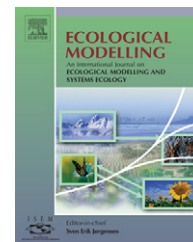


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Abiotic and biotic factors explain independent gradients of plant community composition in ponderosa pine forests

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ABSTRACT

General multivariate models have appeal when analyzing ecological systems because they have the potential to shed light on the relative importance of multifaceted factors. We hypothesized that plant community composition is a function of the interactions among three general constructs: abiotic and biotic factors and disturbance history. We sampled vegetation and soils on 75 randomly located 0.05 ha plots across a broad soil gradient within a 110,000 ha ponderosa pine forest landscape in northern Arizona to evaluate this hypothesis.

The variation in abundances of 271 understory plant species was reduced to two orthogonal axes using non-metric multidimensional scaling. We evaluated the relationships between ordination results and environmental conditions using two types of structural equation models. ‘Specific’ models provided a detailed perspective of hypothesized relationships among observed variables. A ‘general’ model was evaluated to address the general hypothesis stated above. The general model employed composite variables, which specify the combined effects of multiple factors on a response, in order to evaluate the relative importance of the three theoretical constructs.

The results of the final specific model suggested that organic matter and nitrogen explained unique variation in composition, but the ‘total effects’ of organic matter were not significant due to offsetting direct and indirect pathways. Soil texture and pH also constrained where many plant species occurred. Elevation was a strong determinant of species distributions, and its effects could be propagated through a network of processes involving soil mineral and organic properties. Litter depth explained unique variation in community composition, suggesting that plant species differ in their ability to colonize sites with different litter depths independent of the density of pine trees. Composition also differed under varying densities of pine trees since species vary in their tolerance of a competitive overstorey. Finally, heavy grazing tended to favor the abundance of non-palatable species in the community.

The results of the general model provided new insight into the underlying structure of independent plant community gradients in ponderosa pine forests. The model suggested that abiotic factors generated one gradient in community composition, whereas biotic factors, and to a lesser degree, disturbance history, generated a second independent gradient in community composition. Future evaluations of this composition model across a diversity of ecosystems could determine the generality and utility of this multivariate hypothesis.

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1. Introduction

A fundamental interest in community ecology is to understand the main drivers of community composition. Debate over the existence and importance of assembly rules that determine the composition of natural communities is decades old (Diamond, 1975; Stone et al., 1996; Booth and Larson, 1999; Simberloff et al., 1999), and much progress has been made (Weiher and Keddy, 1999b). It is generally agreed that both abiotic factors (e.g., elevation, soil texture) and biotic factors (e.g., shading, herbivory, interspecific competition) determine which species from the regional species pool can exist in a community (Booth and Larson, 1999; Weiher and Keddy, 1999a; but see Wilson, 1999). However, the debate over the relative importance of abiotic and biotic factors in regulating composition has not been adequately resolved (Simberloff et al., 1999), nor has the relative importance of disturbance (such as grazing) in relation to abiotic and biotic factors been addressed (Díaz et al., 1999). Moreover, a multivariate model of composition that permits an evaluation of the relative importance of abiotic and biotic factors and disturbance has not been formally proposed or evaluated. General models such as those proposed by Grace and Pugsek (1997) are useful because they provide ecologists with the ability to test the generality of a theory across systems (Grace, 2006), which is becoming an increasingly important activity in ecology (e.g., Weiher, 2003; Knapp et al., 2004). Such a model could advance current understanding of the main drivers of plant community structure.

Abiotic factors such as climate-driven responses to elevation (Díaz et al., 1999) and soil properties (Grace, 2003) can determine which plant species will colonize a site (Keddy and Weiher, 1999) because plant species differ in their tolerance and utilization of resources. These differences have been proposed as a driving mechanism of species coexistence in similar environments (Tilman, 1982) and can also explain broad-scale compositional differences along multiple resource gradients (Grace, 2003; Kashian et al., 2003). Once the regional species pool passes through the abiotic filters, the remaining species undergo further filtering by biotic interactions and disturbance effects. Biotic factors such as overstory tree density can influence community composition because understory species differ in their ability to tolerate stresses imposed by competitive trees (Grime, 1979; Riegel et al., 1995; Naumburg and DeWald, 1999; Laughlin et al., 2005). Furthermore, disturbances can influence community composition by favoring stress-tolerant species (Grime, 1979) and increasing the abundance of annual and biennial plants (Hayes and Holl, 2003; Laughlin et al., 2004, 2005).

Evaluating community–environment relationships is quantitatively challenging since community matrices represent a complex multivariate response (Legendre and Legendre, 1998). Analyses that simply regress multiple environmental variables on axis scores derived from ordinations may satisfy distributional properties of the data (e.g., Lee and Sampson, 2000), but these analyses have all the same problems of interpretation that befall multiple regression (Grace and Bollen, 2005). These problems include, but are not limited to (1) the unanalyzed and unresolved covariances among interacting explanatory variables and (2) the inability

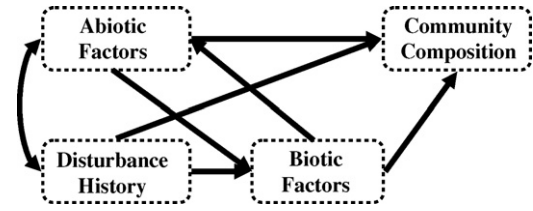


Fig. 1 – Generalized conceptual model of factors influencing community composition. Model structure follows from diversity models developed in grasslands (Grace and Pugsek, 1997; Weiher et al., 2004), savannas (Weiher, 2003) and pine forests (Laughlin and Grace, 2006; Laughlin et al., 2007).

to assign unique explanatory capacity to individual factors (Pedhazur, 1997; Grace and Bollen, 2005). To avoid these problems, structural equation modeling has been proposed for testing multivariate theories of community composition (McCune and Grace, 2002; Grace, 2003).

We developed a generalized conceptual model illustrated in Fig. 1. This model hypothesizes that community composition is controlled by the interactions of abiotic and biotic factors and disturbance history (Weiher and Keddy, 1999b). We included the possibilities that abiotic factors can have reciprocal relations with biotic factors, that disturbance history and abiotic factors could be associated because of land-use patterns, and that disturbance might influence biotic factors.

The *a priori* specific structural equation model is presented in Fig. 2. Following from the logic conceptualized in Fig. 1, we hypothesized that community composition is associated with variations in elevation (Whittaker, 1960), soil properties (Grace, 2003; Kashian et al., 2003), tree density (Riegel et al., 1995; Naumburg and DeWald, 1999; Laughlin et al., 2005), litter depth (Beatty and Sholes, 1988) and grazing (Stohlgren et al., 1999; Cingolani et al., 2005). Our primary purpose was to gain insight into the relative importance of processes that influence plant community composition by incorporating the potential interactions between system components into the model. In conjunction with this analysis, we sought to address a number of specific questions:

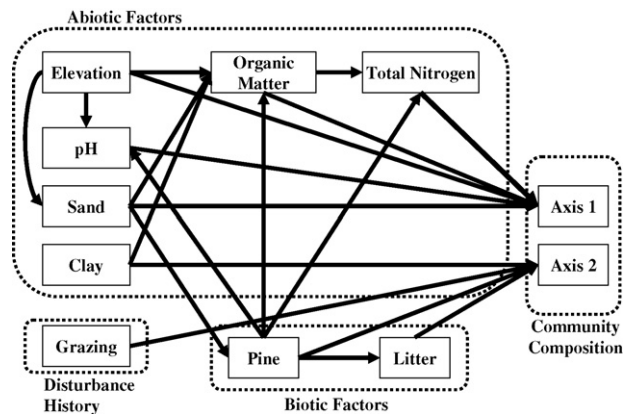


Fig. 2 – *A priori* multivariate hypothesis of specific factors that influence plant community composition in ponderosa pine forest ecosystems.

1. Can organic matter and nitrogen have independent effects on composition?
2. Are associations between soil texture and composition explained entirely by indirect effects mediated through organic soil properties?
3. Can the effects of elevation on composition be propagated through a network of processes involving soil mineral and organic properties?
4. Does litter depth uniquely contribute to the variation observed in composition or is it merely a function of pine density?
5. Does composition differ under varying densities of pine trees?
6. Can grazing affect the composition of the community?

2. Methods

2.1. Study system

The ponderosa pine (*Pinus ponderosa* P. & C. Lawson var. *scopulorum* Engelm.) forest ecosystem covers millions of hectares in the southwestern United States and occurs on a wide variety of soil parent materials including basalt, limestone, sandstone, and cinder soils. In this study we sampled vegetation within a 110,000 ha landscape on the Northern Arizona University Centennial Forest and on the Coconino National Forest between the elevations of 1920–2660 m. In the sampled area, ponderosa pine is the dominant tree species and forms extensive pure stands, but sometimes occurs with Gambel oak (*Quercus gambelii* Nutt.) or quaking aspen (*Populus tremuloides* Michx.). Precipitation ranges from 42 to 56 cm year⁻¹, snowfall from 152 to 233 cm year⁻¹, and mean maximum daily temperatures from 15.7 to 17.5 °C (Western Regional Climate Center, Reno, NV, USA). Topography is primarily flat or undulating (slope gradients <10%), occasionally dissected by cinder cones, ravines, and low hills. Volcanic activity has been widespread, with the most recent eruptions occurring ~900 years ago in the Sunset Crater Volcanic Field in the northeastern part of the study area (Moore et al., 1976). Soil parent materials include basalt, volcanic cinders, benmoreite, mixed igneous rocks, and limestone (Welch and Klemmedson, 1975). Major soil subgroups are Typic and Udic Argiborolls, Typic and Mollic Eutroboralfs, Typic Ustorthents, and Vitrandic Ustochrepts (Miller et al., 1995).

2.2. Data collection

We used a digital Terrestrial Ecosystem Survey (TES) map (Miller et al., 1995) in a Geographic Information System to randomly select mapping units for sampling in each of 11 TES types that encompass a range of soil types. We randomly located 0.05 ha (20 m × 25 m) plots within each mapping unit for a total of 75 plots.

Plots were sampled during the period May–August 2003. At each plot, we collected composite soil samples of 0–15 cm depths from two pits per plot. Samples were air dried, sieved (2 mm), and analyzed for texture (hydrometer method), pH (1:2 soil:0.01 M CaCl₂), total nitrogen (with an elemental carbon/nitrogen analyzer), and organic matter (estimated from

loss-on-ignition at 300 °C for 2 h), following methods outlined in Sparks (1996) and Dane and Topp (2002).

We sampled litter (O_i horizon) thickness and plant species composition in fifteen 1 m² subplots in each 0.05 ha plot. We visually categorized areal percent cover of each species rooted in each subplot as 0.1, 0.25, 0.5, and 1% up to 1% cover, at 1% intervals to 10% cover, and at 5% intervals above 10% cover. We also measured diameters at 1.4 m of all live ponderosa pine >1 cm diameter on each plot to calculate pine basal area.

Evidence of grazing was used to produce a coarse categorical variable where 0=evidence of light grazing and 1=evidence of heavy grazing. This determination was based on field observations of severely grazed vegetation, proximity of plots to livestock tanks, and known areas where sheep and cattle are herded or kept. These determinations resulted in 40% of the plots being coded as having experienced recent heavy grazing.

2.3. Data analysis

If continuous soil properties could accurately predict the correct soil type from which the sample was taken, we decided it could be appropriate to use the continuous soil properties to explain patterns of composition across the landscape in lieu of the less informative alternative of simply using soil types as nominal predictors. To accomplish this, we used discriminant analysis (SAS Institute, 2005). Discriminant analysis showed that continuous soil properties correctly predicted the soil type 88% of the time. An alternative, non-parametric discriminant analysis test indicated that predictions were correct 100% of the time. As a result of these findings, we felt justified in using continuous soil variables in lieu of soil types to represent the relationship between soil gradients and community composition.

Many data reduction methods (e.g., detrended correspondence analysis, and canonical correspondence analysis) used to analyze associations between community and environmental gradients have been shown to perform poorly when applied to ecological community data (Beals, 1984; Minchin, 1987; Jackson and Somers, 1991; Legendre and Legendre, 1998; McCune and Grace, 2002). Non-metric multidimensional scaling (NMS) has been suggested over other ordination techniques for community analysis because it does not ignore community structure that is unrelated to environmental variables and it does not assume multivariate normality (McCune and Grace, 2002). Therefore, with cover values as a measure of species abundance, we used NMS using PC-ORD software (Version 4.25; McCune and Mefford, 1999) to reduce the dimensionality of the community matrix. We used the Bray–Curtis distance measure (Faith et al., 1987) with random starting configurations, 100 runs with real data, a maximum of 400 iterations per run, and a stability criterion of 0.00001. A Monte Carlo test with 99 randomizations was used to determine how likely the observed stress value of the final solution would be by chance alone. Species that occurred on <5% of the plots were omitted from the ordination following guidelines in McCune and Grace (2002).

We used PC-ORD to determine which continuous soil variables could explain at least 10% of the variation of an ordination axis, expressed as a vector on the ordination diagram

(McCune and Grace, 2002). We included in this analysis the following environmental variables: elevation, total nitrogen, organic matter, clay and sand concentrations, pH, pine basal area ($\text{m}^2 \text{ha}^{-1}$), and litter depth (cm). We used Varimax rotation on the ordination axes to maximize variance explained by pH and elevation following the procedure described by Grace (2003).

Prior to evaluating multivariate models, bivariate relations between all variables in the model were assessed. We examined scatterplots for the presence of outliers, evidence of skewness or kurtosis, and non-linear relationships up to second-order polynomials. Non-linear relationships between an explanatory variable and one ordination axis were modeled by freeing paths from the explanatory variable to both ordination axes.

2.4. Structural equation modeling

Collinearity among explanatory variables can be problematic in multiple regression analysis (Asher, 1983; Myers, 1990). However, SEM allows a researcher to theorize about why explanatory variables are correlated and to build directional relationships into their models of a system. For example, explanatory variables are often correlated because they have a common cause or because one factor influences the other (Shipley, 2000). Indeed, these situations often occur in observational studies of complex systems. Therefore, in this study, we took such a systems approach to the analysis and interpretation of composition in an ecosystem where driving forces interact to produce observed compositional patterns across the landscape.

The use of structural equation models to understand ecological systems has gained momentum in recent years (Shipley, 2000; Pugesek et al., 2003; Grace, 2006; Arhonditsis et al., 2006). Structural equation modeling (SEM) is an extension of regression and path analysis that can be used to model multivariate relations and to test multivariate hypotheses (Bollen, 1989). Good-fitting structural equation models do not prove causal relationships (Bollen, 1989). Inferences about the sign and strength of directional paths in SEM can only be made if sound theory guides both the model building and the model-fitting processes (Grace, 2006).

We evaluated two types of structural equation models in this study: 'specific' and 'general' models. 'Specific' models were evaluated to give a detailed perspective of relationships. The initial specific model (Fig. 2) represents what we believed to be the most plausible structural relations based on *a priori* knowledge. We acknowledge that not all processes that act on composition in this system are represented in Fig. 2. Rather, our objective was to determine whether the data were consistent with the expectations of the proposed model. Ultimately, our goal was to arrive at a model consistent with the data using the fewest modifications of the initial model as possible, thereby preserving as much as possible the ability to draw inferences from model parameters. We used maximum likelihood solution procedures and employed chi-square goodness of fit measures to evaluate model adequacy. Residuals and modification indices were also examined to determine if there were apparent model-data discrepancies, which in turn were used to identify alternative models for considera-

tion. Analyses were performed using Mplus software (Muthén and Muthén, 2005). The final structural equation model had a covariance structure that was consistent with the covariance structure of the data; therefore, we used theory to guide our interpretation of the mechanistic nature of the directional paths.

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 to address more general hypotheses. Generalized multivariate models such as these offer tremendous promise to ecology because they permit consideration of general constructs (e.g., disturbance) while allowing the specific factors (e.g., grazing versus flooding) to differ among systems (Grace, 2006). Moreover, ecological constructs such as 'abiotic factors' are very often multifaceted in nature (Grace and Bollen, *in press*). The effects of elevation, pH, clay, organic matter, and nitrogen were composited into effects of 'abiotic factors'. The effects of pine density and litter depth were composited into effects of 'biotic factors'. Since only one disturbance type was measured in this study, grazing represented the effect of recent 'disturbance history'. We followed the general principles developed by Heise (1972) and refined by Grace and Bollen (*in press*) for developing composites that represent general constructs. Composites estimate the combined effects of multiple factors on a single response variable. 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. Abiotic factors were scaled to elevation and biotic factors were scaled to pine density.

Finally, we calculated the so-called 'total effects', which are the sum of direct and indirect pathways from the explanatory variables to composition (Grace, 2006). Indirect effects equal the total sum of the products of all path segments from an explanatory variable to composition. Total effects are a simple summary of the complex and sometimes dual nature (opposing signs) of the relationship between the causal factors and community composition and they provide a calculation of the net effect (i.e., strength and sign) of a relationship.

3. Results

We identified 271 plant species within the plots across the study area. We included the 156 species that were found on >5% of the plots. A satisfactory two-dimensional solution was obtained using NMS ordination (Fig. 3). Thus, each ordination axis represented an independent gradient in species space. Nine variables, expressed as vectors in Fig. 3, appeared to be correlated with composition.

Bivariate correlation analysis determined that axis 1 was significantly ($P < 0.05$) correlated with five of the nine variables in the model. Axis 1 exhibited positive linear relationships with nitrogen, organic matter, and elevation and negative linear relationships with pH and sand (Fig. 4). Axis 2 exhibited positive linear relationships with sand and pine basal area, negative linear relationships with nitrogen and clay, and non-linear relations with litter (Fig. 5). Many of the factors proposed

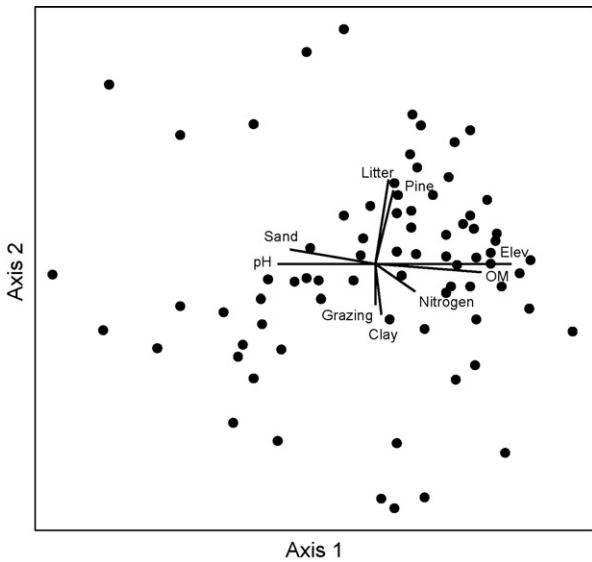


Fig. 3 – Non-metric multidimensional scaling ordination of plant community composition sampled across a 110,000 ha northern Arizona ponderosa pine forest landscape. The plot was constructed using 156 species that were found in 75 plots. The final solution had two-dimensions (stress = 20.1, P = 0.01).

to influence composition were also correlated with each other (Table 1), suggesting that the factors themselves interacted and that indirect effects on composition were likely in this system.

The *a priori* specific structural equation model (Fig. 2) was found to be inconsistent with the data ($\chi^2 = 176$, 31 d.f., $P < 0.001$). After controlling for other variables, sand did not explain unique variation in axis 1 despite its strong bivariate correlation (Table 1), and was therefore dropped to simplify the model. We added paths from clay to litter and nitrogen, and a path from litter to axis 1 (which accounted for the non-linear association with axis 2), since these were indicated to be missing based on modification indices. The resulting model was found to not differ significantly from the data ($\chi^2 = 25.5$, 22 d.f., $P = 0.27$) and explained 71% of the variation in axis 1, 61% of the variation in axis 2, 36% of the variation in litter, 80% of the variation in nitrogen, 48% of the variation in organic matter, and 20% of the variation in pH (Fig. 6).

Elevation exhibited the strongest 'total effect' on axis 1 (Table 2) due to its direct and many indirect relationships with axis 1 (Fig. 6). The negative indirect effects of organic matter on axis 1 (standardized path coefficient = -0.28) offset the relatively strong positive direct effect (standardized path coefficient = 0.44), yielding a non-significant 'total effect' (Table 2).

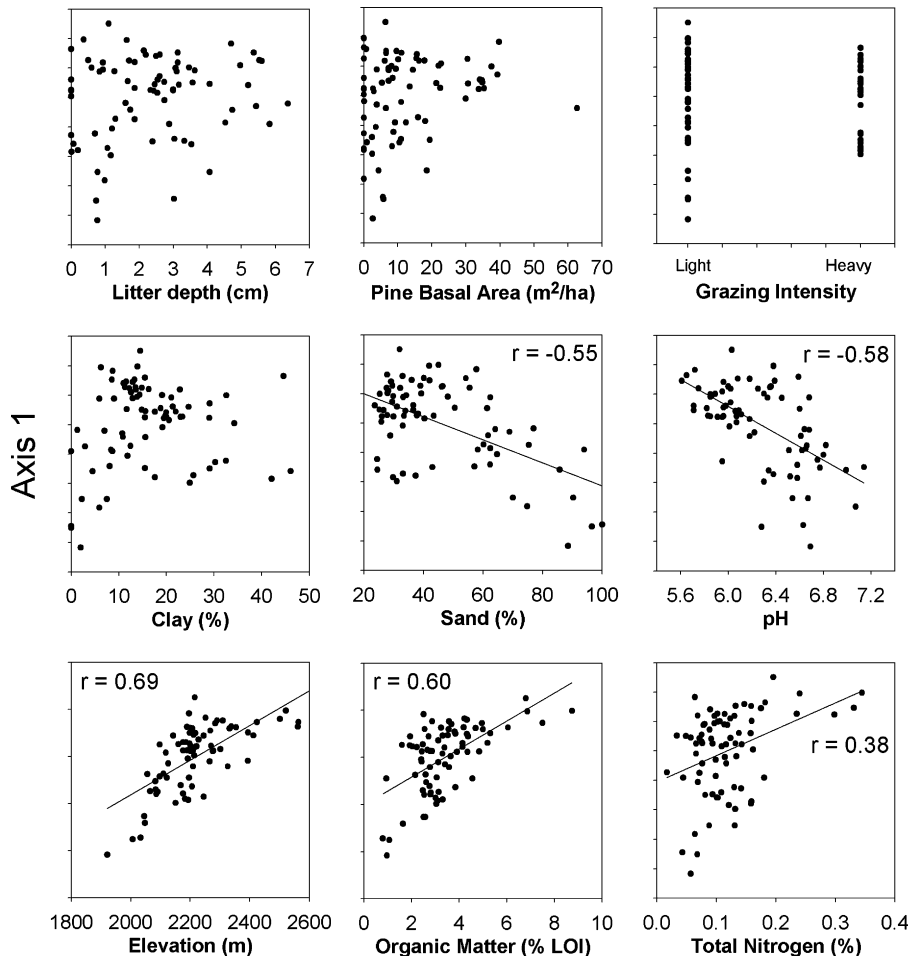


Fig. 4 – Bivariate relationships between explanatory variables and NMS axis 1. Correlation coefficients are shown for significant relationships.

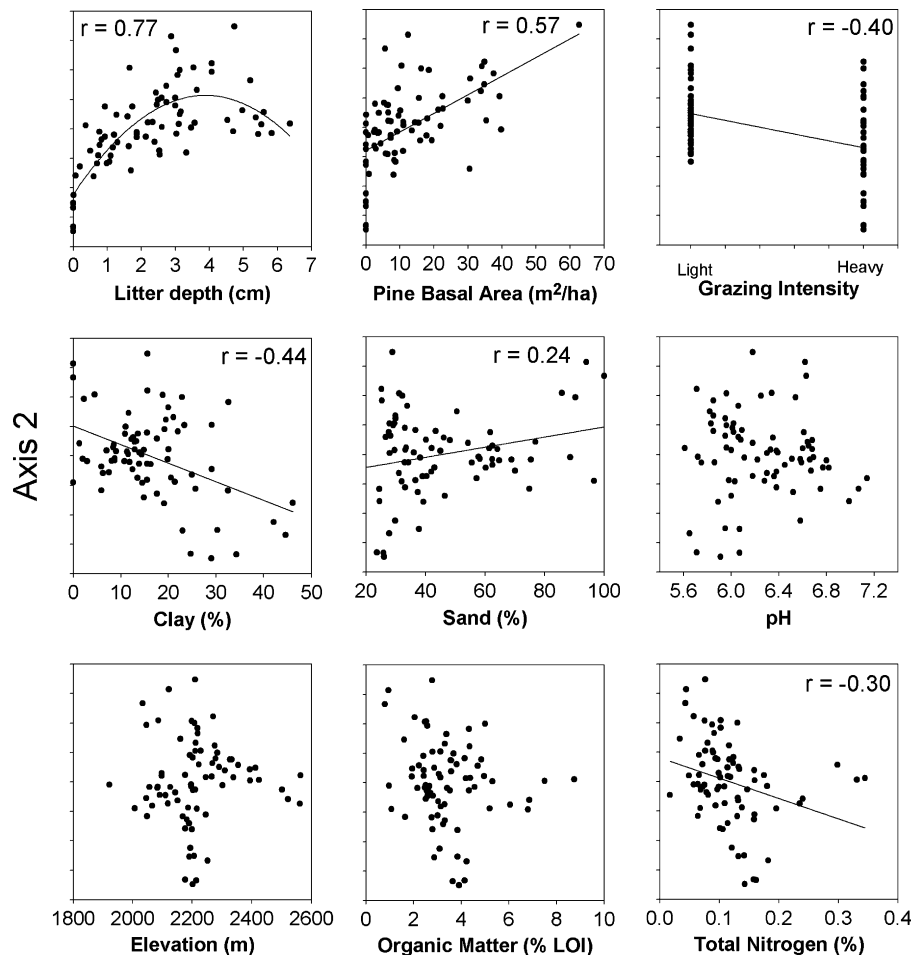


Fig. 5 – Bivariate relationships between explanatory variables and NMS axis 2. Correlation coefficients are shown for significant relationships and include non-linear terms.

Table 1 – Bivariate correlation coefficients (r)

	Axis 1	Axis 2	Litter	N	OM	Sand	Clay	Elev	pH	Pine	Graz
Axis 1	1.0										
Axis 2	0.04	1.0									
Litter	0.16	0.60	1.0								
N	0.38	-0.30	-0.12	1.0							
OM	0.60	-0.19	-0.03	0.83	1.0						
Sand	-0.55	0.24	0.15	-0.28	-0.46	1.0					
Clay	0.13	-0.44	-0.37	0.11	0.17	-0.73	1.0				
Elev	0.69	0.02	0.00	0.66	0.70	-0.44	0.07	1.0			
pH	-0.58	-0.03	-0.06	-0.03	-0.22	0.51	-0.25	-0.26	1.0		
Pine	0.19	0.58	0.47	-0.35	-0.17	-0.21	0.01	-0.06	-0.35	1.0	
Graz	0.02	-0.40	-0.23	-0.06	-0.04	-0.42	0.46	-0.11	-0.17	-0.03	1.0

Significant ($P < 0.05$) correlations are in bold.

Pine density exhibited the strongest 'total effect' on axis 2 (Table 2) due to its direct relationship and indirect relationship mediated through litter depth (Fig. 6).

The analysis of the general model (Fig. 1) in which some effects were composited produced a broader perspective of relationships (Fig. 7). The general model results show that abiotic factors were strongly related to axis 1, biotic factors were strongly related to axis 2, and disturbance exhibited a moderate relationship with axis 2.

4. Discussion

We identified two independent compositional gradients in ponderosa pine forest understory plant communities, suggesting that there were at least two underlying ecological processes that generated these gradients. Interestingly, the general model suggests that abiotic factors generated one compositional gradient and biotic factors and disturbance

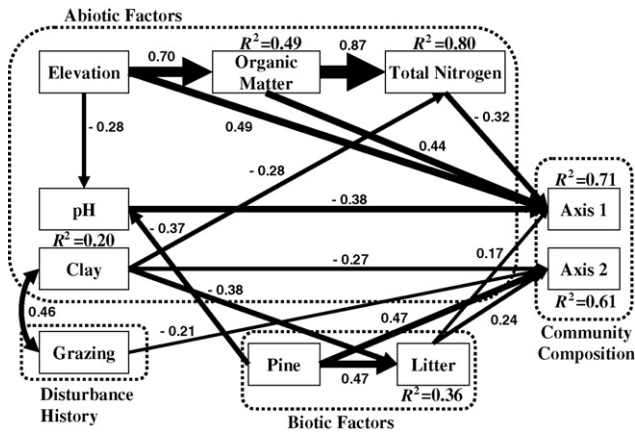


Fig. 6 – Final structural equation model results ($\chi^2 = 25.5$, 22 d.f., $P = 0.27$) with standardized coefficients. All pathways were significant ($P < 0.05$).

Table 2 – Standardized total effects (sum of direct and indirect effects) of factors that influence community composition

Factor	Axis 1	Axis 2
Abiotic filters		
Nitrogen	-0.32**	
Organic matter	0.16 ns	
pH	-0.38***	
Clay	0.03 ns	-0.36***
Elevation	0.72***	
Biotic filters		
Litter	0.17*	0.24*
Pine	0.22***	0.58***
Disturbance		
Grazing		-0.21*

Blank cells indicate that no direct or indirect associations were detected between the factor and the NMS ordination axes. ns: non-significant.
 * $P < 0.05$.
 ** $P < 0.01$.
 *** $P < 0.001$.

history generated the second compositional gradient in this system.

4.1. Abiotic factors

The regional species pool can be strongly filtered by abiotic factors. Variations in total nitrogen, which is primarily a function of organic matter in ponderosa pine forests (Welch and Klemmedson, 1975), have been shown to have profound influences on community composition in many systems (Bradshaw, 1969; Silvertown, 1980; Tilman, 1982; Kirkham et al., 1996; Boyer and Zedler, 1999). This important abiotic gradient influences biotic interactions. Enrichment studies have demonstrated that plant dominance increases and evenness decreases with mineral fertilization (Lawes et al., 1882; Thurston, 1969; Kirchner, 1977; Bakelaar and Odum, 1978). Interestingly, the bivariate relationship between nitrogen and axis 1 is positive, yet when organic matter is statistically controlled, the residual relationship between nitrogen and axis 1 was negative. This suggests that if we were to hold organic matter constant and increased levels of nitrogen, we might see a shift in composition toward the negative end of axis 1 instead of toward the positive end. The structure of the model suggests that organic matter has unique effects on composition independent of soil nitrogen. However, the total effect of organic matter was not significant (Table 2), suggesting that the direct effects and indirect effects mediated through nitrogen were offsetting. Organic matter was a function of elevation because more organic matter is produced at elevations that receive more precipitation and because the higher elevation soils in the study area are finer textured.

Soil moisture availability is determined largely by soil texture, which can influence the composition of the plant community (Rainer, 1990; Barton, 1994) by affecting seedling germination, establishment and growth (Coffin and Lauenroth, 1994). Clay concentration was more important than sand concentration in this model because elevation explained the same information as sand concentration. Soil pH often affects plant community composition because plants differ in nutrient availability requirements and soil acidity/basicity tolerances (van Raamsdonk, 1988; Bridgman and Richardson, 1993). Soil pH was found to be influenced by elevation in our study because soil parent materials of higher pH (e.g., limestone) occurred at lower elevations than soil parent materials of lower pH (e.g., basalt and benmoreite) (Abella and Covington, 2006a). It also is possible that leaching rates were slower on low-elevation sites receiving less precipitation.

Elevation has long been known to influence the composition of plant communities (Whittaker, 1960), and in this analysis elevation had the strongest total effects on one compositional gradient (Table 2). Changes in forest types are often observed along broad elevation gradients (Fisher and Fulé, 2004), but this study was limited to a 740 m elevation zone that encompassed the ponderosa pine ecosystem. The direct effect of elevation is likely due to a precipitation gradient. Thus, plant species that occurred at lower elevations are generally more drought tolerant (Abella and Covington, 2006b). However, the model suggests that three indirect effects of elevation on composition were mediated through pH, organic matter,

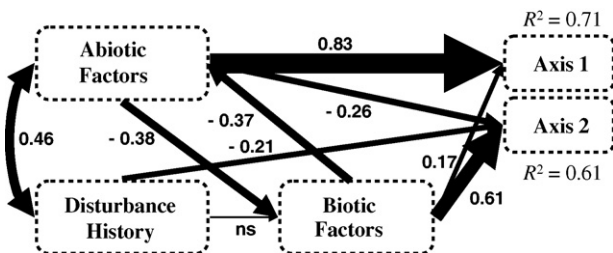


Fig. 7 – Final general model results ($\chi^2 = 25.5$, 22 d.f., $P = 0.27$) with standardized coefficients in which specific paths were composited into general constructs.

and total nitrogen. Thus, the effects of elevation on composition are complex and involve many indirect pathways.

4.2. Biotic factors

Species that pass through the abiotic filters are further affected by biotic interactions. The biotic filters in this model are driven by the density of the overstory pine trees and the amount of needle cast that these pine trees produce. Plant species appeared to respond to varying levels of pine litter depth. This association was independent of pine abundance, suggesting that if pine was held constant, variations in litter depth could shift community composition. Plants are known to respond to experimental manipulation of litter depths (Beatty and Sholes, 1988; Facelli and Pickett, 1991), and the mechanism behind these effects likely involves germination requirements of plants (Sydes and Grime, 1981). Annual species, for instance, have been suggested to respond to litter consumption after fires due to increased availability of exposed mineral soil (Laughlin et al., 2004, 2005). This relation deserves further study, however, since experimental removals of ponderosa pine litter have not induced short-term plant community responses (Abella and Covington, in press).

Pine basal area had the strongest total effect on axis 2 (Table 2). Understory species tolerate different levels of shading (Naumburg and DeWald, 1999), and water and mineral resources (Riegel et al., 1995), both of which vary with pine density (Welch and Klemmedson, 1975; Kaye and Hart, 1998). In addition, pine basal area indirectly affected composition by driving the variation in litter depth.

4.3. Disturbance

Grazing effects appeared less important than abiotic and biotic factors in explaining the observed spatial variation in vegetation. The model results imply that ungulate (cattle, sheep, deer and elk) grazing might directly influence plant community composition. Heavy grazing can shift the community toward greater abundance of unpalatable species (Westoby et al., 1989; O'Connor, 1991). A few unpalatable species, including broom snakeweed (*Gutierrezia sarothrae* (Pursh) Britt. & Rusby) and spreading fleabane (*Erigeron divergens* Torr. & Gray), were most abundant in the heavily grazed plots (Abella and Covington, 2006a).

Ponderosa pine forest structure and plant community composition are strongly influenced by frequent surface fires (Covington and Moore, 1994; Fulé et al., 1997; Moore et al., 2006). Fire as a disturbance process is conspicuously absent from this model due to a lack of data. Future composition models in this system should include fire effects, which have been shown to shift composition by increasing the abundances of annual and biennial forbs (Crawford et al., 2001; Laughlin et al., 2004).

4.4. Conclusions

The model provides an adequate explanation of the variance in composition, but it has limited predictive capacities at present due to the complicated dimensionality of the compositional response variables and to the descriptive nature of the

study design. Nevertheless, this model suggests that community composition is under multivariate control in ponderosa pine forests in the southwestern United States. It seems that the regional species pool is filtered by abiotic gradients, biotic gradients and grazing effects to produce the plant community assemblages that occur across the landscape. Our general model results suggest that abiotic factors drive one compositional gradient and that biotic factors and, to a lesser degree, disturbance history, drive the other independent compositional gradient. Evaluations of multivariate models of species richness across a wide variety of systems have advanced our understanding of the general factors that drive diversity (e.g., Grace and Pugsek, 1997; Weiher, 2003; Laughlin and Grace, 2006; Laughlin et al., 2007). Likewise, future evaluations of the general composition model proposed here across a variety of different systems could determine the generality and utility of this multivariate hypothesis.

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