SPECIES DIVERSITY OF VEGETATION IN THE CAROLINAS: THE INFLUENCE AND INTERACTION OF SCALE OF OBSERVATION, SOIL NUTRIENTS, AND DISTURBANCE EVENTS

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Abstract

Brooke Ellen Wheeler: Species Diversity of vegetation in the Carolinas: The influence and interaction of soil nutrients, scale of observation, and disturbance events
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Ecological determinants of diversity operate across a variety of scales with impacts ranging from small-scale, local influences to ecosystem-wide effects. Because there is no way to know a priori at which scale specific mechanisms influence diversity, observation at multiple scales is essential. In addition, consideration of the influence of resource availability is necessary, in part because the distribution of soil nutrients can be intrinsically spatially patchy, or patchy as a consequence of small-scale disturbance. Although previous studies of forest disturbances and diversity have focused on light, soil nutrient and water availability also affect vegetation response. Thus, to understand patterns in forest diversity it is essential to consider simultaneously scale of observation, disturbance, and availability of resources including light, water, and soil nutrients.

I provide a review and evaluation of multi-scale methodologies for observing forest diversity that can be used as a guide for researchers, managers, and conservationists. I then examine the relationship between soil nutrients and diversity across scales in longleaf pine and southern Appalachian vegetation. I next use structural equation modeling to investigate the productivity-diversity relationship. The previous sections are brought together to cast a new paradigm for how to view gap dynamics within a framework that considers the resource context and its impact on the role of subordinate species as filters and in the context of the structural carbon-nutrient balance hypothesis. Finally, I provide an initial test of this framework with field data from North Carolina forest gaps.

My results emphasize the importance of matching study objectives with methodology and suggest inclusion of multi-scale samples whenever possible. In longleaf pine communities, silt and soil *p*H were the strongest predictors of diversity, and models with soil nutrients and texture predicted diversity well. In mountain forests, soil *p*H and nutrients, especially calcium and manganese, were the best indicators of diversity. Structural equation models demonstrated an influence of productivity on diversity. Mountain models worked best with local predictors, while the best longleaf model had local and regional predictors. Sampling of forest gaps provided some support for the resource context framework for gap dynamics.

To my family and my friends

who believed in me, encouraged me, supported me, and walked with me during this part of my journey.

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Chapter 1: Introduction

Ecological determinants of diversity operate across a variety of scales with impacts ranging from small-scale, local influences to ecosystem-wide effects. Because different mechanisms may be influencing diversity at different scales, the emergent patterns may also differ across scales (Levin 1992). When studying a system to determine the patterns of diversity, there is no “correct” scale at which to observe (Wiens 1989, Levin 1992) and the appropriate scale of observation is not known *a priori*. Thus, in order to examine patterns of diversity, multiple spatial scales must usually be considered.

Beyond evaluating the influence of scale, a consideration of the influence of resource availability is necessary to fully understand diversity in vegetation. Resources are not uniformly distributed or equally available. In addition to light as an energy source, carbon, oxygen, and water, plants require many nutrients acquired from the soil. Plants use larger amounts of the macronutrients nitrogen, phosphorous and potassium. However, they also need small amounts of several trace or micronutrients including manganese, sodium, nickel (Troeh and Thompson 2005). Because the distribution of soil nutrients is spatially patchy, it is important to examine the relationship between diversity and availability of soil nutrients across scales. Differences in soil variables correlated with diversity within communities may be due to mechanisms operating at a smaller scale, or small-scale variability in these variables. However, differences between communities may suggest influences of soil nutrients in determining diversity at larger scales.

An understanding of the relationship between nutrient availability and diversity can contribute to understanding patterns in productivity and diversity. Recent research has suggested that the debate over the relationship between productivity and diversity is driven by differences in proxies for productivity, the use of experimental versus field data, and differences in scale (Cardinale et al. 2009). The perspective that diversity both affects and is affected by productivity has been documented in an experimental predator-prey system (Cardinale et al. 2006) and in an experimental algal community (Cardinale et al. 2009). However, the multivariate productivity diversity hypothesis (Cardinale et al. 2009) has yet to be examined in terrestrial plant communities or with observational data. Therefore, the next step in determining whether this proposed relationship holds true in other systems is testing the relationships between nutrient availability, productivity, and diversity using observational data from other systems.

Soil nutrient availability may also interact with small-scale disturbance in forests. Gaps in forest canopies provide heterogeneity and temporal changes in light availability (Canham 1988, Platt and Strong 1989, Canham et al. 1990) that increase diversity (Pickett and White 1985). However, because light is not the only essential resource for plant growth, the response of vegetation at a given location is also affected by soil nutrient and water availability. It is essential to consider not just a single resource, but rather the synergistic interactions of all these resources.

In this work, I provide a practical discussion of including multiple scales in ecological studies, an investigation of the productivity-diversity relationship using modeling and observational data, and a novel look at factors affecting forest gap dynamics. These discussions are organized to move from a broadly applicable guide to available multi-scale methodologies in Chapter 2, to an examination of nutrients, diversity, and productivity at multiple scales in Chapters 3 and 4, and then to a detailed look at the influence of disturbance in the context of resource availability in Chapters 5 and 6.

Measuring variables of interest at a relevant scale determines both the ability to detect patterns and understand processes in ecology. Selection of the appropriate scale of observation is influenced by a variety of factors including, but not limited to, the study system, funding, available time and aims of the study. Because the scale of observation may determine whether a pattern is detected or missed and the mechanisms influencing variables of interest such as diversity may have different critical scales, a multi-scale methodology is useful and recommended for most studies. In Chapter 2, I review the advantages of multi-scale methodologies for field work in plant communities, and compare available methods with respect to analytical criteria, efficiency of data acquisition, and flexibility. This provides a guide to selection of an appropriate methodology for researchers, managers, and conservationists.

Building on the importance of multi-scale observations, in Chapter 3 I examine a suite of soil nutrients in relation to plant species diversity across multiple scales in longleaf pine communities in the Coastal Plain and forest communities in the southern Appalachian Mountains of the Carolinas. This analysis explores how the relationship of diversity and soil nutrients differs with scale of observation and between two different community types. It provides a basis for modeling the relationship of diversity and soil resources by establishing path models and conducting confirmatory factor analysis for the relationships between soil nutrients and diversity. Models change slightly across scales; however, the models for longleaf pine plots and montane forest plots differ significantly. Diversity in longleaf pine plots is best predicted by soil texture and soil nutrients, whereas in the mountains *p*H and soil nutrients predict diversity.

Building on the soil-diversity models from Chapter 3, in Chapter 4 I model plant productivity and diversity using Structural Equation Modeling in two separate systems: longleaf pine communities in the coastal plain and the southern Appalachian montane forests. The productivity-diversity relationship is one of the most studied, yet most debated relationships in ecology (Waide et al. 1999, Gross et al. 2000, Fridley 2002, Worm and Duffy 2003, Gross and Cardinale 2007). Cardinale et al. (2009) proposed a multivariate productivity-diversity hypothesis to reconcile historical conceptualization of diversity being dependent on productivity with more recent studies that suggest productivity is driven by diversity, but is also indirectly affected by nutrient availability. While there is some experimental evidence to support this hypothesis in streams (Cardinale et al. 2009), it has not been tested in natural systems or terrestrial plant systems. To further our understanding of the diversity-productivity relationship, models of the hypothesis should be tested with data from natural systems. Additionally, the question remains as to whether the pattern of the productivity-diversity relationship is general or system specific. Structural equation modeling is an ideal method for examining the directionality of the productivity-diversity relationship. Models are tested with plot-level data and remotely-sensed data.

Chapter 5 addresses a specific instance of the interplay between multiple ecological parameters on diversity by describing a new framework for gap dynamics: the influence of small disturbances in forests results from both light availability and resource context. In considering plant diversity in forest communities, the importance of disturbance has been well-established. Disturbance in the form of forest gaps opens up resources, allowing individuals to grow into the canopy. Previous work on gaps has focused primarily on light availability; however, light is not sufficient for plant growth. The increase in light availability in and around gaps is overlaid onto the distribution of other necessary nutrients. This necessitates an incorporation of multiple resource gradients into the theory of gap dynamics. In Chapter 5, I conduct a brief review of the literature, and then outline a new unifying model for how to view gap dynamics within a framework that considers the resource context: both the influence of subordinate species as filters (Grime 1998) and the implicaitons of the structural carbon-nutrient balance hypothesis (Graves et al. 2006). This work represents an important departure from the classical theory towards incorporating the synergistic effects of the availability of multiple resources.

This theoretical framework of a resource context for gap dynamics lays out predictions, which have yet to be tested across a range of resource availabilities. Specifically, in temperate forests, gaps are expected to have a greater impact on woody species regeneration at the high end of the nutrient gradient, where there is a strong herb layer filtering regeneration, and at the low end of the nutrient gradient in the presence of a dense evergreen shrub layer. In Chapter 6, I examine the role of soil nutrients in shaping tree regeneration in forest gaps in North Carolina. Fieldwork in gaps from a range of soil types looks at the importance of gaps for tree regeneration with respect to soil nutrient availability as a first step in testing the theoretical framework described in Chapter 5. The density of saplings and diversity of woody species is examined across gaps comparing the advance regeneration present underneath intact canopy to the saplings growing into hurricane gaps. This serves as an initial test of the differences in regeneration in gaps along a soil nutrient gradient.

The aim of this dissertation is to better understand the plant diversity in the Carolinas. First the importance of scale of observation in sampling is considered. The influence of soil nutrients is then examined at multiple scales, and theoretical models of the productivity diversity relationship are tested. Finally the interaction of nutrient availability and small-scale disturbance in the form of forest gaps is addressed both theoretically and with fieldwork.

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Chapter 2: A comparison of multi-scale vegetation survey methods: matching methods with objectives[1]

Abstract

Because community-level processes such as those driving species richness and composition are scale-dependent, selection of an appropriate and efficient method for recording vegetation is an essential initial step towards obtaining accurate and appropriate field measurements for both applied and theoretical purposes. We provide an overview of available multi-scale vegetation plot designs for inventory of species richness and composition. We examine a wide variety of designs with respect to analytical criteria, efficiency of data acquisition, and flexibility. We advocate use of a multi-scale methodology whenever resources permit, with the Dengler and Carolina Vegetation Survey methodologies being the most flexible and efficient options.

Introduction

Selection of an appropriate and efficient method for recording vegetation is a first and critical step toward obtaining field measurements for inventory and monitoring, as well as for answering theoretical questions in ecology. Increased recognition of the variation in ecological patterns and processes when examined across a range of spatial scales has led to evolution and increased application of multi-scale methodologies for recording vegetation. In light of recent publications (e.g. Stohlgren 2007, Dengler 2009) advocating various methodologies, we take a step back to consider how survey design can and should vary and

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[1] Chapter 2 was co-authored with L.A. Reilly, P.S. White, T.R. Wentworth, J.A. Fridley, R.K. Peet.

compare several available multi-scale methodologies. Specifically, we provide an in-depth evaluation of how research goals should influence research methodology through consideration of data collection efficiency, statistical aspects of the data, and applicability of the data obtained. We also emphasize the need to balance efficient collection of data with consideration for broad current and future applicability.

Because processes such as those relating to species richness and composition are typically scale-dependent (Huston 1994, Rosenzweig 1995, Fridley 2001, Fridley et al 2006, Chase and Liebold 2002), it is important that general sampling protocols quantify richness and composition across a variety of spatial scales. In particular, recording richness and composition at multiple spatial scales has at least four distinct benefits: (1) as research questions and objectives evolve, analyses can be shifted to the scale most relevant to the question; (2) multiple scales allow for examination of the mathematical form of the increase in species richness with increasing area, which may be the attribute of greatest interest (Gleason 1925, Williams 1964, Rosenzweig 1995); (3) species richness and composition data spanning multiple spatial scales facilitates comparison with studies at varied scales and extrapolation to larger scales; and (4) when trying to monitor or detect a change in species richness or composition over time, there is no appropriate scale for observation because changes might be different at different scales, or vary with the duration of the monitoring period.

Increased recognition of the value of a multi-scale framework for general purpose vegetation surveys has led to several suggested protocols (e.g., Whittaker et al. 1979, Peet et al. 1998, Stohlgren 2007, Dengler 2009). Although there have been several reviews of methodologies for recording vegetation (Mueller-Dombois and Ellenberg 1974, Stohlgren et al. 1998, Keeley and Fotheringham 2005), none have addressed the issue of scale-sensitivity and how to optimize a design for given objectives. Stohlgren (2007) does make recommendations for multi-scale designs for recording plant diversity and community composition and advocates a particular methodology, but he does not systematically compare the alternative protocols. Dengler (2009) also provides a brief overview of several methodologies, though he too emphasizes one technique and as a consequence omits factors that can be important in selecting an optimal methodology for a particular objective. Given acceptance of a need for multi-scale vegetation records, but with a plethora of available protocols, the individual researcher has to select the most appropriate methodology in the context of the goals of the particular study.

In addition to the recognition of the importance of multiscale methodology, major sampling initiatives in the United States highlight the importance of selecting appropriate methodologies. The National Wetland Condition Assessment, which begins sampling in 2011, is collecting data to assess variables in key taxa and report on the quality of wetlands across the nation. A second broad-scale initiative is the National Ecological Observatory Network (NEON). NEON aims to establish a multiscale network of plots across 20 ecoclimatic domains on the continent. While the multiscale methodology of NEON is inherent in its collection of both field data at sites and remotely sensed data, the goal of standardized, comparable data that can be used for multiple purposes makes the sampling design critical.

When selecting the appropriate methodology for recording vegetation, plot attributes, those variables that must be selected include 1) the plot size and shape, 2) the size, shape, number, and placement of subplots, 3) whether to sample completely or use sub-sampling, and 4) the actual variables to be recorded (e.g., counts of individuals, measurements of individuals, rooted presence, or above-ground presence or cover). These variables affect both the time it takes to acquire the data in the field and the information available after the data have been collected. The size of the plot influences the survey time per plot, the area sampled, and, potentially, whether or not the area is homogeneous, since heterogeneity will increase with larger area. The shape and configuration of the plot determines the difficulty of setting the plot up in the field. The combination of shape and size of the plot influence the comparability of the plot to previously sampled plots and the relationship of increase in grain and extent. The number of subplots of each size entails a tradeoff between survey time and number of replicates of each size; the placement of the subplots should be considered to maximize efficiency and the intended use of the data. Finally, the specific information recorded is driven primarily by research questions and objectives, but again influences the ability to compare to other datasets.

Below, we provide an overview of available multi-scale vegetation plot designs for inventory of species richness and composition. We examine a wide variety of designs with respect to analytical criteria, efficiency of data acquisition, and flexibility, and we provide recommendations on the appropriateness of their usage in various situations. The design selected for a particular project should maximize efficiency of data acquisition in the field, replication and replicability of plots and subplots, and comparability to currently available data, while also minimizing the confounding of grain and extent with increasing subplot size.

Available multi-scale methodologies

In each of the following designs, species presence and cover/abundance values are determined at multiple scales, with species presence/absence being the basic measurement. Stem counts and measurements can be included with any methodology. However, the availability of data from multiple-scales is dependent on the methodology (both arrangement of subplots, and replication of subplots). Below we discuss multi-scale designs for recording vegetation covered by Stohlgren (2007), as well as Peet et al.'s (1998) flexible nested method, Dengler's methodology (2009), and several general gridded designs.

Descriptions of the methodologies and a brief summary of their applicability are presented first, followed by a detailed analysis of how to optimally match methods with goals and objectives. Simple nested plots provide the most straight forward approach and are discussed here primarily because they are often included in a modular fashion within more complex designs. Next we present chronologically the multi-scale plots derived from Whittaker plots, together with a summary of subplots and extent by grain size (Table 2.1). Gridded plots are presented in the last section as they represent the most general but time-intensive of the available approaches.

Simple nested methods

Nested concentric.

This design is also referred to as a target plot (Figure 2.1). Nested circular quadrats of increasing size are centered on a focal point. The size of the quadrats can be tailored to suit the specific aims of the study. This is a seldom-used design (Stohlgren, 2007) presented primarily for illustration. In a forested community, it would be difficult and potentially inefficient to implement because of the height and density of woody stems; however, in a low-growing herbaceous community such as some grasslands, it would be more feasible to use this design. This methodology has the lowest increase in extent with increase in area; however, it only has one replicate for each size of subplot. Although the subplots are of a consistent shape, circular plots are less common, and thus difficult to compare to other data.

Nested quadrats overlapping 50%.

Successively larger quadrats are formed by doubling the initial square quadrat, so that the odd quadrats are squares and the even quadrats are rectangles (Figure 2.1). While the design could be reduced or infinitely expanded, one option starts from 0.5 x 0.5m and expands to 8 x 8m (Mueller-Dombois and Ellenberg 1974, Barbour et al. 1999). The nesting sequence could be altered to increase by a different factor (such as 4 or 10). The species present in each subplot are recorded and, because the quadrats, are nested all species in a given quadrat are also present in the next larger size quadrat. Nesting of the subplots allows for appropriate analysis of species area curves; however, by doubling the subplot sizes, the shape of the subplots alternates between square and rectangular further confounding grain size and extent.

Whittaker plots and their modifications.

In order to clarify the nomenclature and specific designs of currently applied multi-scale methodologies as well as examine their advantages, it is useful to examine the evolution of the Whittaker plot design through time.

Classic Whittaker plot.

When Robert H. Whittaker recorded vegetation for his classic study of the Siskyou Mountains (Whittaker 1960), he used a 20 x 50m plot which had 25 1x1m subplots distributed every other meter on alternating sides along the center line of the plot. This plot was intended primarily to document composition, rather than the effects of scale (Whittaker 1960, Whittaker and Niering 1965).

***Whittaker diversity plot*.**

As part of a broader research agenda to compare vegetation of Mediterranean ecosystems of the world, Whittaker experimented with various modifications of this plot design (e.g., expansion to a 1 ha plot in Australia (Whittaker et al. 1979). In 1975 in Australia (Whittaker et al. 1979), and 1976-1977 in Israel (Naveh and Whittaker 1980) Whittaker used a design that is indistinguishable from the Whittaker plot described much later by Shmida (1984), and which was intended to capture both diversity at multiple scales and the composition of plant communities.

The Whittaker diversity plot design is based on a 20 x 50m vegetation plot that is intended to represent a homogeneous area (Shmida 1984). Ten 1 x 1m contiguous subplots are placed along the center axis of the plot. Two 2 x 5m subplots are overlaid on the smaller subplots, which are then surrounded by a 10 x 10m subplot (Figure 2.1). This yields four scales with ten 1m^2, two 10m^2, one 100m^2, and one 1000m^2 plot.

This Whittaker diversity plot has since been modified independently by various researchers. Below we discuss three of these modifications: the Carolina Vegetation Survey (Peet et al. 1998), the Modified Whittaker (Stohlgren et al. 1995, Stohlgren 2007), and the Keeley plot (Keeley et al. 1995, Carrington and Keeley 1999, Dengler 2009).

Carolina vegetation survey (CVS).

In1988, Peet et al. (1998) designed and began implementing the Carolina Vegetation Survey (CVS) methodology, which is an adaptation of the Whittaker diversity plot design that contains nested subplots. This design has been widely implemented in the southeastern US. The CVS methodology was developed with the goal of having a flexible method to capture the diversity of homogeneous vegetation at multiple scales. The nested design is intended to minimize the confounding of grain and extent and maximize efficiency of recording vegetation.

A standard plot consists of a 20 x 50m plot with ten contiguous 10 x 10m quadrats or "modules" within it. Four intensive modules (modules 2, 3, 8 and 9) are sampled with nested subplots in 2 corners of the module. In each intensive corner, nested square subplots 0.10m, 0.32m, 1m, and 3.16m on each side are sampled (Figure 2.2a, Table 2.1) (Peet et al. 1998). The standard plot layout yields eight 0.01m^2, eight 0.1m^2, eight 1m^2, eight 10m^2, four 100m^2, and one 400m^2 subplot within one 1000m^2 plot. The contiguous placement of intensive modules is advantageous because it allows lumping and splitting of the subplots as needed for analysis or comparison to other data. All subplots are consistently square; however, at the full-plot scale, the shape shifts to rectangular. The plot and subplot shapes and sizes yield data that are easily compared to those from other methods.

The CVS methodology has built-in flexibility for use with various module layouts and levels depending on the study objectives, time available, and study area (Peet et al. 1998, Lee et al. 2008). Thus the methodology has built-in guidelines for separate recording of planted stems for monitoring of restoration efforts, simpler recording at fewer scales if time does not permit a full set of nested subplots, and varying shapes for areas where a full plot may not fit or is not necessary to capture an accurate picture of the vegetation. As a general rule, a full 20 x 50m plot is recommended to fully capture forest communities. Alternative plot layouts include a 20 x 20m plot of 4 intensive modules, and single module plots of either 10 x 10m or 5 x 20m plots (Lee et al. 2008, Figure 2.3, Table 2.1). CVS plots could also be nested into a larger plot (Fridley et al. 2005). A smaller subplot scale could also be incorporated if desired; this is particularly useful in species-rich, fine-scale vegetation (Van der Maarel and Sykes 1993, Willems et al. 1993, Sykes et al. 1994, Fridley et al. 2006).

Modified Whittaker diversity plot.

Stohlgren et al. (1995) also modified the Schmida (1984) Whittaker diversity plot. This method, called "the Modified Whittaker plot" (Stohlgren et al. 1995, Stohlgren 2007), contains non-nested subplots and has been used widely in the western US.

The Modified Whittaker plot layout distributes the subplots within the plot so they are non-nested (Stohlgren et al. 1995, Stohlgren 2007). The 100m^2 subplot is in the center (5x20m), the ten 1 x 1m subplots are distributed around the perimeter of the plot, and the two 2 x 5m subplots are in diagonally opposite corners (Figure 2.2b). Like the Whittaker method, this generates ten 1m^2, two 10m^2, one 100m^2 subplot within one 1000m^2 plot (Table 2.1). The subplots are not nested within each other, but contained within the 20 x 50m plot. The subplot shape varies between square and rectangular, and the distribution of the subplots across the area of the full plot in a non-nested fashion confounds the increase in extent with the increasing area (size) of the subplots.

***Keeley plot*.**

Keeley (1995) published a modification of the Whittaker plot that contains three nested spatial scale, and this method has been used in the western US and the fynbos of South Africa. Keeley's design has also been referred to as a "modified Whittaker plot" (Schwilk et al. 1997, Carrington and Keeley 1999, Keeley and Fotheringham 2003, Keeley et al. 2003). This design has fewer spatial scales of nested plots; however, the subplots are distributed across all of the 100m^2 subplots.

The Keeley plot is a 20 x 50m vegetation plot with ten contiguous 10 x 10m subplots within it (Keeley et al. 1995, Carrington and Keeley 1999). In each 10 x 10m subplot, there are 2 smaller subplots of 1 x 1m positioned on opposite sides (Figure 2.1). This results in 20 1m^2, and ten 100m^2 subplots, within one 1000m^2 plot. Subplots are all square but are contained in a rectangular full plot. In this methodology, only three scales are surveyed, and the subplots are spread over the entire plot.

***Dengler plot*.**

Dengler (2009) adapted his previously used 9m^2 methodology to a log10 based system in order to be more consistent with widely available data based on Whittaker plot variants. Dengler's methodology is a multi-scale design based on its application since 2004, primarily in grassland communities in Europe. The design contains nested square subplots within a 31.62 x 31.62m plot. The methodology has two standard forms: the minimum variant which has three nests of subplots placed along the diagonal of the plot (Figure 2.2c, Table 2.1), yielding three 0.01m^2, three 0.1m^2, three 1m^2, three 10m^2, and three 100m^2 subplots within one 1000m^2 plot, and the intensive variant, which has five nests of subplots one 100m^2 at each corner and one in the center and further subplots placed on diagonal corners, yielding eighty 0.01m^2, forty 0.1m^2, twenty 1m^2, ten 10m^2, and five 100m^2 subplots within one 1000m^2 plot. This design maintains a uniform subplot shape and spacing of plot size. However the subplots are not contiguous, so they cannot be combined to create other plot sizes or compared to plots of different sizes, and the square full plot size is not as easily compared to previous data.

General gridded plots

A gridded system allows for almost infinite variations in measuring vegetation. Almost any schema could be extracted down to the grain size of the grid units and analyzed by incrementally increasing the units in a nested manner. The vegetation data available in a gridded design allow for many different combinations of multi-scale analysis. However, these methodologies tend to be much more time intensive. Often gridded plots are geared more towards long-term measurements or questions regarding spatial analysis, whereas the previously discussed methods are designed for recording many different plots in several areas. Although there are many examples of this type of plot, here we briefly describe three examples: transects, the Palmer/Oosting plot, and the fully mapped plot.

Transects.

In general terms, a transect is a reference line along which subplots are placed, usually with the intent to maximize spatial extent per survey effort. A transect design is flexible and could be modified to suit the specific aims of a study and the size of the study area. If quadrats are contiguous they can be combined to allow for multi-scale analyses.

Quadrat size can also be adjusted if needed to better capture a given vegetation type. As an example, one specific adaptation of this design into a flexible transect methodology was used by Walker et al. (2003) (Figure 2.1). Square quadrats 0.5m on each side were placed every 5m along a transect. In areas of interest, an intensive transect up to 150m long was used with a grid of eight contiguous quadrats set up along the transect (Walker et al. 2003). The intensive transect area allows for analysis of data at multiple scales. While the combining of non-contiguous quadrats could be considered a multi-scale analysis, we consider only quadrats of multiple sizes to be multi-scale units.

Palmer/Oosting Plot.

The Palmer/Oosting plot is an example of a large, gridded, permanent plot (in this case a 16 x16 grid of 16m x16m subplots) that contains fully nested subplots originating at a single corner. The subplots are 0.125, 0.25, 0.5, 1, 2, 4, 8, and 16m on a side (Reed et al. 1993, Palmer and White 1994, Palmer et al. 2007). The Palmer/Oosting plot is similar to those used by the Carolina Vegetation Survey; however the logarithmic interval of increase in scale has a base of 4 rather than 10. This is a fully nested plot with one subplot at each scale.

Fully mapped plot.

A gridded plot with all stems fully mapped also presents opportunities for multi-scale analysis. One example of this type of design is the mapped 50ha plot of old growth tropical forest on Barro Colorado Island (Hubbell et al. 1999) which has since been used in plots across the tropics by the Center for Tropical Forest Science (Condit 1998). With all stems mapped in a given area, typically 25-50m on each side, the data can be analyzed in many ways including multi-scale nested and non-nested approaches. However, this is obviously a very time-intensive approach and probably best suited for permanent long-term research for stem data only.

Discussion

Vegetation data are collected for many purposes. Depending on the goals of a given study, certain aspects of the design will be prioritized. We consider three general attributes of designs: analytical objectives, efficiency of use, and flexibility of the design and the data collected using it. Table 2.2 contains a summary of criteria and methods that are best suited for each. Although we focus on vegetation, all methodologies and considerations discussed here should apply for plots of any sessile organism or group of organisms selected for study.

Analytical objectives

The analytical considerations of importance will vary depending on the specific goals of the study. The goals may include very different general objectives: (1) using this pattern to determine the species-area relationship and contributions that grain, extent, and environment make to this relationship in different communities for the purpose of evaluating process (such as the factors underlying diversity differences among communities), (2) monitoring changes in richness and or the progress of a restoration effort, and (3) inventorying the species in a landscape, community, or region that is larger than the largest grain size surveyed (such as building a species list). Nested multi-scale designs better address the first and second objectives, while the third objective does not require multi-scale methodology; however, use of multi-scale designs for the third objective will result in a more thorough species list and can be attained from available multi-scale plot data. In addition to these objectives, multiscale data can be used to examine compositional change and drivers of composition across scales.

For both process- and pattern-based studies, concepts of spatial grain and extent are central to our reasoning. Spatial grain is the area of the smallest unit surveyed, whereas spatial extent is the distance between the two most distant survey points. Both attributes of scale affect the species-area relationship as well as species accumulation, with grain having a stronger effect on richness (Palmer and White, 1994). For example, Palmer and White (1994) found that the effects of grain and extent interact such that, across small grain sizes (smallest subplots), extent has relatively little effect on increasing richness; however, as grain size increases, the effect of extent on richness also increases. Thus, extent is less important at small scales, but as the size of a subplot increases, it is essential to minimize changes in extent in order to tease apart the effects of grain and extent on species richness. For this reason, we advocate the use of nested subplots, because complete nesting ensures a minimal increase in extent with the necessary increase in grain size. If nested subplots are placed contiguously, the total increase in extent is also minimized allowing for averaging of subplot values with a minimal change in environmental conditions as well as extent (e.g. CVS protocol). However, if nested subplots are not contiguous (such as the nested subplots of Dengler 2009, and all non-nested subplots), there will be a greater increase in extent between subplots as well as greater changes in environmental conditions. Non-nested multi-scale designs only increase extent relative to similar nested methods up to the largest plot size;

total extent is still constrained by the largest plot size (0.1 ha for many of the designs discussed in this paper).

Another concept central to our argument is the species-area relationship. Unfortunately, there is substantial confusion in the literature with respect to species-area curves (SAR) and species-accumulation curves (SAC, also called collector's curves), and this confusion has led to erroneous conclusions about species-area relationships, patterns of richness, and the efficacy of different survey designs. A SAR is created by plotting the number of species versus area sampled (grain size), and thus the number of species encountered would be expected to increase monotonically as a function of the area inventoried. Individual species-area curves developed from non-nested designs may exhibit reversals of richness increase with area if by chance a larger area contains fewer species than the previously measured smaller quadrat. However, with a nested plot design, the SAR will always increase monotonically since each larger area completely contains each smaller area sampled. A SAC is constructed with the number of species encountered (a cumulative list) versus the cumulative area sampled (Rosenzweig 1995). For a fully nested design, the SAC will be the same as the SAR. However, for a non-nested design, the two may differ.

Stohlgren et al. (1995) illustrate the potential for confusion by both plotting the cumulative richness across subplots rather than the number of species observed at particular grain sizes and also accumulating species but not area sampled. For non-nested subplots, the SAR should be constructed by accumulating neither species nor area sampled, but rather by plotting the number of species observed at each grain size against the grain size. A non-nested SAC, on the other hand, should be created by accumulating both species and area. Stohlgren et al. (1995) plotted accumulated species richness against unaccumulated area, rather than adding together the areas of subplots. Dengler (2008) further describes the confusion created when Stohlgren (2007) defined a SAR as: “The species-area curve plots the cumulative number of species against the cumulative area of the quadrats (or area searched) - the quadrats do not have to be of similar size.” As stated above, we disagree. His definition produces a SAC rather than a SAR. For instance, island-based SARs accumulate neither species nor area, which we believe establishes the long-used definition of what a species area analysis is intended to be.

If the sole aim of the research is to build a species list and hence to capture the greatest number of species possible within a specific subsample of a larger area (i.e. when the largest extent is not itself sampled as the largest grain size), then a multi-scale approach would not be necessary but would increase the intensity of the search for species. Perhaps the most thorough inventory design would include plots stratified by environmental factors (Jobe 2006), complemented by strategic searches by teams of experts and volunteers.

Non-nested designs are sometimes rationalized on the premise that non-nested subplots of different scales (grain sizes) are more statistically independent (Stohlgren, Falkner, and Schell, 1995; Stohlgren, 2007). The degree of independence, however, is a function of both the amount of overlapping area and the distance between subplots. Because the subplots are constrained to fall within the largest grain size (0.1 ha in several of the designs compared in this paper), both nested and non-nested plot designs discussed in this paper (Whittaker, Modified Whittaker, Keeley, Dengler and CVS) have some level of spatial autocorrelation in estimates of richness at different scales. Thus, the statistical objective of independence of sub-samples is not achieved by simply moving subplots apart arbitrarily within a larger plot. However, fully nested designs allow explicit investigation of the nature of spatial autocorrelation and allow the separate analysis of the effects of grain size and spatial extent on species richness. When nesting is replicated within a plot (as in the CVS and Dengler methods) it also allows the construction of both nested and non-nested SACs and SARs so that investigators can detect the influence of spatial autocorrelation in their data. Rather than attempting to escape statistical dependence by minimizing autocorrelation, nested designs provide a means to interpret the autocorrelation, both statistically and biologically.

The issue of statistical independence is also related to how the data are used. If subplots are considered to be the sample unit, then subplots within a larger plot are spatially autocorrelated, regardless of whether they are nested within the plot or not. If, on the other hand, the SAR/SAC itself is considered to be the observation to be analyzed (that is, n=1 for a series of quadrats, not n=the number of quadrats), then the independence lies in the independence of the species area relationships from replicate plots, rather than in the data needed to produce a single SAR.

To separate the effects of grain and extent, a nested plot design has the following advantage. Nested designs allow examination of the change in species richness with changing grain size of observation while minimizing the effect of extent, and thus minimizing the confounding effects of grain with extent. Nested concentric, the Palmer/Oosting plot design, the CVS protocol, and Dengler’s plot design have a slower gain in extent with increasing grain size, thereby minimizing the change in the ratio of grain:extent. In contrast, non-nested designs confound the influence of grain with that of extent. The change in extent as measured as the entire area of all measured subplots (areal extent) or the greatest distance between the corners of subplots (linear extent) illustrates that nested plot designs have less change in extent with increasing subplot size (Table 2.1). Different communities are likely to differ in both the species-grain relationship and the species-extent relationship for many reasons, including the sizes and packing of individual plant stems in the community and the history of recent disturbances or mortality. The nested overlapping quadrat and Whittaker designs both have some nesting; however the subplot shapes change from square to rectangular, resulting in greater increases in extent than necessary for an increase in area, in other words, a changing grain:extent relationship.

When SARs will be fit to data, nested designs (nested concentric, nested overlapping quadrats, Palmer/Oosting, Dengler, or CVS) have another advantage because they constrain the species-area relationships to a monotonic form. Undesirable reversals of this relationship (e.g., a higher than average richness when a small quadrat lands in a rich patch and a larger quadrat lands in a species-poor patch) are possible when a non-nested design, such as the modified Whittaker, is employed. Additionally, any extrapolation of the relationships discovered in small-scale data to larger scales is inherently a nested approach, so a nested design is preferred because it maintains a consistent approach to data collection.

Replication of subplots is essential to building SARs representative of a given community/landscape/area. A given curve will be affected by the initial starting point, the smallest subplot. According to Stohlgren (2007), this anchor point will have more variability in species number than the larger subplots. Therefore, having replicated subplots is important for building representative species area curves for a given community. Both the CVS protocol and the Modified Whittaker plots have replicated subplots (Table 2.2 and Figure 2.2). The CVS design has more replication across scales within a plot, with eight replicates for each of the four smallest scales and four replicates of the 100m^2 subplot. The Modified

Whittaker design has 10 and two replicates for its two smallest scales, and only one subplot one size smaller than the full plot. There are two fewer scales in the modified Whittaker design than in the CVS design. Additionally, the CVS design gives the option of constructing both nested and non-nested curves. While the quadrats are not independent replicates in either the nested or non-nested designs, and therefore cannot be used to construct independent curves within a single plot, the replicated quadrats can be used to create multiple curves that can then be averaged to produce a single representative curve for each plot. With its additional small scale replication, the CVS method provides a more representative relationship for each plot.

Efficiency

In all field measurement efforts, efficiency is essential because increased time and effort greatly increase the cost of data collection. In a nested design, the smaller subplot is contained in the next larger subplot, decreasing searching time for new species in the larger subplot and reducing effort of moving through sometimes dense or thorny vegetation. The establishment of nested subplots is also simpler because the subplots all start from the same point. Thus, even for the fewer subplots in the non-nested Modified Whittaker relative to the nested CVS design (Table 2.2), the same field workers would have to spend extra time measuring out all of the non-nested corners and starting a new species list in each non-nested module, rather than adding to an existing list from surveying the next smaller unit in a nested design. The number of species lists required to complete plots ranges from 4-5 for a single CVS module and 8 for a full CVS plot, to 160 for the full Dengler plot (Table 2.1). Stohlgren (2007) remarks that complete non-nesting (scattering subplots outside the full 0.1 ha plot) would increase the rate of encountering new species, but this would result in a design that is extremely inefficient to implement and difficult to resample. In addition to increased efficiency in the field, the nested design also generates more data per unit effort (Table 2.1). A nested multi-scale design with replicated nesting is logistically simpler and more time-efficient than a non-nested design. Setup of a series of nested subplots requires less time than setup of a series of non-nested subplots spanning the same range of scales, except when the nested subplots are not centered from one corner, as in the Dengler (maximum) design. It takes additional time and energy to establish and inventory non-nested subplots in different parts of a larger plot or nested subplots anchored at different points (e.g. Dengler Figure 2.2e).

If plots are to be permanently marked and re-sampled, a nested design requires fewer permanent subplot markers and less effort to relocate the subplots than does a non-nested design, if the anchoring point is in the same corner as in the CVS design (11 stakes for full plot, Table 2.1). However, in the Dengler design with the corners placed diagonally, up to 160 stakes would be necessary to accurately relocate the smallest subplots. For efficiency and cost-effectiveness, the CVS method is recommended.

Applicability

A given design may be ideally suited for a particular habitat or community type, but have little use in other conditions. Other designs may be flexible enough to adjust to a broad range of physical settings. In various situations, it may be necessary to modify a design. Of the vegetation designs discussed here, only the CVS protocol and the Dengler design have built-in flexibility. The Dengler (2009) plot has a minimum and maximum design, allowing effort to match available time and resources. However, the two designs differ substantially in layout, preventing on-the-fly adaptation or re-sampling using a different level of intensity. The CVS protocol (Peet et al. 1998, Lee et al. 2008) has built-in flexibility that allows it to be used in a variety of situations where the standard plot may not be best suited, where time or resources do not permit recording all nested subplots, or when it is desirable to continue nesting up to a larger plot size (Fridley et al., 2005) or down to a smaller size (Van der Maarel and Sykes 1993, Willems et al. 1993, Sykes et al. 1994). A mid-scale plot size may be selected as the total plot size in cases when the community is very homogeneous and additional area would not provide additional information. For example, a single CVS module and its nested subplots may be used in isolation (Figure 2.3a) or four intensive modules (Figure 2.3c) may be used. Plot shape may also be adjusted; for example, a single 5m x 20m module or a strip of modules such as a 10m x 50m half-CVS plot (Figure 2.3b, d) may be more appropriate to capture vegetation along a river levee than would a full 20m x 50m plot (Peet et al. 1998, Brown and Peet 2003). However, flexibility, especially in sub-sampling, could be built into other methods as well, although ideally it would be clearly described in the methodology.

While all the vegetation plot designs discussed are appropriate for use in various communities, the Modified Whittaker, Dengler, and CVS designs are most suited for a wide range of communities. These sample the vegetation using many different grain sizes. Fine-scale values of richness are highly constrained by local variation in the density of individual stems, and increased replication of these smaller scales allows those constraints to be removed to provide a species area relationship that is more representative of the community (Fridley et al., 2006).

It is also important to consider compatibility of data collected with that previously collected. Because of the widespread use of 20x50m plots in the US, the Whittaker, Modified Whittaker, Keeley, and CVS designs are more generally compatible with existing data. The CVS method also uses both 1x1m and 10x10 m quadrats, which are used in a wide variety of vegetation types around the world, making CVS data even more generalizeable. Use of a well established and widely-used design is recommended because there are more data available for comparison. The CVS methodology has been implemented across the southeastern US with over 6000 plots currently in the CVS database. The Modified Whittaker plot design has also been applied widely in the Western US. Although the Dengler design has been used in grasslands in Europe, it has not been widely applied in other systems.

Generalizability refers not only to the use of the design itself in different community types, but also to the use of the data. A design can be devised to test a hypothesis developed a priori; such a methodology will maximize the appropriateness of the data for testing the particular hypothesis, but the data generated may not be appropriate for other applications. Conversely, a design can produce data flexible enough to address a multitude of questions. While the data generated may not maximize appropriateness to test any given hypothesis, the data will serve as a robust archive that can be mined to address many fundamental ecological questions.

Further decisions: taxa of interest and determining presence

Following the selection of a methodology for a study, at least two separate decisions remain regarding how to sample: which taxa will be sampled and how to determine if an individual is present in a plot. First, the researcher must decide which taxa are of interest.

Often this includes all vascular plants, or a subset of interest, such as all woody species. Dengler (2009) states that it is imperative to include bryophytes and lichens rather than limiting data collection to vascular plants, despite the admittedly different patterns exhibited by non-vascular plants. While it is important to also study these groups, the decision of which taxa to study using a design is a separate decision; a methodology could be applied to all taxa, vascular plants, or any subset of taxa of interest. Field workers trained in identification of vascular plants are much more available than experts prepared for field identification of vascular plants, bryophytes, and lichens. One common decision is to focus solely on trees or woody species. In general, data should be collected on all necessary taxa determined by the goals/objectives of the study and constraints determined by availability of time, funding, and taxonomic experts.

A second methodology decision, highlighted by Dengler (2008) and at times ignored or glossed over in discussions of methods, is how to determine an individual's (and therefore a species') presence in a plot. When using the "any-part" system (Williamson 2003, Dengler 2008), a plant is present if any part of the plant is visible within the plot (or subplot) as viewed from directly above the plot. The other widely used system, called the grid-point system (Dengler 2008), uses the rooted presence of a plant to determine its occurrence in a plot (e.g. (Condit 1998, Peet et al. 1998). While both systems of determining plant presence are adequate and have been applied in previous studies, and either system can be applied to a chosen methodology, it is important to be clear which system is used when describing methodologies and understand differences in data collected using each method.

The "any-part" system advocated by Dengler (2008) leads to slightly higher species counts in the smaller subplots as well as less consistency between repeat samples. In the field, this system has the advantage of not requiring a separate rule for rootless plants (non-vascular plants including lichens and bryophytes, if they are also being sampled) and epiphytic plants, and it can be made more accurate (in open vegetation under 1m tall) following Dengler's (2009) recommendation of constructing frames matching the size of each subplot to aid in determining whether plant parts are leaning into the boundary of a subplot. This methodology can be applied in short, open vegetation; however, it quickly becomes much less accurate in woody vegetation. Dengler (2009) points out that it is very difficult to look directly above you at a small (e.g. 10cm^2) subplot. In forests, where there may be multiple layers in the canopy and trees moving in the wind, determining presence using only the any-part system is not advisable, especially for plot sizes smaller than 100m^2, as it would not be repeatable or accurate.

Even in short, open vegetation, such as a grassland, the species count today may not be the same tomorrow if it is re-counted tomorrow, because plants may lean into and out of plots. The inflation of number of species present using the "any-part" system is greater at smaller scales, with an average increase of 1% at the 100m^2 plot size, which drops to only 0.2% at the 1000m^2 plot size (based on analysis of plots in the CVS database comparing species counts from cover and rooted presence).

A grid-point system, requiring a plant to be both rooted in a plot, and only counted in one contiguous subplot, has a clear advantage of replicability. If re-sampled the next day, the species count will be the same. When using a grid-point system, a separate rule for recording rootless plants using their vertical projection onto the plot (any- part system) will allow data to be collected on these plants, while still maximizing repeatability. Using a grid-point system and counting a plant in only one subplot also prevents an over-estimation of a species' presence. If data other than simply presence, such as a stem count of woody species, are also being collected, the grid-point system is also preferable because it prevents repeat counting of an individual or inflated density values.

Dengler (2008) claims that the CVS methodology uses a grid-point system. However, the CVS methodology actually calls for grid-point recording of all vascular plants at all plot sizes, and a presence/cover value for all species at both the $100 m^2$ and $1000 m^2$ plot sizes. We maintain that you can apply either system to any design, thus maximizing compatibility and generalizability of data.

Conclusions

Selection of a methodology for recording vegetation should involve consideration of the analytical objectives of the study, efficiency of field measurements, and flexibility of the methods to address a wide range of pattern- and process-based objectives in vegetation research. When possible, the selection of a multi-scale methodology for recording plant species richness or composition is strongly recommended. We suggest that nested designs, such as those of CVS and Dengler, maximize the greatest number of criteria, and because of the flexibility of their design, are the most generally applicable. As with all nested methodologies, CVS and Dengler have minimal confounding of grain and extent, ensuring monotonicity of species-area relationships. The CVS design is efficient for data collection in the field and is the most flexible design of the nested methods, allowing for adaptation of the design for a specific purpose or a particular plot site.

Tables

Table 2.1: Number of plots and extent comparison of CVS, Dengler, and Modified Whittaker methodologies

	CVS (full)	CVS (1module)	Dengler (min)	Dengler (intensive)	Modified Whittaker
0.01 m^2 Subplots	8	4-5	3	80	0
Linear extent	0.14m	0.14m	0.14m	0.14m	-
Area extent	20x20m	10x10m	~30.86m	31.62x31.62m	-
0.1 m^2 Subplots	8	4-5	3	40	0
Linear extent	0.45m	0.45m	0.45m	0.45m	-
Area extent	20x20m	10x10m	~31.03m	31.62x31.62m	-
1 m^2 Subplots	8	4-5	3	20	10
Linear extent	1.4m	1.4m	1.4m	1.4m	2.06m
Area extent	20x20m	10x10m	~31.99m	31.62x31.62m	20x50m
10 m^2 Subplots	8	1	3	10	2
Linear extent	4.5m	4.5m	4.5m	4.5m	5.24m
Area extent	20x20m	10x10m	~35.04m	31.62x31.62m	20x50m
100 m^2 Subplots	4	0	3	5	1
Linear extent	14.1m	14.1m	14.1m	14.1m	20.62m
Area extent	20x20m	10x10m	31.62x31.62m	31.62x31.62m	5x20m
400 m^2 Subplots	1	0	0	0	0
1000 m^2 Subplots	1	0	1	1	1
Linear extent	53.85m	14.1m	44.72m	44.72m	53.85m
Area extent	20x50m	10x10m	31.62x31.62m	31.62x31.62m	20x50m
Lists needed	8	4-5	24	160	13
Stakes required	11	4-5	24	160	16

Table 2.2: Common objectives of vegetation sampling and methods to optimize each. Methods in the left block of the table are for illustrative purposes, methods in the center block of the table are methodologies designed for multi-scale sampling, and methods in the right block are examples of generic gridded sampling designs.

Objective to maximize	Nested Conc.	Nested Overlap	Whittaker	CVS	Modified Whittaker	Keeley	Dengler	Transect	Palmer/ Oosting plot	Fully Gridded
Nested (Y/N)	Yes	Yes	Some	Yes	No	Yes	Yes	Depends	Yes	Depends
Analytical:										
1) Quadrat independence	Poor	Poor	Poor	Poor	Poor	Poor	Poor	Poor	Poor	Poor
2) Minimizing confounding of grain and extent	Good	Acceptable	Acceptable	Good	Poor	Acceptable	Good	Acceptable/ Poor	Good	Acceptable
3) Monotonicity of SPARC	Good	Good	Fair	Good	Poor	Acceptable	Good	Poor	Good	Possible
4) Replication of subplots	No	No	Some	Yes	Yes	Some	Yes	Depends	Yes	Possible
5) Distributuion of subplots across grains	Poor	Poor	Fair	Good	Fair	Poor	Good	Depends	Fair	Flexible
6) Rate/Increment of increase in area/grain	Linear	Linear	Non-linear	Linear/ Log scale	Non-linear	NA (only 2 sizes)	Linear/ Log scale	Depends	Linear	Depends
Efficiency:										
7) Species found per unit effort sampling	Poor	Acceptable	Acceptable	Good	Acceptable	Acceptable	Good	Good	Acceptable	Acceptable
8) Efficiency, cost-effectiveness	Acceptable	Acceptable	Acceptable	Good	Acceptable	Acceptable	Acceptable	Depends	Good	Poor
9) Permanence, ease of relocating	Acceptable	Acceptable	Good	Good	Acceptable	Good	Acceptable	Good	Good	Good
10) Ease of training	Acceptable	Acceptable	Good	Acceptable	Acceptable	Good	Acceptable	Good	Good	Good

Objective to maximize	Nested Conc.	Nested Overlap	Whittaker	CVS	Modified Whittaker	Keeley	Dengler	Transect	Palmer/ Oosting plot	Fully Gridded
Applicability:										
11) Flexibility of use	Poor	Poor	Poor	Good	Poor	Poor	Fair	Good	Poor	Good
12) Appropriateness for various vegetation types	Acceptable	Acceptable	Acceptable	Good	Good	Acceptable	Good	Good	Good	Good
13) Compatibility with data from other methods	Poor	Poor	Acceptable	Good	Acceptable	Acceptable	Acceptable	Acceptable	Acceptable	Good
14) Use of data to test various hypotheses	Poor	Poor	Acceptable	Good	Acceptable	Poor	Good	Acceptable	Acceptable	Good

Figures

Figure 2.1: Layouts of general methodologies provided for comparison. Transect methods are arranged along a line to maximize extent covered per unit effort. The Nested Concentric sampling method consists of nested, circular subplots. The Nested Quadrat method forms successively larger subplots by doubling the smaller subplot area. Keeley plots are 20m x 50m divided into 10m x10m subplots with two 1m x 1m subplots nested inside each. Whittaker diversity plots are 20m x 50m with ten contiguous 1m x 1m subplots, and two 1m x 5m subplots, surrounded by one 10m x 10m subplot.

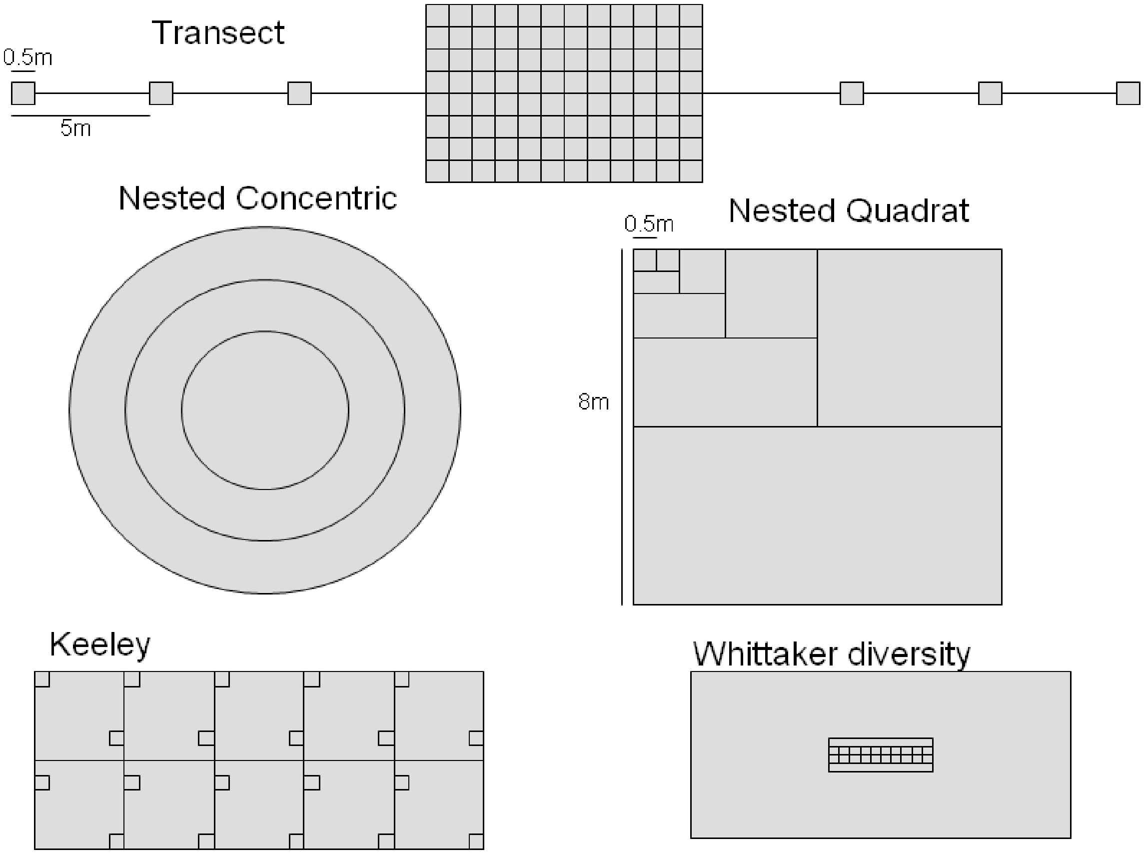


Figure 2.2: Layouts of specific multi-scale methodologies: A) Carolina Vegetation Survey design B) Modified Whittaker design C) Dengler minimum plot design

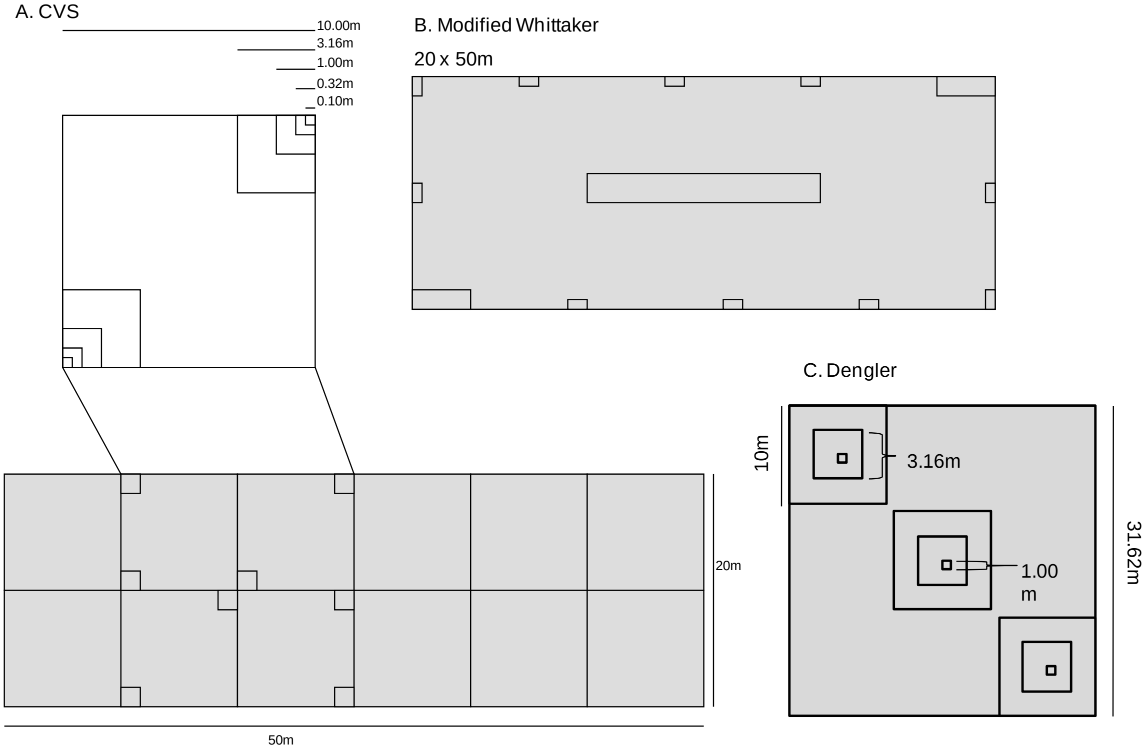
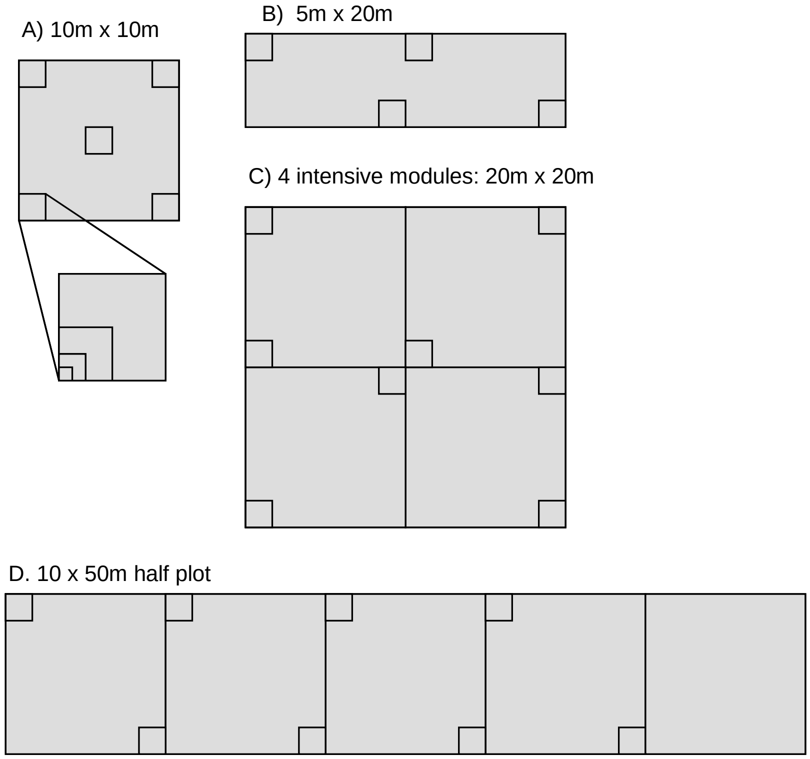


Figure 2.3: A few common adaptations of the CVS protocol. A. Single 10x10m module with five intensive corners consisting of subplots 0.1, 0.32, 1.0, and 3.16m on a side respectively. B. Lengthened module: 5x20m with four intensive corners. C. Partial CVS plot with four 10x10m modules for a 20x20m plot. D. 10 x 50m half CVS plot.



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Chapter 3: A multi-scale analysis of plant diversity along nutrient gradients

Abstract

Although edaphic variation is common in natural systems, the effect of this variation on plant diversity has not been adequately described. Understanding this variation is, however, important because soil nutrients are important drivers of plant community structure. This study takes advantage of multi-scale vegetation sampling along with plot-level soil data from the Carolina Vegetation Survey to examine the relationships between soil nutrients and diversity at multiple spatial scales. I find that there is greater variation in soil characteristics that predict diversity between regions than across scales within regions. In Atlantic Coastal Plain longleaf pine communities, nitrogen, sulfur, iron, soil *p*H, organic matter, and silt are important predictors of diversity. In the Sandhills longleaf pine of the Carolinas manganese, nitrogen, soil *p*H, and silt are the measured variables that best predict diversity. In Florida longleaf pine communities, soil *p*H, iron, nitrogen, and silt are consistently the strongest indicators across all scales from $0.01 m^2$ to $1000 m^2$. In southern Appalachian Mountain communities, soil *p*H, manganese, and calcium are the best diversity indicators. By tailoring models to individual regions, soil characteristics can predict between 39 and 54 percent of the variance in diversity at the 0.1 ha scale.

Introduction

Multiple factors affect plant species diversity, including climatic factors, the species pool, dispersal abilities of species, disturbance, and environmental favorability, which includes nutrient availability. Describing diversity is, however, complicated by the fact that patterns of diversity have also been shown to vary with scale of observation (Gaston 2000). Soil nutrients are critical in driving plant community diversity; however, variation in soil nutrients (i.e. edaphic variation) is poorly represented in regional data (Waring and Running 1998). Soil nutrients vary between regions because of differences in geological history, but diversity may also track fine-scaled differences in soil nutrition. If the significant correlates of diversity vary with scale, this could shed light on which mechanisms of species coexistence are operating at a given scale. However, if correlates vary less with scale and more with region, it highlights the influence of soil nutrients in understanding community composition within a given region.

I examine the relationship between soil characteristics and species diversity across multiple scales in two regions: the longleaf pine communities of the Southeastern United States and the forests of the southern Appalachian Mountains. Small changes in soil moisture and soil texture translate into distinct compositional differences in longleaf pine communities. In fact a combination of soil moisture and percent silt has been used in the classification of longleaf pine communities (Peet 2006). Soil texture has consequences of water relations that affect the moisture availability and the availability of nutrients to plants. Thus, soil texture is particularly important in regulating longleaf pine communities. Soil texture is expected to be a key factor in accounting for variation in diversity across spatial scales from 0.01 m^2 to 1000 m^2 within the coastal plains. Previous work in the southern Blue Ridge Mountains has demonstrated a close relationship between soil *p*H and species diversity (Peet et al. 2003). This is consistent with the correlation between diversity and *p*H seen in other temperate forest communities (e.g. Schuster and Diekmann 2005). Because these distinct regions have different predicted importance of soil characteristics, they allow for examination of consistency of this pattern across scales in a wide range of community types, rather than testing for patterns within one region.

This study takes advantage of multi-scale vegetation sampling (Peet et al. 1998) along with plot-level soil data to examine the relationships between soil nutrients and diversity at different scales. Path analysis is used to determine the relative strength of soil variables in predicting plant species richness and to determine the loadings of soil variables onto latent variables in order to build structural equation models of soil nutrients and diversity. I hypothesize that texture is the driving influence on diversity in longleaf pine communities, while soil *p*H and manganese are the essential variables in the southern Appalachian Mountains. I expect soil minerals to collectively influence diversity in the mountains (Figure 1), but that there will be distinct soil mineral and soil texture influences in longleaf pine communities (Figure 2).

Methods

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

Soil samples were taken from the A horizon in at least one intensive module (a complete suite of soil data was a requirement for plot selection). Because soil samples were taken from each intensive module, they were only nested inside of the $10m^2$ subplot and $1000m^2$ plot. All soil samples were analyzed by Brookside Laboratories. Soil analyses included texture (percent clay, silt, and sand), cation exchange capacity (CEC), *p*H, organic matter (Org), nitrogen (N), phosphorous (P), sulfur (S), manganese (Mn), calcium (Ca), and iron (Fe). Soil nutrient measurements were log-transformed to normalize the distributions.

For each dataset, correlations and covariances were calculated for plant species richness at each scale and for all soil variables. The strongest 5-6 soil variables (correlations $r>0.24$) were selected to model diversity at four scales: $1m^2$, $10m^2$, $100m^2$, and $1000m^2$. Smaller scales were excluded because they were further from the soil sample, and, because of weaker correlations, the models either had poor fit or did not converge. All path models were initially run with the strongest correlates for a given scale and region (Table 3.1). Correlates with strong co-linearity with other predictors were removed. Initial models were refined based on the significance of paths (i.e., insignificant paths were removed from the models until the best model fit was achieved). Confirmatory factor analyses were run on all models to determine the appropriateness of predictors loading onto latent variables (e.g., conceptual variables, such as soil nutrients and soil texture). The confirmatory factor analyses were used to test structural equation models of soil and diversity (Bollen 1989). All analyses were conducted using the MPlus6.1 statistical package (Muthén and Muthén 1998-2010) with maximum likelihood estimation.

Results

Longleaf pine communities

In all three longleaf pine regions, the correlates of diversity had some turnover between scales; Table 3.1 summarizes the strongest correlates at each scale. Silt was a strong correlate across almost every scale in all three regions. Iron, nitrogen, and sulfur had the strongest relationship with diversity across all scales of observation in Atlantic Coastal Plain longleaf, followed by soil organic matter and silt and sand (Table 3.2 for all correlations). In the Sandhills, longleaf diversity correlated most strongly with manganese, *p*H, and nitrogen, but silt, sand, and calcium were also highly correlated with diversity (Table 3.3). In Florida longleaf, soil *p*H, iron, manganese, and silt were the strongest correlates of diversity (Table 3.4).

Path models predicting diversity using the strongest soil nutrient indicators for the $10m^2$, $100m^2$, and $1000m^2$ scales (Table 3.1) had excellent model fit values based on standardized root mean square residuals (SRMR), the comparative fit index (CFI), and the Root Mean Square Error of Approximation (RMSEA) (Table 3.5). The chi-squared values were significant ($p=0.000$), indicating a poor model fit. However, this fit value is heavily influenced by the relatively large sample size. The one exception to the excellent path model fit values was the $1m^2$ path model for Atlantic Coastal Plain longleaf pine, which had a poor to marginal fit (see Table 3.5). While the model fit is not ideal, the $1m^2$ Atlantic Coastal Plain longleaf pine path model has similar patterns to models at larger scales, with nitrogen, sulfur, and iron as strong indicators of diversity.

The path models indicated that nitrogen, sulfur, iron, and *p*H are the best indicators of diversity at all scales in Atlantic Coastal Plain longleaf pine communities, while sand is important at the $1m^2$ scale and organic matter at the 0.1ha scale (Figure 3.3). In the Sandhill longleaf pine path models, manganese and silt were strong predictors of diversity across all scales, and *p*H and nitrogen became more important at the $1 m^2$ and $10 m^2$ scales (Figure 3.4). Florida longleaf pine diversity is best predicted by *p*H, iron, manganese, and silt across all scales (Figure 3.5). The predictability of diversity decreased with decreasing scale in Atlantic Coastal Plain and Florida longleaf pine (Figures 3.3, Figure 3.5); however, the Sandhill longleaf pine path models had the opposite relationship with increasing predictability as scale decreased (Figure 3.4).

The refined conceptual model (Figure 3.2) was supported when measures of soil texture would not load on the same latent variable as soil nutrients. Therefore, silt (and sand in the Florida longleaf pine) was modeled with a separate influence on diversity. Confirmatory factor analysis with soil nutrients as a latent variable and separate measured variables for soil texture had an adequate fit. This base model was used to build an initial structural equation model of soil nutrients, texture, and diversity.

The longleaf pine structural equation models had moderate fit values (Table 3.5, longleaf pine SEM). In the Atlantic Coastal Plain, the longleaf diversity was modeled with soil nutrients having a stronger affect on diversity than silt. Iron, organic matter, *p*H, sulfur and nitrogen were all strong predictors of soil nutrients (Figure3.7). In the Sandhills, soil nutrients and silt also had strong positive loadings on diversity, but the influence of silt was stronger. Manganese, nitrogen, and *p*H were the best indicators of soil nutrients (Figure 3.8). Florida longleaf diversity was also influenced positively by silt and soil nutrients. Sand was a very weak indicator of diversity in this model, and iron, calcium, manganese, and phosphorous were important predictors of soil nutrients (Figure 3.9).

Southern Appalachian Mountains vegetation

The strongest soil correlates of diversity for the mountain database are summarized in Table 3.1. The mountain data demonstrated that *p*H, manganese, and calcium are strong correlates of diversity, regardless of the scale of observation, and soil texture has only a weak correlation with diversity at any given scale (Table 3.6). Soil cation exchange capacity (CEC) is also an important correlate at the smaller scales. At the 1000m^2 scale, iron, and sulfur were the other notable correlates.

Path models using the strongest correlates of diversity (Table 3.1) generated models with good fit values. Both iron and calcium had insignificant or very small factor loadings at several scales. The final path models (Figure 3.6) have excellent model fit values based on CFI, SRMR, and RMSEA (Table 3.5). The path models suggest that manganese, calcium, and *p*H are the strongest indicators of diversity at the 1m^2 scale. At the full plot scale, manganese and *p*H were the best measures for predicting diversity (Figure 3.6).

Confirmatory factor analysis using the single latent variable model (Figure 3.1) failed to converge. However, confirmatory factor analysis with *p*H as an independent indicator, and the other nutrients loading onto a latent variable had an adequate fit. This model was then used for the basis of a structural equation model for soil nutrients, *p*H, and diversity (Figure 3.10). The mountain structural equation model has a moderate model fit (Table 3.5, Mountain SEM). The model accounts for 39 percent of the variation in diversity (Figure 3.10). Soil *p*H positively loads onto diversity; however, it is a strong negative indicator for soil minerals. Soil minerals negatively influence diversity, driven by strong negative indicators (*p*H, Ca, Mn).

Within plot variance was calculated for all plots with four soil samples (Table 3.7). Soil organic matter, cation exchange capacity, calcium, sulfur, magnesium, and manganese have variances on average an order of magnitude larger in the mountains than in the longleaf pine plots. The variances of soil *p*H, and base saturation were the soil variables with the most similar level of within plot variance across all regions.

Discussion

The path models indicated that there are consistent indicators of diversity across scale in both the mountains and longleaf pine communities. The path models of soil and diversity illustrated that soil nutrient indicators differ across scale, but only slightly. In the mountains, sulfur was important at the intermediate scales ($10m^2$, $100m^2$). In the Atlantic Coastal Plain longleaf pine systems, nitrogen was a strong predictor only at the $1m^2$ scale, and *p*H became insignificant at this smaller scale. It was also difficult to fit a path model with an adequate model fit at the smallest scale ($1m^2$). This variation in indicators at the $1m^2$ scale is probably due to the lack of nesting of the soil samples at this smaller scale, because the models using $0.1m^2$, and $0.01m^2$ measures of richness had poor fit or did not converge. However, in the longleaf pine communities, it may also be due to small-scale variation in soil nutrients caused by fire. Fire is inherently patchy, resulting in greater variation in nutrient availability across the landscape from year to year. Binkley et al. (1992) pointed out the high level of variability in mineral soils in longleaf pine systems and called for more precise soil measurements within plots.

As anticipated, texture was consistently significant across scales in the longleaf systems. While silt was a strong indicator at most scales; however, clay was a weak indicator across all scales and systems. Silt has been used to classify longleaf pine communities (Peet 2006), suggesting that it is important in these systems. Silt and sand also had inverse relationships with species richness, with sand negatively correlated to diversity while silt is positively related to diversity. When modeling species diversity, the conceptual model with both texture and nutrients (Figure 3.2) was more effective at capturing the relationship in longleaf pine systems.

The results from the mountain models were in line with expectations. Manganese, *p*H and calcium were consistently strong predictors. Previous work had already identified *p*H and Mn as an important correlates of diversity in the southern Blue Ridge Mountains (Peet et al. 2003). Texture does not seem to be an important indicator of diversity in this region. Because of the higher variance of calcium and cation exchange capacity within plots in the mountains than in the longleaf pine plots (Table 3.7), the higher within plot variation in calcium is probably adding to the importance of these variables in the mountains.

The initial soil structural equation models predicted diversity well in both the longleaf pine and mountain communities, suggesting that this modeling approach and conceptual model can be applied to other regions effectively. Soil nutrients, modeled by calcium, manganese, iron, and phosphorous, along with *p*H were the key predictors of diversity in mountain communities. A similar model was effective in all longleaf pine communities: soil nutrients and silt both positively influenced diversity. Soil *p*H was a key indicator in both longleaf pine communities and the southern Appalachian Mountains. Silt effectively modeled the influence of soil texture across all longleaf pine regions. However, a more detailed examination of the soil nutrient variation within plots, including fully nested soil samples, would add to our understanding of the influence of soil on diversity and the effect of scale of observation.

These findings demonstrate the soil characteristics that closely vary with plant species richness; however, the next step is to determine why these variables are so important.

Manganese may be a surrogate for phosphorous availability, which is difficult to measure. In Atlantic Coastal Plain longleaf pine communities, it is likely that iron and sulfur function as surrogate for water availability. Future research should focus on why these variables are meaningful and how soil nutrient availability influences diversity.

Tables

Table 3.1: Strongest correlates of diversity at different scales in Atlantic Coastal Plan (ACP), Sandhills, and Florida (FL) longleaf pine communities, and southern Appalachian Mountain (Mountain) communities. The strongest correlate is listed on the left and they decrease from left to right.

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

Table 3.2: Correlations between soil nutrients and plant species richness at six scales in Atlantic Coastal Plain (NC, SC, GA) longleaf pine communities. Correlations greater than 0.25 are in bold (see columns 1-7). Organic matter, nitrogen, sulfur, iron, silt, and sand are strong correlates across all scales.

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

Table 3.3: Correlations between soil nutrients and plant species richness at six scales in NC Sandhills longleaf pine communities. Correlations of 0.25 and above are in bold (see columns 1-7). Soil *p*H, organic matter, nitrogen, and silt are strong correlates across all scales.

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

Table 3.4: Correlations between soil nutrients and plant species richness at six scales in Florida longleaf pine communities. Correlations of 0.25 and above are in bold (see columns 1-7). Iron and silt are strong correlates across all scales. Soil *p*H is a strong correlate at the larger scales.

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

Table 3.5: Model fit values for path models and structural equation models of plant diversity and soil nutrients. Models are organized by region and scale: Atlantic Coastal Plain longleaf pine (ACP longleaf), Sandhills longleaf of the Carolinas (Sandhills longleaf), Florida longleaf pine (FL longleaf), and southern Appalachian mountain (Mountain). The comparative fit index (CFI), standardized root mean square residuals (SRMR), and the Root Mean Square Error of Approximation (RMSEA), 90% confidence interval for the RMSEA (90% CI), chi-squared value, degrees of freedom (df), p value (p), and Akaike information criterion (AIC) are all presented. The path models for each region had excellent fit based on CFI, SRMR, and RMSEA, with the exception of the $1m^2$ scale Atlantic Coastal Plain model, which had a marginal fit. SEM models in each region had marginally acceptable fit values.

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

Table 3.6: Correlations between plant species richness across six scales and soil nutrients in Southern Appalachian Mountain communities. Correlations greater than 0.23 are in bold (see first 7 columns). Both manganese and calcium are strong correlates across all scales. Soil *p*H and iron are strong correlates across several scales. Cation exchange capacity, and sulfur are strongly correlated at some scales.

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

Table 3.7: Average within-plot variance of soil characteristics by region. This table depicts the variance in soil characteristics within Atlantic Coastal Plain longleaf pine (ACP longleaf), longleaf pine in the Sandhills of the Carolinas (SH longleaf), Florida longleaf pine (FL longleaf), and southern Appalachian mountains (Mountain) plots. Soil characteristics include organic matter (Organic), soil *p*H (soilPH), soil cation exchange capacity (CEC), base saturation (BaseSat), and nutrients in either parts per million (ppm) or percentages. The variance in organic matter, cation exchange capacity, sulfur, calcium (ppm), magnesium (ppm), and manganese (ppm) are an order of magnitude larger in the mountains than in each of the longleaf regions. The variances of soil *p*H, and base saturation were the variables with the most similar level of within plot variance across all regions.

Region	Organic	soilPH	CEC	BaseSat	S	P	Ca_ppm	Mg_ppm	K_ppm	Na_ppm
ACP longleaf	4.73	0.08	6.10	33.34	24.50	192.36	27851.49	308.86	133.10	66.99
SH longleaf	5.00	0.05	1.71	25.48	27.83	7.13	7628.92	141.20	81.47	3.78
FL longleaf	5.28	0.06	3.52	35.42	13.68	181.17	29015.19	298.08	49.15	153.42
Mountain	79.42	0.08	18.47	39.03	106.32	77.83	121685.68	3161.65	782.07	8.59

Region	%Ca	%Mg	%K	%Na	%Other	Fe_ppm	Mn_ppm
ACP longleaf	29.30	2.09	0.42	0.61	0.29	1765.20	35.60
SH longleaf	20.74	2.35	0.38	0.15	0.20	1485.51	352.72
FL longleaf	31.41	3.57	0.49	1.05	0.22	1824.24	201.82
Mountain	33.47	6.03	1.32	0.20	0.29	3330.06	1463.71

Figures

Figure 3.1: Initial conceptual model showing the influence of soil characteristics on diversity.

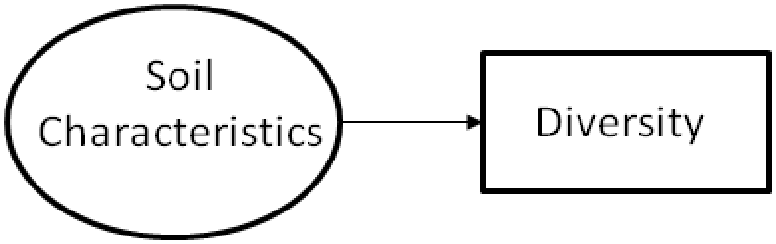


Figure 3.2: Refined conceptual model illustrating the direct and indirect influence of soil texture on diversity.

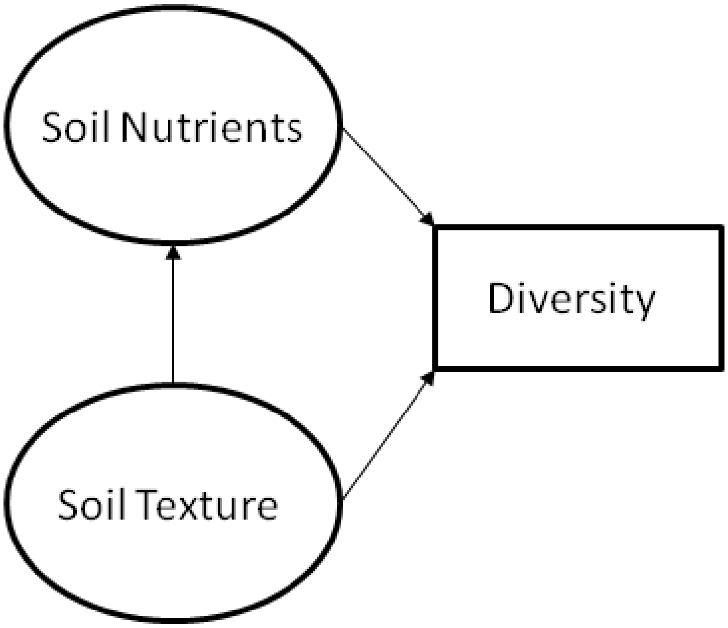


Figure 3.3: Path models of Atlantic Coastal Plain longleaf pine diversity and soil nutrients at the 1m^2, 10m^2, 100m^2, and 1000m^2 scales. The paths show standardized model estimates. The direction of the arrow represents the direction of the regression, with x, or observed variables, pointing to y variables on the right. The strength of the relationship is represented by the weight of the arrow. Solid lines are significant at the $p<0.005$ level; dashed lines are significant at $p<0.10$. In Atlantic Coastal Plain longleaf pine communities, sulfur and iron were significant at all scales. At the three larger scales, *p*H and nitrogen have significant loadings.

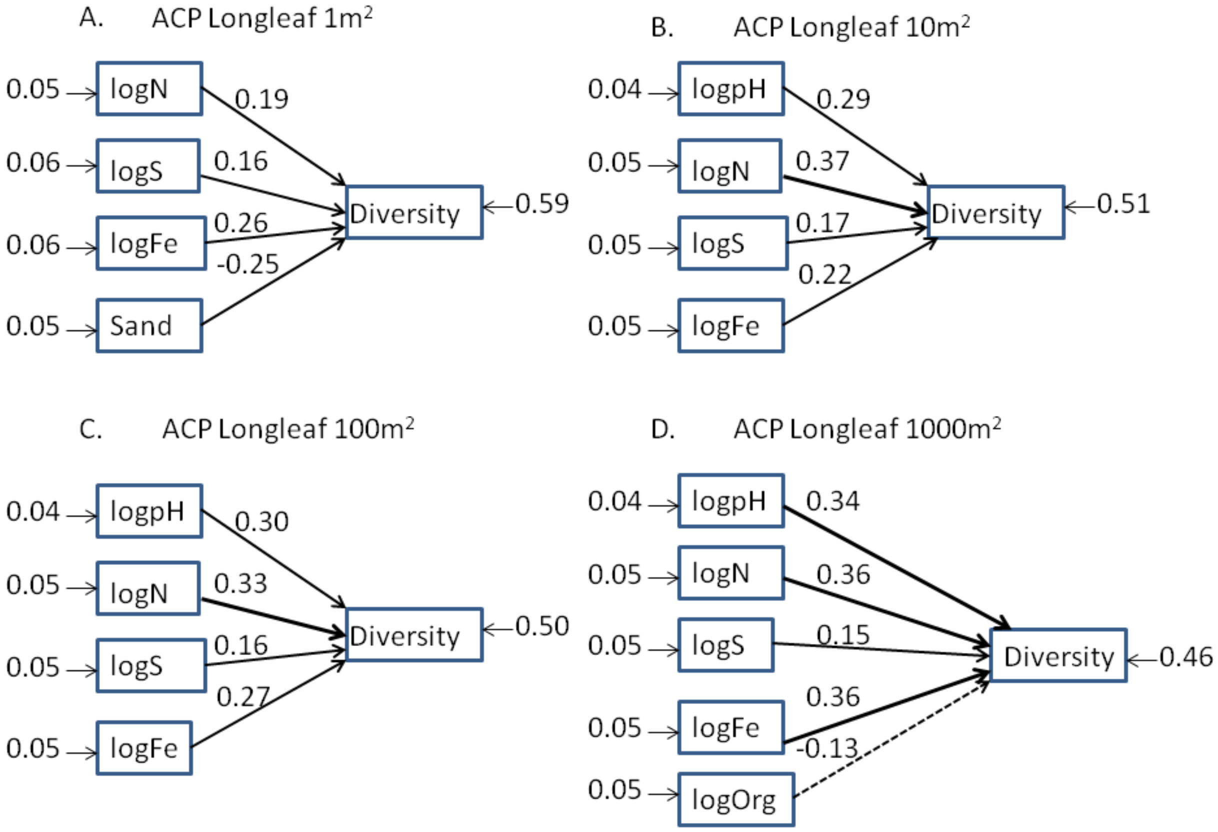
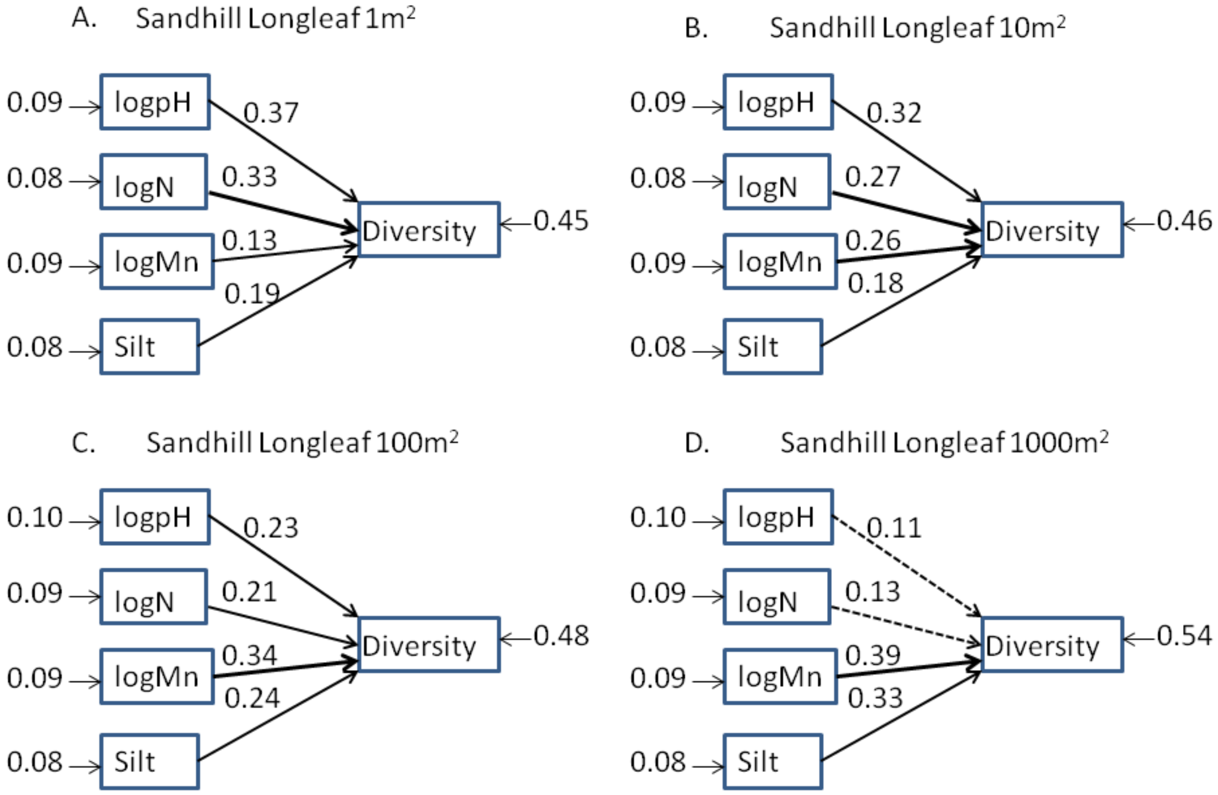


Figure 3.4: Path models of longleaf pine diversity in the Sandhills of North and South Carolina and soil nutrients at the 1m^2, 10m^2, 100m^2, and 1000m^2 scales. The paths show standardized model estimates. The direction of the arrow represents the direction of the regression. The strength of the relationship is represented by the weight of the arrow. Solid lines are significant at the $p<0.05$ level; dashed lines are significant at $p<0.30$. In Sandhill longleaf pine communities, *p*H, nitrogen, manganese, and silt have significant loadings at all scales. However, at the 1000m^2 scale, soil *p*H and nitrogen were not significant.



A. Sandhill Longleaf 1m^2

B. Sandhill Longleaf 10m^2

C. Sandhill Longleaf 100m^2

D. Sandhill Longleaf 1000m^2

Figure 3.5: Path models of Florida longleaf pine community diversity and soil nutrients at the 1m^2, 10m^2, 100m^2, and 1000m^2 scales showing standardized model estimates. The direction of the arrow represents the direction of the regression. The strength of the relationship is represented by the weight of the arrow. Solid lines are significant at the $p<0.005$ level; dashed lines are significant at $p<0.10$. In Florida longleaf pine communities, silt, *p*H, and iron have significant loadings at all scales. Nitrogen is a significant measured variable at the 1m^2 scale, and manganese is significant at the three larger scales.

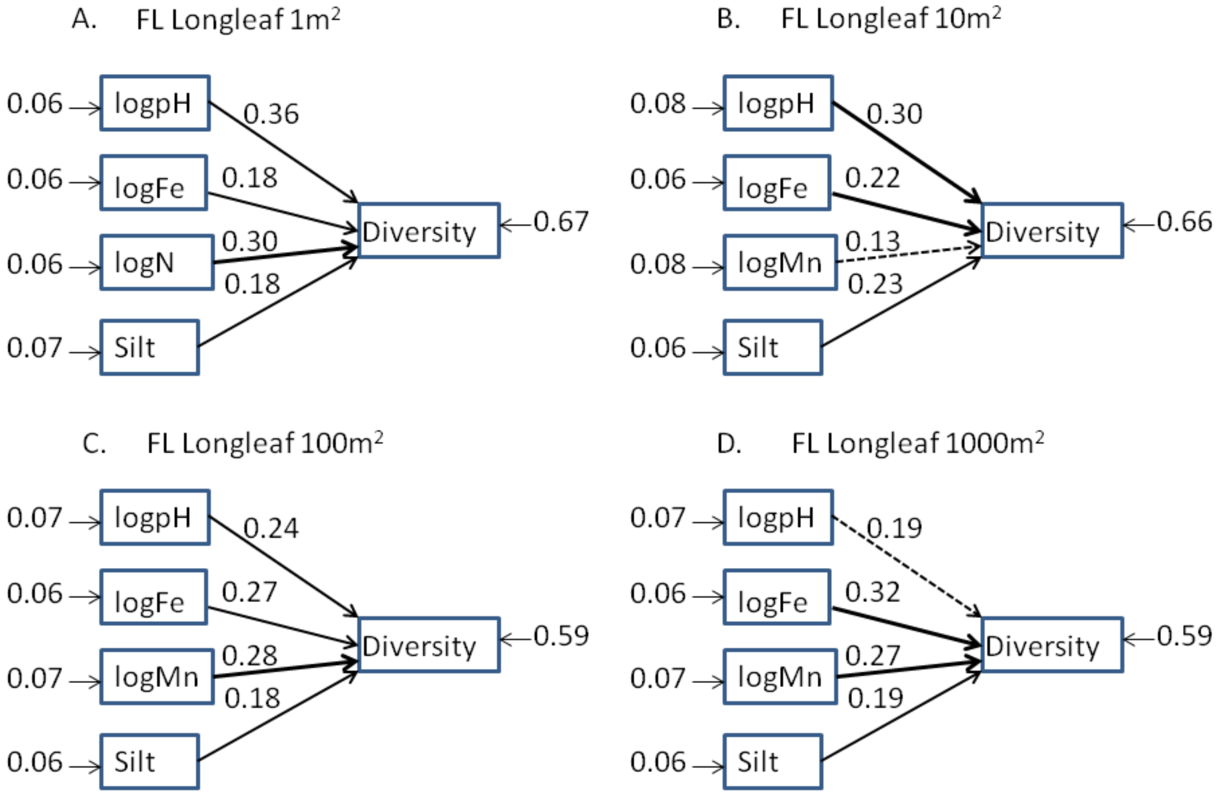


Figure 3.6: Path models of southern Appalachian Mountain community soil nutrients and diversity at the 1m^2, 10m^2, 100m^2, and 1000m^2 scales showing standardized model estimates. The direction of the arrow represents the direction of the regression. The strength of the relationship is represented by the weight of the arrow. Solid lines are significant at the $p<0.001$ level; dashed lines are for loadings with $p<0.1$. In mountain communities, Manganese and *p*H are the strongest indicators for diversity at all scales.

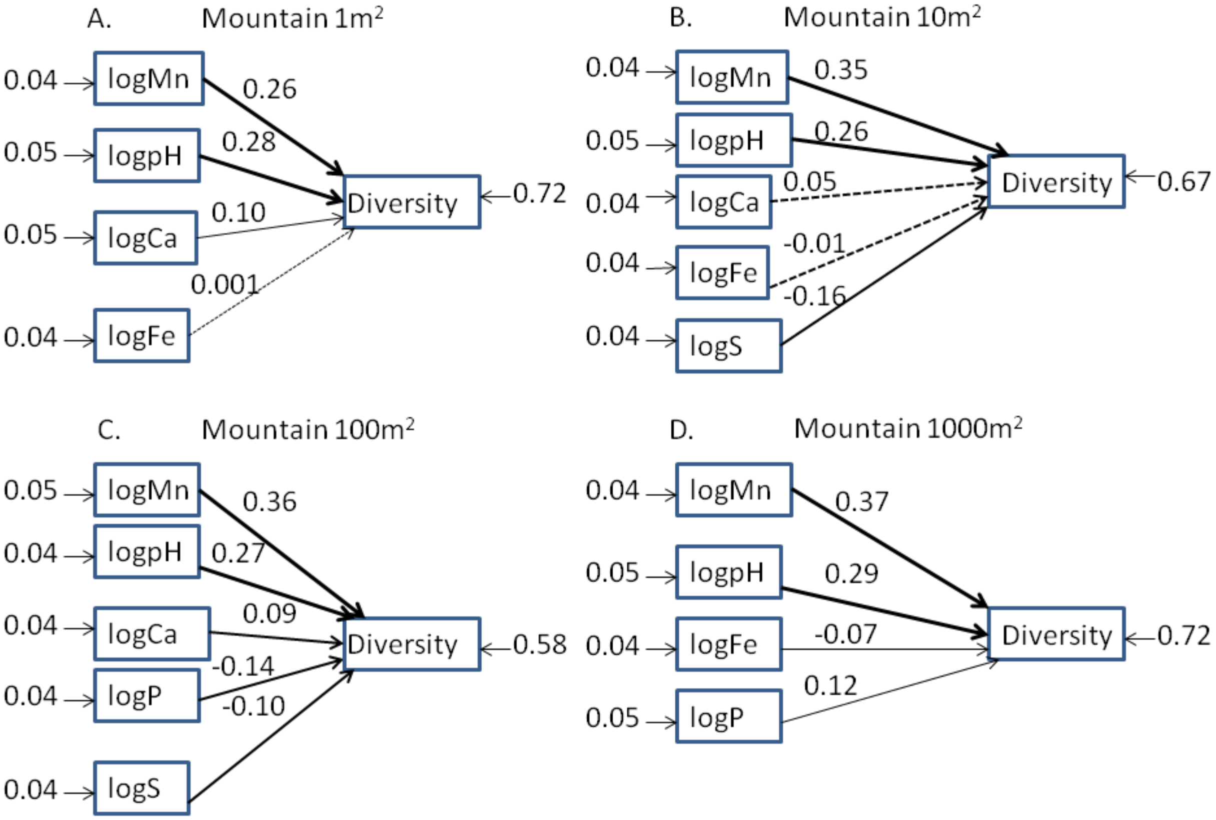


Figure 3.7: Structural equation model for Atlantic Coastal Plain longleaf pine diversity and soil nutrients (1000m^2 scale). The direction of the arrows from the latent variable (Soil nutrients) indicates that this construct is determining the measured values in the field. All other arrows represent the direction of the regression and influence on other variables. Short arrows into the measured variables indicated the measurement error. All loadings are standardized and significant at p<0.001. Iron, sulfur, and organic matter were the strongest indicators of soil nutrients. Silt had a separate affect on diversity. Soil nutrients had a greater influence on diversity than silt. The model explained 54 percent of the variance in diversity.

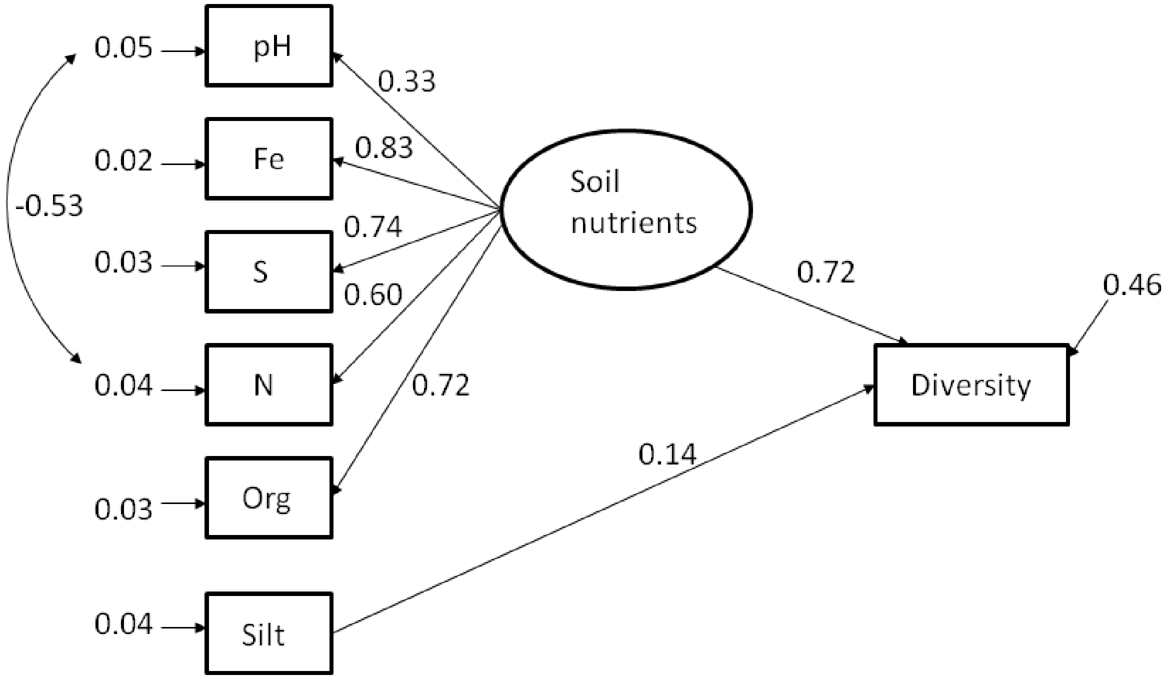


Figure 3.8: Structural equation model for diversity and soil nutrients in longleaf pine communities in the Sandhills of the Carolinas (1000m^2 scale). The direction of the arrows from the latent variable (Soil nutrients) indicates that this construct is determining the measured values in the field. All other arrows represent the direction of the regression and influence on other variables. Short arrows into the measured variables indicated the measurement error. All loadings are standardized and significant at $p<0.001$. Manganese and soil *p*H were the strongest indicators of soil nutrients. Silt had a separate affect on diversity, which was roughly half the influence of Soil nutrients on diversity. The model explained 49 percent of the variance in diversity.

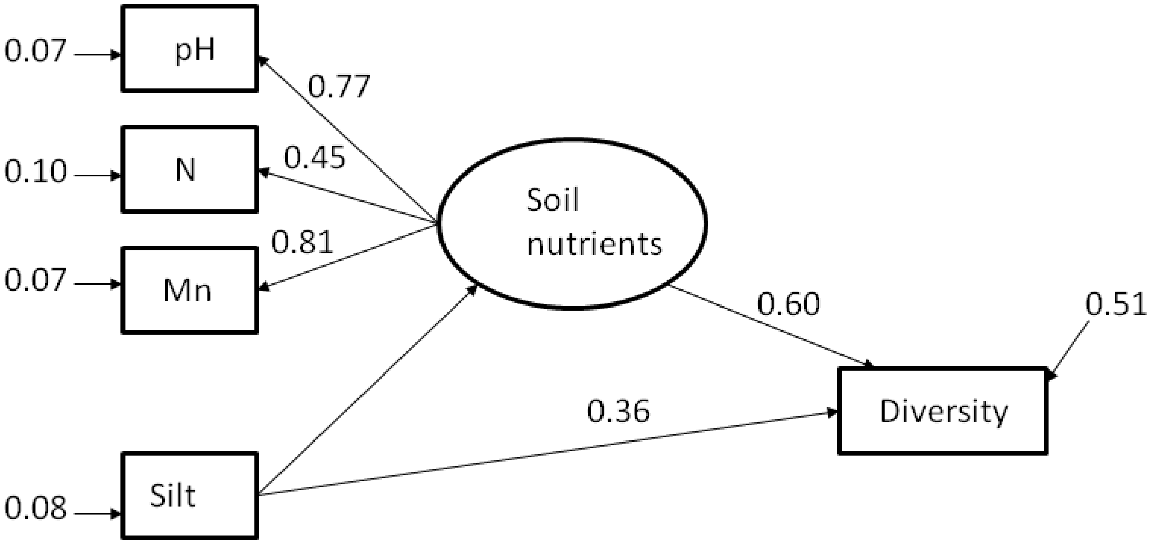


Figure 3.9: Structural equation model for diversity and soil nutrients in Florida longleaf pine communities (1000m^2 scale). The direction of the arrows from the latent variable (Soil nutrients) indicates that this construct is determining the measured values in the field. All other arrows represent the direction of the regression and influence on other variables. Short arrows into the measured variables indicated the measurement error. All loadings are standardized and significant at $p<0.001$, except for the dotted line, which is significant at $p<0.9$. Manganese and soil *p*H were the strongest indicators of soil nutrients. Silt and sand had separate effects on diversity; however the loading for sand was both insignificant ($p<0.9$) and a small number. The model explained 40 percent of the variance in diversity.

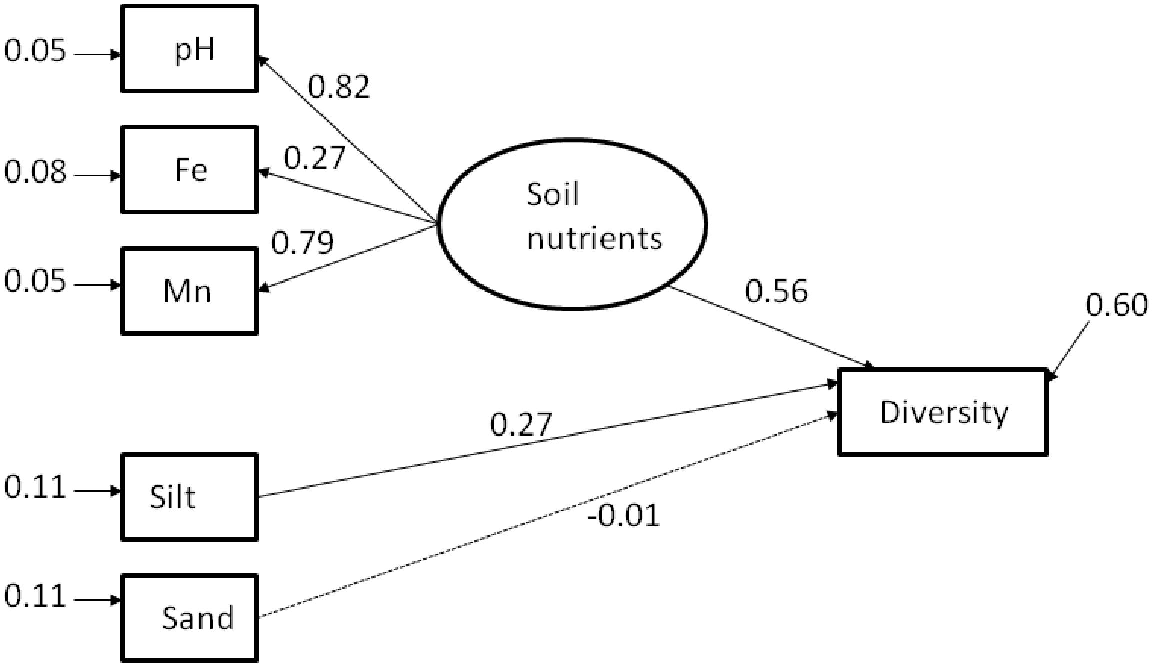
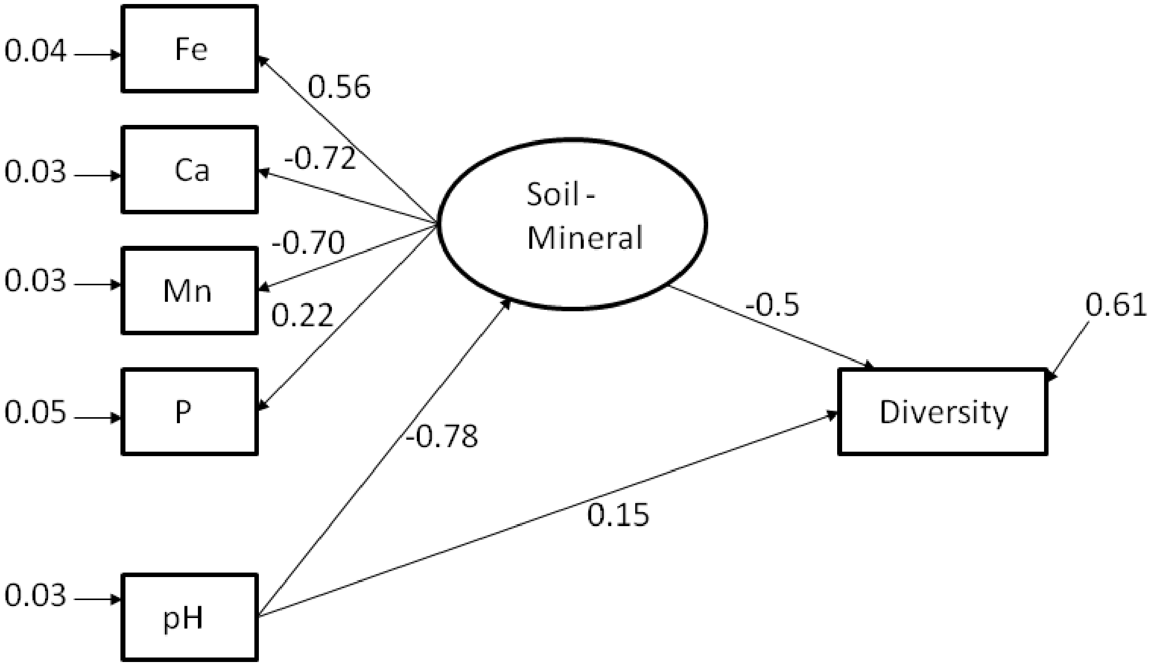


Figure 3.10: Structural equation model for diversity and soil nutrients in southern Appalachian Mountain communities (1000m^2 scale). The direction of the arrows from the latent variable (Soil nutrients) indicates that this construct is determining the measured values in the field. All other arrows represent the direction of the regression and influence on other variables. Short arrows into the measured variables indicated the measurement error. All loadings are standardized and significant at $p<0.001$. Manganese, calcium and iron were the strongest indicators of soil nutrients. Soil *p*H had separate effect on diversity. The model explained 39 percent of the variance in diversity.



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Chapter 4: Structural equation models of plant community diversity and productivity in the southeastern US

Abstract

The relationship between productivity and diversity continues to be a focal point of ecological study. Although Grime's hump-backed productivity diversity curve, showing a peak in diversity at intermediate productivity, is perhaps the most widely known description, debate continues about the nature of the diversity-productivity relationship. Numerous empirical studies have laid the groundwork for a more theoretical analysis of the relationship.

Structural equation modeling allows for the examination of complex multivariate relationships between components of theoretical models, such as the multivariate productivity-diversity hypothesis. This technique is ideal for testing the relationship between multiple predictors of productivity and diversity. Here we compare local, regional and combined Structural Equation Models of productivity, nutrient availability, and diversity. We use plots from the Carolina Vegetation Survey along with remotely-sensed data to model longleaf pine communities and southern Appalachian Mountain communities. Remotely-sensed data on productivity adds another source of information that can be added to plot-level measurements of plant communities in examining this relationship. This allows for further examination of the productivity-diversity relationships at differing scales.

We find that the combined model with both local and remotely-sensed data improves the prediction of diversity for longleaf pine communities, while a local model focusing on soil characteristics is a better predictor of diversity in the southern Appalachian Mountains.

The diversity-productivity relationship was not significant in the mountains; however, in longleaf pine communities there was a significant influence of productivity on diversity.

Introduction

The relationship between productivity and species diversity has long been a focal point of ecological study. Although the productivity-diversity relationship has been studied across many systems, there is still much debate about the nature of the relationship (Waide et al. 1999, Gross et al. 2000, Fridley 2002, Worm and Duffy 2003, Gross and Cardinale 2007). Perhaps the most widely known pattern is Grime's (1977) hump-backed productivity diversity curve, showing a peak in diversity at intermediate productivity. However, different patterns, including increasing, decreasing, and unimodal relationships, may be observed when different measures of diversity (Gramling 2006), or scales of measurement are used (Chase and Leibold 2002). This ongoing debate raises the question of whether there is a general pattern that explains the relationship between productivity and diversity, or whether the relationship is system- or scale- specific.

In addition to the debate over the nature of the relationship, the directionality of the productivity-diversity relationship has also been questioned. Historically, ecologists have framed this relationship with productivity as the independent variable influencing diversity. Taking Grime's (1977) hump-backed curve as an example, the peak of diversity occurs in systems with intermediate productivity. However, some recent studies have argued that diversity drives productivity (or biomass) (Chapin et al. 2000, Naeem 2002, Hooper et al. 2005). Cardinale et al.(2009) claim that the classical view of productivity controlling diversity should be merged with the more recent framing of productivity as the dependent variable affected by diversity. The multivariate productivity-diversity hypothesis proposes that these two perspectives can be clarified by adding a simultaneous consideration of resource availability, stating that 1) the supply of resources directly affects biomass by constraining production based on limiting resources, 2) local diversity directly influences biomass, and 3) resource availability indirectly affects productivity through its influence on diversity (Figure 4.1A, Gross and Cardinale 2007, Cardinale et al. 2009). They further claim that the influence on standing biomass can be extended to the impact on production of new biomass. Under this view, the multivariate productivity diversity hypothesis predicts that diversity influences productivity, and that resource availability has both a direct influence, and an indirect influence, on productivity. Although there is support for the multivariate productivity-diversity hypothesis in an experimental stream system (Cardinale et al. 2009), it has not been tested in terrestrial plant communities.

Part of the confusion and challenge of examining the relationship between productivity and diversity is the ability to measure them. As Cardinale et al. (2009) point out, the different measures used as proxies for productivity (e.g. standing biomass, production of new biomass, environmental correlates of productivity) may not be mechanistically equivalent. However, while it is feasible to directly measure biomass in microcosm experiments, or in small herbaceous plots, it becomes more difficult to obtain direct measures of productivity in natural systems (e.g. cutting down, drying and weighing all standing vegetation in a forest plot).

The next step towards improving our understanding of the productivity diversity relationship is a consideration of both scale and whether the relationship is general or changes from system to system. In this study, we use the Carolina Vegetation Survey (CVS) data from across the Southeastern US to test theoretical models of productivity and diversity. The CVS database contains plots from plant communities across the Carolinas sampled using a flexible, multi-scale methodology based on a 0.1ha plot (Peet et al. 1998). This data provides an ideal set of observed, natural communities with both multi-scale diversity values and environmental variables with which to test the productivity diversity relationship. In addition to the plot-level data on diversity and soil nutrients, remotely-sensed productivity data from NASA provide a larger-scale indicator of productivity in these plots. In order to further examine the generality of this relationship, the dataset can also be extracted into two large subsets: longleaf pine communities and southern Appalachian forests. These two systems were selected to allow examination and comparison of diversity productivity relationships in distinct systems.

The CVS data will be used to test Structural Equation Models (SEM) of the relationships between nutrients, diversity and productivity. Structural equation modeling is ideal for testing the relationship between multiple predictors of plant productivity and diversity because instead of simply examining patterns in data, theoretical models can be compared quantitatively, using either experimental or observational data. We use this technique to explore complex multivariate relationships between components of theoretical models (Grace 2006) with observational data. Given the ongoing debate about the nature and direction of the productivity-diversity relationship, SEMs allow an examination of both direct and indirect effects, such as those in the multivariate productivity diversity hypothesis (Cardinale et al. 2009).

Cardinale et al.(2009) propose a conceptual model for the multivariate diversity productivity hypothesis that incorporates nutrient availability and results in diversity influencing productivity (Figure 4.1A). We also include nutrient availability as an essential component of the conceptual model influencing the productivity-diversity relationship; however, we also incorporate a path representing the influence of productivity on diversity, and paths for the effect of climate on nutrient availability, diversity, and productivity (Figure 4.1B). Our conceptual model of the relationships among nutrient availability, productivity and diversity (Figure 4.1B), incorporates a direct influence of nutrient availability on productivity and diversity, an indirect effect of nutrient availability on productivity (through diversity), and the influence of diversity on productivity.

Structural equation models are used to evaluate whether models using only local measures, regional measures, or a combination of local and regional measures are best for modeling the diversity productivity relationship. Local measures are expected to be better predictors at small plot scales, while regional measures will generate better models of diversity at larger scales. The best model fit is anticipated for a combination of local and remotely sensed data. Models are evaluated using two subsets of data (longleaf pine plots and southern Appalachian mountain plots) and random subsets from the entire dataset to test whether there is a general trend across communities and regions, or the productivity-diversity relationship is system-specific. In examining the productivity relationship, we also examine the direction of the relationship between productivity and diversity. We hypothesize that in plant communities productivity will influence diversity.

Methods

Plot-level data

A dataset of 1602 plots with soil data and nested subplots was generated from the CVS database. Plots were sampled across the southeastern United States in Florida, Georgia, and North and South Carolina in representative vegetation communities. All plots were 0.1ha, following the sampling protocol described by Peet et al. (1998). Two subsets of the data consist of 672 longleaf pine (LL) plots and 578 southern Appalachian mountain (M) plots. The plant species richness for the entire 0.1ha plot is the number of vascular plant species found in the full plot. Richness values for subplots were calculated by averaging the richness in all intensive modules at $0.1m^2$, $1m^2$, $10m^2$, and $100m^2$ scales.

In each 0.1ha plot, the diameter at breast height was measured for each woody individual over 1.3m in height. These values were converted to basal area ($BA = \pi \text{ x } (½ \text{ dbh})^2$) and summed within each 0.1ha plot. Because plant diameter is highly correlated with biomass, basal area of a plot represents a proxy for standing woody plant biomass (Gramling 2006). Thus, the resulting basal area calculation for the plot was used as a plot-level estimate of productivity.

Soil samples were taken from the A horizon of each intensive module in the plots and sent to Brookside Laboratories for analysis. Nine measures of soil nutrition were considered: cation exchange capacity in milliequivalents per 100 grams of soil (CEC), soil *p*H (pH), percentage organic soil content (Org), percentage available nitrogen (N), percentage available sulfur (S), percentage available phosphorous (P), calcium concentration in ppm (Ca), manganese concentration in ppm (Mn), and iron concentration in ppm (Fe). All soil nutrient values were transformed to a log scale, resulting in more normal distributions. Soil texture values consisted of percentage sand, silt, and clay. All variables were scaled to within one order of magnitude of each other.

Regional data

Climatic data were taken from DayMet: temperature is the average annual minimum temperature at the site, radiance is the average daily radiance at the site, and precipitation is average annual precipitation. Location is the specific site location in latitude and longitude, acquired using a handheld GPS unit in a plot.

Using the GPS-based plot locations, remotely- sensed productivity data were extracted from NASA satellite images for 2000-2006 including the Normalized Differential Vegetation Index (NDVI), Leaf Area Index (LAI), Enhanced Vegetation Index (EVI), and Net Primary Productivity (NPP) using the plot locations(NASA 2008). These values were averaged over the growing seasons from 2000-2006. Because of the large values and different ranges of these indices, all variables were scaled to be within an order of magnitude of the other variables.

Analysis

Structural equation models for plant productivity and diversity were used to evaluate the conceptual model in which climate and soil nutrient availability influence productivity and diversity. The model predicts that climate directly affects soil nutrient availability, productivity, and diversity (Figure 1B). Soil nutrient availability influences diversity (Schlesinger 1997), and productivity. Since there are no direct plot-level measures of productivity, basal area was used as a proxy for biomass in local models with the expectation that biomass influences diversity (Gramling 2006), and also influences soil nutrition.

Incorporating multiple variables impacts the SEM fit in two ways: redundant variables unnecessarily complicate models, and variables with a high colinearity negatively affect model fit, potentially preventing convergence of the model. Minimizing colinearity of variables also ensures that each predictor variable adds new information to the model. This also results in the most parsimonious model. To this end, Pearson's product correlations and covariances were calculated for all variables. Measurement variables that correlated highly with diversity were selected. Pairwise plots were examined for each combination of variables. Then correlations between measurement variables predicting the same latent variable were examined to ensure a low level of co-linearity.

The conceptual model (Figure 4.1B) depicts the expected relationship between the latent variables, or inferred constructs of interest. The measured or observed variables are then incorporated into the model via relationships with the latent variables (i.e., measurement models). Soil measurement models are taken from Chapter 3. Climate is predicted by three indicators: temperature, radiance, and precipitation. Productivity is modeled using NDVI, EVI, and LAI in the regional models, and is replaced with biomass (BA) in local models. Since plot diversity (alpha diversity) has only one measurement (species richness), it is modeled as a measured variable rather than a latent variable.

Structural equation models were examined for random subsets of the entire dataset, and two subgroups within the dataset: longleaf pine plots and southern Appalachian Mountain plots (Table 4.1). A local model of productivity and diversity was created using only plot-level data (soil data, diversity, BA) for both longleaf pine and mountain datasets. A regional model was tested using remotely-sensed productivity and climatic data for both datasets. Finally, a combined model was constructed using plot-level indicators (soil nutrients, basal area) as well as remotely sensed data (NDVI, EVI, LAI, NPP) and climatic data (temperature, precipitation). The model was also run using a variety of scales for richness measurements (0.1m^2, 1m^2, 10m^2, 100m^2, and 1000m^2). The scales showed only minor variations, so the 10m^2 (representative of smaller scales) and 0.1ha scale (full plot) models are presented here (Table 4.1).

All analyses were performed in Mplus 6.0 (Muthén and Muthén 1998-2010), using maximum likelihood estimation. The initial models were trimmed using significance values and the theoretically reasonable correlations suggested by modification indices greater than 50, to yield the final models presented in the results. All final models were tested with productivity influencing diversity and diversity influencing productivity to assess the directionality of the relationship.

Results

Model fit

We examined several measures of model fit to evaluate the models: standardized root mean square residuals (SRMR), the comparative fit index (CFI), and the Akaike Information Criteria (AIC). The estimates of model fit are summarized in Table 2. We also examined two other commonly referenced measures of fit (Chi-squared values and the root mean square error of approximation, Appendix A). Within the longleaf pine models the SRMR and CFI values are both adequate and indicate that the longleaf pine local model is the best fit for the data. However, the AIC value is lowest for the longleaf pine combined model, suggesting it has the best fit. Thus, according to model fit indices, both the longleaf pine local and combined models have acceptable fits, while the combined model is preferable.

In the mountain data, the CFI and SRMR for both local models suggest an excellent model fit (Table 4.1). The AIC suggests that the mountain local model is the best fit for the data. Neither of the mountain regional models converged on a solution; therefore, they are not reported in Table 1 because the estimates are not sufficient for interpretation.

All models were run using random sets of data sampled from across the entire dataset. These models either did not converge or had such poor fit indices that the estimates are not dependable. Thus, they were omitted from further examination, since the estimations are meaningless with insufficient fit indices.

Estimations

Model estimates for the longleaf pine local $10m^2$, longleaf pine regional, longleaf pine combined, mountain local, and mountain combined models are depicted in Figures 4.2-4.6. Because the mountain regional models did not converge on a solution, the estimates are not sufficient for interpretation, and therefore are not presented here.

For the longleaf pine data, the directions of all relationships were consistent across the scales of data: soil minerals, climate, and productivity positively loaded on diversity, climate negatively loaded on productivity, and soil texture negatively loaded on diversity (Figures 4.2-4.4). This indicates that for both local and regional models the relationship directions are consistent and statistically significant. Basal area in the local longleaf pine model was the exception (Figure 4.2). At the plot level, it was not significant; however, at the $100m^2$ scale it had a significant, negative loading on diversity.

The local models using mountain data did not converge on a solution when basal area was included. Therefore, basal area was omitted from the models. The mountain local models included *p*H and soil nutrients that both had negative loadings on diversity (Figure 4.5). In contrast to the longleaf pine models, in which sulfur and nitrogen loadings were most significant for soil minerals, manganese and phosphorous were important indicators for soil minerals. Iron and calcium were significant indicators in both longleaf pine and mountain data.

In the longleaf pine plots, the productivity loaded positively onto diversity (Figures 4.3-4.4), except at small scales with basal area as the only indicator for productivity (Figure 4.2). However, in the mountains, the productivity-diversity relationship was less clear: it was not significant in the combined model (Figure 4.6), local models with basal area did not converge, and regional models did not converge. All models were tested with the path for diversity influencing productivity; however, this path was not significant. Therefore, it was excluded from the models and is not depicted in the figures.

Both longleaf pine and mountain models predicted diversity well. The local longleaf pine models and the combined model performed comparably, explaining between 36 and 38% of the variance in plant diversity (Figures 4.2, 4.4). However, the variance in diversity explained decreased to 8 and 14% in the longleaf pine regional models (Figure 4.3). The combined model using the mountain data explained 39% of the variance in diversity (Figure 4.6), while the local models explained 53 and 58% of the variance in diversity (Figure 4.5).

Discussion

In fitting an overall productivity-diversity model to the entire dataset, none of the models converged on a solution or had an adequate model fit. These results combined with the models for the longleaf pine and mountain subsets of the data indicate that communities, or at a minimum regions, should be modeled separately, since the factors driving diversity may differ between regions. This requires a working knowledge of the community or preliminary analyses to determine the relevant measurement and latent variables to use in a model. The system specificity also seems logical when nutrient availability, which is likely to vary between systems, is incorporated into the model, as in the multivariate productivity diversity hypothesis (Cardinale et al. 2009). Thus general productivity-diversity models (e.g., Figure 4.1) must be tested and optimized for specific communities and regions.

The local models fit both the mountain and longleaf pine data well, predicting a significant percentage of the variance in plant diversity (36-58%). However, the local measure of productivity available, basal area, only had an effect on diversity at small scales. At smaller scales, the presence of one large individual (e.g. a tree with large basal area) would decrease the area available for other individuals and species, affecting the potential diversity.

The regional longleaf pine SEM had an adequate model fit; however, the mountain regional model did not even converge. It is likely that the smaller area within which the mountain plots are sampled did not have enough heterogeneity in the climate and productivity variables to drive a model. Although the fit of the regional model was not ideal, the direction of the relationships was consistent. This confirmation of relationship direction using remotely sensed variables increases our confidence in the loadings.

Contrary to expectations, the combined models of productivity and diversity did not always have the best model fit. Although the longleaf pine local models had better model fit indices for CFI and SRMR, the combined model was a better predictor of diversity for the longleaf pine data based on AIC, which helps to select for the most parsimonious model

(Burnham and Anderson 2002). However, the mountain local model was a significantly better predictor of diversity than the combined model. Thus the use of both plot-level and remotely sensed data has a tradeoff: model fit decreases but accuracy of predictions increases. Because diversity is driven by multiple variables, it is important to account for as many of the significant indicators as possible in modeling. The drivers of diversity are likely to vary across communities, so knowledge of a given system and incorporation of relevant variables and scales is essential to estimations of productivity and diversity.

SEMs allow testing of theoretical frameworks, such as the relationship between resource availability, productivity, and diversity. In this case, models indicated that the relationship between productivity and diversity in the mountains is not clear. However, the influence of soil nutrient availability and *p*H on diversity was strong as found in previous studies in the area (Peet et al. 2003). When using remotely-sensed productivity data, the longleaf pine plots show a positive loading of productivity on diversity. In both longleaf pine and mountain models, the influence of diversity on productivity was insignificant, contrary to results from experimental studies in stream systems (Cardinale et al. 2009).

Tables

Table 4.1: List of Structural Equation models of plant productivity and diversity in Longleaf and Mountain datasets. Models, the various data sets used with each model, latent variables (conceptual variables), and measured variables are listed for each model. Italicized data sets did not converge on a solution with a given model, and are therefore not presented in this paper. Abbreviations are as follows, randomized subsamples of the entire dataset (RS), longleaf (LL), mountain (Mtn), basal area (BA), radiance (Rad.), temperature (Temp.), precipitation (Precip.), average Normalized Differential Vegetation Index (AvgNDVI), averaged Leaf Area Index (AvgLAI), averaged Enhanced Vegetation Index (AvgEVI).

Model	Data	Latent Variable	Measured Variable
Local Longleaf	LL 10m^2	Soil Minerals	Fe, S, N, Ca
	LL 1000m^2	Soil Texture	Clay, Sand
	RS		BA
			Diversity
Regional Longleaf	LL 10m^2	Climate	Rad., Temp., Precip.
	LL 1000m^2	Productivity	AvgNDVI, AvgLAI, AvgEVI
	RS		Diversity
Combined Longleaf	LL 10m^2	Soil Minerals	Fe, S, N, Ca
	LL 1000m^2	Soil Texture	Clay, Sand, Precip.
	RS	Productivity	AvgNDVI, AvgLAI, AvgEVI
			Diversity
Local Mountain	Mtn 10m^2	Soil Minerals	Fe, Ca, Mn, P
	Mtn 1000m^2		pH
	RS		Diversity
Regional Mountain	*Mtn 10m*^{2}	Climate	Rad., Temp., Precip., Elev
	Mtn 1000m^2	Productivity	AvgNDVI, AvgLAI, AvgEVI
	RS		Diversity
Combined Mountain	Mtn 10m^2	Soil Minerals	Fe, Ca, Mn, P
	Mtn 1000m^2		pH
	RS	Productivity	AvgNDVI, AvgLAI, AvgEVI
			Diversity

Table 4.2: Fit indices for structural equation models for longleaf and mountain datasets. Fit indices include Comparative Fit Index (CFI), Standardized Root Mean Square Residual (SRMR), Akaike Information Criteria (AIC), and free parameters (free param). Local models fit better using 10m^2 subplot measures of richness. The longleaf regional model had slightly more marginal fit using richness from the 10m^2 subplot. The longleaf and mountain 10m^2 local models and the longleaf combined model had the best overall fit. Values representing the best fit statistic are bolded, except for the CFI and SRMR for both of the mountain local models which are bolded for their excellent fit.

	Fit Index	Local	Local 100m2	Regional	Regional100m2	Combined
Longleaf	CFI	0.896	**0.909**	0.902	0.902	0.871
	SRMR	0.048	**0.046**	0.058	0.058	0.061
	AIC	12412.978	14104.152	8700.109	10424.288	**8253.834**
	Free param	30	30	22	22	40
Mountain	CFI	**0.968**	**0.974**			0.903
	SRMR	**0.027**	**0.026**			0.080
	AIC	**1784.795**	3034.198			3567.806
	Free param	23	23			33

Figures

Figure 4.1: Conceptual models of nutrient availability, productivity, and diversity. A. The relationships predicted in the multivariate diversity productivity hypothesis (Cardinale *et al.* 2009). Diversity influences productivity. Nutrient availability has a direct effect on productivity and an indirect effect through diversity. B. Our conceptual model incorporates the effect of productivity on diversity and climatic influences. Climate influences nutrient availability, productivity, and diversity. Nutrient availability directly impacts productivity and diversity. Nutrient availability indirectly affects productivity. Productivity and diversity influence each other.

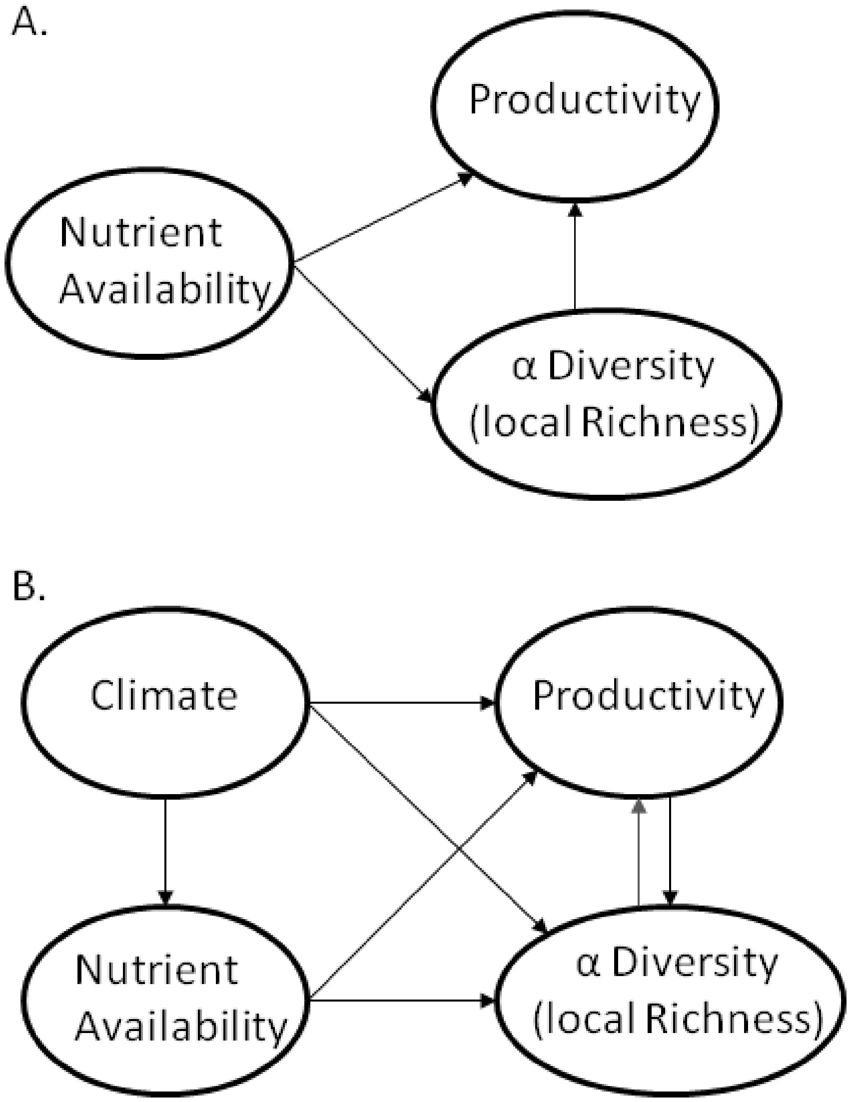
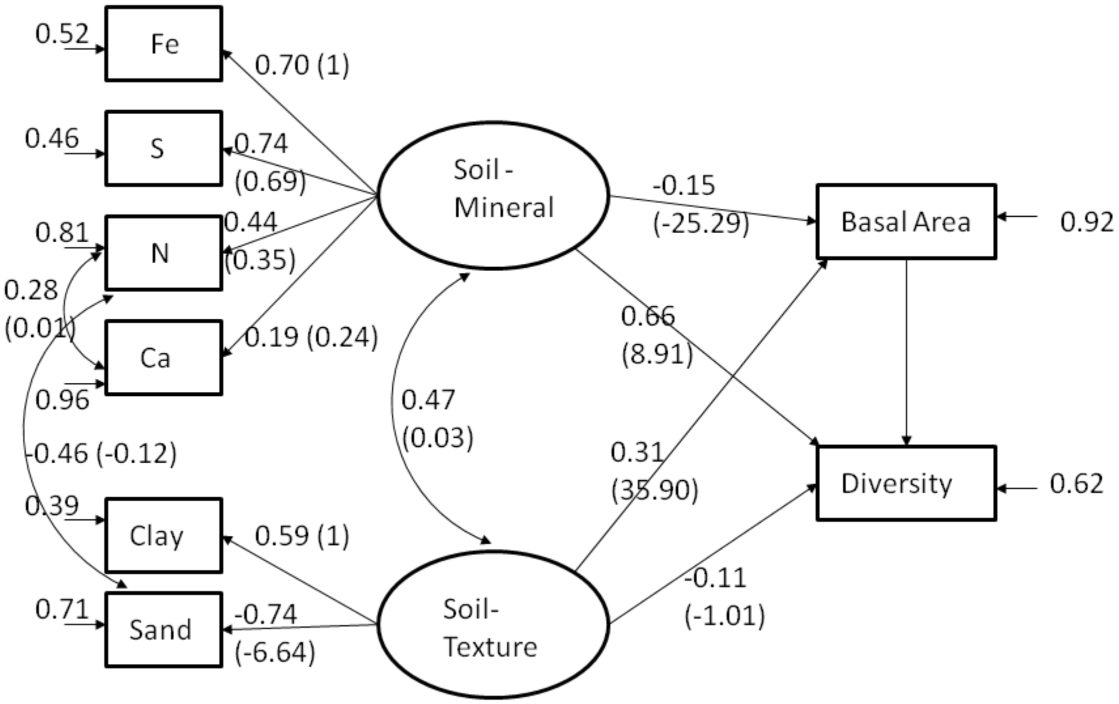


Figure 4.2: Local models of Longleaf species diversity. Figure 2a shows estimates using the 0.1ha diversity measurements; figure 2b shows estimates using the 10m^2 diversity measurements. Note: Loadings on paths are standardized coefficients (unstandardized coefficients), and all measurement errors (arrows going into boxes) are standardized residual variances. All loadings and errors are significant at the $p<0.01$ level, except when no estimate is given, indicating an insignificant loading.

2a.



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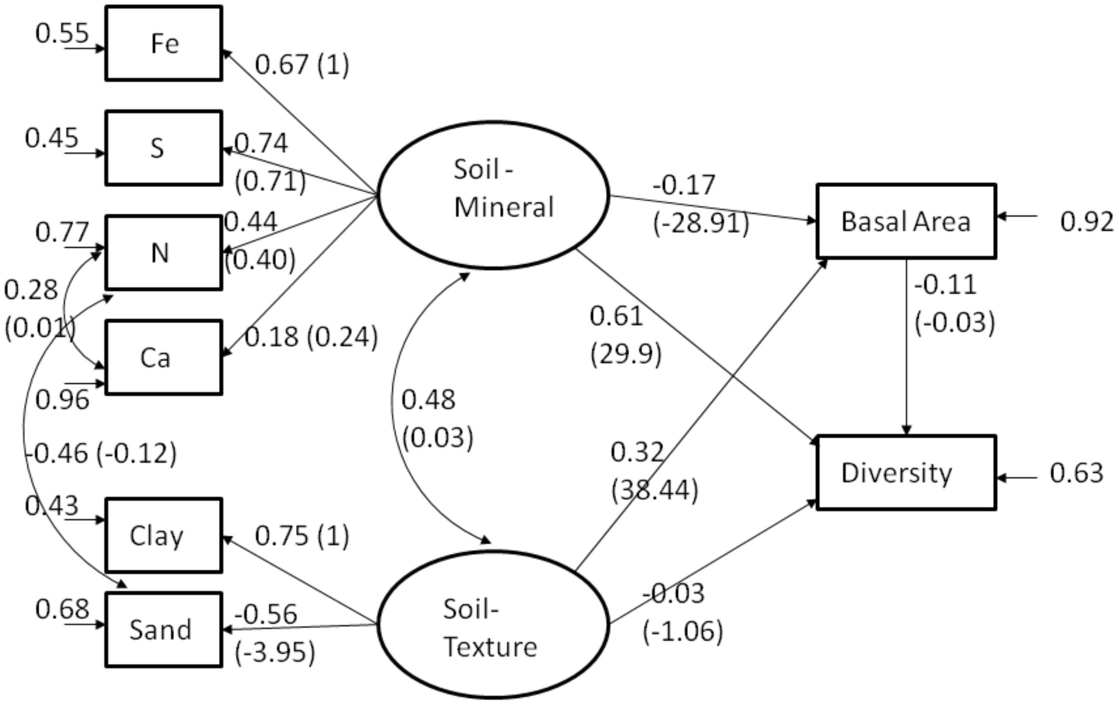


Figure 4.3: Regional models of Longleaf species diversity at the 0.1ha scale. Note: Loadings on paths are standardized coefficients (unstandardized coefficients), and all measurement errors (arrows going into boxes) are standardized residual variances. All loadings and errors are significant at the p<0.01 level.

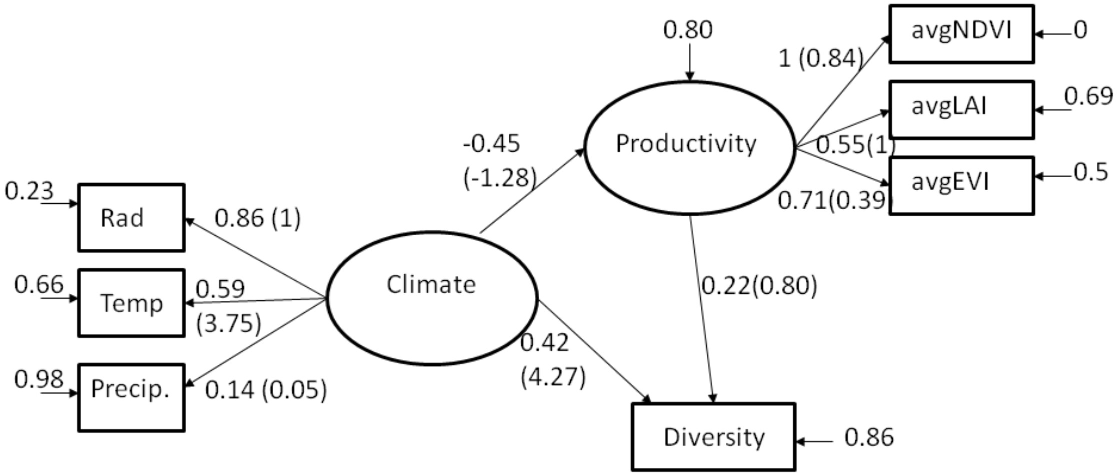


Figure 4.4: Combined model of longleaf species diversity using both local and regional measurements. Soil texture has a negative influence on diversity; however, soil minerals and productivity have a positive influence on diversity. Note: Loadings on paths are standardized coefficients (unstandardized coefficients), and all measurement errors (arrows going into boxes) are standardized residual variances. All loadings and errors are significant at the p<0.01 level.

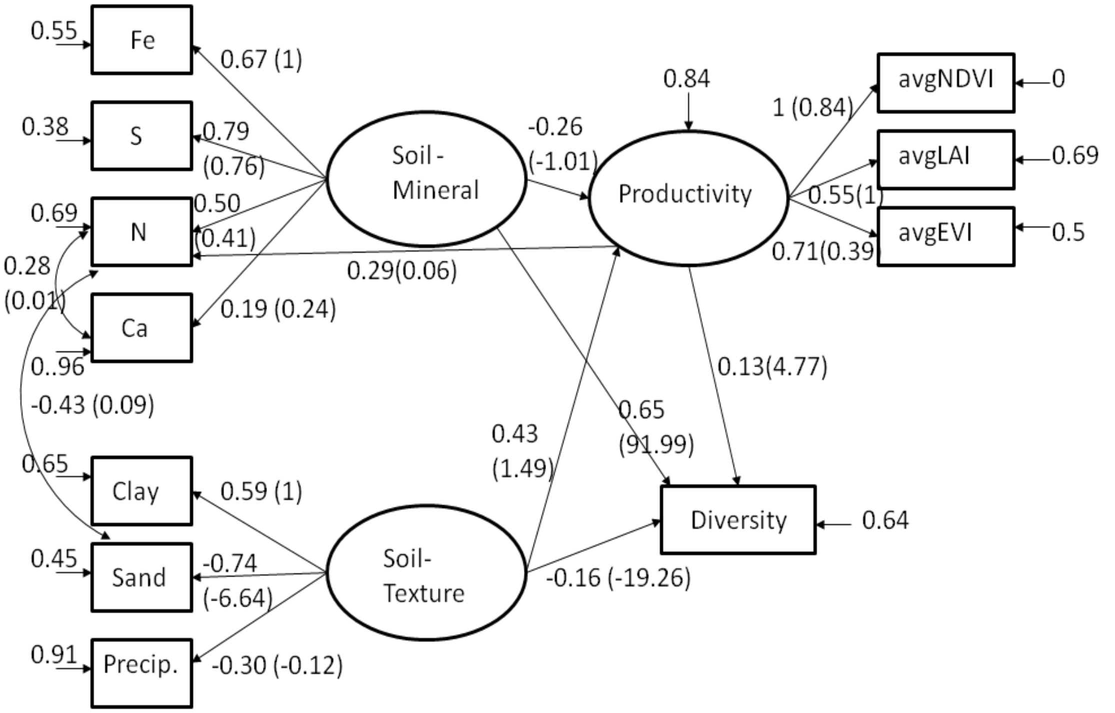


Figure 4.5: Local model of Mountain species diversity at the 0.1ha scale. Note: Loadings on paths are standardized coefficients (unstandardized coefficients), and all measurement errors (arrows going into boxes) are standardized residual variances. All loadings and errors are significant at the p<0.01 level.

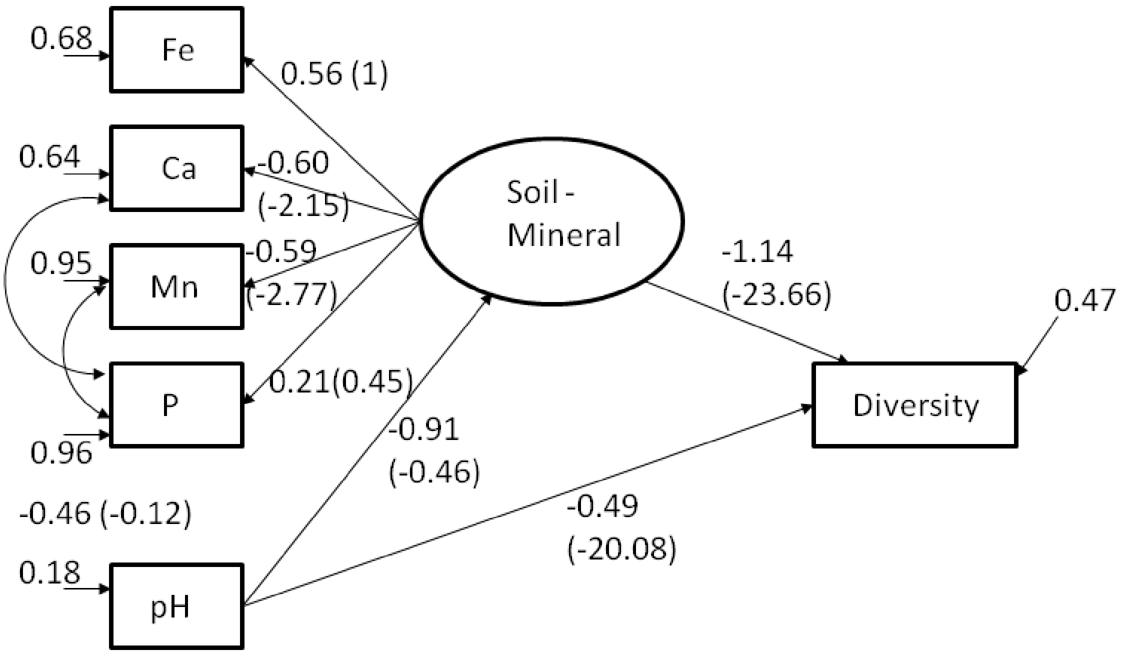
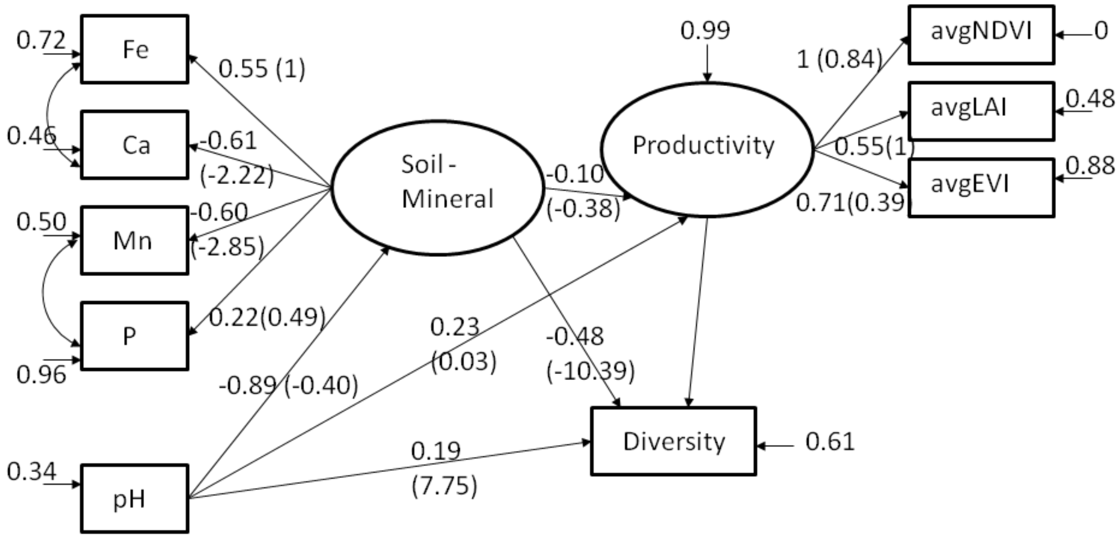


Figure 4.6: Combined model of Mountain species diversity. Note: Loadings on paths are standardized coefficients (unstandardized coefficients), and all measurement errors (arrows going into boxes) are standardized residual variances. All loadings and errors are significant at the p<0.01 level, except when no estimate is given, indicating an insignificant loading.



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Chapter 5: The dependence of gap dynamics on resource context

Abstract

As temporary openings in the competitive matrix, gaps are areas of increased availability of essential resources. Understanding gap dynamics is essential for comprehending community pattern and process as well as structure and diversity. Most previous research on gap processes has focused on one resource, usually light, whereas a multi-dimensional approach to gap dynamics that incorporates availability of multiple resources is needed to represent variation in key gap processes. Building on classical gap dynamics by incorporating two other conceptual frameworks, the herb filter effect (Grime 1998) and the structural carbon-nutrient balance hypothesis (Graves 1995, Graves et al. 2006), provides a more general, multiple-resource approach to gap dynamics.

This resource gradient framework enables a generalization from deciduous temperate forest systems to other forest systems. It predicts that the influence of gaps varies with moisture and nutrient gradients. In deciduous forests at the high end of the nutrient availability gradient, the strong filter effect of the herb layer makes gaps key to tree regeneration. Likewise, on low-nutrient sites in evergreen to mixed deciduous forests, gaps are also important for the growth of many woody species because of the strong filter effect from the evergreen shrub layer. Thus, gaps can be expected to have the lowest influence on tree regeneration at intermediate soil fertility in moderately deciduous to evergreen systems.

Introduction

Gaps are transient openings in a competitive matrix where vital resources such as space, light, moisture and nutrients are more available than elsewhere in the community owing to an event that killed or damaged previously established plants. The important contributions of gap mosaics to pattern and process in plant communities has been recognized since Aubréville's (1938) classic work, which directly or indirectly inspired most subsequent work on gaps. In particular, Watt (1947) built on Aubréville's work to describe how forest trees frequently regenerate through the small-scale successional process he called gap-phase regeneration in which a canopy opening generated by a tree mortality event is filled through colonization by new seedlings or enhanced growth of previously established seedlings and saplings.

Previous research has generally treated all forest canopy gaps as equivalent, usually focusing on the availability of one conspicuous resource such as light, or by treating all resources as a single, undifferentiated contingency. However, the sudden availability of a key resource due to a disturbance event does not guarantee an equivalent availability of other essential resources. For example, tree mortality generally results in increased light levels. However, the availability of essential nutrients can differ significantly among sites. These site differences can, in turn, lead to different recovery patterns, either directly through differences in woody species response to increased resource availability, or indirectly through differences in the amount of competition from herb and shrub species. As a consequence, it is important that studies of gap processes be considered in the context of the availability of multiple, largely independent resources.

Here I evaluate predictions from previous treatments of gap dynamics, describe how gap processes are influenced by subordinate species which are dependent on the background and changing availability of multiple resources, examine how a new synthesis of gap dynamics in a resource gradient framework enhances our understanding of forest community pattern and process, and explore the extent to which this resource-based approach to gap dynamics can be generalized to multiple regions and biomes. I conclude by examining new research opportunities and needs that emerge from adopting a resource-gradient approach to understanding gap dynamics.

The classic gap dynamics model

Previous research has shown that gaps are influential in forest dynamics across a range of biomes (Pickett and White 1985, Platt and Strong 1989, Denslow and Spies 1990). Gap dynamics are a result of disturbances that generate heterogeneity in vegetation cover. In forests, the creation of gaps in the canopy and subsequent growth of new trees into those gaps results in a multi-age stand that is a structurally diverse mosaic (Watt 1947, Whitmore 1978, Bormann and Likens 1979). This mosaic of gaps and former gaps also provides spatial heterogeneity in resource availability within forests. The current understanding of gap dynamics is primarily focused on light availability and falls into four partially overlapping categories: 1) gap formation increases available resources, 2) the influence of gaps is scale dependent, 3) gaps facilitate tree regeneration, and 4) gaps maintain species diversity.

Gap formation increases available resources

Openings in the forest canopy create a heterogeneous pattern of light availability (Canham 1988, Canham et al. 1990). While plant growth in forest systems is typically light-limited, the local abundance of light in forest gaps can result in rapid seedling establishment as well as enhanced growth of already established seedlings and saplings. Although the gap versus non-gap characterization of a forest might better be viewed as a continuum of varying light availability (Lieberman et al. 1989, Canham et al. 1994), forest systems historically have been described as consisting of a mosaic of gap and closed canopy areas, perhaps reflecting the discrete nature of the events that generate the gaps. This approach has resulted in trees that succeed in high-light environments being grouped into a pioneer species category, while the more shade-tolerant life strategies have been grouped into a climax species category (Whitmore 1989).

Although the classic theory of gap dynamics developed around variation in light availability (Platt and Strong 1989), gap formation also increases availability of a variety of other resources, primarily through reduced root competition (Korstian and Coile 1938, Machado et al. 2003). Regardless of the limiting resources in a system, multiple resources should become more available as a consequence of gap formation, including soil nutrients, light, and soil moisture. These other resources can be expected to be particularly important in systems with limited or no canopy development.

The influence of gaps is scale dependent

The heterogeneity created by gap processes can be profitably examined across a range of scales from within individual gaps to across entire forests. Within a gap resulting from a single treefall, Oldeman's (1978) concept of the gap included 4 distinct zones: the epicenter where the crown hits the ground and the impact is maximal, the understory layers that are damaged to some degree as the tree falls, the canopy gap with the understory mostly intact, and peripheral individuals damaged by the creation of the gap. Development in an area of canopy gap with undisturbed understory can be distinctly different from that in a shaded impact zone. This within-gap heterogeneity is further increased by the mineral soil turned up if a tree is uprooted rather than snapped (Putz 1983, Nunez-Farfan and Dirzo 1988, Peterson and Pickett 1990).

Observations and understanding of gap processes are also influenced by the size of the gap. The range of gap size varies from the nearly trivial mortality of a single small stem to a large-scale, multi-tree morality event. Because of the dramatic variance between small patches generated by gradual, individual-stem tree deaths and large-scale, infrequent disturbance events (Turner et al. 1998), where large patches of many tree stems die synchronously, the impact of gap formation on forest heterogeneity varies with the size of the gap generated.

Height of the surrounding trees, gap size, and gap orientation all affect light availability. The heights of the individuals bordering a gap determine local light availability (Canham et al. 1990, Canham et al. 1994). The size or spatial extent of a canopy gap affects the amount of light available in the gap, with larger gaps allowing higher light levels (Chazdon and Fetcher 1984) to reach into the understory and herb layers. In temperate forests, light availability is also dependent on gap orientation, with north-south oriented gaps having higher light levels and slower closure than gaps oriented east-west (Poulson and Platt 1988, Poulson and Platt 1989).

Gaps facilitate tree regeneration

The gap-phase process (Watt 1947) has often been framed as a mechanism crucial for the establishment, growth and maturation of individuals of many canopy species (Pickett and White 1985). In this perspective, the gap is viewed less as a patch of temporarily increased availability of nutrients and light, and more as a patch of enhanced growth of new seedlings and the release and rapid growth of established seedlings, saplings, and understory trees (Canham 1985, Brokaw 1987, Whitmore 1989).

Species differ in their response to increased resource availability: for a significant growth response, some species require large disturbance events, some small tree-fall gaps, and some simply space in the forest interior. Moreover, gap size can influence tree regeneration not only by generating habitat heterogeneity, but also by influencing gap duration. Large gaps can take a long time to fill, whereas smaller gaps may close relatively rapidly and almost entirely by the lateral growth of the surrounding canopy individuals (Uhl et al. 1988, Whitmore 1989). Unless the gap is large and thus slower to close, trees may be dependent on multiple, smaller-gap events, each subsequent gap providing a temporary release from competition from surrounding trees (Canham 1988).

Gaps maintain species diversity

Gaps create varied opportunities for tree regeneration and thereby contribute to tree species diversity within a forest (Hubbell and Foster 1986). Specifically, gaps promote the coexistence of tree species with different regeneration strategies (from the extremely light dependent to the very shade tolerant; Henry and Aarssen 2001, Kaelke et al. 2001), or simply allow more species to become established by reducing competition for resources (Xi 2005, Xi et al. 2008).

Arrival of propagules and establishment of juveniles tend to be highly stochastic, and, as a result, species do not conspicuously sort into particular areas within a gap as might be expected given the distinct zones and within-gap heterogeneity (see above). However, this stochastic establishment also leads to slow competitive exclusion and the maintenance of more species in a forest stand (Brokaw and Busing 2000). Moreover, the maintenance of tree diversity is enhanced by gap isolation in both space and time. Although gaps occur periodically, the high survival rate and longevity of adult trees in comparison to seedlings ensures the maintenance of diversity over time through the storage effect, with long-lived adults providing seed sources for gap colonization (Shmida and Ellner 1984, Warner and Chesson 1985).

The importance of the resource context and subordinate species

The classic conceptualization of forest gap dynamics focuses primarily on competition for light (Figure 5.1A), in part because the spatial variation in light availability is conspicuous, but also because many of the classic studies of forest gap dynamics were conducted in forests with ample moisture and nutrients (e.g., Runkle 1981, Phillips and Shure 1990, Runkle 1998, 2000). However, spatial and temporal variation in light should not be viewed as sufficient for understanding gap dynamics as plant growth can be influenced just as strongly by availability of soil nutrients and water. For example, sapling responses to light availability have been shown to be dependent on nitrogen availability in at least some species (Fownes and Harrington 2004).

Two theoretical constructs from the community ecology literature address the interaction of tree regeneration and the subordinate herb and shrub species in the context of multiple resource gradients: the filter effect (Grime 1998) and the structural carbon-nutrient balance hypothesis (Graves 1995, Graves et al. 2006). A general theory of gap dynamics must incorporate subordinate species and accommodate these two conceptual frameworks in order to account for the influence of subordinate species on tree regeneration.

The filter effect

Plants in the forest herb and shrub layers are often described as subordinate species (Grime 1998) and are frequently overlooked in studies of forest tree dynamics. However, these subordinate species have the potential to dramatically affect the future composition of the forest and the canopy layer. The understory, shrub and herb layers compete directly with and influence tree regeneration in forest systems as diverse as southern beech (Veblen 1989) and Douglas-fir and hemlock forests (Spies and Franklin 1989). Previous studies have shown that the herb and shrub layers influence which species and individuals survive the germination and seedling stages (Graves 1995, George and Bazzaz 1999b, George and Bazzaz 1999a). This filter effect (Grime 1998) is a mechanism through which the herb and shrub layers influence the system, despite having considerably less biomass than the dominants. Consequently, subordinate species impact species composition of the forest canopy and the overall richness of the system both through direct competition with tree seedlings and indirect filtering of which seedlings survive.

The filter effect is expected to be strong where the herb or shrub layer is well developed, and this in turn typically varies with resource availability. Where soil nutrients are readily available, herbaceous plants can more quickly convert nutrients into leaf area than woody species, which invest more energy into creating permanent stems (Givnish 1988). As herb abundance in forests generally increases with soil fertility (Grubb 1987, Peet and Christensen 1988, Peet et al. 2003), the filter effect can be expected to increase with resource availability as well (Figure 5.1B).

Structural carbon – nutrient balance hypothesis

The structural carbon - nutrient balance hypothesis proposes that soil nutrient and water availability strongly affect the interaction between herbs and woody plant regeneration (Graves 1995, Graves et al. 2006). Herbs are generally more efficient at allocating resources to rapid initial vertical growth and subsequent leaf production than woody species because they invest proportionately less carbon in stem tissue (Givnish 1988). As a consequence, in forest understory conditions where nutrients and soil moisture are not limiting (low availability of fixed carbon relative to soil resources; i.e., low C:R ratio), herbaceous plants have an advantage. In these areas, herbs grow faster than woody seedlings, overtopping them and further reducing light availability to woody plant seedlings to a level where those seedlings cannot survive (Graves 1995, Graves et al. 2006). In contrast, where soil resources are limiting, herbs are at a competitive disadvantage as they must re-grow support tissue every year. In these conditions, characterized by moderate available light but limiting soil nutrients (high C:R ratio), woody plant generation is not significantly limited by shade from herbs with the consequence that woody seedling regeneration is generally abundant.

The structural carbon - nutrient balance hypothesis was originally cast in the context of a closed forest canopy and largely did not address the question of how forest trees eventually regenerate on rich sites where herbs are abundant (Graves et al. 2006). At sites with high nutrient and water availability, light is limiting for seedling establishment and growth. On these sites gap formation, which increases light near the forest floor, is expected to be critical for allowing forest tree regeneration (Figure 5.1B). A single gap event might be sufficient for tree seedling establishment since seedlings reaching a height taller than the surrounding herb layer will no longer be competitively inhibited. Indeed, established seedlings and saplings on fertile sites might grow significantly faster than on infertile sites, because of greater availability of soil resources. On the other hand, at nutrient-limited sites the woody vegetation already has an advantage over herbaceous plants with the consequence that gap creation will play a different role in tree regeneration. However, it could play a key role in the interactions among established saplings and understory individuals.

Towards a new synthesis: new predictions with resource gradients

A resource gradient framework clarifies the variation in gap dynamics with essential resources and provides predictions within the resource context. Resources are acquired within a given resource context of competitive interaction from directional, asymmetric competition to diffuse, symmetric competition. Along one axis of this resource context is competition for light, the most obvious resource to consider in gap dynamics. Asymmetrical light competition confers an advantage on taller individuals as they can capture a disproportionate share of resources. In order to compete, plants grow up and towards available light. If light is the primary limiting resource in a system, then the competitive process is weighted heavily towards this vertical competition, and woody species that can germinate and penetrate the filtering herbs and shrubs will eventually have the opportunity to pre-empt available light with their vertical advantage. However, other essential resources are acquired through more diffuse competitive interactions. An example would be soil nutrients for which herbaceous and woody species compete symmetrically underground.

When considering a single resource acquired through asymmetrical competition, the influence of the filter effect will decrease with increasing light availability. As light becomes more available and less limiting, the advantage in the understory shifts from herbaceous plants, with their ability to quickly grow leaf surface area, to woody species, that maintain their initial starting height from the previous growing season with permanent woody stems. Thus the saplings that survive under a filtering layer will eventually grow tall enough that they have a vertical advantage over the filtering layer and are no longer inhibited. Gap creation increases the light availability, shifting the advantage to woody species and facilitating accelerated sapling growth. However, the preexisting soil resource context determines the influence of the filter effect, and thus the influence of a gap. As suggested by the structural carbon – nutrient balance hypothesis, woody species have an advantage over herbs at sites at the low end of the soil resource gradient, and therefore will have little interference from the sparse herb layer. Gaps allow accelerated growth of previously established saplings at this end of the gradient.

The theory discussed thus far pertains to temperate forests with full deciduous seasonality: at the end of each growing season there is a complete dieback of herbaceous species and the trees drop their leaves. This seasonal “restart” provides a window of opportunity for rapid early growth of herbs at the start of the following spring, before the trees leaf out. When considering forests across the gradient of growing season lengths, the herbaceous filter is dominant in areas with high soil nutrients and distinct seasons; however, in areas where seasonality is not important, the herbaceous filter is less central (Figure 5.2A, orange and green isoclines).

Revisiting gap-theory predictions: Gap formation increases available resources

Canopy gaps increase available light in most cases, though the amount of change in light availability is dependent on position along soil nutrient and water availability gradients. In particular, the disparity of light availability in the forest understory between gap and non-gap will vary with soil nutrients and water availability, as well as the size of the gap. In systems with dry or nutrient-poor soils, the canopy is often more sparse than the canopy on nutrient-rich sites. A less dense canopy allows more light to penetrate into the understory, even without a gap-generating disturbance (Coomes and Grubb 2000). Light levels may also be affected by the lack of understory to capture light on richer sites in comparison to the more well-developed understory on low-nutrient sites. Thus, initial disparities in light levels in gaps vs. underneath the canopy are expected to be greater at mesic and high-nutrient-level sites than at low nutrient or dry sites, and the increase in light reaching the understory as a result of a gap is greater at mesic and high nutrient sites.

In systems with plentiful nutrient and water availability, a dense herb layer decreases light levels at the ground level; however, creation of a gap allows woody species to attain a vertical advantage over the herb layer. Because of intense competition for light under closed canopy, gap formation becomes essential for tree regeneration in these high nutrient systems, and more seedlings are found in gaps than underneath the closed canopy. The greater change in light availability at higher-nutrient sites, combined with a greater filter effect, makes gap formation more important for tree establishment at these sites. At nutrient poor sites, gaps still serve a role by releasing established saplings.

Revisiting gap-theory predictions: The influence of gaps is scale and context-dependent

As discussed in the classical gap dynamic model (see above) the scaling and context of a forest gap determine the change in light availability within the gap and surrounding edges. When one or more canopy individuals die, creating a gap, not only light but also available soil nutrients and soil moisture will generally increase. Underneath a forest canopy, the importance of competition for soil moisture and soil nutrients has been clearly demonstrated in forest trenching experiments (Korstian and Coile 1938, Machado et al. 2003). Gap size and severity of the disturbance will determine the amount of increase in resources. Gaps generated by the death of multiple canopy individuals will also cause a greater increase in available soil nutrients.

The influence of gap size may also be context dependent. In nutrient-limited systems, the increase in light in and around even small gaps will often allow the release of advanced regeneration. Larger gaps may allow the establishment of shade-intolerant species on these sites. However, at a nutrient-rich site, the increased light availability in and around a small gap may not be enough to facilitate tree regeneration through the dense herb layer. Larger gaps would be necessary to allow a higher number of saplings in and around gaps to germinate and compete with the herb layer. Once established, the permanent woody stems allow these individuals an advantage in light competition after the annual dieback of herbaceous vegetation during winter, because their permanent stems allow woody species to maintain any height gained the previous growing season, creating a head start on vertical growth. The plentiful soil resources, combined with the release of available light due to the death of canopy individuals, shifts the advantage to woody species, especially any advance regeneration remaining after the disturbance.

Revisiting gap-theory predictions: Gaps facilitate tree regeneration

The extent to which gaps facilitate tree regeneration will depend not only on light, but also on the availability of water and soil nutrients, and perhaps on the timing of the gap creation event. Where all critical resources are simultaneously abundant, high rates of regeneration can be expected. However, gaps should have a different influence on dry, infertile sites than at moist, nutrient-rich sites. Gaps on sites with high nutrient availability allow woody species an opportunity to compete with the already well-developed herb layer. On dry and/or nutrient-poor sites, on the other hand, the most intense competition is not that for light but for soil nutrients and/or water (Coomes and Grubb 2000). Consequently, at these sites a release of light resources in a gap has less of an influence on the ground layer than where soil resources are abundant. Indeed the primary effect of a gap at a nutrient-poor site is the release of the already established woody plants that may require one or several release events to grow into the canopy (Canham 1988).

Revisiting gap-theory predictions: Gaps maintain species diversity

The prediction that gaps maintain diversity was framed around the maintenance of tree diversity through the formation of spatial heterogeneity in light levels, allowing the persistence of species with varying shade tolerances and regeneration requirements. However considering the availability and spatial heterogeneity of resources other than light as well as their influence on the diversity is necessary to have a complete picture of how gaps influence tree diversity.

The resource gradient framework predicts that gaps help to maintain diversity in forests, but that this effect differs along the moisture and nutrient gradients. On dry, low-nutrient sites, the canopy of a forest system is initially sparser and more open, allowing more light through to the forest floor (Coomes and Grubb 2000), in comparison to denser, more closed canopies at nutrient-rich sites. Thus, with the creation of a canopy gap, the release of the species already present as advance generation on nutrient poor sites will have a lesser effect on diversity. At the higher end of the water and soil nutrient availability gradients, there is a greater change in light availability with the opening of a gap. Here the dense herb layer will also have a greater potential effect on diversity, facilitating or filtering out specific species in addition to suppressing regeneration by out-shading seedlings.

As previously examined with dense herb cover under closed canopy (Graves 1995, George and Bazzaz 1999b, George and Bazzaz 1999a), the filter effect (Grime 1998) does have selective influence on the diversity of regeneration. The dense herb layer at high nutrient sites is filtering the woody species successfully regenerating on those sites. Consequently, the maintenance of diversity by gaps is directly influenced by the resource context via this filtering process. Where a strong filter effect is present, different species of woody plants will grow into gaps as compared to the seedlings germinating under closed canopy or already present under the intact canopy at sites.

Generalization to other systems

Although the resource gradient framework for gap dynamics that I present above was constructed for temperate forest systems, it is potentially applicable to other systems.

Forests with evergreen under stories

On sites with intermediate seasonality and lower soil nutrient availability, a dense, evergreen shrub layer may be present. This evergreen shrub layer on low-nutrient sites functions as a filter, similar to the herb layer on high nutrient sites, necessitating gaps in shrub layer to allow establishment of trees (Figure 5.2A, blue isoclines). In low-nutrient environments, evergreen leaves provide an advantage because they conserve nutrients in comparison to deciduous plants. When present, an evergreen shrub layer can have a strong inhibiting and filtering effect on tree regeneration as well as herb growth. In effect, a dense evergreen shrub layer (e.g., *Rhododendron maximum* in the southern Appalachian Mountains) has the potential to behave much like the herbaceous filter, and is perhaps a stronger inhibitor of tree regeneration (Clinton and Boring 1994, Beckage et al. 2000). The presence of an evergreen understory keeps the light availability at low levels year-round and reduces water availability in the soil (Clinton 2003), thereby negating any increase in these resources resulting from formation of a gap. This interaction results in an intense competition and selection process for tree regeneration on such nutrient-poor sites, making gaps essential for the establishment of young trees at sites with a dense evergreen shrub layer (Figure 5.2, blue isoclines). The expected density of seedlings and saplings in this type of system is extremely low under a closed canopy and shrub layer in comparison to the density of young trees in canopy gaps.

Temperate forests in Asia and South America often have an understory dominated by bamboo. The bamboo does not die seasonally and constitutes a dense understory for years until a synchronized flowering and dieback event when the bamboo simultaneously reproduces and then dies (Veblen et al. 1981). In these systems, the bamboo is expected to function as a filter for tree regeneration (Figure 5.2, yellow isocline), similar to the evergreen shrubs in the southern Appalachian mountains. The scarcity of saplings in the understory and gaps in mesic areas can be explained by the intense competition with bamboo in the understory (Veblen 1989); it has been demonstrated that tree regeneration is increased in tree fall gaps in these systems (Veblen et al. 1981). The flowering and dieback events do not have a significant influence on tree establishment; however, these events are important for release of the established seedlings present as a consequence of previous gap events (Holz and Veblen 2006).

Tropical forest systems

The impact of gaps on both structure and diversity has been proven at varying latitudes (Brokaw and Busing 2000) with similar estimates of the importance of gaps in both temperate and tropical systems (Runkle 1989). However, latitude affects the influence of gaps through the incidence angle of the light. At higher latitudes, there are smaller angles of incidence, resulting in a larger effective gap size and increasing light further into the understory, as opposed to lower latitudes where only the area directly below the canopy gap experiences an increase in light levels (Ricklefs 1977, Poulson and Platt 1989), albeit greater changes in light level than found at higher latitudes. In the tropics, the maximum initial light intensity after the creation of a gap is found in the center of the gap with intensity decreasing from the gap center to edges. In northern temperate forests, the light intensity decreases from the northern to the southern end of gaps (Poulson and Platt 1989).

Soils in tropical forests are often assumed to be nutrient poor. However, nutrient-rich soils do occur in the tropics. Weathered ultisols and oxisols are the most common soils in the tropics, but a wide range of soil types, including entisols, andisols and inceptisols are found in some areas of the tropics (Ashton 2004). More fertile alluvial (Ashton 2004) and volcanic soils (also known as andisols; Vitousek and Denslow 1986) are also found in tropical forest systems. Therefore, there is still a gradient of soil nutrients along which gap influence will vary and that needs to be taken into account when predicting the influence of gaps. Although seasonal dieback will only occur in dry tropical forests, the increased influence of sub-canopy layers with nutrient availability should still occur in the tropics.

In temperate systems, seasonality is important in regulating growth, creating a high level of synchronization in the growing seasons; the end of winter defines the start of a growing period for the majority (non-evergreen) of the vegetation (Runkle 1989). This synchronization should also occur in seasonally dry (drought deciduous) tropical forests, creating a similarity in re-growth and regeneration patterns. The synchronization generated in deciduous forests by seasonality creates an advantage of more direct sunlight reaching the forest floor at the beginning of the growing season. This can be advantageous to both herbs and seedlings of woody species. However, the dieback of herbaceous species during the winter or dry season gives a distinct advantage to any woody species that survives until the start of the next growing season. The similarity in synchronization and the importance of gaps means the gradient perspective will fit both forest systems well. Gaps may occur throughout the year in temperate zones (Runkle 1989); however, in tropical systems treefalls predominantly occur during the rainy season (Brokaw 1982). This timing of gap creation creates an added level of synchronization, because all regeneration begins during the same season.

The resource gradient framework for gap dynamics fits several other tropical forest systems, including wet tropical forests. Studies of tropical forest gap dynamics have focused mostly on trees in rainforests with a traditional gap-phase regeneration process dominated by an increase in tree stems that eventually fill in the canopy. Thus, the gradient approach should fit as expected (e.g.,Hubbell and Foster 1986, Brokaw and Scheiner 1989, Whitmore 1989). Gap-generating disturbances are essential in creating structural heterogeneity in tropical forests, maintaining diversity by allowing for light-dependent species to germinate and grow in tropical systems, increasing available resources, and in tree regeneration by release of advance regeneration. Because of the increased vertical stratification in tropical rainforests, the herbs play less of a role than in temperate forests, while repeated release from gaps is crucial for saplings to eventually reach the canopy.

However, in wet tropical forests, there are at least two possibilities of gap regeneration being affected by the understory and resulting in alternative gap regeneration pathways. In rainforests with few dry periods, some proportion of the gaps may be filled by palms (Schnitzer et al. 2000). Thus, towards the high end of the water availability gradient, gaps may proceed through a normal regeneration process or be caught in a palm-dominated stage with the creation of a competitive filter of palms, much like the herb layer in moist, nutrient-rich temperate forests. Alternatively, lianas may dominate a gap; thereby, halting or slowing the regeneration process through intense competition with tree seedlings (Schnitzer et al. 2000, Schnitzer et al. 2005)). Under the structural carbon-nutrient balance hypothesis, this would be expected to occur more often on wetter, more nutrient-rich sites, because like herbs, lianas are investing less energy and fewer resources into supporting structure, instead relying on trees to support them while they grow towards the available light. Both the liana and palm dominated gaps provide an alternative gap regeneration pathway. These gaps are arrested in this stage for a period of time until tree saplings overtop the filtering layer of palms or lianas. The resulting canopy would be strongly influenced by the selective filter of the palms or lianas after the period of suppressed regeneration, and would take much longer to regenerate than a normal gap because of the competition from the dense vine cover. Within various forest types, the gradient perspective on gap dynamics increases the applicability and generality of the gap model.

Different physiognomic types

Non-forest communities have considerably less vertical structure than forests. Thus, the decrease in light competition after a disturbance will be less significant than in forest systems. In communities of lower stature, disturbances as varied as animals, fire, drought (Loucks et al. 1985), and wave action (Sousa 1985) can result in gaps. Although the light gradient may not be as important in these systems because there is less vertical stratification, applying the gradient approach to gaps will still yield more insight into the regeneration in gaps in these systems. Gap generation in these systems will open up space for regeneration and cause a temporary increase in available soil nutrients, increasing species diversity. This effect will be weaker in low nutrient systems where plant establishment and growth are already limited by nutrient availability.

The filtering effect of subordinate species has been demonstrated in grasslands (Boeken and Shachak 2006). Thus, even in systems with less vertical structure than forests, subordinate species can act as a filter in determining the species and individuals that regenerate within a gap. However, in systems such as grasslands, physical disturbances such as fire, wind, and animal damage are more likely to impact individuals of similar stature more equally, as opposed to forested systems where canopy individuals may be blown down in a wind event, leaving some understory individuals, seedlings, saplings and the herbaceous layer intact.

Concluding remarks

Tree regeneration in gaps is influenced by both the light availability gradient (often driven by gaps) as well as the soil nutrient and soil moisture availability gradients. Thus, the theory for the resource gradient framework to gap dynamics laid out here increases our understanding of gap processes through the synthesis gap dynamics with the structural carbon and nutrient balance hypothesis and the subordinate species filter.

In order to generalize the theory, we need to study how tropical and temperate evergreen and seasonal systems differ, and specifically whether the seasonal dieback of both tropical dry forests and the temperate herb layer cause these forests to respond with more tree regeneration in gaps than in tropical rainforests. The applicability of the resource gradient approach to gap dynamics must also be tested in non-forest systems where competition for light is less important. Because of the release of available space and nutrient resources, gaps at nutrient-rich sites should increase regeneration and increase species diversity more markedly than at nutrient-poor sites. This increase in diversity in gaps at the high end of the nutrient availability gradient will include more fast-growing taxa with short life spans (e.g. annuals). However, on nutrient limited sites, there will be fewer of these fast-growing species, because slower-growing perennial species will be favored. In systems containing a dominant species or species with high cover values, gaps will increase regeneration and diversity; gaps in these systems function to interrupt the filtering effect of dominant species, similar to the herbaceous filter on rich sites in forest systems.

The resource gradient approach appropriate for gaps should be examined at different scales. As soil nutrients may be distributed patchily, the scale(s) at which nutrient heterogeneity matters must be determined. Because natural gaps occur in a variety of sizes, the congruence of gaps and resource distribution will vary with larger gaps potentially containing more nutrient variability. Scaling may also influence our predictions: the smaller gaps discussed here will have shorter regeneration time, with more advanced regeneration and intact understory. Large-scale and less frequent disturbance events will have longer recovery time with regeneration depending more on dispersal and germination of seedlings. Large-scale, infrequent disturbance events tend to have a higher severity of disturbance that decreases the influence of herb and shrub layers on tree regeneration in forest systems. A comparison of regeneration in gaps of different sizes would address the influence of scale.

There are several challenges remaining for future fieldwork on gap dynamics. We need to obtain data on gaps of different size, shape, and orientation from across soil nutrient and water availability gradients. In order to fully test the gradient theory of gap dynamics gaps from tropical, temperate, and boreal zones should be examined. The resource context of gaps could also be applied in non-forest systems. A thorough examination of the herb and shrub filters of tree regeneration along entire nutrient gradients is also needed to determine the applicability of the gradient approach to gap dynamics. However, in order to do this, we need complete field measurements of gap parameters including herbaceous cover, soil nutrients, topographic position, and gap age. Application of the resource gradient perspective to gap dynamics improves our insight into the effects of small-scale disturbance on tree regeneration, community structure, and maintenance of species diversity; comparative research in tropical forests and other systems will further our understanding and generalization of gap theory.

Figures

Figure 5.1: The classic model of gap dynamics and gap dynamics in a resource context. A. The classic model of gap dynamics. The importance of gaps to tree regeneration (establishment and growth of seedlings) decreases as the availability of light increases in the absence of a gap. B. Gap dynamics in a resource context. Consideration of soil nutrients illustrates where the herb filter effect is strong at the high end of the nutrient availability increasing the importance of gaps for tree regeneration.

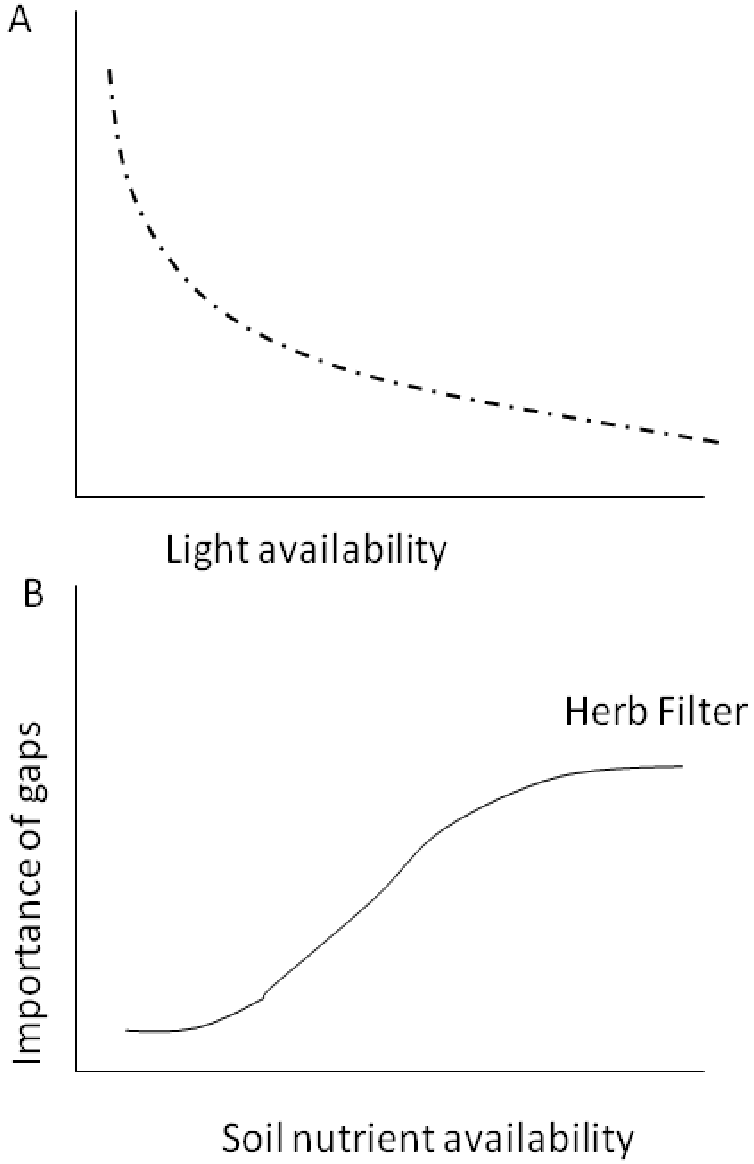


Figure 5.2 A: Strength of the filter effect along fertility gradient (soil nutrient availability) and length of growing season. The influence of gaps can be understood in the context of various filters and the deciduousness of the dominant cover. Shading indicates the strength of each filter effect. Where filter the filter effect is strongest, gaps have a different effect, allowing tree regeneration to break through the filter. Orange isoclines indicate a predominantly deciduous canopy. Blue isoclines indicate the strength of the herb filter; green isoclines correspond to the strength of the evergreen shrub filter. The yellow isocline represents the bamboo filter. Tree seedlings have the highest potential for establishment and growth (maximal seedling survivorship) in areas where the filter effect is lowest, and thus the influence of gaps on tree regeneration is the lowest. On high nutrient sites that are strongly deciduous (e.g. Northern temperate deciduous forests), the herb filter is dominant in the understory. At the low end of the fertility gradient, an evergreen shrub layer functions as a filter (e.g. *Kalmia latifolia* and *Rhododendron maximum* in the Southern Appalachians).

A.

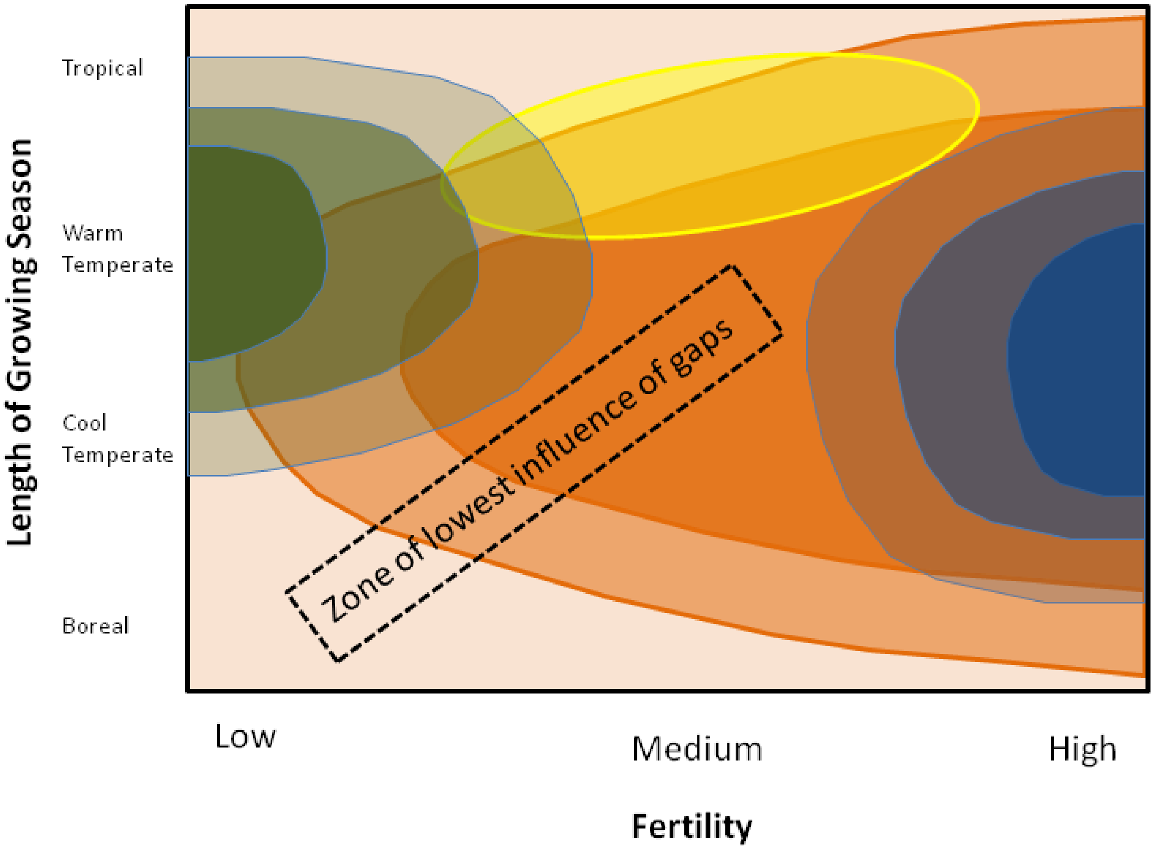
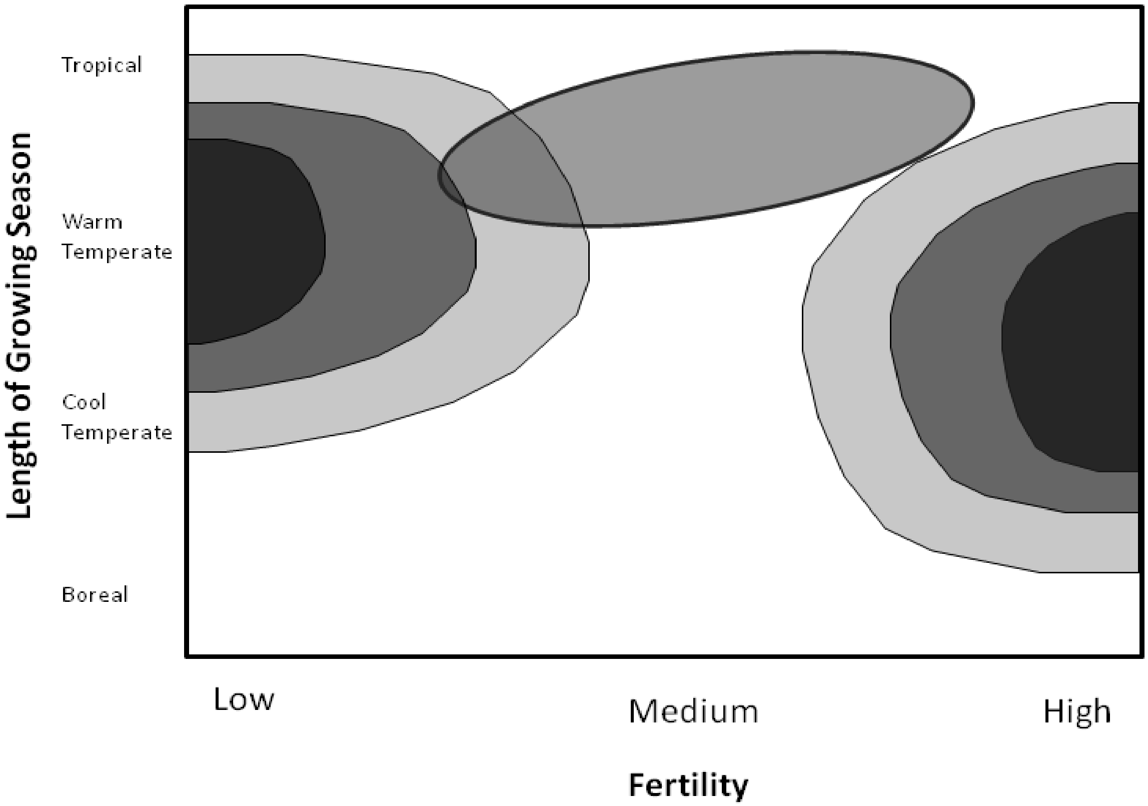


Figure 5.2 B: Overall filter effect. Shading indicates the strength of the overall filter effect. Gaps play a central role in releasing tree regeneration where there is darker shading because of the filter effect.

B.



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Chapter 6: Forest gaps along soil nutrient gradients in North Carolina

Abstract

The classical approach to forest gap dynamics focuses primarily on light availability for plant growth, rather than considering all necessary resources. While this attention to light has established the importance of disturbance to tree regeneration, it neglects possible differences in the influence of gaps in a more comprehensive resource context. Consideration of soil nutrient availability suggests that the importance of gaps to tree regeneration varies with the strength of the subordinate species filter, which is highly correlated with the nutrient gradient. As an initial test of the resource context approach to gap dynamics (see Chapter 5), forest gaps in North Carolina are sampled to assess variation in diversity and density of woody species regeneration across gaps.

Introduction

Examination of disturbances has increased our understanding of community pattern and process. It is accepted in ecology that a variety of disturbances across multiple scales play a major role in maintaining forest diversity (Pickett and White 1985, Platt and Strong 1989, Denslow and Spies 1990). However, studies of forest canopy gaps have primarily emphasized competition for a single resource, typically light (e.g. Lieberman et al. 1989, Canham et al. 1994). This view fails to consider the influence of other essential resources, such as soil nutrients. Previous work on both nutrient availability and competition from other species has generated hypotheses describing mechanisms that affect regeneration but that have not been tested in canopy gaps. Two mechanisms in particular, the filter effect of subordinate species (Grime 1998), and the structural carbon nutrient balance hypothesis (SCNBH; Graves 1995, Graves et al. 2006), suggest that gap resource context determines the relative influence of a gap on tree regeneration (Chapter 5).

With the first mechanism, the subordinate, or non-dominant, species in a community act as a filter altering the success of regeneration. Species in the herb layer in forested systems can be described as subordinate species (Grime 1998) and have received little attention. Herbs influence tree seedling survival directly through competition (Spies and Franklin 1989, Veblen 1989). Additionally, the herb layer may also determine which trees are able to germinate and survive in the seedling stage (George and Bazzaz 1999a, George and Bazzaz 1999b), thus influencing the specific species or individuals surviving. Because herbs act as a filter (Grime 1998) on the dominant species in forests, they play a significant role in community composition and ecosystem function.

The second mechanism, the SCNBH, explains how soil gradients influence vegetation (Graves 1995, Graves et al. 2006). Physiologically, herbs are more efficient than woody species at allocating resources rapidly to leaf production (Givnish 1988). Since herbs invest more in non-permanent leaf area and convert nutrients to leaf area more quickly, the SCNBH proposes that herbs have an advantage in areas where light is limiting, but nutrients and soil moisture are plentiful. Thus, where the amount of available light, which can also be described as the amount of fixed carbon, is low compared to the plentiful available soil resources (a low C:R ratio), herbs compete more effectively than woody species in the ground layer of the forest, resulting in a high cover of herbaceous plants and fewer woody individuals (Graves 1995, Graves et al. 2006). In contrast, where soil nutrients or water availability are limited, woody species will have an advantage over herbs, because the ability to retain nutrients in permanent stems or semi-permanent leaves becomes a competitive advantage. Thus, on high-light, low-nutrient sites (high C:R ratio), woody plant cover and stem density will be high in the understory, because woody species have an advantage over herbs (Graves 1995, Graves et al. 2006).

Although the SCNBH has only been tested under a closed canopy, I hypothesize that it will hold true for gaps as well. A new resource-context perspective on gap dynamics emerges with the application of both the SCNBH and the filter effect of subordinate species to gaps (Chapter 5, Figure 5.2). Under this framework, I expect the filter effect to generate a differential importance of gaps to tree regeneration across the nutrient gradient. The influence of the herb layer is expected to remain strong under closed canopy at high-nutrient sites, but this influence will be consistently low, both in and out of gaps, at nutrient-poor sites. I hypothesize that gaps will have a different influence on tree regeneration on low nutrient sites: the number of established saplings will be little affected by the opening of a canopy gap, while established saplings will be released from competition to grow into the canopy. There will be a gradual increase in number of saplings from closed canopy to edge of gaps, to the center of gaps. In contrast, on nutrient-rich sites, pre-existing dense herbaceous cover will act as a filter to influence tree regeneration, necessitating gaps to increase light levels sufficiently for woody plants to break through the herbaceous layer. Immediately after gap formation, the herbs may grow denser; however, the increased light in the gap will eventually shift the C:R ratio, favoring woody species. Therefore, richer sites with a higher herbaceous cover should have a greater disparity in sapling density between closed canopy and gaps in comparison to nutrient poor sites.

Tip up mounds cause mechanical disturbance of the forest floor, opening up both space and soil resources. Tip up mounds should have greater number of stems than other positions within a gap on high nutrient sites because the mechanical disturbance of the forest floor will disrupt the herbaceous filter. However, because of the decrease in soil competition that has been demonstrated in forest trenching experiments (Korstian and Coile 1938), larger numbers of stems are also expected on tip up mounds on low nutrient sites. The increased light availability and exposed mineral soil may also allow for establishment of a larger number of species, particularly early successional species. Based on previous findings that species diversity increased in gaps following Hurricane Hazel (Xi 2005), I expect gap subplots to be more diverse than non-gap subplots.

The framework of resource context in Chapter 5 predicts that gaps in temperate forests have a greater impact at the high end of the soil nutrient gradient because of the dense herb layer, and I expect to see this pattern in small-scale wind-disturbance gaps in North Carolina forests. As an initial test of this framework, I sampled gaps across a range of soil nutrient availability and herb layer cover. I expect to see a greater difference in the number of saplings present in gaps versus underneath closed canopy on high nutrient sites with dense herbaceous cover than on low nutrient sites.

Methods

Fieldwork

In order to maximize the similarity in gap age and cause, I selected gaps from two hurricanes, Hugo and Fran, which had substantial impacts on North Carolina forests. Examining a gap several years after a disturbance event has the added benefit of allowing researchers to identify individuals that have survived for several years and are successfully growing into the gap. In the years immediately after a disturbance, the researcher only has access to seedlings initially recruiting into a gap, and these have a high level of mortality. Gaps were sampled in August 2007 and May through August 2008 in three areas of North Carolina: the Triangle, Charlotte, and Mount Jefferson areas (Table 6.1). Gaps from Hurricane Fran (1996) were identified and sampled using canopy tree mortality data in Duke Forest and the North Carolina Botanical Garden. At Swift Creek Bluffs, gaps of a similar age were identified and sampled. Gaps from Hurricane Hugo (1989) were sampled in the Charlotte, NC area on the Redlair property in Gaston County with guidance from the owner, and at Reedy Creek Preserve and McDowell Creek in Mecklenburg County. To capture the high end of the nutrient gradient, sites with high fertility in the Amphibolite region of Ashe and Watauga Counties, including Bluff Mountain, Mount Jefferson State Park, and Paddy Mountain were also sampled (Mountain region). These gaps were of a similar age to the Charlotte gaps, and one gap at Bluff Mountain was identified by a volunteer as occurring during Hurricane Hugo.

All gaps were sampled using a transect (Figure 6.1) placed in a north-south orientation (Canham et al. 1990), starting under the closed canopy, and crossing through the canopy gap and back into closed canopy. Plots were positioned to cross the center of the gap, and ideally placed the mid-point of the transect in the center of the gap. All transects were 5m wide and most were 50m long, although some transects were shortened to prevent entry into an adjacent gap. The 5x50m transects were subdivided into 5x5m subplots in which all woody stems taller than diameter at breast height (dbh, 1.3m above the ground) were recorded by dbh size classes (following Peet et al. 1998): 0-1cm, 1-2.5cm, 2.5-5cm, 5-10cm, 10-15cm, 15-20cm, 20-25cm, 25-30cm, 30-35cm, 35-40cm, and over 40cm, the latter in 1cm dbh increments. Woody stems less than dbh were tallied in 1x5m subplots along the center line of the 5x5m subplots. Each subplot was also assigned to a qualitative class based on its location in relation to the original canopy gap: Gap with tip up mound (tip up), Gap, Edge, Not Gap (Figure 6.1). Plot data including both a general description and GPS measurement of location, percent cover by strata, slope, and soil description were recorded (following Peet et al. 1998).

Plots were analyzed by region. Within each region, plots were divided into high and low herb covers to determine if there were different effects on number of woody individuals depending on the strength of the herb filter. In the Triangle area, plots were split into greater or less than 35% herb cover. In the mountains and Charlotte area plots were divided at 40% herb cover, in order to roughly split the data into two equal subsets.

Nine soil samples were taken for each plot in clusters of three: three samples spaced 1m apart in the center of the plot in the gap, and three samples spaced 1m apart, in the first and last subplot of the transect (Figure 6.1). Soils were dried in an oven, and sieved. One sample from each cluster of three was randomly selected for analysis. Soils were sent to Brookside Laboratories for texture and nutrient analysis.

The significance of the gap position (not gap, edge, gap, tip up) and the herb cover (high or low) was evaluated using Poisson regression models. All regressions were performed using Stata 11 (StataCorp. 2009).

Results

Soil samples demonstrated by sampling in the West Jefferson mountain area the range of nutrient availability included higher nutrient levels than in the Triangle (Table 6.2). The mountain transects had large within-transect ranges in copper, iron, calcium, organic matter, aluminum, and cation exchange capacity (Table 6.3). A few soil characteristics, such as *p*H and bulk density, had similar ranges within transects from all three regions.

In the Triangle area, there were fewer woody species in non-gap and gap subplots on sites with low herb cover than in high herb cover sites (Figure 6.2). In the mountains, the woody species diversity was relatively consistent from closed canopy to the center of gaps on sites with both low and high herb cover (Figure 6.3). In the Charlotte area, there were fewer woody species in not gap and tip up subplots on low herb cover sites than high herb cover sites (Figure 6.4). However the expected trend of higher species diversity in gaps compared to closed canopy was not evident.

In the Triangle area, the dominant trend was a general increase in number of stems from not gap to gap subplots, and no significant difference between low and high herb cover sites. Results of Poisson regression models evaluating each size class are presented in Tables 6.5 through 6.9. There is a steady increase in number of woody stems under breast height present on low herb cover sites from closed canopy to the center of gaps (Figure 6.5). However, on high herb cover sites, there are more seedlings under the canopy and at the edge of the canopy than in corresponding low herb sites. These trends hold true for the next larger size class of saplings, 0-1cm dbh, except that there is no significant difference between non-gap plots in different herb covers (Figure 6.6). While there are no differences between herb cover classes, the number of stems 1-2.5cm dbh increase from closed canopy to gap subplots (Figure 6.7), and the number of individuals in gap and tip up subplots and non-gap subplots are significantly different (Table 6.7). In the 2.5-5cm dbh class, the number of individuals near tip up mounds was greater on low herb cover sites (Figure 6.8). In the 5-10cm size class, there were no individuals in this size class under closed canopy on high herb cover sites

(Figure 6.9). Near tip up mounds, the number of saplings in this size class was greater on low herb cover sites.

In the mountains, where there were higher herb cover values, there were some significant differences between low and high herb cover sites. Results of Poisson regression models evaluating each size class are presented in Tables 6.10 through 6.14. There are more woody stems under breast height present on low herb cover sites at the edge of gaps and inside of gaps. However, on high herb cover sites, there are more stems under breast height in subplots with a tip up mound than on low herb cover sites (Figure 6.10). All coefficients in the Poisson regression were significant, indicating that herb cover class is a significant predictor of number of stems, and edge, gap, and tip up mound subplots were different than non-gap subplots (Table 6.10). In the 0-1cm dbh size class, high herb cover and low herb cover sites have similar numbers of saplings across gaps (Figure 6.11). The number of saplings in the 1-2.5cm size class decreases from subplots not in gaps to the center of gaps regardless of the herb cover. However, in subplots with a tip up mound, there were more stems on high herb cover sites than low herb cover sites (Figure 6.12). High and low herb cover sites had similar counts of 2.5-5cm dbh stems under closed canopy and in gaps (Figure 6.13). However, at the edge of gaps there were greater numbers of stems on low nutrient sites, and in subplots with a tip up mound there were more stems on high herb cover sites. In the 5-10cm dbh size class, the number of stems gradually decreased from not gap subplots to the center of gaps for both herb cover classes (Figure 6.14). The gap plots had statistically different numbers of individuals than non-gap plots (Table 6.14).

In the Charlotte area, the number of stems under breast height present on high herb cover sites is greater than low herb cover sites across all gap positions (Figure 6.15, Table

6.15). On low herb cover sites, the number of saplings with 0-1cm dbh increases steadily from closed canopy to the center of the gaps. There are greater numbers of stems on high herb sites in non-gap subplots, edges of gaps and in gaps (Figure 6.16, Table 6.16). The number of saplings in the 1-2.5cm size class increases from subplots not in gaps to the center of gaps regardless of the herb cover. There are more stems of this size class on high herb cover sites that low herb cover sites in gaps (Figure 6.17, Table 6.17). Herb cover influenced the number of stems, and edge, gap and tip up subplots were significantly different from non-gap subplots in the 2.5-5cm dbh size class (Figure 6.18, Table 6.18). There is a steady increase in number of 5-10cm dbh stems from not gap to gap plots. However there is no significant difference between high and low herb cover sites for this size class (Figure 6.19, Table 6.19).

Discussion

The high level of variation in several soil characteristics across gaps (Table 6.3) indicates that there are differences across gaps in resource availability. This may be due to consistent differences in availability of soil nutrients in and around gaps. Denslow et al. (1998) demonstrated a higher level of nitrogen availability in experimental gaps in Costa Rica during the first year after gap formation. However, given the high level of variance of some of the soil characteristics, it would be interesting to study the duration of the changes in soil characteristics through time.

The differences in number of species across transects were not clear. In the Triangle area, there were fewer woody species on low herb cover sites than in high herb cover sites, both in not gap and gap subplots. However, overall there was no significant trend in number of woody species across gaps in any region.

In the Triangle transects, there was a gradual increase in number of stems from under the canopy to the center of gaps. However there was no difference between low and high herb cover sites, because the highest herb cover only reached 40%. There were larger numbers of stems in tip up subplots on low herb sites, which was probably due to a decrease in soil competition.

In the mountain tip up subplots, there were more individuals less than breast height on high herb sites than on low herb cover sites, as expected. This same pattern was also evident in the 1-2.5cm dbh size class. This trend was expected in gap and tip up subplots; however, perhaps the combination of mechanical soil disturbance and a canopy gap is necessary.

The resource framework of gap dynamics (Chapter 5) through the application of the herb filter effect (Grime 1998) and the SCNBH (Graves 1995, Graves et al. 2006) is most evident in the 0-1cm dbh size class in the Charlotte area; however, herb cover is significant in the Poisson regression models for stems under breast height in the mountains, stems 0-1cm dbh in Charlotte, and stems 2.5-5cm dbh in Charlotte. Because of the herb filter effect and the need for increased light availability in and around gaps to release woody vegetation from the effect of the herbaceous filter, I expected a greater difference in number of stems in gaps versus closed canopy on sites with a strong herb filter. In the Charlotte plots, there were more stems 0-1cm dbh in the center of gaps in tip up subplots on high herb cover sites than at low herb cover sites. This suggests that the gap, and soil disturbance from the tip up are playing a larger role on sites with high herbaceous cover, at least for this size class of woody stems.

The trends between sites with low herb cover and high herb cover may have been partly obscured by a particular case of gap regeneration. In several transects, the gap subplots were covered in vine seedlings, often those of *Vitus rotundifolia*. This may represent a special case of regeneration where vines halt or slow the process of tree regeneration in gaps. In tropical gaps, this path of gap regeneration has been observed and described with either lianas or palms dominating and "freezing" the regeneration of the gap by filtering out trees (Schnitzer et al. 2000). A weaker version of this vine filter may also occur in temperate forests and deserves further study as a special type of filter in gap regeneration.

Although there was some evidence in support of the resource context for gap dynamics in Chapter 5, further study is necessary to test this framework. Truly high herb cover (>80%) would be preferable for testing the filter effect, so a more extensive survey in areas with dense herbaceous cover is needed because the high herb cover in this study (40-70%) may not have been dense enough to see the full impact of the herbaceous layer. Studies assessing the differences in regeneration in gaps across nutrient availability gradients comparing tropical, temperate and boreal gaps would best assess the generality of the resource content framework for gaps. Following gaps through time to assess when the filter effect shifts in gaps would help to understand this framework.

Tables

Table 6.1: Gap plots by location. The total number of plots is broken down into plots with a high understory herbaceous cover (greater than or equal to 35% for the Triangle and Charlotte and 40% for West Jefferson) and low herbaceous cover (less than 35% for the Triangle and Charlotte and 40% for West Jefferson).

Area in NC	Site	Total Plots	High Herb	Low Herb
Triangle	Duke Forest	7	1	6
	NC Botanical Garden	6	2	4
	Swift Creek Bluffs	4	4	0
Charlotte	Red Lair	8	2	6
	Reedy Creek	6	4	2
	McDowell Creek	5	0	5
West Jefferson	Paddy Mountain	4	4	0
	Mount Jefferson	10	1	9
	Bluff Mountain	6	5	1

Table 6.2: Range of soil variables in gap plots by region. This table shows the range of soil measures found in the gap transects: Cation exchange capacity (CEC), soil *p*H (pH), estimated nitrogen release (Est. N Release).

	Triangle		Mountain		Charlotte	
Soil Measure	Min	Max	Min	Max	Min	Max
CEC (meq/100 g)	4.15	20.4	5.09	33.24	2.87	17.17
pH	4	6.2	3.7	5.7	3.9	6.1
OrganicMatter (%)	1.95	10.73	5.81	83.75	1.83	14.63
Est. N Release (N/acre)	59	125	104	130	57	127
S (mg/kg)	11	22	14	41	10	31
P (mg/kg)	4	31	5	38	4	41
Ca (mg/kg)	159	1587	114	3528	90	1988
Mg (mg/kg)	40	266	38	381	28	373
K (mg/kg)	31	142	36	159	24	143
Na (mg/kg)	19	41	23	55	20	46
Ca (%)	14.74	64.08	11.2	63.41	13.12	69.03
Mg (%)	6.67	20.83	2.57	13.99	4.43	20.26
K (%)	0.6	4.22	0.6	4.71	0.55	3.69
Na (%)	0.57	3.49	0.46	3.01	0.72	4.32
Other Bases (%)	5.2	9.4	6	10	5.2	9.6
Fe (mg/kg)	65	277	32	483	52	385
Mn (mg/kg)	4	351	5	572	4	249
Cu (mg/kg)	0.47	2.12	0.64	12.13	0.41	2.65
Zn (mg/kg)	0.93	7.69	0.99	12.45	0.58	5.01
Al (mg/kg)	287	1018	190	1773	417	1185
Bulk Density (g/cm3)	0.66	1.11	0.2	0.96	0.54	1.19
Sand (%)	31.77	56.64	49.85	72.68	34.55	75.86
Silt (%)	30.73	56.08	22.75	34.42	16.44	43.97
Clay (%)	9.83	26.68	4.57	17.45	6.63	27.91

Table 6.3: Average range for each soil characteristic by area. For each transect, the range was determined by subtracting the minimum value from the maximum. These ranges were then averaged by region: Triangle area, mountains near West Jefferson (Mountain), and Charlotte area.

Soil Measure	Triangle	Mountain	Charlotte
CEC (meq/100g)	4.54	7.59	3.83
pH	0.64	0.54	0.61
Org (%)	2.66	14.86	2.61
S (mg/kg)	3.44	6.95	5.11
P (mg/kg)	7.00	6.75	7.05
Ca (mg/kg)	444.33	745.50	402.11
Mg (mg/kg)	52.22	57.50	76.32
K (mg/kg)	32.44	29.60	34.42
Na (mg/kg)	6.89	7.40	6.63
Ca (%)	15.31	12.73	13.37
Mg (%)	4.13	3.19	4.29
K (%)	1.46	1.03	1.14
Fe (mg/kg)	61.67	111.95	84.05
Mn (mg/kg)	94.22	99.85	64.74
Cu (mg/kg)	0.32	2.10	0.46
Zn (mg/kg)	1.93	2.55	1.35
Al (mg/kg)	231.00	367.15	242.68
Bulk Den (g/cm3)	0.15	0.20	0.15
Other Bases (%)	1.27	1.08	1.22
Est. N Release (N/acre)	18.11	7.65	20.63

Table 6.4: Average density of woody individuals by dbh size class per 5x5m plot for low (less than 35% herbaceous cover) and high (greater than 35% herbaceous cover) cover plots.

		0-1cm	1-2.5cm	2.5-5cm	5cm-	10cm-	15cm-	20cm-	25cm-	30cm-	35cm-	40cm+
Low Herb Cover	Not Gap	2.50	1.00	1.00	2.00	0.50	1.50					1.00
	Edge	4.79	1.97	2.53	1.27	1.19	1.00	1.00	1.09	1.00	1.00	1.09
	Gap	5.44	2.30	2.35	1.77	1.36	1.34	1.06	1.00	1.13	1.00	1.06
	Tip up	9.33	3.06	2.94	1.63	3.86	1.00	1.00	1.00		1.00	1.00
High Herb Cover	Not Gap	4.00	1.00		1.50	1.00				1.00	1.00	1.50
	Edge	8.39	1.87	2.22	1.30	1.35	1.10	1.17	1.14	1.50	1.00	1.15
	Gap	8.48	2.74	2.24	1.44	1.38	1.12	0.96	1.15	1.17	1.00	1.08
	Tip up	9.35	2.47	2.42	1.14	1.00	1.00	1.00		1.00		1.00

Table 6.5: Poisson regression model of the number of woody stems less than breast height by gap position and herb cover in the Triangle area. Gap position was classified as gap, edge of gap (edge), gap, or tip up. Herb cover was low (less than 35% herb cover) or high (greater than 35% herb cover). This model was significant (N=80, Wald chi-square= 18.98, df= 4, p=0.00), indicating that at least one model coefficient is also significant. Bold values indicate significant z values at p<0.05. In this model, the counts of stems in edge, gap, and tip up subplots were different from not gap subplots.

lessdbh	Coef.	Robust Std.Err.	z	P>|z|	95% Confidence Interval	
Not Gap						
Edge	0.63	0.17	**3.79**	**0.00**	0.31	0.96
Gap	0.48	0.18	**2.65**	**0.01**	0.12	0.84
Tip Up	0.75	0.21	**3.63**	**0.00**	0.34	1.15
HerbCover	-0.05	0.12	-0.39	0.70	-0.28	0.19
_cons	4.78	0.26	18.23	0.00	4.26	5.29
Model	Obs	ll(null)	ll(model)	df	AIC	BIC
lessdbh	80	-2578.73	-2381.8	5	4773.68	4785.59

Table 6.6: Poisson regression model of the number of woody stems 0-1cm dbh by gap position and herb cover in the Triangle area. Gap position was classified as gap, edge of gap (edge), gap, or tip up. Herb cover was low (less than 35% herb cover) or high (greater than 35% herb cover). This model was insignificant (N=80, Wald chi-square= 7.51, df= 4, p=0.11), indicating that none of the coefficients are statistically significant. Thus there are no statistical differences between these groups.

0-1cm dbh	Coef.	Robust Std.Err.	z	P>|z|	95% Confidence Interval	
Not Gap						
Edge	0.13	0.28	0.46	0.65	-0.42	0.68
Gap	0.23	0.29	0.81	0.42	-0.33	0.80
Tip Up	0.59	0.30	1.98	0.05	0.00	1.18
HerbCover	-0.19	0.16	-1.18	0.24	-0.50	0.13
_cons	2.40	0.37	6.52	0.00	1.68	3.12
Model	Obs	ll(null)	ll(model)	df	AIC	BIC
0-1cm dbh	80	-352.28	-338.31	5	686.62	698.53

Table 6.7: Poisson regression model of the number of woody stems 1-2.5cm dbh by gap position and herb cover in the Triangle area. Gap position was classified as gap, edge of gap (edge), gap, or tip up. Herb cover was low (less than 35% herb cover) or high (greater than 35% herb cover). This model was significant (N=80, Wald chi-square= 23.45, df= 4, p=0.0001), indicating that at least one model coefficient is also significant. Bold values indicate significant z values at p<0.05. In this model, the counts of stems in gap, and tip up subplots were different from not gap subplots.

1-2.5cmdbh	Coef.	Robust Std.Err.	z	P>|z|	95% Confidence Interval	
Not Gap						
Edge	0.59	0.37	1.60	0.11	-0.13	1.32
Gap	1.30	0.38	**3.45**	**0.00**	0.56	2.04
Tip Up	1.10	0.40	**2.75**	**0.01**	0.32	1.89
HerbCover	-0.13	0.22	-0.57	0.57	-0.57	0.31
_cons	0.05	0.53	0.10	0.92	-0.99	1.09
Model	Obs	ll(null)	ll(model)	df	AIC	BIC
1-2.5cmdbh	80	-185.81	-172.063	5	354.13	366.04

Table 6.8: Poisson regression model of the number of woody stems 2.5-5cm dbh by gap position and herb cover in the Triangle area. Gap position was classified as gap, edge of gap (edge), gap, or tip up. Herb cover was low (less than 35% herb cover) or high (greater than 35% herb cover). This model was insignificant (N=80, Wald chi-square= 0.46, df= 4, p=0.98), indicating that none of the model coefficients are significant.

2-5cm dbh	Coef.	Robust Std.Err.	z	P>|z|	95% Confidence Interval	
Not Gap						
Edge	-0.10	0.41	-0.25	0.80	-0.91	0.71
Gap	0.00	0.39	-0.01	0.99	-0.77	0.76
Tip Up	-0.10	0.43	-0.23	0.82	-0.95	0.75
HerbCover	-0.06	0.18	-0.35	0.73	-0.41	0.29
_cons	0.89	0.48	1.85	0.06	-0.05	1.82
Model	Obs	ll(null)	ll(model)	df	AIC	BIC
2-5cm dbh	80	-150.73	-150.45	5	310.90	322.81

Table 6.9: Poisson regression model of the number of woody stems 5-10cm dbh by gap position and herb cover in the Triangle area. Gap position was classified as gap, edge of gap (edge), gap, or tip up. Herb cover was low (less than 35% herb cover) or high (greater than 35% herb cover). This model was insignificant (N=80, Wald chi-square= 3.42, df= 4, p=0.49), indicating that none of the model coefficients are significant.

5-10cm dbh	Coef.	Robust Std.Err.	z	P>|z|	95% Confidence Interval	
Not Gap						
Edge	0.62	0.62	1.00	0.32	-0.59	1.83
Gap	0.95	0.60	1.58	0.11	-0.23	2.13
Tip Up	0.86	0.74	1.17	0.24	-0.58	2.31
HerbCover	0.16	0.25	0.63	0.53	-0.34	0.65
_cons	-1.39	0.73	-1.91	0.06	-2.82	0.04
Model	Obs	ll(null)	ll(model)	df	AIC	BIC
5-10cm dbh	80	-87.18	-85.69	5	181.38	193.29

Table 6.10: Poisson regression model of the number of woody stems less than breast height by gap position and herb cover in the mountain area. Gap position was classified as gap, edge of gap (edge), gap, or tip up. Herb cover was low (less than 35% herb cover) or high (greater than 35% herb cover). This model was significant (N=198, Wald chi-square= 26.49, df= 4, p=0.00), indicating that at least one model coefficient is also significant. Bold values indicate significant z values at p<0.05. In this model, the counts of stems in edge, gap, and tip up subplots were different from not gap subplots. The effect of herb cover was also significant.

lessdbh	Coef.	Robust Std.Err.	z	P>|z|	95% Confidence Interval	
Not Gap						
Edge	0.63	0.16	**4.08**	**0.00**	0.33	0.94
Gap	0.50	0.14	**3.51**	**0.00**	0.22	0.77
Tip Up	0.79	0.25	**3.15**	**0.00**	0.30	1.27
HerbCover	0.29	0.09	**3.14**	**0.00**	0.11	0.48
_cons	3.70	0.21	17.72	0.00	3.29	4.11
Model	Obs	ll(null)	ll(model)	df	AIC	BIC
lessdbh	198	-5223.94	-4909.645	5	9829.29	9845.73

Table 6.11: Poisson regression model of the number of woody stems 0-1cm dbh by gap position and herb cover in the mountain area. Gap position was classified as gap, edge of gap (edge), gap, or tip up. Herb cover was low (less than 35% herb cover) or high (greater than 35% herb cover). This model was insignificant (N=198, Wald chi-square= 5.2, df= 4, p=0.27), indicating that none of the model coefficients are significant.

0-1cm dbh	Coef.	Robust Std.Err.	z	P>|z|	95% Confidence Interval	
Not Gap						
Edge	0.35	0.17	2.04	0.04	0.01	0.69
Gap	0.30	0.16	1.89	0.06	-0.01	0.60
Tip Up	0.24	0.30	0.81	0.42	-0.34	0.82
HerbCover	-0.05	0.12	-0.41	0.68	-0.29	0.19
_cons	1.38	0.25	5.60	0.00	0.90	1.87
Model	Obs	ll(null)	ll(model)	df	AIC	BIC
0-1cm dbh	198	-664.59	-663.2256	5	1336.45	1352.89

Table 6.12: Poisson regression model of the number of woody stems 1-2.5cm dbh by gap position and herb cover in the mountain area. Gap position was classified as gap, edge of gap (edge), gap, or tip up. Herb cover was low (less than 35% herb cover) or high (greater than 35% herb cover). This model was insignificant (N=198, Wald chi-square= 2.11, df= 4, p=0.72), indicating that none of the model coefficients are significant.

1-2.5cm dbh	Coef.	Robust Std.Err.	z	P>|z|	95% Confidence Interval	
Not Gap						
Edge	-0.35	0.47	-0.75	0.45	-1.28	0.57
Gap	-0.47	0.46	-1.02	0.31	-1.38	0.43
Tip Up	-0.50	0.57	-0.88	0.38	-1.61	0.61
HerbCover	0.08	0.13	0.58	0.57	-0.18	0.33
_cons	0.97	0.52	1.88	0.06	-0.04	1.99
Model	Obs	ll(null)	ll(model)	df	AIC	BIC
1-2.5cm dbh	198	-373.78	-372.262	5	754.52	770.97

Table 6.13: Poisson regression model of the number of woody stems 2.5-5cm dbh by gap position and herb cover in the mountain area. Gap position was classified as gap, edge of gap (edge), gap, or tip up. Herb cover was low (less than 35% herb cover) or high (greater than 35% herb cover). This model was insignificant (N=198, Wald chi-square= 4.87, df= 4, p=0.30), indicating that none of the model coefficients are significant.

2.5-5cm dbh	Coef.	Robust Std.Err.	z	P>|z|	95% Confidence Interval	
Not Gap						
Edge	0.17	0.29	0.59	0.55	-0.40	0.74
Gap	-0.09	0.27	-0.35	0.73	-0.61	0.43
Tip Up	-0.11	0.49	-0.23	0.82	-1.06	0.84
HerbCover	0.31	0.16	2.02	0.04	0.01	0.62
_cons	0.16	0.36	0.45	0.66	-0.55	0.87
Model	Obs	ll(null)	ll(model)	df	AIC	BIC
2.5-5cm dbh	198	-386.08	-379.8773	5	769.75	786.20

Table 6.14: Poisson regression model of the number of woody stems 5-10cm dbh by gap position and herb cover in the mountain area. Gap position was classified as gap, edge of gap (edge), gap, or tip up. Herb cover was low (less than 35% herb cover) or high (greater than 35% herb cover). This model was significant (N=198, Wald chi-square= 8, df= 4, p=0.09), indicating that at least one of the model coefficients is significant. Bold values indicate significant z values at p<0.05. In this model, the counts of stems in gap subplots were different from not gap subplots.

5-10cm dbh	Coef.	Robust Std.Err.	z	P>|z|	95% Confidence Interval	
Not Gap						
Edge	-0.89	0.47	-1.90	0.06	-1.81	0.03
Gap	-1.08	0.45	**-2.39**	**0.02**	-1.96	-0.20
Tip Up	-1.16	0.62	-1.86	0.06	-2.39	0.06
HerbCover	0.25	0.18	1.44	0.15	-0.09	0.60
_cons	0.42	0.51	0.82	0.42	-0.59	1.42
Model	Obs	ll(null)	ll(model)	df	AIC	BIC
5-10cm dbh	198	-247.48	-242.9583	5	495.92	512.36

Table 6.15: Poisson regression model of the number of woody stems less than breast height by gap position and herb cover in the Charlotte area. Gap position was classified as gap, edge of gap (edge), gap, or tip up. Herb cover was low (less than 35% herb cover) or high (greater than 35% herb cover). This model was significant (N=177, Wald chi-square= 37.94, df= 4, p=0.00), indicating that at least one model coefficient is also significant. Bold values indicate significant z values at p<0.05. In this model, the effect of herb cover was significant.

lessdbh	Coef.	Robust Std.Err.	z	P>|z|	95% Confidence Interval	
Not Gap						
Edge	0.13	0.22	0.60	0.55	-0.30	0.56
Gap	0.24	0.21	1.14	0.26	-0.17	0.64
Tip Up	-0.16	0.24	-0.67	0.50	-0.62	0.30
HerbCover	-0.50	0.09	**-5.46**	**0.00**	-0.68	-0.32
_cons	6.16	0.24	26.16	0.00	5.70	6.62
Model	Obs	ll(null)	ll(model)	df	AIC	BIC
lessdbh	177	-9582.94	-8160.7	5	16331.47	16347.35

Table 6.16: Poisson regression model of the number of woody stems 0-1cm dbh by gap position and herb cover in the Charlotte area. Gap position was classified as gap, edge of gap (edge), gap, or tip up. Herb cover was low (less than 35% herb cover) or high (greater than 35% herb cover). This model was significant (N=177, Wald chi-square= 23.52, df= 4, p=0.00), indicating that at least one model coefficient is also significant. Bold values indicate significant z values at p<0.05. In this model, the effect of herb cover was significant.

0-1cm dbh	Coef.	Robust Std.Err.	z	P>|z|	95% Confidence Interval	
Not Gap						
Edge	0.34	0.41	0.83	0.41	-0.47	1.15
Gap	0.58	0.40	1.46	0.14	-0.20	1.36
Tip Up	0.62	0.42	1.46	0.14	-0.21	1.44
HerbCover	-0.67	0.15	**-4.42**	**0.00**	-0.97	-0.37
_cons	2.38	0.43	5.48	0.00	1.53	3.22
Model	Obs	ll(null)	ll(model)	df	AIC	BIC
0-1cm dbh	177	-722.55	-664.32	5	1338.63	1354.52

Table 6.17: Poisson regression model of the number of woody stems 1-2.5cm dbh by gap position and herb cover in the Charlotte area. Gap position was classified as gap, edge of gap (edge), gap, or tip up. Herb cover was low (less than 35% herb cover) or high (greater than 35% herb cover). This model was significant (N=177, Wald chi-square= 20.58, df= 4, p=0.00), indicating that at least one model coefficient is also significant. Bold values indicate significant z values at p<0.05. In this model, the counts of stems in edge, gap and tip up subplots were different from not gap subplots.

1-2.5cm dbh	Coef.	Robust Std.Err.	z	P>|z|	95% Confidence Interval	
Not Gap						
Edge	1.60	0.50	**3.17**	**0.00**	0.61	2.59
Gap	1.91	0.49	**3.89**	**0.00**	0.95	2.86
Tip Up	2.14	0.51	**4.18**	**0.00**	1.14	3.15
HerbCover	-0.26	0.18	-1.48	0.14	-0.61	0.09
_cons	-0.87	0.52	-1.66	0.10	-1.90	0.16
Model	Obs	ll(null)	ll(model)	df	AIC	BIC
1-2.5cm dbh	177	-324.30	-309.69	5	629.39	645.27

Table 6.18: Poisson regression model of the number of woody stems 2.5-5cm dbh by gap position and herb cover in the Charlotte area. Gap position was classified as gap, edge of gap (edge), gap, or tip up. Herb cover was low (less than 35% herb cover) or high (greater than 35% herb cover). This model was significant (N=177, Wald chi-square= 9.88, df= 4, p=0.04), indicating that at least one model coefficient is also significant. Bold values indicate significant z values at p<0.05. In this model, the counts of stems in edge, gap, and tip up subplots were different from not gap subplots. Herb cover was also significant.

2.5-5cm dbh	Coef.	Robust Std.Err.	z	P>|z|	95% Confidence Interval	
Not Gap						
Edge	0.87	0.42	**2.08**	**0.04**	0.05	1.68
Gap	0.93	0.40	**2.31**	**0.02**	0.14	1.73
Tip Up	1.02	0.44	**2.30**	**0.02**	0.15	1.89
HerbCover	0.28	0.14	**2.00**	**0.05**	0.01	0.55
_cons	-0.73	0.46	-1.57	0.12	-1.63	0.18
Model	Obs	ll(null)	ll(model)	df	AIC	BIC
2.5-5cm dbh	177	-318.65	-310.43	5	630.87	646.75

Table 6.19: Poisson regression model of the number of woody stems 5-10cm dbh by gap position and herb cover in the Charlotte area. Gap position was classified as gap, edge of gap (edge), gap, or tip up. Herb cover was low (less than 35% herb cover) or high (greater than 35% herb cover). This model was significant (N=177, Wald chi-square= 12.03, df= 4, p=0.02), indicating that at least one model coefficient is also significant. Bold values indicate significant z values at p<0.05. In this model, the counts of stems in gap subplots were marginally different (p=0.06) from not gap subplots.

5-10cm dbh	Coef.	Robust Std.Err.	z	P>|z|	95% Confidence Interval	
Not Gap						
Edge	0.56	0.56	1.01	0.31	-0.53	1.65
Gap	1.00	0.54	1.86	0.06	-0.05	2.06
Tip Up	0.03	0.64	0.04	0.96	-1.23	1.29
HerbCover	0.06	0.20	0.29	0.77	-0.33	0.45
_cons	-0.99	0.60	-1.65	0.10	-2.17	0.18
Model	Obs	ll(null)	ll(model)	df	AIC	BIC
5-10cm dbh	177	-236.08	-227.75	5	465.49	481.37

Figures

Figure 6.1: Gap plot design. Ten 5x5m subplots are placed contiguously from the south edge of a gap (represented by the grey figure), across the gap to the north end. Black dots represent locations of soil samples along the center line. All woody species are measured and tallied by dbh class, except for woody seedlings shorter than breast height that were sub-sampled in 1x5m subplots along the center line. Subplots under closed canopy were classified as "not gap". Subplots in the center of the gap were classified as "gap", and subplots on the edge or not clearly in the gap were classified as "edge".

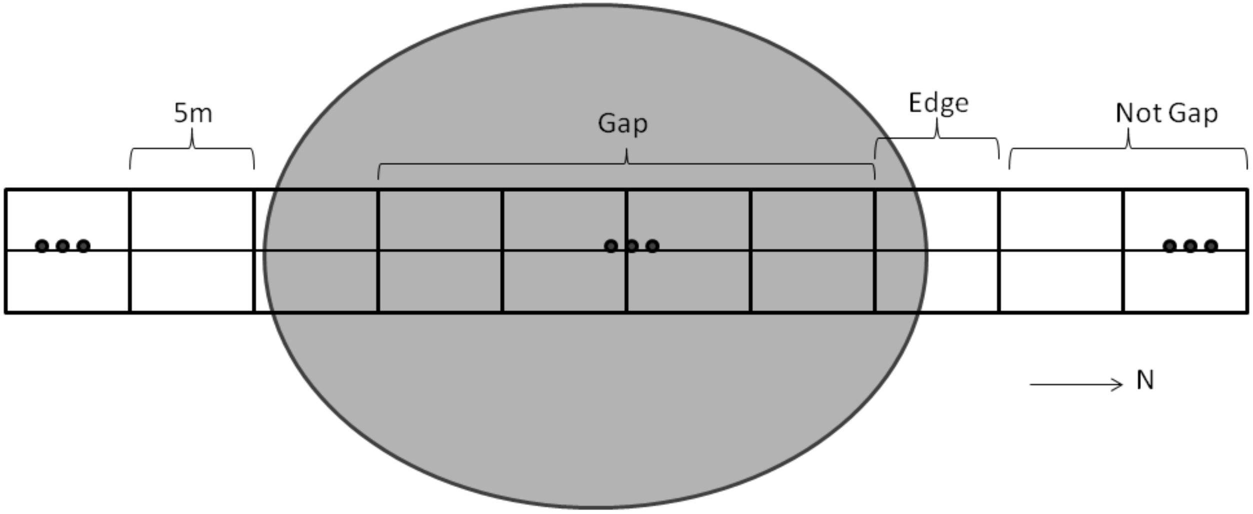


Figure 6.2: Woody species diversity across gaps in the Triangle region. This figure depicts the average number of woody species, including seedlings and trees, in 5x5m subplots across gaps, with standard error bars. There are fewer species of saplings under the canopy in areas with low herb cover and in the gap.

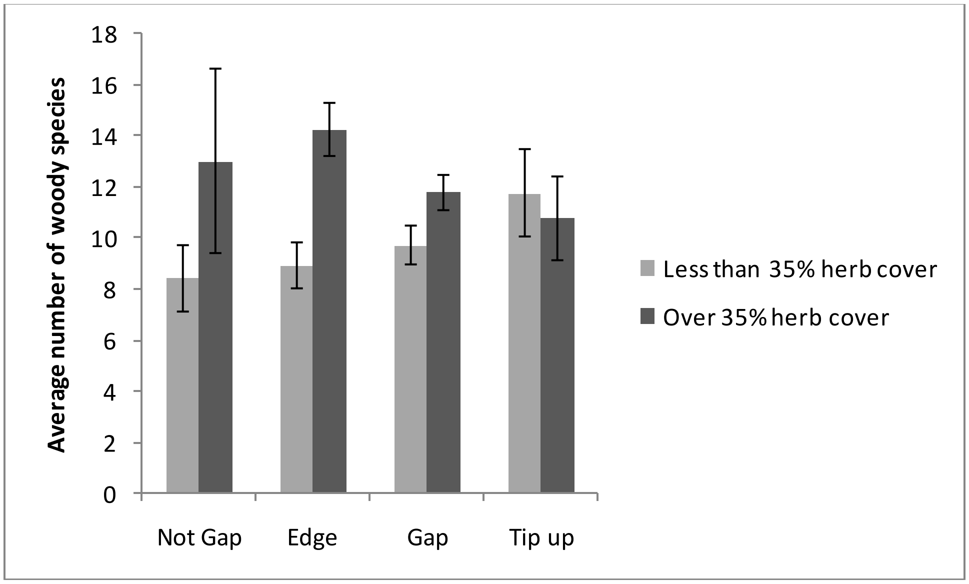


Figure 6.3: Woody species diversity across gaps in the mountains. This figure depicts the average number of woody species in 5x5m subplots across gaps. There are fewer woody species at gap edges and gaps in areas with high herb cover.

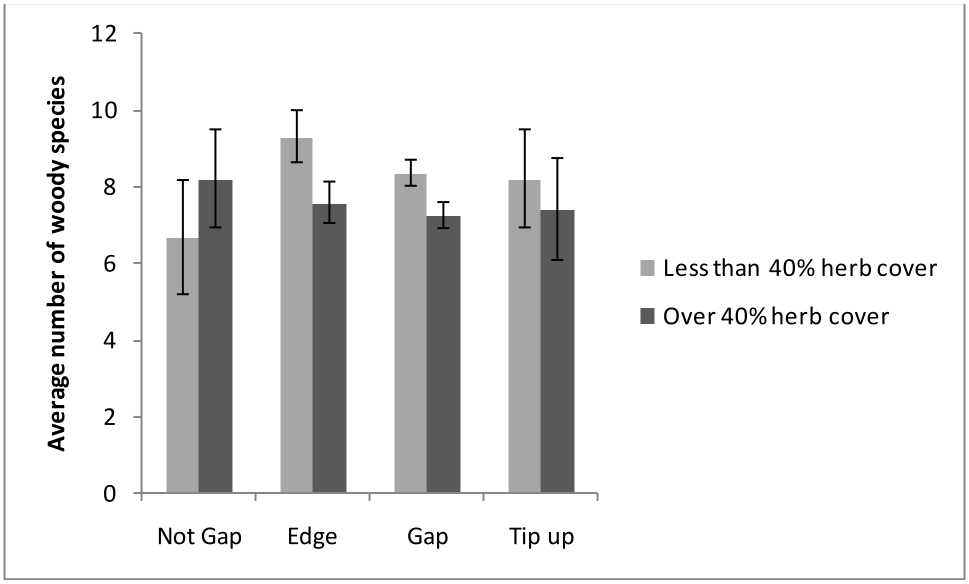


Figure 6.4: Woody species diversity across gaps in the Charlotte area. This figure depicts the average number of woody species in 5x5m subplot across gaps. There are fewer species of saplings under the canopy and in tip up subplots in areas with low herb cover.

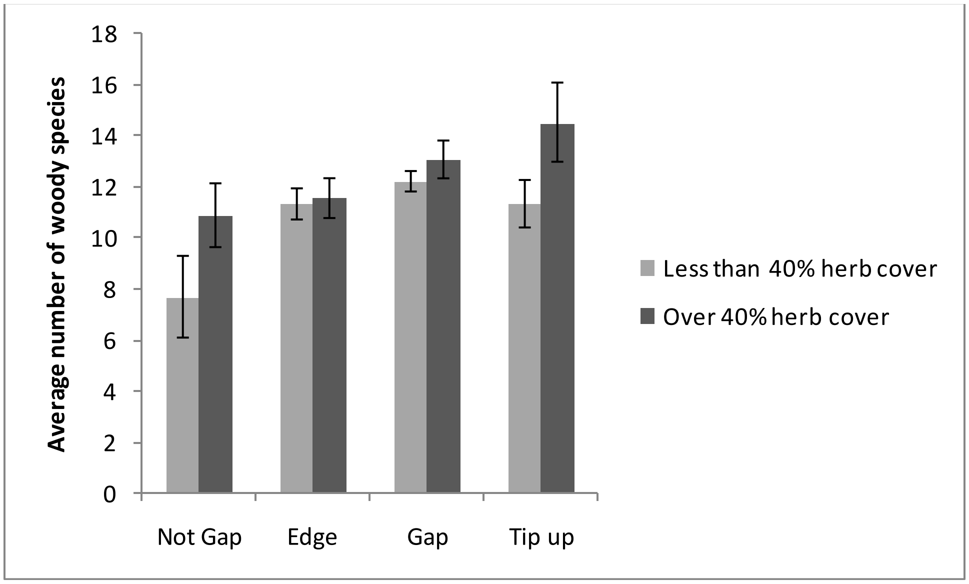


Figure 6.5: Average number of woody stems under breast height in a 5x5m subplot in the Triangle region. The number of woody stems present on low herb cover sites increases steadily from closed canopy to the center of gaps. However, on high herb cover sites, there are more seedlings under the canopy and at the edge of the canopy than in corresponding low herb sites.

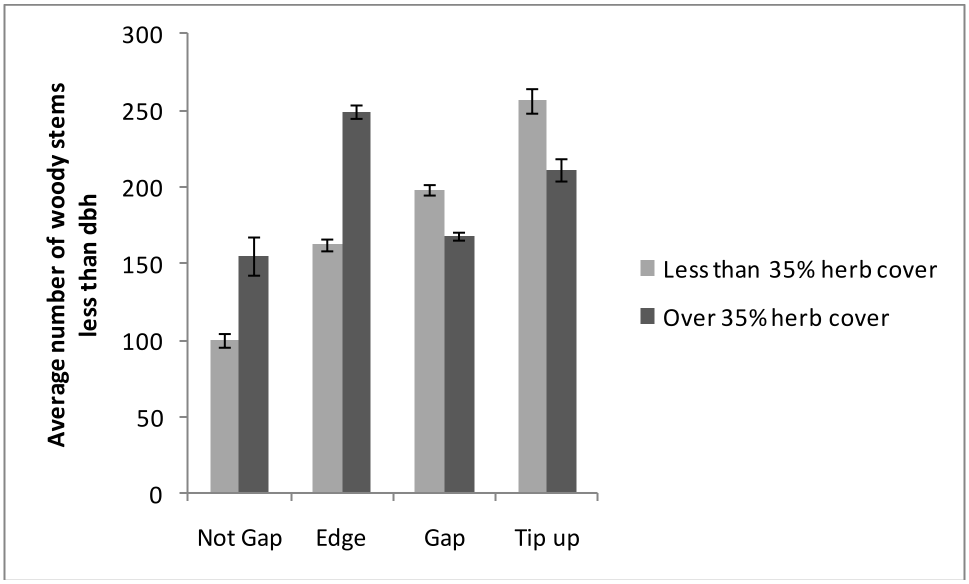


Figure 6.6: Average number of saplings with a dbh of 0-1cm in a 5x5m subplot in the Triangle region. The number of saplings increases gradually from closed canopy to the center of the gaps on both low and high herb cover sites. The number of stems present at the edge of gaps is greater on high herb sites than on sites with low herb cover.

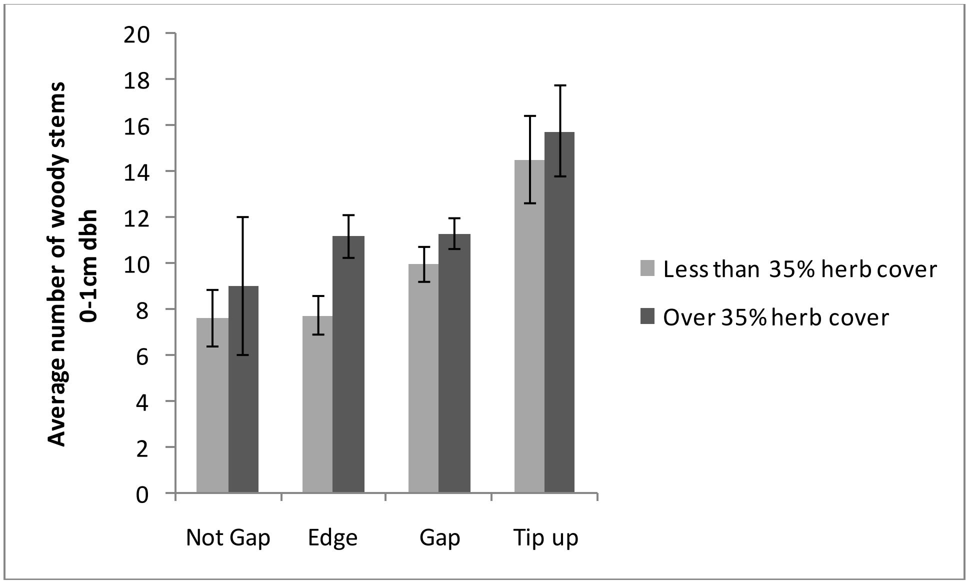


Figure 6.7: Average number of saplings with a dbh of 1-2.5cm per 5x5m plot in the Triangle. The number of saplings in this size class increases from subplots not in gaps to the center of gaps regardless of the herb cover.

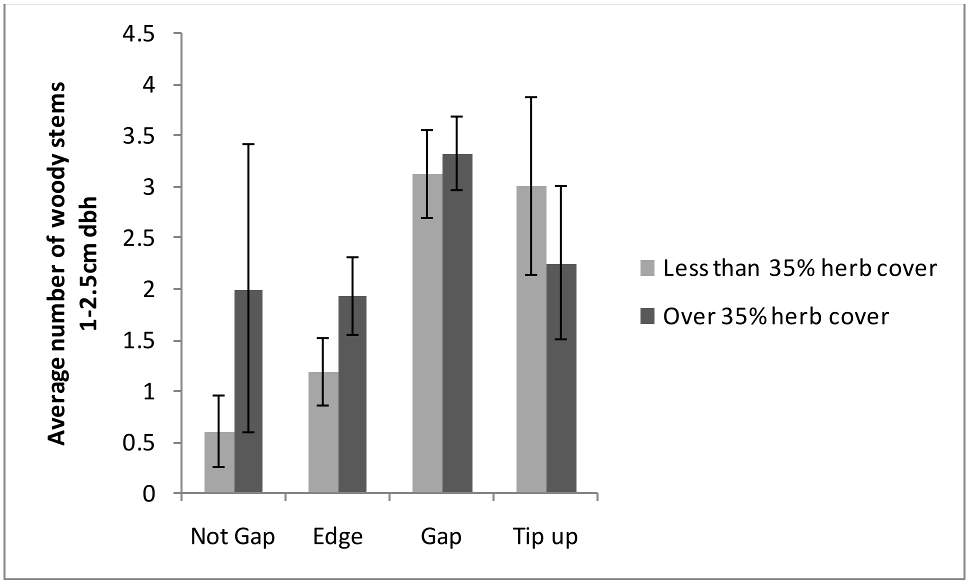


Figure 6.8: Average number of saplings with a dbh of 2.5-5cm per 5x5m plot in the Triangle. The number of individuals near tip up mounds was greater on low herb cover sites.

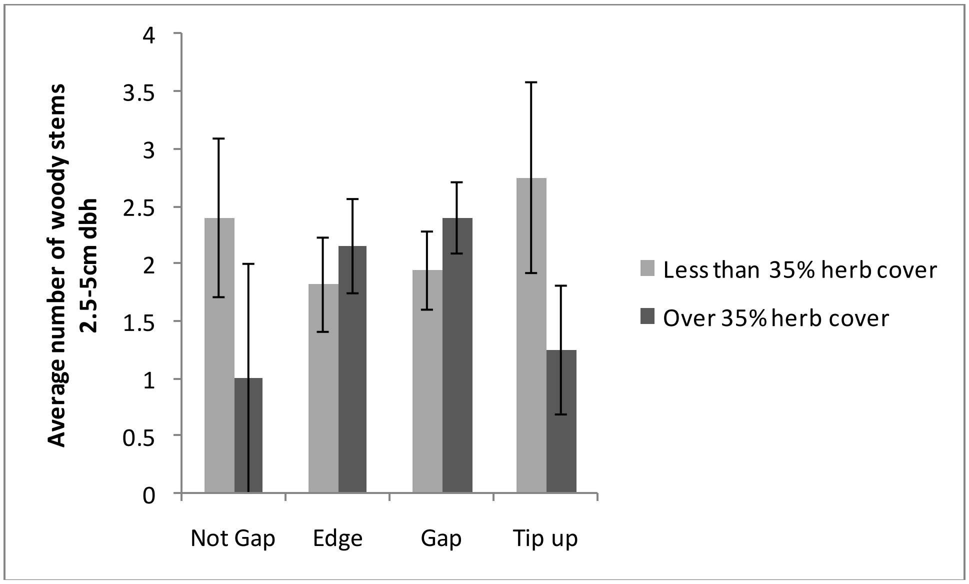


Figure 6.9: Average number of saplings with a dbh of 5-10cm per 5x5m plot in the Triangle. There were no individuals in this size class under closed canopy on high herb cover sites. Near tip up mounds, the number of saplings in this size class was greater on low herb cover sites.

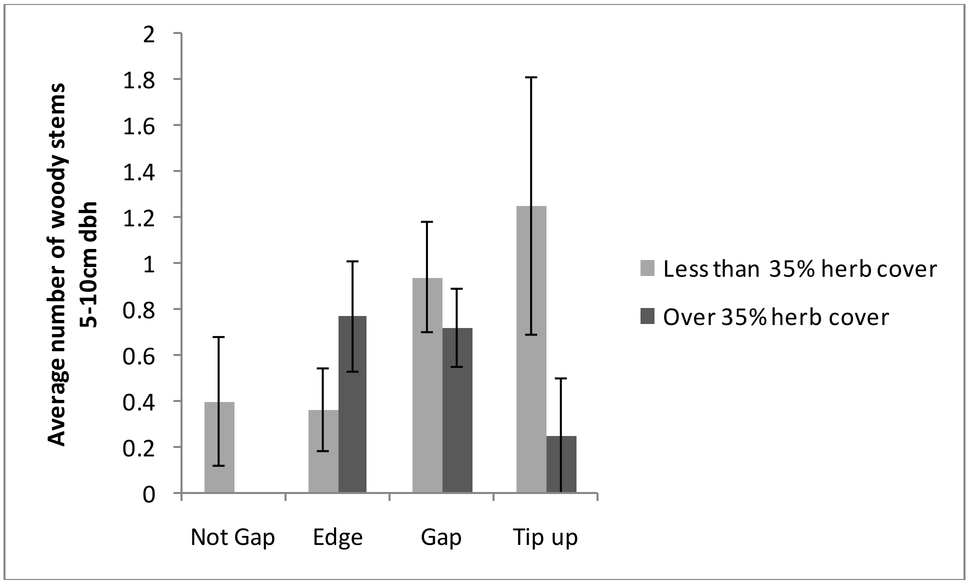


Figure 6.10: Average number of woody stems less than breast height in a 5x5m subplot in the mountains. There are more woody stems present on low herb cover sites at the edge of gaps and inside of gaps. However, on high herb cover sites, there are more seedlings in subplots with a tip up mound than on low herb cover sites.

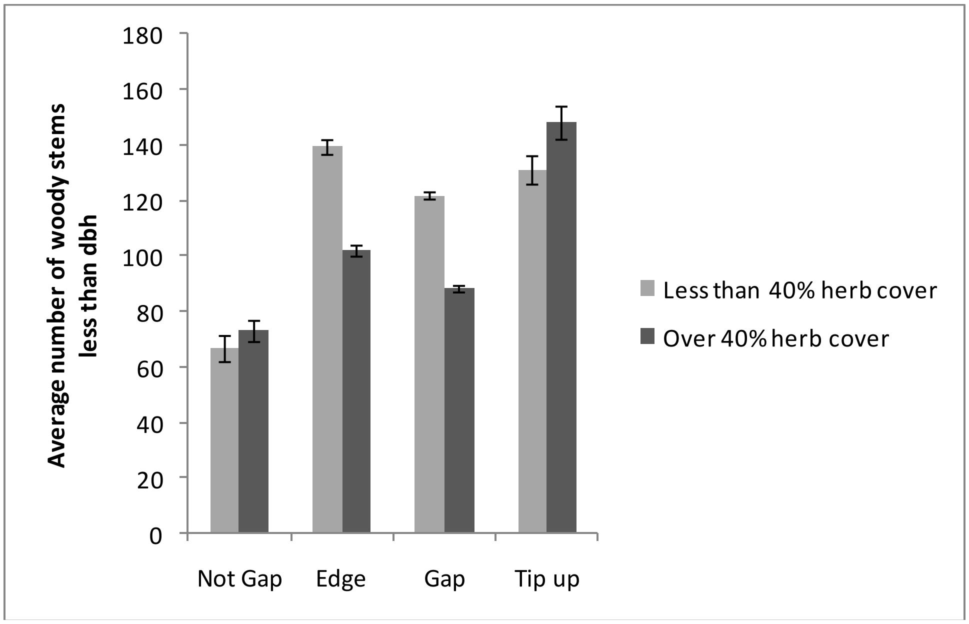


Figure 6.11: Average number of saplings with a dbh of 0-1cm in a 5x5m subplot in the mountains. In this size class, high herb cover and low herb cover sites have similar numbers of saplings across gaps.

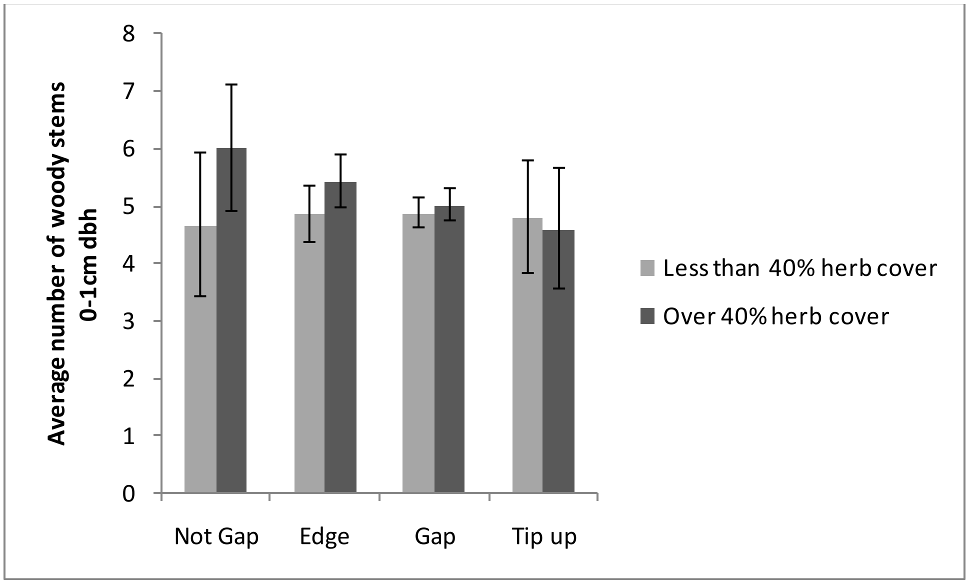


Figure 6.12: Average number of saplings with a dbh of 1-2.5cm per 5x5m plot in the mountains. The number of saplings in this size class decreases from subplots not in gaps to the center of gaps regardless of the herb cover. However, in subplots with a tip up mound, there were more stems on high herb cover sites than low herb cover sites.

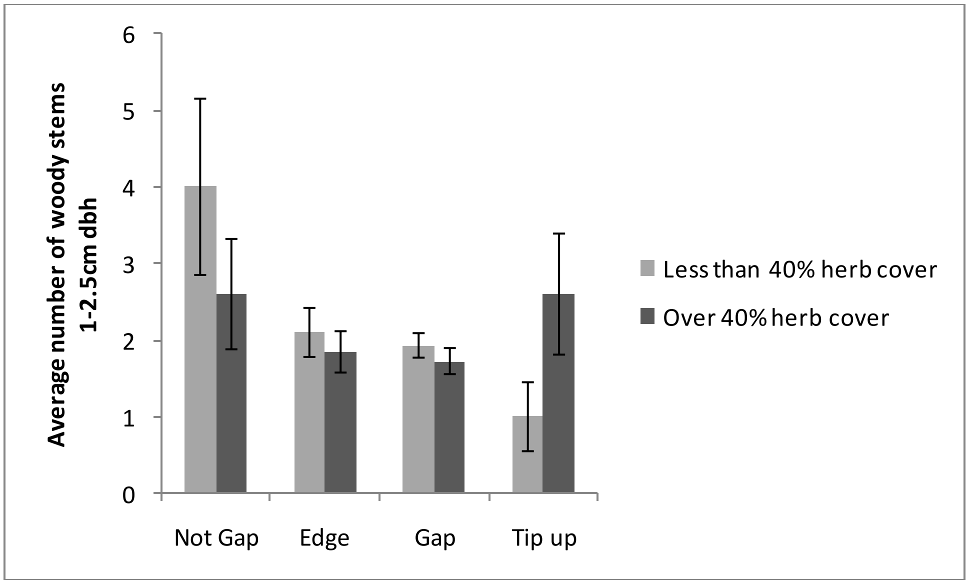


Figure 6.13: Average number of stems with a dbh of 2.5-5cm per 5x5m plot in the mountains. High and low herb cover sites had similar counts of stems under closed canopy and in gaps. However, at the edge of gaps there were greater numbers of stems on low nutrient sites, and in subplots with a tip up mound there were more stems on high herb cover sites.

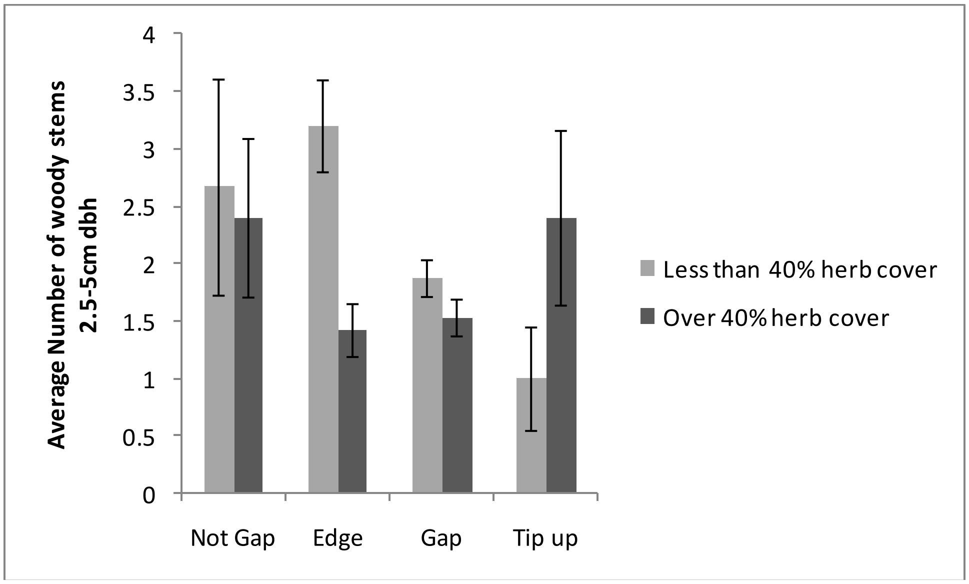


Figure 6.14: Average number of stems with a dbh of 5-10cm per 5x5cm plot in the mountains. On both high and low herb cover sites, the number of stems in this size class decreased gradually from not gap subplots to the center of gaps.

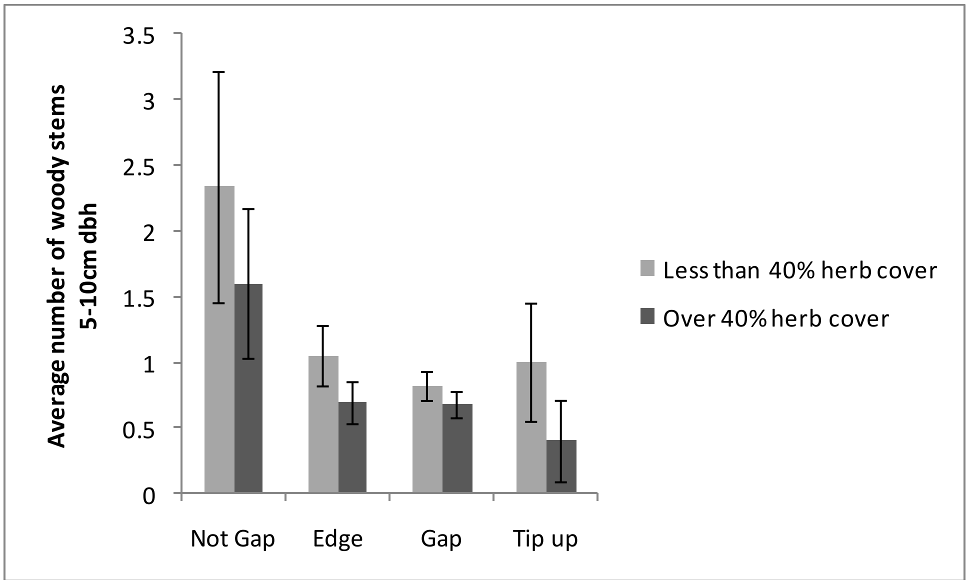


Figure 6.15: Average number of woody stems under dbh in a 5x5m subplot in the Charlotte area. The number of stems present on high herb cover sites is greater than low herb cover sites across all gap positions.

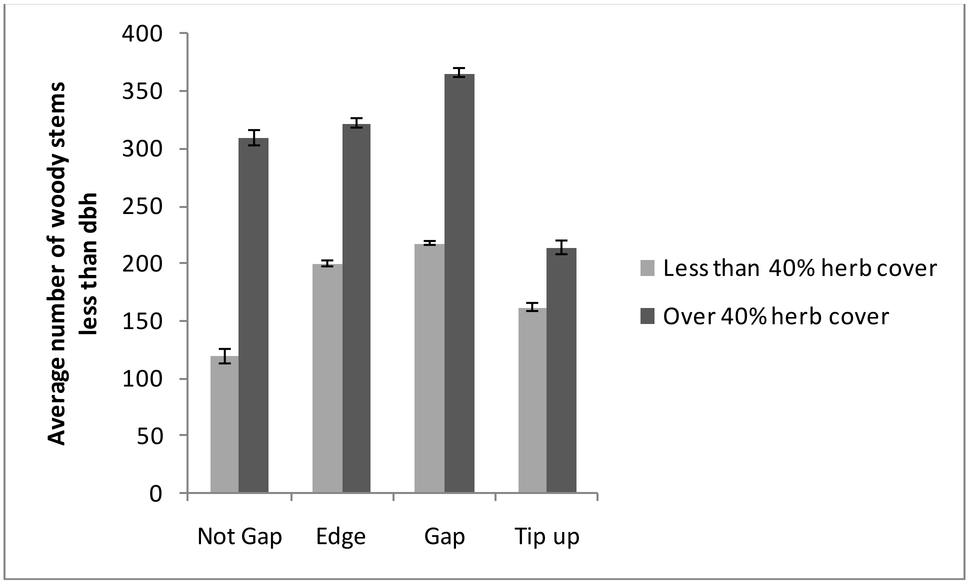


Figure 6.16: Average number of saplings with a dbh of 0-1cm in a 5x5m subplot in the Charlotte area. The number of saplings increases steadily from closed canopy to the center of the gaps on low herb cover sites. There are greater numbers of stems on high herb sites in non-gap subplots, edges of gaps and in gaps.

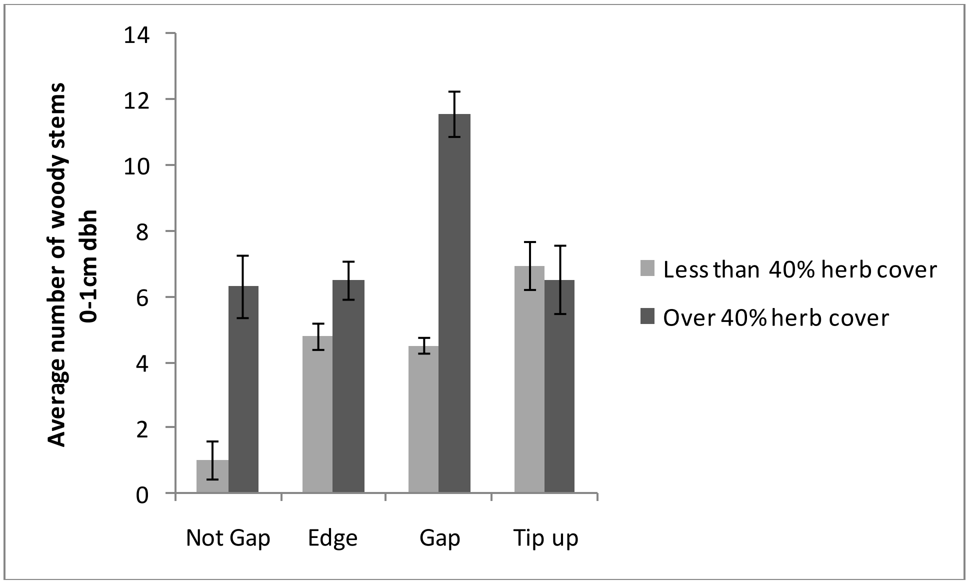


Figure 6.17: Average number of saplings with a dbh of 1-2.5cm per 5x5m plot in the Charlotte area. The number of saplings in this size class increases from subplots not in gaps to the center of gaps regardless of the herb cover. There are more stems of this size class on high herb cover sites that low herb cover sites in gaps.

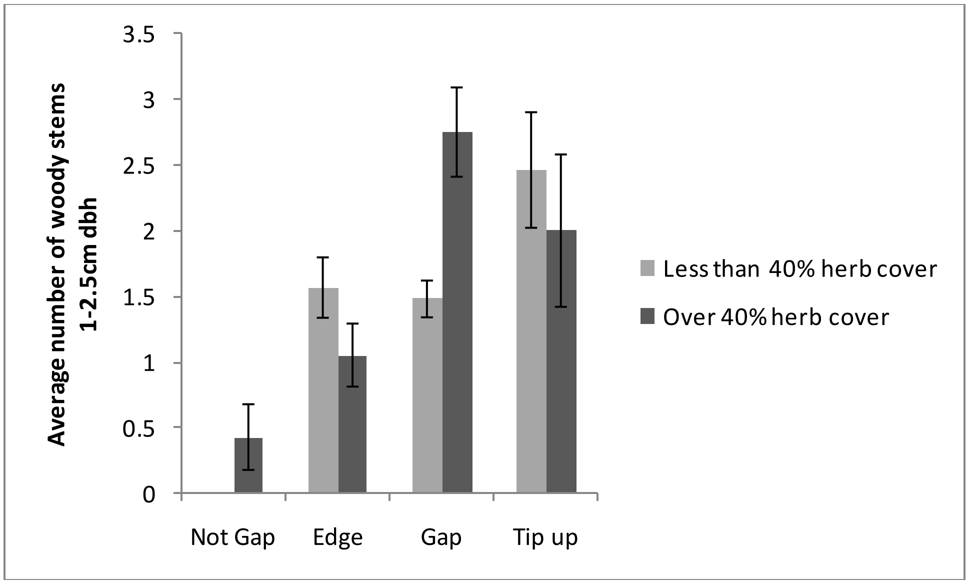


Figure 6.18: Average number of woody stems with a dbh of 2.5-5cm per 5x5m plot in the Charlotte area.

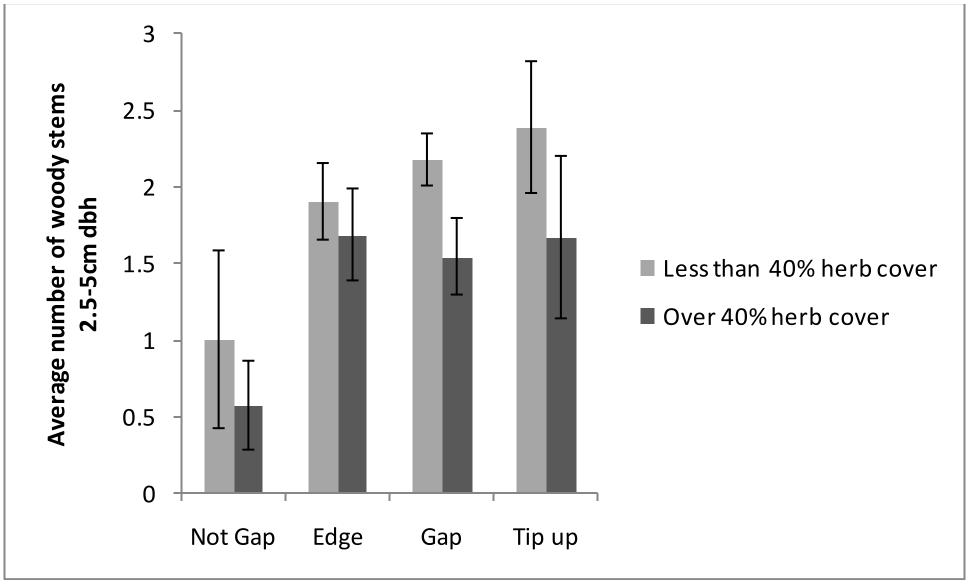
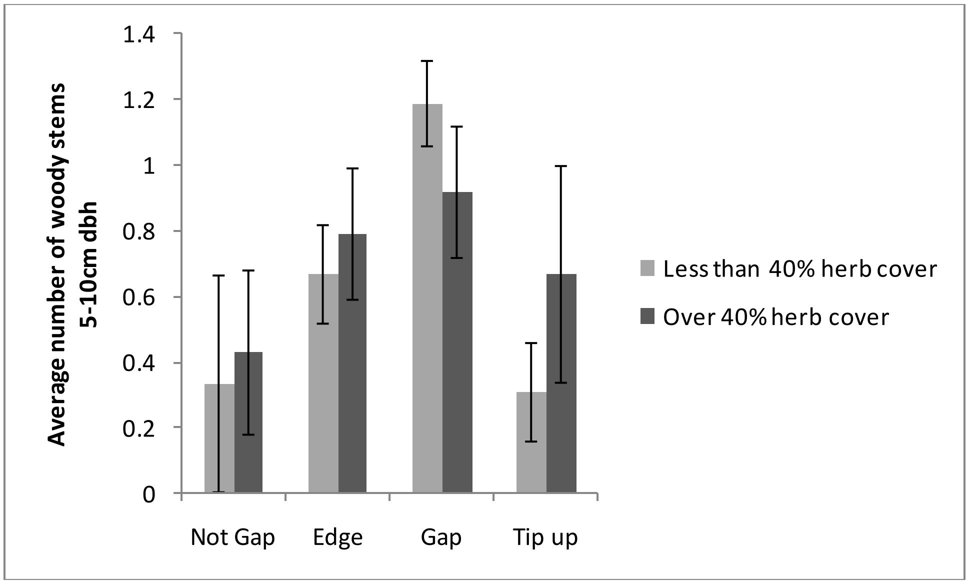


Figure 6.19: Average number of woody stems with a dbh of 5-10cm per 5x5m plot in the Charlotte area. There is a steady increase in number of stems from not gap to gap plots. However there is no significant difference between high and low herb cover sites for this size class.



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Chapter 7: Conclusion

Through an examination of multi-scale methodologies, models of soil nutrients, diversity, and productivity, and theory and fieldwork on the resource context of forest gaps, this dissertation demonstrates the importance of scale of observation, soil nutrient availability, and disturbance to our understanding of plant diversity. Building on the findings from each chapter, there are several suggested directions for future research.

Chapter 2 lays out a framework for comparison of the available multi-scale sampling methodologies. While the overall importance of observing at multiple scales is emphasized, the key message is that the objectives of the research should be carefully considered in planning the methodology. In particular, the efficiency of data collection in the field, the flexibility of the plot design, and the ability to compare with other data should be accounted for in determining methodology. Multi-scale methodologies such as Dengler's design (Dengler 2009) and the Carolina Vegetation Survey's methodologies (Peet et al. 1998, Lee et al. 2008) seem most applicable in this regard.

Hopefully this framework for matching methodologies with objectives of studies will be considered by ecologists, conservationists and managers in planning sampling initiatives. This can also serve as a starting point for a more in-depth discussion of survey design that could inform such large scale (both in time and space) sampling initiatives such as the National Ecological Observatory Network and the National Wetland Assessment Inventory.

The multi-scale approach is applied in Chapter 3 to an examination of the relationship between soil nutrients and diversity. Path models and initial structural equation models of soil characteristics and diversity demonstrated that soil measures are strong indicators of diversity and predicted 40 percent of the variance in diversity. However, the particular soil indicators do vary slightly across scales within regions, and significantly between regions. In longleaf pine systems silt and soil *p*H were the strongest indicators of diversity across all scales; in the Southern Appalachian Mountains soil *p*H, manganese, and calcium were consistent indicators across all scales. Soil texture was more important in the longleaf pine plots than in the mountains as expected. Although there were some consistent indicators of diversity across scales, there was also variation, more so in the longleaf pine plots than in the mountains. Further study of the within-plot variation in soil nutrients and texture would add to our understanding of how particular soil characteristics influence diversity. Additionally, the predictors of diversity identified should be studied to further understand why they are meaningful and what is actually driving species diversity.

Building on the work from Chapter 3, the relationship between productivity, diversity, and soil nutrients is examined with structural equation models in Chapter 4. The use of observational data to test models of productivity and diversity yielded several insights. General models for vegetation throughout the Carolinas did not converge, suggesting that there is not a general model that works for a wide range of plant communities from the coastal plain to the mountains. The difference in the models for the longleaf pine and mountain data suggests that models tailored to a specific region or community are necessary to effectively model this relationship. The diversity in the southern Appalachians is best modeled without productivity measures, with *p*H and soil micronutrients as strong predictors.

However, diversity in longleaf pine plots is modeled with a combination of remotely sensed productivity data and local soil texture and nutrients.

Future research should focus on testing nutrient-productivity-diversity models in other systems. Specifically, the question remains as to whether productivity and diversity have reciprocal effects as suggested in experimental systems (Cardinale et al. 2006, Gross and Cardinale 2007, Cardinale et al. 2009), or whether productivity influences diversity as found my longleaf pine models. As ecologists examine this question, particular attention should be paid to scale of observation, and how diversity and productivity are measured, since both the scale of observation and the variety of proxies for productivity and measures of diversity are likely driving the debate in the literature. One of the problems with examining productivity is that direct measures of productivity are possible in some systems (e.g. algal communities, and grasslands) while they are usually impractical in others (e.g. forests). The difference in direction of the diversity-productivity relationship in the literature may also be directly related to whether productivity is examined within one environment or across environments.

After examining the relationship between productivity and diversity at multiple scales, I added in the consideration of disturbance. Chapter 5 explains a new paradigm for gap dynamics, emphasizing both light availability and soil nutrient availability. Consideration of the resource context of a disturbance reveals that the influence of gaps is variable. Gaps are essential for woody species regeneration in temperate zones at the high and low end of the nutrient gradient because of the filter effect of the herb layer and evergreen shrub layer respectively.

Chapter 6 is an initial test of the resource context framework for gap dynamics in North Carolina's temperate forests. There was only weak evidence for the influence of the herb filter on tree regeneration: herb cover was significant in the Charlotte area in the 0-1cm dbh and 2.5-5cm dbh size classes and in the mountains in stems less than breast height. This suggests the expected release from the herbaceous filter due to increased light in and around gaps hypothesized in Chapter 5.

This was the first step towards testing the resource context for gap dynamics. However, it was limited to temperate forests of North Carolina and a relatively small sample size. Sampling gaps in areas with very high (>80%) herb cover would be ideal to test for the herbaceous filter effect. Further studies are needed to determine whether this framework for gap dynamics is general. Studies comparing tropical, temperate, and boreal gaps across a range of soil fertility levels would be ideal. Future work should pay particular attention to whether there is a separate path of gap regeneration similar to the delayed regeneration in tropical gaps covered in lianas (Schnitzer et al. 2000) in temperate zones.

Appendix A

The chi-squared values were significant at the p=0.000 level for all models (see Table 4.3), indicating poor model fit. However, this result is driven by the large sample sizes used; with large sample sizes, chi-squared values should be significant. Thus, while a commonly referenced fit value for SEMs, chi-square values are not an appropriate measure of fit for this study.

Within the longleaf models, the Root Mean Square Error of Approximation (RMSEA) is adequate and indicated that the Longleaf local model is the best fit for the data. The RMSEA indicates that the 10m^2 mountain local model is also recommended.

Tables

Table A.1: Fit indices for structural equation models for longleaf and mountain datasets. Fit indices include Chi-squared values (χ^2), degrees of freedom (df), p-values (p), Root Mean Squared Error of Approximation (RMSEA), 90% Confidence intervals for RMSEA (90% CI).

	Fit Index	Local	Local 100m2	Regional	Regional100m2	Combined
Longleaf	χ^2	127.583	112.879	134.271	130.071	303.435
	df	14	14	13	13	37
	p	0.000	0.000	0.000	0.000	0.000
	RMSEA	0.110	**0.103**	0.118	0.116	0.104
	90% CI	0.093-0.128	0.085-0.120	0.100 -0.136	0.098-0.134	0.093-0.114
Mountain	χ^2	40.205	33.916			198.834
	df	4	4			21
	p	0.000	0.000			0.000
	RMSEA	0.125	**0.114**			0.121
	90% CI	0.092-0.162	0.080-0.151			0.106-0.137

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