

**SPATIAL PATTERNS IN A 40-YEAR-OLD SLASH PINE (*PINUS ELLIOTTII*
ENGELM.) FOREST IN THE COASTAL PLAIN OF SOUTH CAROLINA**

by

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(ABSTRACT)

A study was conducted at the Savannah River Site near Aiken, SC to: 1) characterize the spatial patterns of soil and forest floor variables (moisture, pH, soil phosphate, forest floor and soil carbon and nitrogen, and soil available nitrogen), 2) assess the spatial patterns of the plant community, and 3) investigate spatial relationships among the variables and between the variables and woody vegetation. Spatial soil and litter samples were collected on five 0.25 hectare plots, and relationships were explored using Pearson's correlation tests, canonical correlation analysis, variogram modeling and kriging.

The average range of spatial autocorrelation for the forest floor variables was >45 m, while that for soil variables was 12 m. Woody stem basal area exhibited spatial autocorrelation at ranges of less than 12 m, and was only weakly correlated with forest floor and soil resource patterns. Few strong spatial correlations among the forest floor and soil variables were observed. The means and variances of the variables were low, and differences in resource levels probably had little impact on the spatial pattern of vegetation. Results indicate a weak, differential effect of species group on litter quality, a weak relationship between large pine trees and soil nitrogen patterns, and a general homogeneity of the stands.

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INTRODUCTION AND RATIONALE

Background

It is universally accepted that spatial pattern exists at many scales in natural systems. Traditionally, studies of pattern in ecology have been associated with large-scale phenomena, such as the response of species to regional landscape patterns and other biogeographical factors (Forman 1994, 1995). This scale of study, however, while applicable to regional and global species conservation problems, has little relevance to the finer scale processes that mediate many ecological interactions. Pickett and Cadenasso (1995) discussed two concepts of landscape, one which is at the traditionally broad scale, and one which is an abstraction, representing spatial heterogeneity at any scale. Similarly, Ehrenfeld *et al.* (1997) discussed the three scales of variation commonly arising in ecological studies. The coarsest scale, extending up to hundreds of meters, they term the "gradient scale". The "patch scale" extends into the tens of meters, and reflects local changes in physical and chemical attributes of the site. The finest scale, or "meter-scale" variation, occurs at distances of centimeters or meters.

With respect to plant communities, one of the most obvious characteristics is spatial structure. In the Coastal Plain of the Southeastern United States, for example, certain species associations occur at higher frequencies than would be expected by chance (e.g., *Pinus palustris* Mill./*Aristida stricta* Michaux), as do nonrandom spatial patterns (e.g. the lack of nearby neighbors to individual *Myrica cerifera* L. shrubs (Tolliver *et al.* 1995)). Similarly, the presence of non-random, clumpy distributions of conspecifics suggests that an observed community structure is due to mechanisms other than chance dispersal of propagules. Spatial patterns in plant communities may be the result of soil nutrient and water heterogeneity (Snaydon 1962, Lodhi and Johnson 1989, Palmer 1990, Hook *et al.* 1991, Willems *et al.* 1993, Meredieu *et al.* 1996, Ehrenfeld *et al.* 1997), patchy distribution of herbivory and other disturbances (Janzen 1971), asymmetric interactions among neighboring plants (Fowler 1982, Mitchell *et al.* 1993, Tolliver *et al.* 1995, Mou *et al.* 1995), uneven seed dispersal (Lechowicz and Bell 1991), uneven distribution of microsites for seed germination (Harper *et al.* 1965, Huenneke and Sharitz 1986) and random chance (Halpern 1988).

It is also well documented that many soil properties do not vary smoothly across the landscape at various scales (Trangmar *et al.* 1985). Hypotheses as to the origin of patchiness in soils include bedrock mineralogy (Meriedieu *et al.* 1996), patterns of soil-dwelling vertebrate (Inouye *et al.* 1987) and invertebrate (Gosz 1984) activity, effects of different litter types (Hendrickson and Robinson 1984, Gonzalez and Zak 1994, Finzi *et al.* 1998*a* and *b*, Tappeiner and Alm 1975), plant canopy-related phenomena such as differential rainsplash (Schlessinger *et al.* 1996), stemflow (Lechowicz and Bell 1991) and canopy gaps (Bormann and Likens 1979), plant physiological activity (Kellman 1979), and finally past disturbance such as fire (Schlessinger *et al.* 1996), forestry practices (Preston 1996) and ice and wind damage (Jonsson *et al.* 1990).

Differences in the levels and uptake of resources in the edaphic environment impact plant-plant interactions, particularly competition (Harper 1977, Tilman 1988, Bazzaz 1990, Grieg Smith 1979, Mou *et al.* 1995). This has been confirmed by numerous studies in natural communities and agricultural systems which have shown that the alteration of soil chemistry and moisture status or the manipulation of light levels (i.e., the imposition of a heterogeneous environment) favors one species over another with respect to some measure of competitive success (Harper 1977, Grieg Smith 1979, Tilman 1990). Environmental gradients, particularly of moisture and nutrients, are well correlated with plant distribution and productivity (e.g., Austin 1990, Austin and Austin 1980). There is a need, however, for studies that examine the relationships between plants and the soil environment at a finer, i.e., community-level scale. To address this need, I have conducted a study in a 40-year-old slash pine (*Pinus elliottii* Engelm.) forest in which the spatial patterns of edaphic variables and the plant community were characterized, and their relationships assessed.

Rationale

1) Generally needed by the ecological community is a better understanding of the relationship between competition, ecological heterogeneity (functional and structural) and plant community structure, as well as insights into the mechanisms responsible for succession.

Although most of these studies of the plant community-soil environment relationship have effectively quantified spatial heterogeneity or the interrelationships among spatial patterns, they have not adequately addressed the issue of functional heterogeneity. In other words, it is relatively straightforward to describe and classify spatial patterns of ecological phenomena based on some arbitrary standard (structural, or measured heterogeneity), but it is much more difficult to assess the biological impact these patches might have on ecological entities (functional heterogeneity) (Kolasa and Rollo 1991). Kolasa and Rollo (1991) discussed the difficulties associated with distinguishing measured heterogeneity from functional heterogeneity. With respect to a resource “patch”, for example, they pointed out that one can only define threshold levels of a resource which might affect an ecological entity from the perspective of that entity; if the size of a measured patch is larger than the ecological realm of an organism or assemblage of organisms, the existence of that patch is functionally meaningless. To address this issue, they suggested that only increased knowledge of a system and its constituents, such as that imparted by performing manipulative experiments, can clarify the relevance of measured heterogeneity to inhabitants of that system.

2) Methodology for effective manipulative experiments that can reveal the effects of spatial heterogeneity on plant competition for scarce resources and on community structure is needed.

There are different methods that have been used conventionally to assess the impact of competition on plant community structure. One method is the manipulative experiment, in which plants are grown in an environment where some resource is limiting, and their physiological and morphological responses are measured in response to inter and intra-specific competition (e.g., Campbell *et al.* 1991, Tilman 1990). An inherent assumption of this approach is that the experimental plants have equal access to the limiting resource, and thus are in direct competition for its uptake. Often the growth medium is homogenized to eliminate any heterogeneity that might lead to a violation of this assumption. However, plants in natural settings infrequently experience broad-scale homogeneity of resources, because light, moisture and nutrient resources are inherently

patchy at scales relevant to individual plants (Ehrenfeld *et al.* 1997, Robertson *et al.* 1988).

3) An understanding of the nature and sources of ecological variability in pine forests, which is necessary when attempting to quantify and describe forest resources and avoid statistical errors, is needed.

There is a paucity of information about the spatial structure of Southeastern U.S. Coastal Plain pine forest soils, as well as about the interaction between spatial patterns of forest vegetation and the spatial patterns of soil factors in these systems. In addition to improving the theoretical foundation for manipulative competition experiments, studying the spatial structure of these forest ecosystems will help forest managers to better characterize forest resources. Riha *et al.* (1986) and Liu and Burkhart (1994) recognized that samples which exhibit spatial autocorrelation confound forest scientists by violating the assumption of statistical independence (Appendix 1); this leads to a bias and an unfounded loss of conservatism in the determination of the critical values of test statistics such as the F ratio or the T value (Legendre 1993).

4) Finally, a better understanding is needed of ecological heterogeneity that could improve site preparation and nutrient management techniques for agriculture and industrial forestry, such as improved vegetation management strategies, more efficient use of fertilizers, and better ecological restoration practices.

VRT (Variable Rate Technology) is an automated fertilization method in which heterogeneous parcels of agricultural land receive variable rates of application based on their specific needs. A prerequisite of this approach is recognition of the spatial heterogeneity of soil resources and of crop production, and their relationship (Thompson and Robert 1995). As GIS and GPS technology become ubiquitous, VRT might be extended to not only more agricultural uses, but also to the silvicultural arena.

OBJECTIVES AND HYPOTHESES

The current study will attempt to characterize the spatial structure of a Southeastern Coastal Plain pine plantation. The objectives of the study are:

- i. to quantify soil resource spatial heterogeneity in a 40-year-old pine plantation;
- ii. to characterize the spatial patterns of biomass of vegetation in this forest;
- iii. and to assess the relationships between soil and vegetation patterns.

Specifically, I hypothesize that:

1) The soil resources will exhibit relatively low amounts of variability and be at relatively low levels. Several studies predict that more mature communities should have broader-scale homogeneity due to the exploitation of the soil by roots and the input of organic matter (Gross *et al.* 1995, Robertson *et al.* 1988, and Robertson and Gross 1994). I expected the same because our site is near the point of maximum biomass accumulation typically associated with plantation forests (i.e. similar to the peak of Bormann and Likens' (1979) aggradation phase). Furthermore, I expected that soil resource levels would be drawn down to low levels by aggressive exploitation by roots.

2) The soil and forest floor variables will exhibit spatial heterogeneity at scales similar to that of individual trees (< 10 m). Several studies have assessed the spatial variability of edaphic variables in forests, including those of Palmer (1990) and Gross *et al.* (1995), which found that a number of edaphic variables exhibit spatial autocorrelation within approximately 10 m. However, these studies were in hardwood forests; very few or no spatial heterogeneity studies have been conducted in pine plantations.

3) There will exist several cross-correlations among the forest floor and soil variables due to the interrelationships among biological and chemical processes. For example, moisture, pH, and the availability of nitrogen and phosphorous are related (Pritchett and Fisher 1987). Tappeiner and Alm (1975) showed that forest floor nitrogen content and that of the mineral soil were closely related, and Berendse (1994) cites a study that found that organic matter content of the humic and mineral horizons were correlated. I further

hypothesized that physical properties of the forest floor (depth and dry mass) and soil moisture will be correlated.

4) The vegetation community will exhibit spatial autocorrelation of measurements at different scales. Results of ordination and other plant distribution studies have revealed that within a site, species are distributed non-randomly (Harper 1977). For example, Zedler and Zedler (1969) reported that groups of species were associated with certain features of the environment (elevation, soil moisture content and soil organic matter content) in a Wisconsin old field-prairie ecotone. Similarly, specific species groups are known to colonize canopy gaps in plantation forests based on their tolerance of shade (Smith *et al.* 1997).

5) The dominance of different species groups will be correlated with levels of forest floor and soil nitrogen, carbon, C:N ratios and available soil nutrients, as well as soil moisture content and pH. Tappeiner and Alm (1975), Berendse (1994), Lodhi *et al.* (1989), and several others have shown that species differences in litter quality can affect the nutrient content of the forest floor and mineral soil. Others studies have shown that there exists a strong degree of correlation between plant community structure and edaphic heterogeneity (Jackson and Caldwell 1993, Schlessinger *et al.* 1996, Hook *et al.* 1991, and Finzi *et al.* 1998*a* and *b*). Jones *et al.* (1998) hypothesized that in mature forests, the vegetation community will exert a homogenizing influence on the edaphic environment, while at earlier seral stages, soil heterogeneity will exert a de-homogenizing effect on the vegetation community.

6) There will be no substantial difference between the plots within the putatively homogeneous forest with respect to variogram form and range of autocorrelation. A unique feature of my study is that we replicated the sampling plots, allowing us to characterize a larger area, and to make inter-plot comparisons of autocorrelation indices. The studies of Gross *et al.* (1995) and Robertson *et al.* (1988) do not have any replication, and that of Schlesinger *et al.* (1996) only has minimal replication.

LITERATURE REVIEW

Background and Definition of Spatial Heterogeneity

Watt (1947), in considering the nonrandom distribution of plant species across the landscape, discussed the truism that one cannot study a system as a whole, nor simply individuals; rather, one must study patches and the mosaics which they form. These patches can be both autogenic and allogenic, and can exist at varying scales. In the past decade, ecologists have begun to recognize the importance of ecological heterogeneity to the patterns and processes occurring in nature. For example, Dutilleul and Legendre (1993) found that 41,000 research articles contained the keyword “heterogeneity”, and that 850 of those contained the phrase “spatial heterogeneity”. Although much is being written about spatial heterogeneity, it is surprising that its exact definition is still unclear. In its broadest sense, heterogeneity means the absence of homogeneity, or the absence of sameness. Kolasa and Rollo (1991), however, pointed out that heterogeneity is a multi-faceted concept, the meaning of which is very case specific. In addition, there are shades of difference between temporal and spatial heterogeneity, and between heterogeneity that is quantifiable and that which is actually experienced by an organism (Li and Reynolds 1995, Dutilleul and Legendre 1993, Kolasa and Rollo 1991). One approach that might eliminate some of the confusion associated with the term is that advocated by Li and Reynolds (1995). Rather than attempting to create composite indices of spatial heterogeneity by decomposing several disparate measures, it is more appropriate to attempt to quantify its ecologically-meaningful components.

In fact, the most important feature of heterogeneity is probably its ecological significance. Given that many ecological phenomena exist in patches, i.e. in areas with clearly defined boundaries and biological differences from their surroundings (Forman 1994), the relationship between patches of resources and resource users is of particular interest. At certain scales, resources such as soil nutrients vary smoothly across the landscape, necessitating the loosening of the definition of “clear boundary”, and the classification of levels of a resource based on their positions relative to some threshold of biological significance. Kolasa and Rollo (1991) pointed out that in order to determine this threshold, one must be intimately acquainted with the system under study. Many

studies, however, either fail to address this issue of functional heterogeneity, or avoid the problem of environmental heterogeneity altogether.

For example, although soil resource heterogeneity has been shown to strongly influence plant species distribution at many scales (Hook *et al.* 1991, Armesto *et al.* 1991, Gross *et al.* 1995), most studies dealing with the origin of plant community structure do not take into account the influence of environmental heterogeneity, specifically heterogeneity of belowground resources (Robertson and Gross 1994). Along the same lines, many computer models that are used to predict the outcome of plant-plant interactions do not consider the effects of spatial and temporal heterogeneity of soil resources (Tilman 1988, Proe *et al.* 1994, Grime 1994). Mou *et al.* (1995) stated that competition models that assume symmetrical distributions of roots below plants are flawed; in many cases, plants concentrate their roots in nutrient-rich patches. Grime (1994) criticized Tilman's (1988) resource-ratio hypothesis, which assumes a tradeoff between allocation of photosynthate toward production of roots and production of shoots, on similar grounds. Finally, Campbell *et al.* (1991) and Mou *et al.* (1995) reported evidence that subordinate species more precisely forage for soil resources as compared with more dominant species in a community, emphasizing the importance of the relationship between heterogeneity of belowground resources and plant community structure.

Many studies that do consider the effects of soil resource heterogeneity only consider environmental variation in two horizontal dimensions (Ehrenfeld *et al.* 1997). However, numerous studies have shown that vertical traits, such as depth to a hardpan or other limiting soil horizon, can have dramatic effects on plant growth and community composition (Pritchett and Fisher 1987, Ehrenfeld *et al.* 1997). For example, in a study conducted in the Coastal Plain Pine Barrens of New Jersey, Ehrenfeld *et al.* (1997) found that patterns of soil properties exist that vary vertically, i.e. with depth. Meredieu *et al.* (1996) found that red oak (*Quercus rubra* L.) survivorship and productivity were most strongly correlated with spatial patterns of soil depth and depth to a calcareous layer.

An understanding of the nature of soil resource heterogeneity is not only important to the study of mechanisms governing plant community structure and dynamics, but also to the science of soil analysis as related to agronomy and silviculture.

For example, Snaydon (1962) showed that the mean levels of soil factors from samples collected over a short distance were very different from those collected with widespread sampling. This implies that sampling schemes designed to assess the fertility of soil for agriculture or silviculture must consider the spatial heterogeneity of soil resources (Jackson and Caldwell 1993, James and Wells 1990, Hook *et al.* 1991). Many statistical designs have been created to eliminate the confounding effects of heterogeneity in experiments (e.g., randomized block, Latin square and split plot designs), as have soil sampling techniques (e.g., compositing of soil samples and stratified random sampling) (Jackson and Caldwell 1993, James and Wells 1990). More recently, however, the use of geostatistics to quantify the spatial heterogeneity of soil resources has taken on added importance (James and Wells 1990, Robertson and Gross 1994, Trangmar *et al.* 1985).

One final impetus for the assessment of the spatial heterogeneity of soil resources is given by Schlessinger *et al.* (1990), who advocated the use of measures of soil heterogeneity as indices of the effects of habitat change. Specifically, their study suggested that processes such as land degradation and cattle grazing which increase the scale of soil resource heterogeneity could increase the rate of desertification of grasslands in arid regions. Measuring changes in soil heterogeneity over time can thus indicate the rate of desertification of a region.

Examples of Soil Resource Spatial Heterogeneity

Characterizing the variability of belowground resources is very important if one is to study the effects of resource heterogeneity on ecological processes (Robertson and Gross 1994). Environmental variability can be studied at many scales, from the ecosystem level to scales relevant to individual plants (Lechowicz and Bell 1991, Ehrenfeld *et al.* 1997). Stark (1994) believed that scales of heterogeneity greater than the reach of an individual plant's roots are not perceived by the plant; however, he failed to consider that mycorrhizal symbioses could greatly increase the volume of soil available to a plant for resource foraging (Pritchett and Fisher 1987). There are few studies that attempt to quantify fine scale soil resource heterogeneity, with some notable exceptions.

Robertson *et al.* (1988) assumed, in their study of the effects of nitrogen availability on old field succession, that there exists a scale at which patchiness of

nitrogen is ecologically significant, i.e. important to plants. Nitrogen mineralization potential and nitrification and denitrification rates exhibited substantial spatial dependence at a scale of one to approximately 20 meters. However, soil respiration, which was used as an index of soil organic matter content, was not spatially autocorrelated at any of the scales they studied.

In a sagebrush steppe in Utah, levels of soil organic matter, gravimetric water content, root mass, soil respiration, nitrogen mineralization potential, several macronutrient cations and phosphate all varied greatly within a distance of 12 meters (Jackson and Caldwell 1993). In the same study, the pH of some soil samples separated by less than 0.5 meters varied by up to 1.3 units. At a scale of less than 1 meter, levels of organic matter, phosphate, potassium, nitrate and ammonium were all autocorrelated. Microbial processes, however, were not spatially dependent at such a fine scale.

Robertson *et al.* (1993) investigated old fields in Michigan, and found that there was a substantial amount of variation between measured soil factors including pH, soil moisture, total carbon, inorganic phosphorous and nitrogen mineralization potential; all variates showed high degrees of spatial dependence within distances of 7 to 108 m. The scale of heterogeneity was much smaller in fields that were undisturbed (7-26 m) compared with fields that had been subjected to frequent cultivation (48-108 m).

Studies by Snaydon (1962) and Lechowicz and Bell (1991) further illustrate the high degree of spatial variation of soil factors over short distances. They showed that pH, levels of calcium, phosphate, nitrate and other factors varied substantially within a distance of 2 meters. Kabrick *et al.* (1997) determined that the log of total % carbon on drumlin tops in Minnesota exhibited significant autocorrelation at scales smaller than 1 meter, possibly due to perturbations in the soil caused by fallen trees and differences in aeolian cap thickness.

Gross *et al.* (1995) found that soil nitrogen levels were spatially dependent at scales of less than 20 m. In addition, the scale of spatial dependence of nitrogen availability changes over time, suggesting that spatial as well as temporal characteristics of resource heterogeneity might be related to changes in community structure. Armesto *et al.* (1991) also discussed the temporal dynamics of spatial heterogeneity with reference to their effects on succession and community structure, as did Campbell *et al.* (1988).

Goovaerts and Chiang (1993), on the other hand, found that the mean values and spatial patterns of several of the variables they investigated, including pH, electrical conductivity, ammonium, oxidizable carbon, gravimetric water content, and potentially mineralizable nitrogen, showed temporal stability between winter and spring in an old field in Belgium. A significant amount of the spatial autocorrelation occurred within a distance of 1 meter, and most factors were autocorrelated within 12 meters.

Spatial autocorrelation not only exists at the meter and patch scale, but also at the gradient scale. A study by Ovalles and Collins (1988) reported patterning of particle size class distribution at the scale of tens of kilometers for soils in northwest Florida. The percent sand and clay content of their soils exhibited autocorrelation within 35 kilometers, but A horizon organic C content was spatially dependent at distances of less than 10 km, their shortest sampling interval. They hypothesized that the observed ranges of spatial dependence were related to the distribution of physiographic provinces within their study region. In an investigation at a similar scale, Rahman *et al.* (1996) studied spatial variability of Wyoming mountain soils. Soil pH, organic carbon content and solum coarse fragments exhibited spatial dependence within distances greater than the length of their sampling transect, 7 km. However, the depth and coarse fragment contents of the A and B soil horizons as well as solum thickness were spatially autocorrelated at scales smaller than their shortest sampling distance, 200 m. Again, they attributed these patterns to large-scale processes such as slope position, parent material composition and age of soil. It is probable that these factors would have also exhibited autocorrelation at smaller scales had the sampling been more intensive, reflecting more fine-scale processes such as micro-topographic changes and vegetation patterns.

Results of studies of spatial structure in agricultural fields, while not necessarily being applicable to less-disturbed systems, can yield valuable information about soil processes. Berndtsson *et al.* (1993) showed that 20 trace and major elements showed high degrees of spatial dependence within 30 m in a Tunisian agricultural field. Cambardella *et al.* (1994) conducted a similar study in central Iowa, where physical and chemical properties of soils from a tilled field all exhibited varying degrees of spatial dependence.

One thing these and most other studies do not consider is the relation of soil heterogeneity to microsite physical variability. Huenneke and Sharitz (1986) classified

16 different microsite (substrate for seed germination and establishment) types in a cypress-tupelo swamp in South Carolina, each of which presumably differs with respect to physical and chemical properties. Similarly, Zedler and Zedler (1969) related vegetation patterns to differences in microtopography and associated differences in soil physical and chemical properties. These and the other studies indicate that there does exist a high degree of spatial variability of soil factors at scales that might be perceived by individual plants or plant communities.

In summary, it is clear from many of these studies that spatial structure exists at measurable scales in many different systems. Without a clear understanding of the characteristics of this spatial structure, those attempting to quantify soil resource levels might obtain non-representative samples, and might draw erroneous conclusions from their statistical tests. My current study of the characteristics of spatial patterns in a slash pine plantation will help fill a gap in the knowledge about these systems, and possibly lead to new insights into the mechanisms behind plant community dynamics in pine-dominated ecosystems.

Causes of Spatial Heterogeneity

What are the mechanisms that cause a patchy distribution of soil resources? There are several hypotheses, including differences in parent material, climate, soil physical properties, effects of soil organisms, and disturbance (Stark 1994), as well as plant activity (Harper 1977). It is often difficult, however, to pinpoint the exact cause of soil resource heterogeneity (Snaydon 1962), because there are several factors which might be acting together to form resource patches at certain scales. Variations in soil moisture content might cause variations in nutrient movement, microbial activity and thus nutrient availability (Dawson 1993, Stark 1994). All of these factors can be influenced by soil organic matter content, bulk density, texture and vegetation cover (Pritchett and Fisher 1987, Aber and Melillo 1991). Similarly, depth of soil is a highly variable soil property, and is one that can interact with many other factors (Stark 1994, Ehrenfeld *et al.* 1997).

Animals can have a powerful influence on soil heterogeneity (Armesto *et al.* 1991, Stark 1994, Pritchett and Fisher 1987). For example, an investigation by Inouye *et*

al. (1987) showed that pocket gophers at the Cedar Creek study area in Minnesota create mounds of soil with lower average nitrogen content than surrounding areas. In addition, they increased the point to point variability of nitrogen, deposited feces, and altered the soil structure, aeration, and moisture content, all of which influenced plant species composition by slowing the rate of succession. Other studies have shown how soil meso- and macrofaunal activity, especially that of earthworms, can influence the spatial pattern of soil resources by mixing the soil and by depositing feces, as described in Gosz (1984), Pritchett and Fisher (1987), and Campbell *et al.* (1988).

Differences in physical factors inherent to a site can cause soil spatial heterogeneity. For example, Meredieu *et al.* (1996) concluded that the spatial variation of microtopography and that of tree growth were due to the effects of variability of the calcareous bedrock in a French red oak (*Quercus rubra* L.) forest. Similarly, Zacharias *et al.* (1997) found that spatial trends in soil pH and soil clay content corresponded, supporting the hypothesis that trends in soil and parent material physical properties affect spatial patterns of chemical properties related to plant growth.

Agricultural and silvicultural manipulation of the soil can obviously alter nutrient patterns. Tillage can create ridges and furrows that provide microsites that allow for differential seed germination, different moisture levels and thus different chemical properties (Armesto *et al.* 1991). In one study, the levels of total carbon were reported to be lower and the levels of phosphorous and pH to be higher on frequently tilled, agricultural lands than on abandoned farmland, possibly due to the effects of liming and fertilization (Robertson *et al.* 1993). This study also revealed the homogenizing effects a monoculture plantation can have on cultivated fields; the scale of variability was smaller on the untilled study site than on the tilled, recently cultivated site, possibly due to the accumulated effects of longer-lived perennials on small areas of soil in the untilled site.

Other types of disturbance that might alter the scale of the heterogeneity of soil resources include fire and flooding. Huenneke and Sharitz (1986) showed that the addition of thermal effluent and silt to a cypress-tupelo swamp lowered the diversity of microsites (relative to a control), and made the remaining microsites more homogenous by lowering the intersite variability. Schlessinger *et al.* (1996) hypothesized that fire would make soil resources more homogeneous by converting a shrub-dominated

community to grassland in Nevada. There was, however, little change in the scale of heterogeneity due to fire.

Another important factor influencing soil resource heterogeneity is plant activity. Several studies have shown how root activity and litter degradation can affect soil chemistry (e.g., Hendrickson and Robinson 1984, Parmelee *et al.* 1993). This phenomenon has been studied much in deserts, where the sparseness of vegetation lends itself to the study of ecological patchiness. Schlessinger *et al.* (1996) and Hook *et al.* (1991) pointed out that shrubs, especially sagebrush (*Artemisia spp.*), can act as “islands of fertility”, concentrating nutrients in their environs. These shrub-scale patches of nutrients might form by differential rainsplash (which allows topsoil to accumulate in protected areas), the accumulation of wind-borne particles, the effects of litterfall on the biogeochemical cycle, or the concentration of nutrients near plants as a result of below-ground processes. Below-ground processes are driven largely by the moisture regime of the plant-soil system. The flow of water into the roots draws water convectively through the soil; in addition, it creates a difference in water potential between the drier areas adjacent to roots and the wetter areas within the soil aggregates, leading to a further flow of water toward the plant (Pritchett and Fisher 1987). These processes create a flow of dissolved nutrients toward the plant via diffusion and mass flow (Barber 1977), leading to localized areas of nutrient enrichment.

Higher soil moisture levels under some plants also affect nitrogen mineralization, microbial activity, mycorrhizal functions, pH, and other processes which cause localized nutrient accumulations (Barber 1977, Hendrickson and Robinson 1984, Dawson 1993, Parmelee *et al.* 1993). Tilman (1988) found that soil moisture levels might be a factor affecting vegetation pattern by enhancing microbial mineralization of a limiting nutrient.

In a study by Hook *et al.* (1991) in a shortgrass steppe in Utah, total organic carbon, total nitrogen, the carbon : nitrogen ratio, potential nitrogen mineralization, and soil respiration were all higher under clumps of bunchgrass than in spaces between plants, possibly due to the production of organic exudates by the plants, as well as to some of the erosion-filtering processes discussed above. Similar patterns of accumulation of soil organic matter, phosphorous and potassium were under individual plants of wheatgrass (*Pseudoroegneria spp.*) and sagebrush (*Artemisia spp.*) (Jackson and

Caldwell 1993), as well as under clover (*Trifolium repens* L.) (Snaydon 1962). Berendse (1994) found that the increase of nitrogen mineralization potential of the soils under study was linearly correlated with the production of plant biomass.

Kellman (1979) reported how individual trees in a neotropical savanna act as “nutrient pumps”, sequestering calcium, magnesium, potassium, sodium and phosphorous in the soil below them. The mechanisms behind this, he hypothesized, include the production of organic matter, the withdrawal of nutrients from deeper soil layers, the establishment of associations with mycorrhizae and the interception of nutrients found in rainfall. Lechowicz and Bell (1991) discussed how stemflow, differential patterns of decomposition under individual trees, and canopy gaps can influence the patchiness of soil factors.

Plant cover can change the nutrient content and biomass of not only the mineral soil horizons, but also the organic horizon in forests. Gonzalez and Zak (1994) believed that fine-scale heterogeneity of nitrogen dynamics in a tropical dry forest soil was due to overstory litter inputs. Tappeiner and Alm (1975) found that birch trees (*Betula spp.*) produced litterfall that was lighter but higher in nitrogen, phosphorous and potassium than pine trees (*Pinus spp.*). Furthermore, understory vegetation, specifically the shrub *Corylus cornuta* Marshall, significantly increased the weight of litterfall biomass as well as soil nutrient content in forests in Minnesota. Campbell *et al.* (1988) reported that canopy distribution could play a large role in causing O horizon heterogeneity. They stated that the weights of catches of litter from traps separated by only 7 meters in an African woodland varied by a factor of 1.5. Furthermore, there existed a correlation between the concentrations of various nutrients in the O horizon with proximity to tree trunks. Riha *et al.* (1986) obtained similar results in *Pinus resinosa* Aiton, *Picea abies* L. and *Acer saccharum* Marshall stands: pH varied slightly when samples were collected beneath different species. Across all species, the variance in pH of samples collected at the bases of individual trees was greater than that of samples taken nearly a meter away.

Effects of Spatial Heterogeneity

On plant community structure

Few studies have adequately addressed the issue of how soil resource patchiness is related to the patchiness of plant community structure. The difficulty of disentangling the exact relationship is typified by the comments of Snaydon (1962), who suggested three possible explanations for why *Trifolium repens* L. is associated with nutrient-rich patches of soil: that the presence of *T. repens* causes the patch, that the patch causes the presence of *T. repens*, or that some other factor, such as microtopography, causes both to occur together.

More confusion arises from the difficulty of determining what scale of resource heterogeneity is perceivable by the plant. Stark (1994) pointed out that plants might perceive heterogeneity at scales that are different from those at which we typically measure it. Furthermore, when grown at lower nutrient levels, plants will respond to smaller changes in levels of soil factors than plants grown at high levels of soil resources. Finally, the heterogeneity of the light environment also plays a strong role in plant community organization, and its effects are difficult to separate from those of soil factors (Baldocchi and Collineau 1994). These problems aside, several studies have explored the role that edaphic spatial variability plays in the structuring of plant communities.

Lechowicz and Bell (1991) hypothesized that members of the genus *Impatiens* found in the understory of a southern Quebec forest may adapt to soil heterogeneity at a scale of less than 5 m. They found that the genetic variation of the populations occurs at the same scale as the edaphic variability, suggesting that the populations have adapted evolutionarily to the scale of soil heterogeneity that they encounter in the understory. They offered further evidence by citing a study where plants from one population were transplanted into a population where resources exhibited a different scale of heterogeneity and suffered lower fitness, implying a morphological or physiological adaptation to different scales of soil variability (i.e. fine scale adaptation). Hence at least in *Impatiens*, spatial heterogeneity of edaphic factors caused evolution of adaptations which favor the exploitation of localized patches, such as low seed dispersal distance, low pollen transport distance, and cleistogamy.

Patches of high levels of soil resources under individual trees in a neotropical savanna created fertile sites for the establishment of rainforest trees, explaining the periodic invasions of rainforest into the nutrient-poor savannas (Kellman 1979). Klinka *et al.* (1990) found that several groups of British Columbian understory species were correlated with variations in nitrogen dynamics and forest floor type in western hemlock forests. Ehrenfeld *et al.* (1997) determined that although temporal variability of many soil chemical properties might mitigate the effect of soil resource patterns on vegetation, some Coastal Plain understory species did show relationships with spatial patterns of moisture.

Soil factor variability can be especially important in deserts, where plant cover is low, exposure to the elements is more intense, and there are greater extremes of weather (Hook *et al.* 1991). The soil erosion created by activities such as cattle grazing and off-road vehicle use can change the scale of soil resource heterogeneity in arid regions and can exacerbate desertification (Schlessinger *et al.* 1990). This causes a loss of plant-available nitrogen and creates conditions that are favorable for the invasion of exotic species such as shrubs, speeding the loss of native grassland. The ecological ramifications of arid region edaphic variability include erosion, desertification and consequent local and possibly global climatic perturbations (Schlessinger *et al.* 1990).

The heterogeneity of microsites suitable for plant growth can also affect plant distribution. Zedler and Zedler (1969) found that differences in microtopography of a few centimeters caused sharp boundaries between clumps of the grass *Andropogon scoparius* Michaux and other species in old fields. Harper *et al.* (1965) argued that the availability of suitable microsites might be one of the major factors affecting the germination of seeds which fall to the ground, or which are spread manually. Similarly, Huenneke and Sharitz (1986) reported that vegetation patterns were altered by the differential trapping and germination of seeds in favorable microsites in a South Carolina swamp.

Finally, some researchers have studied the effects of spatial patterning of soil resources on spatial patterns of crop productivity. Stein *et al.* (1997) investigated how several soil properties (pH, total phosphorous, organic carbon, ammonium, mineralizable nitrogen, CEC, base saturation and crust hardness) affected patterns of millet yield in

India. CEC had the strongest effect on millet yield, and patterns of millet yield and those of several soil factors exhibited significant though low correlation coefficients. Similarly, Samra *et al.* (1992) studied the effects of pH heterogeneity on rice and wheat yields in India, and reported that both yield and pH exhibited spatial pattern at the measured scale, and that the effects of heterogeneity of soil pH on rice yield were lower in magnitude than those on wheat.

On plant-plant interactions: nutrients

Vegetation patterns are highly correlated with spatiotemporal soil nutrient patterns (Grieg Smith 1979, Berendse and Elberse 1990, Austin 1990). For hundreds of years, it has been well known that manipulating nutrient levels of agronomic soils can enhance crop biomass production. More recently, however, interest has been paid to nutrient variability that might govern plant-plant interactions. It is generally accepted that nutrients, especially nitrogen, are a significant limiting resource in most terrestrial ecosystems (Tilman 1990, Pritchett and Fisher 1987). Few plants have more than 3 or 4 limiting mineral resources (Tilman 1990); among these, plant-available nitrogen, phosphorous, potassium, calcium, and magnesium (the macronutrients) are important (Grieg Smith 1979, Aber and Melillo 1991).

The importance of the effects of nutrient heterogeneity on plant community structure and competition can be seen in a study performed in South Africa, where Cowling (1985) found that broad scale patches of highly-leached, nutrient poor soils acted as an “edaphic barrier” to the migration of plants from neighboring communities. Other studies have shown that density, composition, and biomass yield of plant assemblages were closely related to a nutrient gradient, implying that heterogeneity might affect community structure (Austin and Austin 1980, Austin *et al.* 1985). Using phosphorous isotopes in a different approach to studying nutrient competition, Caldwell *et al.* (1987) showed that sagebrush (*Artemisia tridentata* Nutt.) competed directly for phosphorous with various grass species in a desert shrubland, suggesting that a patchy distribution of phosphorous could differentially affect the success of these species.

Many researchers have found evidence for the historical importance of competition for patchy resources in the life history strategies and different morphologies

of plant species. The existence of differing root morphologies among coexisting species is thought to be a result of selective pressures created by competition for nutrients that are heterogeneously distributed in a vertical dimension. Fitter (1986) showed that coexisting species had differences in root activity at a given depth, giving evidence that niche differentiation exists. He suggested, however, that this resulted more from morphological plasticity than from a coevolutionary process. Bazzaz (1990) also pointed out the differing rooting depths and root morphologies of 3 plant species growing together: *Setaria faberii* Hermann (shallow rooting), *Abutilon theophrasti* Medicus (intermediate depth) and *Polygonum pennsylvanicum* L. (deep rooting). An alternative explanation for these differences in rooting depths, however, is an avoidance of allelochemicals (Williamson 1990).

Foraging precision, nutrient uptake efficiency, and foraging scale are characteristics that differ among plant species and are adaptations for improving exploitation of microheterogeneity. Mou *et al.* (1997) discovered that competing tree species have differing abilities to detect fertile microsites and have differing scales (mass and extent or root systems), as did Einsmann *et al.* (1998). In a review article, Robinson (1994) cited evidence that nutrient uptake efficiency was enhanced when nutrients were supplied locally to plant roots, but that only 30% of the studies he encountered reported enhanced root growth due to localized enrichment. Berendse and Elberse (1990) pointed out that *Paulownia tomentosa* Thunberg, a species common in more nutrient-rich sites, has a higher nitrogen-use efficiency than *Pinus sylvestris* L., a potential competitor. This suggests that *P. tomentosa* might have outcompeted *P. sylvestris* where nitrogen was limiting and heterogeneously distributed.

Possibly the most compelling indirect evidence for the importance of the limiting, patchy nature of nutrient distribution, however, is the existence of symbioses between many plant species (especially those of the family Fabaceae) and nitrogen-fixing bacteria, as well as symbioses between many plant species and mycorrhizal fungi. The investment of photosynthate and structural material in the maintenance of these relationships is often relatively high, suggesting that the enhanced nutrient uptake capability (foraging scale) gained by the plant from the symbioses is worth the decrease of investment in reproduction or growth (Berendse 1982, Aber and Melillo 1991).

On plant-plant interactions: moisture

Water is the least temporally reliable of all of the vital plant resources (Harper 1977), and its availability is often cited as one of the key factors influencing carbon fixation, growth and net primary production (Dawson 1993). The availability of water can vary dramatically within a small area, due to the effects of microtopography, differences in soil texture, organic matter content, and vegetation-induced factors such as shading. Competition for spatiotemporally heterogeneous water exists and has been a strong force influencing plant adaptations and distributions (Grieg Smith 1979, Dawson 1993). For example, Walker and Peet (1985) showed the importance of the effects of a moisture gradient on species composition in longleaf pine/wiregrass communities in the Green Swamp savannas in North Carolina. Similarly, Grieg Smith (1979) cited a study showing that vegetation pattern was highly correlated with patterns of soil moisture because of microtopographic variation.

Obviously, the desert is a ripe area for studying competition for spatiotemporally heterogeneous water resources. Removing conspecifics from clumps of *Encelia farinosa* Blake, a desert aster, raised the leaf water potential and increased the growth rate of remaining individuals (Ehleringer 1984). In a similar study, the desert shrub *Artemisia tridentata* Nutt. and two species of *Agropyron* grass were tested to assess their relative competitive abilities. The survival of *A. tridentata* was differentially affected by competition with similar densities of the two grasses, suggesting that the distribution of these three species might be affected by patterns of moisture heterogeneity. Mitchell *et al.* (1993) discovered that loblolly pine (*Pinus taeda* L.) seedlings exhibited lower leaf water potentials during drought conditions when grown in proximity to high densities of broomsedge (*Andropogon* spp.) and sweetgum (*Liquidambar styraciflua* L.), two potential competitors. During times of higher moisture availability, however, the broomsedge and sweetgum actually increased the availability of moisture, suggesting that the competitors acted to lower the soil temperature and decrease evaporation. In this case, the spatial heterogeneity of the vegetation community has a positive effect on water availability.

As with competition for nutrients, the historical importance of a heterogeneous, limiting water supply can be seen in plants' morphological and physiological adaptations.

For example, Dawson (1993) reported that *Acer saccharum* Marshall practices hydraulic lift, or the nocturnal uptake of water via deep roots and subsequent release of water into upper soil layers. This water can be used by the tree to maintain a proper leaf water balance at times of the following day when moisture is limiting. Further circumstantial evidence for the importance of water as a limiting resource in these systems arises from the observation that higher species diversity is associated with *A. saccharum*, possibly due to the localized area with higher soil moisture associated with the tree (Dawson 1993).

Schaffer and Gadgil (1975) speculated that the evolution of an annual (vs. perennial) life history is in part an adaptation to the effects of temporally heterogeneous water availability. They believed that in highly variable environments such as deserts, annuals are competitively superior because they produce seeds that are able to resist periods of drought better than the rhizomatous roots of perennials. Further evidence is that on wet, stable sites they found a low percentage of annuals (~1%), vs. a very high percentage of annuals (~95%) on dry, unstable sites (Schaffer and Gadgil 1975). Similarly Wilson and Harris (1970) reported that some annual grasses are better competitors for moisture than perennials when started from seed, due to their more rapid elongation of roots during periods of high moisture availability. These examples of adaptations to temporally heterogeneous, unstable moisture regimes support the idea that competition for moisture exerts a strong influence on plant community structure and composition.

On plant-plant interactions: light

The availability of light is the most fundamental variable which influences plant growth rate and structure, and thus competition for it is keen (Harper 1977). It is thought to be one of the most important factors driving succession (Harper 1977, Bazzaz 1990), vertical vegetation structure (Givnish 1982), and other plant-plant interactions. For example, manipulating the amount of canopy in a forest affected the structure of the understory community and relative growth rates of associated species (Mitchell and Arnott 1995). In addition, successful efforts have been made to model the effects of

canopy structure and other factors on plant-plant interactions using a spatially-explicit, resource-mediated, mechanistic model (Mou *et al.* 1993).

More interesting, however, is an investigation of the life history and structural adaptations that result from competition for spatiotemporally heterogeneous light. For example, many species become shade adapted (Mitchell and Arnott 1995); they have physiologically specialized to grow in low-light levels to the extent that exposure to direct sunlight inhibits their growth (Bazzaz 1990). Several species of goldenrod (*Solidago spp.*) drop their lower leaves when grown at high densities; this plasticity is thought to be a strategy with which the individual can best invest its energy into producing optimally-photosynthesizing tissues, normally at the upper part of the plant (Bazzaz 1990).

Both leaf area and leaf weight exhibit plastic responses to the spatial heterogeneity of light. For example, the development of sun and shade leaves on the same plant can be seen as a mechanism with which plants adapt to vertical heterogeneity of light levels (Fitter and Hay 1987). Givnish (1982) discussed the benefits of the plasticity of shoot growth in response to competition, but assumes it is secondary to genetically-determined leaf heights. Furthermore, he believed that plants growing in patches of conspecifics might benefit by limiting their height growth, because taller individuals might lower their inclusive fitness by outcompeting relatives.

Other adaptations that enhance plants' abilities to respond to a heterogeneous light environment include reproductive strategies and complex morphological changes. *Myrica cerifera* L. forms clonal thickets, which might be a strategy by which it can alter the light environment of its surroundings and reduce interspecific competition (Tolliver *et al.* 1995). Many species of rainforest plants have evolved adaptations such as red undersides, blue tint, and epidermal lenses (raised epidermal surfaces) in order to better compete for light (Lee 1983). Finally, the evolution of leaf solar tracking and optimal leaf and branch orientation are examples of further indirect evidence for the strength of light as a limiting resource (Givnish 1982).

On succession

Not only are the effects of small-scale edaphic variability on localized plant-plant interactions significant, but also are their effects on succession. In an old field community in Michigan, nitrogen availability was patterned at scales from 1-40 meters, the same scale at which plant community composition varies during early succession; this suggests close relationships among patterns of nutrient availability and successional dynamics (Robertson *et al.* 1988). Pilmanis and Schlesinger (1997) revealed that the range of autocorrelation of nitrogen, carbon and phosphorous changes across a gradient of desertification; the ranges of autocorrelation generally got shorter as grassland degraded to shrubland.

Stark (1994) believed that since plants create edaphic heterogeneity via production of litter, concentration of nutrients, water movement and stimulation of microbial activity, their persistence in a community is tied to their ability to exploit that heterogeneity better than competitors. This concept gave rise to the hypothesis that a plant's ability to exploit ecological heterogeneity relates to its competitive ability during succession. Jackson and Caldwell (1993) believed that nutrient foraging capacity could be a strong determinant of a plant's competitive ability. Campbell *et al.* (1991) found that competitively dominant plants produce the greatest biomass of their roots in nutrient rich soil zones, but are less precise with respect to the proportion of new growth they produce in these patches.

Species which persist in low numbers in communities are typically more precise foragers. Mou *et al.* (1997) found that in sweetgum (*Liquidambar styraciflua* L.) and loblolly pine (*Pinus taeda* L.) plantings, fine root production was not correlated spatially with aboveground biomass, but rather with patches of fertile soil. Jackson and Caldwell (1993) reported that root mass is well correlated with levels of soil potassium and organic matter, suggesting that differential root proliferation occurs. Einsmann *et al.* (1998) also found that species that coexist and presumably compete have different abilities to respond to nutrient enrichment.

It is possible that early successional species may not exploit fine scale environmental heterogeneity as well as can later successional species (Stark 1994, Grime 1994), a characteristic that leads to their demise. Annual plants are favored in early

succession because they can produce “cheap”, non-lignified structural material which allows them to rapidly exploit large volumes of soil (Fitter 1994, Givnish 1982). As succession occurs, however, smaller-scale patches of resources form due to the accumulation of a litter layer and changes in site chemistry, light levels and hydrology, allowing for trees and shrubs to move in. The progression to later successional stages causes a re-homogenization of the edaphic matrix, with some finer-scale patches forming around decaying vegetation (Gross *et al.* 1995). The above studies show that species differ in their response to environmental heterogeneity, and that the differing responses are important determinants of community structure.

Geostatistics

Geostatistics is a field of statistics based on the theory of the “regionalized variable”, as opposed to that of the “random variable” of conventional statistics. Regionalized variable theory states that many phenomena are locally autocorrelated in time and/or space. Legendre and Fortin (1989) defined autocorrelation as a characteristic of random variables which causes pairs of variables found separated by a given distance to exhibit more or less similarity on average than expected by chance. They believed that many ecological variables exhibit spatial autocorrelation due to certain biological properties, for example patchiness of dispersal, home range phenomena, and localized nutrient releases. The assumptions of many conventional statistics, e.g. the F and t tests, include randomly-distributed independent samples, and thus are violated when one is sampling an autocorrelated environmental variable. In other words, a variable’s value at one location can be predicted by the value at a different location (one within the range of autocorrelation), and so the samples are not statistically-independent of one another (Legendre and Fortin 1989). Basically, geostatistics assumes that the variation in a group of samples comes from a mixture of deterministic (spatial dependence) and random variation (Rossi *et al.* 1992).

Variogram analysis is one geostatistical technique frequently used to quantify spatial autocorrelation (Appendix 1). Trangmar *et al.* (1985) discussed the utility of using geostatistics in spatial studies of soil properties, and several researchers have followed suite by conducting geostatistical studies of soil variables (e.g., Rahman *et al.*

1996, Kabrick *et al.* 1997, Robertson *et al.* 1997). Rossi *et al.* (1992) and Legendre and Fortin (1989) described how the recognition of spatial autocorrelation could greatly improve ecological studies. They detailed the results of studies that were found to be erroneous after determining that the variables measured were not statistically independent as assumed.

Variogram modeling not only allows us to characterize spatial patterns of autocorrelated phenomena, but is also a tool with which to perform spatial interpolation. Kriging, an interpolation technique initially created by the mining industry, uses the variogram to provide weights for the terms in a series of simultaneous equations, the solution of which yields an interpolated value for a variate at an unknown point. Knowledge of the form of the variogram allows the kriging procedure to perform better in many instances than traditional techniques such as regression or inverse distance weighting (Cressie 1993, Isaaks and Srivastava 1989). Advantages of kriging include low estimation error, ability to provide estimated values for specified points as well as estimation standard deviation for each point, and honoring the control points. While kriging is basically a mapping technique, allowing for a visual assessment of spatial patterns of the soil variates, it can also produce values that can be used in future analyses.

SAVANNAH RIVER SITE EXPERIMENT

INTRODUCTION

Watt (1947) showed that many plant communities are not homogeneous, but are in fact a mosaic of patches. Spatial patterns in plant communities may be the result of soil nutrient and water heterogeneity (Snaydon 1962, Lodhi and Johnson 1989, Palmer 1990, Hook *et al.* 1991, Willems *et al.* 1993, Meredieu *et al.* 1996, Ehrenfeld *et al.* 1997), patchy distribution of herbivory and other disturbances (Janzen 1971), asymmetric interactions among neighboring plants (Fowler 1982, Mitchell *et al.* 1993, Tolliver *et al.* 1995, Mou *et al.* 1995), uneven seed dispersal (Lechowicz and Bell 1991), uneven distribution of microsites for seed germination (Harper *et al.* 1965, Huenneke and Sharitz 1986) and random chance (Halpern 1988).

It is also well documented that many soil properties do not vary smoothly across the landscape at various scales (Trangmar *et al.* 1985). Hypotheses as to the origin of patchiness in soils include bedrock mineralogy (Meredieu *et al.* 1996), patterns of soil-dwelling vertebrate (Inouye *et al.* 1987) and invertebrate (Gosz 1984) activity, effects of different litter types (Tappeiner and Alm 1975, Hendrickson and Robinson 1984, Gonzalez and Zak 1994, Finzi *et al.* 1998*a* and *b*), plant canopy-related phenomena such as differential rainsplash (Schlessinger *et al.* 1996), stemflow (Lechowicz and Bell 1991), canopy gaps (Bormann and Likens 1979), plant physiological activity (Kellman 1979), and finally past disturbance such as fire (Schlessinger *et al.* 1996), wind and ice storm-related treefall and soil mounding (Jonsson *et al.* 1990), and forestry practices (Preston 1996). While it is recognized that soil properties vary at scales of centimeters to tens of kilometers (Ehrenfeld *et al.* 1997), many studies deal with heterogeneity at the plant community level. For example, Gross *et al.* (1995), Robertson *et al.* (1997), Ehrenfeld *et al.* (1997) and Palmer (1990) all focus their soil heterogeneity studies at the scale of one to several meters; i.e., they examine heterogeneity at scales relevant to plant community structure.

In recent years, several studies have found correlation between plant community structure and edaphic heterogeneity. For example, Jackson and Caldwell (1993) found

that the spatial distribution of desert shrubs and grasses was related to soil resource patterns. Schlessinger *et al.* (1996) and Hook *et al.* (1991) reported that desert shrubs tend to concentrate nutrients below their canopies. In forests, Finzi *et al.* (1998a and b) found spatial correlation among tree species and chemical properties of the forest floor and soil. Meredieu *et al.* (1996) showed that patterns of productivity of *Quercus rubra* L. were correlated with patterns of soil depth. Palmer (1990) found that species composition of a North Carolina hardwood forest was spatially correlated with soil calcium content.

Not all studies reveal strong relationships between community or smaller-scale patterns of soil properties and plant growth or community structure, however. Lodhi *et al.* (1989) did not find any significant correlation between understory woody plant biomass and soil cations, nitrogen, or moisture. Robinson (1994) reported that 30% of the studies he reviewed did not show significant correlation between measurements of root growth or overall plant biomass and fine scale nutrient heterogeneity. Tappeiner and Alm (1975) did not find a significant relationship between total forest floor nutrient levels and different understory species groups. Ehrenfeld *et al.* (1997) showed that neither individual forest understory species patterns nor those of species groups were strongly related to patterns of soil properties. Similarly, Robertson *et al.* (1997) found that biomass production in an old field community was only weakly correlated with soil properties. Finally, Chapin (1980) and Chapin *et al.* (1986) hypothesized that biomass production of plants adapted to nutrient poor sites will not be well-correlated with nutrient levels.

One explanation for the lack of a clear, consistent relationship between spatial patterns of soil resources and of vegetation might be temporal fluctuations in resource levels. For example, Jones *et al.* (1998) hypothesized that the temporal dynamics of spatial heterogeneity parallel the dynamics of biomass accumulation following a clearcut, as described by Bormann and Likens (1979). As succession progresses and vegetation begins to dominate an area, fine-scale, localized patches of resources tend to become homogenized by a combination of litter layer accumulation, root exploitation of soil, and uptake of nutrients. Robertson *et al.* (1993) and Gross *et al.* (1995) proposed a similar though less explicit model of the spatiotemporal dynamics of heterogeneity; along the

same lines, Ehrenfeld *et al.* (1997) suggested that temporal heterogeneity of environmental variables could have as large an impact as spatial heterogeneity on plant community structure.

A second possible explanation for the lack of agreement among studies assessing the correlation of vegetation and environmental variability is the distinction between structural and functional heterogeneity. In other words, it is relatively straightforward to describe and classify spatial patterns of physical environmental factors and ecological phenomena independently based on some arbitrary standard (structural heterogeneity), but much more difficult to assess the biological impact these patterns might have on ecological entities (functional heterogeneity) (Li and Reynolds 1995). Thus, for nutrient-poor sites in particular, small changes in nutrient levels might lead to some measurable spatial structure, but they might not be functionally significant. While it is difficult to determine if functional heterogeneity exists without a manipulative experiment, correlations between the heterogeneous resource (soil) and the entities affected (plant communities) can provide evidence that it exists.

Incorrect scale of sampling is the third possibility for a lack of measured correlation between plant communities and soil variables. Since soil physical and chemical characteristics are a result of processes operating at a variety of spatial and temporal scales, it is necessary to measure them using a sampling methodology that accurately captures this nested pattern of heterogeneity (Trangmar *et al.* 1985). For example, the spatial structure of edaphic resources in one community might be very different from that of a floristically similar community (e.g., Kelly and Canham 1992), or one separated by a short geographic distance, due to a lack of correspondence between the scale of sampling and the scale of variability. Many of the studies of soil heterogeneity found in the ecology literature, however, restrict their experiments to one large plot within each community type, possibly failing to account for the fact that spatial structure at the community scale varies across the landscape.. For example, Robertson *et al.* (1988) used one 0.5 ha study plot, Gross *et al.* (1995) employed only one 0.025 ha study plot in each of three community types, and Schlesinger *et al.* (1996) used only one or two small (96 m²) plots at each of 11 study sites.

In this paper, I explore spatial heterogeneity of soil properties and vegetation in a nutrient-poor forest and attempt to determine if functional spatial heterogeneity is indicated. I consider spatial heterogeneity to be an integration of three elements: global variability, patchiness and the autocorrelation scale. *Global variability* is the variation of the measured variable without regard to sample location. I define a *patch* as a contiguous area within which values of a variable exhibit spatial autocorrelation and have clear differences from their surroundings. *Patchiness* consists of patch number, quantity of patch types, and the transition features between patches. *Autocorrelation scale* is the spatial range at which the measured variables exhibit autocorrelation, or are spatially structured. While there are numerous metrics used to quantify spatial autocorrelation, I prefer the variogram because of its intuitive appeal, its ease of interpretation and its ubiquitous use in the literature (Isaaks and Srivastava 1989, Dutilleul and Legendre 1993).

The specific objectives of my study were to: a) characterize the spatial patterns of soil and forest floor variables in an aggrading pine forest, b) characterize the spatial patterns of the vegetation community, and c) explore relationships among vegetation and forest floor variables. I tested three hypotheses: first, in a mature forest plantation dominated by one species, soil and forest floor resources would exhibit low global variability; second, the variables would have broad autocorrelation ranges; and third, this low spatial heterogeneity at the community scale would be consistent across the landscape. I chose a relatively simple, pine-dominated ecosystem with a patchy understory distribution for my study with the expectation that although the overall heterogeneity would be low, the measurable correlation among the edaphic variables and plant community would be strong.

MATERIALS AND METHODS

Site Description

The study was conducted in a 40-yr-old slash pine (*Pinus elliottii* Engelm.) plantation at the U.S. Department of Energy's (DOE's) Savannah River Site, on the Upper Coastal Plain near Aiken S.C. The mean July maximum, January minimum and

annual temperatures are 27°, 9° and 24° C, respectively. The mean annual precipitation is 113 cm, distributed roughly evenly throughout the year (South Carolina State Climatology Office, SC Dept. of Natural Resources, Columbia, SC 1998). The soil series encompassing the study plots is the Dothan (fine-loamy, kaolinitic, thermic Plinthic Kandiudult), which was formed in sandy marine sediments, is well-drained, has a low nutrient-holding capacity, and has a low organic matter content (Rogers 1988). Prior to establishment of the plantation, the area consisted of pastureland and agricultural fields (Rogers 1988). The stand was thinned on at least two occasions since its inception, and was last burned in 1993 in order to reduce fuel load and prevent uncontrolled fires. In addition to the pine that comprised ca. 90% of the forest's basal area, other relatively abundant species included several species of oaks (*Quercus spp.*), waxmyrtle (*Myrica cerifera* L.), and black cherry (*Prunus serotina* Ehrhart). Total herbaceous plant cover was less than 5%.

Data Collection

Five 1 hectare plots (100 m x 100 m) were randomly selected for the study. A 0.25 ha survey plot (50 m x 50 m) was located at the center of each plot with a 25 m buffer strip on each side. Each survey plot was divided into 100 5.0 x 5.0 m grid cells (Figure 1). Soil sampling locations were systematically established at 41 of the grid intersections. Within each large plot, two 5.0 x 5.0 m grid cells were randomly chosen to contain an additional 41 sampling points each, with the sample layout being identical to that of the larger scale, except the minimum distance between points was 50.0 cm rather than 5 m.

My soil and forest floor sampling scheme was chosen in order to optimize variogram modeling with a uniform number of pairs of points separated by a given distance (lag) class, and to allow for an accurate resolution of the variogram close to its y axis (Isaaks and Srivastava 1989). For the soil and forest floor variables, distance classes were created so that there were an average of ca. 2000 pairs of points in each lag class for each variogram constructed with data from all five plots, with a minimum of 500 and a maximum of 2800 pairs.

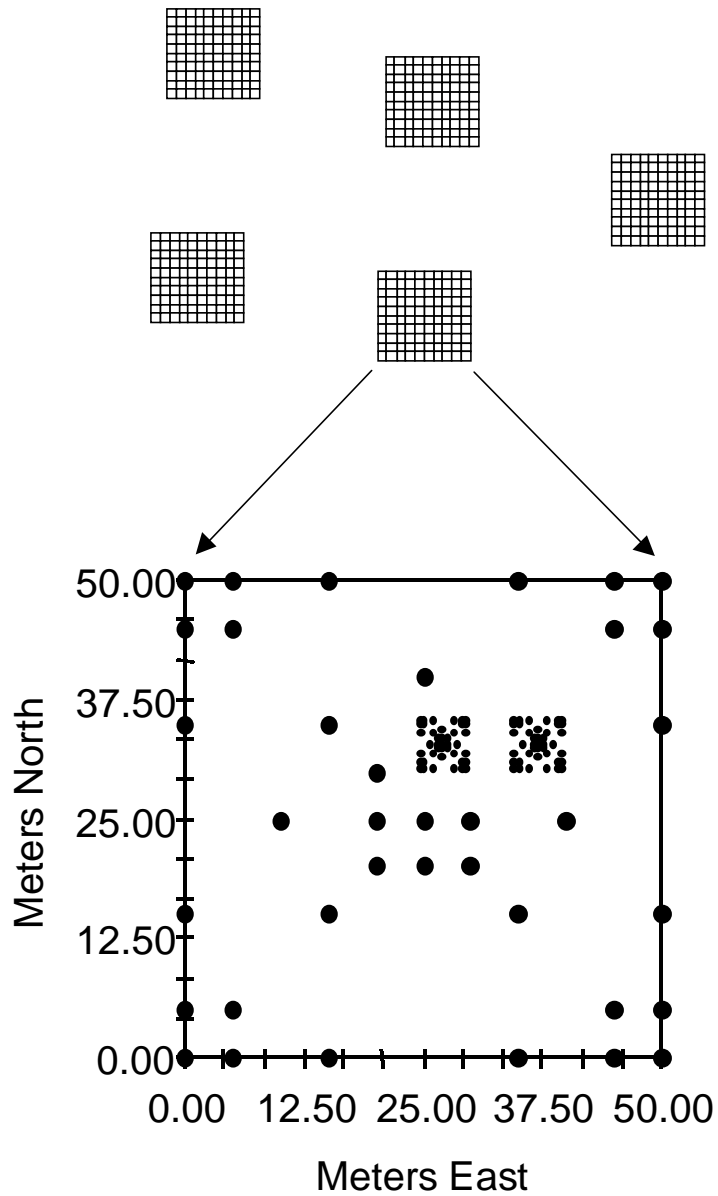


Figure 1. Schematic layout of survey plots at the Savannah River Site. On each of five plots, 41 points were located on the nodes of a grid partitioned into 100 5 x 5 m cells, in a configuration whose goal was to optimize variography. Forty-one points were also located inside each of two randomly chosen cells, each cell having the same sample configuration as the large scale grid, and the smallest sampling interval being 50 cm.

In Spring 1997, a 2 cm diameter soil core of the A horizon was taken from 0-20 cm depth at each sampling location. The soil samples were returned to the lab and dried to a constant weight at room temperature prior to analysis. On one of the five plots, a 4.8 cm diameter core of mineral soil was taken from the A horizon between a depth of 5 and 10 cm at each of the 41 points at the large scale using a bulk density hammer. The cores were dried to a constant weight at 65° C and soil bulk density was determined. Forest floor samples were collected at each point using a specially constructed, 9 cm diameter steel pipe with sharpened edges, and the forest floor depth was measured. Samples were dried at 65° C to a constant weight prior to analysis. Pairs of 20 cm long stainless steel rods were inserted into the top 20 cm of mineral soil at each point, and in May 1997 a Tektronix model 1502C cable tester (Tektronix, Inc., Wilsonville, OR 97070) was used for TDR (Time Domain Reflectometry) measurement of volumetric soil moisture content (Topp *et al.* 1980). Ion resin membranes (Ionics Corp., Watertown, MA 02172) of 2.5 x 5.0 cm in size were vertically inserted into the A horizon soil between a depth of 5 and 10 cm at each sampling location in order to obtain bioavailability indices for nitrogen (NO_3^- and NH_4^+), and phosphorous (HPO_4^-) (Lundell 1989, Abrams and Jarrell 1992, Qian *et al.* 1992). Membranes were removed after a period of 14 days and immediately refrigerated at 3° C until extraction.

In the laboratory, dried soil samples were passed through a 2 mm sieve and analyzed for pH and total soil C and N (% by weight) after removing the coarse fragments (> 2 mm). A random sample of ca. 30 samples of coarse fragments were weighed to determine the % of the bulk soil made up of coarse fragments. The pH in water was determined using standard methods (McLean 1982). Approximate 25 mg subsamples of the remaining soil were ground (<0.2 mm) and oxidized in a Perkin Elmer Model 2100 CHN analyzer (Perkin-Elmer Corporation, Norwalk, CT 06859) to determine total C and N. Dried forest floor samples were weighed and ground (<0.2 mm), and approximate 20 mg subsamples were also oxidized in the CHN analyzer for total C and N determination.

Membrane-bound NO_3^- and NH_4^+ were extracted with 2.0 M KCl, and membrane-bound HPO_4^- was extracted with 0.5 M HCl. The extracts were analyzed with a Lachat Model 4000 autoanalyzer (Lachat Instruments, Inc., Milwaukee, WI

53022). The bioavailability indices for N and P were used in determining the relative spatial variation of the soil nutrient pool.

In March 1997, the spatial location, species and diameter of each tree (> 4.0 m in height) and shrub (< 4.0 m in height) were recorded on all five plots. For all species except waxmyrtle, diameters at breast height (DBH) were measured. Waxmyrtle diameters were measured at the base of the stem, just above the swell of the root collar.

The height and crown width of ca. 100 pines, hardwoods and waxmyrtle were randomly sampled and regression models of the relationship between DBH and tree height and between DBH and canopy dimensions were established (Table 1). Using these models, a canopy map for each species group was created for each plot in order to assess spatial patterns of tree crowns and species group dominance. All data were entered into a GIS (Arc-Info and Arc-View (ESRI, Redlands, CA 92373)) for further analyses.

Table 1. Regression equations derived from Savannah River Site vegetation data. Trees were chosen from throughout the study area for inclusion, their diameters were measured, and the relationship between their diameter and their crown dimensions were established.

Species group	Crown diameter regression*	R ²	n
Oaks	Y=36.781x + 119.957	0.931	13
Other hardwood	Y=40.3856x - 0.959x ² + 74.654	0.909	14
Waxmyrtle	Y=25.425x + 59.728	0.873	34
Pines	Y=15.984x - 0.13x ² + 41.77	0.897	45

* Y=crown diameter (m); x = DBH (cm)

Data analyses

Mean, variance and coefficient of variation (CV) were calculated for each forest floor and soil variable. Data sets that did not visually approximate a normal distribution were log transformed prior to statistical analysis. Variogram analysis was used to examine spatial autocorrelation for both the soil and the forest floor variables for all 5 plots combined. Cambardella *et al.* (1994) considered significant autocorrelation to be that captured by a regression model fitting the semivariogram with a ratio of autocorrelated variance to total model variance of > 0.5. In order to assess the degree of spatial autocorrelation of basal area of different species, the geographic coordinates of

each tree were determined and variograms for basal area were calculated using each tree as a sample point. All variography was performed with GS + software (Gamma Design Software, Plainwell, MI 49080).

On each plot, ten 5 x 5 m grid cells that had a sample location on each of their four corners were chosen. The averages of the four values of the forest floor and soil variables were calculated, as was the sum of the basal area of members of each species group found within that cell. Pearson's correlation tests were performed (n=50) to assess the relationship between cell-based average levels of soil and forest floor variables, and between these and dominance (basal area) of different species and species groups. In addition, canonical correlation analysis was performed in order to investigate the relationship between a weighted combination of the forest floor variables and a weighted combination of the mineral soil variables, as well as between these and a weighted combination of the hardwood and pine dominance.

Finally, in order to assess the continuity of spatial autocorrelation across the landscape and the ability of my sampling scheme to accurately characterize it, confidence intervals were calculated for each point of each soil and forest floor variogram calculated on a per-plot basis. The degree of confidence interval overlap was assessed, and the ranges of autocorrelation for each variable for each plot were compared. Kabrick *et al.* (1997) employed this method to examine the similarity of variograms calculated from data collected in different geographic areas. To visually assess the spatial patterns of the forest floor and soil variables and their continuity across the landscape, kriged maps of the variables were produced using Surfer software (Golden Software, Golden, CO 80401), and interpolated values were assigned to classes based on functional significance.

RESULTS

Using the CV as a measure, global variation of soil and litter variables ranged from 4.3 to 166.7% (Table 2). CV's were greatest for nutrient bioavailability indices (>100%) and lower for all other variables (<41%). Table 2 also lists variances and means

of the variables in order to assist a thorough evaluation of CV's, which usually are inflated when the means of measured variables are low.

Table 2. Mean, standard deviation and CV % of several forest floor and soil variables in a mature upland slash pine forest at the Savannah River Site, near Aiken, SC.

Variable	Mean	StDev	CV%
litter depth (cm)	10.0	3.6	35.3
dry mass (kg/m ²)	2.1	0.7	35.3
litter N (%)	0.76	0.16	21.1
litter C (%)	36.82	5.75	15.61
soil ammonium (ppm*)	0.353	0.588	166.676
soil nitrate (ppm*)	0.169	0.180	106.932
soil phosphate (ppm*)	0.106	0.158	148.966
soil C (%)	0.61	0.14	22.89
soil N (%)	0.02	0.01	40.58
soil moisture (vol. %)	10.8	2.7	24.85
soil pH	4.90	0.21	4.34
soil bulk density (g/cm ³)**	1.49	0.06	3.97
soil coarse fragments (%)***	0.01	0.01	87.82

*values are ppm ion extracted from resin membrane

**calculated on a subset of 41 points

***coarse fragments are >2 mm in diameter; calculated on a subset of 30 points

Six of the eight soil variables exhibited significant spatial autocorrelation, with ranges of spatial dependence varying from 1.3 m to 36.3 m, and an average range of 12 m (Figure 2). All of the forest floor variables exhibited significant spatial dependence, with all ranges and the average range being >45 m (Figure 2).

Pines were clearly the dominant species in the sample plots, making up 88.9% of the basal area (Table 3). Oaks, waxmyrtle, and black cherry were the most abundant among the hardwoods. The canopy maps I developed based on the regression models indicate that pines were evenly distributed and made up the vast majority of the overstory. Understory hardwoods (especially waxmyrtle), however, exhibited a clumpy, irregular distribution (Figure 3). The semivariograms of species dominance indicate that the basal area of all species groups exhibits significant spatial autocorrelation within short ranges, with understory hardwood (including waxmyrtle) dominance exhibiting autocorrelation within 1.2 m, and large pine trees exhibiting autocorrelation within 11.2 meters (Figure 4).

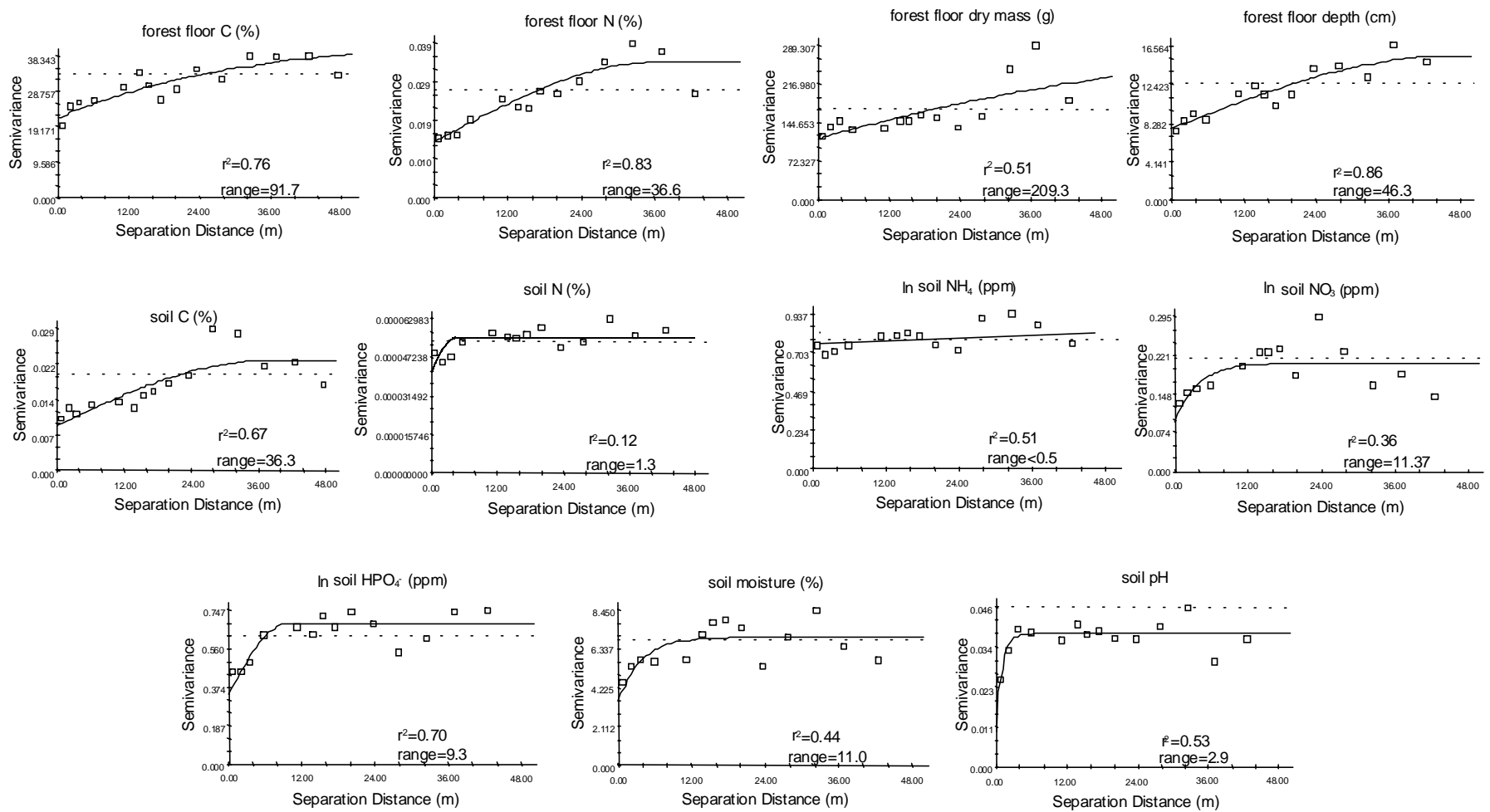


Figure 2. Variograms of soil and forest floor variables collected at the Savannah Rivers Site, SC. Each semivariance lag class is calculated using an average of 1500 pairs of points. The dashed line represents the sample variance. Range is the distance in meters within which samples exhibit spatial autocorrelation.

Table 3. Summary description of species composition, dominance and density of woody vegetation community within five 0.25 ha plots at the Savannah River Site.

SPECIES	basal area (m ² /ha)	% of total	
		basal area	#stems/ha
<i>Pinus elliottii</i> Engelm.	30.7748	82.51	2942
<i>Myrica cerifera</i> L.	2.8702	7.70	1151
<i>Pinus taeda</i> L.	2.3853	6.40	95
<i>Quercus nigra</i> Wangenh.	0.5193	1.39	207
<i>Prunus serotina</i> Ehrhart	0.2534	0.68	114
<i>Quercus incana</i> Bartr.	0.1272	0.34	45
<i>Quercus falcata</i> Michaux	0.0923	0.25	50
<i>Quercus hemispherica</i> Michaux	0.0829	0.22	71
<i>Ilex opaca</i> Aiton	0.0389	0.10	20
<i>Crataegus</i> spp.	0.0313	0.08	6
<i>Sassafras albidum</i> Nuttall	0.0309	0.08	10
<i>Liquidambar styraciflua</i> L.	0.0258	0.07	6
<i>Nyssa sylvatica</i> Marshall	0.0213	0.06	12
<i>Disopyros virginiana</i> L.	0.0174	0.05	26
<i>Cornus florida</i> L.	0.0136	0.04	6
<i>Vaccinium arboreum</i> Marshall	0.0092	0.02	3
<i>Ulmus alata</i> Michaux	0.0016	<0.01	1
<i>Quercus laurifolia</i> Michaux	0.0010	<0.01	3
<i>Acer rubrum</i> L.	0.0008	<0.01	3
<i>Rhus copallinum</i> L.	0.0001	<0.01	1
<i>totals</i>	37.2900	100	4774

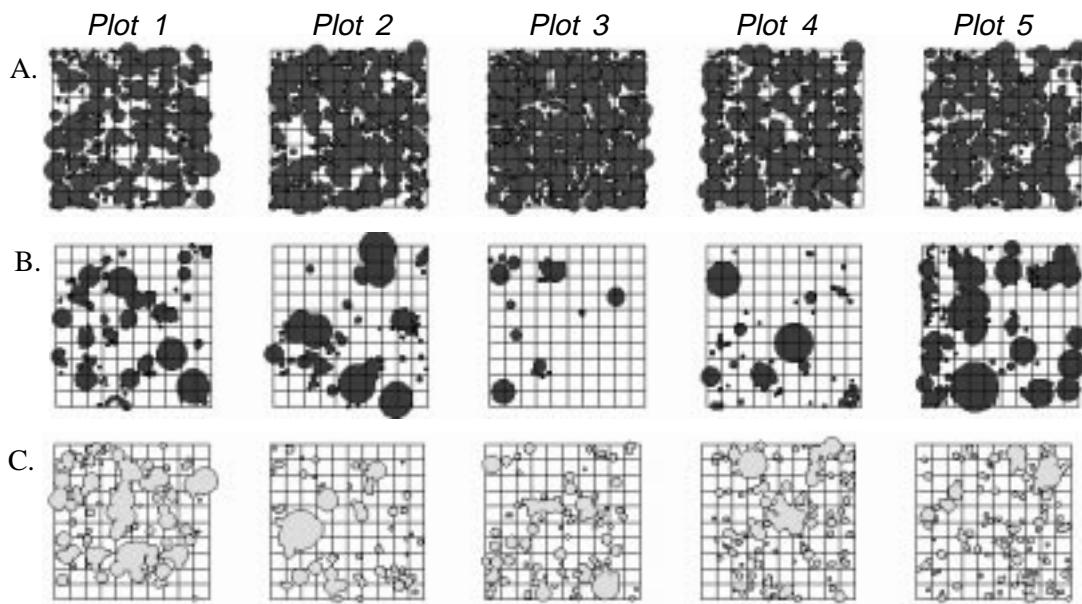


Figure 3. Distribution of different species groups across all 5 plots, shown by canopy area derived from regression equations in Table 1. A. pines; B. waxmyrtle; and C. hardwoods. Each plot is 50 x 50 m, and each grid cell is 5 x 5 m. Plots are arranged such that plots in same column overlap.

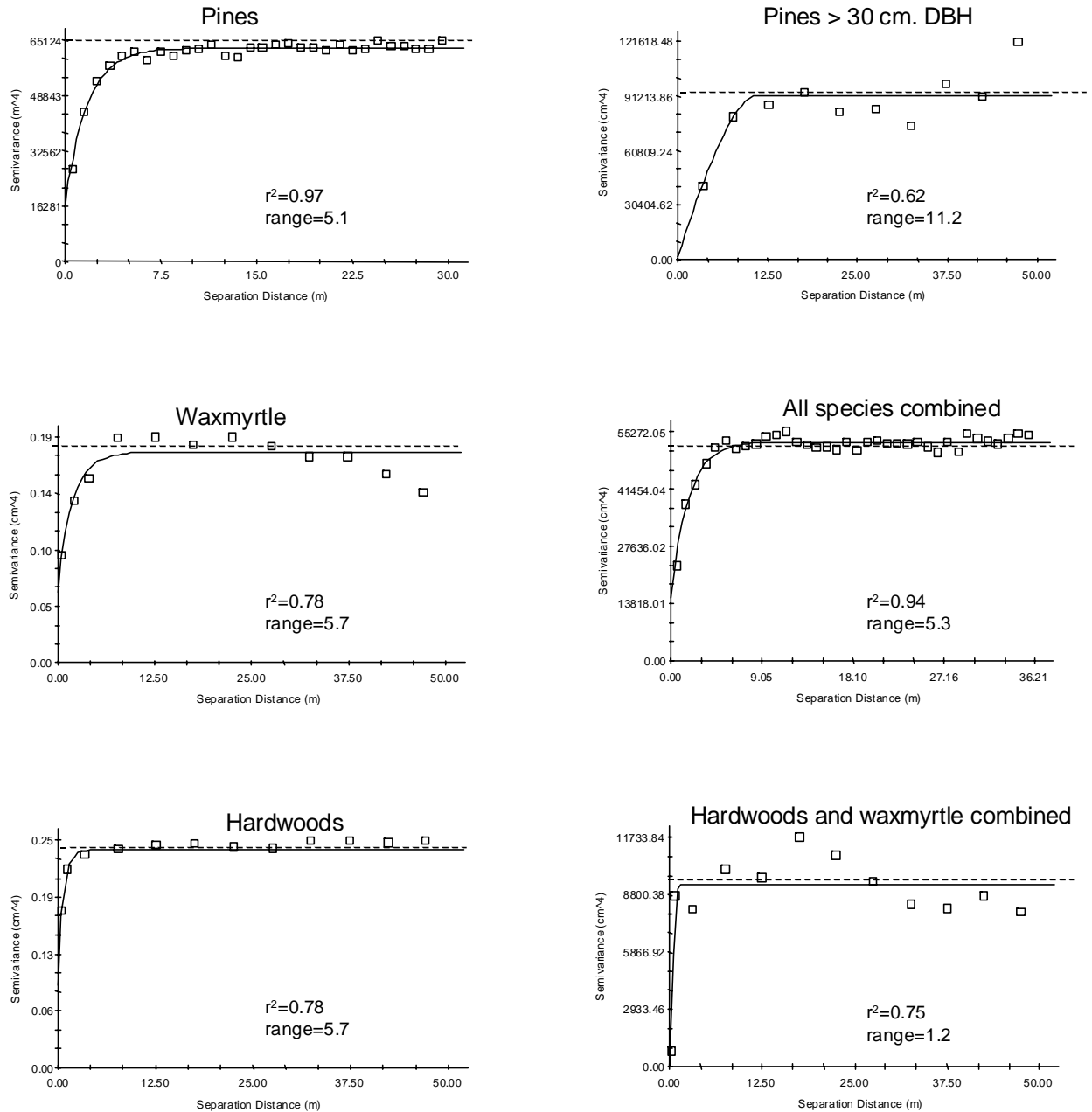


Figure 4. Semivariograms produced with basal area data from the Savannah River Site survey plots. Semivariograms represent local spatial patterns, i.e. data for basal area were used only for locations where trees occurred (no zero values were used). Each semivariance value was calculated with an average of 5000 pairs of points.

Pearson's correlation tests between forest floor and soil variables that we had expected to be well correlated demonstrated few significant cross-variable correlations, and those that were significant yielded low correlation coefficients (Table 4). The strongest correlation was seen between the forest floor N concentration and its depth ($r=-0.66$, $p<0.001$). The nitrogen concentration of the forest floor was also significantly, though weakly, correlated with the log of soil NO_3^- and soil pH. Contrary to our expectations, several variables were not significantly correlated, for example forest floor total nitrogen concentration vs. soil ammonium, soil total nitrogen concentration vs. that of the forest floor, forest floor carbon concentration vs. forest floor nitrogen concentration, soil pH vs. soil available phosphorous, and soil nitrate vs. soil ammonium (all $p>0.05$).

Few of the correlation tests between forest floor and soil variables and vegetation dominance revealed significant correlation, and again, their correlation coefficients were low (Table 4). In general, the correlation was higher between understory hardwoods (including waxmyrtle) and decomposition-related soil and forest floor variables. For example, the log of hardwood (including waxmyrtle) dominance was negatively correlated with forest floor C:N ($r=-0.55$, $p<0.001$), and the log of hardwood (not including waxmyrtle) dominance was positively correlated with soil moisture ($r=0.50$, $p<0.01$), and with the log of nitrate ($r=0.40$, $p<0.05$). The basal area of all pines combined, on the other hand, was not significantly correlated with any of the soil or forest floor variables. When only large pines (>30.0 cm DBH) were considered, a significant negative correlation was found between them and the log of nitrate ($r=-0.43$, $p<0.05$).

Results of canonical correlation tests reveal a similar pattern. Neither the set of soil variables ($r=0.41$) nor the set of forest floor variables ($r=0.47$) was significantly correlated with the weighted combination of overstory pine and understory hardwood vegetation ($p>0.05$). The set of forest floor variables, however, was significantly correlated with that of the soil variables ($r=0.68$, $p<0.001$). Forest floor depth ($r=0.74$) and forest floor nitrogen ($r=-0.85$) were most highly correlated with the first forest floor canonical variate,

Table 4. Correlation test results of relationships among cell-based average values for soil and forest floor variables and cell-based dominance of different species and species groups. Significance levels: * = < 0.05; ** = < 0.01; *** = < 0.001. Only relevant correlation coefficients are shown.

	Vegetation						Forest Floor					Soil								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
Vegetation	all species combined (m ² /ha) (1)	1																		
	all pines (m ² /ha) (2)	---	1																	
	large pines (m ² /ha) (3)	---	---	1																
	ln hardwood (m ² /ha) (4)	---	---	---	1															
	ln waxmyrtle (m ² /ha) (5)	---	---	---	---	1														
	ln hardwood incl. waxmyrtle (m ² /ha) (6)	---	---	---	---	---	1													
Forest floor	forest floor depth (cm) (7)	-0.14	-0.12	-0.06	-0.27	-0.07	-0.37*	1												
	forest floor dry mass (kg/m ²) (8)	-0.08	-0.13	0.00	0.17	0.01	-0.09	---	1											
	forest floor C (%) (9)	-0.04	-0.01	0.02	-0.47**	-0.15	-0.15	-0.16	-0.46***	1										
	forest floor N (%) (10)	-0.01	-0.10	-0.17	0.20	0.11	0.46**	-0.66***	-0.27	0.10	1									
	forest floor C:N (11)	0.01	0.13	0.20	-0.32	-0.27	-0.55***	0.47	0.25	---	---	1								
Soil	soil C (%) (12)	0.01	-0.05	0.15	-0.15	0.37*	0.12	0.01	-0.13	0.01	0.13	-0.12	1							
	soil N (%) (13)	0.01	-0.08	0.41	0.01	0.24	0.15	-0.24	0.17	-0.06	0.23	-0.16	0.29*	1						
	soil C:N (14)	-0.04	-0.01	-0.38	-0.18	0.02	-0.16	0.24	-0.25	0.05	-0.17	0.12	---	---	1					
	ln soil ammonium (ppm) (15)	-0.02	-0.19	-0.31	-0.26	0.14	0.10	0.24	0.09	0.15	0.08	-0.09	0.02	0.00	0.01	1				
	ln soil nitrate (ppm) (16)	0.06	0.01	-0.43*	0.40*	0.02	0.23	-0.29	-0.16	-0.24	0.49***	-0.50***	0.02	0.18	-0.19	0.04	1			
	ln soil phosphate (ppm) (17)	-0.03	-0.05	0.25	-0.07	0.14	-0.01	0.24	0.01	0.05	-0.19	0.20	0.33*	-0.07	0.30	-0.20	-0.19	1		
	soil moisture (%) (18)	0.01	0.06	-0.28	0.50**	-0.07	0.15	-0.03	-0.01	-0.20	0.00	-0.06	-0.09	-0.16	0.08	-0.25	0.31*	0.00	1	
	soil pH (19)	0.02	0.06	0.12	0.09	-0.01	-0.23	0.32*	0.15	-0.29*	-0.45***	0.36*	-0.04	0.01	-0.02	-0.12	-0.17	-0.02	0.09	1

and the log of nitrate ($r=-0.78$) and pH ($r=0.42$) were most highly correlated with the first soil canonical variate. However, redundancy analysis revealed that the first soil canonical variate did not explain a large proportion of the standardized variance of the forest floor variables (16.3%), nor did the first forest floor canonical variate explain a large proportion of the standardized variance of the soil variables (8.4%).

The comparison of confidence intervals of soil and forest floor variograms calculated on a per plot basis revealed that most of the variograms contained several points whose confidence intervals did not overlap with those of the other plots (Figure 5), indicating significant dissimilarity among the variograms according to the criteria of Kabrick *et al.* (1997). Along the same lines, the ranges of autocorrelation of the different variables changed dramatically across the study area (Table 5). Finally, an assessment of the kriged maps of soil and forest floor properties revealed that patches varied dramatically in size and arrangement from plot to plot across the landscape (Figure 6).

DISCUSSION

As predicted, I found that soil and forest floor resources in the mature slash pine plantation were spatially homogeneous relative to other forests, and thus at the community level, the functional significance of existing spatial heterogeneity is probably minimal. My first basis for this conclusion is my finding that for many of the soil resources that are important to plant growth, the global variability (range of values) was low and the coefficients of variation were typical of those reported in the literature (Beckett and Webster 1971). For example, the standwide variation of soil nitrogen and soil carbon concentrations (Table 2) were quite low compared to studies in other forest types (Vitousek *et al.* 1982, Finzi *et al.* 1998b), and were typical of values found in pine forests with nutrient-poor, sandy soils (Montes and Christensen 1979, Burger and Pritchett 1988, Rogers 1988, Wood *et al.* 1992, Polgase *et al.* 1992, Schultz 1997). Total soil nitrogen often shows a strong positive correlation with potentially mineralizable nitrogen and with pine growth (Maimone *et al.* 1991). The narrow variation range of total soil nitrogen values in this forest suggests a low variation of

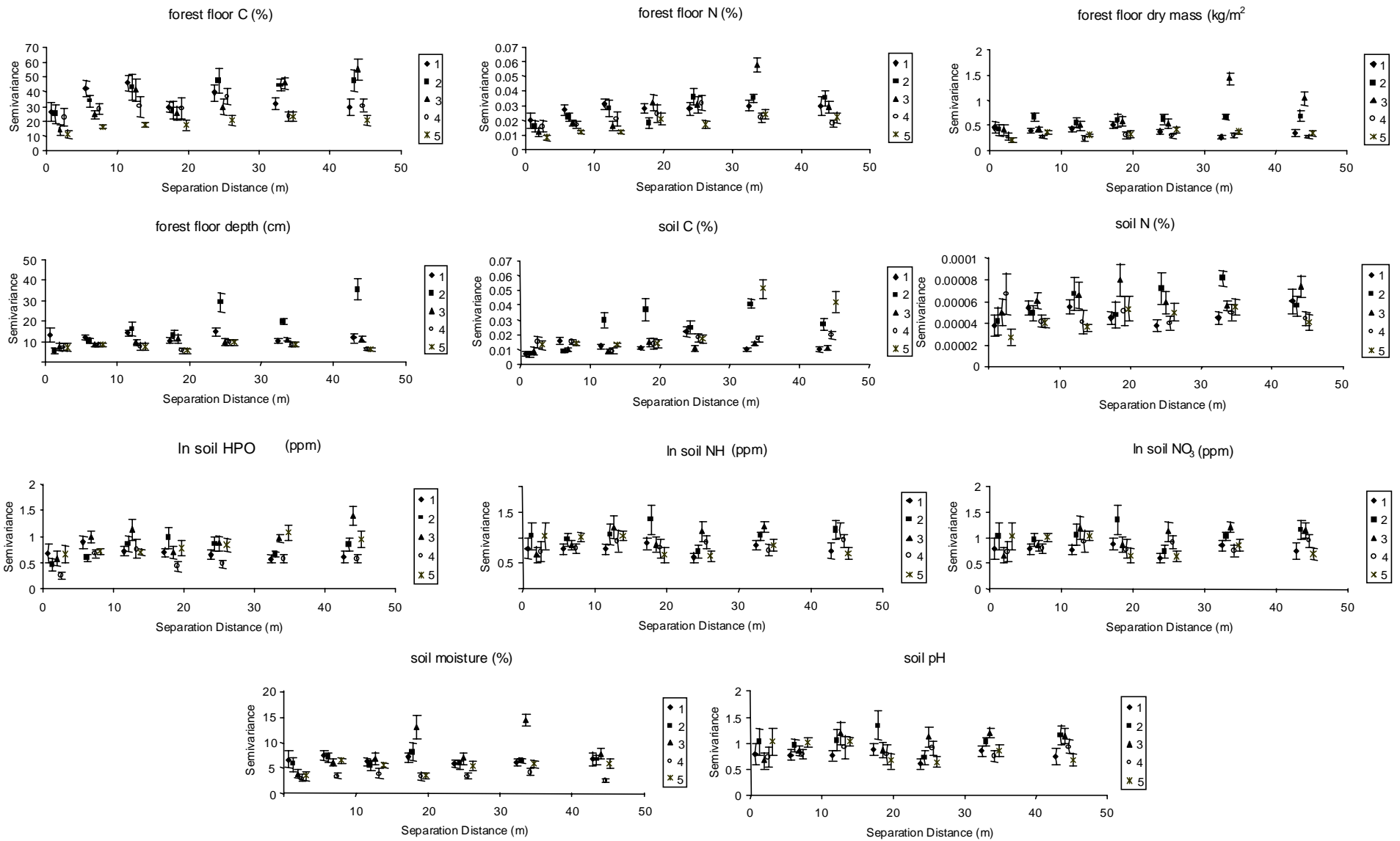


Figure 5. Variograms and confidence intervals for each point and each of five plots, calculated for several variables measured at the Savannah River Site, SC. Each group of points represents a single lag class; points were offset to facilitate interpretation.

Table 5. Comparison of ranges of autocorrelation for variograms calculated on a per-pl basis from soil and forest floor variables collected on five 0.25 ha survey plots at the Savannah River Site.

plot	----- Ranges of autocorrelation (m)-----										
	forest floor dry mass	forest floor depth	forest floor % N	forest floor % C	soil % N	soil % C	ln soil ammonium	ln soil nitrate	ln soil phosphate	soil vol. moisture	soil pH
1	<1.0	<1.0	8	1.4	2.5	6.4	<1.0	27.2	<1.0	<1.0	7.4
2	5.2	>45.0	>45.0	>45.0	15.2	16.88	<1.0	2.1	14.4	<1.0	<1.0
3	>45.0	1.8	39.2	>45.0	2.1	<1.0	15.3	<1.0	7.4	18.1	2.9
4	<1.0	<1.0	22.2	2	<1.0	<1.0	12	<1.0	>45.0	<1.0	<1.0
5	6.2	28	37.6	6.5	5.1	>45.0	<1.0	13.2	>45.0	7.9	<1.0

nitrogen mineralization potentials, and thus probably is not sufficiently broad to differentially impact plant community structure.

Global variability of soil moisture was typical of those in other well-drained, Eastern U.S. pine forest soils (e.g., Burger and Pritchett 1988, Zutter *et al.* 1986, Ehrenfeld *et al.* 1997, Schultz 1997), but was low compared to that in other forest types (e.g., Lodhi *et al.* 1989, Kelley and Canham 1992, Boerner and Koslowsky 1989) due mainly to the coarse texture and low organic matter content of the soils in my study area.

Global variability of soil pH was also typical of those in other mature pine forests (Montes and Christensen 1979, Vitousek *et al.* 1982, Hart and Binkley 1985, Rogers 1988, Reese and Moorhead 1996); the mean level was perhaps slightly higher than normal, possibly due to the effects of past liming of the agricultural fields on which the forest was established. Slash pine forests are adapted to acid soil conditions (Pritchett and Smith 1968), so the narrow range of pH values in my study probably do not have a strong effect on soil biological activity (Swift *et al.* 1979, Tisdale *et al.* 1985) or seedling growth (Reiner *et al.* 1996); furthermore, compared to the range of pH values (4.3-7.3) obtained by Kelting (1998, unpublished data) from lower Coastal Plain (ca. 160 km east of SRS) pine forest soils collected two years after harvest, my range of values (4.3-5.6) was much narrower.

The global variability of forest floor characteristics in my study area was also typical of that in other pine forests, and low compared to other forest types. For example, the mean forest floor nitrogen concentration and biomass were similar to those reported in other studies in slash, loblolly (*Pinus taeda* L.), and longleaf pine (*Pinus palustris* Mill.) forests (Van Lear and Goebel 1976, Jorgensen *et al.* 1980, Hough 1982, Schultz



Figure 6. Kriged maps based on semivariograms obtained using data from edaphic variables collected at the Savannah River Site, SC. Nitrate, ammonium and phosphate values were log transformed for variography, and backtransformed prior to kriging. Each plot is 50 x 50 m, and each grid cell is 5 x 5 m. Plots are arranged so that the same plots are found in columns.

1997), but low compared to the mean levels for these variables reported by the review of Vitousek *et al.* (1982) and by Finzi *et al.* (1998b). Assuming that forest floor decomposition is the dominant source of nitrogen nutrition for trees in mature pine forests (Jorgensen *et al.* 1980), the relatively low range of forest floor nitrogen concentrations and contents in this forest would have little differential impact on forest nutrition and community structure.

The second basis for the conclusion of broad scale homogeneity in the mature pine forest was the lack of correspondence between ranges of autocorrelation of the soil, forest floor, and vegetation variograms (Figures 2 and 4). I had expected to find that the ranges of autocorrelation for the forest floor and mineral soil variables and the species group dominance would be similar due to the known effects of leaf litter nutrient content on that of the soil (Tappeiner and Alm 1975, Boerner and Koslowsky 1989, Pritchett and Fisher 1987). For example Gonzalez and Zak (1994) found that forest floor dry mass and soil nitrogen variables were both spatially autocorrelated within 18 m, and Finzi *et al.* (1998a and b) found differences between forest floor and soil physical and chemical properties under hardwoods and those under conifers in the same forest. The results of this study, however, indicate that spatial patterns of forest floor properties exhibit a dramatically broader scale of autocorrelation (coarser-scale patterns) than those of the soil variables and the species group dominance (Figures 2 and 4). This was probably due to the overwhelming pine dominance across the site and decades of more evenly distributed pine litter inputs that had led to a large patch size for forest floor variables. The soil properties on the other hand were more variable at a finer scale, possibly because they are modified by finer-scale phenomena such as effects of canopy gaps, root uptake, or differences in litter quality and soil biotic activity associated with small patches of hardwoods. The finer scale heterogeneity of the understory species dominance probably stems from the clonal nature of reproduction in the case of waxmyrtle, and the invasion of hardwoods into canopy gaps and their growth as cohorts in the case of the other hardwoods. Peterson and Squiers (1995) found that this might be the mechanism of understory patch formation that explains gap dynamics of an aspen-white-pine forest.

The poor correlation among theoretically-related covariates also supports a conclusion of broad scale homogeneity (Table 3). For example, the carbon:nitrogen ratio

of fresh organic matter of a given type is known to be relatively constant (Tisdale *et al.* 1985), and carbon and nitrogen in forest soil organic matter are well-correlated (e.g., Powers 1980, Kelting 1998, unpublished data). However, my data indicate that forest floor carbon and nitrogen are not significantly correlated ($r=0.187$, $p>0.05$). Similarly, Hart and Binkley (1985) found that ion exchange resin-extractable nitrate and ammonium were extremely highly correlated ($r=0.94$, $p=0.0001$), as were soil pH and resin-extracted phosphorous ($r=0.74$, $p=0.001$). However, I did not find statistically significant relationships between my nitrate and ammonium values ($r=0.037$, $p>0.05$), nor did I find them between my pH and phosphorous values ($r=-0.023$, $p>0.05$). I attribute these weak relationships to the low global variability of these properties; the expected covariates did not respond to one another because most of the values were not sufficiently high to elicit a measurable functional response.

With respect to patchiness of the forest, I also conclude that general broad-scale ecological homogeneity exists. I found only weak correlation between vegetation and soil and forest floor variables (Table 4). If a resource patch exists, there should be some measurable, consistent effect of it on an ecological entity (Li and Reynolds 1995). The lack of strong correlation among edaphic features and between edaphic features and vegetation, however, indicates that the degree of edaphic patchiness is low, i.e., the patches may exist at a broader scale than that at which I focused my study. Were the understory hardwoods to have a greater abundance than that in my study site (i.e., >10%), these results might be substantially different; we plan to conduct future research of this type in hardwood forests and in forests at different successional stages.

The weak, marginally significant correlations among decomposition-related variables (e.g., forest floor nitrogen and soil available nitrogen, soil moisture and pH, forest floor nitrogen and depth) indicate an effect of fine scale, local hardwood abundance on soil properties, and were probably due to the influence of differences in litter quality among species groups. For example, it was not surprising to uncover the significant correlations among soil moisture, forest floor and soil nitrogen, litter depth and understory hardwood dominance (Table 4). Hardwood litter generally contains more mineralizable nitrogen, bases and sugars than does that of pines (Tappeiner and Alm 1975, Gosz 1984, Tisdale *et al.* 1985, Keenan *et al.* 1996, Moorhead and McArthur

1996). Differences in litter quality (e.g., C:N) are correlated with mineralization rates, forest floor depth and dry mass, and other soil chemical properties (Swift *et al.* 1979, Tisdale *et al.* 1985, Finzi *et al.* 1998a and b). The results of this research support those of other studies in this respect.

I suspect that at the time of sampling, the higher nitrogen litter and higher moisture levels below small patches of hardwoods produced a forest floor environment in which the magnitude of mineralization and nitrification was greater at the scale of individual trees or clumps of trees. The dominance of large pines and the log of soil NO_3^- were negatively correlated due to the probable higher density of pine roots and thus greater uptake in these areas. These processes might explain the shorter ranges of autocorrelation of the soil variables; the approximate 10 m ranges of spatial dependence correspond with the average canopy diameter of a clump of hardwoods, and with the diameter of the area of highest root intensity surrounding large pines. At the coarser scale, however, the homogeneous input of pine needles and overwhelming effects of associated broad-scale rhizosphere biological activity tended to dampen this finer scale heterogeneity, in part explaining the larger ranges of autocorrelation for the input-related (forest floor) variables.

This mechanism agrees with that proposed by the model of spatiotemporal dynamics of Jones *et al.* (1998) and the hypotheses of Robertson *et al.* (1993) and Gross *et al.* (1995); as vegetation begins to dominate a site during succession, broad scale, plant community-mediated processes tend to homogenize the edaphic environment. I thus conclude that at the fine scale, local vegetation variation tended to increase the spatial heterogeneity of the edaphic environment, but broad scale phenomena such as litter input, mycorrhizal activities and broad scale uptake processes led to a general broad scale homogeneity that I observed. Furthermore, we are currently testing the hypothesis that in early successional forests, the situation would be reversed: the heterogeneity of the soil and forest floor will affect plant-plant interactions and successional dynamics.

My general finding of broad-scale functional homogeneity supports the claim that the lack of agreement in the literature among studies assessing the relationship between vegetation and soil spatial patterns is due in part to the lack of functional heterogeneity in many of the systems studied. Although it is possible to measure autocorrelation and

define structural heterogeneity at a variety of scales, global variability may not be large enough to significantly affect community structure. In certain community types, such as forest plantations, it is probable that broad-scale gradients such as elevation or changes in soil texture have more functional significance than do chemical properties that are known to impact plant growth.

The results of this study also emphasize the importance of attention to the issue of scale. Kolasa and Rollo (1991), Ehrenfeld *et al.* (1997), and Li and Reynolds (1995) pointed out the importance of the correspondence between the scale of sampling and the relevant scale of the ecological process under study. In order to assess the consistency of levels of autocorrelation properties across the landscape and thus gain insight into the best manner in which to measure it, we distributed my survey plots randomly throughout a putatively homogeneous pine stand. This unique, replicated study design allowed us to assess how levels of autocorrelation vary across the landscape by calculating variograms on a per-plot basis, and comparing them using confidence intervals.

My findings from my comparisons of confidence intervals calculated for each point on a per-plot basis indicate that for most of the variables, the scale of autocorrelation and degree of autocorrelation I measured had apparent variation across the landscape, and within a visually homogeneous area (Figure 5, Table 5). An assessment of the kriged maps reveals similar trends (Figure 6). For those variables that exhibit low global variability, I arbitrarily grouped my kriged values into three broad classes of equal magnitude (assuming that any finer division of classes would preclude any possibility of creating functionally-significant classes). Kriged maps that were classified in this manner indicate that spatial patterns of most of the variables vary at quite a broad scale, and that the shape and configuration of patches varies drastically from plot to plot.

It is possible that many of the studies which have attempted to draw conclusions about the relationships between spatial patterns of vegetation and edaphic variables have not fully recognized changes in edaphic heterogeneity across the landscape, even within a relatively small geographic area. My results further indicate that an alternative to measuring a large, contiguous land area might be the use of several smaller, replicate plots and a subsequent pooling of the variability data. In this manner, a larger geographic

area can be sampled at less cost, and a clearer picture of the spatial structure of a forested ecosystem might possibly emerge. Future studies of edaphic variability and its effect on plant community dynamics should pay more attention to the issue of functional spatial heterogeneity, as well as to that of sampling methodology and scale.

SUMMARY AND CONCLUSIONS

1) *As expected, the forest floor and soil variables I measured generally exhibited low amounts of global variability (i.e., were found at low levels and had low CV's). I had expected to find this because the forest was located on sandy, upland soils. The past land use had probably been pastureland, which is normally relegated to poorer sites in this area. Finally, the maturity of the forest as well as the density and dominance of trees suggested that a large portion of the resources on the site had been incorporated into living biomass, and that any resources made available by decomposition or other inputs would quickly be absorbed by aggressive uptake by roots.*

2) *As expected, the ranges of autocorrelation of the soil properties and those of the vegetation corresponded; however, those of the forest floor properties did not correspond with those of the soil or the vegetation. The ranges of autocorrelation of forest floor variables were much larger than those of the soil and vegetation community. I attribute this to the overwhelming input of pine litter and its associated broad scale effects on the forest floor, and to the localized influences of small patches of understory hardwoods on the soil environment.*

3) *There were several cross-correlations among the edaphic variables, and among the edaphic variables and the vegetation, but very few were biologically meaningful. While there were several significant correlation coefficients for the cross- soil and forest floor variable and the soil- forest floor- vegetation correlation tests, the correlation coefficients were in general low (<0.6). Those relationships which were significant were among soil and forest floor variables which are related to decomposition, such as forest floor nitrogen and depth, soil pH, soil moisture, and soil nitrate. The higher quality litter of understory hardwoods appeared to be driving these relationships. I thus conclude that at the broad scale, the vegetation community tends to homogenize the forest floor and soil, at the fine scale, understory hardwoods have a marginally de-homogenizing effect.*

4) *Contrary to expectations, there was a substantial difference in the ranges of the variograms and the spatial patterns of the edaphic variables separated by a relatively small distance across the landscape.* Surprisingly, a large number of the confidence intervals of the variograms calculated on a per-plot basis did not overlap, nor did the interpolated maps of forest floor and soil properties exhibit similar patterns. In addition, ranges of the variograms differed in some cases by several hundred percent. I attribute this to the lack of correspondence between my scale of sampling and the landscape-level variation of these properties; had I used only a single large plot, I may not have achieved as accurate a characterization of the forest's spatial patterns as I did by spreading my sample plots across the landscape. I would, of course, have benefited from using a larger plot size or more replications. The extra cost associated with increasing the volume of samples, however, precluded this.

There are several avenues for future research in this area. First, the scale of investigation could be expanded. It has long been recognized that there exist several scales of ecological heterogeneity. My study, however, focused on scales of 50 cm to about 50 m. The results of this study (specifically the finding that the size and configuration of resource patches varied from plot to plot across the landscape) suggest that an increase in scale might be appropriate. Along the same lines, a significant amount of autocorrelation occurred at scales smaller than my smallest sampling interval (50 cm). Evidence for this can be found by examining the nugget variance (Appendix 1) of the semivariograms in Figure 2. Future studies could be designed with the goal of capturing variability at a broader range of scales: from the scale of centimeters to the scale of hundreds of meters.

This study has attempted to characterize the spatial patterns in a Coastal Plain pine forest. In addition to lending some valuable insight into the spatial structure of this system, the data are being used to test a model of the temporal dynamics of spatial heterogeneity. In early successional systems, it is likely that relatively small differences in levels of soil resources or that microsite heterogeneity (i.e., patchiness) will have a dramatic effect on a plant community's development via the creation of microhabitats for seed germination and arenas for plant-plant interactions. As vegetation begins to

dominate the site, however, the scale of heterogeneity that is significant gradually increases, and eventually, plant community structure is more influenced by chance environmental events and broader scale, topographical factors. At this point, the vegetation community begins to influence the soil environment, the exact opposite of what occurs in early succession. The results of this study will help test this hypothesis, and hopefully continue to add to the body of knowledge of the effects of ecological heterogeneity.

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APPENDIX 1

To illustrate the steps leading to the production of a variogram, the following generalized example is presented: Assume that a transect has been established across an area of land (Figure 8). Soil sampling locations have been established at 1.0 m intervals. At each sampling location, the value for a soil variable (e.g., pH) has been measured. The semivariance for points that are separated by a distance of h along this transect is given by:

$$\Upsilon = \frac{1}{2n} \sum_{i=1}^{N(h)} (x_i - x_{i+h})^2$$

where Υ is the semivariance value for lag class h , x is the value for pH at point i , h is the distance interval (or lag class) for which the semivariance is being calculated, N is the number of pairs of points separated by distance h , and n is the number of pairs of points used to calculate the semivariance for interval h . In other words, the semivariance is $\frac{1}{2}$ the average squared difference between pairs of values separated by a given distance.

The origin of semivariance lays with a statistic called the moment of inertia (Isaaks and Srivastava 1989, Rossi *et al* 1992). The moment of inertia is basically an index of the spread of points that are plotted on a diagram called an h-scatterplot. An example of an h-scatterplot is shown in figure 9. The moment of inertia is described as:

$$\text{moment of inertia} = \frac{1}{2n} \sum (x_i - y_i)^2$$

where x_i and y_i are the x and y coordinates of each point on the h scatterplot, and n is the number of points. The statistic serves as an index of the amount of variability of the points about the 45° line, hence the use of the $\frac{1}{2}$ in the formula; if the points fell directly on this line, there would be no difference between samples separated by distance h (Isaaks and Srivastava 1989).

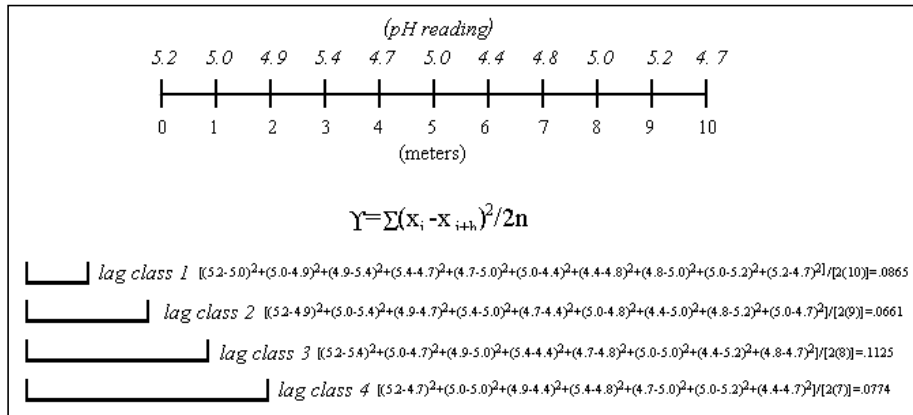


Figure 7. Example of a 10 m long transect at which soil pH measurements were taken every meter. The semivariance for the first four lag classes was calculated below, next to the measurement bars. Each measurement bar represents the distance separating each pair of points used to calculate the semivariance for each lag class.

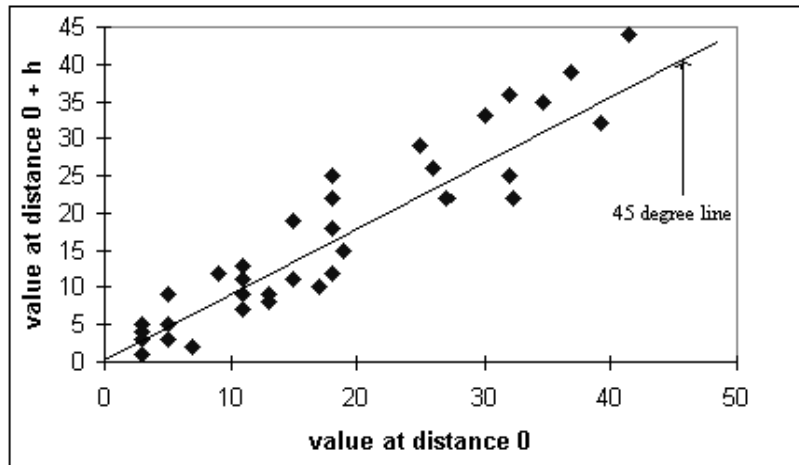


Figure 8. H scatterplot of contrived geographic data. For a given direction, for example N-S, the values for pairs of points are plotted, e.g. for the point at the far right, the value at distance 0 is 42, and the value of variable at distance 0 + h is 44, where h is a given distance class. Note that a point at distance 0 can have several points at distance 0 + h with which it is paired. The average sum of the distances of each point from the 45° line is the moment of inertia.

An idealized semivariogram using contrived data is given in figure 10. A least squares regression line is fit to the semivariance data, and from this model the characterization of the spatial patterns of the phenomenon of interest can be obtained. The range (A_0) is the average distance over which spatial autocorrelation exists, i.e. the samples are not statistically independent of one another. The sill, or C_0+C , is the semivariance value around which the values for lags greater than the range fluctuate. If no trend exists in the data, the sill should approximately equal the sample variance because at distances beyond the range, the samples are no longer autocorrelated, and thus their value is independent of location. The structural variance, or C , is the portion of the model variance attributed to spatial autocorrelation of the phenomenon under study. The nugget, or C_0 , should theoretically be equal to zero (sample pairs that are 0 distance apart should have zero variance). However, nonzero nuggets are common, and indicate either spatial autocorrelation at distances smaller than the smallest lag, or experimental error. Assuming no experimental error, the ratio of structural variance to total model variance ($C:C+C_0$) has been used as an index of the degree of spatial autocorrelation measured by one's sampling scheme (Robertson *et al.* 1997). A ratio of 1.0 would indicate that the sampling scheme measures a high degree of spatial autocorrelation; similarly, a value close to zero would indicate that the phenomenon shows a high degree of spatial dependence at scales smaller than the smallest sampling interval.

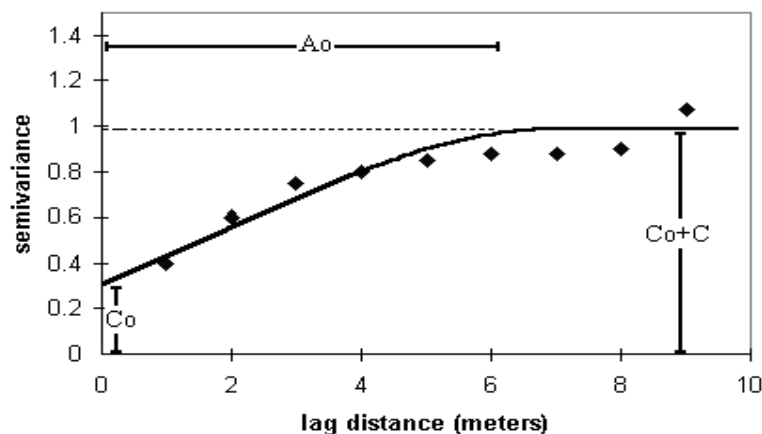


Figure 9. A contrived, idealized semivariogram. The range (A_0) is the distance from the origin at which the semivariogram reaches its sill (C_0+C). The nugget, or C_0 , is the amount of the model variance which is unexplainable due to experimental error or autocorrelation at scales smaller than the smallest sampling interval.

There are certain assumptions of variogram modeling that must be met prior to use, foremost of which is the assumption of stationarity. Non-stationarity of the mean occurs if the average value of a variable changes as one moves across the study area (i.e., there is a trend), and non-stationarity of the variance occurs if the variability of the samples changes as one moves across the study area. These concepts are not clearly defined, and of course are relative to the size of the area within which the mean and variance are calculated. For variogram analysis, non-stationarity of the variance is of little concern, but non-stationarity of the mean needs to be addressed (Jongman *et al.* 1995). Rossi *et al.* (1992) suggested that creating a series of h-scatterplots, one for each lag class, is a method by which one can check for a trend. If the cloud of points does not more or less straddle the 45° line, a trend might exist. A trend can be defined as a pattern whose dimensions are larger than the sampling area (Rossi *et al.* 1992). Hence, if a variogram increases exponentially and never reaches a sill, one should attempt to eliminate the trend. Finally, a first or second order trend surface can be fit to the data; if a significant model can be found, the data should be detrended.

There have been various methods proposed for detrending data. Cressie (1993) discussed a technique called “median polishing”, which leaves residual values that can be used to create the semivariogram. Similarly, Jongman *et al.* (1995) suggested “pre-whitening”, in which the fitted trend surface is subtracted from the data and the residuals are then used as the x_i 's for the variogram calculation.

Other considerations of variogram modeling include non-normally distributed values and anisotropy. Non-normal distributions should be avoided because they might lead to erratic variograms (Jongman *et al.* 1995, Rossi *et al.* 1992). Anisotropy, or the tendency for semivariance to change preferentially in a given geographic direction, can be dealt with by calculating anisotropic variograms. This is done by only including pairs of points in the semivariance calculation which fall along the pre-defined anisotropy axis.

APPENDIX 2

The TDR trace was interpreted by visually determining the location of the inflection point of each waveform produced by the cable tester. The waveform is a visual display of the path of the current pulse leaving the machine, reaching the end of the waveguide, and returning to the machine. From this waveform, one can directly determine the distance value, or $c\Delta t/2$, given by the Tektronix machine, where c is the speed of light in a vacuum ($3 \times 10^8 \text{ ms}^{-1}$) and t in seconds is the transit time of a current pulse sent from the cable tester to the ends of the waveguides and back. The quantity $[(c\Delta t/2)L]^2$ (where L is the length of the waveguide in meters) yields K_a , the apparent dielectric constant of the soil through which the current is passing. In other words, the K_a of soil is basically the ratio of the speed of light to the speed of propagation of an electric current through the rods buried in the soil. The dielectric constant of soil is affected by its moisture content, so Topp *et al.* (1980) derived the empirical relationship between K_a and the volumetric moisture content of several types of soil across several levels of moisture:

$$\theta_v = -5.3 \times 10^{-2} + 2.92 \times 10^{-2} K_a - 5.5 \times 10^{-4} K_a^2 + 4.3 \times 10^{-6} K_a^3$$

The validity of the use of this equation for my soils was tested in the laboratory and confirmed by constructing tubes filled with soil with a known volumetric water content and using the TDR to confirm this value.

VITA

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Andrew Lister was born in Hartford, Connecticut on July 31, 1970. He lived for 18 years in Simsbury, Connecticut, and attended Tufts University in Massachusetts where he had a double major in biology and in environmental studies. After working on Army bases conducting botanical surveys, he joined the Peace Corps, where he worked in Panama for two years conducting community-based environmental education and development projects. After returning from Panama, he again worked conducting botanical surveys until he enrolled in a Master's degree program in the forestry department at Virginia Tech.