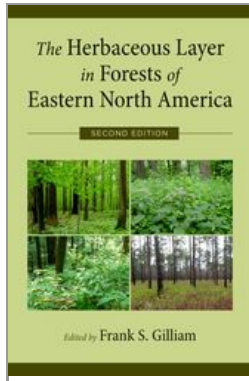


University Press Scholarship Online

Oxford Scholarship Online



The Herbaceous Layer in Forests of Eastern North America

Frank Gilliam

Print publication date: 2014

Print ISBN-13: 9780199837656

Published to Oxford Scholarship Online: May 2015

DOI: 10.1093/acprof:osobl/9780199837656.001.0001

Herbaceous Layer Species Richness of Southeastern Forests and Woodlands

Patterns and Causes

Robert K. Peet

Kyle A. Palmquist

Samantha M. Tessel

DOI: 10.1093/acprof:osobl/9780199837656.003.0010

[–] Abstract and Keywords

This chapter examines species richness patterns in the herbaceous layer vegetation of forests and woodlands of southeastern North America. It demonstrates the changing importance of various drivers of species richness across environmental and geographic gradients and across vegetation types, and shows how the relative importance of those drivers varies with scale of observation. The most important processes structuring species diversity patterns in southeastern forests and woodlands appear to be cation availability (environmental favorableness), disturbance (flooding, fire, grazing), mass effects, and the relative size of the species pool.

Herbaceous Layer Species Richness of Southeastern Forests and Woodlands

Keywords: herbaceous layer diversity, herb layer, vegetation, woodlands, species richness, Blue Ridge Mountains, Piedmont, Coastal Plain, southeastern North America

Numerous factors have been shown or asserted to influence the species richness of natural plant communities. Species richness has variously been suggested to be high where propagule supply is high, competition is low, disturbance is intermediate or low, or soils are of intermediate to high fertility (e.g., Grime 1973; Huston 1979, 1994; Shmida and Wilson 1985). However, attempts to test the generality of these broad hypotheses have generally met with inconclusive or inconsistent results (e.g., Adler et al. 2011; Willig 2011). Part of the challenge is that the dominant patterns and processes vary with environmental and ecological context, as well as spatial scale. Moreover, the dominant patterns and processes may be system-specific. In this chapter, we explore the patterns in herbaceous layer species richness of forests and woodlands of southeastern North America, identify their likely drivers, and examine how these fit into a global context.

Numerous patterns have been reported for understory species richness in southeastern forests and woodlands. The upland forests of the southern Appalachian Mountains are famous for their herb-rich cove forests. Species richness in these systems has been widely reported to vary with elevation and topographic position (the work of Whittaker [1956] being best known), but subsequent work (e.g., Newell and Peet 1998; Newell et al. 1999; Peet et al. 2003; Wheeler 2011) has added a third gradient of increasing species richness with increasing soil nutrient status. The fire-maintained **(p.256)** pine woodlands of the southeastern Coastal Plain, extending from southeastern Virginia south to southern Florida and west to eastern Texas, look superficially monotonous with mostly one tree species and a grass-dominated herbaceous layer, but previous studies have shown small-scale (1 m²) and plot-scale (1,000 m²) species richness to range from trivially low to among the highest reported for temperate North America, despite the generally infertile soils and lack of topographic diversity (Walker and Peet 1983; Peet 2006). Piedmont forests occupy an ancient landscape of highly weathered soils that is widely ignored by ecologists because it lacks the charismatic taxa and dramatic topography that characterize the Coastal Plain and Blue Ridge Mountains respectively. The herbaceous layer in these forests and woodlands exhibits a striking signature of underlying rock type evidenced by species richness showing a strong positive correlation with soil cation content and basic parent material (Peet and Christensen 1980b, 1988). Finally, riparian forests and woodlands are quite different from upland systems of the Southeast due to the important role of water in dispersal of propagules by flowing water, episodic flooding, and redistribution and supply of soil particles and nutrients. Species richness in these systems at the 1,000 m² scale has been reported to range from very low in chronically flooded swamps to among the highest levels reported for temperate North America in scour areas along Blue Ridge Mountain rivers (175 species / 1000 m²; Brown and Peet 2003).

Previous reports of specific patterns of species richness largely result from independent and spatially isolated studies that largely fail to address variation in these patterns across the landscape and region, or their broader generality. In addition, these studies have been conducted at a range of different spatial scales, leaving uncertainty as to whether

different species richness patterns might have been observed under different scales of observation. Various authors have argued that species richness should be studied in the context of multiple potential determinants and across a range of spatial scales (e.g., Shmida and Wilson 1985; Stohlgren et al. 1995; Brown et al. 2007; Dengler 2009). Giladi et al. (2011) have gone as far as to conclude that species richness is determined by the combined effect of multiple determinants acting at multiple scales and that conclusions from studies that do not employ multi-scale sampling across the range of potential drivers are restricted and likely misleading.

We draw on a large, multi-scale plot database to explore patterns of herbaceous layer diversity and the processes likely maintaining those patterns across contrasting sets of vegetation types. We use data from a set of > 5,000 vegetation plots collected across the Southeast and sampled at multiple scales (0.01 m² to 1,000 m²) following the Carolina Vegetation Survey (CVS) protocol (Peet et al. 1998; Peet et al. 2012). These plots have full floristic inventories at each scale and thus capture the diversity and composition of the herbaceous layer. This is currently the largest vegetation plot dataset in the world that spans six orders of magnitude in subplot size.

We compare the results from four cohesive subsets of our data to provide greater clarity and synthesize general patterns in richness in southeastern forests and woodlands. The forests and woodlands of southeastern North America are often broken into subsets based on composition, history, and ecology. For our study area in the Carolinas, and more broadly across the Southeast, Braun (1950) recognized three major forest regions of the Eastern Deciduous Forest Formation corresponding to the southern Appalachian Mountains (Oak, Chestnut Forest), the Piedmont (Oak, Pine Forest), and the Coastal Plain (Southeastern Evergreen Forest). The EPA level-3 Ecoregion Map (fig. 10.1; Omernik 1987; USEPA 2011) makes similar divisions recognizing the **(p.257)**

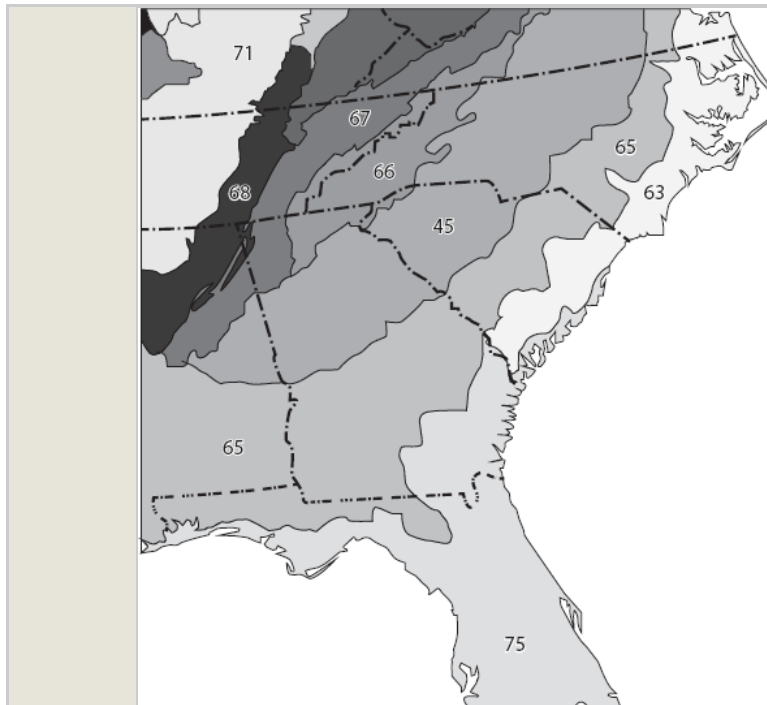


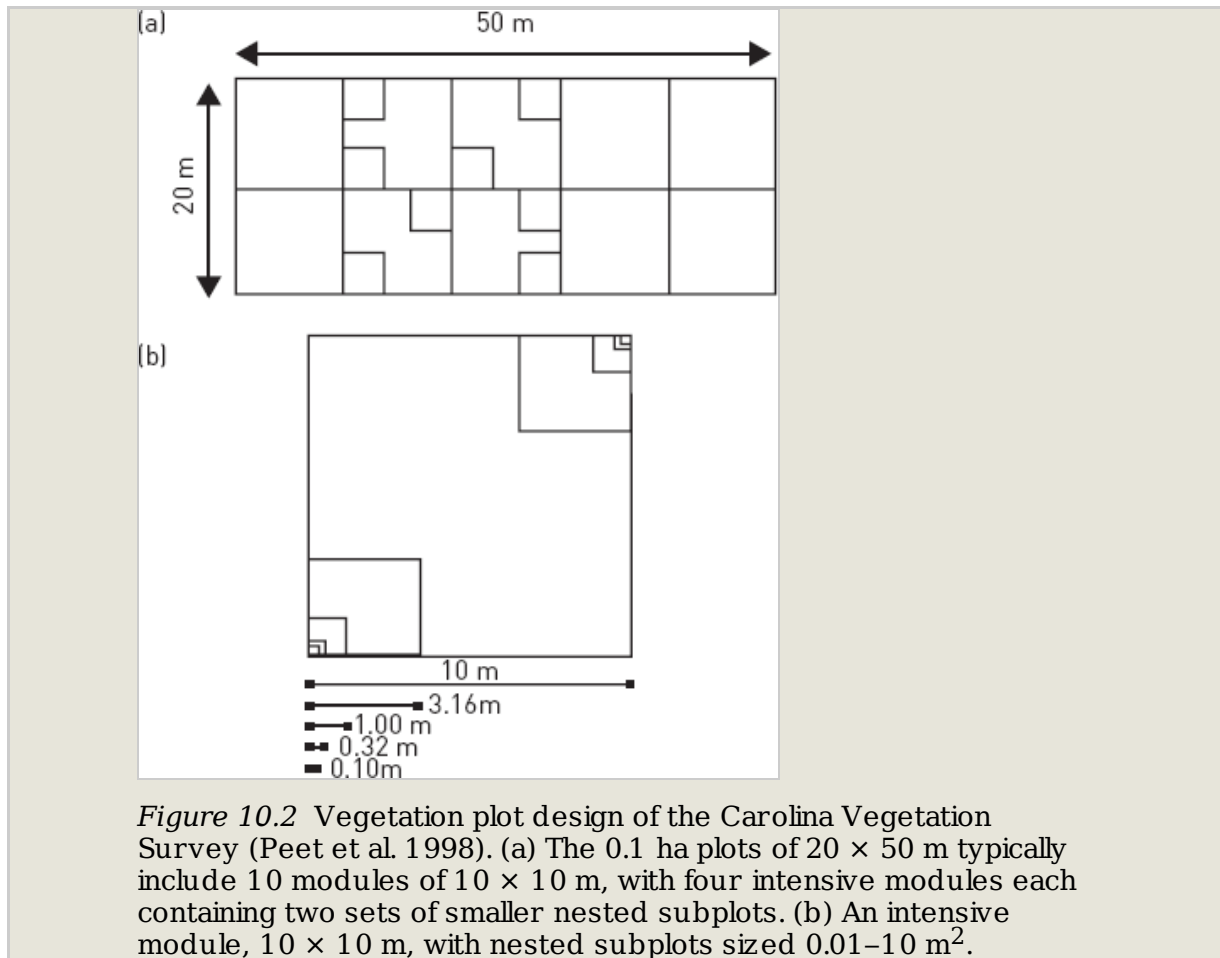
Figure 10.1 Ecoregions of the southeastern United States (U.S. EPA 2011). The three focal regions for this chapter are the Blue Ridge Mountains (Ecoregion 66), the Piedmont (Ecoregion 45), and the Southeastern Coastal Plain (Ecoregion 63: Middle Atlantic Coastal Plain, 65 Southeastern Plains, and 75 Southern Coastal Plain).

Blue Ridge Mountains, the Piedmont, and the Coastal Plain, albeit with the Coastal Plain divided into three sections. Here we recognize the Blue Ridge Mountains, the Piedmont, and the Coastal Plain as regions with distinct flora, climate, and geology, suggesting that patterns of plot-scale species richness might well differ among regions, and we examine their patterns and drivers separately. In addition, we look at brown-water riparian forests of North Carolina as a fourth focal vegetation type likely dominated by different ecological processes than upland forests and woodlands.

Data and Methods

In this chapter, we identify patterns in species richness in the herbaceous layer vegetation of forests and woodlands of southeastern North America. We define forests and woodlands as areas with greater than 10 percent cover of trees, consistent with the definitions used by F.A.O. (2001), the U.S. Forest Service Forest Inventory and Analysis Program (Gray et al. 2012), and the U.S. National Vegetation Classification (U.S. FGDC 2008). We include in our analysis all vascular plant species present in the herbaceous layer, regardless of whether they are herbaceous or woody (chapter 1, this volume). We define species richness as the count of all vascular plant species rooted in a quadrat of fixed area.

(p.258)



We use vegetation plot data drawn from the CVS database (Peet et al. 2012) that comply with the CVS protocol (Peet et al. 1998) and have intensive sampling down to 0.01 m². The standard plot (fig. 10.2) is 1,000 m² and consists of ten 10 × 10 m modules arranged as a 20 × 50 m rectangle. Typically, a square of four contiguous modules is designated as containing intensive modules, and each intensive module contains two sets of nested square subplots with areas of 0.01, 0.1, 1, and 10 m². Thus, in a typical plot we have eight species counts at scales of 0.01 m², 0.1 m², 1 m², and 10 m²; four counts at 100 m²; and one count each at 400 m² and 1,000 m². Occasionally, when there is insufficient homogeneous vegetation for a 1,000 m² plot, fewer modules are recorded. Thus, while our analysis is organized around seven plot sizes, occasionally the two largest sizes are not available. When only one intensive module is recorded, four sets of nested quadrats are recorded to assure that no plot has fewer than four sets of subplots less than or equal to 10 m². This is important because small plots are much more sensitive to chance variation in species occurrences. In total, we initially examined 5,051 CVS plots, of which 2,703 contained the full set of seven plot sizes. Our final analysis employs four subsets of plots spread across a total of 3,264 plots drawn from across North Carolina, South Carolina, Georgia, and Florida.

In addition to information on species composition across a range of spatial scales, CVS plot data include location, slope, aspect, elevation, and topographic position (including for the

Blue Ridge Mountain dataset McNab's terrain shape index [TSI] and land form index [LFI]; McNab 1989, 1993). Soil samples were collected from the top 10 cm of mineral soil in the center of each intensively sampled module. Total cation exchange capacity (meq/100g), pH, percent humic matter, estimated N release, easily extractable P, exchangeable cations (Ca, Mg, K, Na in ppm), percent base saturation, **(p.259)** extractable micronutrients (B, Fe, Mn, Cu, Zn, Al in ppm), soluble sulfur, and bulk density values were determined for each subsample. Extractions were carried out using the Mehlich III method (Mehlich 1984), and percent humic matter was determined by loss on ignition. Texture analysis employed the Bouyoucos hydrometer method (Patrick 1958) with a composite sample of the four subsamples from each plot. All soil values for a plot (typically four) were averaged to obtain a single value per plot.

Many of the vegetation plots in the CVS database were placed subjectively to represent a particular place or range of composition variation. Ideally, all plots would be selected objectively, but this is not practical when trying to capture more than the most common vegetation types. Roleček et al. (2007) have explained that while simple random sampling, systematic sampling, and stratified random sampling better meet certain statistical assumptions, preferential sampling yields datasets that cover a broader range of vegetation variability and allow inclusion of rare types that might otherwise be missed. Michalcová et al. (2011) further considered the problems inherent in using large plot databases wherein many of the plots are likely to represent preferential sampling. In their analysis, they found that preferentially sampled datasets contain more endangered species and have higher beta diversity, whereas estimates of species richness are not consistently different between preferentially and stratified randomly sampled datasets.

Vegetation plot databases often contain unbalanced representations of the range of compositional variation encountered in nature. In the CVS database, a few common vegetation types are represented by nearly 200 plots, whereas uncommon types are in some cases represented by just a few plots. Care must be taken not to allow the attributes of the most heavily represented types to dominate the analysis. Lengyel et al. (2011) have proposed that plot databases be sampled to provide even coverage in geographically broad studies. Knollová et al. (2005) proposed several methods for stratified resampling of vegetation databases where some of their methods divide the database into groups according to geography or according to environmental variables expected to influence between-plot variation in species composition. As a way of comparing across a broad range of communities with uneven sampling, we summarize our data as community types recognized at the association level in the U.S. National Vegetation Classification (NVC). Nationally, approximately 6,500 associations are currently recognized (see <http://usnvc.org>), and the CVS database contains plots assigned to over 500 NVC types that occur in the Carolinas. The types recognized in the NVC have been defined to be roughly equivalent in terms of their distinctiveness in composition and setting (Jennings et al. 2009). By summarizing plot data by NVC types, we minimize the problem of uneven sample size. For riparian vegetation, in some cases, we use new community classifications designed to replace the current NVC types, but which are not yet incorporated in the system (Brown 2002 for the Blue Ridge Mountains, Matthews et

al. 2011 for the Piedmont, and Faestel 2012 in part for the Coastal Plain).

To determine the important drivers that structure plant communities in each of the four focal areas, we conducted principle components analysis (PCA) on 28 environmental variables: soil nutrients (N, P, Al, B, Ca, Cu, Fe, H, K, Mg, Mn, Na, S, Zn), bulk density, aspect, slope, elevation, base saturation, cation exchange capacity, pH, Ca/Mg ratio, soil texture (% sand, silt, clay), organic matter, latitude, and longitude. Also included for the Blue Ridge Mountains analysis were LFI and TSI. Each environmental variable was averaged across all plots within each NVC type prior to analysis. PCA was used because many of the pertinent soil variables were strongly correlated (**p.260**) and were proxies for larger potential drivers of richness (e.g., nutrient and water availability). Prior to analysis, soil nutrient content variables measured in parts per million (ppm) were log-transformed to normalize the data. After we ran PCA on the environmental matrix, we examined which axes explained the most variation in species richness across the various scales of observation. Pearson correlations were calculated to assess the degree to which PCA axes represented the observed environmental variables.

Median richness values were calculated at seven spatial scales (.01 m², 0.1 m², 1 m², 10 m², 100 m², 400 m², and 1,000 m²) for each community type. We used Pearson correlations to identify the strength and direction of influence of all potential environmental drivers of species richness and the latent variables represented by PCA axes. Linear models were used to calculate variation in species richness explained by environmental variables or PCA axes, and to test the significance of these relationships. To visualize relationships between the important PCA axes and richness most effectively, we log₂ transformed richness. For some vegetation associations, the median richness at .01 m² was 0; therefore, to avoid undefined values when taking the log₂ of 0, we added 1 to median richness values across all spatial scales. To examine latitudinal patterns of species richness in Coastal Plain pine woodlands, we extracted richness values at 1,000 m² for each plot and tabulated a mean richness value for each of five major longleaf pine vegetation types recognized in Peet 2006 (see fig. 10.7).

Regional Patterns in Species Diversity

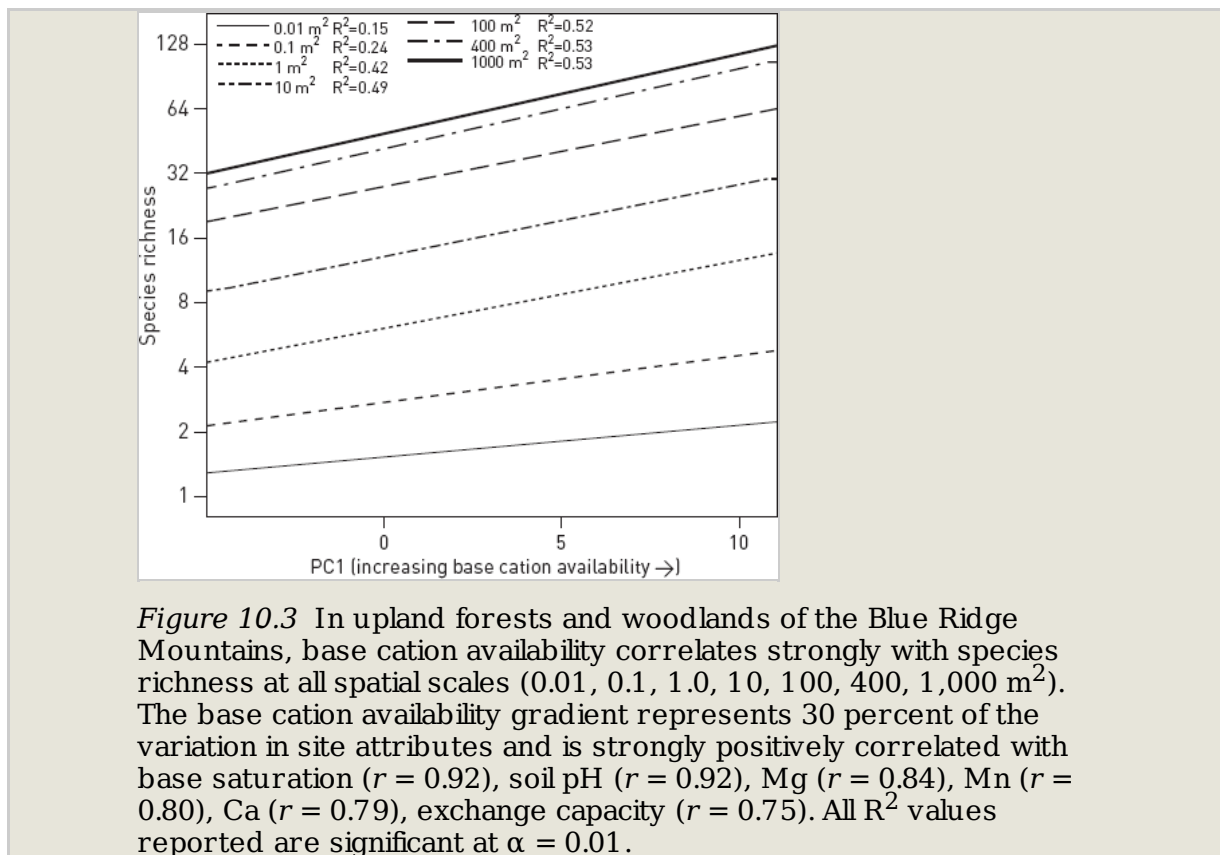
Local studies have reported sometimes similar and sometimes conflicting patterns in herbaceous layer species diversity. Here we discuss richness across four specific subsets of southeastern North American vegetation types.

Upland Forests and Woodlands of the Blue Ridge Mountains

The subset of data representing upland forests and woodlands of the Blue Ridge Mountains contains 1,184 vegetation plots distributed across 56 NVC associations in North Carolina and South Carolina. The first PCA axis of the site variables associated with those 56 associations was strongly correlated with pH ($r = 0.92$), percent base saturation (0.92), cation exchange capacity (0.75), calcium (0.79), magnesium (0.84), and manganese (0.80). This gradient, which we refer to as base cation availability, shows a strong positive correlation with species richness at all spatial scales from 0.01 to 1,000 m² (fig. 10.3), though the strength of the signal drops off below 1 m² where larger plant size damps the

increase in species richness on rich sites (see Fridley et al. 2004).

The importance of base cation availability for prediction of species richness in this region has been underappreciated in the broader literature and is not evident in Whittaker's (1956) seminal work on the Great Smoky Mountains where he described elevation and topographic position as predictors of richness. However, subsequent work (e.g., Newell et al. 1999; Ulrey 2002; Peet et al. 2003; Wheeler 2011) has shown that when Blue Ridge Mountain forests are examined over a broad geographic extent, rather than from just one study area where parent rock can be relatively homogeneous, pH and soil cation availability are strong predictors of richness. The extent to which this pattern is a consequence of higher resource availability on high-base sites **(p.261)**



versus a larger species pool size (*sensu* Eriksson 1993) is difficult to assess, though a region-wide analysis for the Blue Ridge Mountains by Peet et al. (2003) showed high pH sites to have generally larger species pools.

Species richness did not show a strong relationship to PCA axes other than axis 1, with the exception that there is a negative correlation at the two smallest plot sizes (0.01 and 0.1 m²; $r = -0.51$ and -0.40 respectively) with axis 3 (PC3), but this relationship fades with increasing plot size and reverses to become modestly positive at large scales. PC3 is correlated with a broad range of variables including terrain shape index ($r = 0.51$), land form index ($r = 0.49$), and elevation ($r = -0.46$), indicating a connection to topographic position. The lower richness at small scales in topographic lows is likely a consequence of the larger mean plant size in these sites, limiting the number of species that can be

packed into a very small area (Fridley et al. 2004).

The richest herb communities of the Blue Ridge Mountain forests and woodlands are often reported to occur in coves and valley bottoms, though not all coves and valley bottoms have high species richness. One reason Whittaker's (1956) interpretation of species richness in the Great Smoky Mountain forests did not include soil cations was likely because he examined compositional variation relative to a complex topographic position gradient that he referred to as "moisture." As soils weather, water-soluble nutrients tend to be transported downhill, accumulating in coves and valleys. Thus, Whittaker's moisture gradient combines a range of variables including temperature, moisture availability, and cation availability. Interestingly, we found that some of the most species-rich herbaceous layers are found in areas of moderately high base cation availability, but in an intermediate topographic position. As a case study, rich oak-hickory communities of mid-slopes are generally more species rich than the rich (p.262) cove community types found in topographic lows, despite a similar pool of relatively high pH herb species (Schafale 2012). This may be attributed to asymmetric competition for light by species in the lush herb layer of rich coves with high soil moisture, whereas the herb cover is lower and richness higher on the somewhat higher and drier mid-slope oak forests.

We attempted to separate the contributions of soil cation availability from topographic position by graphing richness simultaneously against base saturation (representing cation availability) and McNab's Land Form Index (mean percent slope of an azimuth to the horizon), which ranges from zero at a local topographic high to a high value deep in a cove. fig. 10.4 shows the results for 1 m² and 1,000 m² plots. Species number is strongly correlated with base saturation as already described, the signal being slightly stronger at 1,000m². However, the higher richness values at 1,000 m² usually occur on sites with high LFI values (i.e., coves and valley bottoms), but not all sites with high LFI values have high richness. This reflects the very low diversity that can occur in low base-availability coves ("acidic coves" *sensu* Schafale 2012) dominated by evergreen shrubs such as great laurel (*Rhododendron maximum* L.), which can limit herb development through both decreased light availability (Wheeler 2011) and allelopathic impacts (Nilsen et al. 1999). The base cation signal is not as strong at 1 m² because of the limitation of how many lush herbs can fit into a small plot.

Although elevation is known to constitute a strong environmental gradient that accounts for much of the variation in species composition in the southern Appalachian Mountains (e.g., Whittaker 1956; Newell et al. 1999) and is often correlated with soil pH and nutrients, it is only a weak determinant of species richness in our dataset (fig. 10.5). Elevation shows a weak negative relationship with species richness at large scales and a weak positive (though non-significant) relationship at small scales. The negative correlation with elevation at large scales may result from mass effects (Shmida and Wilson 1985) because at low elevations, multiple habitats are in close proximity, and propagules from plants in neighboring habitats frequently arrive and survive short periods in suboptimal community types (see Grime 1998), whereas the restricted area and isolation of higher

elevation forests results in a more limited species pool (sensu Eriksson 1993). The small-scale, weak positive relationship may result

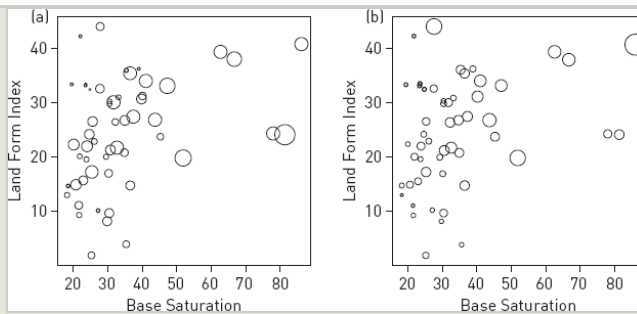


Figure 10.4 Species richness (scaled with the size of the circle) relative to base saturation and topographic position (Land Form Index sensu McNab 1989, high levels being in more sheltered locations) for (a) 1 m², and (b) 1,000 m² plots. Maximum richness values shown are 137 species for 1,000m² and 13 species for 1 m².

(p.263)

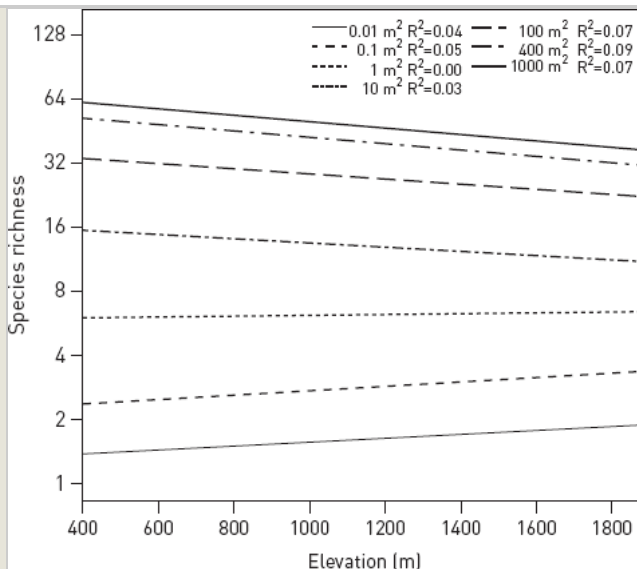


Figure 10.5 Elevation in Blue Ridge Mountain upland forests and woodlands is weakly negatively correlated with species richness at large scales, but weakly positively correlated at small scales. R² values for scales 100–1,000 m² are significant at $\alpha = 0.05$.

from a fairly high number of individuals per unit area in the generally mesic habitats of higher elevation forests, whereas the number of individuals in lower elevation forests varies more strongly as a function of topographic position.

Another factor known to significantly influence species richness in Blue Ridge Mountain forests and woodlands is fire (chapter 14, this volume). However, only limited data were available in our dataset for recently burned sites. Oak forests of eastern North America are widely appreciated to have developed in the context of chronic fire (e.g., Abrams 1992), and there are frequent reports in the literature of increased species richness with frequent fire, especially at small scales (e.g., Hutchinson et al. 2005). In two cases, Blue

Ridge Mountain forests previously sampled using the CVS protocol have been resampled after fire. In 2003, Reilly et al. (2006a, b) resampled 20 plots from Linville Gorge Wilderness previously sampled by Newell and Peet (1998) in 1992 and examined the vegetation change at 0.01, 0.1, 1, 10, 100, and 400 m². While there was considerable variation in the impact of the fire, species richness increased across all scales and across four broad community types, roughly doubling in number. The increase at 400 m² ranged from a few species to 60. In a second study, Marx (2007) resampled six plots established on a serpentine barren community after 10 years and approximately three fires. She observed at the 100 m² scale a decline in woody species, but an increase in density and richness of herbaceous species. In both cases, a major contributor to increased plant establishment appeared to be the removal of the litter layer, allowing seedlings to become established in exposed soil.

Piedmont Upland Forests

The subset of data representing upland forests and woodlands of the Piedmont contains 851 vegetation plots distributed across 53 NVC associations and two states (**p.264**) (North Carolina and northern South Carolina). PCA revealed two important axes that may structure plant species richness in Piedmont uplands: base cation availability (PC1) and soil moisture (PC2). The variables that strongly load on PC1 and their respective correlations include base saturation ($r = 0.95$), pH (0.94), calcium (0.97), and magnesium (0.90). Thus, PC1 represents a base cation availability gradient across Piedmont upland forest associations. Compared to the other PCA axes, base cation availability has the strongest correlation with richness in the herbaceous layer, a result consistent with the findings of Peet and Christensen (1980b). Base cation availability and species richness are positively correlated across all scales; however, the strength of this relationship increases with increasing spatial scale (fig. 10.6). The extent to which the higher species richness on high-base sites is a consequence of greater resource availability or greater species pool size is unclear, but we expect that species pool size is important, at least at larger scales.

We identified PC2 as a soil moisture axis based on strong loading of nitrogen ($r = 0.88$), organic matter ($r = 0.63$), and sulfur ($r = 0.53$). This reflects, in part, the increased accumulation of organic matter in anaerobic soils and the storage of nitrogen and sulfur in organic matter in anaerobic soils. Thus, as soil moisture increases, organic matter, nitrogen, and sulfur increase. Soil moisture (PC2) is the second most important driver of richness patterns in Piedmont uplands; as soil moisture increases, species richness increases. This relationship is especially prominent at small spatial scales ($r = 0.35$ at .01 m² versus $r = 0.18$ at 1,000 m²).

In addition to the environmental axes described above, human modifications of the landscape (e.g., agriculture, tree harvest, urbanization, fragmentation, and climate change) impact diversity patterns in the Piedmont region. Peet (1992) and Peet and Christensen (1988) (chapter 11, this volume) report that during old-field succession on the Piedmont, the strength of the correlation between species richness and pH varies with stand development. The correlation first increases through the natural thinning phase as species become more strongly sorted relative to environment and

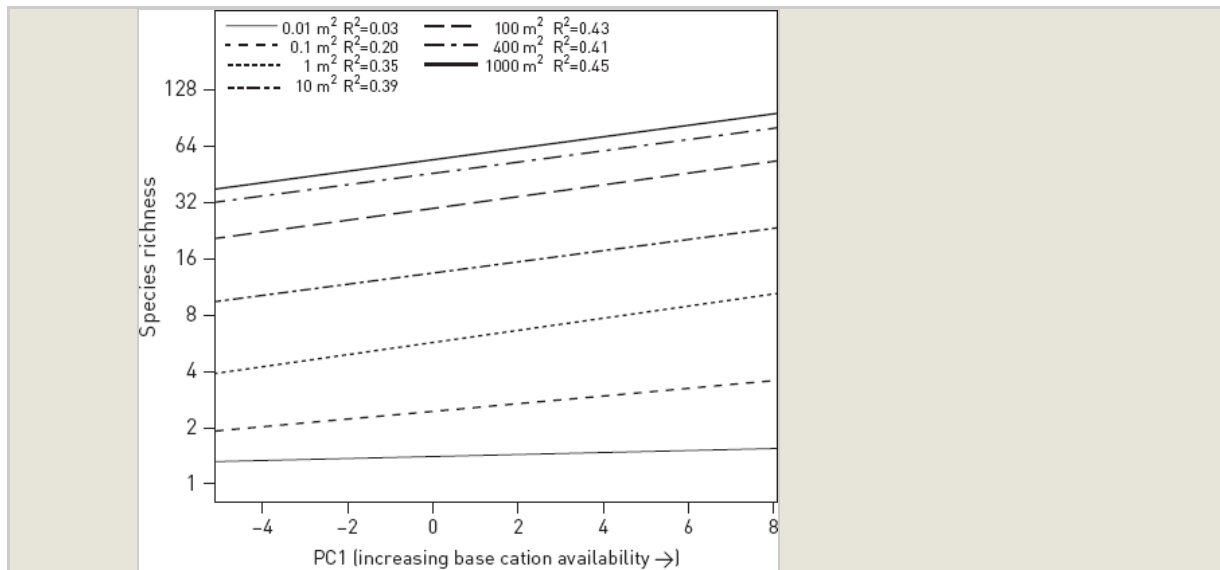


Figure 10.6 Relationship between PC1 (base cation availability) and log₂ richness across seven spatial scales in Piedmont upland forests and woodlands of southeastern North America.

(p.265) uncommon species have time to arrive. The correlation subsequently declines during the breakup of the original pine population owing to decreased competitive sorting, but then increases again into the mature hardwood phase with renewed competitive sorting. However, further work is needed to examine the importance of the various human impacts relative to environmental drivers of richness.

Disturbance in the form of heavy grazing and browsing also has important consequences for plant species richness in the Piedmont region. With the removal of predators and the decline in hunting, the white-tailed deer population has increased dramatically in many areas with severe negative impacts on plant community structure and diversity (Israel 2012; Cote et al. 2004; chapter 16, this volume), which is consistent with patterns documented in heavily grazed systems throughout the world (Fleischner 1994; chapter 14, this volume). Taverna et al. (2005) and Israel (2012) resampled permanent vegetation plots in the Duke Forest (in the Piedmont region of North Carolina) after 22 and 33 years during a period of dramatic increase in deer populations. They found that species richness declined steadily and significantly at both the 1 m² and 1,000 m² scale.

Coastal Plain Pine Woodlands

At the time of European settlement, fire-maintained longleaf pine (*Pinus palustris* P. Miller) woodlands and savannas dominated much of the southeastern Coastal Plain from southern Virginia south to south-central Florida and west to eastern Texas. Here we use a comprehensive sample of the remaining fire-maintained pine woodlands and savannas from northern North Carolina south to central Florida and west to the western edge of the Florida Panhandle. Our dataset contains 785 vegetation plots distributed across 58 NVC associations (see Peet 2006; Carr et al. 2009).

PCA revealed three potentially important environmental factors structuring plant species

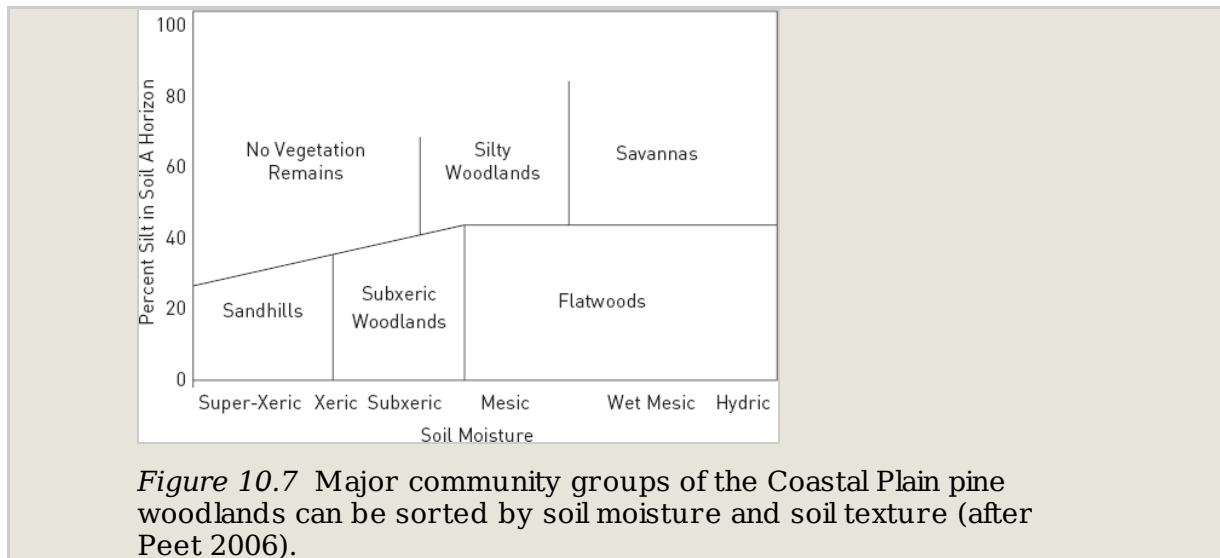
richness in Coastal Plain pine woodlands: soil moisture (PC2), soil texture (PC3), and base cation availability (PC1). The correlation strength of these three predictors with herbaceous layer richness varies across the spatial scales examined, but soil moisture is the most important driver, regardless of scale (table 10.1). Individual environmental variables that load on the soil moisture PCA axis and their respective correlations with the axis include bulk density ($r = -0.70$), sulfur (0.73), and organic matter (0.71). Linear models revealed that soil moisture is a highly significant predictor of species richness across all spatial scales examined (table 10.1). As soil moisture increases, richness increases in the herbaceous layer.

Soil texture is the second most important predictor in structuring species richness patterns in coastal plain pine woodlands after soil moisture. Environmental variables that load on the soil texture axis (PC3) and their respective correlations include aluminum ($r = 0.84$), iron (0.72), clay (0.64), sand (-0.63), and silt (0.57). As fine-textured soil components increase (clay % and silt %), richness increases significantly across all spatial scales (table 10.1). Fine-textured soils have greater water- and nutrient-holding capacity, which increases the number of species that can be supported in a given area.

The third PCA axis represents a base cation gradient across the Coastal Plain woodland community types with pH ($r = 0.89$), base saturation (0.88), and calcium (0.90) loading strongly on PC1. However, unlike Piedmont and Blue Ridge Mountain upland forests and riparian forests, base cation availability is only weakly correlated with richness, and the correlations shift from negative at small scales to positive at **(p.266)**

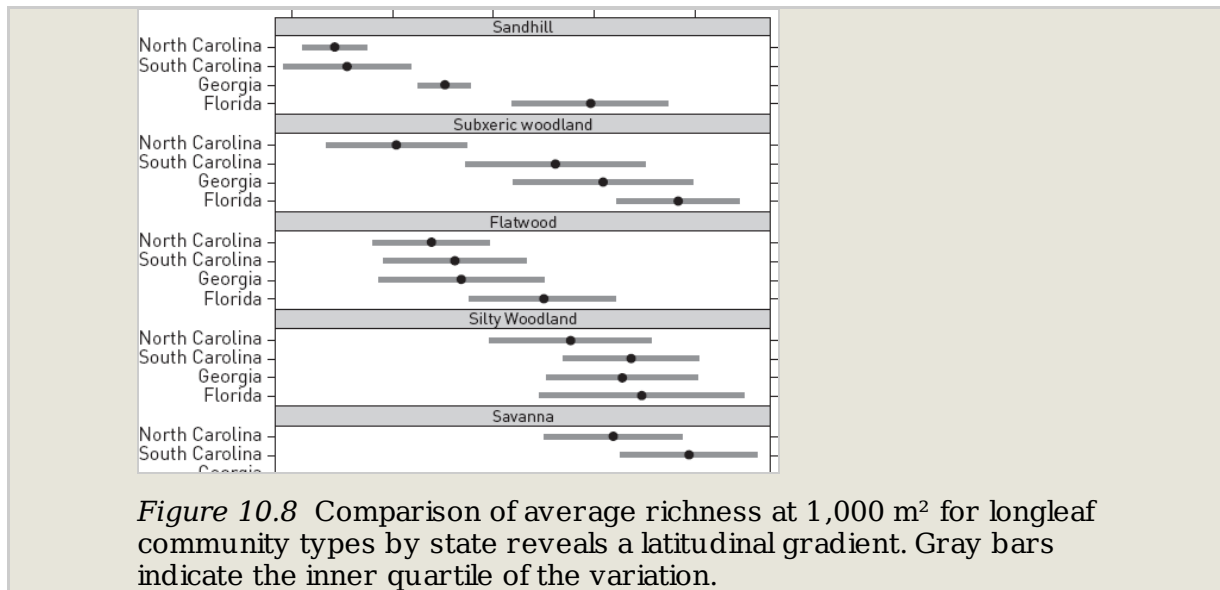
Table 10.1 Correlations of species richness in Coastal Plain pine woodlands with axes of soil moisture, soil texture, and soil cation availability. * indicates significant relationships ($p = .01$ to $.05$), and ** indicates highly significant relationships ($p < .01$).

Richness	Soil Moisture	Soil Texture	Cation Availability
.01 m ²	0.50 **	0.29 *	-0.32 *
.1 m ²	0.55 **	0.36 **	-0.25
1 m ²	0.55 **	0.39 **	-0.09
10 m ²	0.54 **	0.43 **	0.06
100 m ²	0.53 **	0.45 **	0.13
400 m ²	0.56 **	0.44 **	0.17
1000 m ²	0.57 **	0.44 **	0.18



large scales (table 10.1). At small scales, the more infertile sites can contain more small plants as competition for space is relatively modest, whereas at large scales, competition for space is less important and more species can persist on the more fertile soils. Interestingly, some of the highest species richness values reported for North America at small scales (e.g., 52/1 m²) have been reported for infertile longleaf pine savannas (Walker and Peet 1983), whereas some of the highest species richness values reported for North America at large spatial scales (1,000 m²) have been reported for longleaf woodlands on relatively fertile soils (161/1,000 m²; see Orzell and Bridges 2006; Platt et al. 2006; Gilliam 2007).

In addition to the environmental drivers of richness, there is a geographic trend in species richness across latitude in Coastal Plain pine woodlands (Peet 2006). Species richness increases with decreasing latitude in four of the five major vegetation types, with the pattern especially strong for the xeric longleaf community types (fig. 10.8). This geographic signal is likely due to a combination of climatic factors and biogeographic history. The length of the growing season and average mean temperature (**p.267**)



increase with decreasing latitude in southeastern North America; this may allow for the persistence of a larger suite of species. During the last glacial maximum (~ 18 ka), species refugia were concentrated on the Gulf Coastal Plain and in parts of peninsular Florida, and as climate warmed, species migrated eastward and northward to their current locations. Hence, the southern portion of the Coastal Plain pine woodlands may be more species rich due to fewer drastic fluctuations in climate, more speciation events, and less extinction over geologic and evolutionary time (Sorrie and Weakley 2001). Interestingly, species richness of Coastal Plain pine woodlands drops off again as one descends the Florida peninsula (Carr et al. 2009), probably owing to a smaller species pool resulting from the intrinsic isolation of communities on islands and peninsulas.

Fire history and current fire regimes (fire frequency, fire return interval, time since fire, season of fire) are also extremely important for the maintenance of plant species richness in Coastal Plain pine woodlands (Walker and Peet 1983; Glitzenstein et al. 2003; Kirkman et al. 2004). Historically, Coastal Plain pine woodlands burned every one to five years, depending on site productivity, topographic position, and landscape context, with annual fire on the flat outer Coastal Plain and less frequent fire in the dissected and topographically complex inner Coastal Plain (Frost 2006). Frequent fire maximizes species richness by reducing the density of litter and the abundance of dominant species and by increasing resource availability in the form of light, space, and nutrients (Sparks et al. 1998; Kirkman et al. 2004). Without fire, species richness decreases rapidly (Glitzenstein et al. 2003), especially in mesic to wet community types where competitive exclusion by bunch grasses eliminates the small-statured species that constitute the bulk of biodiversity.

(p.268) Carolina Riparian Forests

Riparian forests may have different patterns of herbaceous layer richness compared to upland forests and woodlands because of the movement and persistence of water. We look only at rivers that originate in the Blue Ridge Mountains or the Piedmont, thereby excluding the smaller, black-water rivers of the Coastal Plain, which have very different

hydrologic, geomorphic, and edaphic attributes. The subset of data representing brown-water riparian forests and woodlands of North Carolina includes 444 plots spanning 44 NVC or equivalent association units.

Analysis of all 44 riparian, brown-water forest community types across the Blue Ridge Mountains, Piedmont, and Coastal Plain revealed strong geographic, elevation, soil nutrient, and soil texture gradients, with montane riparian forests generally richer in species, base cations, and percentage of sand in the soil (fig. 10.9). It is difficult to interpret ecological drivers of species richness when there is such a strong geographic trend, other than to observe that Blue Ridge Mountain riparian forest community types, which are among the most species-rich communities in the region at large scales (100–1,000 m²), are likely to be richer in species because of propagule pressure from the wide variety of communities in close proximity and the limited duration of flooding events on these steep-gradient streams (Brown and Peet 2003). We therefore split the communities in this dataset into three subgroups, where each community in the full dataset was assigned to a dominant physiographic province. This resulted in 11 Blue Ridge Mountain riparian forest communities, 13 Piedmont

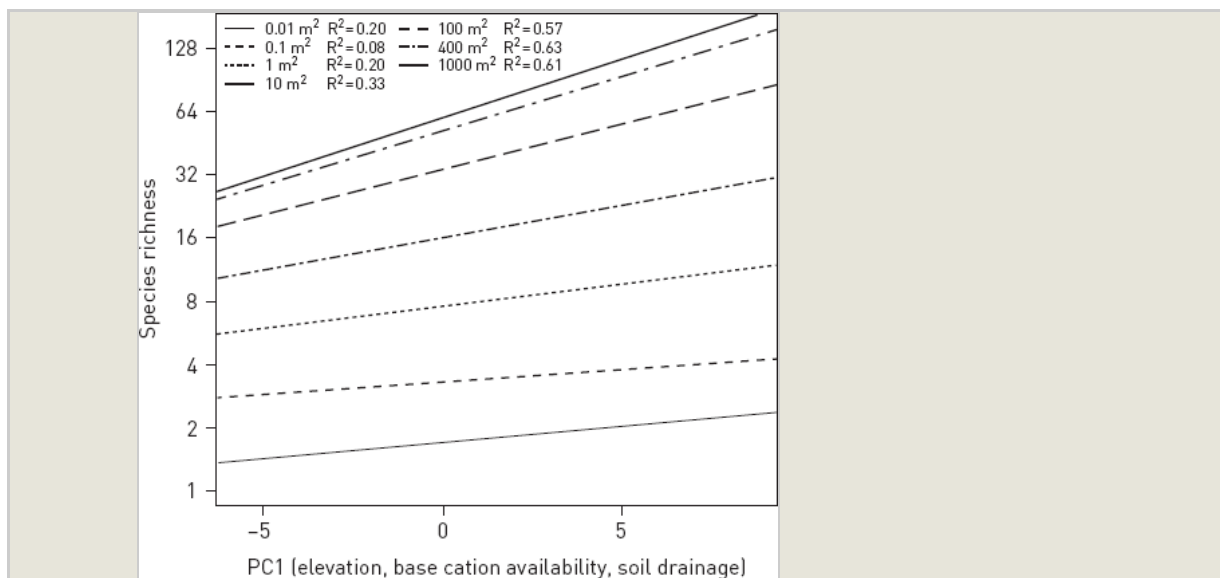


Figure 10.9 PCA axis 1 for explanatory variables of riparian brown-water forest community richness. PC1 represents 43 percent of the variation in environmental conditions and shows a strong geographic trend in richness, as well as environmental variables, where Blue Ridge Mountain riparian plots are richest in species, base cations, and percent sand. Variables strongly correlated with PC1 include elevation ($r = 0.75$), longitude ($r = -0.81$), pH ($r = 0.76$), base saturation ($r = 0.76$), cation exchange capacity ($r = -0.82$), nitrogen ($r = -0.86$), percent sand ($r = 0.88$), percent silt ($r = -0.76$), percent clay ($r = -0.86$), bulk density ($r = 0.81$), and soil organic matter ($r = -0.75$). R^2 values for all scales have $p < 0.01$ except 0.1 m² with $p < 0.05$.

(p.269) riparian communities, and 20 Coastal Plain riparian communities. Species richness patterns were analyzed separately for these three subgroups.

Soil calcium and magnesium are very important determinants of species richness in Blue Ridge Mountain riparian forests, especially at smaller scales ($r = 0.80$ for Ca and 0.76 for Mg at 0.1 m^2 , $p < 0.01$). Base saturation and pH, often correlated with calcium and magnesium, are not as strong predictors (r up to 0.55 for base saturation and 0.54 for pH, not significant). Higher species richness in areas with more base nutrients is a common pattern in plant community ecology (e.g., Peet et al. 2003), and similar relationships were detected for upland forests of the Piedmont and Blue Ridge Mountains. Terrain Shape Index (TSI) was another strong determinant of species richness at small scales (r up to -0.74 , $p < 0.05$ for scales 0.01 m^2 to 100 m^2 , not significant at larger scales); sites with high richness occur predominantly on local topographic high points such as ridges and levees, while low flats and depressions have lower richness. Sites that had concave local topography (high TSI) probably have fewer species because of greater duration of flooding and local dominance of flood-tolerant species.

The predictive power of most environmental variables at large scales in Blue Ridge Mountain riparian habitats is low. This is likely because propagule pressure is the dominant driver in this system, with stream-facilitated disturbance and seed dispersal allowing temporary occurrence of many species that would not otherwise be competitive. The highest known species richness values for the Carolinas and possibly temperate North America at scales of 100 to $1,000 \text{ m}^2$ (table 10.2) have been reported for scour woodlands along Blue Ridge Mountain rivers where chronic disturbance decreases competition and frequent, brief flooding provides a steady supply of propagules from throughout the adjacent watershed (Brown and Peet 2003).

In Piedmont brown-water forests, soil nutrients and texture, probably reflecting flooding regime and moisture, were strong determinants of species richness. Phosphorous was the strongest predictor at all scales (r ranges -0.60 to -0.85 , $p < 0.05$ at all scales) and

Table 10.2 Highest values of species richness recorded for the Carolinas at different scales. At larger scales, scour zones along Blue Ridge Mountain rivers have the highest richness values reported, whereas at small scales, the most species-rich communities are moist, fire-maintained longleaf pine savannas.

Scale- m^2	Richness	USNVC Name
1,000	175	<i>Alnus serrulata</i> — <i>Xanthorhiza simplicissima</i> Shrubland
400	146	<i>Alnus serrulata</i> — <i>Xanthorhiza simplicissima</i> Shrubland
100	129	<i>Alnus serrulata</i> — <i>Xanthorhiza simplicissima</i> Shrubland
10	72	<i>Pinus palustris</i> / <i>Arundinaria tecta</i> — <i>Liquidambar</i> / <i>Andropogon glomeratus</i> — <i>Sarracenia minor</i> Woodland
10	72	<i>Liquidambar</i> — <i>Liriodendron</i> —(<i>Platanus</i>)/ <i>Carpinus</i> — <i>Halesia tetraptera</i> / <i>Amphicarpaea</i> Forest
1	52	<i>Pinus palustris</i> — <i>Pinus serotina</i> / <i>Sporobolus pinetorum</i> — <i>Aristida stricta</i> — <i>Eryngium integrifolium</i> Woodland

0.1	35 <i>Pinus palustris</i> — <i>Pinus serotina</i> / <i>Sporobolus pinetorum</i> — <i>Aristida stricta</i> — <i>Eryngium integrifolium</i> Woodland
0.01	15 <i>Pinus palustris</i> — <i>Pinus serotina</i> / <i>Ctenium aromaticum</i> — <i>Muhlenbergia expansa</i> — <i>Rhynchospora latifolia</i> Woodland

(p.270) was strongly correlated with sulfur and iron, suggesting that flood events have resulted in storage of organic matter in swamps behind levees. In addition, soil clay was a strong negative predictor of species richness at larger spatial scales ($r = -0.72$ at 400 m^2 , $p < 0.05$), again indicating swamps with poor drainage and sediment accumulation.

In Coastal Plain brown-water river forests, there is again a geographic trend in species richness, with species richness higher in more southerly areas and in the community types more common in the inner Coastal Plain ($r = -0.45$ with latitude and -0.51 with longitude at 100 m^2 , $p < 0.05$). Distance to coast is an insignificant determinant of species richness, and though latitude, longitude, and elevation are among the few predictors of species richness, their contribution is weak or insignificant at most scales. Elevation is the strongest predictor of species richness at the scale of 100 m^2 ($r = 0.54$, $p < 0.05$), and it also primarily reflects river distance from the coast, as sites further inland tend to be higher in elevation. The richest community types in the Coastal Plain brown-water riparian forest data subset were (1) point bars with many vagrant, ephemeral species due to propagule pressure; and (2) herb-rich bottomlands and low slopes with good to moderate drainage. These community types were sampled mostly from the Cape Fear and Neuse River basins, whereas community types with geographic centroids along the Roanoke River more often had saturated soil, thereby supporting fewer individuals and species.

Differences in abundances of community types across river basins may arise from variation between rivers in hydrologic processes. The Cape Fear River, for instance, is entrenched due to geologic uplift in the Cape Fear Arch region resulting in a larger levee-to-swamp ratio and infrequent flooding. In contrast, the Roanoke River meanders broadly because of a history of crustal subsidence in the region. The river also has a history of altered hydrology over the last 50 years due to dam construction. Management of these dams has resulted in longer-lasting but less dramatic flooding events, which may have homogenized community composition along the river (Townsend 2001; Pearsall et al 2005). Annual variability in flooding may also affect species richness in the herb layer of riparian forests. A 2009 resurvey of Roanoke River plots originally sampled in the wet year of 1994 had consistently higher species counts than in the original sample (J. White, unpublished data). It is therefore possible that perceived differences in species richness between river basins may also be caused by annual hydrologic variability between rivers sampled in different years.

Synthesis

Numerous hypotheses have been proposed to explain patterns in plant species richness and coexistence (see Whittaker 1972; Huston 1994; Palmer 1994; Wilson 2011). Here we examine several that seem to have particular relevance to the forests and woodlands of southeastern North America and that appeared with varying importance in our

discussion of the four groups of plots considered above. Our intent is not to catalogue proposed mechanisms, something already done by Palmer (1994) and others, but to examine how the most important factors vary with ecological context and scale of observation.

Environmental Favorableness and Plant Size

Herbaceous richness has been linked to numerous factors that might best be collectively referred to as environmental favorableness. For example, richness peaks in moist **(p.271)** but well-drained sites and drops off in very wet and very dry sites. In our data, we observed riparian sites with chronic inundation to have lower richness than better drained sites, and we observed that Coastal Plain pine woodlands, Piedmont upland forests, and Blue Ridge Mountain upland forests on moist soils support higher richness than those on xeric sites. Whittaker (1956) reported richness to decline with elevation in the Blue Ridge Mountains, and in our data we see a decline with elevation, at least at large scales. Of variables that might be considered components of favorableness, soil cation availability is most consistently correlated with species richness across our vegetation subsets. In general, as soil fertility increases, so does richness, especially at the larger spatial scales examined. Greater cation availability allows more species to coexist as nutrients are less limiting.

Although species richness increases with soil cation availability at large scales for all four subsets of our data, the highest richness values at small scales occur consistently in Coastal Plain pine woodlands, which are characterized by low cation availability and pH in comparison to the sites with high small-scale richness in the other subsets of our data. This reflects the smaller size of plants in fire-maintained Coastal Plain pine woodlands and the number of species that can be packed into a small area. In fact, for small scales in Coastal Plain pine woodlands, the normal pattern between species richness and soil cation availability is reversed (negatively correlated), whereas in all other regions, there is a consistent positive correlation. Plant size and density are also important in the Piedmont, Blue Ridge Mountain, and Riparian datasets as indicated by the generally weaker correlation between soil cation availability and richness at small scales than at large scales for each of these datasets.

Species Pool and History

Species richness increases with decreasing latitude in Coastal Plain pine woodlands (fig. 10.8) and at least weakly along a northeast-to-southwest axis down the spine of the Blue Ridge Mountains. These gradients are likely a consequence of geographic variation in the available species pool. The number of species available at a site, or the “species pool” (sensu Pärtel et al. 1996), generally reflects evolutionary history, historical events, and local context. For example, the pool is generally larger in or near areas where species persisted during the Pleistocene epoch or is larger because of conditions that are more prominent on the landscape. Within refugial areas, species richness may be higher due to fewer extinctions over geologic time and a longer period for evolutionary divergence in isolated habitats. Consistent with this, the species pool for Coastal Plain pine woodlands appears to vary with proximity to places of Pleistocene persistence, such as the

Apalachicola region of Florida and, to a lesser extent, the Florida Peninsula and the Cape Fear Arch (located in southeastern North Carolina; see Sorrie and Weakley 2001). Similarly, the southwest end of the Blue Ridge Mountains has somewhat higher richness than in northern North Carolina, probably because of Pleistocene persistence along the southern edge of the Blue Ridge escarpment. An anomaly relative to the expectation that larger areas should have larger species pools (Pärtel 2002) is the observation of Peet et al. (2003) that species richness in Appalachian forests increases consistently with pH, despite most of the landscape having low-pH soils. This seeming anomaly likely results from the generally more favorable conditions for plant growth on high-cation sites.

(p.272) Propagule Pressure and Mass Effect

Ever since MacArthur and Wilson (1967) proposed their classic theoretical framework for island biogeography, community assembly has been widely appreciated to represent a balance between immigration and extinction. Numerous papers have emphasized the importance of the immigration side of the equation, documenting how high species arrival rates can lead to high species richness. For example, Brown and Peet (2003) found that riparian vegetation of the Blue Ridge Mountains is sometimes exceptionally species rich because of propagules carried by water from throughout the adjacent watershed.

Grime (1998) noted that a large proportion of species occurring in plant communities are waifs, species that we should not expect to persist, but which simply dropped in via dispersal and generally persist for only a modest period. Shmida and Wilson (1985) referred to this process as spatial mass effect and also noted that proximity to other environmental conditions can increase species number through increased chance arrival. In regions of rapid environmental turnover, such as in mountain ranges, mass effects can be particularly important as species more frequently have propagules land and become established in habitats inadequate for long-term persistence. Thus, landscape context alone can be an important driver of species richness and could explain why Blue Ridge Mountain vegetation is generally more species rich than equivalent Piedmont vegetation.

Disturbance

Disturbance, both human-mediated and natural, represents an important set of processes that influence herbaceous richness patterns across all four data subsets. Recurrent scouring by floods maintains species richness in riparian forests of the Blue Ridge region (Brown and Peet 2003) through the removal of dominant species and the arrival of waifs. Fire is an essential process for the maintenance of biodiversity in several Piedmont and Blue Ridge Mountain community types, including both oak and pine woodlands (e.g., Reilly et al. 2006a, b). In the fire-maintained Coastal Plain pine woodlands, a reduction in fire frequency rapidly leads to decreased species richness at all scales for all except the most xeric sites, first owing to increased accumulation of litter and ultimately to increased growth of woody plants (Walker and Peet 1983; Glitzenstein et al. 2003; Kirkman et al. 2004).

Disturbances ranging from episodic canopy gaps following wind disturbance in closed forests to the frequent fires of the Coastal Plain pine woodlands create areas of

temporary availability of resources and space that can be exploited by colonizing species, allowing persistence until the next disturbance event. This represents an example of the temporal mass effect of Shmida and Wilson (1985), a mechanism that explains local perpetuation of a species that cannot become established under current conditions. Consistent with this interpretation is the phenomenon that flowering in Coastal Plain pine woodlands increases by an order of magnitude following a fire, probably a consequence of selection for maximum reproduction when conditions for establishment are optimal.

Productivity

Herbaceous layer richness has been reported to increase, decrease, or show a bell-shaped curve along gradients of productivity, these typically being gradients (p.273) of soil chemistry and especially gradients of nitrogen and phosphorus supply (e.g., Grime 1973; Huston 1979; Adler et al. 2011). Most studies where richness has been reported to exhibit a bell-shaped curve were conducted in relatively nutrient-poor grassland systems, essentially the same situation encountered in Coastal Plain pine woodlands. In contrast, many studies conducted in forested systems report a nearly monotonic positive correlation between production and species richness, as suggested by soil moisture and cation availability in our Piedmont and Blue Ridge Mountain datasets. However, Graves et al. (2006) observed that forest herbaceous layer richness will drop at the most productive extreme of a soil-fertility gradient. This is consistent with our observation that cove forests in the Blue Ridge Mountains are somewhat less species rich than equally fertile mid-slope sites.

Peet and Christensen (1988) suggested that the explanation for the relationship between productivity and small-scale richness in grasslands can be found in the changing character of competition across the fertility gradient. For grasslands at low levels of fertility, competition is symmetric (*sensu* Schwinning and Weiner 1998) in the sense that ability to capture resources is proportional to size (essentially, amount of root surface area). In this situation, many plant species can coexist. However, at higher fertility levels, the larger individuals overtop and preempt light from the smaller ones (see Lamb et al. 2009). Thus, when productivity is high, the taller plants win at competition and the smaller ones are excluded. At both a regional and a global scale, the most species-rich plant communities at scales on the order of 1 m² are infertile grasslands (sometimes with in excess of 40 species/m²) that are subject to chronic disturbance from some factor like mowing, grazing, or fire that removes the tops of the plants on a regular basis (Peet and Christensen 1988; Sykes et al. 1994; Wilson et al. 2012), reducing the degree of competition for light (asymmetry of competition) and allowing high species richness to occur on more fertile sites than would be the case in the absence of such disturbance (fig. 10.10). De Bello et al. (2007) observed, in a synthetic evaluation of the impact of grazing on richness, that grazing increases species richness of Spanish grasslands at all spatial scales except on arid sites. This is consistent with

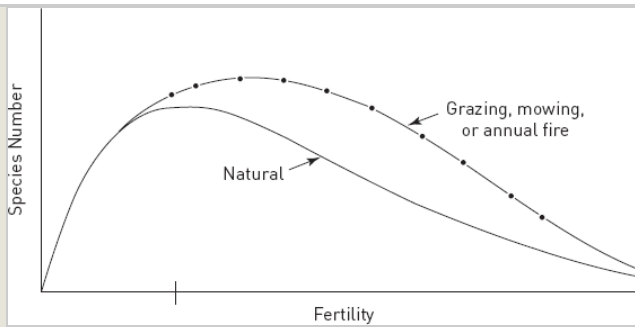


Figure 10.10 Species richness has frequently been reported to peak at low to intermediate levels along a gradient of fertility or primary productivity in grasslands and open savannas, after which competition for light becomes important and the shorter species are lost, reducing richness. Grasslands with very high richness are chronically disturbed by some factor such as fire or grazing or mowing that reduces plant height and thus reduces competition for light, allowing richness to increase along a fertility gradient longer before the asymmetric competition for light becomes a factor.

(p.274)

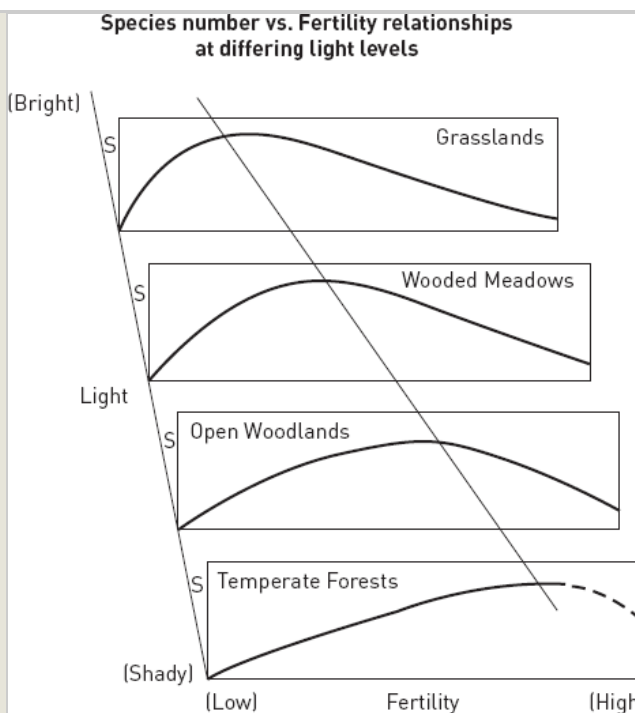


Figure 10.11 With increasing canopy cover from open grasslands through open woodlands to closed canopy temperate forests, the light available to the herbaceous layer steadily declines. As the available light declines, it takes greater fertility for the herbaceous layer to become sufficiently robust for asymmetric light competition to become important, with the consequence that the peak in richness shifts progressively toward more fertile sites.

grazing increasing richness where competition is asymmetric, but decreasing richness where competition is symmetric. This interpretation is also consistent with our observation that fire does not have a significant influence on the richness of the most

xeric Coastal Plain pine woodlands, whereas it does on all other sites.

The mechanism behind the shift in the peak of richness encountered along the fertility gradient in forests relative to grasslands can again be explained in terms of a shift from symmetric to asymmetric competition. With increasing cover of woody plants, the amount of light penetrating to the herbaceous layer declines. This allows for richness to keep increasing with fertility until the lushness of the herbaceous layer becomes such that competition for light within the herbaceous layer becomes important. At this point, richness starts to decline. Thus, one can envision a sequence from grassland to open woodland to closed forest with the peak in richness moving progressively toward the more fertile conditions (fig. 10.11).

Scale

One way of searching for general patterns in and drivers of richness across datasets is to examine which sites have the highest richness at each scale. In table 10.2, we report for each scale the NVC community type for which we have the highest species richness in our southeastern database. At large scales (100–1,000 m²), the scour zones of Blue Ridge Mountain riparian areas have by far the highest species number. At small scales (**p.275**) (0.01–1 m²), moist, infertile longleaf pine savannas on silty substrate have the highest richness values. At the intermediate scale of 10 m², the honors are split between Blue Ridge Mountain alluvial forests and somewhat fertile, moist, and silty longleaf pine savannas. Thus, we see the large-scale records driven by propagule pressure, fertility, and chronic but brief flooding, and the small-scale records driven by chronic fire on moist sites with low nutrient status and low productivity. A comparison with other records from the United States reveals no examples with higher values, but some close contenders for the most at 1,000 m² in cation-rich, fire-maintained longleaf savannas and prairies of Florida and Louisiana (e.g., 161 sp. in loess soil longleaf in Louisiana, William Platt pers. comm.; Orzell and Bridges 2006; Gilliam 2007). Globally, we find higher richness at small scales in oligotrophic, chronically grazed European grasslands (27 per 0.01 m², 43 per 0.1 m²; van der Maarel and Sykes 1993; Dengler et al. 2009) and in oligotrophic, grazed montane tropical grasslands in South America (89 per 1 m²; Cantero et al. 1999).

The first clear synthesis of changes in the processes driving richness with change in spatial scale appeared in two overlapping papers by Shmida (Shmida and Ellner 1984; Shmida and Wilson 1985). These papers proposed niche relationships (i.e., competition) as most important at smallest scales, habitat diversity and mass effects at intermediate scales, and ecological equivalency (i.e., species pool) at larger scales. These predictions fit well with our observations in southeastern North America. At smallest scales, we found plant interactions via space preemptions (size) and competition for light as mediated by chronic disturbance as critical. At larger scales, mass effects (propagule pressure) and species pool size appeared to be the critical drivers.

Conclusions

Examination of species richness patterns of the herbaceous layer of southeastern forests and woodlands reveals the changing importance of various drivers of species richness

across environmental and geographic gradients and across vegetation types, and shows how the relative importance of those drivers varies with scale of observation. The most important processes structuring species diversity patterns in southeastern forests and woodlands appear to be cation availability (environmental favorableness), disturbance (flooding, fire, grazing), mass effects, and the relative size of the species pool.

Numerous previous studies have examined species richness, but typically in the context of a single spatial scale, and for a single region, vegetation type, or environmental gradient. Different community assembly processes operate at different spatial scales, with biotic interactions and local environmental filtering operating at smaller spatial scales, and dispersal and species pool size becoming increasingly important at broader spatial scales. By looking at richness across a broad range of regions, community types, and spatial scales, we show that to understand patterns in richness, a holistic approach that examines all of these components concurrently must be taken.

Acknowledgments

Thomas Wentworth, Alan Weakley, and Michael Schafale have been longtime collaborators in organizing the Carolina Vegetation Survey (see Peet et al. 2012), and Susan **(p.276)** Carr collaborated in collection of data from longleaf pine sites in Florida. Without their continued dedication to building our dataset, this project would not have been possible. We are pleased to thank the 900+ persons who have participated in the collection of the vegetation plots in the CVS database. Collection of these data was supported by the Ecosystem Enhancement Program of the state of North Carolina, the U.S. Forest Service, and numerous other groups, programs, and persons. Michael Lee and Forbes Boyle provided invaluable assistance with data management and analysis.



Access brought to you by: University of North Carolina -
Chapel Hill Libraries

Literature cited

- Abrams, M. D. 1992. Fire and the development of oak forests. *BioScience* 42: 346-353.
- Adler, P.B., and 57 others, 2011. Productivity is a poor predictor of plant species richness. *Science* 333:1750-1753.
- Braun, E.L. 1950. Deciduous forests of eastern North America. Blakiston Co., Philadelphia Pennsylvania. 596 pp.
- Brown, R.L. 2002. Biodiversity and exotic species invasion in southern Appalachian riparian plant communities. Ph.D. Dissertation. University of North Carolina at Chapel Hill, Chapel Hill, North Carolina. 136 pp.
- Brown, R.L. L.A. Jacobs, and R.K. Peet. 2007. Species richness: small scale. *Encyclopedia of Life Sciences*. <http://onlinelibrary.wiley.com/doi/10.1002/9780470015902.a0020488/pdf>.
- Brown, R.L., and R.K. Peet. 2003. Diversity and invasibility of southern Appalachian plant communities. *Ecology* 84:32-39.
- Cantero, J. J., M. Pärtel, and M. Zobel. 1999. Is species richness dependent on the neighbouring stands? An analysis of the community patterns in mountain grasslands of central Argentina. *Oikos* 87:346-354.
- Carr, S.C., K.M. Robertson, W.J. Platt, and R.K. Peet. 2009. A model of geographic, environmental and regional variation in vegetation composition of pyrogenic pinelands of Florida. *Journal of Biogeography* 36:1600-1612.
- Cote, S.D., T.P. Rooney, J.P. Trembly, C. Dussault, and D.M. Waller. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology Evolution and Systematics* 35: 113-147.
- De Bello, F., J. Lepš, and M.T. Sebastia. 2007. Grazing effects on the species-area relationship: Variation along a climatic gradient in NE Spain. *Journal of Vegetation Science* 18:25-34.
- Dengler, J. 2009. A flexible multi-scale approach for standardised recording of plant species richness patterns. *Ecological Indicators* 9:1169-1178.
- Dengler, J., E. Ruprecht, A. Szabó, D. Turtureanu, M. Beldean, E. Uğurlu, H. Pedashenko, C. Dolnik, and A. Jones. 2009. EDGG cooperation on syntaxonomy and biodiversity of *Festuco-Brometea* communities in Transylvania (Romania): report and preliminary results. *Bulletin of the European Dry Grassland Group* 4:13–19, Hamburg.
- Eriksson, O. 1993. The species-pool hypothesis and plant community diversity. *Oikos* 68:371-374.
- F.A.O. [Food and Agriculture Organization]. 2001. Global Forest Resources Assessment 2--Main Report. FAO Forestry Paper 140. Food and Agriculture Organization of the United Nations, Rome. 482 pp. [N01FAO01ICEC]
- Faestel, M. 2012. Classification and description of alluvial plant communities of the North Carolina Coastal Plain. M.S. thesis, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina.
- Fleischner, T.L. 1994. Ecological costs of livestock grazing in western North America. *Conservation Biology* 8: 629-644.

- Fridley, J.D., R.L. Brown, and J.F. Bruno. 2004. Null models of exotic invasion and scale-dependent patterns of native and exotic species richness. *Ecology* 85: 3215-3222.
- Frost, C. 2006. History and future of the longleaf pine ecosystem. Pages 9-48 in S. Jose, E. Jokela and D. Miller, editors. *Longleaf pine ecosystems: ecology, management, and restoration*. Springer, New York.
- Giladi, I., Y. Ziv, F. May, and F. Jeltsch. 2011. Scale-dependent determinants of plant species richness in a semi-arid fragmented agro-ecosystem. *Journal of Vegetation Science* 22:983-996.
- Gilliam, F.S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. *BioScience* 57: 845-858.
- Glitzenstein, J.S., D.R. Streng, and D.D. Wade. 2003. Fire frequency effects on longleaf pine (*Pinus palustris* P. Miller) vegetation in South Carolina and northeast Florida, USA. *Natural Areas Journal* 23: 22-37.
- Graves J.H., R.K. Peet, and P.S. White. 2006. The influence of carbon-nutrient balance on herb and woody plant abundance in temperate forest understories. *Journal of Vegetation Science* 17:217–226.
- Gray, A.N., T.J. Brandeis, J.D. Shaw, W.H. McWilliams, and P.D. Miles. 2012. Forest inventory and analysis database of the United States of America (FIA). *Biodiversity and Ecology* 4: 225-232
- Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation *Nature* 242:344-347.
- Grime, J.P. 1998. Benefits of Plant Diversity to Ecosystems: Immediate, Filter and Founder Effects. *Journal of Ecology* 86:902-910.
- Huston, M.A. 1979. A general hypothesis of species diversity. *American Naturalist* 113:81-101.
- Huston, M.A. 1994. *Biological Diversity: The Coexistence of Species on Changing Landscapes*. Cambridge University Press, Cambridge, UK
- Hutchinson, T. F., R. E. J. Boerner, S. Sutherland, E. K. Sutherland, M. Ortt, and L. R. Iverson. 2005. Prescribed fire effects on the herbaceous layer of mixed-oak forests. *Canadian Journal of Forest Research* 35: 877-890.
- Israel, K. 2012. Vegetation change in the Duke Forest, 1977-2010. M.S. Thesis, University of North Carolina, Chapel Hill, North Carolina.
- Kirkman, L.K., P.C. Goebel, and B.J. Palik. 2004. Predicting plant species diversity in a longleaf pine landscape. *Ecoscience* 11: 80-93.
- Knollová, I., M. Chytrý, L. Tichý, & O. Hájek. 2005. Stratified resampling of phytosociological databases: some strategies for obtaining more representative data sets for classification studies. *Journal of Vegetation Science* 16:479-486.
- Jennings, M.D., D. Faber-Langendoen, O.L. Loucks, R.K. Peet, and D. Roberts. 2009. Characterizing Associations and Alliances of the U.S. National Vegetation Classification. *Ecological Monographs* 79:173-199.
- Lamb, E.G., S.W. Kembel, and J.F. Cahill. 2009. Shoot, but not root, competition reduces community diversity in experimental mesocosms. *J. Ecol.* 97: 155–163.

- Lengyel, A., M. Chytrý, and L. Tichý. 2011. Heterogeneity-constrained random resampling of phytosociological databases. *Journal of Vegetation Science* 22:175-183.
- MacArthur, R.H., and E.O. Wilson 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Marx, E. 2007. Vegetation dynamics of the Buck Creek serpentine barrens, Clay County, North Carolina. B.S. Thesis, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina. 44 pp.
- Matthews, E.M., R.K. Peet, and A.S. Weakley. 2011. Classification and description of alluvial plant communities of the Piedmont region. North Carolina, U.S.A. *Applied Vegetation Science* 14:485-505.
- McNab, W.H. 1989. Terrain Shape Index: quantifying effect of minor landforms on tree height. *Forest Science* 35:91-104.
- McNab, W.H. 1993. A topographic index to quantify the effect of mesoscale landform on site productivity. *Canadian Journal of Forest Research* 23:1100-1107.
- Melich, A. 1984. Mehlich 3 soil test extractant: a modification of Mehlich 2 extractant. *Communications in Soil Science and Plant Analysis* 15: 1409–1416.
- Michalcová, D., S. Lvončík, M. Chytrý, and O. Hájek. 2011. Bias in vegetation databases? A comparison of stratified-random and preferential sampling. *Journal of Vegetation Science* 22:281-291.
- Newell, C.L., and R.K. Peet. 1998. Vegetation of Linville Gorge Wilderness, North Carolina. *Castanea* 63:275–322.
- Newell, C.L., R.K. Peet, C.J. Ulrey, T.R. Wentworth, K.D. Patterson, and D.E. McLeod. 1999. Geographic variation in forest distribution across five landscapes in the Southern Appalachian Mountains of North and South Carolina. In R.P. Eckerlin, editor. *Proceedings of the Appalachian Biogeography Symposium, Special Pub., Virginia Mus. Nat. Hist.* 7: 19–34.
- Nilsen, E.T., J.F. Walker, O.K. Miller, S.W. Semones, T.T. Lei, and B.D. Clinton. 1999. Inhibition of seedling survival under *Rhododendron maximum* (Ericaceae): could allelopathy be a cause? *American Journal of Botany* 86:1597-1605.
- Omernik, J.M. 1987. Ecoregions of the conterminous United States. Map (scale 1:7,500,000). *Annals of the Association of American Geographers* 77:118-125.
- Orzell, S.L., and E.L. Bridges. 2006. Floristic composition and species richness of subtropical seasonally wet *Muhlenbergia sericea* prairies in portions of Central and South Florida. In R.F. Noss, editor. *Land of fire and water: the Florida dry prairie ecosystem*. E.O. Painter Printing Company, DeLeon Springs, Florida. Pp 136-175.
- Palmer, M.W. 1994. Variation in species richness: towards a unification of hypotheses. *Folia Geobotanica* 29:511-530.
- Pärtel, M., M. Zobel, K. Zobel, and E. van der Maarel. 1996. The species pool and its relation to species richness: evidence from Estonian plant communities. *Oikos* 75: 111-117.
- Pärtel, M. 2002. Local plant diversity patterns and evolutionary history at the regional scale. *Ecology* 83:2361-2366.

- Patrick, W.H. 1958. Modification of particle size analysis. Soil Science Society of America, Proceedings. 22:366-367.
- Pearsall, S.H., B.J. McCrodden, and P.A. Townsend. 2005. Adaptive management of flows in the lower Roanoke River, North Carolina. Environmental Management 35: 353-367.
- Peet, R.K. 1992. Community structure and ecosystem function. Pages 103-151 in D.C. Glenn-Lewin, R.K. Peet, and T.T. Veblen, editors. Plant Succession: Theory and Prediction. Chapman & Hall, Cambridge, UK.
- Peet, R.K. 2006. Ecological classification of longleaf pine woodlands. In: Pages 51-94 in S. Jose, E. Jokela and D. Miller, editors. Longleaf pine ecosystems: ecology, management, and restoration. Springer, New York.
- Peet, R.K., and N.L. Christensen. 1980. Hardwood forest vegetation of the North Carolina Piedmont. Veröff. Geobot. Inst. ETH Stiftung Rübel 69:14-39.
- Peet R.K., and N.L. Christensen. 1988. Changes in species diversity during secondary forest succession on the North Carolina USA Piedmont. Pages 233-246 in H.J. During, W.H.J. Werger, and J.H. Willems, editors. Diversity and Pattern in Plant Communities; International Symposium on Vegetational Structure, Woudschoten, Utrecht, Netherlands, July 14–18, 1987. Academic Publishing BV. The Hague, The Netherlands.
- Peet, R.K., J.D. Fridley, and J. M. Gramling. 2003. Variation in species richness and species pool size across a pH gradient in forests of the southern Blue Ridge Mountains. Folio Geobotanica 38:391-401.
- Peet, R.K., M.T. Lee, M.F. Boyle, T.R. Wentworth, M.P. Schafale, and A.S. Weakley. 2012. Vegetation-plot database of the Carolina Vegetation Survey. Biodiversity and Ecology 4: 243-253.
- Peet, R.K., T.R. Wentworth, and P.S. White. 1998. A flexible, multipurpose method for recording vegetation composition and structure. Castanea 63: 262-274.
- Platt, W.J., S.C. Carr, M. Reilly, and J. Fahr. 2006. Pine savanna overstory influences on ground-cover biodiversity. Applied Vegetation Science 9: 37-50.
- Reilly, M.J., M.C. Wimberly, and C.L. Newell. 2006a. Wildfire effects on plant species richness at multiple spatial scales in forest communities of the southern Appalachians. Journal of Ecology 94:118-130.
- Reilly, M.J., M.C. Wimberly, and C.L. Newell. 2006b. Wildfire effects on β -diversity and species turnover in a forested landscape. Journal of Vegetation Science 17:447-454.
- Roleček, J., M. Chytrý, M. Háyek, S. Lvoncik, and L. Tichý, L. 2007. Sampling in large-scale vegetation studies: Do not sacrifice ecological thinking to statistical puritanism. Folia Geobotanica 42, 199-208.
- Schwinning, S., and J. Weiner. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia 113:447-455.
- Schafale, M.P. 2012. Guide to the natural communities of North Carolina. Fourth Approximation. North Carolina Natural Heritage Program. Department of Environment and Natural Resources. 208 pp.
- Shmida, A., and S. Ellner 1984. Coexistence of plants species with similar niches. Vegetatio 58:29-55.

- Shmida, A., and M.V. Wilson. 1985. Biological determinants of species diversity. *Journal of Biogeography* 12:1-20.
- Sorrie, B.A., and A.S. Weakley. 2001. Coastal Plain vascular plant endemics: phytogeographic patterns. *Castanea* 66:50-82.
- Sparks, J.C., R.E. Masters, D.M. Engle, M.W. Palmer, and G.A. Bukenhofer. 1998. Effects of late growing-season and late dormant-season prescribed fire on herbaceous vegetation in restored pine-grassland communities. *Journal of Vegetation Science* 9: 133-142
- Stohlgren, T. J., M.B. Falkner, and L.D. Schell. 1995. A modified-Whittaker nested vegetation sampling method. *Vegetatio* 117:113-121.
- Sykes, M.T., E. van der Maarel, R.K. Peet, and J. Willems. 1994. High species mobility in species-rich plant communities: an intercontinental comparison. *Folia Geobot. Phytotax.* 29:439-448.
- Taverna, K., R.K. Peet, and L. Phillips. 2005. Long-term change in ground-layer vegetation of deciduous forests of the North Carolina Piedmont, USA. *Journal of Ecology* 93:202-213.
- Townsend, P.A. 2001. Relationships between vegetation patterns and hydroperiod on the Roanoke River Floodplain, North Carolina. *Plant Ecology* 156:43–58.
- Ulrey, C.J. 2002. The relationship between soil fertility and the forests of the Southern Appalachian region. Ph.D. dissertation. North Carolina State University, Raleigh, NC, 234 pp.
- US EPA [U.S. Environmental Protection Agency]. 2011. Level III ecoregions of the continental United States. National Health and Environmental Effects Research Laboratory. ftp.epa.gov/wed/ecoregions/us/Eco_Level_III_US.pdf
- US FGDC [U.S. Federal Geographic Data Committee] 2008. National Vegetation Classification Standard, Version 2. FGDC-STD-005-2008 (Version 2). http://www.fgdc.gov/standards/projects/FGDC-standards-projects/vegetation/NVCS_V2_FINAL_2008-02.pdf
- van der Maarel, E., and M.T. Sykes. 1993. Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. *Journal of Vegetation Science* 4:179–188.
- Walker, J., and R.K. Peet. 1983. Composition and species diversity of pine-wiregrass savannas of the Green Swamp, North Carolina. *Vegetation* 55: 163-179.
- Wheeler, B.E. 2011. Species diversity of vegetation in the Carolinas: The influence and interaction of scale of observation, soil nutrients, and disturbance events. Ph.D. Dissertation. University of North Carolina at Chapel Hill, Chapel Hill, North Carolina. 181 pp.
- Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. *Ecological Monographs* 26:1-80.
- Whittaker, R.H. 1972. Evolution and measurement of species diversity. *Taxon* 21: 213-251.
- Willig, M.R. 2011. Biodiversity and productivity. *Science* 333:1709-1710.
- Wilson, J.B. 2011. The twelve theories of co-existence in plant communities: the doubtful, the important and the unexplored. *Journal of Vegetation Science* 22:184-195.
- Wilson, J.B., R.K. Peet J. Dengler, and M. Pärtel. 2012. Plant species richness: the world records. *Journal of Vegetation Science* 23: 796-802.