FIRE SEVERITY AND ECOSYTEM RESPONSES FOLLOWING CROWN FIRES IN CALIFORNIA SHRUBLANDS

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Abstract. Chaparral shrublands burn in large high intensity crown fires. Managers interested in how these wildfires affect ecosystem processes generally rely on surrogate measures of fire intensity known as fire severity metrics, which typically measure organic matter loss above- and belowground. In California shrublands burned in the autumn of 2003, a study of 250 sites distributed across five fires, investigated factors determining fire severity in these ecosystems and the extent to which fire severity ecosystem responses.

Using structural equation modeling we showed that stand age, prefire shrub density and the shortest interval of the prior fire history had significant direct effects on fire severity, explaining over 50% of the variation in severity.

Fire severity *per se* is of interest to resource managers primarily because it is presumed to be an indicator of important ecosystem processes such as vegetative regeneration, community recovery and erosion. Our bivariate models as well as structural equation modeling showed that fire severity contributed relatively little to explaining patterns of vegetative regeneration after fire, measured as cover of all species or as resprouting success of shrubs. Where fire severity did affect recovery, two generalizations can be drawn: fire severity effects are mostly short-lived, i.e., by the second year they are greatly diminished, and fire severity may have opposite effects on different functional types.

Species richness exhibited a highly significant negative relationship to fire severity in the first year but fire severity impacts were substantially less in the second postfire year and varied by functional type. Much of this relationship was due to alien plants that are sensitive to high fire severity; at all scales from 1 – 1000 m^2, the percentage of alien species in the postfire flora declined with increased fire severity. Other aspects of disturbance history are also important determinants of alien cover and richness as both increased with the number of times the site had burned and decreased with time since last fire.

A substantial number of studies have shown that remote-sensing indices are correlated with field measurements of fire severity. Across our sites, absolute dNBR was strongly correlated with field measures of fire severity and with fire history at a site but relative dNBR was not. Despite being correlated with fire severity, absolute dNBR showed little or no relationship with important ecosystem responses to wildfire such as shrub resprouting or total vegetative regeneration. These findings point to a critical need for further research on interpreting remote sensing indices as applied to postfire management of these shrublands.

Key-words: *dNBR; ecosystem responses; fire intensity; fire severity;* Landsat*; postfire regeneration, postfire resprouting;* ΔNBR

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INTRODUCTION

California chaparral comprises closed-canopy fire-prone shrublands that burn in large high intensity crown fires. Understanding how variations in fire intensity affect ecosystem responses such as soil erosion and community recovery is important to managing these landscapes, particularly where urban development interfaces with these wildlands. Studies of prescribed burns have shown direct effects of fire intensity on ecosystem responses such as resprouting and seedling recruitment (Davis et al. 1989, Borhert and Odion 1995, Tyler 1995). However, after wildfires one must rely on surrogate measures of intensity and these are called fire severity measures. A number of sources define fire severity broadly as ecosystem impact (e.g., NWCG 2006), but, operationally, fire severity metrics have a common basis in that they measure various aspects of organic matter loss, above- and belowground (Keeley in press). Measurement of fire severity varies with the ecosystem and management need. In forests a common measure is the volume of canopy scorch and sometimes tree mortality, and studies have shown that these are strongly correlated with fire intensity as measured by flame length (e.g., Wade 1993, Cram et al. 2006). In shrublands and some crown fire forest types the diameter of the smallest twig has been widely used as a fire severity metric, and it also has been shown to be strongly correlated with measures of fire intensity related to heat production (Moreno and Oechel 1989, Perez and Moreno 1998, Keeley et al. 2005a). Mortality is not a good measure of fire severity in these ecosystems because all aboveground biomass is typically killed, and the mortality of entire genets (i.e., above- and belowground parts) is more a function of community composition (i.e., presence of resprouting species), than it is a function of fire intensity. US federal agencies routinely participate in immediate postfire assessments under the Burned Area Emergency Response (BAER) program that measures fire severity impacts on soils, although they typically use the term burn severity rather than fire severity (Robichaud et al. 2000). As with other fire severity assessments, these burn severity measures also focus on loss of organic matter through their assessment of ash deposition, loss of duff layers and related parameters (Stronach and McNaughton 1989, Christensen 1994, Neary et al. 1999, NWCG 2006).

In shrublands, a multitude of parameters affect fire severity, including both abiotic factors such as slope aspect and inclination (Keeley et al. 2005d) as well as biotic factors, in particular fuels. Fire severity is strongly affected by the quantity of fuels and the proportion of dead fuels retained in the shrub canopy (Bond and van Wilgen 1996, Schwilk 2003). Stand age is considered to be one of the more critical factors because biomass accumulates due to moderate growth rates and relatively slow decomposition of dead organic matter (Keeley and Fotheringham 2003). It is commonly assumed that fire intensity and fire severity increase as stands age, indeed this is one of the basis for fuel management strategies in this vegetation type (Minnich 1995). However, the only study that has looked for such a relationship failed to find a connection between fire severity and stand age in chaparral across 40 sites, but did find such a relationship in sage scrub across 50 sites (Keeley et al. 2005a).

In terms of postfire management, direct measurements of fire intensity or fire and burn severity per se are important only to the extent to which they affect ecosystem responses to fire (Fig. 1). There is a substantial body of literature showing that fire has a significant impact on ecosystem functioning, affecting both vegetation and watershed processes. What is less clear is the extent to which fire severity, or burn severity as it sometimes called, controls ecosystem responses. In forests and shrublands some of the more important ecosystem responses to fire are changes in watershed hydrology. Assessments that focus on soil burn severity are thought to be good predictors of changes in hydrologic functioning, and although fire *per se* has marked impacts on hydrology, there is not a lot of evidence for shrubland systems that the degree of fire severity is strongly linked to processes such as erosion and debris flows (Robichaud et al. 2000, Doerr et al. 2006).

Studies of other ecosystem responses to the degree of fire or burn severity have shown variable relationships, dependent on the response variable and vegetation type. Studies in forests with surface fire regimes commonly report a strong relationship between fire severity metrics such as crown scorch and duff consumption and tree mortality (e.g., Wade 1993, Wang and Kemball 2003, Franklin et al. 2006). However, in crown fire shrublands, aboveground mortality is generally a 100% regardless of differences in fire severity. For chaparral shrubs capable of resprouting, fire severity does affect belowground survivorship and thus resprouting success (Rundel et al. 1987, Moreno and Oechel 1989), but fire severity is not as critical in determining resprouting of sage scrub subshrubs (Keeley 2006). In terms of overall vegetative recovery, one study in California chaparral showed no significant effect of fire severity, although in the lower stature sage scrub there was a significant effect (Keeley et al. 2005a). Of particular interest from that study is the observation that fire severity had opposite effects on different functional types; subshrub cover in the first growing season was inversely related to fire severity, whereas cover of the suffrutescents (chamaeophyte) was positively associated with fire severity. Several studies have shown that although seedling recruitment in general is inhibited by high fire severity, obligate seeding *Ceanothus* recruitment is positively associated with high fire severity (Moreno and Oechel 1994, Keeley et al. 2005a, 2005d). Alien plant invasion also has exhibited a variable response to fire severity; it increased with fire severity in sage scrub but not in chaparral (Keeley et al. 2005c).

A substantial number of studies have shown that remote-sensing indices are correlated with field measurements of fire or burn severity, which could greatly facilitate postfire assessments (Rogan and Franklin 2001; Miller and Yool 2002; Chafer et al. 2004; Hammill and Bradstock 2006). In recent studies utilizing remote sensing data, field validation has used the term severity in a way that diverges from previous usage as a measure of organic matter loss; these studies have incorporated ecosystem responses such as plant regeneration in their measure of fire severity (Epting et al. 2005;

Cocke et al. 2005; Chuvieco et al. 2006). This approach is described as the *composite burn index* and it is designed to provide a single index that represents many different phenomena of interest to land managers (Key and Benson 2006). Thus, the composite index combines fire severity metrics and ecosystem response metrics, but the applicability of this approach to some ecosystems has been questioned (Keeley in press).

The present study investigates the factors that affect fire severity in chaparral across several large wildfires that burned at about the same time in the autumn of 2003 in southern California. Our focus was on those factors that affect fire severity, the relationship between fire severity and ecosystem responses, and the extent to which remote sensing data could predict fire severity and ecosystem responses. Previous chaparral studies with 40 sites revealed few significant relationships with fire severity (Keeley et al. 2005a, 2005b), and so we increased our sampling effort to 250 sites in this study.

SITES AND METHODS

Study sites

Sites were distributed across five fires that burned in autumn 2003 (Fig. 2). The Grand Prix Fire ignited 21 Oct and the remaining fires started within the subsequent five days. Shrublands were the main vegetation type burned, comprising from south to north: 83% in the Otay, 83% in the Cedar, 81% in the Paradise, (Fig. 2a) and 73% in the Grand Prix / Old fire complex (Fig. 2b) (http://frap.cdf.ca.gov/socal03/tables/fuels.html; accessed April 2007). The Otay Fire was largely on BLM land, the Cedar Fire a mixture of mostly USFS lands plus State Parks, BLM, Tribal lands, County Parks and private property, and the Grand Prix/Old fires mostly on USFS and private land.

A total of 250 sites were divided between fires based roughly on size of fire, accessibility and diversity of stand ages (Table 1). Site locations were recorded with a Garmin 3+ GPS unit (Garmin, Olathe, Kansas, USA), and GIS data layers of all sites were generated. Sites were selected to include roughly comparable numbers of apparently low and high severity fires from stands of varying ages, which was initially assessed by differences in shrub skeleton height. This landscape has a very complex geology and sites were located on granitic fault block uplift, volcanic extrusions, marine terraces and alluvial deposits, although these factors were not included in our analysis.

Field methods

Sampling was conducted in the spring and early summer of the first and second years following the fires. Each site consisted of a 20 x 50 m sample plot, positioned parallel to the elevational contour of the slope in order to capture the greatest variation in community composition (Keeley and Fotheringham 2005). Each of these tenth hectare plots were subdivided into 10 nested 100-m^2 square subplots, each with a single nested 1-m^2 square quadrat in an outside corner (see Figure 4 in Keeley et al. 2005a). Cover and density were recorded for each species within the quadrats and a list of additional species was recorded from the surrounding subplot. Cover was visually estimated and a percentage of ground surface covered was recorded for each species. Density was recorded for each species with counts where density was less than approximately 30 individuals, and with estimates at higher densities. Seedlings and resprouts of the same species were counted and recorded separately. All plant nomenclature follows Hickman (1993).

Prefire shrub densities were estimated by recording the number of skeletons of individual species of shrubs in each 100-m^2 plot during the first postfire year. Each skeleton was identified to species based on form, branching pattern, bark characteristics and root-crown shape (Keeley *et al*. 2005a). The number of resprouting shrubs was also recorded for each species.

For fire severity estimates, the diameter of the smallest twig remaining on the two *Adenostoma fasciculatum* skeletons nearest to each 1-m^2 quadrat was recorded. On sites where *Adenostoma* density was low, one *Adenostoma* and one other shrub species were measured and these data were used to predict *Adenostoma* twig diameter when that species was sparse or missing. Another measure of biomass loss from fire is skeleton height, and this was measured on the same two *Adenostoma* skeletons.

Site factors recorded were slope aspect and inclination. Latitude, longitude, and elevation were taken from GIS layers and radiation load was calculated from slope aspect, inclination, and latitude (McCune and Keon 2002). Three soil samples were collected in the first growing season from the top 6 cm of soil from alternating plots within the 20 x 50 m site and combined and dried in paper bags. A texture analysis was done according to (Cox 1995) and total soil Kjeldahl nitrogen and phosphorous were determined on a sub-sample at the DANR Analytical Laboratory, University of California, Davis. Precipitation data were obtained from the Western Regional Climate Center (http://www.wrcc.dri.edu/summary/Climsmsca.html; accessed April 2007) for climate stations distributed within the range of sites for postfire years 1 and 2. Totals for the growing season (September-August) were averaged from stations within each fire for each year. Prefire stand age was determined for each site by counting the rings from two shrub skeleton basal stem sections. At most sites stand age was determined from obligate-seeding *Ceanothus* or *Arctostaphylos* species. These species provide an accurate estimate of the time since last fire due to the rarity of missing or extra rings (Keeley 1993) and the nearly exclusive restriction of seedling recruitment to the first postfire year (Keeley et al. 2006). In a few cases when neither species was present, ages were based on the largest stem from the resprouting *Adenostoma fasciculatum*. Stand ages based on ring counts were compared with data on fire history from statewide fire perimeter GIS data layers of these fires (California Department of Forestry and Fire Protection 2004; http://frap.cdf.ca.gov/data/frapgisdata/select.asp; Oct 2007).

Data analysis

Fire severity was based on the diameter of the smallest twig remaining on *Adenostoma fasciculatum* skeletons. The foundation for this estimate is the demonstration that higher fire intensities are correlated with the diameter of terminal branches on burned skeletons of a number of species (Moreno and Oechel 1989, Perez and Moreno 1998). Least squares regression analysis was used to relate diameters of *Adenostoma* with diameters of associated species at the same site and this relationship was used to predict the expected twig diameter of *Adenostoma* on three sites where it was absent.

Data were organized in an Access database and analyses were conducted with Systat 11.0 (Richmond, CA, USA). Least squares regression was used to test bivariate models of hypothesized dependence on fire severity. Other relationships were explored with correlation analysis using the Pearson correlation. This exploratory analysis used the Bonferroni adjustment for *P*-values $(1 - (1 - P)^x)$, where x = the number of correlations in the exploratory analysis; this correction is arbitrary in that it depends on the number of analyses packaged in a single test and it provides a conservative estimate of significance at the cost of rejecting some significant relationships. Considering the multiple sources of error associated with field studies, this more conservative approach seemed appropriate.

Structural equation modeling

In order to evaluate the role of the many factors determining fire severity and ecosystem responses, we utilized structural equation modeling (Grace 2006). This approach allows one to test hypothesized models of direct and indirect effects by comparing the covariance structure of the data against that expected for the model. Our hypothesized model for factors determining fire severity included the following conceptual or latent variables for direct effects: stand age, prefire community structure, course-grain topographic variation, fine-grain topographic variation and substrate (Fig.

3a). Our model for factors determining ecosystem responses included these same variables plus fire severity as a direct effect (Fig. 3b).

These latent variables are characterized by observed indicator or measurement variables, which were initially evaluated for inclusion with bivariate regression and for linearity with scatter plots. Some variables were log-transformed to improve their linearity. The path coefficients between indicator and latent variables can be biased by measurement error and structural equation modeling allows these errors to be included in the model. In most cases the nature of the measurement variable did not suggest any measurement error, e.g. elevation, stand age, radiation load etc. For other measurement variables with multiple samples within a site we estimated reliability (i.e., repeatability) by randomly assigning measures to one of two groups and determining their average correlation across sites. Reliability was used to specify error variances, defined as: error variance = (1- reliability squared) times the variance. In a couple cases, e.g., soil texture and phosphorous, samples had been combined prior to analysis and no measurement error estimate was possible.

Estimation of model fit to the data was based on maximum likelihood with MPlus (Muthén and Muthén 2003). Adequacy of model fit was evaluated using the model chi-square and associated *P* -value. Path coefficients were evaluated using z-tests and by testing the effect of their removal on the model chi-square. Results presented are for models with no significant difference between expected and observed covariances based on a critical *P*-value of 0.05.

Remote sensing fire severity

Remote sensing studies have found a good correlation between Landsat signals, particularly the Normalized Difference Vegetation Index (NDVI), and fire severity estimates based on biomass loss (e.g., Miller and Yool 2002, Chafer et al. 2004). A widely used measure of fire severity calculates the difference between prefire and postfire Landsat signals from sites for the ratio of reflectance from bands 4 and 7; this is the differenced Normalized Burn Ratio (dNBR), defined as (R4 – R7) /

(R4 + R7). This dNBR index was provided by the USGS EROS data center (Sioux Falls, SD, USA) and was scaled from 0 – 250. Typically USGS and USFS dNBR assessments are done both immediately postfire and in the subsequent growing season. Due to cloud cover, the only immediate assessments available were for the Grand Prix/Old Fire Complex and that assessment had very little variation across our study sites. However, all fires had assessments available for the spring and summer following fires; the spring assessment used images taken on 11 May 2003, 4 months before the fire, and on 11 April 2004, 5 months after the fire and the summer assessment was taken on 14 July 2003 and 14 July 2004. Recently Miller and Thode (2007) have proposed that the relative dNBR (dNBR/prefire NBR) has advantages in detecting postfire changes and so we also added this index to our analysis. With GIS we overlaid the locations of our plots on these dNBR maps (Fig. 2) and investigated the relationship of fire severity and ecosystem response variables to dNBR. To evaluate the relationship between dNBR and past disturbance history we overlayed the statewide fire history (California Department of Fire and Forestry, FRAP database) and determined the average dNBR for all the pixels within a particular fire perimeter.

RESULTS

A total of 250 sites distributed across these five fires (Fig. 2) exhibited a range of fire severities and other site variables (Table 1). Precipitation throughout the region was below average in the first postfire year and well above average in the second year (Table 1). Sites from the Cedar Fire, the largest of all the fires, exhibited the greatest range of environmental conditions, however, in all fires a diversity of different aspects, inclinations, soils, stand ages, prefire shrub density, and fire severity were sampled. Stand age used in this analysis was determined from ring counts since there were 70 sites that did not have a record of past fires on FRAP fire maps. Of the remaining 180 sites, the mapped age matched the stem age on 53% of those sites and in nearly all cases where it didn't, the stem age was younger; stem age apparently recorded fires not captured by fire maps and was interpreted for this study as the correct stand age. In general, fire-map age was a modestly good, but far from perfect, predictor of stand age ($r^2 = 0.65$, $P < 0.001$, n = 180). This study included stands less than 5 years of age and ones over 40, with the bulk of sites falling between 21 – 35 years (Fig. 4).

Fire severity metric

Our metric for fire severity was diameter of the smallest twig on *Adenostoma fasciculatum* skeletons. Although this species occurred at 247 of the sites, density of prefire skeletons was insufficient to produce an adequate sample at 60 sites, so at those sites we predicted *A. fasciculatum* twig diameter from measurements on other species. This extrapolation was supported by the determination that there was a highly significant relationship between *A. fasciculatum* postfire twig diameter and associated species at sites where both were measured (Table 2).

Our fire severity metric was also weakly related to another measure of biomass loss, specifically the height of *Adenostoma* skeletons; $r^2 = 0.14$, $P < 0.001$, n = 250. Skeleton height, however, was not significantly related to any other site variable. Fire severity was not correlated with elevation, slope incline, estimated annual solar insolation or rock cover, but was highly correlated with percentage sand, nitrogen and phosphorous in the soil (Table 3).

Bivariate regression analysis showed stand age was a very good predictor of fire severity, explaining 50% of the variation (Fig. 5a). Another significant predictor of fire severity was prefire shrub density (Fig. 5b), however, shrub density and stand age were not significantly related to each other ($P = 0.32$, n = 250). Multiple regression with both stand age and prefire shrub density gave an adjusted $r^2 = 0.50$, $P < 0.001$, n = 250), this did not improve with addition of other independent variables including times burned or shortest interval between fires. For the 10 most common shrub species (present at more than 50 sites), correlation analysis with Bonferroni adjusted *P*-values showed that fire severity was negatively correlated with *Adenostoma* density (r = - 0.32, $P < 0.001$, n = 247), positively correlated with *Ceanothus greggii* density (r = 0.30, P = 0.006, n = 87) and not correlated with the prefire density of another eight shrub species (P > 0.34, the lowest for these other species).

Fire severity effects on postfire recovery

Total vegetative regeneration in the first growing season ranged from near zero to over 50% of the ground surface covered, yet there was only a very weak relationship between total plant cover and fire severity (Fig. 6a). In the second postfire year total cover ranged between 25 – 100% and there was no significant relationship with fire severity (Fig. 6b). Focusing on just the woody cover showed that in the first growing season it did not respond to fire severity (Fig. 6c). Also, there was no correlation between fire severity and any life history type, but there was a significant negative correlation in both years with alien cover (Table 4). Only three native annual species occurred at more than 50 sites; cover of two of these, *Emmenanthe penduliflora* and *Filago californica*, was not significantly related to fire severity (Bonferroni adjusted P = 0.75 and 0.20, n = 53, 57, respectively), but the third, *Antirrhinum nuttalianum*, was positively related to fire severity (r = 0.30, Bonferroni adjusted P = 0.041, n = 67).

Seedling recruitment of one woody species, *Ceanothus leucodermis*, was positively correlated (r = 0.40, Bonferroni adjusted P = 0.032, n = 51), and another, *Helianthemum scoparium*, was negatively correlated with fire severity (r = -0.36, Bonferroni adjusted P < 0.001, n = 172). The remaining species with seedling recruitment at 50 or more sites exhibited no significant relationship with fire severity (P > 0.10, the lowest observed for this group, which included *A. fasciculatum*, *Ceanothus greggii*, *C. tomentosa*, *Lotus scoparius*, *Malosma laurina, and Salvia mellifera*).

Resprouting capacity was variable between species. For the most widespread shrub, *Adenostoma fasciculatum*, percentage of the prefire population resprouting varied from 3 to 100%, but it was not predicted by fire severity (Fig. 6d). Correlation analysis also showed that resprouting of other common species found at more than 50 sites, *Arctostaphylos glandulosa, Malosma laurina, Quercus berberidifolia*, *Rhamnus crocea* and *Xylococcus bicolor*, was not related to fire severity (Bonferroni adjusted $P > 0.32$, the lowest for this group) but resprouting of *Ceanothus leucodermis* was ($r = -0.45$, $P = 0.044$).

Regression analysis showed that species richness exhibited a highly significant negative relationship with fire severity in the first year, although there was much site to site variability, and thus less than 15% of the variance was accounted for by this model (Fig. 6e). Fire severity impacts on diversity were substantially less by the second postfire year (Fig. 6f). The correlation of fire severity with species richness varied between the different life history types (Table 5); herbaceous species richness was negatively correlated with fire severity, subshrubs exhibited no correlation and shrubs exhibited a positive correlation.

Much of the decline in species richness observed in this study was due to alien plants being highly sensitive to high fire intensity. Regression analysis showed that at all scales the percentage of alien species in the postfire flora declined sharply with increased fire severity (Fig. 7). This relationship is important because the first year diversity of alien species was highly predictive of the cover of aliens in subsequent postfire years (Fig. 8). The vast majority of aliens were annual grasses and forbs and each of the most common aliens, *Bromus madritensis, Brassica nigra, Hypochoeris glabra, Erodium cicutarium* and *Centaurea melitensis* increased cover by about an order of magnitude in the second postfire year. The most widespread alien was *B. madritensis* and density and cover were negatively correlated with fire severity ($r = -0.51$, -0.34, Bonferroni adjusted $P < 0.001$, 0.01, respectively, $n = 67$). Disturbance history is an important determinant of alien cover success. The number of times a site burned was positively correlated with alien cover ($r^2 = 0.10$, $P < 0.001$) and with species richness ($r^2 = 0.13$, $P < 0.001$) and time since last fire (i.e., stand age) was negatively correlated with both of these response variables ($r^2 = 0.15$, $P < 0.001$ for both of these dependent variables).

Structural equation modeling

Examination of bivariate relationships of all relevant parameters led us to the decision that all latent variables were best represented by a single measurement variable and these are presented with the model results. For several variables the log of the indicator variable provided a better linear relationship.

Our model of fire severity used the log of skeleton diameter as the indicator for fire severity, annual ring counts for stand age, log prefire shrub density for prefire stand structure, elevation and radiation load as the indicators for coarse-grain and fine grain topographic effects, respectively (Fig. 9). Most indicators were assumed to not have any measurement error and reliability is indicated as 1 on the outward arrows from latent variable to indicator variable. The estimated reliabilities for log skeleton diameter and log prefire shrub density were relatively high. Our original model (Fig. 3a) fit the data well, as shown by no significant departure between the covariance structure of the indicator data set and the covariance structure implied by the latent variable model ($\chi^2 = 0.86$, 1 degree of freedom, $P = 0.36$). The model explained over half of the total variance in fire severity ($R^2 = 0.52$). Standardized path coefficients shown in Fig. 9 indicated that stand age contributed most strongly to fire severity, but significant effects were contributed by short fire intervals and prefire stand structure. Significant indirect effects included fine grain topographic effects and shortest fire interval on prefire structure. Stand age and shortest interval between fires were strongly correlated, indicating that short intervals between fires were more common recently than earlier in the record.

We investigated how fire severity related to ecosystem response variables in a multivariate context with other ecosystem parameters (Fig. 3b). The first ecosystem response variable was total plant cover in the first postfire year and the data gave a good fit to the full model (χ2 = 3.13, df = 4,

P = 0.54), however, the direct path of one of the latent variables, prefire structure, was not significant and was removed. The remaining model (Fig. 10) gave a good fit ($\chi 2$ = 2.59, df = 3, P = 0.46) and explained nearly 80% of the variability in first year cover. Fire severity had a significant but relatively minor effect on postfire cover. The strongest determinants were topographic effects such as elevation and substrate. Substrate was significantly correlated with stand age suggesting different substrates have different fire histories. Soil nutrients were correlated with substrate, elevation, and stand age.

Species diversity at the tenth-ha scale showed a good fit to the model ($\chi 2$ = 4.40, df = 3, P = 0.22) after prefire structure was removed, but explained only 17% of the variation (model not shown). At the smallest scale, 1-m^2, the R^2 = 0.42 for the model with prefire structure but without substrate ($\chi 2$ = 5.33, df = 3, P = 0.15; model not shown).

Alien cover in the first postfire year did not fit the full model (Fig. 3b) due to lack of a coarse-grain topographic (elevational) effect. With that variable removed (Fig. 11) the modified model explained 35% of the variance ($\chi 2$ = 0.16, df = 2, P = 0.92). The strongest direct effects were the negative impacts of prefire stand age and fire severity. All of the remaining latent variables showed negative effects on alien cover.

First year alien diversity at the tenth-ha scale also did not fit the full model (Fig. 3b) because neither prefire stand age nor substrate had significant effects. The final model (Fig. 12) was significant ($\chi 2$ = 5.45 df = 3, P = 0.14) and explained 35% of the variation. Fire severity had by far the strongest effect on alien diversity.

Predicting fire severity and ecosystem responses with remote sensing

The differenced Normalized Burn Ratio (dNBR) mapped on each of the fires studied here is shown along with the field sites in Figure 2. This remote sensing index measured in the spring at the peak of the growing season was a significant predictor of fire severity measured in the field (Fig.

13a), and summer dNBR exhibited a similar strong relationship ($r^2 = 0.42$, $P < 0.001$; not shown). In contrast to the strong relationship between the absolute dNBR and fire severity, the relative dNBR was only very weakly related to fire severity (Fig. 13b) and not used in further analysis. Stand age was significantly related to dNBR ($r^2 = 0.20$ and 0.24 for spring and summer, respectively, $P < 0.001$). Across the entire span of the fire severity map the number of times an area burned was an important factor determining the dNBR (Fig. 14).

Considering the fact that our field measurements of fire severity showed little relationship to vegetative recovery (Fig. 6), it is not surprising that ecosystem response variables such as plant cover and percentage of *Adenostoma fasciculatum* resprouting were not significantly related to dNBR (Fig. 15).

DISCUSSION

Chaparral fires are generally considered high intensity because fire intensity in these shrublands is several times higher than in other vegetation types (Pyne et al. 1996). Even so, there is substantial variation between and within chaparral fires determined by species-specific differences in fuel structure and chemistry as well as wind speed and topography (Rundel 1981). Although there are a few experimental studies in chaparral that have related measures of fire intensity to changes in ecosystem properties (Borchert and Odion 1995, Tyler 1995, Odion and Davis 2000), most of what we know about fire intensity effects is based on surrogate measures known as fire severity metrics. Operationally, fire severity measures the aboveground and/or belowground organic matter loss (Keeley in press), and these metrics are correlated with measures of fire intensity (McCaw et al. 1997, Perez and Moreno 1998).

As shown in this study fire history is an important determinant of fire severity. As stands increase in age they accumulate greater biomass and a higher proportion of dead fuels (Keeley and Fotheringham 2003). We expect that more fuels would lead to higher fire intensity and thus fire severity would increase with stand age (Fig. 5a). This is consistent with expectations about the relationship between stand age and fire behavior (Green 1981, Philpott 1977). Age, however, is only one of several factors affecting fire severity. In this study another factor that affected fire severity was the prefire stand structure (Fig. 9), which is affected by the shortest interval between fires, which acts to thin shrub density (Jacobson et al. 2004). Stand composition also plays a key role in affecting fuel loads (Specht 1981, Riggan et al. 1988), and composition and other site factors affect the live:dead ratio (Paysen and Cohen 1990, Conard and Regglebrugge 1994), which affect fire intensity and severity. These factors were not considered in our model (Fig. 9). Other sources of variation in fire severity that were not considered in this study are effects of climate and weather during the fire event (Borchert and Odion 1995).

Fire severity per se is not a measure of direct interest to resource managers, but rather the extent to which severity is indicative of ecosystem responses, in particular vegetative regeneration, community recovery and erosion (Fig. 1). It is apparent that fire severity is not a good predictor of vegetative regeneration after fire, either in the immediate postfire years (Fig. 6a-d) or later years (Keeley et al. 2005a). Fire severity may have a negative effect on diversity in the first year (Fig. 6e, Grace and Keeley 2006). This should not be surprising since diversity is commonly related to disturbance severity (Huston 1994), and in chaparral these effects are evident at different scales from micro-habitats (Odion and Davis 2000) to landscapes (Keeley et al. 2005a). Regardless of the scale, the effect of fire severity is short-lived, being weak (Fig. 6f) or non-existent (Keeley et al. 2005b) in the second and subsequent years.

This negative effect of fire severity on species diversity is consistent with the generally understood effect of severity on ecosystem processes. However, in chaparral shrublands, high fire severity also has impacts on ecosystem responses that managers would find to be positive with respect to goals of minimizing alien plant invasion (Figs. 7, 8, 11 and 12). In general, high fire frequency alters shrub community structure, which concomitantly affects fire severity in ways that favor alien plant invasion (Keeley et al. 2005c). As fire frequency increases, stands become more open due to thinning of native shrubs. with the interstitial spaces being filled by alien annuals (Haidinger and Keeley 1993, Jacobsen et al 2004). This has two important impacts: a much greater alien seed bank present at the time of subsequent fires (Keeley et al. 2005c) and a change in fire behavior. Fires in these vegetation mosaics shift from strictly active crown fires to a combination of surface- and passive crown fires, with lower fire intensity, and lower fire intensities favor survival of alien seed banks (Keeley 2006).

Predicting fire severity and ecosystem responses with remote sensing

The absolute Landsat dNBR index is strongly correlated with field measurements of fire severity in these crown fire shrublands (Fig. 13a), justifying its description as a fire or burn severity measure (Lentile et al. 2006). However, the relative dNBR (Miller and Thode 2006) does not seem to distinguish different levels of fire severity (Fig. 13b), and thus may not be an appropriate index for severity in these shrublands. These remote sensing data are also linked to fire history on the site (Fig. 14), however, the mechanism leading to this relationship is unclear. What is very clear is that just like field measures of fire severity are not good predictors of ecosystem response variables involving vegetative regeneration (Fig. 6), the same is true with dNBR (Fig. 15). These studies show that while dNBR is significantly correlated with field measurements of fire severity, this signal is not necessarily a good predictor of important ecosystem responses. It seems that combining fire severity and ecosystem responses into a single composite index as suggested by some recent papers (e.g., Key and Benson 2006, Lentile et al. 2006) may not be the appropriate analytical tool for these crown fire ecosystems.

CONCLUSIONS

In crown fire shrubland ecosystems, fire severity is not a reliable measure of postfire recovery. Chaparral shrublands are not only well adapted to these fire-prone environments, but are highly resilient to high intensity burning. This has implications for fire management of these landscapes. For example, prefire fuel manipulations are sometimes justified as having positive resource benefits because they reduce subsequent fire intensity and severity. However, lower fire intensity/severity does not contribute to better native regeneration. In fact, reductions in fire intensity or severity may have negative impacts because lower fire intensities are likely to favor alien plant invasion. The potential for remote sensing techniques to contribute to postfire management has not yet been fully realized and it is suggested that this will develop best if we parce out the separate contributions of fire severity and ecosystem responses.

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TABLE 1. Environmental characteristics of burned sites used in this study. Two fires, the Grand Prix and Old fires merged and were treated here as one fire complex.

	Fire				
Site characteristics	**All combined**	**Otay**	**Cedar**	**Paradise**	**GrandPrix /Old**
Number of sites	250	59	79	53	59
Elevation (m)	143 - 1444	257 - 1069	143 - 1265	539 - 818	668 - 1444
Aspects represented	N,S,E,W	N,S,E,W	N,S,E,W	N,S,E,W	N,S,E,W
Inclination (^{o})	1 - 32	3 - 29	2 - 32	1 - 27	2 - 27
Insolation ($MJ/cm^2/yr$)	0.51 - 1.08	0.55 - 1.05	0.51 - 1.08	0.68 - 1.07	0.58 - 1.04
Prefire age (yrs)	3 - 63	7 - 43	3 - 42	9 - 44	7 - 63
Rock cover (%)	1 - 83	3 - 80	2 - 54	1 - 57	2 - 83
Soil rock (%)	0.0 - 0.6	0.1 - 0.6	0.1 - 0.5	0.0 - 0.3	0.1 - 0.6
Soil sand (%)	38 - 91	38 - 83	44 - 86	64 - 91	52 - 88
Soil clay (%)	0 - 28	9 - 28	0 - 26	4 - 13	5 - 28
Soil P (ppm)	2 - 183	2 - 82	3 - 103	6 - 100	9 - 183
Soil Kjeldahl N (%)	0.1 - 0.8	0.1 - 0.6	0.1 - 0.4	0.1 - 0.3	0.1 - 0.8
Prefire shrub density (#/ha)	134 - 2910	169 – 2892	134 - 2910	156 - 2093	149 – 1399
Fire severity (twig dia, mm)	0 – 49	0 – 40	2 – 28	3 - 29	0 – 49
Precipitation year 1 (% of average)	50 – 80	60	50 – 60	55	70 – 80
Precipitation year 2 (% of average)	135 – 260	170	135 – 170	165 – 190	190 – 260

TABLE 2. Regression analysis of diameter of smallest twig on shrub skeletons of *Adenostoma fasciculatum* vs associated shrub species at the same site for 187 sites; r^2 values presented for regressions with $P < 0.05$. Equation coefficients for predicting *A. fasciculatum* twig diameter; $y = mx + b$, SE = standard error of estimate.

	Twig diameter			Predictive equation		
Independent variable	N	*P*	r^2	m	b	SE
Arctostaphylos glauca	19	< 0.001	0.61	2.92	0.574	3.35
A. glandulosa	94	< 0.001	0.76	0.679	0.741	2.61
Ceanothus greggii	26	< 0.01	0.32	5.55	0.152	2.55
C. leucodermis	22	< 0.001	0.54	5.19	0.355	2.92
C. tomentosus	18	< 0.001	0.85	0.486	0.786	2.53
Cneoridium dumosum	15	< 0.001	0.66	1.25	0.902	1.48
Malosma laurina	27	< 0.001	0.67	1.95	0.270	1.15
Pickeringia montana	21	< 0.01	0.42	1.01	0.622	0.490
Quercus berberidifolia	51	< 0.001	0.50	3.82	0.714	3.12
Rhamnus crocea	54	< 0.001	0.25	3.74	0.534	3.76
Rhus ovata	30	< 0.001	0.33	4.44	0.361	3.43
Xylococcus bicolor	49	< 0.001	0.69	1.82	0.817	1.98

TABLE 3. Correlation of average log fire severity at a site with environmental parameters; Bonferroni-adjusted probabilities and, for significant correlations ($P < 0.05$), Pearson correlation coefficient (n = 250).

	P	r
Elevation	0.96	
Inclination	0.40	
Insolation	0.99	
Rock cover	0.91	
Soil sand	< 0.001	0.266
Soil total N	0.04	0.210
Soil P	< 0.001	0.355

TABLE 4. Correlation of average log fire severity at a site with

cover of life history types and natives and annuals in the first and second postfire years; Bonferroni-adjusted probabilities and, for significant correlations (P < 0.05), Pearson correlation coefficient (n = 250).

	Species / m^2	
	P	r
1st year		
Annuals	0.99	
Herb. perennials	0.99	
Suffrutescents	0.82	
Subshrubs	1.00	
Shrubs	1.00	
Native species	1.00	
Alien species	< 0.001	-0.33
2nd year		
Annuals	1.00	
Herb. perennials	0.25	
Suffrutescents	1.00	
Subshrubs	1.00	
Shrubs	1.00	
Native species	1.00	
Alien species	0.023	-0.23

TABLE 5. Correlation of average log fire severity at a site with species richness of

life history types at two scales in the first and second postfire years; Bonferroni-adjusted probabilities and, for significant Correlations ($P < 0.05$), Pearson correlation coefficient (n = 250).

	Species / m^2		Species / 1000 m^2	
	P	r	*P*	r
1st year				
Annuals	< 0.001	-0.42	< 0.001	-0.43
Herb. perennials	< 0.001	-0.39	< 0.001	-0.34
Suffrutescents	< 0.001	-0.39	< 0.001	-0.22
Subshrubs	0.077		1.00	
Shrubs	0.005	0.26	1.00	
Native species	< 0.001	-0.42	< 0.001	-0.28
Alien species	< 0.001	-0.51	< 0.001	-0.53
2nd year				
Annuals	< 0.001	-0.38	1.00	
Herb. perennials	< 0.001	-0.34	< 0.001	-0.31
Suffrutescents	< 0.001	-0.47	0.007	-0.25
Subshrubs	0.066		1.00	
Shrubs	< 0.001	0.31	1.00	
Native species	< 0.001	-0.35	1.00	
Alien species	< 0.001	-0.41	1.00	

Figure Legends

Fig. 1. Relationship of fire intensity, fire severity and ecosystem responses.

Fig. 2. Fires in (a) Los Angeles and San Bernardino and (b) San Diego counties studied in this investigation shown in colors reflecting the Landsat differenced Normalized Burn Ratio (dNBR). Plot locations indicated with closed circles.

Fig. 3. Hypothesized models of direct and indirect effects on (a) fire severity and (b) ecosystem responses to be tested in the structural equations models.

Fig. 4. Age distribution of sites included in this study.

Fig. 5. (a) Stand age and (b) prefire density as predictors of fire severity (n = 250 sites).

Fig. 6. Fire severity as a predictor of (a) total plant cover expressed as percentage of ground surface covered (% GSC) in the first and (b) second postfire year, (c) woody cover in the first year, (d) resprouting success of *Adenostoma fasciculatum*, (e) species richness in the first year and (f) second year.

Fig. 7. Fire severity as a predictor of alien species richness, expressed as a percentage of total species at (a) 1-m^2, (b) 100-m^2, and (c) 1000-m^2.

Fig. 8. First year alien species richness as a predictor of second year alien cover (a) 1-m^2, (b) 100-m^2, and (c) 1000-m^2; cover expressed as percentage ground surface covered (% GSC).

Fig. 9. Structural equation model of conceptual or latent variables (circles) affecting fire severity. Measurement variables (rectangles) considered to have no measurement error were number of annual rings as indicator of STAND AGE, shortest interval between fires available from fire records as indicator of SHORTEST INTERVAL, and calculated radiation load as indicator for FINE-GRAIN TOPOGRAPHIC effects. Measurement error was calculated from the reliability estimate (above outward arrow from latent variable to indicator variable) for log prefire shrub density as an indicator of PREFIRE STRUCTURE, and for log skeleton diameter for FIRE SEVERITY.

Fig. 10. Structural equation model of latent variables (circles) affecting the ecosystem response of cover in the first postfire year. Indicator variables (rectangles) presumed to not have measurement error (annual rings and elevation) or not sampled in a manner that allowed for estimate of error (phosphorous and soil texture) are indicated with 1 above the outward arrow from the latent variable to the indicator variable. Double headed arrows indicate correlations not explicitly part of the model structure.

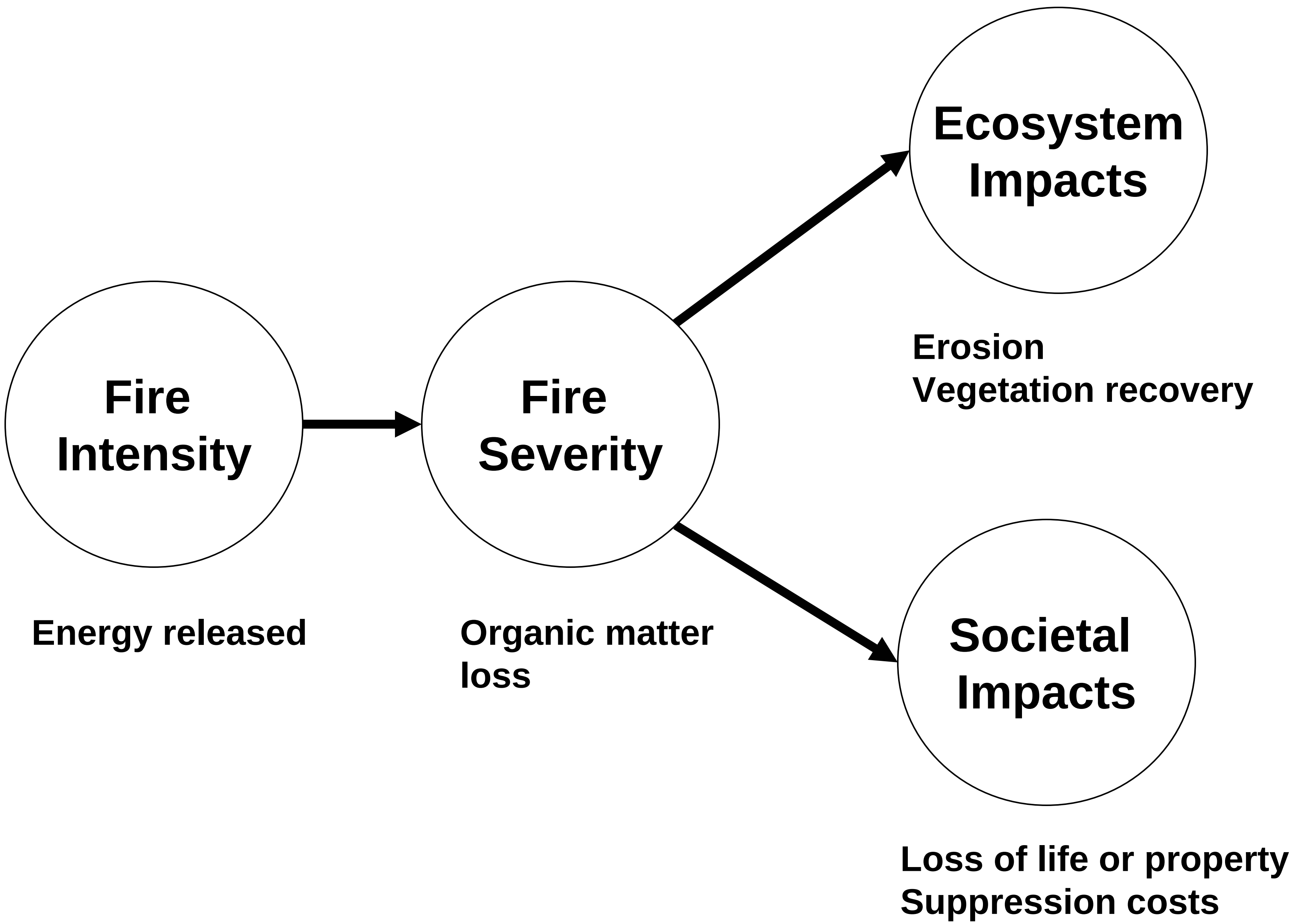
Fig. 11. Structural equation model of latent variables (circles) affecting the ecosystem response of alien plant cover in the first postfire year. Other details as in Figure 10 legend.

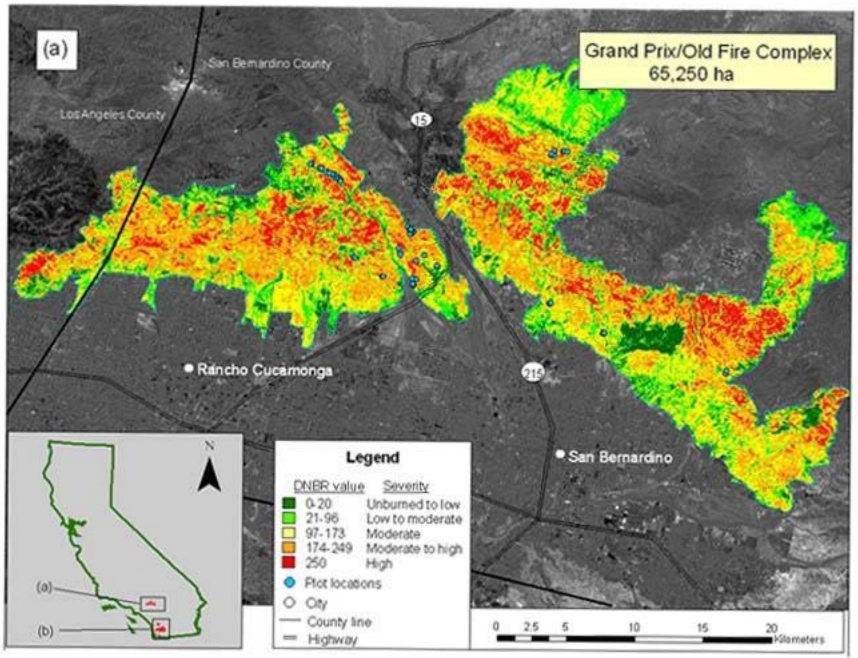
Fig. 12. Structural equation model of latent variables (circles) affecting the ecosystem response of alien diversity at the 1000-m^2 scale in the first postfire year. Other details as in Figure 10 legend.

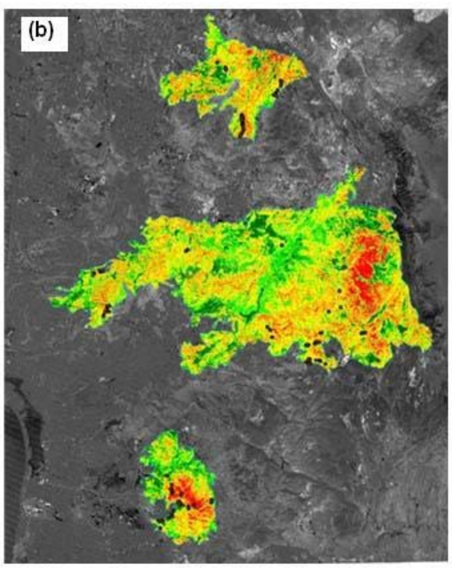
Fig. 13. Prediction of field measured fire severity by the remote sensing index dNBR for (a) the absolute index in spring and (b) the relative dNBR index.

Fig. 14. Times burned as a predictor of dNBR (absolute value, spring assessment).

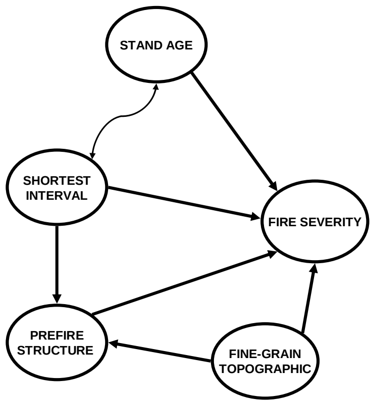
Fig. 15. dNBR (absolute spring assessment) as a predictor of (a) total plant cover, expressed as percentage ground surface covered, and (b) resprouting success of *Adenostoma fasciculatum* in the first postfire year.


Ecosystem Impacts
Erosion
Vegetation recovery
Fire Intensity
Fire Severity
Energy released
Organic matter loss
Societal Impacts
Loss of life or property
Suppression costs

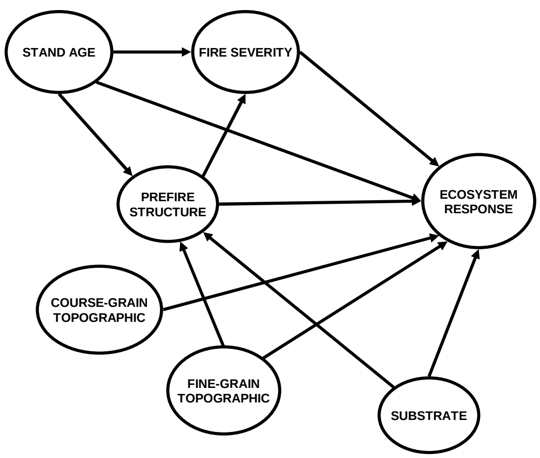

(a)
Grand Prix/Old Fire Complex
65,250 ha
San Bernardino County
Los Angeles County
15
215
Rancho Cucamonga
San Bernardino
N
(a)
(b)
Legend
DNBR value Severity
0-20 Unburned to low
21-96 Low to moderate
97-173 Moderate
174-249 Moderate to high
250 High
Plot locations
City
County line
Highway
0 2.5 5 10 15 20 Kilometers

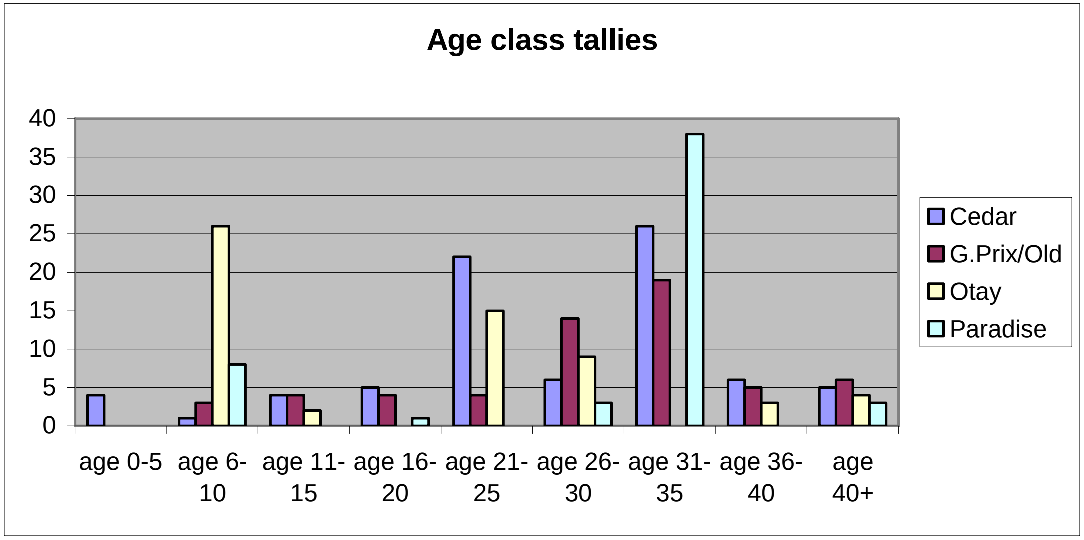

(b)

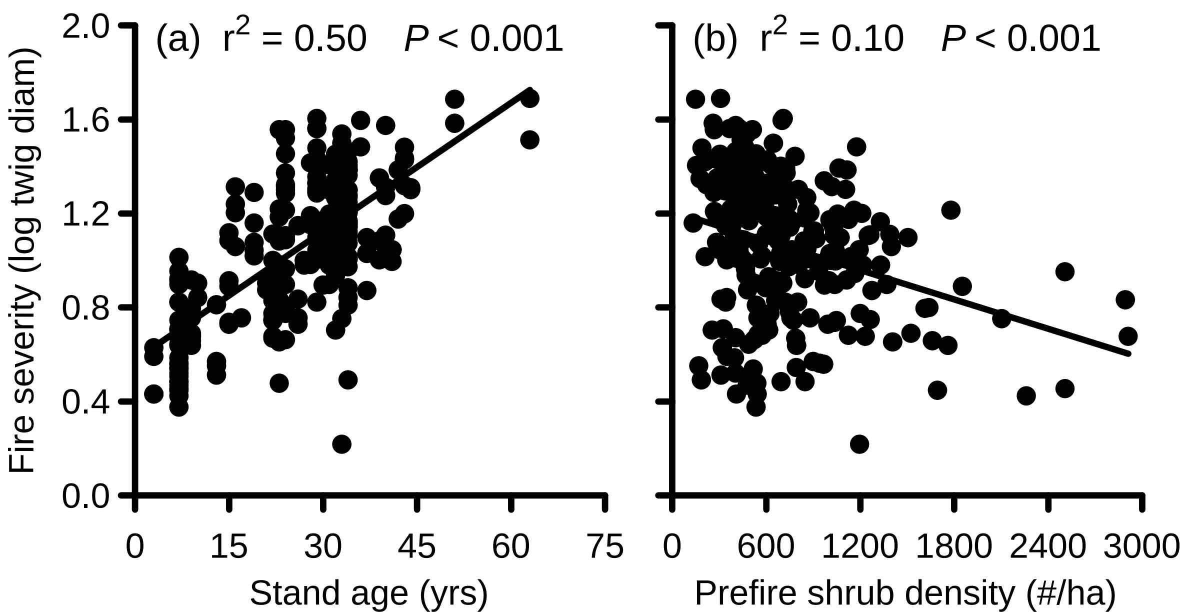
a)


STAND AGE
SHORTEST INTERVAL
FIRE SEVERITY
PREFIRE STRUCTURE
FINE-GRAIN TOPOGRAPHIC

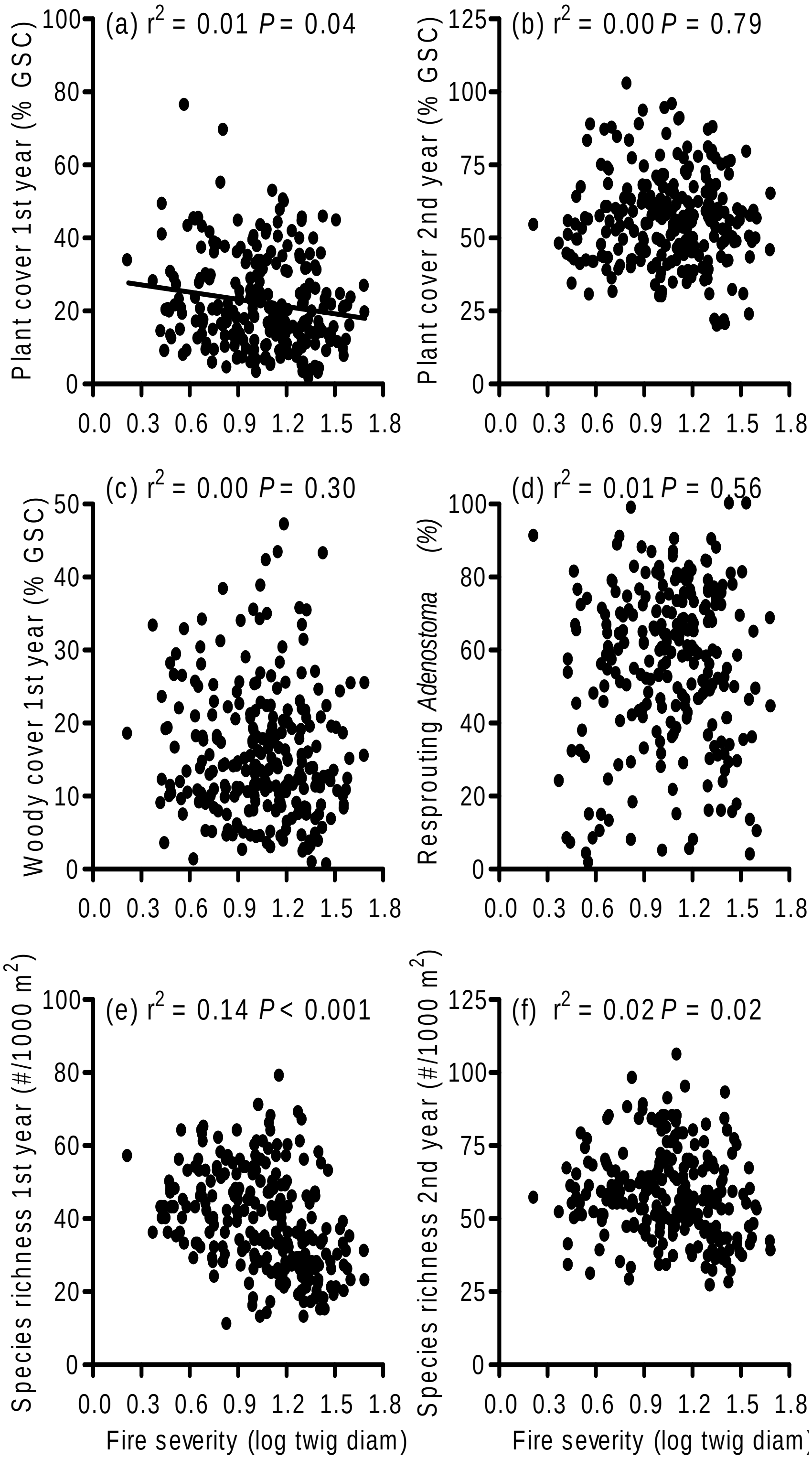
b)


STAND AGE
FIRE SEVERITY
PREFIRE STRUCTURE
ECOSYSTEM RESPONSE
COURSE-GRAIN TOPOGRAPHIC
FINE-GRAIN TOPOGRAPHIC
SUBSTRATE

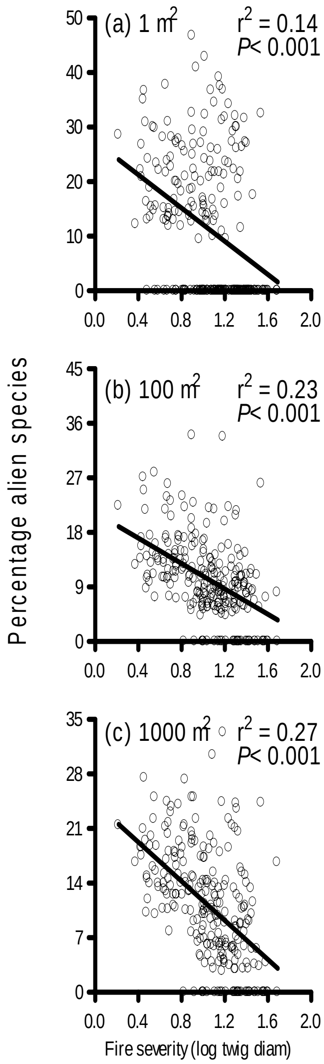

Age class tallies
40
35
30
25
20
15
10
5
0
age 0-5
age 6-10
age 11-15
age 16-20
age 21-25
age 26-30
age 31-35
age 36-40
age 40+
Cedar
G.Prix/Old
Otay
Paradise

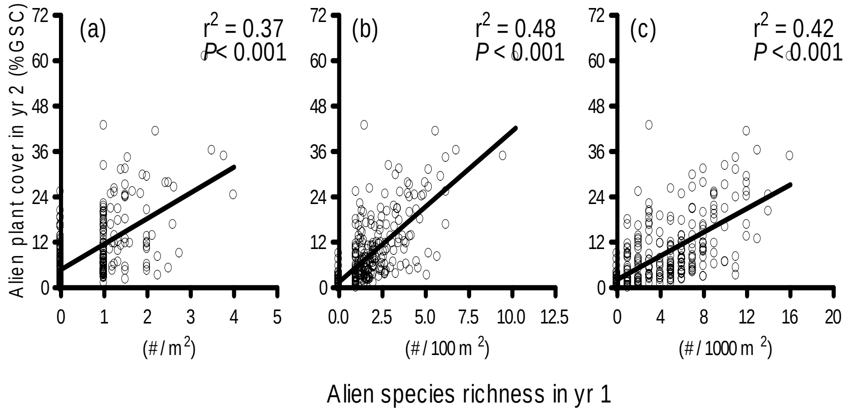


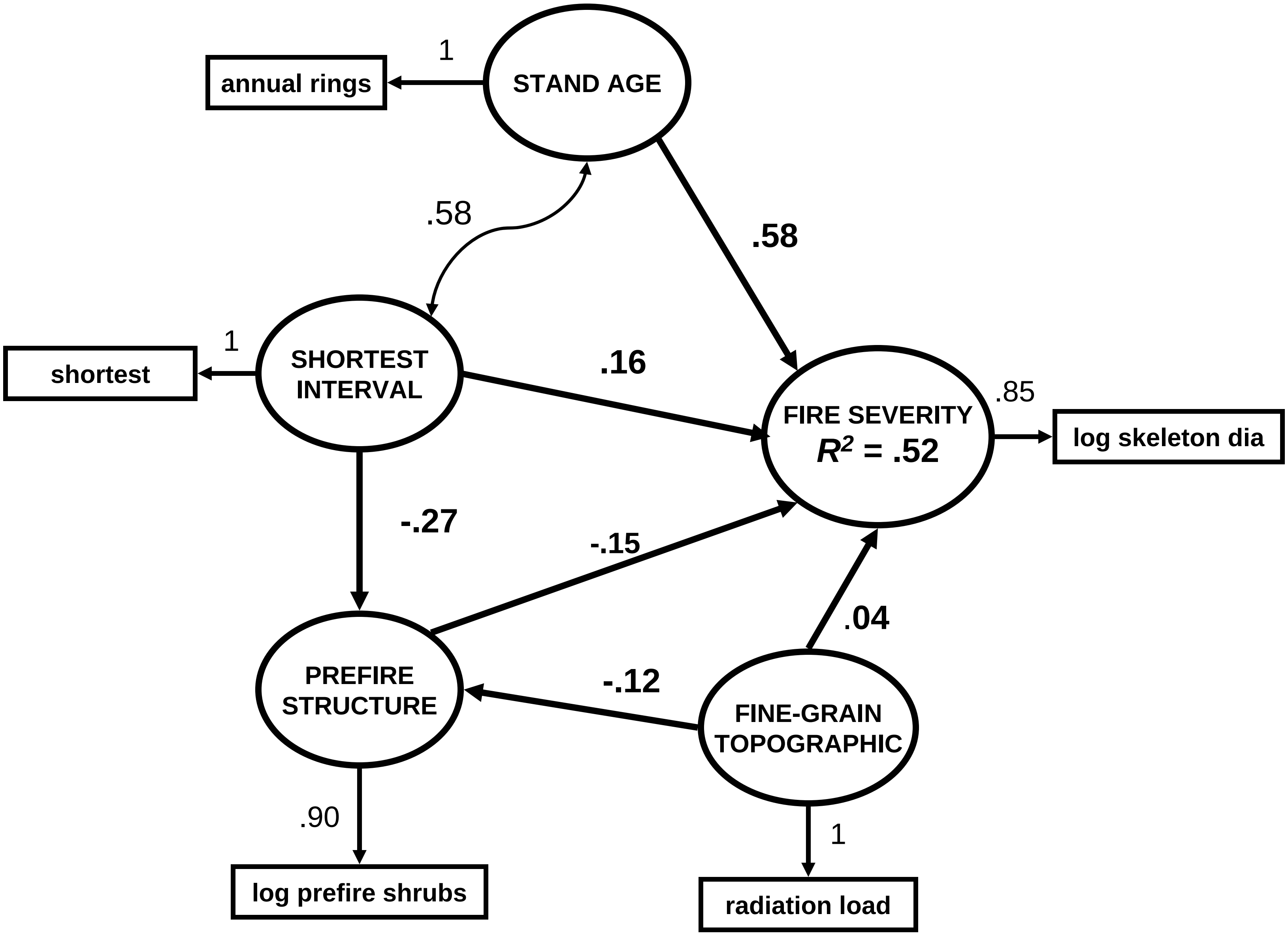
(a) r2 = 0.50 P < 0.001
(b) r2 = 0.10 P < 0.001
Fire severity (log twig diam)
2.0
1.6
1.2
0.8
0.4
0.0
0
15
30
45
60
75
Stand age (yrs)
0
600
1200
1800
2400
3000
Prefire shrub density (#/ha)

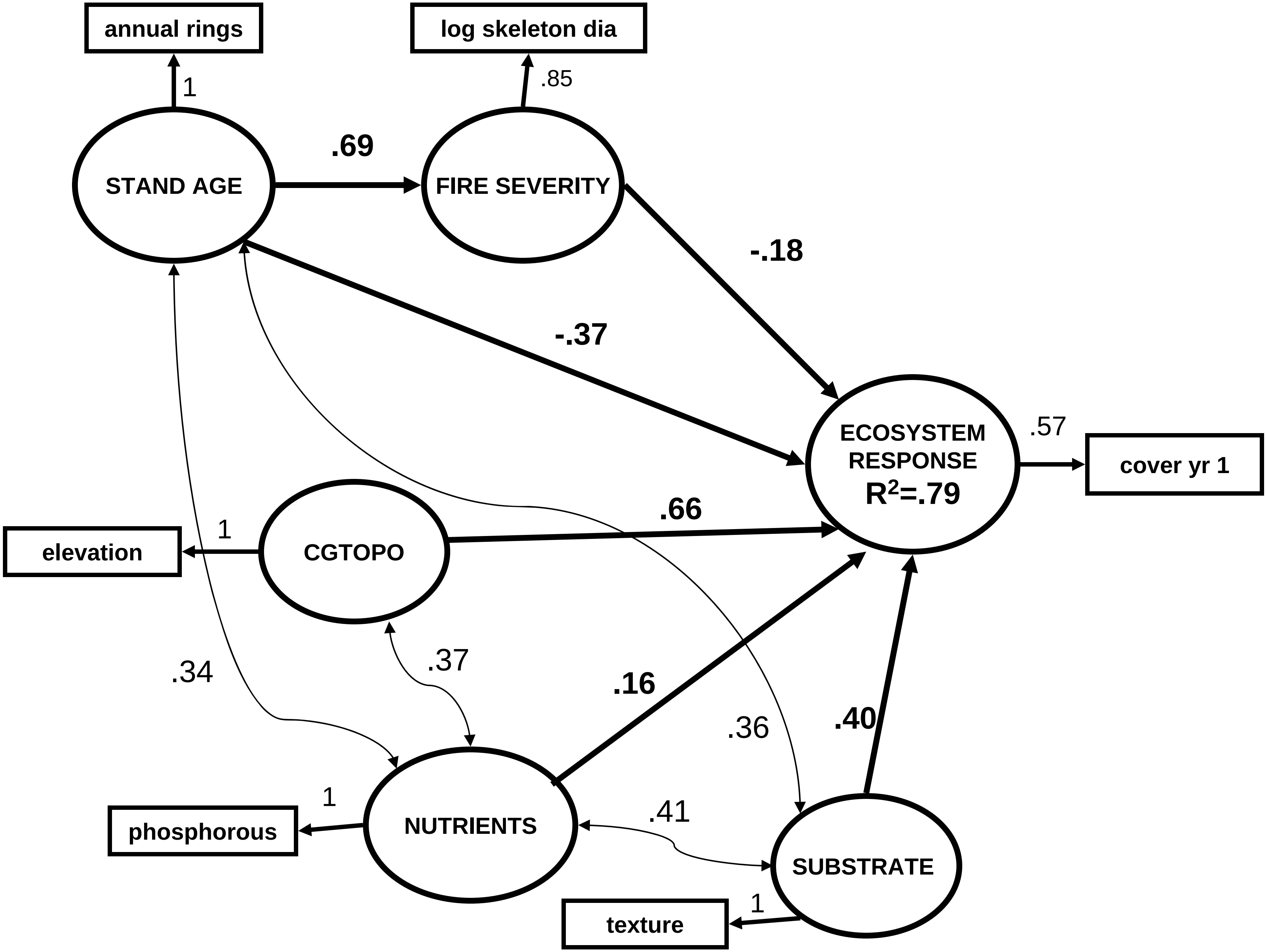


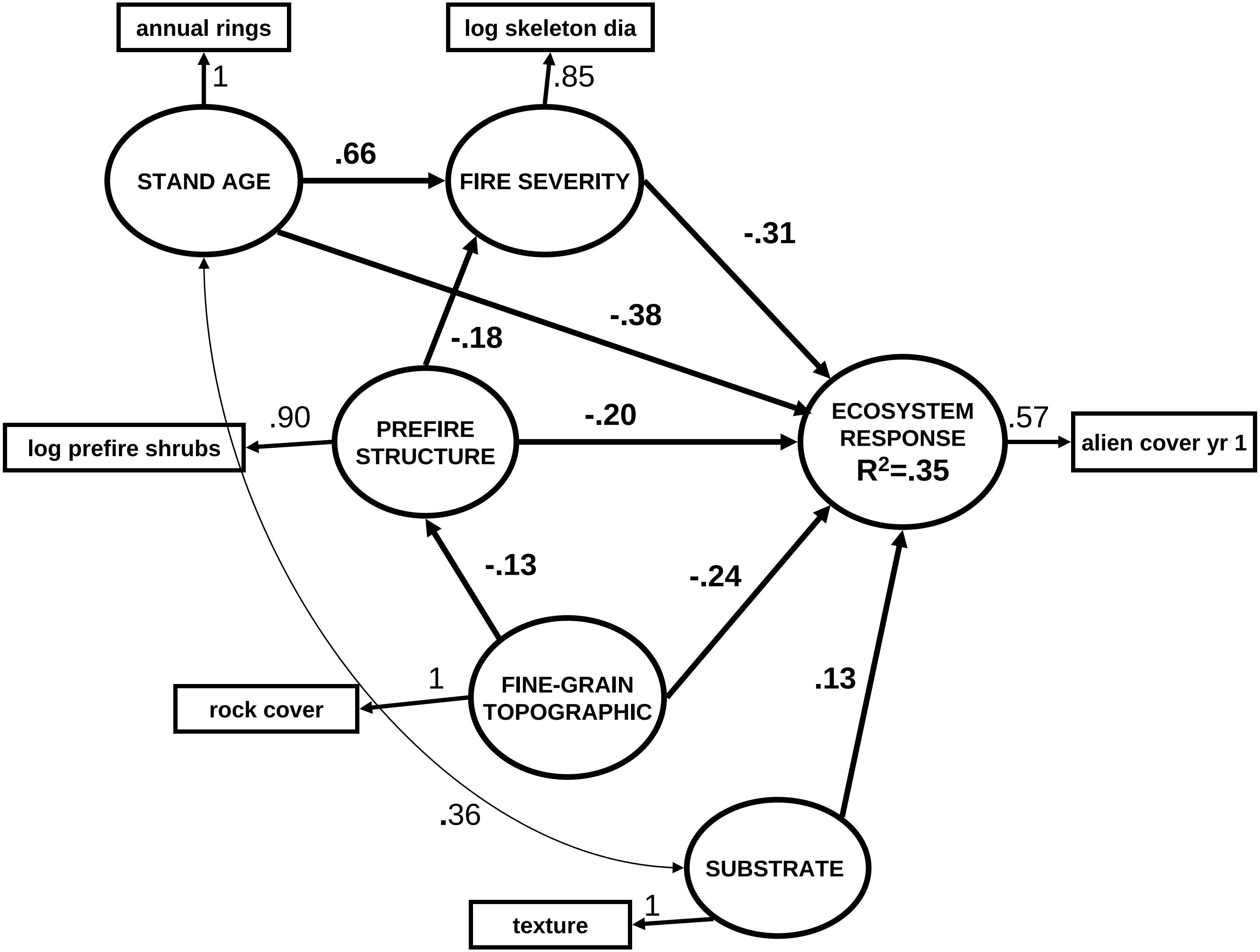
(a) r2 = 0.01 P = 0.04
Plant cover 1st year (% GSC)
(b) r2 = 0.00 P = 0.79
Plant cover 2nd year (% GSC)
(c) r2 = 0.00 P = 0.30
Woody cover 1st year (% GSC)
(d) r2 = 0.01 P = 0.56
Resprouting Adenostoma (%)
(e) r2 = 0.14 P < 0.001
Species richness 1st year (#/1000 m2)
(f) r2 = 0.02 P = 0.02
Species richness 2nd year (#/1000 m2)
Fire severity (log twig diam)
Fire severity (log twig diam)

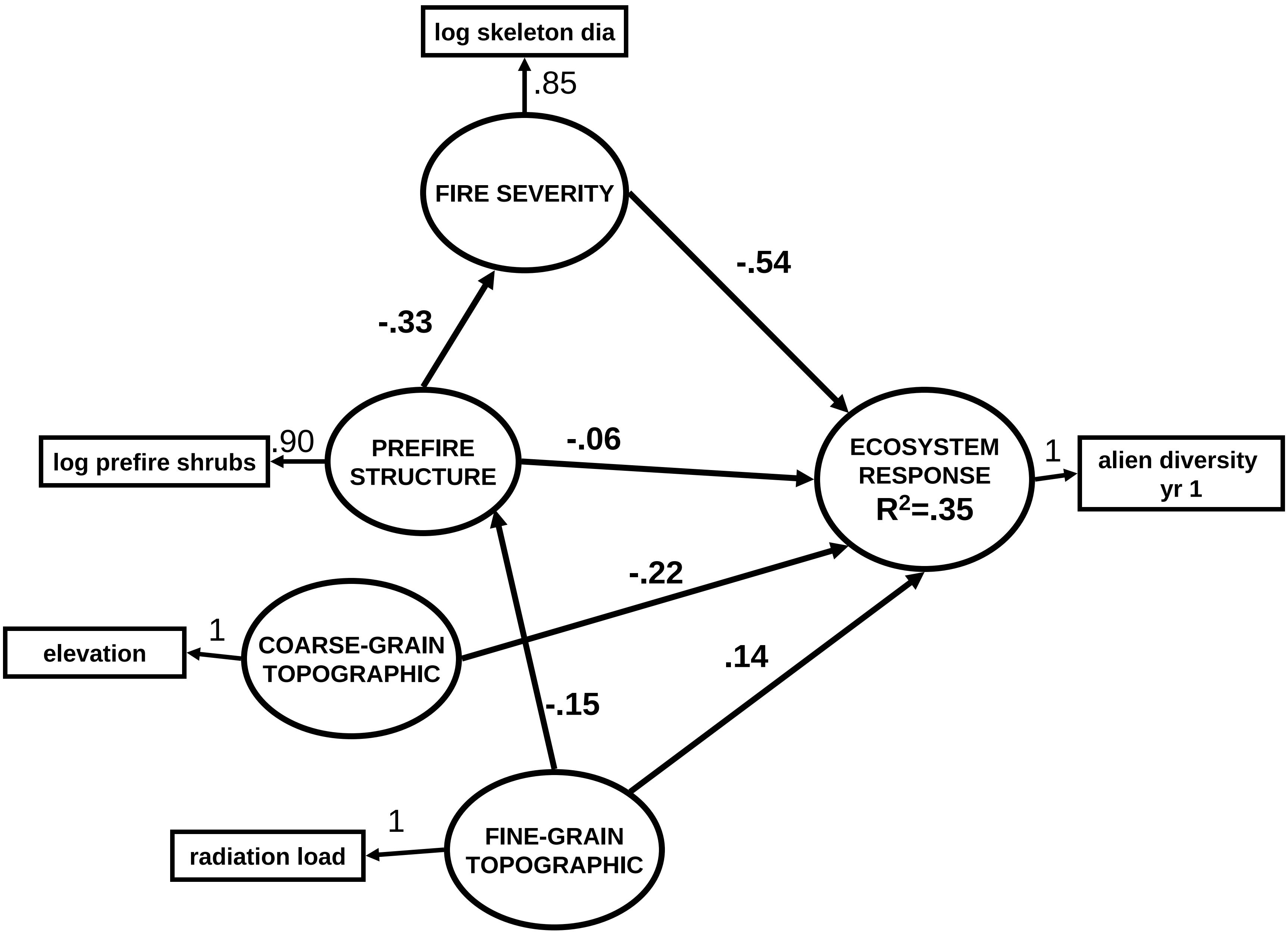

(a) 1 m2
r2 = 0.14
P< 0.001
(b) 100 m2
r2 = 0.23
P< 0.001
(c) 1000 m2
r2 = 0.27
P< 0.001
Percentage alien species
Fire severity (log twig diam)
0.0
0.4
0.8
1.2
1.6
2.0
0
10
20
30
40
50
9
18
27
36
45
7
14
21
28
35

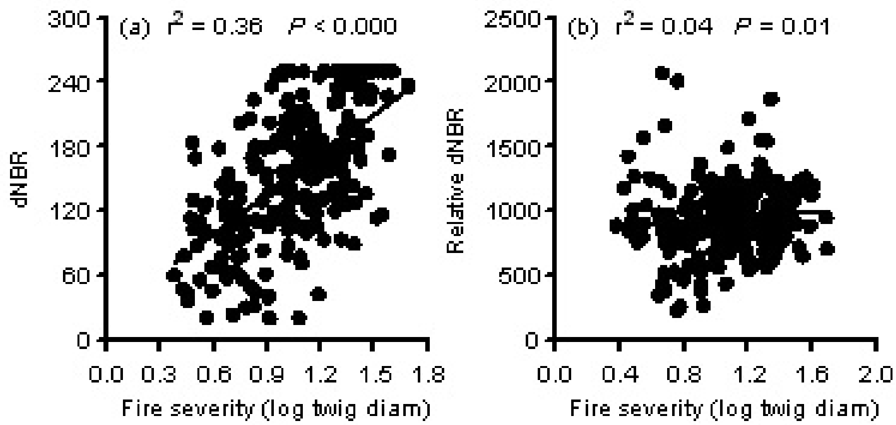

(a)
$r^2 = 0.37$
$P < 0.001$
(b)
$r^2 = 0.48$
$P < 0.001$
(c)
$r^2 = 0.42$
$P < 0.001$
Alien plant cover in yr 2 (%GSC)
(#/m^2)
(#/100 m^2)
(#/1000 m^2)
Alien species richness in yr 1


STAND AGE
annual rings
1
.58
.58
SHORTEST
INTERVAL
shortest
1
.16
FIRE SEVERITY
R^2 = .52
.85
log skeleton dia
-.27
-.15
PREFIRE
STRUCTURE
.04
-.12
FINE-GRAIN
TOPOGRAPHIC
.90
log prefire shrubs
1
radiation load

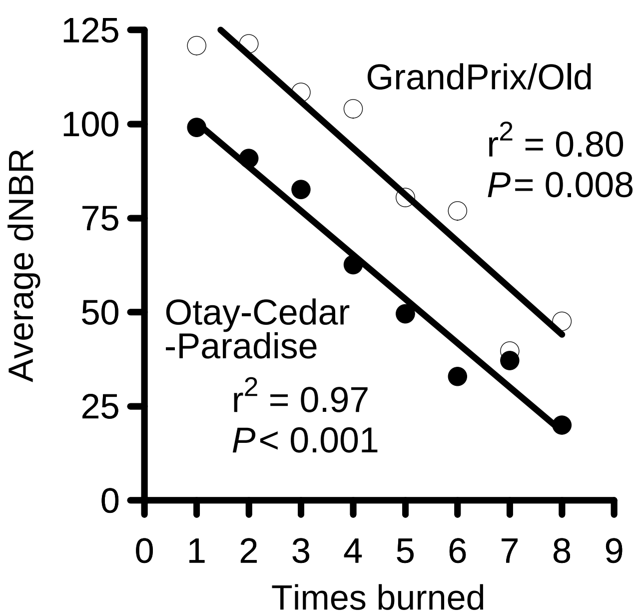

annual rings
log skeleton dia
1
.85
.69
STAND AGE
FIRE SEVERITY
-.18
-.37
ECOSYSTEM
RESPONSE
R2=.79
.57
cover yr 1
.66
1
elevation
CGTOPO
.37
.34
.16
.36
.40
1
phosphorous
NUTRIENTS
.41
SUBSTRATE
1
texture


annual rings
log skeleton dia
1
.85
STAND AGE
.66
FIRE SEVERITY
-.31
-.38
-.18
PREFIRE STRUCTURE
.90
log prefire shrubs
-.20
ECOSYSTEM RESPONSE
R²=.35
.57
alien cover yr 1
-.13
-.24
FINE-GRAIN TOPOGRAPHIC
1
rock cover
.13
.36
SUBSTRATE
1
texture

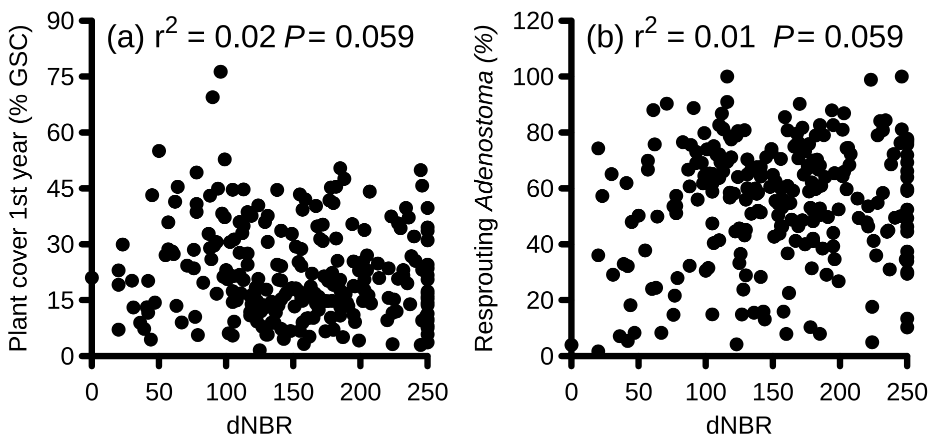

log skeleton dia
.85
FIRE SEVERITY
-.54
-.33
log prefire shrubs
.90
PREFIRE
STRUCTURE
-.06
ECOSYSTEM
RESPONSE
R^2=.35
1
alien diversity
yr 1
-.22
elevation
1
COARSE-GRAIN
TOPOGRAPHIC
.14
-.15
1
radiation load
FINE-GRAIN
TOPOGRAPHIC



(a) r^2 = 0.36 P < 0.000
dNBR
300
240
180
120
60
0
0.0 0.3 0.6 0.9 1.2 1.5 1.8
Fire severity (log twig diam)
(b) r^2 = 0.04 P = 0.01
Relative dNBR
2500
2000
1500
1000
500
0
0.0 0.4 0.8 1.2 1.6 2.0
Fire severity (log twig diam)



GrandPrix/Old
r2 = 0.80
P= 0.008
Otay-Cedar
-Paradise
r2 = 0.97
P< 0.001
Average dNBR
Times burned
125
100
75
50
25
0
0 1 2 3 4 5 6 7 8 9


(a) r2 = 0.02 P= 0.059
Plant cover 1st year (% GSC)
90
75
60
45
30
15
0
0
50
100
150
200
250
dNBR
(b) r2 = 0.01 P= 0.059
Resprouting Adenostoma (%)
120
100
80
60
40
20
0
0
50
100
150
200
250
dNBR