explained by an indirect association through plant cover, (5) local abiotic conditions had unique effects on richness, (6) richness was higher in plots high in heterogeneity, and (7) the association between richness and landscape position can be apportioned among four different pathways, including ones

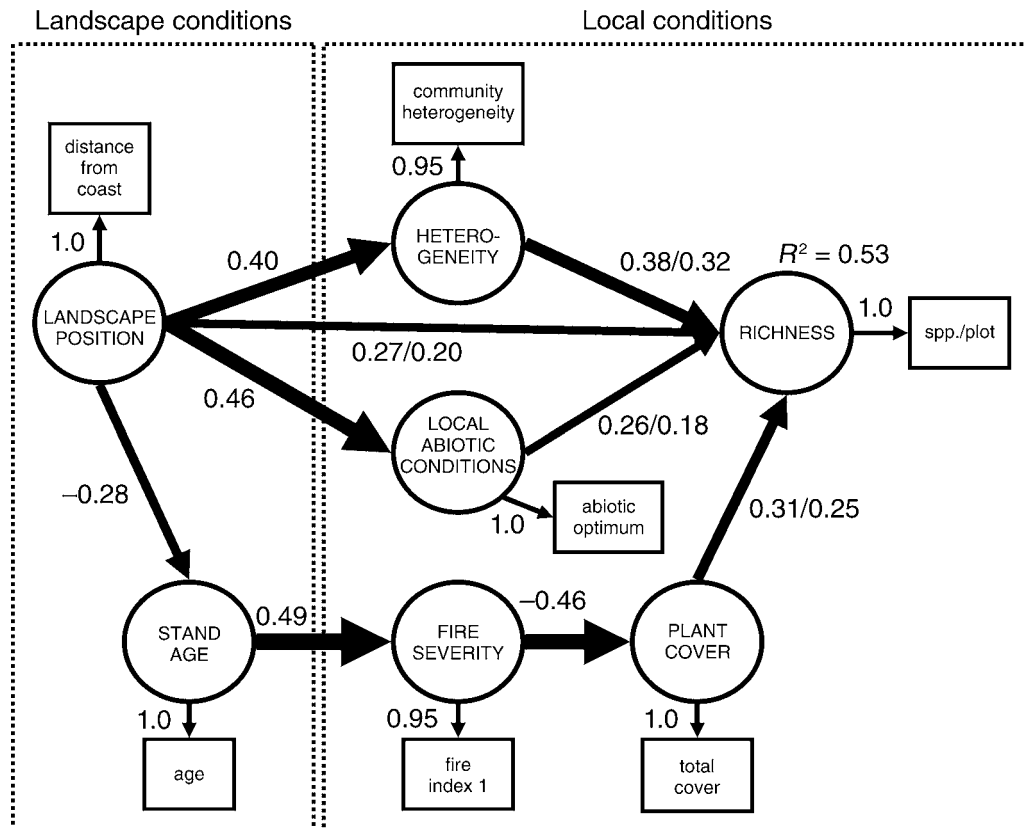


FIG. 4. Results for final model ( $\chi^2 = 26.6$ ,  $df = 25$ ,  $P = 0.38$ ). Circles signify latent variables used to represent theoretical concepts of interest, while boxes represent observed variables that serve as indicators of latent variables. Numbers associated with paths from latent to observed variables represent loadings, while numbers associated with paths between latent variables represent path coefficients. Estimates of measurement error were included in the analysis for community heterogeneity and fire severity, which explains why the loadings for these variables are  $<1.0$ . Path coefficients presented are standardized values (standardized by the standard deviations of the variables) and are of two types. For paths where two numbers are presented separated by a slash, the first number is the conventional path regression coefficient while the second number is the semipartial coefficient (which represents the unique influence of that variable; see *Results: SEM results*).

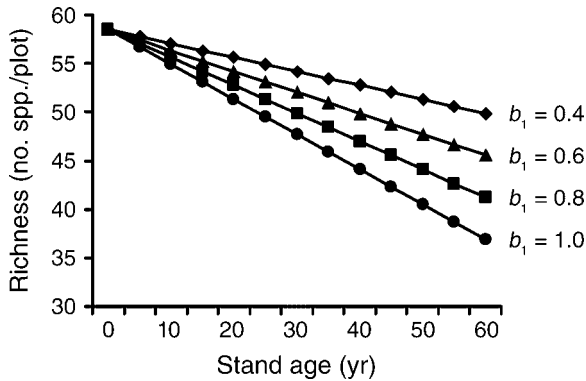


FIG. 5. Predicted sensitivity of richness to stand age at various levels of fire intensity (as a proportion of natural strength):  $b_1 = 1.0$  represents the average fire severity observed in these wildfires, while values  $< 1.0$  represent expectations if fire intensity were lower, for example, through the use of prescribed burning techniques under more moderate weather and fuel conditions.

involving stand age, local abiotic conditions, heterogeneity, and a residual direct path. At the level of local vs. landscape variables, nearly all of the variance explained for richness is attributed to local variables, with the sole exception of a modestly important path from landscape position. On the other hand, all local variables are associated with position along a landscape gradient, and the total effect (sum of all paths) of the relationship between landscape position and richness ( $=0.562$ ) is quite strong.

Unstandardized coefficients provide measures of the expected change in response variables in absolute units. Such coefficients derived from reduced-form equations

were used to explore the changes in richness that would be expected if we were able to reduce fire severity for any given aged stand using controlled burning. If we assume that proportional reductions in the relationship between stand age and fire intensity might be achieved using controlled burning (such reductions are represented by values of  $b < 1.0$ ), this yields a series of converging richness-response lines. Examination of these predicted response lines illustrates that in young stands, fire severity has little effect on richness and this leads to the prediction that reductions in fire intensity in young stands would have little effect on postburn richness. However, in older stands, reductions in fire severity could substantially enhance the recovery of vegetative richness (Fig. 5). At the fire intensities found in the wildfires that burned through this system ( $b_1 = 1.0$ ), there is an average loss of about 22 species per plot in the oldest stands compared to the youngest (36 vs. 58). If fires burning under more moderate fire conditions reduced the impact of stand age on fire severity to 40% of the intensity created by wildfires, for example, the expected loss of species in the oldest stands would be only about 7 (51 vs. 58).

#### Temporal dynamics in richness

Examination of temporal patterns for variables measured over time (Fig. 6) indicates that (1) in the absence of annual variations in precipitation, species richness would decline over time following fire, (2) elevated precipitation in years 2 and 5 was associated with higher diversity for those two years, (3) total plant cover increased over time following fire, particularly in wet years, (4) stem density increased and then decreased

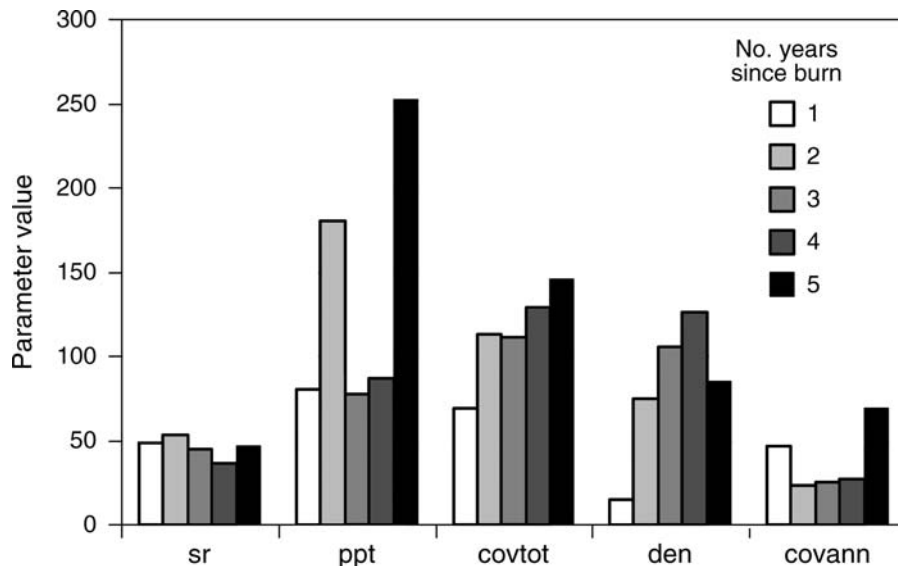


FIG. 6. Temporal variation as a function of years since burn (1–5) for species richness, sr (no. species/0.1-ha plot); annual precipitation, ppt (expressed as a percentage of normal); total plant cover, covtot (%); stem density, den (no. stems/m<sup>2</sup>); and the cover of annuals, covann (%). Analysis of these time course data was accomplished using latent growth curve modeling (see Results: Temporal dynamics in richness).



as colonization and then thinning took place, and (5) the cover of annuals was initially high (perhaps because of release by the fire) and thinned in year 2, but recovered in year 5 when rainfall was very high.

The effects of time and precipitation were evaluated further using latent growth curve analysis (Grace 2006: Chapter 7). This analysis is based on a model in which data are analyzed using a repeated-measures approach allowing for random slopes and intercepts for each individual plot. Results showed negative slopes for richness in plots over time, indicating that there was indeed an underlying declining trend for richness, though it was not strictly linear in all years. The average rate of decline was  $-4.351$  (number of species lost per year,  $t = -12.859$ ,  $P < 0.001$ ). On top of this declining trend, there was a highly significant positive relationship between annual precipitation and richness ( $t = 14.954$ ,  $P < 0.001$ ). For the model overall, a robust chi-square of 14.2 was found with 9 df ( $P = 0.115$ ), indicating no major deviations between data and model. Finally, the variances in richness explained by the model for years 1–5 were 34.3, 62.2, 68.5, 75.5, and 59.7%, respectively.

#### DISCUSSION

The spatial patterns in richness within the postfire landscape that we observed can be related to a substantial body of theory derived from the study of many systems. Historically, most models have tried to explain diversity patterns based on one or two factors. However, recent reviews of the literature and theoretical analyses have emphasized that plant species richness is under strong multivariate control (Diamond 1988, Grace 1999, 2001). The results of the present study support this view. In the discussion that follows, we consider in sequence the eight questions posed at the beginning of the paper.

As in many other studies, here we found a moderately strong relationship between richness and plant abundance. In this case, we found that richness generally increased up to the point of  $\sim 100\%$  total cover and then leveled off once canopy layers started to overlap (Fig. 2). This pattern suggests that positive influences (an increase in richness with increasing colonization) are involved and that at the highest levels of cover, negative influences (suggesting some form of competition) are detectable. However, within the context of the full model, the observed negative effect of cover on richness at high cover values was not sufficiently strong to be detectable.

Temporal dynamics are consistent with the idea that as cover exceeds some value, richness may decline, showing a loss of species with increasing plant cover over time (note that cover was much higher in later years than in year 1). In addition, a gain of species with high rainfall was observed. The evidence of a positive influence of precipitation on richness supports the general contention that resource availability variations

in time are important to species richness dynamics in this system (Keeley et al. 2005c).

While the results of this study are consistent with the often proposed idea that richness is related to habitat productivity (Grime 1979, Tilman 1988, Huston 1994), they are also consistent with other multivariate studies that indicate important roles for additional local factors (e.g., Grace and Pugsek 1997, Weiher et al. 2004). In this case, local abiotic conditions appeared to have significant effects on richness independent from associated variations in plant abundance. Specifically, conditions of either high or low (but not intermediate) levels of soil nitrogen, high sand content, and high rock cover were especially high in richness. These conditions, which were found to be optimal for diversity, were unrelated to plant cover, suggesting another type of influence, such as an association with diversity hot spots. In these arid land ecosystems open sandy or rocky sites favor herbaceous elements, which comprise the bulk of the regional species pool. Thus, we interpret this relationship as being consistent with the premise that environmental gradients filter species pools independent from effects mediated by productivity (Zobel 1992, Gough et al. 1994).

Richness was strongly associated with within-plot heterogeneity in species composition in this study. It is tempting to interpret this measure of heterogeneity as reflective of the spatial variation in environmental conditions, though strictly speaking, this requires some extrapolation deserving of further study. Other studies examining richness in small plots, in the range of 1–10 m<sup>2</sup>, have generally not reported substantial relationships with heterogeneity (Grace 1999). However, the results from our study, where 1000-m<sup>2</sup> plots were examined, would seem to support the contention that heterogeneity and associated niche complementarity are quite important in promoting high diversity (Grubb 1977, Diamond 1988, Tilman 1988, Cody 1991). Interestingly, across all sites there was a significant relationship between our measure of site heterogeneity and richness at 1-m<sup>2</sup> through 1000-m<sup>2</sup> scales during the first postfire year. By the fifth postfire year, heterogeneity at the lowest scale no longer appeared to contribute to diversity, though the effect persisted at the larger scale. Thus it would seem that the scale of habitat heterogeneity can change during succession.

Disturbance severity is often related to richness (Huston 1994). It is well known that fires create a high degree of spatial heterogeneity in their effects (Bond and van Wilgen 1996) and for this reason, disturbance severity was treated as a locally varying factor in this case. We found that postfire richness was lower in plots where fire severity was high. It is possible that this relates in part to the heat tolerance of seeds (Keeley 1991).

Landscape relationships to richness have been studied in the California flora and climatic variables taken

together are the strongest predictors of diversity (Richerson and Lum 1980). One of the strongest climatic predictors was annual precipitation. In this region the marked orographic gradient also causes a strong relationship between elevation and precipitation, and elevation has been found to be a strong predictor of plant diversity (Qi and Yang 1999). In this study we were not able to isolate the effect of elevation from the overall effect of landscape position. Thus, we must conclude that part of the effect of landscape position on richness (the part not mediated through indirect effects in the model in Fig. 4) remains unexplained. We also conclude that identity of the community type (chaparral vs. sage) did not provide unique information about richness patterns above and beyond that provided by the other landscape and local variables considered.

A second landscape relationship of interest was the tendency for older stands to have lower postburn richness (Fig. 2). There are several reasons why such a pattern might be observed. Since richness generally declines as stands mature in these systems, it could be that older stands have suffered a greater amount of competitive exclusion and, in conjunction, the seed bank is depauperate. Another possibility is that older stands have greater reserves for resprouting, and these exhibit a greater suppression of seedling establishment for herbs. The results from this study suggest that the reason older stands had lower richness following fire is entirely because fire intensity was greater (presumably due to greater fuel buildup), and fire severity was higher on average. Taken at face value, the structural equation modeling (SEM) results do not indicate that stand age had any additional effects on richness (such as a loss of species from the system over long fire-free periods) above and beyond its influence on fire severity.

Overall, this study supports the contention that patterns of richness are influenced by a complex of factors. In this context, it is interesting to consider the relative importance of factors as controlling agents. One way that relative importance can be quantified is in terms of so-called "total effects," which include both indirect as well as direct pathways. Total effects, in contrast to individual path coefficients, represent the degree to which richness should respond if we were to manipulate a variable and allow the variables it influences to simultaneously vary (note that path coefficients represent the expected change if all other variables were held constant). In this study, the total effects based on standardized coefficients were as follows: (1) landscape position = 0.562, (2) heterogeneity = 0.385, (3) plant cover = 0.307, (4) local abiotic conditions = 0.257, (5) fire severity = -0.141, and (6) stand age = -0.069. Thus, it can be argued that position in the landscape is one of the strongest single predictors of postfire richness, though this can be largely explained by the local and landscape conditions associated with particular locations. Spatial heterogeneity and plant

cover were the two local factors most related to richness variations, while abiotic conditions and disturbance intensity were of lesser importance.

An alternative view of relative importance can be obtained by asking how variables contribute to explaining the variations in richness that were observed. This question relates to the issue of unique explanatory importance. When predictors are intercorrelated, unique explanatory importance can best be quantified in terms of unique variance explanation. The unique role each variable plays within the model can be quantified using semipartial coefficients. In this case, the standardized semipartial coefficients were: (1) heterogeneity = 0.32, (2) plant cover = 0.25, (3) landscape position = 0.20, and (4) local abiotic conditions = 0.18, with fire severity, stand age, and landscape position having no unique variance explanation ability (because they have no direct paths to richness).

Based on these results, we suggest that diversity at the scale of 1000-m<sup>2</sup> plots in this system appears to be predominantly controlled by local factors, particularly by the degree of spatial heterogeneity in vegetation, which presumably reflects niche partitioning, and by intermediate levels of productivity, which likely reflect a point where colonization is favorable and competitive exclusion is modest. It also appears to be true that there are variations in the local species pool controlled by particular abiotic conditions (represented by direct effects of abiotic conditions on richness), though this effect is not as pronounced as has been reported for systems with strong abiotic gradients (e.g., Grace and Pugsek 1997).

Plant diversity in California shrublands has long been known to follow a marked temporal pattern with the greatest diversity concentrated in the early postfire years (Keeley 2000). Woody growth forms increase in size, cover, and biomass during early postfire succession (Guo and Rundel 1997, Guo 2001, Keeley et al. 2006), and thus time since disturbance likely affects diversity through the inhibitory effect of shrub cover on herbaceous diversity (Carrington and Keeley 1999, Safford and Harrison 2004). In the present study, time course results indicate that there was a general trend of declining species richness during the first five postfire years, with an additional influence by variations in annual rainfall. Thus, it seems likely that precipitation may be an important temporal (and possibly spatial) factor behind diversity patterns after fire. The primary effect of annual variation in precipitation appears to be the inhibitory effect of low rainfall on annual species germination (Keeley et al. 2006).

#### MANAGEMENT IMPLICATIONS

Commonly applied management operations in southern California shrublands include prescribed burning to diminish hazardous wildfires. Of prime interest is reducing the threat of fires burning into the urban

environment, but the threat to natural resources is also a concern to many land managers. Oftentimes prescription burning is justified on the grounds that by burning under moderate weather conditions one can produce less severe fires than those associated with uncontrolled wildfires. Part of the reduction in fire severity is achieved by burning using prescriptions that call for modest winds, moderate humidities, and nonextreme fuel moisture conditions. Ignition techniques and preburn fuel management can also be selected so as to restrict fire intensity and rates of spread. The results presented in this study support the notion that low intensity prescribed burns may indeed reduce adverse impacts on postburn diversity. However, as the converging lines in Fig. 4 indicate, this moderating effect of prescribed burning is only of substantial significance in older stands. In younger stands, we would project that prescribed fire would have little benefit for diversity recovery.

In the real world of fire management, multiple constraining factors must be considered. Keeley et al. (2005b) have examined the invasion of burned-over areas by exotic plant species and have raised concerns about the potential for frequent burns to facilitate invasions and spread of exotics in these systems. They suggest caution in the use of prescribed burning for southern California shrublands, in part because of the potential to increase exotic plant invasions and in part because some of these exotic species (especially various species of *Bromus* L.) can act to intensify fire risk. They further argue that the greatest potential for harm is from frequent prescribed fires, which maintain shrubs in a young stage of development.

When the potential for prescribed burning to reduce impacts on postburn recovery of diversity is balanced against the risk of spreading exotic species using frequent burns, it would seem that prescribed fire may be most useful when applied on an infrequent basis and primarily in older stands. In older stands of sage and chaparral, prescribed burning can reduce adverse impacts on diversity, which is expected to be high. At the same time, it may be that confining burning to older stands (and, therefore, infrequent burning) is less likely to permit exotics to invade these systems by reducing the period of time when shrub domination is relaxed. We recognize that in areas where wildfire threatens urban areas, other considerations will override concerns about biodiversity. However, for areas managed for conservation purposes, use of prescribed fire for managing older stands may be beneficial if it can be done without encouraging persistent populations of exotics. This possibility needs further evaluation before a strong recommendation can be made. From the broadest perspective, the development of appropriate recommendations for managing biodiversity will require us to go beyond an understanding of the current dynamics of systems to also include additional factors not yet in play.

Among the most severe of these are those that relate to invasive exotic species (Brooks et al. 2004), which can interact with existing processes in complex ways and for which we need substantially more information than currently available.

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