



# A model of geographical, environmental and regional variation in vegetation composition of pyrogenic grasslands of Florida

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## ABSTRACT

**Aim** To develop a landscape-level model that partitions variance in plant community composition among local environmental, regional environmental, and purely spatial predictive variables for pyrogenic grasslands (prairies, savannas and woodlands) throughout northern and central Florida.

**Location** North and central Florida, USA.

**Methods** We measured plant species composition and cover in 271 plots throughout the study region. A variation-partitioning model was used to quantify components of variation in species composition associated with the main and interaction effects of soil and topographic variables, climate variables and spatial coordinates. Partial correlations of environmental variables with community variation were identified using direct gradient analysis (redundancy analysis and partial redundancy analysis) and Monte Carlo tests of significance.

**Results** Community composition was most strongly related to edaphic variables at local scales in association with topographic gradients, although geographically structured edaphic, climatic and pure spatial effects were also evident. Edaphic variables explained the largest portion of total variation explained (TVE) as a main effect (48%) compared with the main effects of climate (9%) and pure spatial factors (9%). The remaining TVE was explained by the interaction effect of climate and spatial factors (13%) and the three-way interaction (22%). Correlation analyses revealed that the primary compositional gradient was related to soil fertility and topographic position corresponding to soil moisture. A second gradient represented distinct geographical separation between the Florida panhandle and peninsular regions, concurrent with differences in soil characteristics. Gradients in composition corresponded to species richness, which was lower in the Florida peninsula.

**Main conclusions** Environmental variables have the strongest influence on the species composition of Florida pyrogenic grasslands at both local and regional scales. However, the limited distributions of many plant taxa suggest historical constraints on species distributions from one physiographical region to the other (Florida panhandle and peninsula), although this pattern is partially confounded by regionally spatially structured environmental variables. Our model provides insight into the relative importance of local- and regional-scale environmental effects as well as possible historical constraints on floristic variation in pine-dominated pyrogenic grasslands of the south-eastern USA.

## Keywords

Climatic variation, edaphic variation, environmental–vegetation model, Florida, floristic variation, grasslands, spatial variation, species composition, USA, variation partitioning.

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## INTRODUCTION

Natural variability in plant community species composition is shaped by complex interactions of biotic and abiotic factors acting at both local and regional spatial scales. Most studies of plant community composition have focused on variation associated with local environmental gradients. Comparisons among such studies reveal regional-scale variation in species composition (Hubbell & Foster, 1986; Collins *et al.*, 2002; Svenning & Skov, 2005). However, few studies have attempted to interpret the relative influence of local environmental gradients, regional environmental gradients, and historical effects for a given ecosystem type (Ricklefs, 1987; Partel, 2002). Such an approach requires systematic, spatially explicit measurement of vegetation and environmental variables at both local and regional scales (Legendre & Legendre, 1998).

Fire-maintained grasslands of the south-eastern US Coastal Plain provide a model system for investigating the relative influences of environmental vs. spatial factors, given their high local and regional floristic diversity and large number of endemic and restricted-range species. Local variation in species composition is related to environmental factors, including soil properties, topography and associated moisture regimes (Peet & Allard, 1993; Grace *et al.*, 2000; Weiher *et al.*, 2004). These findings are consistent with general ecological models of 'abiotic controls' (environmental control models), which emphasize environmental gradients, resource limitations and niche specialization as determinants of community structure and composition (Whittaker, 1956; Bray & Curtis, 1957). Biotic control models might also apply, emphasizing organism interactions such as competition and herbivory as well as historical influences of dispersal limitation, speciation and extinction (Hubbell, 2001; Collins *et al.*, 2002; Foster & Tilman, 2003). Although testing effects of species interactions requires rigorous experimental approaches beyond the scope of this study, insights into historical controls on species distributions may be investigated empirically by measuring the relative contributions of environmental vs. spatial variance towards limitations on species distributions. Such an approach must incorporate a wide range of species compositions and environmental and spatial contexts to distinguish purely spatial autocorrelation from environmental effects (Borcard & Legendre, 1994; Legendre *et al.*, 2005).

The primary goal of our study was to determine the relative influence of local environmental, regional environmental and historical influences on plant species composition in Florida grasslands (prairies, savannas and woodlands). We hypothesized that each of these factors act simultaneously, and predicted that plant species composition would vary according to local topographic position and edaphic characteristics, regional gradients of edaphic conditions and climate, and purely spatial patterns. Our approach was to census a large number of natural community remnants to develop a statistical model that partitions species composition variance among these factors and their interactions.

## MATERIALS AND METHODS

### Study region

The study area includes the Florida panhandle and most of the central and northern peninsula of Florida, USA (Fig. 1). As most of Florida's native pyrogenic grassland ecosystems are classified as, or associated with, pine savannas (*sensu* Houghton *et al.*, 2006) dominated by longleaf pine (*Pinus palustris* P. Mill.), the study region was delineated based on the historical range of this species (Fig. 1a). This region includes roughly 9 million ha, extending from *c.* 31°00' to 28°80' N latitude and 87°30' to 80°00' W longitude.

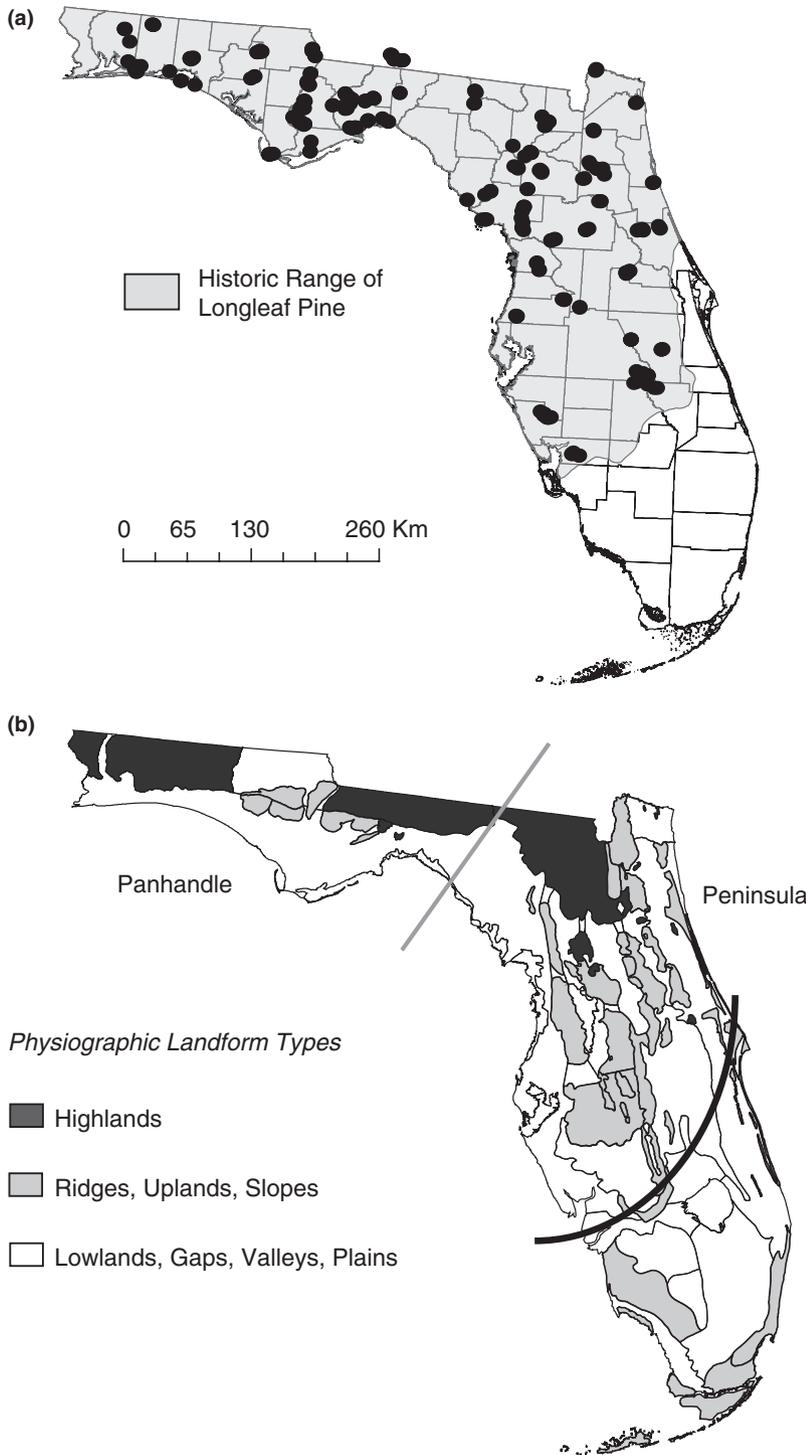
The study region falls within the 'warm temperate moist forest' bioclimate zone (Holdridge, 1967). Mean annual maximum temperatures, minimum temperatures and short-wave radiation increase southward (25–29°C, 13–17°C, 345–361 MJ m<sup>2</sup> day<sup>-1</sup>, respectively; Fernald, 1981; Thornton *et al.*, 1999). Average annual rainfall is highest in the western panhandle and declines further east and south, ranging from 173 to 124 cm year<sup>-1</sup> (Fernald, 1981).

Grasslands within the study region have soils ranging from droughty, coarse sands to poorly drained organic soils. Entisols are common in the dry uplands of the Northern and Central Highlands physiographical landforms, while finer-textured and more fertile ultisols and alfisols are typical of the lowland landforms (Fig. 1b; Puri & Vernon, 1964; Myers & Ewel, 1990). Grasslands in the coastal lowlands of the panhandle (Fig. 1b) have little topographic relief, with sandy, acidic spodosols in the higher areas and histosols (organic soils) in low-lying wetlands (Brady & Weil, 2000).

### Vegetation and environmental data

Our overall model development approach was to record vegetation abundance in standardized plots, measure or gather edaphic and climatic environmental data for each plot location, and calculate geographical distances among plot locations. We focused on fire-dependent herbaceous plant communities (grasslands) in our selection of plot location. Most locations contained woodlands and savannas dominated by longleaf or, to a smaller extent, slash pine (*Pinus elliotii* Engelman var. *elliotii* and *P. elliotii* Engelman var. *densa* Little & K.W. Dorman). These included sandhills, upland pine forests, and wet, mesic and scrubby (xeric) flatwood communities (Florida Natural Areas Inventory, 1990). Other sites had few to no trees and included wet and dry prairie, bog, lake margins and seepage slope communities (Florida Natural Areas Inventory, 1990). Scrub and maritime pinelands were not included, as they represent a fuel structure and fire regime different from those of grasslands (Florida Natural Areas Inventory, 1990; Myers & Ewel, 1990).

To minimize problems common to statistical descriptions of large-scale observational studies (Lajer, 2007), we followed recommendations by Lepš & Šmilauer (2007). Specifically we



**Figure 1** (a) Locations of the 271 vegetation plots (many overlapping at this scale) studied in northern and central Florida. The shaded area indicates the historical range of longleaf pine (*Pinus palustris*) in Florida. (b) Three major physiographical landform types, modified from Puri & Vernon (1964), depicted by shaded regions. The grey line separates panhandle and peninsular regions. The black line represents the approximate southern boundary of the study area.

stratified plot selection over a broad range of geographical and physiographical delineations, included a large sample size, and applied statistical methods to develop descriptive response models rather than hypotheses (Lepš & Šmilauer, 2007). Thus, sample sites within the study region were selected in each of three generalized physiographical landforms delineated by Puri & Vernon (1964): (1) highlands, (2) ridges, uplands and slopes, and (3) lowlands, gaps, valleys and plains (Fig. 1b). We further stratified sampling according to 19 ‘ecoregions’ in

north and central Florida based on physiography, climate and historical vegetation, as delineated elsewhere (Puri & Vernon, 1964; Davis, 1967; Brooks, 1982; Bailey *et al.*, 1994). Ninety-eight sites were selected so that there were two to four sites in each ecoregion. Each site was further stratified into three or four zones of topographic–moisture conditions (1 = highest, 4 = lowest) to encompass the range of local edaphic conditions, and one vegetation plot was established in each zone (271 plots in total; Fig. 1).

Sample sites were restricted to those with: (1) little or no evidence of historical soil disturbance, (2) absence of invasive exotic species, (3) native overstorey and mid-storey trees (if present), and (4) evidence of fire within the previous 5 years, preferably with a history of frequent fires (1–7-year intervals). When possible, plots were located on an intact, continuous topographic moisture gradient. However, in some cases we pieced together a representative gradient using multiple proximate locations. Candidate sites were identified from the Florida Natural Areas Inventory and from consultation with regional natural resource professionals. Twelve plots (at three sites) were located in southern Georgia, within 20 miles of the Florida state border (Fig. 1a), to represent plant community types in the adjacent Florida ecoregion.

Each plot covered 1000 m<sup>2</sup> (50 × 20-m rectangle) following the Carolina Vegetation Survey sampling protocol (Peet *et al.*, 1998). Within each plot, all vascular plants were identified to the most specific taxonomic identity possible. Plant cover for each species in each 1000-m<sup>2</sup> plot was calculated as an average of the four 100-m<sup>2</sup> subplots, in which each plant taxon was assigned an aerial cover class: 1 = 0–1%, 2 = 1–2%, 3 = 2–5%, 4 = 5–10%, 5 = 10–25%, 6 = 25–50%, 7 = 50–75%, 8 = 75–95%, 9 = > 95%. Additional plant species encountered in the remaining 600-m<sup>2</sup> area within the plot were recorded and assigned a nominal cover estimate. Within the 1000-m<sup>2</sup> plot, all woody stems > 1 cm diameter at breast height (d.b.h.) were tallied by species in 10 size classes ranging from 1–40 cm d.b.h., and stems > 40 cm d.b.h. were measured to the nearest centimetre.

The 271 plots were sampled during the late summer until the early winter months (August–December) over a 4-year period (2000–2004). Botanical nomenclature followed Kartesz (1999), although several references were used in the field and herbarium (Godfrey & Wooten, 1979, 1981; Clewell, 1985; Godfrey, 1988; Wunderlin, 1998; Weakley, 2006). The vast majority of taxa were identified to species or variety; low-resolution taxa (family or genus) were omitted from further analyses unless identification was consistent throughout the data set. The term ‘species’ is used hereafter to refer to the lowest recognized taxonomic group.

At each plot location, one subsurface (*c.* 50 cm depth) and four surface (0–10 cm depth) soil samples were collected for nutrient and texture analysis (Brookside Labs, New Knoxville, OH, USA) to determine total cation-exchange capacity (meq 100 g<sup>-1</sup>); pH; estimated nitrogen release, extractable phosphorus, exchangeable cations (Ca, Mg, K, Na) and extractable micronutrients (B, Fe, Mn, Cu, Zn, Al) (p.p.m.); soluble sulfur and bulk density. Nutrient analyses used the Mehlich III extractant (Mehlich, 1984), and percentage organic matter was determined by loss-on-ignition. Texture analysis quantified percentage sand (2 mm–63 µm), silt (63–8 µm) and clay (< 8 µm) of soil samples.

Climate data were obtained for each plot location using the DayMet climatological model (<http://www.daymet.org>; Thornton *et al.*, 1999) based on daily parameter values from 1980 to 1998. We calculated annual and growing season (March–

October) means for daily maximum air temperature, daily minimum air temperature and daily average air temperature, and means and standard deviation for total daily precipitation and total daily shortwave radiation. Elevation estimates for each plot were downloaded from the HYDRO North America Digital Elevation Model webpage ([http://edc.usgs.gov/products/elevation/gtopo30/hydro/na\\_dem.html](http://edc.usgs.gov/products/elevation/gtopo30/hydro/na_dem.html)).

### Numerical data assembly and analysis

The goal of numerical analyses was to develop a model to compare main, two-way and three-way interaction effects of edaphic, climatic and spatial explanatory variables on variation of plant community composition. Explanatory variables were grouped into three matrices of explanatory variables (edaphic variable matrix, climate variable matrix and spatial variable matrix) in which Euclidean distances represent inter-plot similarities in explanatory variables. A response variable matrix was calculated from species cover data from the 271 plots. Cover values for pine species (genus *Pinus*) were omitted to minimize compositional effects of past logging and tree planting. Species with fewer than three occurrences were deleted from the data matrix (McCune & Grace, 2002). The raw species cover matrix was transformed via ‘relativization by maximum’ (Legendre & Gallagher, 2001; McCune & Grace, 2002). We used a Hellinger transformation of species-response data, which is appropriate for community composition data containing many zeros and long beta-diversity gradients (Legendre & Gallagher, 2001; Legendre *et al.*, 2005).

Edaphic and climate variables were transformed to approximate normal distributions when necessary. Soil variables measured in p.p.m. were log-transformed and logit transformations were applied to proportional data (Tabachnick & Fidell, 1996). Because of varying measurement scales of soils and climate variables, all variables in the edaphic and climate variable matrices were standardized to z-scores, expressed as standard deviations from the mean (Legendre & Legendre, 1998).

The spatial variable matrix quantified spatial patterns among plots using a multi-order model of geographical locations. This approach allowed modelling of spatial trends that are more complex than linear gradients (Legendre & Fortin, 1989). The spatial variable matrix initially contained nine terms of a third-order polynomial regression of X and Y geographical coordinates (Borcard *et al.*, 1992; Borcard & Legendre, 1994). Seven terms were retained for both redundancy analysis (RDA) and partial redundancy analysis (pRDA) following forward selection (see below).

Individual variables of each explanatory matrix (edaphic, climate and spatial) were screened using the forward selection procedure and associated Monte Carlo tests to facilitate selection of variables with the largest effect on species response. Variables with the highest marginal effects (eigenvalue from individual constrained ordinations) were initially selected and sequential variables were selected by decreasing values of marginal effects. Only variables with high partial correlations

**Table 1** List of variables retained following the forward selection procedure of variables with largest correlation with variation of species data.

Abbreviation	Variable	Eigenvalue	RDA			pRDA	
			A1	A2	A3	A1	A2
Edaphic variable matrix							
Topo	Relative position on slope (1–4)	0.08	<b>0.79</b>	0.05	0.06	<b>0.82</b>	0.03
Org	Organic matter surface soil (%)	0.03	<b>0.37</b>	–0.21	<b>0.28</b>	<b>0.41</b>	–0.03
Sand A	Sand in surface soil (%)	0.03	<b>–0.25</b>	<b>–0.52</b>	–0.19	<b>–0.39</b>	–0.18
Sand B	Sand in subsoil (%)	0.03	–0.04	<b>–0.63</b>	–0.08	–0.15	–0.24
N	Estimated total extractable nitrogen (p.p.m.)	0.03	<b>0.42</b>	–0.16	0.25	<b>0.43</b>	–0.12
Density	Bulk density (mg m <sup>–3</sup> )	0.03	<b>–0.41</b>	0.09	<b>–0.34</b>	<b>–0.44</b>	–0.03
Elev	Digital Elevation Model coverage	0.02	–0.14	<b>0.50</b>	0.23		
Clay A	Clay in surface soil (%)	0.02	0.04	<b>0.50</b>	0.04		
pH	pH surface soil	0.02	–0.25	<b>0.26</b>	0.25	<b>–0.27</b>	<b>0.43</b>
P	Extractable phosphorus (p.p.m.)	0.02	–0.09	<b>–0.36</b>	<b>0.42</b>		
Ca	Calcium (p.p.m.)	0.02	–0.12	<b>–0.39</b>	<b>0.42</b>	–0.19	0.12
B	Boron (p.p.m.)	0.02	<b>–0.29</b>	0.07	<b>0.37</b>	<b>–0.33</b>	<b>0.42</b>
Mn	Manganese (p.p.m.)	0.02	0.04	<b>0.54</b>	<b>–0.34</b>		
Fe	Iron (p.p.m.)	0.01	–0.14	<b>0.29</b>	0.04	–0.20	0.14
Al	Aluminum (p.p.m.)	0.01				0.22	<b>–0.40</b>
Climate variable matrix							
Temp mean	Mean annual daily temperature (°C)	0.05	<b>0.79</b>	0.08	–0.13		
Temp max	Mean annual minimum temperature (°C)	0.05	<b>0.76</b>	0.15	–0.17		
Srad GS std	Standard deviation mean growing season shortwave radiation (MJ m <sup>–2</sup> day <sup>–1</sup> )	0.05	<b>–0.78</b>	–0.04	0.17	0.02	<b>0.50</b>
Srad std	Standard deviation mean annual shortwave radiation (MJ m <sup>–2</sup> day <sup>–1</sup> )	0.04	<b>–0.67</b>	0.05	<b>0.32</b>		
Prcp_ann	Mean total annual precipitation (cm)	0.03	<b>–0.50</b>	<b>–0.33</b>	<b>0.36</b>		
Srad	Mean daily shortwave radiation (MJ m <sup>–2</sup> day <sup>–1</sup> )	0.02	<b>0.38</b>	0.16	<b>–0.38</b>		
Prcp GS	Mean total growing season precipitation (cm)	0.02	<b>0.30</b>	<b>–0.27</b>	<b>0.45</b>	<b>0.47</b>	0.16
Prcp std	Standard deviation of mean total growing season precipitation (cm)	0.02	<b>–0.27</b>	<b>–0.36</b>	<b>0.36</b>	<b>0.48</b>	<b>0.33</b>

The selected edaphic variables had the highest eigenvalues, indicating partial correlations of specific variables from a redundancy analysis (RDA) including all other edaphic variables as constraining variables. The selection of relevant edaphic variables was repeated in the context of partial redundancy analysis (pRDA) with the effects of climate variables removed (covariables in the model). The same procedure was repeated for individual climatic variables. Eigenvalues indicate the conditional correlation of individual environmental variables. Correlation coefficients are listed for each set of environmental variables, for first the three constrained RDA axes and second the two constrained pRDA axes. Bold type indicates significant correlation between environmental variable and ordination axis scores ( $P < 0.05$ ).

were retained in this stepwise procedure in CANOCO ver. 4.5 (ter Braak & Šmilauer, 2002; Lepš & Šmilauer, 2003). The selection process was then repeated in the context of pRDA. Table 1 provides the list of variables retained following forward selection procedures for inclusion in subsequent RDA and pRDA ordinations.

To quantify the main and interaction effects on species composition of three explanatory matrices (environmental and spatial), we used a series of constrained and partial constrained canonical ordinations (RDAs and pRDAs; Borcard *et al.*, 1992; Økland & Eilersten, 1994; Økland, 2003). Despite recent warnings regarding eigenanalysis for analysis of community data (Faith *et al.*, 1987; McCune & Grace, 2002), we determined canonical ordinations to be appropriate for our study questions, given our intention to measure community structure related to measured environmental and spatial explanatory variables only (McCune & Grace, 2002). Further-

more, quantification of interactions of these variables is compatible with canonical variation partitioning (Legendre *et al.*, 2005). Recent literature supports numerical methods based on partitioning sums of squares of raw community data when beta-diversity across sites with fixed location is of interest (Legendre *et al.*, 2005; Tuomisto & Ruodolainen, 2006).

The null hypothesis tested was that of independence of species-response data from explanatory variable sets. Main effects of explanatory matrices were tested via Monte Carlo permutation tests. Fractions representing two- and three-way interactions, and the fraction of ‘unexplained’ variation, were calculated indirectly from simple and partial terms and were not statistically testable (Legendre & Legendre, 1998; Peres-Neto *et al.*, 2006). Variation partitioning and statistical tests were performed using the vegan community ecology package ver. 1.8 for R software (Oksanen *et al.*, 2007).

The total explained variance (TVE) of explanatory effects on species composition was partitioned into seven variation fractions representing main and interaction effects of explanatory variable matrices (see Venn diagram in Fig. 2). The TVE was calculated as the sum of constrained eigenvalues of variation fractions for main and interaction effects (Fig. 2). In addition, TVE represents the portion of 'total inertia' attributable to explanatory factors in the model (ter Braak & Šmilauer, 2002). Following the convention of Økland (1999), we present explained variance in terms of proportions of TVE only, rather than as proportions of total inertia.

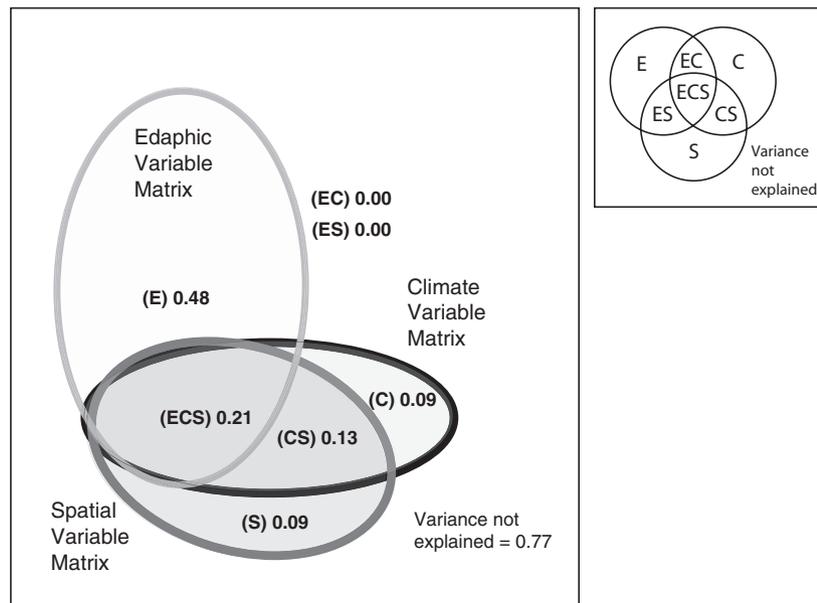
We also quantified correlations between individual explanatory variables and species-response data within the variation-partitioning model using RDA and pRDA canonical ordinations, Monte Carlo permutation tests, and simple Pearson's correlation analysis. We determined correlations of species variation with (1) edaphic, and (2) climatic variables, both with (RDA) and without (pRDA) using the remaining spatial and environmental variables as covariates. Significance of canonical axes in each of the constrained ordinations was tested via Monte Carlo randomization tests. Higher-order canonical axes were tested by including lower-order axes scores as covariables (Lepš & Šmilauer, 2003).

Simple correlations of individual explanatory variables with species data were presented as vector biplots (correlation

coefficient  $P < 0.05$ ). Vector angles and lengths correspond to the degree and strength of correlations. Significant correlations between canonical axes scores and species richness (number of species per 1000 m<sup>2</sup>) are similarly presented. All canonical ordinations, Monte Carlo randomization tests and correlation analyses were run in CANOCO ver. 4.5 (ter Braak & Šmilauer, 2002).

## RESULTS

A total of 1009 plant taxa were recorded from 271 vegetation plots (see Appendix S1 in Supporting Information). Following deletion of infrequent taxa, 670 species were retained for analysis. Mean species richness was 79 per 1000-m<sup>2</sup> plot, ranging from 29 to 168. The majority of species were herbs, of which most were forbs (Table 2). Herbaceous species also contributed most of the vegetation cover (Table 2). Grass and grass-like species of the families Poaceae, Cyperaceae and Juncaceae comprised the most plant cover, followed by woody and forb species. Both understorey and overstorey plant cover varied widely among plots, with basal area of trees ranging from 0 to 39.1 m<sup>2</sup> ha<sup>-1</sup> basal area. Specific community types and environmental features of vegetation samples are described in detail elsewhere (Carr, 2007).



**Figure 2** Venn diagrams of the variation partitioning model, with shaded portions representing variation in species data explained by main and interaction effects of three explanatory variable matrices. Each ellipse represents total variation explained by individual variable matrices (edaphic, climate and spatial). Area within all ellipses = total variance explained (TVE: 23% of total inertia). Shaded and labelled Venn diagram segments represent fractions of TVE and variation explained by main and interaction effects of explanatory variable matrices as derived from a series of constrained ordinations (see reference diagram top right for variation fraction labels). Fractions add up to 1.0. (E) = variation attributable to edaphic variables only, (C) = variation attributable to climatic variables only, (S) = variation attributable to spatial variables only, (CS) = interaction effect of climatic and spatial variables, (ECS) = interaction effect of edaphic, climatic and spatial variables. The interaction effect of edaphic and climatic (EC) and the interaction effect of edaphic and spatial (ES) fractions are negligible and are not displayed. Variance not explained = remaining fraction of total inertia not in TVE (0.77).

**Table 2** Summary data from 271 pineland samples in Florida, including means, standard deviation (SD), and minimum and maximum values for descriptive variables.

Variable	Mean	SD	Min	Max
BA (m <sup>2</sup> ha <sup>-1</sup> )	9.41	7.10	0.00	39.10
Total cover	139.73	46.62	53	357
Herb cover	89.91	41.85	11	257
Forb cover	33.93	20.30	3	114
Grass cover	55.97	31.06	3	182
Woody cover	49.82	36.85	0	235
Total richness	79.03	26.41	26	166
Herb richness	64.08	23.71	15	148
Forb richness	41.76	18.45	5	98
Grass richness	22.31	7.23	7	62
Woody richness	14.95	6.01	2	35

BA = total basal area (m<sup>2</sup> ha<sup>-1</sup>) of all woody stems > 1 cm d.b.h. Cover means are in m<sup>2</sup> per 100 m<sup>2</sup> derived from cover class mid-points for all species (total), herb species (herb), grass and grass-like species (grass), non-woody forb species (forb), and woody species (woody). Richness means are mean number of species per 1000-m<sup>2</sup> sample area.

### Variation-partitioning models

The largest fraction of TVE was explained by the edaphic variable matrix (69%; fractions E + ECS, Fig. 2) followed by effects of the climate and spatial variable matrices (43% of TVE each; fractions C + CS + ECS and S + CS + ECS, respectively). The main effect of the edaphic variable matrix comprised the largest single fraction (48%; fraction E). The three-way interaction with climatic and spatial variable matrices comprised the remainder of the edaphic matrix effect (21%; fraction ECS). In contrast, most of the TVE attributable to climatic and spatial variable matrices was partitioned as interactions between the two (13%; fraction CS) and in the

three-way interaction (21%, fraction ECS), with relatively little variance attributable to their main effects (9% each; fractions C and S). Total variation explained (TVE, the sum of all variation fractions) comprised 23% of total inertia (sum of eigenvalues = 0.727). TVE as a fraction of total inertia should be interpreted with caution, following the warning of Økland (1999; see Methods).

### Environmental explanatory variables

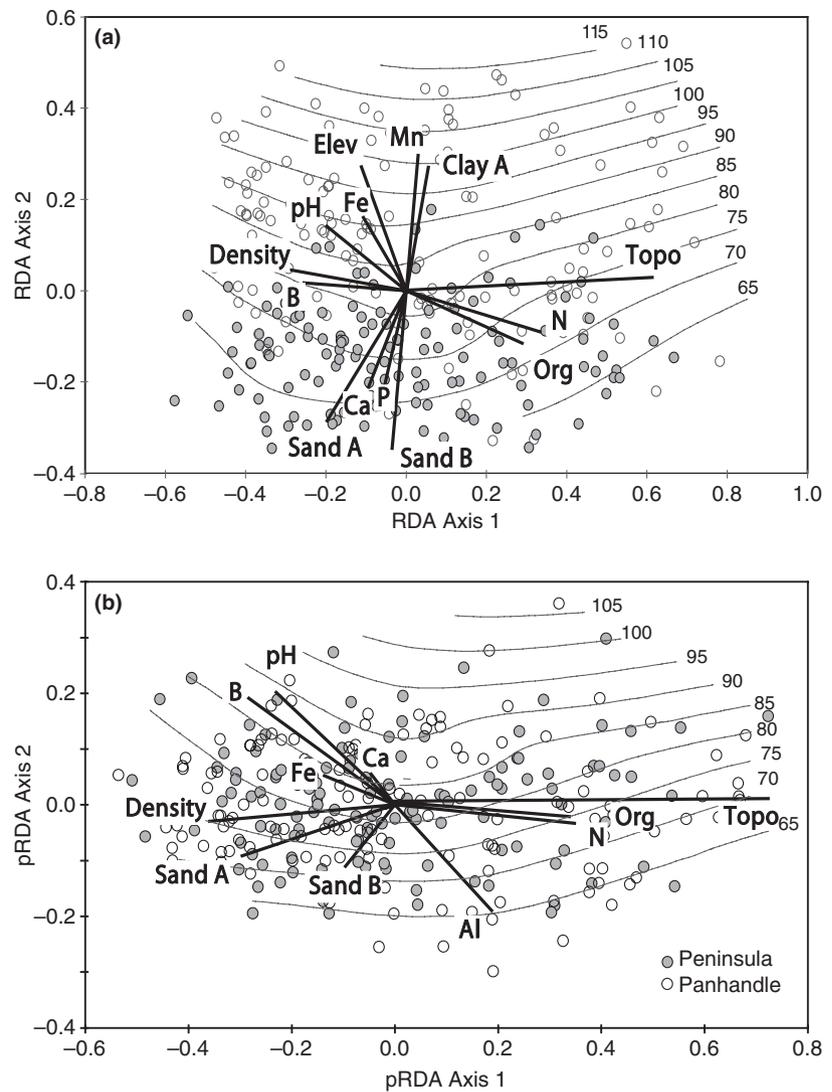
A four-dimensional RDA represents the main and interaction effects of the edaphic variable matrix on species composition (fractions E + ECS, Fig. 2). The first four axes account for 78.7% of the variation attributed to species–edaphic correlations (Table 3). All component variables of the edaphic variable matrix were significantly correlated with either RDA axis 1 or 2 ( $P < 0.05$ , Table 1; Fig. 3a). Axis 1 represents a complex gradient of topographic position (Topo), available nitrogen (N), organic matter (Org), boron (B), soil density (Density), percentage surface soil sand (Sand A) and pH (all  $r^2 > 0.2$ ,  $P < 0.05$ , Table 1; Fig. 3a). Axis 2 represents a combination of soil nutrient and texture properties (Sand A, Sand B, Clay A, P, Ca, B, Mn, Fe), absolute elevation (Elev) and pH (Table 1; Fig. 3a). Variables correlated with axis 2 clearly display edaphic differences between plots in the panhandle vs. peninsular regions, which correspond to a trend in species richness (Fig. 3a).

The removal of effects attributable to the climate and spatial variable matrices had little influence on the relationship between edaphic variables and species composition, as shown by the two-dimensional pRDA of the edaphic variable matrix (Table 1; Fig. 3b). This solution corresponds to fraction E of the variation-partitioning model (Fig. 2). Complexity of the pRDA ordination was reduced compared with the previous RDA constrained by the edaphic variable

Canonical model	Axis	Axis eigenvalue	Cumulative percentage spp-env	F	P
RDA edaphic variable matrix (14 variables)	1	0.095	45.1	26.67	0.002
	2	0.042	65.0	12.29	0.002
	3	0.019	73.4	5.73	0.002
	4	0.014	78.7	4.38	0.002
pRDA edaphic variable matrix (12 variables)	1	0.081	57.6	26.06	0.002
	2	0.012	66.2	3.83	0.004
RDA climate variable matrix (8 variables)	1	0.055	42.8	15.27	0.002
	2	0.028	64.4	7.97	0.002
	3	0.017	77.4	4.88	0.002
	4	0.010	85.2	2.93	0.006
pRDA climate variable matrix (4 variables)	1	0.010	39.6	3.60	0.002
	2	0.005	72.7	1.87	0.016

Cumulative percentage spp-env = variation attributed to explanatory variables as cumulative percentages of variation explained by constrained ordination axes. *F* and *P* are shown for each test of significance per canonical axis after removal of variation attributed to lower dimension axes.

**Table 3** Results for Monte Carlo tests of canonical axes for redundancy analysis (RDA) and partial redundancy analysis (pRDA) constrained ordinations of species data by explanatory environmental variable matrices.



**Figure 3** Biplots of ordinations of species data constrained by edaphic variables. (a) Axes 1 vs. 2 of redundancy analysis (RDA) constrained by the edaphic variable matrix with no covariables (corresponding to fraction E + ECS in Fig. 2). Contours indicate significant correlation of species richness with axis 2 ( $r^2 = 0.23$ ). (b) Axes 1 vs. 2 of partial redundancy analysis (pRDA) constrained by the edaphic variable matrix, and including the climate and spatial variable matrices as covariables (corresponding to fraction E in Fig. 2). Eigenvalues, percentage of variance explained and significance values for all ordination axes (four for RDA and two for pRDA with edaphic variables) are listed in Table 3. Vectors display correlations of individual edaphic variables with ordination axes; variable definitions and correlation coefficients are listed in Table 1. Symbols denote plot locations (panhandle vs. peninsula).

matrix. The first two pRDA canonical axes were related to species variation and represented 66.2% of variation attributed to species–edaphic correlations (Table 3). Furthermore, gradients of soil texture and nutrients associated with geographical region (Florida panhandle vs. peninsula) were absent in the pRDA solution.

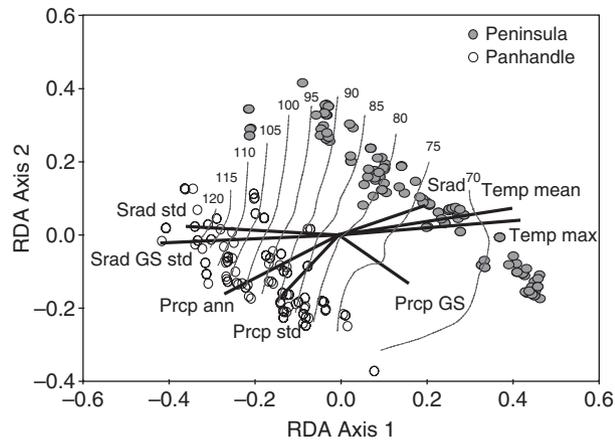
The RDA ordination constrained by the climate variable matrix (fractions C + CS + ECS, Fig. 2) illustrates dramatic geographical separation of plots (Fig. 4). The first four canonical axes were significantly related to species variation and accounted for 85.2% of the variation attributed to species–climate correlations (Table 3). Axis 1 (Fig. 4) was correlated with eight variables representing variations in temperature, daily radiation and precipitation, these variables being regionally segregated between peninsular and panhandle plots. Species richness was negatively correlated with variables represented by axis 1 and was highest for panhandle plots. Axis 2 was related to the standard deviation of annual and growing-season mean precipitation (Fig. 4). Likewise, axis 3 (not shown) represents a gradient in precipitation (annual,

growing season and standard deviation) and radiation (daily mean and standard deviation, Table 1).

The effect of the climate variable matrix following the removal of edaphic and spatial variable matrix variation was small, and is represented by a simple ordination solution (Table 1). The pRDA of climate variable matrix ‘pure’ effects represents fraction C of the variation-partitioning model (Fig. 2). Only three climate variables were included in this canonical solution, and these were significantly correlated with axis 1 or 2 (mean and standard deviation of growing season precipitation, standard deviation of shortwave radiation, Table 1). Separation of plots by panhandle vs. peninsular regions was not evident, but species richness was negatively correlated with axis 1 (biplot not shown).

**DISCUSSION**

Our empirically derived model shows the influence of edaphic conditions, climate, spatial distribution, and their joint effects on plant species composition and cover in pyrogenic grass-



**Figure 4** Biplot of redundancy analysis (RDA axis 1 vs. axis 2) of species data constrained by the climate variable matrix (corresponding to fraction C + CS + ECS in Fig. 2). Symbols indicate panhandle vs. peninsular plots. Variable definitions and correlation coefficients are listed in Table 1. Eigenvalues, percentage of variance explained and significance values for all four ordination axes are listed in Table 3. Contours display significant correlation of species richness with first canonical axes ( $r^2 = 0.35$ ).

lands of Florida. The results support our hypothesis that these factors act simultaneously at a wide range of spatial scales, from local topographic gradients to an area spanning several 100 km. It must be noted that the model explained a relatively small portion of total variance (23%). However, percentages of TVE in variation-partitioning models of species data are typically small, and these results are not unusual (Økland & Eilersten, 1994; Økland, 1999). We present the following specific interpretations based on the variation explained in our model.

Our first interpretation is that edaphic conditions have the strongest influence on species composition and richness, and are most prominent at local scales. Almost half of TVE was uniquely attributable to non-spatially structured (local) edaphic variables. Given that topographic position was the strongest single predictor of species composition, this gradient is also likely to represent variation in unmeasured edaphic variables (e.g. aeration, water stress, microbial activity). Similar results have been noted elsewhere in the Southeastern Coastal Plain (Bridges & Orzell, 1989; Kirkman *et al.*, 2001; Drewa & Platt, 2002). Topographic position, as a proxy for a complex gradient, explains much of the variation in species composition, but not in species richness.

Our model is consistent with other studies that have recognized nitrogen as a limiting resource in temperate grasslands, where nitrogen availability is related to primary productivity and diversity (Seastedt *et al.*, 1991; but cf. Turner *et al.*, 1997). The relationship between nitrogen and soil moisture in our study, as found elsewhere (Vitousek, 1982), can be attributed to the accumulation of organic matter in wet soils (Brady & Weil, 2000). However, this observation contradicts other more localized studies in the Southeastern

Coastal Plain (Foster & Gross, 1998; Wilson *et al.*, 1999; Kirkman *et al.*, 2001).

Our second interpretation is that variation in grassland species composition is regionally segregated and corresponds to regional variation in soil texture, soil nutrient availability and climate. Spatial trends in compositional variation were strongly segregated between the Florida panhandle and peninsula, which in turn corresponded to variation in climate variables. The peninsula is warmer and receives less annual rainfall, but more rain during the growing season (Chen & Gerber, 1990). About half of spatially structured variation in species composition was also related to regional differences in soil texture, as documented elsewhere in the Coastal Plain (Peet & Allard, 1993; Dilustro *et al.*, 2002). Phosphorus and calcium were more abundant in peninsular soils related to the carbonate Florida platform and the abundance of phosphorite in Pleistocene sediments (Puri & Vernon, 1964; Brown *et al.*, 1990).

Our third interpretation is that spatially related compositional variation independent of environmental determinants is attributed to biogeographical and evolutionary history. This interpretation is based on the small (9% of TVE) but measurable contribution of pure spatial effects on species composition in the variation-partitioning model (Ricklefs, 1987). Furthermore, almost half of total TVE was spatially structured, presenting the possibility that historical effects are confounded with environmental patterns, especially those separating the geographically and historically distinct Florida panhandle and peninsular regions. These regions represent different sources and timing of sediment deposition and sea-level fluctuations (Randazzo & Jones, 1997; Myers, 2000), and were apparently separated by the 'Suwannee Strait' between 12 and 30 Ma (Hull, 1962; Myers, 2000). The boundary between these two regions marks the southern extent of many plant species (Carr, 2007) and contributes strongly to the regionally restricted distribution of nearly a quarter of the plant taxa included in our data set.

The relative contribution of pure spatial effects to species variation was small compared with other studies of local to meso-scale community variation (10–1000 km<sup>2</sup>: Wiser *et al.*, 1996; Cushman & McGarigal, 2002; Dilustro *et al.*, 2002; Svenning & Skov, 2005; Laughlin & Abella, 2007). This is surprising, given the large extent of our study (c. 137,000 km<sup>2</sup>), and suggests the relative importance of environmental over historical determinants of community structure in our study region. One caveat is that interpretation of 'unexplained' variation is difficult in the light of problems related to canonical ordination methods (difficulties in separating actual variation from polynomial distortions; Økland, 1999). In addition, the signature of smaller-scale historical processes may have been underdetected in our model of coarse-scale spatial trends (Borcard *et al.*, 2004).

Unmeasured anthropogenic alterations to the natural landscape may contribute to community variation in our model. Population levels and associated land-management impacts of pre-Columbian Native Americans on the land-

scape are poorly understood. It is generally agreed that their most wide-ranging potential impact on the south-eastern US landscape was through the frequent use of fire (Hammett, 1992). However, considerable evidence suggests that Florida grasslands not recently burned by humans were frequently burned through lightning-ignited fires (Robbins & Myers, 1992; Huffman *et al.*, 2004). Burning by Native Americans may have altered the season of fires, where applied, but research shows that season of burning primarily affects relative abundance of woody species, with little effect on herbaceous species composition (Robbins & Myers, 1992; Streng *et al.*, 1993). Soil disturbance through agriculture probably had a stronger local effect on vegetation, but evidence to date suggests that Native American agriculture occurred as relatively small patches within the larger forested landscape (Hammett, 1992; Foster *et al.*, 2004), except in portions of the Tallahassee Red Hills (Paisely, 1989). Post-Columbian human influences, from grazing, logging and alteration of fire regime, may be spatially related to plant community composition. The Florida panhandle was settled earlier, and settlers of this region were first to abandon cattle ranching and associated frequent burning (Myers & Ewel, 1990; Frost, 1993; Bridges, 2006). However, a longer era of fire suppression and related habitat degradation would predict lower species richness of panhandle native grasslands, contrary to our results. It is possible that a significant amount of the unexplained variance in our model originates from the considerable historical variation among landowners in fire application, grazing and timber removal (Mealor & Prunty, 1976; Hart, 1979). However, we conclude that such influences are likely to have a relatively small influence on the broader edaphic and spatial patterns described in this study.

Our final interpretation is that gradients in community composition are related to species richness and are apparent at local and regional scales. The richness gradient is most obvious at the regional scale, as panhandle plots are consistently richer than their peninsular counterparts with similar soil moisture and fertility conditions. Regional differences in local species richness are well documented and may be related to the 'species pool' effect of available propagules. The species pool effect is shaped by processes operating at multiple spatial and temporal scales (Zobel, 1997; Collins *et al.*, 2002). Some studies suggest that regional variation in pineland species richness is related to gradients of local environmental heterogeneity (Grace *et al.*, 2000; Kirkman *et al.*, 2001; Weiher *et al.*, 2004).

Based on comparison among canonical ordinations with and without spatial trends included, the species-richness gradient associated with local edaphic variables and topographic position appears to be independent of spatially structured variation. This spatially independent richness gradient is weakly associated with soil pH, available nutrients (N, Ca) and soil texture. This finding is consistent with other studies documenting local species-richness gradients associated with soil pH and calcium (Partel, 2002; Palmer *et al.*, 2003; Peet *et al.*, 2003), suggesting either larger pools of species

adapted to basic soils (regional 'species pool' effect) or more favourable local conditions for plant colonization and growth (local environmental effect). Alternatively, soil reaction is a proxy variable for other unmeasured causative factors, such as competition for light or space (Grace *et al.*, 2000; Weiher *et al.*, 2004). For example, density of woody biomass increases more rapidly during fire-free intervals on more fertile sites, which hinders understorey herbaceous species richness via competition for light and other resources (Streng *et al.*, 1993; Grace & Pugsek, 1997; Weiher *et al.*, 2004).

In summary, our interpretations derived from our model of floristic variation in native fire-dependent prairies, savannas and woodlands in Florida support the hypothesis of both local and regional influences on plant community structure and diversity. Local topographic gradients and associated edaphic variables have a strong influence on local community composition, which is largely orthogonal to regional edaphic and climatic relationships. However, spatially structured environmental variables and pure spatial effects also influence species variation. Species composition consistently differs between panhandle and peninsular sites with similar environmental conditions, suggesting historical regional divergence of species pools (Ricklefs, 1987; Zobel, 1997). Our model contributes to an understanding of the relative contributions of environmental and historical factors on plant community composition and structure at widely varying spatial scales.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Locations of sample plots and sites in Florida.

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## BIOSKETCHES

**Susan Carr** has a BSc from the University of Florida and an MSc from Louisiana State University. She completed her PhD in Wildlife Ecology and Conservation at the University of Florida in 2007. Her research experience and interests involve the description and restoration of pine savannas and grasslands. She currently lives in Denver, Colorado.

**Kevin Robertson** received his BSc in Botany from Louisiana State University. He received his PhD in Plant Biology at the University of Illinois, where he studied primary forest succession in relation to the geomorphology of meandering rivers of the south-eastern USA. He is currently the Fire Ecology Research Scientist at Tall Timbers Research Station, where he studies the plant community ecology of south-eastern US pine ecosystems, fire regime effects on plant communities, soils and fire behaviour, and the natural history of the Gulf Coastal Plain. He also provides extension and education on the use of prescribed burning in fire-dependent ecosystems of the south-eastern USA.

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