A Multi-scale Analysis of Plant Diversity Along Soil Nutrient Gradients

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Abstract Although edaphic variation is common in natural systems, and has often been described as a major driver of plant species diversity, the effect of this edaphic variation on plant diversity has not been described in a comprehensive, synthetic fashion. Understanding this variation is essential, however, as soil nutrients are important drivers of plant community structure. This study takes advantage of multi-scale vegetation sampling along with plot-level soil data from the Carolina Vegetation Survey to examine the relationships between soil nutrients and diversity in forests and woodlands at multiple spatial scales and across floristic regions. We find that there is greater variation in soil characteristics that predict diversity between regions than across scales within regions. In Atlantic Coastal Plain longleaf-pine communities, nitrogen, sulfur, iron, soil pH, organic matter, and silt are important predictors of diversity. In the Fall-line Sandhill longleaf-pine communities of the Carolinas, manganese, nitrogen, soil pH, and silt are the measured variables that predict diversity best. In longleaf-pine communities of Florida, soil pH, iron, nitrogen, and silt are consistently the strongest indicators across all scales from 0.01 to 1000 m^2. In southern Appalachian Mountain forest communities, soil pH, manganese, and calcium are the best diversity indicators. By tailoring models to individual regions, soil characteristics can predict between 39 and 54 % of the variance in diversity at the 0.1 ha scale.

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Introduction

Multiple factors affect plant species diversity, including climatic factors, species pool, dispersal abilities of species, disturbance, and environmental favorability, which includes nutrient availability. Describing diversity is complicated, however, by the fact that patterns of diversity have also been shown to vary with scale of observation (Gaston 2000; Peet et al. 2014). Giladi et al. (2011) emphasize the importance of studying the multiple drivers of diversity across scales of observation in order to determine influences on plant diversity accurately. Soil attributes are critical in driving plant community diversity, but variation in soil attributes is poorly represented in most regional data (Waring and Running 1998; Box and Fujiwara 2011). In particular, soil nutrients and texture vary between regions because of differences in geological history and context, but diversity may also track fine-scaled variation in soil attributes. If the significant correlates of diversity vary with scale, this could shed light on which mechanisms are influencing species coexistence. However, if correlates vary less with scale and more with region, this highlights the dominance of broader-scale factors, such as soil, climate and regional geology, over local coexistence mechanisms.

Path models and structural equation models provide a basis for determining the complex relationship of diversity with soil resources and its variation with scale. We use these approaches to examine the relationship between soil characteristics and species diversity across multiple scales in forests of two floristic regions: the longleaf-pine woodlands of the southeastern United States coastal plain and the forests of the southern Appalachian Mountains.

Small changes in soil moisture and soil texture translate into distinct compositional differences in longleaf-pine communities. In fact, a combination of soil moisture and percent silt has been used as the primary basis for classification of longleaf-pine communities (Peet 2006; Peet et al. 2014). Soil texture has consequences for water relations and nutrient storage that affect the availability of moisture and nutrients to plants. Based on prior research (e.g., Peet 2006), we expected soil texture to be a key factor driving variation in diversity across spatial scales from 0.01 to 1000 m^2 within the coastal plain. In contrast, previous work in southern Blue Ridge Mountains forests has demonstrated a close relationship between soil pH and species diversity (Peet et al. 2003, 2014). This is consistent with the correlation between diversity and pH seen in other temperate forest communities (e.g., Schuster and Diekmann 2005). Because these distinct regions differ in expected importance of soil characteristics, they provide a case study for examination of consistency of patterns across scales in a wide range of community types.

Examination of the herbaceous richness of forests and woodlands in eastern North American indicates the changing importance of edaphic variables, both across scale of observation and across regions (Peet et al. 2014). This study takes advantage of multi-scale vegetation sampling (Peet et al. 1998, 2012) along with plot-level soil data to examine the relationships between soil nutrients and diversity

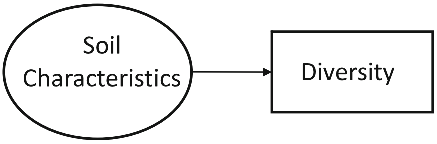

Fig. 1 Initial conceptual model showing the influence of soil characteristics on diversity

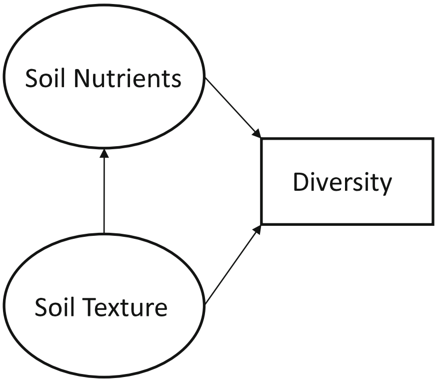

Fig. 2 Refined conceptual model illustrating the direct and indirect influence of soil texture on diversity

of vascular plants at different scales. Path analysis is used to determine the relative strength of soil variables in predicting plant species richness and to determine the loadings of soil variables onto latent variables in order to build structural equation models of soil nutrients and diversity. We hypothesize that texture is the driving influence on diversity in longleaf-pine communities, while soil pH and manganese are the essential variables in the southern Appalachian Mountains. We expect soil minerals to influence diversity collectively in the mountains (Fig. 1) but that there will be distinct soil mineral and soil texture influences in longleaf-pine communities (Fig. 2).

Methods

Data were assembled from the Carolina Vegetation Survey database (CVS; Peet et al. 2012) for forests of the southern Appalachian Mountain region (578 plots) and longleaf-pine woodlands of the Southeastern Coastal Plain (642 plots). The longleaf-pine data were subdivided into three geographic regions: one representing the Atlantic Coastal Plain ($n = 343$), the second the Fall-line Sandhill region of North and South Carolina ($n = 94$), and the third Florida ($n = 203$). These plots are 1000 m^2 and were surveyed using the CVS methodology (Peet et al. 1998, 2012). Plant species richness was measured in 0.01, 0.1, 1, 10, and 100 m^2 subplots within the 1000 m^2 plot, with two nests in each of four 100 m^2 intensive modules within the 1000 m^2. Richness values were averaged across the four intensive modules for each subplot size.

Soil samples were taken from the A horizon in at least one intensive module. Because soil samples were generally taken from each intensive module, they were typically located inside each 100 m^2 subplot, and in all cases there was a sample within the 1000 m^2 plot. All soil samples were analyzed by Brookside Laboratories, New Oxford, Ohio, using Mehlich-3 extraction (Mehlich 1984) for nutrient analyses. Soil analyses included texture (percent clay, silt, and sand), cation exchange capacity (CEC), pH, organic matter (Org), and availability of nitrogen (N), phosphorous (P), sulfur (S), manganese (Mn), calcium (Ca), and iron (Fe). Soil nutrient measurements were log-transformed to normalize the distributions in order to facilitate the comparison of covariances to diversity through structural equation modeling.

Conceptual models were initially specified for structural equation modeling (see above, Figs. 1 and 2), based on theory, previous work, and knowledge of the systems (e.g., Peet et al. 2003, 2014; Peet 2006). An iterative process was used to refine the models: (1) checking the specification of a model, (2) using the estimates based on the model fit to the covariance data and model fit indices to evaluate the model, and (3) making adjustments to the model if necessary. A model with suitable fit can then be interpreted. In this analysis, we used path models (only including measured variables) to eliminate unnecessary measured variables before running the structural equation models that include conceptual variables (e.g., soil nutrients). For a more thorough description of structural equation modeling, see Bollen (1989), or Grace (2006). For each dataset, correlations and covariances were calculated for plant species richness at each scale and for all soil variables. The strongest 5–6 soil variables (correlations $r > 0.24$) were selected to model diversity at four scales: 1, 10, 100, and 1000 m^2. Finer scales were excluded because they were further from the soil sample; also, because of weaker correlations, the models either fit poorly or did not converge. All path models were run initially with the strongest correlates for a given scale and region (Table 1). Correlates with strong co-linearity with other predictors were removed. Initial models were refined based on the significance of paths (i.e., insignificant paths were removed from the models until the best model fit was achieved). Confirmatory factor analyses were run on all models to determine the appropriateness of predictors loading onto latent variables (e.g., conceptual variables, such as soil nutrients and soil texture). The confirmatory factor analyses were used to test structural equation models (Bollen 1989) of soil and diversity. All analyses were conducted using the MPlus6.1 statistical package (Muthén and Muthén 1998–2010) with maximum likelihood estimation.

Table 1 Strongest correlates of diversity at different scales in Atlantic Coastal Plan (ACP), Sandhills, and Florida (FL) longleaf-pine communities, and southern Appalachian Mountain forest (Mountain) communities. The strongest correlate is listed on the left, and they decrease from left to right

ACP longleaf	0.01 m^2	N	Sand	Silt	S	Fe	Org
	0.1 m^2	N	Sand	Silt	S	Fe	Org
	1 m^2	N	Fe	S	Sand	Silt	Org
	10 m^2	Fe	S	N	Sand/Org	Silt	Clay
	100 m^2	Fe	S	N	Org	Sand	Silt/pH
	1000 m^2	Fe	S	N	Org	pH	Clay
Sandhills longleaf	0.01 m^2	N	Sand/pH	Silt	Org		
	0.1 m^2	N	pH	Sand	Silt/Mn	Ca/Org	Clay
	1 m^2	pH	N	Mn	Ca	Sand	Silt
	10 m^2	pH	N/Mn	Ca	Sand	Silt	Org
	100 m^2	Mn	pH	N	Ca	Silt/Sand	Org
	1000 m^2	Mn	Silt/Sand/pH	N/Ca	Org		
FL longleaf	0.01 m^2	N	Silt/Org	Fe	Sand		
	0.1 m^2	Silt	N	Sand	Org	Fe	P
	1 m^2	Silt	Sand/Fe/pH	N			
	10 m^2	pH	Fe	Mn	Silt	Sand	
	100 m^2	pH	Mn	Fe	Silt		
	1000 m^2	Fe	pH	Mn	Silt	Sand	
Mountain	0.01 m^2	Ca	pH	CEC	Mn		
	0.1 m^2	pH	Ca	Mn	CEC		
	1 m^2	pH	Mn	Ca	Fe	CEC	
	10 m^2	pH, Mn	Ca	Fe	S		
	100 m^2	pH	Mn	Ca	Fe	S	
	1000 m^2	pH	Mn	Ca	Fe	S	

Results

Longleaf Pine Communities

In all three longleaf-pine regions, the correlates of diversity had some turnover between scales (Table 1 summarizes the strongest correlates at each scale). Silt was a strong correlate across almost every scale in all three regions. Iron, nitrogen, and sulfur had the strongest relationship with diversity across all scales of observation in longleaf pine of the Atlantic Coastal Plain, followed by soil organic matter, silt, and sand (Table 2). In the Sandhills, longleaf diversity correlated most strongly with manganese, pH, and nitrogen, but silt, sand, and calcium were also highly correlated with diversity (Table 3). In Florida longleaf stands, soil pH, iron, manganese, and silt were the strongest correlates of diversity (Table 4).

Table 2 Correlations between soil nutrients and plant species richness at six scales in Atlantic Coastal Plain (NC, SC, GA) longleaf-pine communities

	0.01 m^2	0.1 m^2	1 m^2	10 m^2	100 m^2	1000 m^2	logCEC	logPH	logOrg	logN	logS	logP	logCa	logFe	logMn	Silt	Clay	Sand
0.01 m^2	1.00																	
0.1 m^2	0.94	1.00																
1 m^2	0.87	0.95	1.00															
10 m^2	0.77	0.86	0.96	1.00														
100 m^2	0.66	0.77	0.89	0.97	1.00													
1000 m^2	0.60	0.70	0.83	0.92	0.97	1.00												
logCEC	0.06	0.06	0.05	0.03	0.04	0.03	1.00											
logPH	0.01	0.07	0.20	**0.30**	**0.33**	**0.37**	−0.15	1.00										
logOrg	**0.28**	**0.29**	**0.37**	**0.40**	**0.40**	**0.41**	0.12	0.18	1.00									
logN	**0.49**	**0.51**	**0.51**	**0.49**	**0.47**	**0.45**	0.39	−0.20	0.53	1.00								
logS	**0.39**	**0.42**	**0.48**	**0.52**	**0.53**	**0.51**	0.23	0.14	0.58	0.45	1.00							
logP	0.00	0.04	0.10	0.16	0.18	0.19	0.21	0.24	0.39	0.31	0.47	1.00						
logCa	0.04	0.08	0.16	0.21	0.24	**0.26**	0.76	0.48	0.17	0.16	0.25	0.33	1.00					
logFe	**0.36**	**0.40**	**0.50**	**0.58**	**0.61**	**0.64**	−0.01	0.27	0.58	0.46	0.64	0.42	0.16	1.00				
logMn	−0.15	−0.10	0.03	0.13	0.16	0.19	0.05	0.70	0.08	−0.11	−0.03	0.34	0.48	0.11	1.00			
Silt	**0.46**	**0.48**	**0.43**	**0.36**	**0.33**	**0.28**	0.17	−0.27	−0.04	0.53	0.25	−0.05	−0.04	0.18	−0.27	1.00		
Clay	0.23	0.24	**0.27**	**0.31**	**0.31**	**0.35**	0.01	0.19	0.27	0.26	0.32	−0.03	0.06	0.33	0.06	0.20	1.00	
Sand	**−0.48**	**−0.50**	**−0.46**	**−0.40**	**−0.36**	**−0.33**	−0.16	0.23	−0.01	−0.54	−0.29	0.06	0.02	−0.23	0.25	−0.99	−0.36	1.00

Correlations greater than 0.25 are in bold (see columns 1–7). Organic matter, nitrogen, sulfur, iron, silt, and sand are strong correlates across all scales

Table 3 Correlations between soil nutrients and plant species richness at six scales in North Carolina Sandhills longleaf-pine communities

	0.01 m^2	0.1 m^2	1 m^2	10 m^2	100 m^2	1000 m^2	logCEC	logPH	logOrg	logN	logS	logP	logCa	logFe	logMn	Silt	Clay	Sand
0.01 m^2	1.00																	
0.1 m^2	0.86	1.00																
1 m^2	0.74	0.93	1.00															
10 m^2	0.64	0.85	0.95	1.00														
100 m^2	0.60	0.79	0.90	0.97	1.00													
1000 m^2	0.52	0.72	0.81	0.88	0.95	1.00												
logCEC	0.00	0.02	0.08	0.06	0.09	0.18	1.00											
logPH	**0.36**	**0.53**	**0.61**	**0.61**	**0.55**	**0.44**	−0.20	1.00										
logOrg	**0.32**	**0.32**	**0.36**	**0.30**	**0.32**	**0.35**	0.57	0.09	1.00									
logN	**0.45**	**0.58**	**0.60**	**0.55**	**0.50**	**0.42**	0.14	0.42	0.51	1.00								
logS	0.20	0.22	0.23	0.19	0.19	0.19	−0.14	0.19	0.48	0.47	1.00							
logP	−0.02	−0.06	−0.02	0.00	0.03	0.11	0.23	0.07	0.43	−0.23	0.11	1.00						
logCa	0.21	**0.32**	**0.42**	**0.41**	**0.41**	**0.42**	0.78	0.41	0.56	0.30	−0.07	0.33	1.00					
logFe	−0.22	**−0.25**	**−0.28**	**−0.28**	−0.24	−0.19	0.17	−0.22	0.05	−0.02	0.14	−0.11	−0.03	1.00				
logMn	0.23	**0.35**	**0.48**	**0.55**	**0.57**	**0.54**	0.14	0.62	0.29	0.30	0.10	0.37	0.54	−0.18	1.00			
Silt	**0.35**	**0.35**	**0.38**	**0.34**	**0.39**	**0.44**	0.50	0.10	0.65	0.40	0.23	0.03	0.43	0.05	0.11	1.00		
Clay	0.22	**0.31**	**0.32**	**0.26**	**0.25**	**0.25**	0.11	0.19	0.45	0.59	0.51	−0.11	0.10	−0.15	−0.04	0.45	1.00	
Sand	**−0.36**	**−0.37**	**−0.39**	**−0.35**	**−0.39**	**−0.44**	−0.47	−0.12	−0.67	−0.46	−0.28	−0.01	−0.41	−0.03	−0.09	−0.99	−0.56	1.00

Correlations of 0.25 and above are in bold (see columns 1–7). Soil pH, organic matter, nitrogen, and silt are strong correlates across all scales

Table 4 Correlations between soil nutrients and plant species richness at six scales in Florida longleaf-pine communities

	0.01 m^2	0.1 m^2	1 m^2	10 m^2	100 m^2	1000 m^2	logCEC	logPH	logOrg	logN	logS	logP	logCa	logFe	logMn	Silt	Clay	Sand
0.01 m^2	1.00																	
0.1 m^2	0.88	1.00																
1 m^2	0.73	0.91	1.00															
10 m^2	0.54	0.75	0.93	1.00														
100 m^2	0.39	0.62	0.83	0.95	1.00													
1000 m^2	0.33	0.55	0.74	0.86	0.94	1.00												
logCEC	−0.06	−0.05	−0.03	−0.09	−0.12	−0.12	1.00											
logPH	−0.01	0.16	**0.33**	**0.45**	**0.50**	**0.45**	−0.19	1.00										
logOrg	**0.31**	**0.32**	0.24	0.10	0.04	0.10	0.56	−0.31	1.00									
logN	**0.33**	**0.36**	**0.28**	0.14	0.08	0.13	0.52	−0.26	0.98	1.00								
logS	0.13	0.09	0.11	0.11	0.12	0.13	0.39	−0.13	0.42	0.44	1.00							
logP	−0.22	**−0.25**	−0.15	−0.07	−0.02	0.00	0.35	0.14	0.14	0.16	0.59	1.00						
logCa	−0.11	−0.03	0.08	0.10	0.09	0.08	0.88	0.26	0.37	0.36	0.33	0.46	1.00					
logFe	**0.28**	**0.31**	**0.33**	**0.38**	**0.41**	**0.46**	−0.31	0.22	0.02	0.05	0.15	−0.01	−0.21	1.00				
logMn	−0.24	−0.05	0.17	**0.35**	**0.47**	**0.44**	−0.09	0.66	−0.24	−0.21	0.01	0.17	0.23	0.13	1.00			
Silt	**0.31**	**0.37**	**0.37**	**0.32**	**0.28**	**0.30**	−0.12	0.07	0.30	0.34	0.09	−0.25	−0.10	0.33	−0.02	1.00		
Clay	0.06	0.16	0.14	0.09	0.08	0.09	0.14	0.03	0.18	0.20	0.05	−0.09	0.11	0.19	0.02	0.26	1.00	
Sand	**−0.25**	**−0.35**	**−0.33**	**−0.27**	−0.24	**−0.26**	0.01	−0.06	−0.32	−0.35	−0.09	0.22	0.01	−0.33	0.01	−0.84	−0.74	1.00

Correlations of 0.25 and above are in bold (see columns 1–7). Iron and silt are strong correlates across all scales. Soil pH is a strong correlate at the larger scales

Table 5 Model fit values for path models and structural equation models of plant diversity and soil attributes

Location	Scale	CFI	SRMR	RMSEA	90 % CI	χ^2	df	P	AIC
ACP longleaf	1 m^2	0.60	0.09	0.26	0.22–0.30	123.16	5	0.00	1004.84
	10 m^2	1.00	0.00	0.00	0.0–0.0	230.954	4	0.00	2381.84
	100 m^2	1.00	0.00	0.00	0.0–0.0	240.706	4	0.00	2714.44
	1000 m^2	1.00	0.00	0.00	0.0–0.0	265.78	5	0.00	1452.47
	SEM	0.74	0.12	0.25	0.23–0.27	1079.23	21	0.00	346.55
Sandhills longleaf	1 m^2	1.00	0.00	0.00	0.0–0.0	75.636	4	0.00	500.79
	10 m^2	1.00	0.00	0.00	0.0–0.0	72.734	4	0.00	607.95
	100 m^2	1.00	0.00	0.00	0.0–0.0	68.285	4	0.00	731.18
	1000 m^2	1.00	0.00	0.00	0.0–0.0	57.518	4	0.00	414.56
	SEM	0.87	0.11	0.19	0.11–0.27	138.51	10	0.00	101.08
FL longleaf	1 m^2	0.00	0.00	0.00	0.0–0.0	80.461	4	0.00	1195.02
	10 m^2	1.00	0.00	0.00	0.0–0.0	83.75	4	0.00	1404.92
	100 m^2	1.00	0.00	0.00	0.0–0.0	107.453	4	0.00	1609.93
	1000 m^2	1.00	0.00	0.00	0.0–0.0	106.528	4	0.00	848.40
	SEM	0.82	0.11	0.17	0.13–0.21	259.49	14	0.00	368.75
Mountain	1 m^2	1.00	0.00	0.00	0.0–0.0	193.38	4	0.00	2299.71
	10 m^2	1.00	0.00	0.00	0.0–0.0	229.064	5	0.00	649.65
	100 m^2	1.00	0.00	0.00	0.0–0.0	314.19	5	0.00	3734.31
	1000 m^2	1.00	0.00	0.00	0.0–0.0	289.88	4	0.00	1446.17
	SEM	0.94	0.04	0.16	0.13–0.19	1153.43	15	0.00	1818.53

Models are organized by region and scale: Atlantic Coastal Plain (ACP) longleaf-pine woodlands, Sandhills longleaf pine, Florida longleaf pine, and southern Appalachian mountain forests (Mountain). The comparative fit index (CFI), standardized root mean square residuals (SRMR), and the root mean square error of approximation (RMSEA), 90 % confidence interval for the RMSEA (90 % CI), chi-squared value, degrees of freedom (df), p value (p), and Akaike information criterion (AIC) are presented. The path models for each region had excellent fit based on CFI, SRMR, and RMSEA, with the exception of the 1 m^2 scale Atlantic Coastal Plain model, which had a marginal fit. SEM models in each region had marginally acceptable fit values

Path models predicting diversity using the strongest soil indicators for the 10, 100, and 1000 m^2 scales (Table 1) had excellent model fit based on standardized root mean square residuals (SRMR), the comparative fit index (CFI), and the Root Mean Square Error of Approximation (RMSEA) (Table 5). The chi-squared values ($p = 0.000$) suggest a poor model fit to the covariance data, but this fit value is influenced heavily by the relatively large sample size. The one exception to the excellent path-model fit values was the 1 m^2 path model for Atlantic Coastal Plain longleaf pine, which had a poor to marginal fit (see Table 5). Although the model fit is not ideal, the 1 m^2 Atlantic Coastal Plain longleaf-pine path model has patterns similar to those of models at coarser scales, with nitrogen, sulfur, and iron as strong indicators of diversity.

The path models indicated that nitrogen, sulfur, iron, and pH are the best indicators of diversity at all scales in Atlantic Coastal Plain longleaf-pine communities, while sand is important at the 1 m^2 scale and organic matter at the 1000 m^2 scale (Fig. 3). In the Sandhill longleaf-pine path models, manganese and silt were strong predictors of diversity across all scales, and pH and nitrogen became more

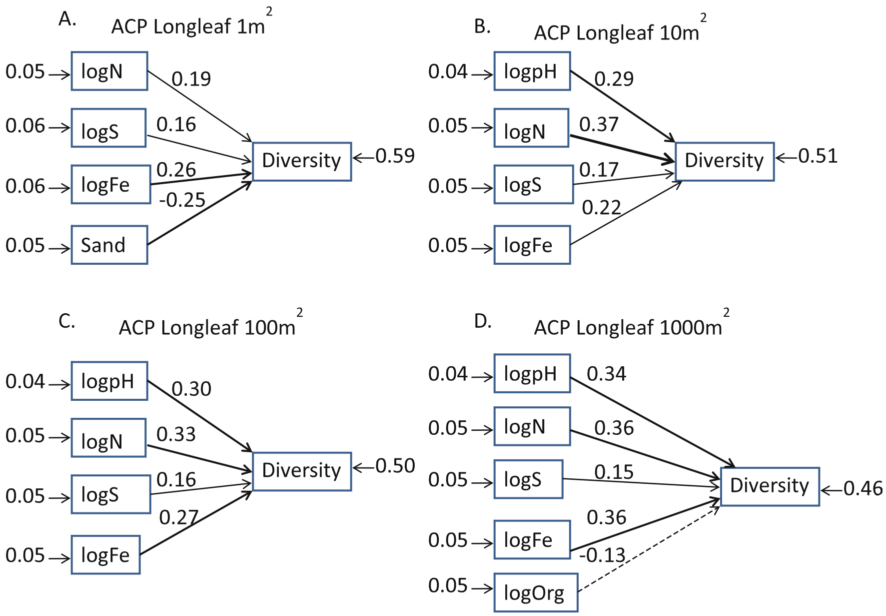

Fig. 3 Path models of Atlantic Coastal Plain longleaf-pinediversity and soil nutrients at the 1, 10, 100, and 1000 m^2 scales. The paths show standardized model estimates. The direction of the *arrow* represents the direction of the regression, with x, or observed variables, pointing to y variables on the *right*. The strength of the relationship is represented by the weight of the *arrow*. *Solid lines* are significant at the $p < 0.005$ level; *dashed lines* are significant at $p < 0.10$. In Atlantic Coastal Plain longleaf-pine communities, sulfur and iron were significant at all scales. At the three coarser scales, *p*H and nitrogen have significant loadings

important at the 1 and 10 m^2 scales (Fig. 4). Florida longleaf-pine diversity is best predicted by pH, iron, manganese, and silt across all scales (Fig. 5). The predictability of diversity decreased with increasingly finer scale in Atlantic Coastal Plain and Florida longleaf-pine (Figs. 3 and 5), but the Sandhill longleaf-pine path models showed the opposite relationship, with increasing predictability at increasingly finer scale (Fig. 4).

The refined conceptual model (Fig. 2) was supported when measures of soil texture would not load on the same latent variable as soil nutrients. Therefore, silt (and sand in the Florida longleaf pine) was modeled with a separate influence on diversity. Confirmatory factor analysis with soil nutrients as a latent variable and separate measured variables for soil texture produced an adequate fit. This base model was used to build an initial structural equation model based on soil nutrients, texture, and diversity.

The structural equation models for longleaf pine had moderate fit values (Table 5, longleaf pine SEM). In the Atlantic Coastal Plain, diversity in longleaf stands was modeled with soil nutrients having a stronger effect on diversity than silt. Iron, organic matter, pH, sulfur and nitrogen were all strong predictors of soil

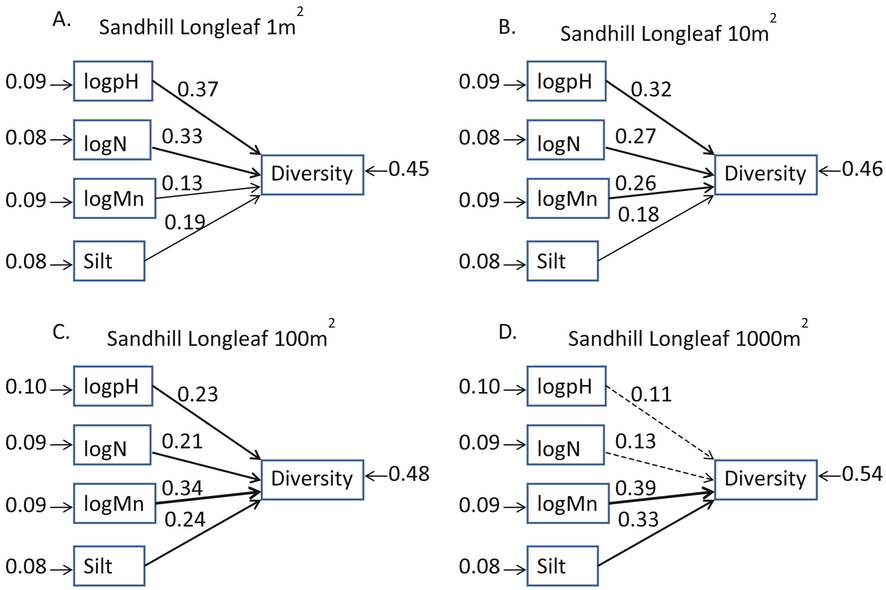

Fig. 4 Path models of diversity in longleaf-pine stands in the Sandhills of North and South Carolina and soil nutrients at the 1, 10, 100, and 1000 m^2 scales. The paths show standardized model estimates. The direction of the *arrow* represents the direction of the regression. The strength of the relationship is represented by the weight of the *arrow*. *Solid lines* are significant at the $p < 0.05$ level; *dashed lines* are significant at $p < 0.30$. In Sandhill longleaf-pine communities, *p*H, nitrogen, manganese, and silt have significant loadings at all scales. However, at the 1000 m^2 scale, soil *p*H and nitrogen were not significant

nutrients (Fig. 6). In the Sandhills, soil nutrients and silt also had strong positive loadings on diversity, but the influence of silt was stronger. Manganese, nitrogen, and pH were the best indicators of soil nutrients (Fig. 7). Diversity in Florida longleaf stands was also influenced positively by silt and soil nutrients. Sand was a very weak indicator of diversity in this model, and iron, calcium, manganese, and phosphorous were important predictors of soil nutrients (Fig. 8).

Southern Appalachian Mountain Vegetation

The strongest soil correlates of diversity for the mountain plots are summarized in Table 1. The mountain data demonstrate that pH, manganese, and calcium are strong correlates of diversity, regardless of the scale of observation, and soil texture has only a weak correlation with diversity at any given scale (Table 6). Soil cation exchange capacity (CEC) is also an important correlate at the finer scales. At the 1000 m^2 scale, iron, and sulfur were the other notable correlates.

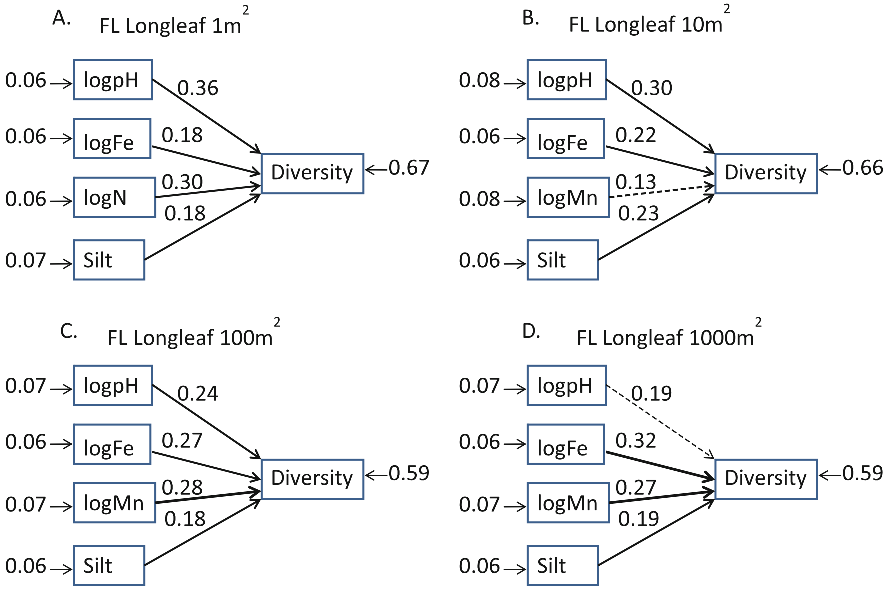

Fig. 5 Path models of Floridalongleaf-pine communitydiversity and soil nutrients at the 1, 10, 100, and 1000 m^2 scales, showing standardized model estimates. The direction of the *arrow* represents the direction of the regression. The strength of the relationship is represented by the weight of the *arrow*. *Solid lines* are significant at the $p < 0.005$ level; *dashed lines* are significant at $p < 0.10$. In Florida longleaf-pine communities, silt, *p*H, and iron have significant loadings at all scales. Nitrogen is a significant measured variable at the 1 m^2 scale, and manganese is significant at the three coarser scales

Path models using the strongest correlates of diversity (Table 1) generated models with good fit values. Both iron and calcium had insignificant or very small factor loadings at several scales. The final path models (Fig. 9) have excellent model fit values based on CFI, SRMR, and RMSEA (Table 5). The path models suggest that manganese, calcium, and pH are the strongest indicators of diversity at the 1 m^2 scale. At the full-plot scale, manganese and pH were the best measures for predicting diversity (Fig. 9).

Confirmatory factor analysis using the single-latent-variable model (Fig. 1) failed to converge. However, confirmatory factor analysis with pH as an independent indicator and the other nutrients loading onto a latent variable showed an adequate fit. This model was then used as the basis of a structural equation model for soil nutrients, pH, and diversity (Fig. 10). The mountain structural equation model has a moderate model fit (Table 5, Mountain SEM), accounting for 39 % of the variation in diversity (Fig. 10). Soil pH loads positively onto diversity, but it is a strong negative indicator for soil minerals. Soil minerals influence diversity negatively, driven by strong negative indicators (pH, Ca, Mn).

Within-plot variance was calculated for all plots with four soil samples (Table 7). Soil organic matter, cation exchange capacity, calcium, sulfur, magnesium, and

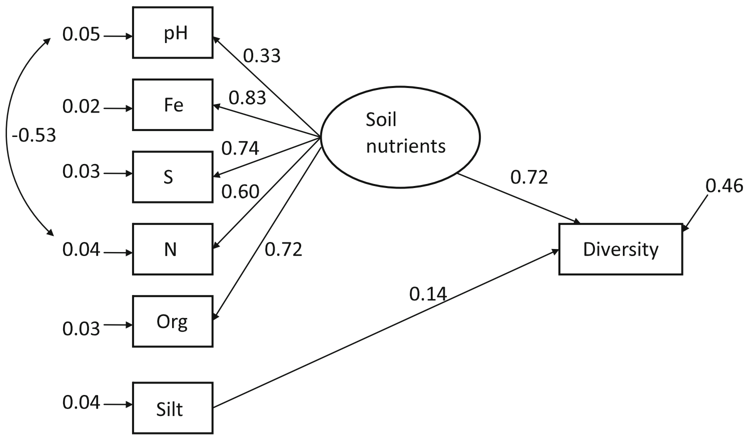

Fig. 6 Structural equation model for Atlantic Coastal Plain longleaf-pine diversity and soil nutrients (1000 m^2 scale). The direction of the *arrows* from the latent variable (Soil nutrients) indicates that this construct is determining the measured values in the field. All other *arrows* represent the direction of the regression and influence on other variables. *Short arrows* into the measured variables indicate the measurement error. All loadings are standardized and significant at $p < 0.001$. Iron, sulfur, and organic matter were the strongest indicators of soil nutrients. Silt had a separate affect on diversity. Soil nutrients had a greater influence on diversity than silt. The model explained 54 % of the variance in diversity

manganese have variances that are, on average, an order of magnitude larger in the mountains than in the longleaf-pine plots. The variances of soil pH and base saturation were the soil variables with the most similar level of within-plot variance across all regions.

Discussion

The path models indicate that there are consistent indicators of diversity across scale in both the mountain forests and longleaf-pine woodlands. The path models of soil and diversity illustrate that soil nutrient indicators differ across scale within 1000 m^2 nested plots, but only slightly. In the mountains, sulfur was important at the intermediate scales (10, 100 m^2). In the Atlantic Coastal Plain pine systems, nitrogen was a strong predictor only at the 1 m^2 scale, and pH became insignificant at this finer scale. It was also difficult to fit a path model with an adequate model fit at the finest scale (1 m^2). This variation in indicators at the 1 m^2 scale is probably

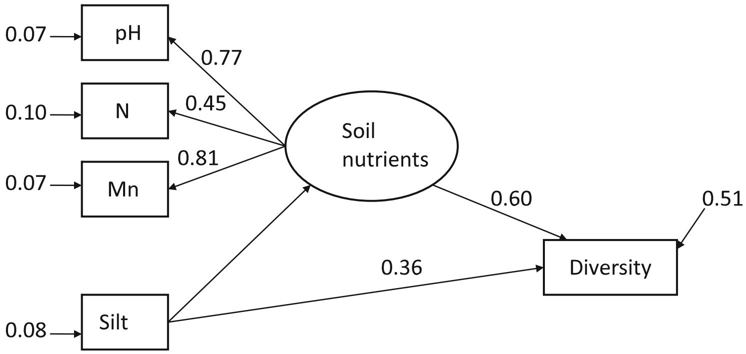

Fig. 7 Structural equation model for diversity and soil nutrients in longleaf-pine communities in the Sandhills of the Carolinas (1000 m^2 scale). The direction of the *arrows* from the latent variable (Soil nutrients) indicates that this construct is determining the measured values in the field. All other *arrows* represent the direction of the regression and influence on other variables. *Short arrows* into the measured variables indicate the measurement error. All loadings are standardized and significant at $p < 0.001$. Manganese and soil pH were the strongest indicators of soil nutrients. Silt had a separate effect on diversity, which was roughly half the influence of Soil nutrients on diversity. The model explained 49 % of the variance in diversity

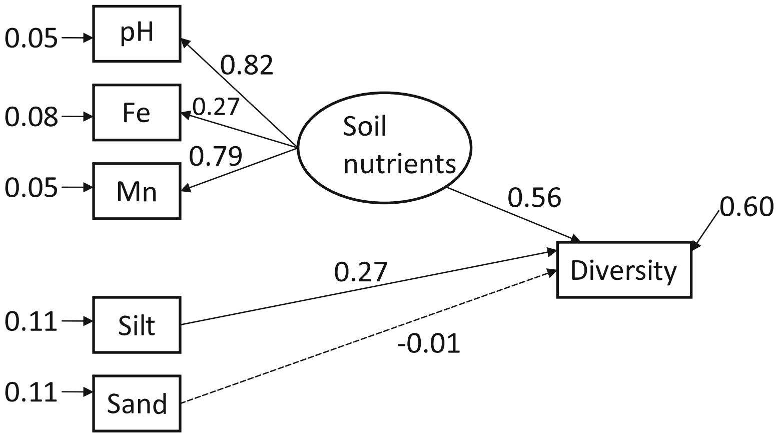

Fig. 8 Structural equation model for diversity and soil nutrients in Florida longleaf-pine communities (1000 m^2 scale). The direction of the *arrows* from the latent variable (Soil nutrients) indicates that this construct is determining the measured values in the field. All other *arrows* represent the direction of the regression and influence on other variables. *Short arrows* into the measured variables indicate the measurement error. All loadings are standardized and significant at $p < 0.001$, except for the *dotted line*, which is significant at $p < 0.9$. Manganese and soil *p*H were the strongest indicators of soil nutrients. Silt and sand had separate effects on diversity; however the loading for sand was both insignificant ($p < 0.9$) and a small number. The model explained 40 % of the variance in diversity

Table 6 Correlations between plant species richness across six scales and soil nutrients in southern Appalachian Mountain communities

Mountain	0.01 m^2	0.1 m^2	1 m^2	10 m^2	100 m^2	1000 m^2	logCEC	logpH	logOrg	logN	logS	logP	logCa	logFe	logMn	Clay	Silt	Sand
0.01 m^2	1.00																	
0.1 m^2	0.86	1.00																
1 m^2	0.66	0.87	1.00															
10 m^2	0.48	0.71	0.92	1.00														
100 m^2	0.37	0.60	0.83	0.95	1.00													
1000 m^2	0.33	0.54	0.75	0.88	0.96	1.00												
logCEC	**0.24**	**0.24**	**0.24**	0.21	0.19	0.17	1.00											
logpH	**0.25**	**0.36**	**0.46**	**0.51**	**0.55**	**0.54**	0.22	1.00										
logOrg	0.00	−0.04	−0.08	−0.13	−0.19	−0.22	0.34	−0.44	1.00									
logN	0.05	0.07	0.07	0.02	−0.04	−0.09	0.17	−0.31	0.81	1.00								
logS	−0.12	−0.18	−0.22	**−0.23**	**−0.24**	**−0.25**	0.24	−0.26	0.20	0.07	1.00							
logP	−0.09	−0.13	−0.17	−0.16	−0.15	−0.12	0.41	−0.19	0.21	−0.06	0.50	1.00						
logCa	**0.28**	**0.35**	**0.40**	**0.41**	**0.41**	**0.39**	0.86	0.55	0.13	0.08	−0.08	0.28	1.00					
logFe	−0.01	−0.14	**−0.26**	**−0.32**	**−0.35**	**−0.34**	−0.12	−0.53	0.09	0.09	0.35	0.05	−0.38	1.00				
logMn	**0.23**	**0.34**	**0.45**	**0.51**	**0.52**	**0.52**	0.40	0.50	0.00	0.13	0.02	0.16	0.57	−0.29	1.00			
Clay	−0.13	−0.11	−0.06	−0.03	−0.02	−0.05	−0.31	0.00	−0.24	−0.05	−0.01	−0.22	−0.25	0.06	0.00	1.00		
Silt	−0.20	−0.21	−0.21	−0.20	−0.21	−0.22	−0.05	−0.35	0.33	0.27	0.21	0.12	−0.17	0.14	0.01	0.18	1.00	
Sand	0.22	0.22	0.21	0.19	0.20	0.21	0.13	0.32	−0.22	−0.23	−0.19	−0.04	0.23	−0.15	−0.01	−0.47	−0.95	1.00

Correlations greater than 0.23 are in bold (see first 7 columns). Both manganese and calcium are strong correlates across all scales. Soil pH and iron are strong correlates across several scales. Cation exchange capacity and sulfur are strongly correlated at some scales

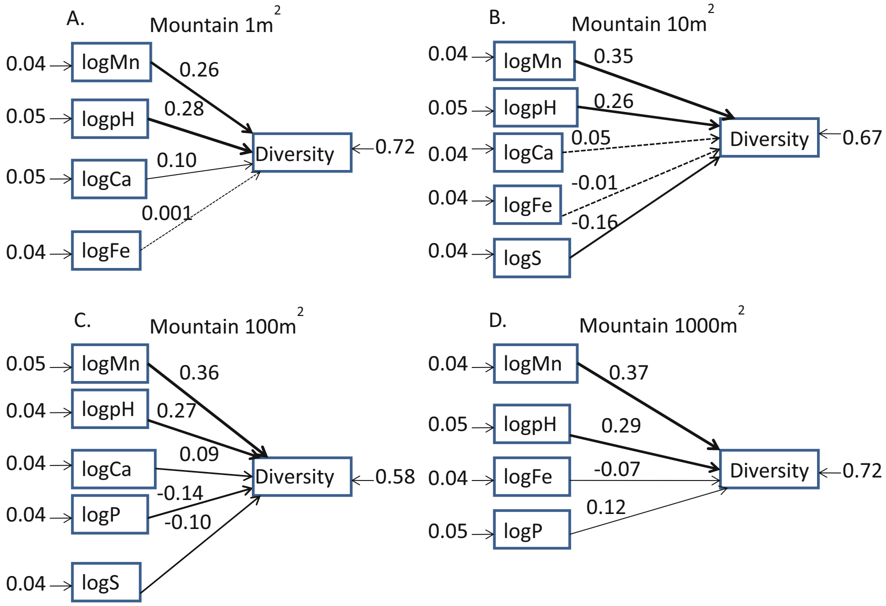

Fig. 9 Path models of southern Appalachian Mountain community soil nutrients and diversity at the 1 m^2, 10 m^2, 100 m^2, and 1000 m^2 scales showing standardized model estimates. The direction of the *arrow* represents the direction of the regression. The strength of the relationship is represented by the weight of the *arrow*. *Solid lines* are significant at the $p < 0.001$ level; *dashed lines* are for loadings with $p < 0.1$. In mountain communities, Manganese and pH are the strongest indicators for diversity at all scales

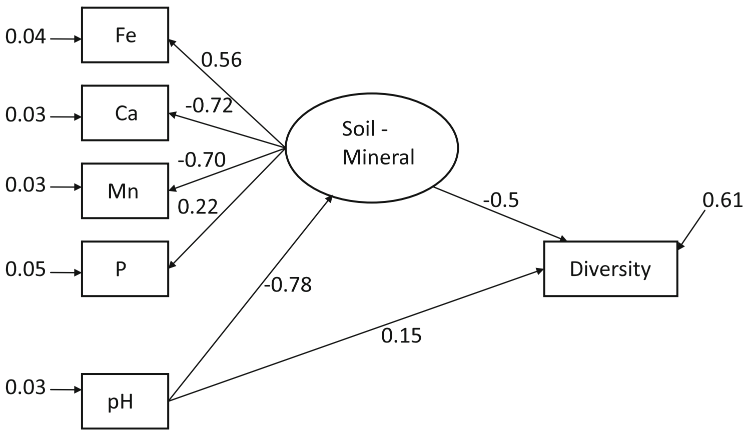

Fig. 10 Structural equation model for diversity and soil nutrients in southern Appalachian Mountain communities (1000 m^2 scale). The direction of the *arrows* from the latent variable (Soil nutrients) indicates that this construct is determining the measured values in the field. All other *arrows* represent the direction of the regression and influence on other variables. *Short arrows* into the measured variables indicate the measurement error. All loadings are standardized and significant at $p < 0.001$. Manganese, calcium and iron were the strongest indicators of soil nutrients. Soil pH had a separate effect on diversity. The model explained 39 % of the variance in diversity

Table 7 Average within-plot variance of soil characteristics by region

Region	Organic	soilPH	CEC	BaseSat	S	P	Ca_ppm	Mg_ppm	K_ppm	Na_ppm
ACP longleaf	4.73	0.08	6.10	33.34	24.50	192.36	27851.49	308.86	133.10	66.99
SH longleaf	5.00	0.05	1.71	25.48	27.83	7.13	7628.92	141.20	81.47	3.78
FL longleaf	5.28	0.06	3.52	35.42	13.68	181.17	29015.19	298.08	49.15	153.42
Mountain	79.42	0.08	18.47	39.03	106.32	77.83	121685.68	3161.65	782.07	8.59
Region	**%Ca**	**%Mg**	**%K**	**%Na**	**%Other**	**Fe_ppm**	**Mn_ppm**			
ACP longleaf	29.30	2.09	0.42	0.61	0.29	1765.20	35.60			
SH longleaf	20.74	2.35	0.38	0.15	0.20	1485.51	352.72			
FL longleaf	31.41	3.57	0.49	1.05	0.22	1824.24	201.82			
Mountain	33.47	6.03	1.32	0.20	0.29	3330.06	1463.71			

This table depicts the variance in soil characteristics within Atlantic Coastal Plain longleaf-pine plots (ACP longleaf), longleaf pine in the Sandhills of the Carolinas (SH longleaf), Florida longleaf pine (FL longleaf), and southern Appalachian Mountains (Mountain) plots. Soil characteristics include organic matter (Organic), soil pH (soilPH), soil cation exchange capacity (CEC), base saturation (BaseSat), and nutrients in either parts per million (ppm) or percentages. The variance in organic matter, cation exchange capacity, sulfur, calcium (ppm), magnesium (ppm), and manganese (ppm) are an order of magnitude larger in the mountains than in each of the longleaf regions. The variances of soil *p*H, and base saturation, were the variables with the most similar level of within-plot variance across all regions due to the lack of nesting of the soil samples at this finer scale, which is consistent with the results that the models using 0.1 and 0.01 m^2 measures of richness had poor fit or did not converge. However, in the longleaf-pine communities, this may also be due to fine-scale variation in soil nutrients and plant mortality caused by frequent fire. Fire is inherently patchy, resulting in fine-scale variation in intensity and nutrient availability across the landscape from place to place and year to year. Binkley et al. (1992) pointed out the high level of variability in mineral soils in longleaf-pine systems and called for more precise soil measurements within plots. In addition, our data lack a good indicator of soil moisture, but iron, organic matter and nitrogen may track the moisture gradient collectively (Peet et al. 2014).

As anticipated, texture was significant consistently across scales in the longleaf systems. Silt was a strong indicator at most scales. Clay was a weak indicator across all scales and systems, perhaps because few longleaf sites have soils with high clay content, thereby reducing the range of variation. Silt has been used previously to classify longleaf-pine communities (Peet 2006; FGDC 2013), suggesting that it is important in these systems. Silt and sand also had inverse relationships with species richness, with sand negatively correlated with diversity and silt positively related to diversity. When modeling species diversity in longleaf-pine woodlands, the conceptual model with separate texture and nutrient variables (Fig. 2) was more effective at capturing the relationship than was a simple soil-characteristics model (Fig. 1). Subsequent work analyzing herbaceous diversity in longleaf systems indicated that principle component analysis axes of environmental variables corresponding to soil moisture and soil texture are important in determining richness of the herbaceous layer (Peet et al. 2014). The key variables loading on these axes were bulk density, sulfur, organic matter aluminum, iron, clay, sand, and silt. With the exception of bulk density and the inclusion of only silt and/or sand as a proxy for soil texture, these variables were all key indicators in at least one of the longleaf structural equation models. However, the structural equation models produced here indicate that the soil variables that predict diversity most closely vary with the specific physiographic regions of longleaf pine.

The results from the mountain models match our expectations. Manganese, pH and calcium were consistently strong predictors, as observed by Peet et al. (2003) and Newell and Peet (1998). This also matches closely the results of the principle components analysis for the herbaceous species richness in southern Appalachian forests by Peet et al. (2014), in which base cation availability, including soil pH, cation exchange capacity, calcium, magnesium, and manganese, was the primary correlate of diversity. Texture does not seem to be an important indicator of diversity in this region. Because the variance of calcium and cation exchange capacity within plots in the mountains was higher than in the longleaf-pine plots (Table 7), the higher within-plot variation in calcium is probably adding to the importance of these variables in the mountains.

The initial soil structural equation models predict diversity well in both the longleaf-pine and mountain communities. Soil nutrients, modeled by calcium, manganese, iron, and phosphorous, along with pH, are the key predictors of diversity in mountain communities. A similar model is effective in all longleaf-pine communities: both soil nutrients and silt influenced diversity positively. Soil pH is a key indicator in both longleaf-pine communities and the southern Appalachian Mountains. Silt modeled the influence of soil texture effectively across all longleaf pine regions. However, a more detailed examination of the soil nutrient variation within plots, including fully nested soil samples, would add to our understanding of the influence of soil on diversity and the effect of scale of observation.

The structural equation models for both longleaf-pine and mountain communities suggest that this modeling approach and conceptual model could be applied effectively to other regions in order to further understanding of the influence of soil attributes on diversity. Specifically, this methodology could be applied: (1) to generate and test theoretical models of how soil attributes influence diversity and whether those impacts are direct or indirect; and (2) to confirm regional or community classifications that are based in part on soil attributes.

These findings demonstrate that soil characteristics vary closely with plant species richness. Further study of the within-plot variation in soil nutrients and texture would add to our understanding of how particular soil characteristics influence diversity. Manganese is a particularly strong but unexplained predictor and may be a surrogate for soil weathering or for phosphorous availability. In Atlantic Coastal Plain longleaf-pine communities, it is likely that iron and sulfur function as surrogates for water availability. Future research should focus on why these variables are meaningful and how soil nutrient availability influences diversity.

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References

Binkley D, Richter D, David MB, Caldwell B (1992) Soil chemistry in a loblolly-longleaf pine forest with interval burning. Ecol Appl 2:157–164

Bollen KA (1989) Structural equations with latent variables. Wiley, New York, 514 pp

Box EO, Fujiwara K (2011) Sorting plots not taxa for studying vegetation structure and plant species richness. Plant Biosyst 145(Supplement):46–53

Gaston KJ (2000) Global patterns in biodiversity. Nature 405:220–227

Giladi I, Ziv Y, May F, Jeltsch F (2011) Scale-dependent determinants of plant species richness in a semi-arid fragmented agro-ecosystem. J Veg Sci 22:983–996

Grace JB (2006) Structural equation modeling and natural systems. Cambridge University Press, Cambridge, 378 pp

Mehlich A (1984) Mehlich 3 soil test extractant: a modification of Mehlich 2 extractant. Commun Soil Sci Plant Anal 15:1409–1416

Muthén L, Muthén B (1998–2010) MPlus version 6. Base program and combination add-on (32-bit)
Newell CL, Peet RK (1998) Vegetation of Linville Gorge Wilderness, North Carolina. Castanea 63(3):275–322
Peet RK (2006) Ecological classification of longleaf pine woodlands. In: Jose S, Jokela EJ, Miller DL (eds) The longleaf pine ecosystem: ecology, silviculture, and restoration. Springer, New York, pp 51–94
Peet RK, Wentworth TR, White PS (1998) A flexible, multi-purpose method for recording vegetation composition and structure. Castanea 63:262–274
Peet RK, Fridley JD, Gramling JM (2003) Variation in species richness and species pool size across a pH gradient in forests of the southern Blue Ridge Mountains. Folia Geobotanica 38:391–401
Peet RK, Lee MT, Boyle MF, Wentworth TR, Schafale MP, Weakley AS (2012) Vegetation-plot database of the Carolina vegetation survey. Biodivers Ecol 4:243–253
Peet RK, Palmquist KA, Tessel SM (2014) Herbaceous-layer species richness of southeastern forests and woodlands: patterns and causes. In: Gilliam FS, Roberts MR (eds) The herbaceous layer in forests of eastern North America, 2nd edn. Oxford University Press, Oxford
Schuster B, Diekmann M (2005) Species richness and environmental correlates in deciduous forests of Northwest Germany. For Ecol Manage 206:197–205
U.S. Federal Geographic Data Committee (FGDC), Vegetation Subcommittee (2013) U.S. National Vegetation Classification. http://usnvc.org
Waring RH, Running SW (eds) (1998) Forest ecosystems: analysis at multiple scales, 2nd edn. Academic, New York, 370 pp