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Species richness and soil properties in *Pinus ponderosa* forests: A structural equation modeling analysis

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Abstract

Question: How are the effects of mineral soil properties on understory plant species richness propagated through a network of processes involving the forest overstory, soil organic matter, soil nitrogen, and understory plant abundance?

Location: North-central Arizona, USA.

Methods: We sampled 75 0.05-ha plots across a broad soil gradient in a *Pinus ponderosa* (ponderosa pine) forest ecosystem. We evaluated multivariate models of plant species richness using structural equation modeling.

Results: Richness was highest at intermediate levels of understory plant cover, suggesting that both colonization success and competitive exclusion can limit richness in this system. We did not detect a reciprocal positive effect of richness on plant cover. Richness was strongly related to soil nitrogen in the model, with evidence for both a direct negative effect and an indirect non-linear relationship mediated through understory plant cover. Soil organic matter appeared to have a positive influence on understory richness that was independent of soil nitrogen. Richness was lowest where the forest overstory was densest, which can be explained through indirect effects on soil organic matter, soil nitrogen and understory cover. Finally, model results suggest a variety of direct and indirect processes whereby mineral soil properties can influence richness.

Conclusions: Understory plant species richness and plant cover in *P. ponderosa* forests appear to be significantly influenced by soil organic matter and nitrogen, which are, in turn, related to overstory density and composition and mineral soil properties. Thus, soil properties can impose direct and indirect constraints on local species diversity in ponderosa pine forests.

Keywords: Diversity; Nitrogen; Organic matter; *Populus tremuloides*; Soil texture; Structural equation modeling.

Abbreviations: SEM = Structural Equation Modeling; TES = Terrestrial Ecosystem Survey.

Introduction

The dominant theories that seek to explain patterns of species diversity often focus on one or two important factors such as productivity and disturbance (e.g., Grime 1979; Huston 1979, 1994; Tilman 1982; Rosenzweig 1995). However, ecological systems are too complex for these elegant, yet simple, models to always have predictive power since diversity is likely under multivariate control (Grace 1999; Weiher 2003). Indeed, the generality of the relationships between diversity and disturbance and between diversity and productivity has been called into question by reviews, meta-analyses (Gross et al. 2000; Mackey & Currie 2001; Mittelbach et al. 2001), and a modeling study (Cordonnier et al. 2006). Other factors, such as abiotic gradients, species pools, and spatial heterogeneity have been proposed as factors that regulate plant diversity patterns across landscapes (see reviews in Grace (1999) and Keddy (2005)). Recent efforts to understand diversity have begun to incorporate a variety of factors in multivariate models (Grace and Pugesek 1997; Grace & Jutila 1999; Gough & Grace 1999; Grace et al. 2000; Weiher 2003; Weiher et al. 2004; Laughlin & Grace 2006).

Grace & Pugesek (1997), for example, have proposed a multivariate model of plant species richness that incorporates several interacting factors, including community biomass, disturbance history, and abiotic environmental conditions. Richness is often, but not always, highest at intermediate levels of biomass (Grime 1979; Keddy 2005) and disturbance (Connell 1978), and can be regulated by spatially heterogeneous soil resources (Tilman 1982; Grace et al. 2000). In addition, several experiments have suggested that richness positively affects primary production (e.g., Tilman et al. 2001; Spehn et al. 2005). Thus, the debate about diversity-productivity relationships suggests that richness and production may be reciprocally related. Structural equation modeling (SEM) permits the simultaneous statistical evaluation of these many plausible relation-

ships, including reciprocal relationships (e.g., Weiher et al. 2004; Kline 2005; Laughlin & Grace 2006). Grace & Pugesek's (1997) model, which was originally developed in herbaceous communities, was recently expanded to include overstory trees as factors controlling understory plant communities (Weiher 2003; Weiher et al. 2004; Laughlin & Grace 2006). These new models for forested systems illustrate the importance of overstory structure in explaining diversity patterns across landscapes.

In this study, we consider how mineral soil properties can interact with forest structure and organic soil properties to influence understory plant abundance and richness. We used SEM to evaluate the a priori statistical model (Fig. 1). Our primary purpose was to gain insight into the relative importance of various processes that may influence understory richness by partitioning covariances among variables into pathways. In this model (Fig. 1), soil organic matter and total soil nitrogen are presumed to be influenced by both mineral soil conditions and forest density and composition (Harradine & Jenny 1958; Ovington 1968; Welch & Klemmedson 1975; Kaye & Hart 1998; Abella & Covington 2006). Consistent with previous models (e.g., Weiher et al. 2004), we hypothesized that mineral soil components and forest overstory are capable of influencing understory conditions (e.g., plant cover and litter) as well as understory species richness.

Structural equation modeling analyses range from confirmatory to exploratory. This particular analysis was exploratory in nature since the effects of soil properties on understory plant communities in western US pine forests have been little studied. Hence, each pathway in Fig. 1 represents an individual question that we sought to answer by evaluating how well the proposed model fits the data. Specifically, we asked:

1. Does richness increase monotonically with increasing understory plant cover or is there a point above which richness declines, indicating competitive regulation at high levels of cover (Grime 1979)?

2. Is cover greatest where richness is highest (Tilman et al. 2001; Spehn et al. 2005)?

3. Do deep litter layers beneath dense *Pinus ponderosa* var. *scopulorum* stands depress richness (Laughlin et al. 2004)?

4. Is richness lower in soils having high concentrations of soil nitrogen, as often observed (e.g., Tilman 1987; Foster &Gross 1998; Collins et al. 1998; Seastedt & Vaccaro 2001)? Can such an effect be explained by high levels of understory cover or is there evidence for an influence of nitrogen on richness that is independent of cover (Gough & Grace 1999)?

5. Can the association between organic matter and richness be explained by relations with nitrogen, or does it have independent effects?

6. How does overstory composition and density relate to soil organic matter and nitrogen? Do forests containing *Populus tremuloides* (quaking aspen) trees have higher levels of soil organic matter and nitrogen than those dominated primarily by pine (Daubenmire 1953; Reich et al. 2001), and do such stands have elevated richness (Langenheim 1962; Fonda & Bliss 1969; Despain 1973)?

7. To what degree does understory richness change with variations in mineral soil properties (Grace et al. 2000; Weiher 2003; Weiher et al. 2004)?

Methods

Study system

The *Pinus ponderosa* forest ecosystem covers millions of hectares of land across uplands in the southwestern United States. Our study was conducted within a 110 000 ha landscape on the Northern Arizona University Centennial Forest and on the Coconino National Forest at elevations from 1920 to 2660 m. *P. ponderosa* ('pine') is the dominant tree species and forms extensive pure stands, but sometimes occurs with *Populus tremuloides* (quaking aspen, 'aspen') or *Quercus gambelii*. Annual precipitation ranges spatially throughout the study area from 42-56 cm/year, snowfall from 152-233 cm/year, and mean maximum daily temperatures from 15.7-17.5 °C (Western Regional Climate Center, Reno, NV, USA). Topography is primarily flat or undulating (slope gradients < 10%), occasionally punctuated by cinder cones, ravines, and low hills. Volcanic activity has been widespread, with the most recent eruptions occurring ca.

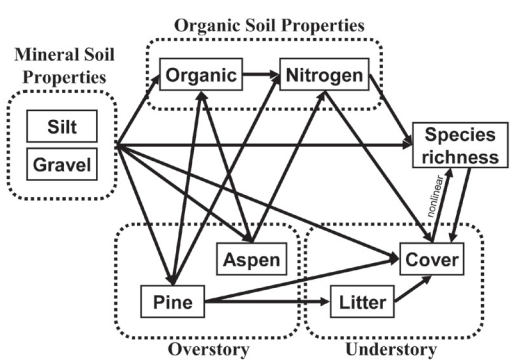

Fig. 1. *A priori* structural equation model. Model structure is based on earlier work in grasslands (Grace & Pugesek 1997; Weiher et al. 2004), savannas (Weiher 2003) and pine forests (Laughlin & Grace 2006). Each arrow drawn from the 'mineral soil properties' construct indicates that pathways from each of the two variables were included in the model (e.g., the two paths from silt and gravel to organic matter are represented by a single arrow).

900 years ago in the Sunset Crater Volcanic Field in the northeastern part of the study area (Moore et al. 1976). Pine forest occurs on a wide variety of soil parent materials including basalt, volcanic cinders, benmoreite, mixed igneous rocks, limestone, and mixed limestone/sandstone (Welch & Klemmedson 1975; Miller at al. 1995). Major soil subgroups are Typic and Udic Argiborolls, Typic and Mollic Eutroboralfs, Typic Ustorthents, and Vitrandic Ustochrepts (Miller et al. 1995). Lightning-ignited surface fires in pre-settlement forests on average occurred historically at least once every 10 years, maintaining open forest structure (Fulé et al. 1997; Heinlein et al. 2005). The study area, however, has experienced fire exclusion, timber harvest, and heavy livestock grazing since settlement, which may have influenced contemporary understory structure (Covington & Moore 1994).

Data collection

We used a digital Terrestrial Ecosystem Survey (TES) map (Miller et al. 1995) in a GIS to randomly select mapping units for sampling in each of 11 TES types (out of about 40 total types within our targeted elevational belt on the Coconino National Forest) that encompass a range of soil types in ponderosa pine forests (Abella & Covington 2006). We sampled 0.05 ha (20 m × 25 m) plots that were randomly located within each mapping unit. At least six plots were sampled in separate mapping units within each TES type, but we were able to sample three additional plots in 3 of the 11 TES types for a total of 75 plots.

Plots were sampled in May-August 2003. At each plot, we collected composite soil samples of 0-15 cm depths from two pits per plot. Soil samples were air dried, sieved through a 2-mm sieve, and analysed for texture (hydrometer method), gravel content (by weight), total N (with a C/N analyzer), and loss-on-ignition (LOI; heating 5 g of each sample in a muffle furnace at 300 °C for two hours), following methods outlined in Sparks (1996) and Dane & Topp (2002). We used LOI as a surrogate measure of soil organic matter (Schulte & Hopkins 1996).

We visually estimated plant cover to the nearest percent in 15 1-m^2 subplots per 0.05-ha plot. The average cover across these subplots was used as the value of plant cover for each plot. We also conducted a plant species census of the entire plot to determine understory plant species richness per 0.05 ha. We measured tree densities and diameters for all tree species over breast height. We used pine basal area as our measure of pine abundance. Aspen was present on only six of the 75 plots; therefore, we used aspen presence as a categorical variable, rather than basal area of this species, in our analyses because of the distributional properties of this variable.

Data analysis

If continuous soil properties could accurately predict the correct soil type from which the sample was taken, we felt it could be appropriate to use the continuous soil variables to explain patterns of richness across the landscape. We used stepwise discriminant analysis (Anon. 2005) to determine how well the continuous soil variables could predict the correct TES soil type (Miller et al. 1995). Discriminant analysis showed that continuous soil properties correctly predicted the soil type 88% of the time. An alternative, non-parametric discriminant analysis test (Anon. 2005) 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 mineral soil variation and richness.

Prior to evaluating multivariate models, bivariate relations between richness and the other variables in the model were assessed. We examined bivariate plots for the presence of outliers, evidence of skewness or kurtosis, and for non-linear relations up to third-order polynomials.

Structural equation modeling

Structural equation modeling is an extension of regression and path analysis that can be used to model multivariate relations and to evaluate multivariate hypotheses (Bollen 1989). Maximum likelihood solution procedures were used (data distributions were sufficiently normal) and we relied on χ^2 goodness of fit measures to evaluate model adequacy. Residuals and modification indices were also examined to determine if there were obvious model-data discrepancies, which in turn could be used to identify new alternative models for consideration.

The structural equation model initially evaluated is shown in Fig. 1. Variables associated with various constructs (mineral soil properties, organic soil properties, overstory, and understory) were incorporated into the model. The model represents what we believed to be the most plausible structural relations based on a priori knowledge. We acknowledge that not all causal processes that act in this system are represented in Fig. 1. Indeed, disturbance processes such as fire and grazing were not included in this study. Rather, our objective was to determine whether the data were consistent with the expectations of the proposed model.

It should be clear that 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). 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 the ability to draw inferences from model parameters. The final structural equation model predicts a covariance structure that is consistent with the covariance structure of the dataset; therefore, theory can guide our interpretation of the mechanistic nature of the directional paths.

Our initial model included a squared term for plant cover since there was an expectation of a non-linear relationship between cover and richness. In this model, the cover^2 variable was allowed to freely intercorrelate with cover and with the predictors of cover. Since silt was highly negatively collinear with sand and since clay was not correlated with richness, we used percent silt to represent soil texture. Because presence of pine represents a categorical response variable, special solution procedures were used to model the effects of mineral soil properties on aspen using a probit procedure, which correctly estimates parameters of categorical outcomes. Analyses were performed using Mplus software (Muthén & Muthén 2005).

In our final model, a composite variable was used to model the endogenous quadratic relationship between cover and richness (Grace & Bollen in press). The purpose of including the composite was to capture the combined effects of the multiple parameters used to fit the non-linear effect. The composite modeling procedure used involves a two-stage approach in which models are first estimated without composites to validate that the individual terms are statistically significant. 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. The single path from the composite to the response variable then represents the overall non-linear effect of the predictor.

We calculated the so-called 'total effects', which are the total sum of direct and indirect pathways from the predictors to richness. Indirect effects equal the total sum of the products of all path segments from a predictor to richness. Total effects are a simple summary of the complex and sometimes dual nature (opposing signs) of the relationship between the factors and species richness. They also provide a calculation of the net effect (i.e., strength and sign) of a relationship. Estimates of these effects and their standard errors were calculated with Mplus software (Muthén & Muthén 2005).

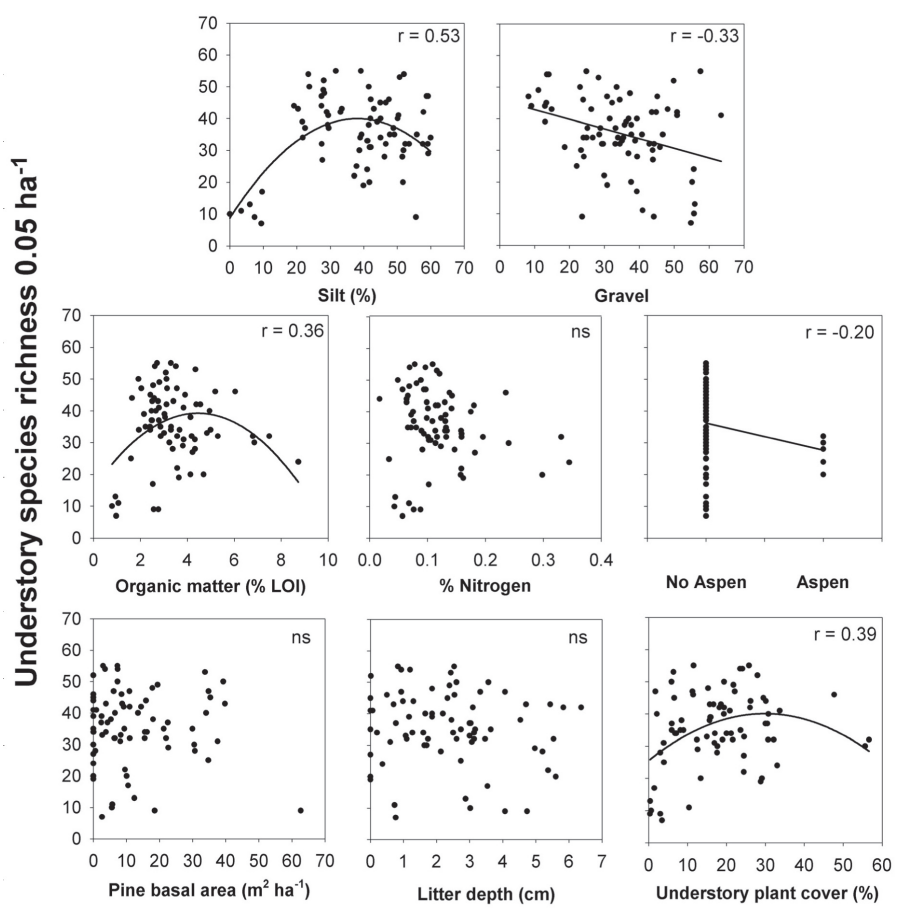

Fig. 2. Bivariate relations between richness and all other variables evaluated in the model. Fitted least-square regression lines represent either first or second-order polynomials. All relationships with correlation coefficients (r) reported were significant ($P < 0.05$); ns = not significant.

Results

Bivariate correlations

Bivariate correlations between richness per 0.05 ha and the other variables indicated that five of eight variables had significant ($P < 0.05$) relationships to richness (Fig. 2). Understory plant cover exhibited a quadratic relationship with richness, where maximum richness occurred at approximately 30% aerial plant cover. Litter depth was not significantly correlated with richness. Soil total nitrogen was not correlated with richness, but soil organic matter exhibited a second-order polynomial relationship to richness. Presence of aspen was negatively correlated with richness, and abundance of pine was not correlated with richness. Silt exhibited a quadratic relationship with richness, and gravel was negatively correlated with richness.

Bivariate correlations between plant cover and the other variables in the model indicated that seven of the eight variables had significant ($P < 0.05$) relationships to plant cover (Fig. 3). Species richness was weakly positively related to plant cover. Litter depth was negatively correlated with plant cover. Soil nitrogen and organic matter exhibited positive linear relations with plant cover. Aspen presence was positively correlated with plant cover, and pine density was negatively correlated with plant cover. Silt exhibited a second-order polynomial relationship to cover, but gravel was not correlated with cover.

Table 1. *A priori* model results showing the estimates, standard errors (SE), and standardized estimates of paths from predictor variables to response variables. Fit statistics for a priori model: $\chi^2 = 27.7$, $df = 17$, $P = 0.049$ ($n = 75$).

	Estimate		SE	Std. Estimate
Pine =				
silt	0.238	*	0.099	0.27
gravel	–0.101	ns	0.112	–0.10
Aspen				
silt	0.004	*	0.002	0.23
gravel	0.004	ns	0.002	0.18
Organic =				
silt	0.047	***	0.008	0.48
gravel	< 0.001	ns	0.009	< 0.01
aspen	2.630	***	0.403	0.51
pine	–0.023	**	0.009	–0.22
Nitrogen =				
organic	0.027	***	0.003	0.65
aspen	0.057	***	0.015	0.27
pine	–0.001	***	< 0.001	–0.21
Litter =				
pine	0.060	***	0.013	0.47
Cover =				
litter	–0.507	ns	0.499	–0.08
pine	–0.366	***	0.079	–0.42
silt	0.109	ns	0.082	0.14
gravel	–0.254	**	0.081	–0.29
nitrogen	79.379	***	17.085	0.41
richness	–0.057	ns	0.121	–0.06
Richness =				
silt	0.274	**	0.081	0.34
gravel	–0.090	ns	0.097	–0.09
nitrogen	–87.048	**	27.825	–0.43
cover	0.722	***	0.203	0.69
cover^2	–1.760	**	0.517	–0.42

* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, ns = not significant.

Structural equation model

The results from the a priori structural equation model (Fig. 1) are summarized in Table 1. While the χ^2 of the initial model was not indicative of major discrepancies between data and model ($\chi^2 = 27.7$, $df = 17$, $P = 0.049$), results suggested that seven pathways were nonessential to the model (Table 1). Litter depth did not have significant relationships with either cover or richness. In addition, modification indices suggested that adding a path from gravel to soil nitrogen might substantially improve model fit.

With non-sigificant paths eliminated and with litter dropped from the model, the addition of a path from gravel to soil nitrogen reduced the χ^2 by 5.68 units, indicating a significant improvement in model fit (the criterion for a significant change in model χ^2 for a single change = 3.84). However, the standardized path coefficient (0.14) was rather weak. Theoretical justification for including this path is not well developed, so we added this pathway provisionally. This relationship is in need of further substantiation in future multivariate analyses.

Examination of the revised model revealed that the path from silt to aspen was not stable (did not retain its significance) and also indicated the need to add a second pathway, this one from soil organic matter to richness. The inclusion of a direct pathway from organic matter to richness was considered for theoretical significance and found to have merit.

The changes made to the second model led to a stable model that only included essential pathways. To obtain the final model used for reporting results, a composite variable was added to capture the effects of cover and cover squared on species richness. This had no effect on model fit or on the values of the other path coefficients. The resulting model showed good consistency with the data ($\chi^2 = 15.2$, $df = 13$, $P = 0.30$) and explained 41% of the variation in richness, 48% of the variation in plant cover, 58% of the variation in organic matter, and 77% of the variation in nitrogen (Fig. 4).

The total, direct, and indirect ‘effects’ of factors on richness are presented in Table 2. Understory plant cover had a positive (yet non-linear) total effect on richness. Nitrogen had strong negative total effects on richness, which included a strong direct negative path and indirect

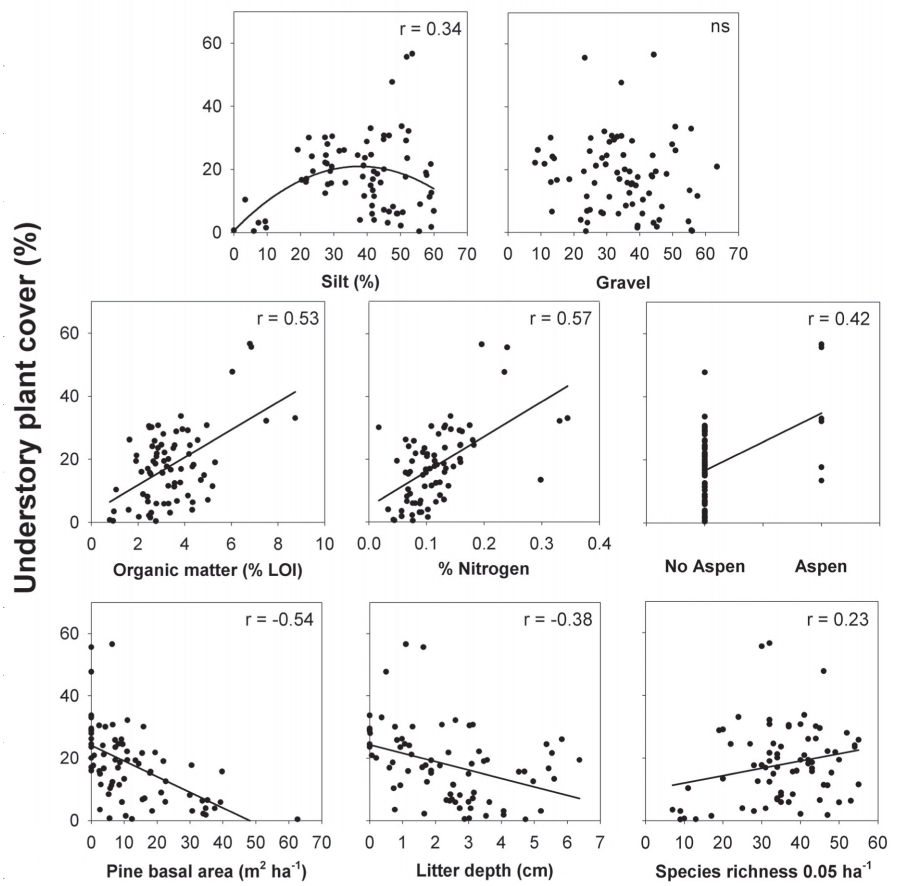

Fig. 3. Bivariate relations between plant cover and all other variables evaluated in the model. Fitted least-square regression lines represent either first or second-order polynomials. All relationships with correlation coefficients (r) reported were significant ($P < 0.05$); ns = not significant.

non-linear paths mediated through plant cover (Fig. 4). Soil organic matter had a non-significant positive total effect on richness because its positive direct path was offset by its negative indirect paths mediated through nitrogen (Fig. 4). Pine basal area had negative total effects on understory species richness, driven primarily by a negative effect on plant cover, though total effects were slightly offset by indirect effects mediated through soil organic and nitrogen content (Fig. 4). Aspen had non-significant total effects on richness since aspen's effects on organic matter and nitrogen were offsetting. Soil silt content had a positive total effect on richness, despite a negative indirect effect mediated through nitrogen. Soil gravel content had a negative effect on richness, and these effects were entirely indirect through its association with plant cover and soil nitrogen.

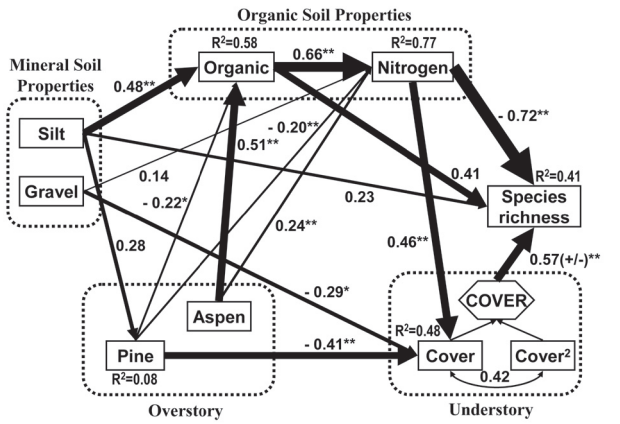

Fig. 4. Final structural equation model with standardized path coefficients ($\chi^2 = 15.2$, $df = 13$, $P = 0.30$). Pathway significance is denoted by the following: no asterisk = $P < 0.05$, * = $P < 0.01$; ** = $P < 0.001$.

Discussion

Understory

Species richness per 0.05 ha was highest at intermediate levels of plant cover. The bivariate second-order

correlation between richness and plant cover ($r = 0.39$; Fig. 2) underestimated the strength of the residual quadratic relationship between these two variables (standardized coefficient = 0.57; Fig. 4). Multivariate analyses that evaluate residual relationships in the presence of important covariates provide a more comprehensive and accurate result (Grace 2006). This 'hump-backed' relationship (*sensu* Grime 1973, 1979) between cover and richness suggests that both colonization success and competitive exclusion can limit richness in open stands where pine abundance is generally low and also where aspen is present.

The results of this analysis indicate a central role of understory plant abundance in the regulation of richness.

Table 2. Standardized total, direct, and indirect effects of factors that influence understory species richness per 0.05 ha and their standard errors. We only report the standardized specific indirect effects that were significant ($P < 0.05$) and > 0.10. Note that non-significant effects can be the result of offsetting effects.

Effects	Estimate	SE	Std. Effect
Effects from Cover to Richness			
Total	0.696 ***	0.122	0.57
Direct	0.696 ***	0.122	0.57
Total indirect	NA	NA	NA
Effects from Nitrogen to Richness			
Total	–86.059 *	34.700	–0.46
Direct	–147.897 ***	34.448	–0.72
Total indirect	61.838 ***	14.933	0.26
Specific indirect			
Nitrogen→Cover→Richness	61.838 ***	14.933	0.26
Effects from Organic to Richness			
Total	1.177 ns	1.039	0.11
Direct	3.509 *	1.508	0.41
Total indirect	–2.333 *	0.972	–0.30
Specific indirect			
Organic→Nitrogen→Richness	–4.009 ***	1.025	–0.47
Organic→Nitrogen→Cover→Richness	1.676 ***	0.442	0.17
Effects from Pine to Richness			
Total	–0.199 **	0.072	–0.17
Direct	NA	NA	NA
Total indirect	–0.199 **	0.072	–0.17
Specific indirect			
Pine→Nitrogen→Richness	0.129 **	0.048	0.14
Pine→Organic→Nitrogen→Richness	0.094 *	0.042	0.10
Pine→Cover→Richness	–0.247 ***	0.060	0.23
Effects from Aspen to Richness			
Total	–1.353 ns	3.109	–0.06
Direct	NA	NA	NA
Total indirect	–1.353 ns	3.109	–0.06
Specific indirect			
Aspen→Organic→Richness	9.220 *	4.197	0.21
Aspen→Nitrogen→Richness	–7.638 **	2.826	–0.18
Aspen→Organic→Nitrogen→Richness	–10.532 **	3.125	–0.24
Effects from Silt to Richness			
Total	0.193 *	0.079	0.24
Direct	0.187 *	0.088	0.23
Total indirect	0.006 ns	0.052	0.01
Specific indirect			
Silt→Organic→Richness	0.164 *	0.076	0.20
Silt→Organic→Nitrogen→Richness	–0.187 **	0.057	–0.23
Effects from Gravel to Richness			
Total	–0.230 ***	0.067	–0.23
Direct	NA	NA	NA
Total indirect	–0.230 ***	0.067	–0.23
Specific indirect			
Gravel→Nitrogen→Richness	–0.091 *	0.043	–0.10
Gravel→Cover→Richness	–0.177 **	0.061	–0.16

* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, ns = not significant, NA = not applicable.

Thus, factors that influence understory abundance (as indicated by plant cover) can be seen as indirect drivers of richness patterns. Approximately half of the variation in plant cover appears to be related to positive relations with nitrogen, and negative relations with pine abundance and gravel content. This suggests that soils with greater nitrogen content can sustain greater understory plant abundance, and that soils with greater gravel content impede plant establishment and production independent of overstory densities. Consistent with earlier studies, sites with high pine densities are unable to sustain abundant understory plant growth due to intense competitive effects from trees (McLaughlin 1978; Moore & Deiter 1992; Riegel et al. 1995; Moore et al. 2006).

Recent studies have suggested that biodiversity may maintain ecosystem functions. Specifically, a few experiments have suggested that species richness has a positive effect on plant production (e.g., Tilman et al. 2001; Spehn et al. 2005). Thus, we modeled the possibility that richness and cover (a surrogate measure of plant production in this system) could have reciprocal relations. However, despite a significant positive linear bivariate relationship (Fig. 3), we did not detect a reciprocal positive path from richness to cover in the context of the model. Similar to Weiher et al. (2004), when the non-linear effect of production on richness has been accounted for, the data do not indicate a reciprocal positive effect of richness on production.

Litter depth did not explain unique variation in plant cover or species richness in the presence of pine. This result contrasts with a univariate analysis that suggested litter (i.e., duff) reduction with fire might stimulate richness (Laughlin et al. 2004). This implies that litter accumulation has less of an effect on plant abundance than pine density at the scale of 0.05 ha. This finding may have implications for ecological restoration efforts since the reduction of pine densities through thinning and the consumption of litter through prescribed fire are both common treatment prescriptions (Covington et al. 1997). Moore et al. (2006) demonstrated that thinning-only treatments produced equal increases in herbaceous production compared to thinning plus burning treatments, and Abella & Covington (in press) detected no increase in plant cover or richness after two years of pine litter removal. Perhaps pine basal area reduction is more important for increasing understory production and species richness than reducing litter depths.

Soil nitrogen and organic matter

Richness at the 0.05 ha scale was lower in soils with greater nitrogen content, as observed in studies across many ecosystems (Tilman 1987; Foster & Gross 1998; Collins et al. 1998; Seastedt & Vaccaro 2001). Soils with greater nitrogen content can sustain increased herbaceous production, which is often the proposed mechanism behind the non-linear relationship between productivity and diversity (Huston 1979; Tilman 1982). However, we detected an additional direct, negative association of nitrogen with richness (standardized coefficient = −0.72) independent of effects on plant cover. These multivariate relations were also detected in structural equation model results from coastal wetlands (Gough & Grace 1999). Such a strong direct path from nitrogen to richness independent of cover is intriguing and it may represent filtering effects on the species pool (Gough & Grace 1998, 1999; Foster & Gross 1998). Further study is needed, however, to ascertain why richness was depressed by elevated soil nitrogen in this system.

Interestingly, the bivariate correlation between nitrogen and richness was not significant. However, once the covariation among predictors was controlled in the context of the multivariate model, the path from nitrogen to richness was the strongest path. This result illustrates the capacity of SEM to reveal masked and suppressed relationships within multivariate space (Grace & Pugesek 1998; Grace 2006).

Organic matter was strongly and positively correlated with total nitrogen, and regressing nitrogen on organic matter resulted in a y-intercept that was not significantly different than zero (data not shown), suggesting that most total nitrogen in these forest soils is derived from organic matter. This concurs with Welch & Klemmedson's (1975) finding that only 2% of total nitrogen in this system was inorganic nitrogen. Soil organic matter also contributes to soil fertility by contributing other nutrients and by increasing both cation exchange and water holding capacity (Brady & Weil 1999). In addition to these indirect associations with richness, the initially hypothesized structural equation model was inconsistent with the data until we included a direct path from organic matter to richness. This suggests that organic matter has effects on richness independent of its association with nitrogen. We interpret its inclusion as allowing for a greater number of species to occur on soils richer in organic matter, while at the same time, for organic-rich soils to include higher levels of nitrogen, which can be detrimental for species coexistence (Bobbink et al. 1998). It would seem, in retrospect, that a direct pathway from organic matter to richness in such models should be expected in many circumstances based on underlying mechanisms. Soils with abundant organic matter might provide additional

nutrients to plants besides nitrogen and might provide more suitable sites for successful establishment than do soils with low organic matter.

Overstory

The effects of aspen and pine trees on understory species richness were entirely indirect within the context of the model (Table 2), which is consistent with the results found by Laughlin & Grace (2006). This implies that the effects of the overstory on understory richness in ponderosa pine forests can be explained by the mediating influences on soils and understory cover.

The presence of aspen in the overstory has complex implications for understory structure. Many studies have suggested a positive relationship between aspen abundance and understory production and species richness (Langenheim 1962; Fonda & Bliss 1969; Despain 1973; Reich et al. 2001), likely due to higher litter quality (Daubenmire 1953) and greater litterfall nitrogen (Reich et al. 2001) in aspen stands compared to conifer stands. Recently, understory species richness at scales > 1 m^2 has been reported to be generally moderate to low in the presence of aspen in northern Arizona forests (Fisher & Fulé 2004; Abella & Covington 2006; Laughlin et al. 2005). Our model suggests that if such a general result holds, it may be the ability of aspen to increase soil nitrogen that causes a reduction in understory richness. Such a mechanism is supported by the results from a study in boreal forests that determined that aspen forests had greater litter nitrogen concentrations and total litter nitrogen than conifer forests (Reich et al. 2001). However, these negative indirect influences are partially offset by the greater abundance of organic matter in aspen stands (Table 2).

Dense pine forests contain fewer understory species than open pine forests (Laughlin et al. 2005; Laughlin & Grace 2006). In this case, model results imply that pine densities indirectly reduce richness by reducing understory plant cover, but that these influences are partially offset by the lower levels of organic matter and nitrogen found in dense pine stands.

Mineral soil properties

In this study, sampling was conducted across a broad range of soil conditions. Sites included in the sample represent influences from both recent and ancient volcanic activity as well as from weathering of sedimentary materials. Soil texture (silt content, specifically) and gravel content were found to be the mineral soil properties most associated with variations in the other system properties examined. The results suggest a variety of mechanisms whereby mineral soil properties can influence richness in this system. These mechanisms involve the forest overstory and the effects it has on soils and understory plant abundance. However, we found that the overstory was only weakly related to mineral soil properties, consistent with the notion that *Pinus ponderosa* and *Populus tremuloides* have broad soil tolerances.

Model results suggest that high gravel content is associated with low species richness (Table 2). Gravel might inhibit herbaceous plant growth by reducing establishment sites and by altering soil moisture availability and drainage properties. We observed low species richness on black cinder soils that contained high gravel content and high species richness on other soils that contained lower gravel content (Abella & Covington 2006).

The results of our analyses suggest that mineral soil properties can have specific influences on understory richness in this system. While siltier soils have a higher density of pine, higher organic matter, higher nitrogen, and support greater understory cover, we found evidence of a specific enhancement of richness by silt independent from the influences of other variables. Influences of gravel on richness, in contrast, can be explained by its association with lower understory cover. These results, and in particular specific effects of soil properties on richness, are consistent with previous studies in grasslands (Grace & Jutila 1999; Grace et al. 2000). Grace (2001) suggested that such specific effects represent a filtering of the species pool by abiotic influences, which is why they operate independently from associations with plant abundance. The overall importance of abiotic conditions as filters of richness patterns has received increasing support in multivariate studies, and additional support for this idea can be found in our results for ponderosa pine ecosystems.

Conclusions

This study demonstrates how traditional univariate analyses can sometimes be misleading when studying complex natural systems (Grace 2006). The incorporation of covariates into an analysis strengthens the validity of the results, especially when factors are not experimentally controlled (Weins & Parker 1995). The bivariate correlations examined in this study suggested that a few variables were only weakly or not correlated with richness. However, if we limited the analysis to bivariate relationships, we would have erroneously concluded that nitrogen had no effect on richness, contrary to many experiments and diversity theories (e.g. Bobbink et al. 1998; Tilman 1982). This SEM analysis revealed a strongly negative residual relationship between richness and nitrogen. In addition, the SEM analysis showed a stronger non-linear relationship between richness and

plant cover than was suggested by bivariate plots. Further, ponderosa pine exhibited no bivariate relationship to richness, yet pine was found to be indirectly negatively related to richness in the context of the model.

The southwestern ponderosa pine forest ecosystem occurs across a wide breadth of soil variation, and our results suggest that soil properties can impose direct and indirect constraints on local species diversity. These constraints should be considered when setting targets for understory plant abundance and diversity in restoration and management projects. Other multivariate studies in the ponderosa pine system (e.g., Laughlin & Grace 2006) have suggested that disturbance factors, such as fire, have strong effects on species richness. Future studies should consider abiotic and disturbance effects simultaneously to determine the relative importance of each in regulating richness patterns. In all cases examined thus far, understory richness is under multivariate control with overstory and understory abundance having predictable roles mediating the influences of disturbance history and abiotic environmental conditions.

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