

## A multivariate model of plant species richness in forested systems: old-growth montane forests with a long history of fire

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Laughlin, D. C. and Grace, J. B. 2006. A multivariate model of plant species richness in forested systems: old-growth montane forests with a long history of fire. – *Oikos* 114: 60–70.

Recently, efforts to develop multivariate models of plant species richness have been extended to include systems where trees play important roles as overstory elements mediating the influences of environment and disturbance on understory richness. We used structural equation modeling to examine the relationship of understory vascular plant species richness to understory abundance, forest structure, topographic slope, and surface fire history in lower montane forests on the North Rim of Grand Canyon National Park, USA based on data from eighty-two 0.1 ha plots. The questions of primary interest in this analysis were: (1) to what degree are influences of trees on understory richness mediated by effects on understory abundance? (2) To what degree are influences of fire history on richness mediated by effects on trees and/or understory abundance? (3) Can the influences of fire history on this system be related simply to time-since-fire or are there unique influences associated with long-term fire frequency? The results we obtained are consistent with the following inferences. First, it appears that pine trees had a strong inhibitory effect on the abundance of understory plants, which in turn led to lower understory species richness. Second, richness declined over time since the last fire. This pattern appears to result from several processes, including (1) a post-fire stimulation of germination, (2) a decline in understory abundance, and (3) an increase over time in pine abundance (which indirectly leads to reduced richness). Finally, once time-since-fire was statistically controlled, it was seen that areas with higher fire frequency have lower richness than expected, which appears to result from negative effects on understory abundance, possibly by depletions of soil nutrients from repeated surface fire. Overall, it appears that at large temporal and spatial scales, surface fire plays an important and complex role in structuring understory plant communities in old-growth montane forests. These results show how multivariate models of herbaceous richness can be expanded to apply to forested systems.

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A profusion of hypotheses exist concerning specific factors that control plant species richness (reviewed by Grace 1999). A few of the most important factors include primary production and competitive exclusion, disturbance history, and the species pool. However, there has been no resolution of the question of the relative importance of each factor nor an adequate synthesis of

the subject (Palmer 1994, Waide et al. 1999, Gross et al. 2000, Mittlebach et al. 2001). Methods that allow for multivariate hypothesis development and testing, specifically structural equation modeling, have, in the past few years, inspired efforts to evaluate hypotheses about interacting networks of controlling factors (Grace and Pugsek 1997, Gough and Grace 1999, Weiher 2003).

Accepted 15 November 2005  
Subject Editor: Heikki Setälä

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ISSN 0030-1299

Such methods depend on the use of theoretically-specified models of plausible relationships and seek to determine which models, if any, are consistent or inconsistent with the multivariate relations in the data (Bollen 1989, Grace 2006). When acceptable models are obtained, the results have the potential to indicate the roles that different factors play in a system and the strengths of different pathways. Such models have provided evidence for a rich array of processes acting to regulate species richness in herbaceous plant communities. While only a limited number of such studies have been conducted to date, the results thus far indicate strong influences of abiotic factors, disturbance history, colonization, and in productive communities, competitive interactions (Grace and Pugsek 1997, Gough and Grace 1999, Grace and Jutila 1999, Grace et al. 2000).

More recently, there has been an interest in expanding the range of factors considered in multivariate investigations of richness patterns. Grace and Guntenspergen (1999) evaluated hypotheses about the residual influences of past disturbances (specifically, hurricanes and tropical storms) in wetlands. Non-equilibrium processes, such as fire, have been shown to exhibit both direct (Weiher 2003) and indirect (Grace and Keeley 2006) effects on diversity. Disturbance can directly affect plant species composition through opening niches for fire-tolerant species (Watson and Wardell-Johnson 2004) and can indirectly affect richness through direct effects on light availability and plant structure (Grace and Pugsek 1997). In addition, landscape influences can affect post-fire richness patterns in chaparral (Grace and Keeley 2006). Hypotheses about the roles of historic, geographic, regional, and local factors on patterns of endemic richness have been considered by Harrison et al. (2006) and exemplify the capacity of multivariate hypothesis testing to aid in the interpretation of complex intercorrelated relationships at multiple scales.

The variety of community types considered has also recently expanded. Weiher (2003) evaluated the multivariate model developed by Grace and Pugsek (1997) in oak savannas and concluded that the inclusion of trees creates a new set of relationships to consider in models of richness. Further studies by Weiher et al. (2004) in prairie containing scattered red cedar trees have provided additional support for the idea that trees can act to both mediate and alter influences of abiotic factors on herbaceous richness. It would seem based on the limited information currently available that the factors influencing understory richness in woodlands and forests potentially include all those occurring in grasslands plus the moderating and interacting effects of trees. In this study, we extend the range of communities considered using multivariate modeling to include old-growth montane forests and we seek to evaluate multivariate hypotheses that consider the ability of trees to

moderate influences from fire history on understory richness.

## Methods

### The study system

This study was conducted in old-growth montane ponderosa pine (*Pinus ponderosa* P. & C. Lawson) forests (at 2200–2350 m elevation) on the North Rim of Grand Canyon National Park (GCNP), USA. Interspersed throughout the pine forest are clumps of Gambel oak (*Quercus gambelii* Nutt.), a deciduous species that resprouts following fire. Montane plant communities in the southwestern United States have evolved in an environment that experienced low-intensity surface fires every 2–20 years (Swetnam and Baisan 1996, Moore et al. 1999). However, the vast majority of montane forests in the western United States have been affected by commercial logging, by over-grazing from domestic livestock (Belsky and Blumenthal 1997), and by the exclusion of surface fires (Agee 1993). As a result, many western montane landscapes have grown into overly dense forests of small trees with subsequent low understory productivity and diversity. In contrast, Grand Canyon National Park (GCNP) contains the largest never-harvested, minimally grazed, and naturally burned (Fulé et al. 2003) forest ecosystem in Arizona. As a result, these relict sites are rare examples of western forest landscapes close to the historic range of natural variability (Fulé et al. 2002). As such, they offer a place to consider how plant community structure is related to abiotic and biotic factors under conditions of minimal anthropogenic disturbance.

Laughlin et al. (2005) used model selection to determine the best fitting multiple regression model to explain variation in species richness in a broad span of montane forests. Understory abundance and species richness was negatively correlated with the number of years since the last surface fire (hereafter, 'time-since-fire') and pine abundance (Laughlin et al. 2005). Fire is known to affect forest structure (Agee 1993), and pine abundance is well known to negatively impact understory production (Moore and Deiter 1992) through competition for light, water and soil nutrients (McLaughlin 1978, Riegel et al. 1995). However, multiple regression does not allow the researcher to interpret why predictor variables, such as pine abundance and time-since-fire, were correlated (Grace and Bollen 2005). It is likely that time-since-fire directly affects pine abundance, which in turn directly affects understory plant abundance; hence, in this study we use a structural equation modeling approach to test a variety of theoretically-specified multivariate models having compound pathways.

## Sampling methods

We sampled understory and overstory characteristics on eighty-two 0.1 ha plots. The plots were separated by at least 300 m and arranged on a grid across the landscape (i.e. plots were located at intersections of lines on a grid; see Fulé et al. (2002) and Laughlin et al. (2005) for study site figures). Plots were oriented uphill-downhill and percent slope for each plot was determined using clinometer readings. Understory plant communities were sampled using belt and point intercept transects that were 50 m in length with points every 30 cm (Laughlin et al. 2005). Understory vegetation was dominated by C<sub>3</sub> graminoids and annual and perennial forbs; few shrubs were detected (Laughlin et al. 2005). Species richness was determined as the number of vascular plant species below breast height that occurred within the 0.1 ha plot. Percent foliar cover was calculated by dividing the number of points containing a plant along the point intercept transect divided by the total number of points (=332). Trees greater than 15 cm diameter at breast height (dbh) were measured on the entire plot and trees between 2.5 and 15 cm dbh were measured on one quarter-plot; all diameters and species of trees were recorded (Fulé et al. 2002).

Previous studies of fire effects on understory vegetation have noted potential confounding effects of time-since-fire and fire frequency, and have therefore held one variable constant to study the effects of the other (Fox and Fox 1986) or have taken a multivariate approach (Weiher et al. 2004, Watson and Wardell-Johnson 2004). We estimated time-since-fire for each plot in the montane forests with two complimentary sources: fire perimeter maps and interpolation of fire scar data (Farris et al. 2004, Laughlin et al. 2005). We also estimated fire frequency since 1880, which is the date of region-wide fire exclusion corresponding to the arrival of Euroamericans (Fulé et al. 2003), by counting the number of fires that overlaid each plot. This method was quite conservative since we only included fires that scarred at least 10% of the recording trees and fire maps derived from fire scars can underestimate fire size.

## Multivariate hypotheses

The general hypotheses of interest in this paper are presented in Fig. 1. This model represents an expansion of the one presented by Grace and Pugsek (1997) with the inclusion of overstory abundance as an important element. All of the hypotheses represented are based on what we believe to be a plausible set of assumptions that include, (1) that current forest overstory abundance may be influenced by past disturbance events and abiotic gradients, (2) that the abundance of understory plants may be influenced by overstory abundance, disturbance events, and abiotic gradients, and (3) that understory

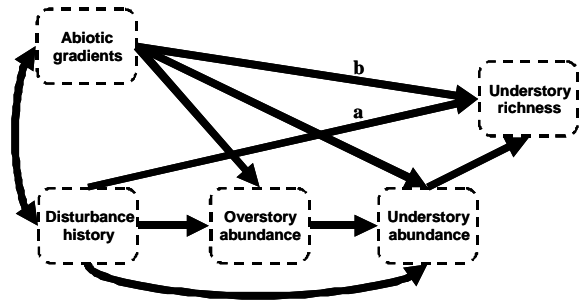


Fig. 1. General conceptual (construct) model that expands on the model in Grace and Pugsek (1997, Fig. 1) by including overstory abundance. Dashed rounded rectangles represent general constructs and arrows denoted by 'a' and 'b' represent pathways of a priori interest. Thus, this diagram represents a set of alternative models, all of which contain the solid arrows, but which differ in the inclusion of direct paths from a) disturbance history and b) abiotic gradients to understory richness.

richness may respond to all four of the other system properties. We recognize that it cannot be guaranteed that the causal relations implied by these assumptions fully represent all the processes operating in this system. Indeed, potentially important abiotic gradients, such as soil properties (which were not measured), are missing from the model. Rather, through the analyses in this paper we seek to determine whether the relations in the data are consistent with expectations from any of the multivariate hypotheses considered (Bollen 1989).

All the hypotheses represented by Fig. 1 seek to determine if understory richness relates in some way to disturbance (specifically, fire) history in this system. There is also interest in seeing what role gradients in topographic slope play in this system. Further, we have an interest in evaluating hypotheses about moderating or altering effects of trees and understory abundance on understory richness. By 'moderating' we refer to the degree to which a presumed effect of fire history or topographic slope on understory richness can be explained by an intervening effect on either forest overstory or understory abundance. For example, if understory abundance completely moderates the effects of disturbance history and forest overstory on richness, all compound pathways would go through understory abundance and no other pathways would go directly to richness. By 'altering' we refer to the situation where the presence of information about intervening variables (in this case, overstory and understory abundance) alters our view of the effects of an influencing factor (fire history or slope) on a response (understory richness). Both kinds of relations are of interest in models that imply a cascading chain of influences, as in Fig. 1.

A number of initial expectations are represented in Fig. 1 and are based on previous studies of this system (Crawford et al. 2001, Gildar et al. 2004, Laughlin et al. 2004, 2005, Huisinga et al. in press). First, it is expected that forest overstory density varies as a function of fire

history. The relations can be potentially complex depending on the effects of fires on seedlings and saplings, the effects on canopy tree growth, and the absolute frequency of fires. Generally, fires in this system, though frequent prior to 1880, occurred only 0–5 times per plot since 1880, and none were stand-replacing. This means that relations of tree abundance to components of fire history (time-since-fire or fire frequency) might be either positive or negative. Second, it is strongly expected that low understory abundance will be associated with high abundance of ponderosa pine, the dominant tree in this system. Finally, it is expected that where conditions are unfavorable for abundant understory growth, there will be a low level of species richness due to a lack of opportunities for establishment. It is also possible that richness is reduced somewhat where understory growth is very high, though it is not clear whether understory abundance in this system is sufficient to drive a loss of species.

What is less certain for this system is whether overstory and understory abundance completely moderate effects of fire history. It is quite possible that there are influences of forest overstory on richness that either intensify or ameliorate the influences of fire history. It is also possible that fire history has had influences on understory richness that are unrelated to overstory or understory abundance. The same questions can be asked about topographic slope. These less certain pathways, arrows denoted by the letters a and b, represent alternative models of a priori interest. These alternatives will be considered in both specific models (presented later in the paper) representing relations among the measured properties of the system and in general models of the form in Fig. 1.

## Data analyses

Prior to evaluations of multivariate hypotheses, bivariate examinations of relationships among variables were examined. All relationships were considered for the presence of outliers, evidence of skewness or kurtosis, and nonlinear relations. A log transform of understory plant cover was used to linearize relations with richness; all other variables were analyzed in their native scale. Spatial autocorrelation in richness was also examined to determine whether there might be contagion in the data (Laughlin et al. 2005). Results found no evidence of autocorrelation; therefore, the data were analyzed as independent samples without modeling proximity.

## Structural equation modeling

Two types of structural equation models were analyzed in this study: ‘specific’ and ‘general’ models. ‘Specific’ models were evaluated to give a detailed perspective of

relationships. Figure 2 represents the a priori specific model evaluated. In this model, the abundance of Gambel oak was separated from the abundance of ponderosa pine because of the potential unique effects each species may have on understory vegetation (Laughlin et al. 2005). In addition, two components of fire history were represented separately, time-since-fire and the frequency of fires during the past 118 years. Time-since-fire and fire frequency covary in the model since plots that burned recently tended to have burned frequently as well (Fulé et al. 2003, Laughlin et al. 2005). Because oak abundance varied with topographic slope, this landscape feature was included in the specific model.

The models in this paper were formulated using latent variables (in circles) and single indicators (observed variables represented by rectangles). Two possible indicators were considered for both oak abundance and pine abundance, total basal area ( $\text{m}^2 \text{ha}^{-1}$ ) and tree density ( $\text{trees ha}^{-1}$ ). Ponderosa pine, which was the dominant canopy species in the great majority of plots, showed much stronger relationships to all other variables when expressed as total basal area compared to when expressed as tree density. This is understandable given the fact that these trees grow to a large size in low-density stands in these forests. Gambel oak, in contrast, showed stronger relationships to other variables when expressed as tree density. This species is one that resprouts, often forming dense thickets, but which does not often grow into stands of large trees in these forests. Another reason for using oak density rather than oak basal area as an indicator of oak abundance is because we have observed that understory plants can be abundant beneath single large oaks, but not beneath dense oak thickets; in contrast, plant abundance is often low beneath single large pines and beneath dense pine thickets.

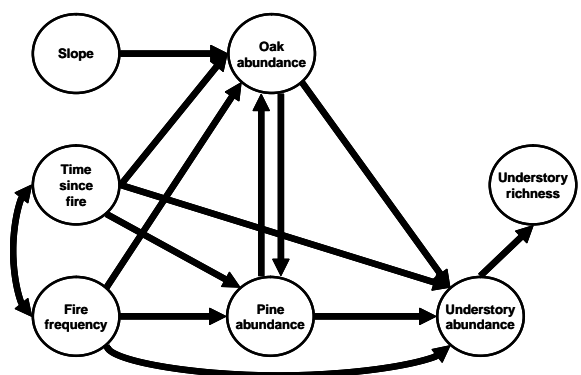


Fig. 2. A priori ‘indirect effects’ (specific) structural equation model representing hypothesized relations between species richness and fire history, slope, forest structure, and understory abundance. Latent variables are represented by circles and the single-indicator observed variables are not shown here for simplicity. Model structure follows from earlier work in grasslands and woodlands.

We considered whether estimates of indicator reliability (repeatability) should be used to specify the degree of measurement error in the model. This was done because appropriate assignments of measurement error can reduce bias in path coefficients (Bollen 1989, Grace 2006), and because we were fairly confident that some of the indicators were not measured perfectly (and, therefore, without error). Indications of the degree of repeatability (reliability) were obtained by correlating readings taken in different years. Such readings provided an underestimate of reliability because they incorporated both measurement error and temporal variation. Still, reliabilities estimated in this way were generally high (up to 90%). Because only approximate measures of reliability could be obtained, conservative estimates of percent error were used in the analyses. Based on our scientific judgement, experience, and available data, we assigned values of 10% error to the indicators of fire frequency and understory richness, 5% to understory abundance and time-since-fire, and 0% to pine abundance, oak abundance, and slope. The effects of reliability estimates on the stability of model results were explored by rerunning the final model using higher or lower reliabilities. For comparison, runs were made using zero estimates for measurement error (equivalent to an observed variable model analysis) and using values double those specified.

We used a competing models approach to compare models of initial interest. The structural relationships (pathways involving latent variables) shown in Fig. 2 describe one of the hypotheses of initial interest, which we refer to as the 'indirect effects' hypothesis. In this hypothesis, all effects of slope, fire, and trees on understory richness can be explained by their effects on understory abundance. The model included both first- and second-order polynomial terms for oak density to allow for nonlinear relations between this and other variables (initial examination of the data indicated that the bivariate relation between oak density and both richness and plant cover fit a second-order polynomial). Though included in the model, we do not illustrate these non-linear relations in the final model for simplicity.

Alternative models to the one shown in Fig. 2 that were investigated were those with direct paths to understory richness from variables other than understory abundance. Analyses proceeded by comparing competing models using chi-square difference tests, without reference to modification indices. The best model selected using this procedure was further examined for indications of lack of fit using residual covariances and modification indices, as well as by examining the significance of pathways. Analyses were performed using the program Mplus (Muthén and Muthén 2005) and normal theory maximum likelihood estimation.

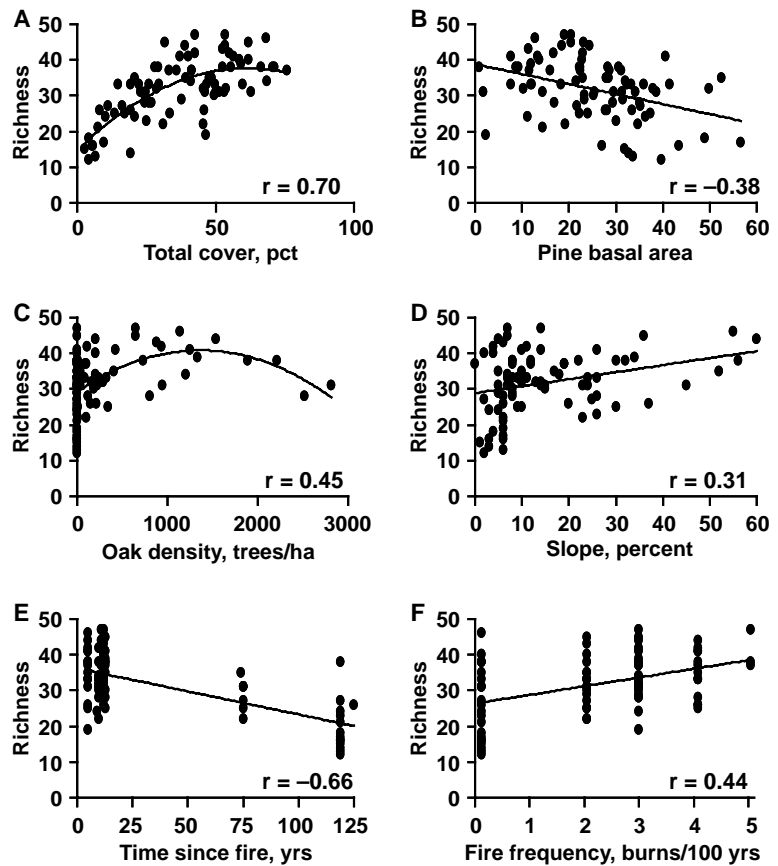
The second type of structural equation model examined in this study was a 'general' model. These models are of the form in Fig. 1 and include composite variables in which combinations of effects are aggregated so we can address more general hypotheses. The effects of time-since-fire and fire frequency were combined into effects of disturbance. Also, the effects of oak and pine were combined into an estimate of the effects of overstory abundance. Composite variable modeling was performed based on the principles in Heise (1972) using the procedures developed by Grace and Bollen (described in Grace 2006, Ch. 6). These procedures use a two-stage approach in which models are estimated without composites in the first stage. In the second stage, composites are included with zero error variance and with one incoming path fixed to a value of 1 so as to set the scale for the composites.

## Results

Understory richness was significantly correlated ( $P < 0.01$ ) with all six of the observed variables in the model (Fig. 3). Richness fit a curvilinear relation to total understory cover (Fig. 3a). Visual examination indicated that richness leveled off when total cover was approximately 50–60%. A clear drop in richness at the highest values of cover was not observed in these data, however. For the purposes of modeling a linear relation with richness, a log transformation of cover yielded a linear graph and a correlation of 0.70. Richness declined linearly with increasing pine basal area (Fig. 3b). Oak density fit a second-order polynomial relation with richness, with richness declining where oak density exceeded approximately 1500 trees  $\text{ha}^{-1}$  (Fig. 3c). Positive linear relations to richness were found for slope and fire frequency, and a negative linear relation to richness was found for time-since-fire (Fig. 3d–e). Correlations among all variables are given in Table 1.

Analysis of specific structural equation models found that the indirect effects model, which includes only those paths shown in Fig. 2, was not consistent with the data ( $\chi^2 = 21.8$ , 9 df,  $P = 0.01$ ; indicating significant differences between model and data). The first alternative model (developed from theoretical justifications) included a direct path from time-since-fire to understory richness and yielded a chi-square of 8.80 (8 df,  $P = 0.36$ ). The drop in chi-square of 13.0 was highly significant ( $P < 0.01$ ), indicating this model was more appropriate. The second alternative model included a direct path from fire frequency to understory richness and yielded a chi-square of 6.6 (7 df,  $P = 0.47$ ). This decline in chi-square was not significant, indicating this path should not be included in the model. Inclusion of a direct path from slope to understory richness likewise failed to improve model fit significantly. Thus, the first alternative

Fig. 3. Bivariate relations between richness and all other observed variables in the model. All relationships were significant ( $P < 0.01$ ).



model was deemed the best of those initially considered. Examination of residuals and modification indices did not reveal substantial discrepancies. However, significance tests for pathways revealed that the paths from the fire variables to oak abundance were not significant, therefore, we decided to delete these from the final model. These deletions permitted estimates of separate effects between oak abundance and pine abundance (instead of a single net relationship) because the resulting model could be ‘identified’ (i.e. unique estimates of all parameters were possible).

The final model (Fig. 4) fit the data well ( $\chi^2 = 11.7$ , 9 df,  $P = 0.23$ ), indicating that the covariance structure of the data did not significantly deviate from the

covariance structure implied by the model. The final model explained the majority of total variance in understory richness ( $R^2 = 0.64$ ) and understory abundance ( $R^2 = 0.72$ ), but explained less of the total variance of oak abundance ( $R^2 = 0.21$ ) and pine abundance ( $R^2 = 0.22$ ). Standardized path coefficients for this model are shown in Fig. 4 and the prediction equations that include unstandardized coefficients are provided in Table 2.

The results of our sensitivity analyses showed that model fit was not significantly affected by varying the amount of measurement error (Table 3). Both the model without measurement error and the model with double the estimated measurement error fit the data. Also,

Table 1. Correlations among observed variables. Significant correlations are in bold.

	Rich	LogCov	PineBA	Oakden	Oakden <sup>2</sup>	Pctslope	Firetime	Firefreq
Rich	1.0							
LogCov	<b>0.67</b>	1.0						
PineBA	<b>-0.38</b>	<b>-0.58</b>	1.0					
Oakden	<b>0.29</b>	<b>0.44</b>	<b>-0.26</b>	1.0				
Oakden <sup>2</sup>	<b>0.14</b>	<b>0.29</b>	<b>-0.14</b>	<b>0.94</b>	1.0			
Pctslope	<b>0.31</b>	<b>0.39</b>	<b>-0.21</b>	<b>0.44</b>	<b>0.33</b>	1.0		
Firetime	<b>-0.66</b>	<b>-0.63</b>	<b>0.32</b>	<b>-0.25</b>	<b>-0.18</b>	<b>-0.17</b>	1.0	
Firefreq	<b>0.44</b>	<b>0.23</b>	<b>-0.02</b>	0.15	0.12	<b>-0.06</b>	<b>-0.66</b>	1.0

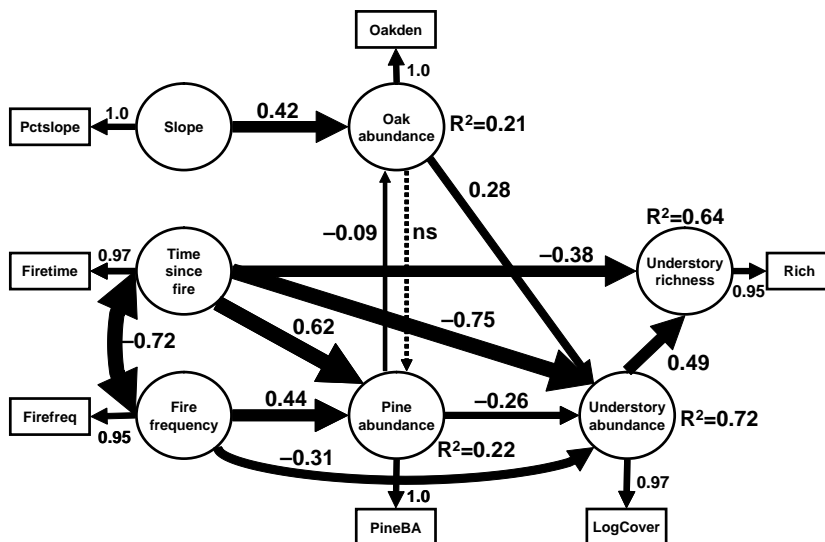


Fig. 4. Specific model results ( $\chi^2 = 11.7$ , 9 df,  $P = 0.23$ ) with standardized path coefficients. The size of the arrow is proportional to the strength of the path.

results supported retention of all the same pathways, thus, model structure was stable. As expected, the magnitude of certain pathways was found to be sensitive to variations in specified measurement error. Most responsive were the paths from time-since-fire to understory abundance and to pine abundance. The paths from fire frequency to pine abundance and to understory abundance were also moderately responsive. All other path coefficients were relatively unresponsive to variations in measurement error.

Indirect relations contribute to the so-called ‘total effects’, which represent the sum of direct and indirect pathways (Table 4). Results indicate that for most variables, their relationships with understory richness were entirely indirect. The one exception was time-since-fire, which contributed directly to the explanation of variation in understory richness. Even for time-since-fire, though, the majority of its total effect on understory richness ( $-0.84$ ) was indirect ( $-0.46$ ), through relationships with pine and understory abundance.

The analysis of the general model in which some effects were composited produced a broader perspective

Table 2. Prediction equations with unstandardized coefficients.

Prediction equations\*

$$\begin{aligned} \text{RICH} &= 25.66 + 28.52 \cdot \text{ABUN} - 0.0731 \cdot \text{FIRETIME} \\ \text{ABUN} &= 0.480 - 0.003 \cdot \text{PINE} + 0.00015 \cdot \text{OAK} - 5.07e^{-8} \cdot \\ &\quad \text{OAK}^2 - 0.000244 \cdot \text{FIRETIME} - 0.035 \cdot \text{FIREFREQ} \\ \text{PINE} &= 11.98 + 0.1715 \cdot \text{FIRETIME} + 4.2 \cdot \text{FIREFREQ} \\ \text{OAK} &= 153.546 + 18.526 \cdot \text{SLOPE} - 4.71 \cdot \text{PINE} \end{aligned}$$

\*Where, RICH = understory richness = number of species per 0.1 ha; ABUN = understory abundance =  $\text{Ln}(\% \text{cover} / 100 + 1)$ ; FIRETIME = time-since-fire = years since last burn; PINE = pine abundance = ponderosa pine basal area per hectare; OAK = oak abundance = Gambel oak trees per hectare;  $\text{OAK}^2$  = square of OAK; FIREFREQ = number of fires since 1880/118 years; SLOPE = % slope

of relationships (Fig. 5). The general model had a chi-square of 13.0 (10 df,  $P = 0.23$ ). The structure of this model fit with the findings for specific models, in that there was evidence for a direct path from disturbance history to understory richness and no support for a direct path from overstory abundance.

## Discussion

Partitioning direct and indirect effects on community structure has advanced the understanding of patterns of diversity across landscapes. In old-growth montane forests that are evolutionarily adapted to a surface fire regime, the evidence from this analysis suggests that understory richness is influenced by direct and indirect effects of fire history. Indirect effects of fire history on understory richness are apparently mediated through direct effects on pine abundance and understory abundance. Therefore, over large temporal and spatial scales, surface fire plays an important role in structuring understory plant communities in old-growth montane forests.

Understory plant abundance was not found to be unimodally related to understory richness in this study, though a leveling off of richness did occur where plant cover was high. This may indicate that competitive exclusion limits seedling establishment and persistence at high levels of understory plant abundance (Grime 1979).

The observation that understory richness was lower where overstory abundance was higher can be explained entirely by the fact that understory abundance was low where overstory abundance was high. Thus, we found no evidence of unique effects of forest structure on richness. This contrasts with Weiher’s (2003) finding that tree

Table 3. Sensitivity analysis of model parameters and model fit with respect to changes in estimated measurement error.

Model pathways	Measurement error		
	Zero	Used in model (Fig. 4)	Double
Understory abundance to understory richness	0.46	0.49	0.52
Time-since-fire to understory richness	-0.36	-0.38	-0.42
Oak abundance to understory abundance	0.28	0.28	0.27
Pine abundance to understory abundance	-0.29	-0.26	-0.19
Time-since-fire to understory abundance	-0.62	-0.75	-1.0
Fire frequency to understory abundance	-0.20	-0.31	-0.53
Slope to oak abundance	0.42	0.42	0.42
Pine abundance to oak abundance	-0.09	-0.09	-0.10
Oak abundance to pine abundance	ns	ns	ns
Time-since-fire to pine abundance	0.51	0.62	0.80
Fire frequency to pine abundance	0.33	0.44	0.61
Time-since-fire with fire frequency	-0.72	-0.72	-0.72
Model fit			
Chi-square	14.0	11.7	9.8
df	9	9	9
P	0.12	0.23	0.37

canopy had a direct effect on richness, yet virtually no effect on herbaceous biomass. In this system, pine trees intercept light (Naumburg and DeWald 1999), intercept precipitation (McLaughlin 1978), produce abundant needle-fall, and can compete for soil nutrients, all of which can negatively impact herbaceous productivity. Riegel et al. (1995) concluded that limiting resources such as light, water, and nutrients affected understory species composition in ponderosa pine forests based on individual species responses' to resource manipulation. It would seem that ponderosa pine has a strong influence on the understory plant community. Furthermore, our evidence implies that pine abundance may have a slight negative effect on oak abundance, likely due to resource competition, but oak abundance had no detectable reciprocal effect on pine abundance in this case.

Oak abundance was positively related to topographic slope in this system. This result may be specific to North Rim forests, as Gambel oak can readily grow on flat terrain in other pine forests in northern Arizona. Oak abundance was unimodally related to understory abundance (data not shown). Low to moderate densities of oak trees had a positive association with understory production, which may be mediated by oak litter, as oak positively influences soil fertility (Klemmedson 1987, 1991). Soil nutrient content, which was not measured in this study, may have contributed to unexplained variance in the model (Grace et al. 2000, Weiher 2003, Weiher

et al. 2004). However, understory abundance began to decline as oak densities surpassed 1500 trees ha<sup>-1</sup>. Therefore, the positive path (0.28) should be interpreted as showing that intermediate levels of oak are associated with maximum understory abundance. This result clarifies the relationship found in Laughlin et al. (2005), where pine-oak forests had much greater plant cover and slightly greater plant species richness than pure ponderosa pine forests, and agrees with Weiher (2003) who found weak positive effects on a variety of plant species when oak canopy was moderate.

Time-since-fire appears to have a strong negative total effect on understory richness (-0.84) in this system, with some of the influence mediated by positive influences on overstory abundance, some mediated by negative influences on understory abundance, and some of the influence represented by a negative direct path. Several different processes would seem to be operating here. The strong positive association between time-since-fire and pine abundance exists because pine abundance increases during long, fire-free intervals (>100 years in some cases). Long-term absence of fire allowed pine seedlings and saplings to develop into

Table 4. Standardized direct, indirect, and total effects on understory richness (ns refers to a nonsignificant effect).

Factors	Direct	Indirect	Total
Understory abundance	0.49		0.49
Oak abundance		0.14	0.14
Pine abundance		-0.13	-0.13
Time-since-fire	-0.38	-0.46	-0.84
Fire frequency		-0.21	-0.21
Slope		0.06 ns	0.06 ns

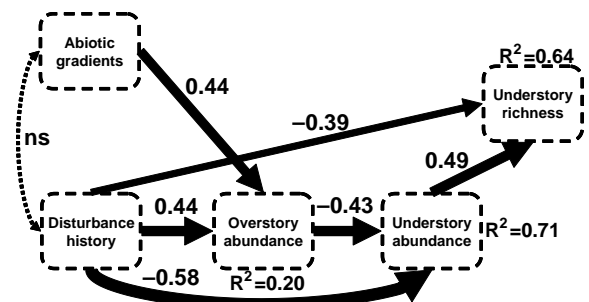


Fig. 5. General model results ( $\chi^2 = 13.0$ , 10 df,  $P = 0.23$ ) with standardized path coefficients. Constructs variously represent individual or collections of latent variables. The size of the arrow is proportional to the strength of the path.



mature trees and thereby contribute to larger stand volumes. In contrast, the strong negative direct path from time-since-fire to understory abundance may represent post-fire stimulation of herbaceous primary production, either through the release of nutrients into the soil (Covington and Sackett 1992), or a reduction of built-up plant litter on the soil surface. Thus, forests without fire show a decline in understory abundance above and beyond what can be explained simply by increases in pine abundance. These processes ultimately resulted in a loss of approximately one plant species per 0.1 ha per decade (Fig. 3) when fire is excluded from these forests.

The direct path from time-since-fire to understory richness implies an effect that is independent of overstory or understory abundance. We think it is possible that this represents post-fire stimulation of richness, either by creating previously unavailable habitat, or by stimulating fire-tolerant and fire-dependent species. Low intensity fires can produce high amounts of small-scale heterogeneity, since slight variability in fuel load and moisture can determine whether an area will burn or not (Huston 1994, Bond and van Wilgen 1996). This heterogeneity can potentially create opportunities for fire-tolerant species (Watson and Wardell-Johnson 2004), allowing for the coexistence of numerous species. Heat and smoke from fires can also stimulate germination of understory species (Keeley 1991). For example, germination of *Penstemon barbatus*, a native forb, increased dramatically after exposure to smoke (Abella 2005). This may be another important mechanism of post-fire stimulation of plant richness that has been little studied in this system. Furthermore, the increased availability of light to the soil surface following a burn allows for the germination of annual species (Grime 1977, Gibson 1988). Pine forests that have not burned for over 70 years had significantly fewer annual species than forests that burned recently (Laughlin et al. 2005), and annual species responded positively to a low-intensity fire on the North Rim of GCNP (Laughlin et al. 2004).

The implied effects of fire frequency are perhaps the most counterintuitive results in the model. The bivariate relationships between fire frequency and understory abundance and richness (Table 1) were significant and positive ( $r=0.23, 0.44$ , respectively). However, once time-since-fire was statistically controlled, model results implied that areas with more frequent fires have lower richness than otherwise expected. In other words, these results suggest that if we could hold time-since-fire constant for all plots, we would see that those plots with high fire frequencies have comparatively low richness. This appears to result primarily from a positive association between frequent fires and pine abundance and negative association between frequent fires and understory abundance. We interpret the positive

association with pine abundance as an indication that multiple fires have a thinning effect on pine seedlings and saplings, thereby allowing the old-growth pine trees to grow larger faster and contribute to greater stand volumes (Feeney et al. 1998). We interpret the negative association of frequent fires with understory abundance as an indication that multiple fires can harm understory production, possibly by depletion of soil N after repeated exposure to surface fire (Binkley et al. 1992, Wright and Hart 1997). Because of the counterintuitive nature of the results and the fact that fire frequency was very conservatively measured, we consider paths from fire frequency as tentative until later confirmed in subsequent multivariate studies. However, these results exemplify the strength of structural equation modeling as a tool for analyzing complex relationships among many variables, since traditional univariate techniques could not have detected these residual effects (Grace and Pugsek 1997, 1998). In other studies, herbaceous species richness has been found to be negatively related to fire frequency in tallgrass prairie (Collins et al. 1995), but positively related to fire frequency in loblolly pine forests (Lewis and Harshbarger 1976, Waldrop et al. 1987). Based on the limited data available at present, it appears that fire frequency may not have a consistent relationship to richness across systems.

General theories about disturbance and species diversity are well supported in surface fire-adapted montane forests. Moderate disturbance frequencies increase diversity by reducing rates of competitive displacement, but high frequencies can reduce diversity through direct species loss. In montane systems, fire history is clearly a strong influence on plant species richness, but the structural equation model results suggests that there is a delicate balance between time-since-fire and fire frequency and that some of these effects are mediated through overstory–understory interactions.

These data and analyses also suggest that multivariate models of richness, such as those used to understand patterns in herbaceous communities (Grace and Pugsek 1997, Gough and Grace 1999, Grace and Jutila 1999, Grace et al. 2000), can be expanded to incorporate the mediating effects of the forest overstory (Fig. 5). It would seem that in general, forest overstories can, among other things, reduce understory abundance and the importance of competition among herbaceous species in regulating richness. At the same time, while not found in this study, there are other cases where the overstory has been found to have unique influences on understory richness (Weiher 2003), which remain to be explored fully. In this case, the overstory completely moderated the effects of abiotic gradients on understory abundance. Disturbance, on the other hand, had unique influences on both understory abundance and richness, representing cumulative effects of fire history.

This example contributes to a growing body of literature indicating that abiotic and biotic factors and their complex interactions are important in regulating spatial and temporal variation in plant species richness across landscapes. Structural equation models, while often reflecting specific influences in each system studied, appear to be consistent with a general multivariate model in which variations in disturbance, abiotic conditions, overstory, and understory conditions combine to explain broad patterns of plant species richness. Further studies, including both a greater range of conditions and those that seek to test model predictions, either experimentally or with additional observational data, should provide additional insight into the adequacy of this model to represent diversity regulation in fire-adapted forest systems.

*Acknowledgements* – We thank P. Fulé, E. Weiher and M. Bowker for their insight early on in the development of this paper, and we are grateful to the National Park Service, the Bureau of Land Management, and the Joint Fire Science Program for support.

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