

Understanding local and regional plant diversity: species pools, species saturation, and the multi-scalar effects of plant productivity

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ABSTRACT

Joel M. Gramling: Understanding local and regional plant diversity: species pools, species saturation, and the multi-scalar effects of plant productivity
(Under the direction of Robert K. Peet)

The different patterns of plant species diversity that occur at local to regional scales are examined across the southeastern United States. The relationship between the species pool (large-scale community diversity) and local species richness is reviewed to clarify the species pool concept and set the stage for the analyses that follow. Techniques for estimating the species pool are demonstrated using mapped ranges, county records, co-occurrence patterns, and the environmental preferences for woody species in the southeastern United States. Species pool estimates for sites across the region are then compared to the recorded plant species richness at those sites. Species pools constructed from ecological information better predict the patterns of community assembly than pools built from phytosociological data. Local versus regional richness assessments and the productivity-diversity relationship have been the subject of much debate. Local versus regional relationships are investigated for signs of community saturation and resistance to plant invasions. Community saturation is not found to be a major structuring force, but the dynamic between local and regional richness and species invasion is linked to disturbance frequency. The generality of the productivity-diversity relationship is assessed across ecologically-distinct plant communities and by using various methods for estimating plant productivity. Productivity-diversity relationships are shown to vary with respect to how local and landscape assessments of productivity are linked to richness at different scales. Collectively, this dissertation draws

upon new and old techniques to link ecological processes with plant diversity patterns across the southeastern United States. Plant species diversity is revealed to be a multi-scalar phenomenon that cannot be fully addressed by local interactions alone. A set of tools and guidelines is provided to help researchers study complex relationships involving plant diversity dynamics at various scales.

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CHAPTER 1

INTRODUCTION

The determinants of species diversity have been linked to ecological and evolutionary processes at varying spatial scales (Schmida & Wilson 1985). Regional, community, and plot-level studies may provide different insights into the mechanisms responsible for the observed patterns of diversity at each level (Ricklefs 1987). Long-term processes (evolution) and large-scale processes (mass extinction, migration events) may be most deterministic of diversity at the regional or continental scales (Rosenzweig 1995: Ch. 9). At the smallest scales, species-species interactions are thought to determine richness. As the sample size increases from small scales with fewer individuals to larger sample units, environment becomes more strongly correlated with species presence (Reed *et al.* 1993), culminating in the well-known latitudinal gradient in diversity. Throughout this dissertation when plant diversity is addressed at the regional scale reference will generally be to the southeastern United States, and when addressed at the local scale reference will generally be to 0.1 ha or smaller study areas.

This project sets out to ask the broad question of “what determines plant species diversity?” I approach this question at many different scales using a variety of statistical and computational methods. The first objective of this project is to address plant species diversity trends and provide evidence of possible mechanisms that may be responsible for these patterns across the southeastern United States. In response to these observations, several

approaches are presented that quantify the relationships between the observed diversity patterns in plant communities and environmental factors that may result in these patterns.

Initially, the relative contributions of large-scale mechanisms to locally-observed plant diversity are reviewed (Chapter 2). This review provides an introduction to some of the concepts, mechanisms and techniques that will be developed in the analyses that follow. Specifically, it explores the idea of a regional pool of species from which local communities are assembled: *the species pool*. The application of the species pool concept to understanding local species diversity is critiqued in order to clarify the theoretical basis for linking local and regional species diversity. The species pool is not only a concept, but a conceptual tool for investigating ecological processes.

The application of the species pool concept to ecological studies typically requires an estimate of the pool of available species. Several methods have been put forth suggesting how species pools might be constructed (Pärtel *et al.* 1996, Dupré 2000, Ewald 2002), but little has been done to actually link species pools to individual study sites. As abiotic conditions vary across the landscape, one would expect the pool of species capable of occupying different sites across the landscape to vary as well. The actual process of linking pools of species to a set of study sites is demonstrated (Chapter 3). Two general methods of estimating the species pool for a local study site are presented that assign site-specific species pools across a region. Each technique demonstrates the importance of producing a unique species pool that accounts for the specific characteristics of a given locale. The construction of a species pool for ecological analysis can be viewed as the application of “filters” (based upon range and habitat) to a regional flora or list resulting in a subset of the regional species that are capable of arriving at and surviving at a study site (Zobel 1997). The first method of

approximating the woody species pool combines published range maps or county records with the environmental preferences of Southeastern tree species. The second method uses patterns of species co-occurrence to estimate the species pool. Both sets of species pool estimates are compared to actual plot observations. The inclusiveness and exclusiveness of these estimates are quantified (*sensu* Dupré 2000). To provide an intermediate scale between the region and the local study site, range maps were used to estimate the species pools for counties. These mid-scale pools are evaluated using the same metrics as the locally-assigned species pools. Evaluating pool-building techniques at various scales provides insight into their generality and may be a useful tool for addressing ecological processes that are scale-dependent.

Ecological processes at the smallest scales (where individuals interact) may be responsible for the patterns of diversity at much greater scales. Ecological and evolutionary theory asserts that species evolve to maximize exploitation of available resources and that community assembly is a process that leads to the suite of species that optimizes resource exploitation for a particular site. These expectations led Charles Elton to suggest that ecological communities may be saturated with species to the extent that no new species may establish there (1958). One assay of saturation is to examine whether local and regional species richness co-vary in a linear fashion, or whether there is an apparent upper limit to local diversity (Terborgh and Faaborg 1980). The species richness of plots is compared to the size of species pool estimates for those plots to assess linearity. Inferences are made from the observed relationship between regional richness estimates and local richness observations. The degree to which plant communities are saturated with species should be reflected by richness values at multiple scales, and trends in non-native plant occurrences.

The observed relationships between native and non-native richness at the plot level are described for several communities to demonstrate whether the most diverse sites are subject to species invasion. Natural plant communities and anthropogenically-disturbed habitats are compared to provide insight into the relative effects of species invasion and species saturation on observed species richness in the southeastern United States. Scaling is essential to understanding the relationship between species saturation and species invasion: large-scale dispersal by non-native species is weighed against the strength of local competition for niche space.

Plant diversity may be affected by ecosystem function at local (< 0.1 ha) or landscape scales (1 km²). The relationship between plant productivity and plant diversity can be approached at various levels and using various techniques for assessing productivity. The ecological literature on productivity-diversity relationships is highlighted by many studies but little consensus (Waide *et al.* 1999, Gross *et al.* 2000, Mittlebach 2001). A comparison of plot observations from montane upland forests and fire-maintained coastal pinelands is used to test the generality of this fundamental ecological relationship (Chapter 4). Productivity-diversity relationships may result from differences in how productivity was estimated (Groner and Novoplansky 2003). The strengths and weaknesses of several common estimators of productivity are presented with respect to the different ecological processes that may act upon each estimator in the study communities. Analyses are presented that assess the relationship between both locally- and remotely-observed productivity estimates and species diversity at the 0.1 ha scale and below. Specifically, monotonic and unimodal models of the productivity-diversity relationship are tested for each

of the plant communities and across the region. Productivity-diversity patterns may expose different processes occurring at different scales of observation.

This dissertation explores patterns of plant species diversity across the southeastern United States at local, landscape, and regional scales. New and traditional ecological relationships addressing diversity at different scales are explored using novel techniques that draw upon modern and conventional data sources. The tools and techniques exhibited in this document may be applied to other regions or questions beyond the scope of this project. This work demonstrates that plant species diversity is a multiscalar phenomenon that cannot be fully described by local observations or local ecological processes alone.

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CHAPTER 2

THE SPECIES POOL CONCEPT AND PLANT DIVERSITY

Introduction

Linking regional and local diversity

Understanding diversity and the processes that shape it is of great importance to scientists interested in applied and theoretical aspects of ecology. This task has become more complex as researchers have addressed diversity issues across scales ranging from small quadrats (10^{-2} - 10 m^2) to plot-level (10 - 10^5 m^2), local (10^5 - 10^9 m^2) and regional (10^9 - 10^{13} m^2) scales. At the smallest scales where individual organisms directly interact, ecological processes, such as competition, will likely have the most impact on diversity. As the scale of observation increases, the relative contribution of landscape-, biogeographic- and evolutionary-scale processes has a more observable impact on diversity. The cumulative effects of larger-scale processes (in space, time or both) have not always been accounted for in local diversity studies. If such processes are having an impact on diversity that is not readily detectable until a coarser sample size is studied, research focusing on how local ecological mechanisms relate to diversity may be neglecting critical factors. Inclusion of both plot and coarser-scale components may be necessary to adequately address community diversity. In particular, examination of the regional species pool for a local study area provides a better vantage point from which to view the various factors shaping diversity within the local community.

What is a species pool?

The species pool is defined as those species capable of dispersing to and surviving at a given site. Conceptually, the species pool may be envisioned to include the group of species from which a community will be or was assembled. Locally observed species are viewed as members of the species pool that have been filtered by local ecological processes, typically competitive exclusion (Zobel 1997). In practice, the species pool has often been delimited as a subset of the regional flora or fauna (Pärtel *et al.* 1996, Zobel 1997, Dupré 2000).

Researchers attempting to define the species pool for a study area have used two primary criteria: proximity and survival. Regional species have been placed in species pools based upon their ability to disperse to the study area (range-limited pools) or their ability to establish in the study area (habitat-limited pools) (Table 2.1). In the first scenario, species are included based solely upon their proximity to the study area, despite habitat preferences. The application of range-limited pools is not very common in the literature and is more prevalent in studies of animals (Table 2.2: Range-limited). Niche similarities or habitat preferences are used as the decisive factor in designating membership in a habitat-limited pool. Habitat-limited pools focus on the regional species that are known to occur in a given habitat type or establish under a set of abiotic conditions. Most species pools are derived from both dispersal criteria and habitat criteria (see Figure 2.1) where preference for the habitat of a given study site has been inferred from past ecological studies of the habitat (Table 2.2: Habitat-limited 1), species observed within the habitat surrounding the local study site (Table 2.2: Habitat-limited 2) and environmental conditions associated with species occurring in the habitat across the region (Table 2.2: Habitat-limited 3).

The appropriateness of criteria used to designate membership in a species pool will depend upon the ecological question being addressed by the study. Although species pool concepts have been invoked in the context of many observational, experimental and theoretical discussions, a few recurrent topics in ecology are inextricably linked to the idea of a species pool such as community assembly, saturation of communities, and regional influences on local diversity.

Using species pool approaches in the study of plant diversity

For much of the last 50 years diversity studies have focused on experimental treatments and approached species richness as a locally regulated phenomenon. More recently, there has been a shift toward studying species richness as a link between large-scale processes and observed local interactions. Focusing on regional species richness and making multiscalar comparisons of diversity results in a more thorough assessment of the factors responsible for observed richness patterns. Viewing the regional species (or a subset of the regional species) as members of a species pool provides a useful way of bridging local and regional processes.

Species pool membership has been shaped over time by distinct historical and evolutionary forces whose effects might not be discernable at small scales (Ricklefs and Schluter 1993, Ericksson 1993, Pärtel 2002). It has been shown that in a given area or habitat, the pool of available species may be just as significant in determining the potential richness of a study site as the local interactions between species (Taylor *et al.* 1990, Eriksson 1993, Zobel 1997). In some habitats, the competitive interactions among species may be less important for microsite occupancy than a propagule's ability to get there in the first place

(Tilman 1997, Zobel *et al.* 2000, Foster 2001). For these reasons, evaluating the species pool can provide an added dimension in the study of diversity that may not be available when examining local richness alone.

A review of past species pool approaches, terminology and results is presented to provide a conceptual context for future study of species pool phenomena. The idea of a cumulative species pool effect, the advantages of a species pool approach to niche assessment, and the integration of species pools in diversity models are highlighted as important new applications of species pool approaches. These approaches make up a diverse set of techniques relating the species pool to local- and plot-level observations for investigating the determinants of species richness in plant communities. The species pool is explored, not just as a concept, but also as a conceptual tool for evaluating ecological hypotheses.

Established species pool approaches

The species pool hypothesis of Taylor et al. (1990)

Although the terms *species pool hypothesis* and *species pool effect* have been used interchangeably by some authors, I will make a distinction between these terms as a way of focusing on the different ways species pool approaches have been applied in the study of plant communities (Table 2.3). In a narrow sense, the strict species pool hypothesis has evolved from the debate over the observed (and predicted) relationship between productivity and diversity. The species pool hypothesis has often referred to the availability of habitat as a determinant of the species pool, which in turn contributes to patterns of diversity. In a broader sense, species pool effects have become a common way to address the idea that

regional or historical processes that shaped the species pool can be as, or more, deterministic of local diversity than local ecological factors. The species pool hypothesis proposes a correlation between habitat availability and diversity that may be the result of evolutionary or ecological processes over time. The species pool effect is applied to many large-scale processes that may affect diversity. The species pool effect is applied so broadly, that the species pool hypothesis falls under the umbrella of a species pool effect.

Originally, the species pool hypothesis was suggested by Taylor *et al.* (1990) as an alternative theory to Grime's assertion that competitive exclusion is responsible for the low species richness observed in the most productive plant assemblages as explained by the hump-backed model (a unimodal productivity-diversity relationship; see Figure 2.2). In Grime's triangular model of competitors, stress-tolerators and ruderal species (also known as the C-S-R Model), the best competitors are the ones that prevail on the most productive sites via competitive exclusion (Grime 1979, 2001). The triangular model dictates that as disturbance and environmental stress decrease competition becomes more intense. The rationale behind this is that once plant species are free from resource limitation and disturbance (including chronic disturbance such as herbivory), species will only have each other to contend with. Since diversity in these most productive sites has typically been found to be low, it has been concluded that this must be a result of competition. Experimental results have been put forth as confirmation of this relationship (Tilman 1982), but there is some debate over the generality of fertility experiments with respect to natural plant community dynamics (Stohlgren 2002, Stohlgren *et al.* 2003).

Taylor *et al.* (1990) argue that there is no reason to suggest that competition is inherently more intense in highly productive habitats than in moderately productive ones.

Their argument proposes that historically, high-productivity sites may have been few, resulting in a smaller pool of species adapted to these sites. Regardless of competitive effects, local diversity could be shaped by neutral processes where any member of the species pool would have an equal likelihood of being found at a given site (van der Maarel and Sykes 1993, Hubbell 2001). The species pool hypothesis suggests that the availability of habitat over time has shaped the pool of available species adapted to that habitat, which is ultimately responsible for modern patterns of diversity (Taylor *et al.* 1990). While Grime's explanation of the unimodal productivity-diversity relationship required intense competition in high productivity sites, the species pool hypothesis allows for a historical or evolutionary explanation for why the observed diversity at high-productivity sites is often found to be relatively low. This suggestion of a regional-level mechanism for explaining local diversity has engaged other scientists to address the relative contributions of local and regional processes and fueled investigations into other species pool effects.

Tests of the species pool hypothesis

Taylor *et al.*'s species pool hypothesis led to the use of new datasets and techniques to address productivity-diversity relationships at the local scale (ex. *Folia Geobotanica* 36 (1) 2001), although the basic concepts did not originate with their work (see Goodall 1963, and more recently Ricklefs 1987 and Hodgson 1987). One approach to the species pool hypothesis as framed by Taylor *et al.* is to test whether productive habitats have been limited in space or time. Showing that these most productive sites are limited would verify a key assumption of this premise (although failure to do so does not preclude other mechanisms for increased species pools at intermediately productive sites).

Support for the species pool hypothesis could come from consistent correlations between local richness and the historical availability of productive habitats across multiple regions. Unfortunately, estimating the historical extent of habitats is a difficult task complicated by anthropogenic impacts and the limitations of paleoecology. Some authors have worked to approximate the current range and past evolutionary centers of regional habitats as a way of relating factors that are thought to shape a regional species pool (Pärtel 2002, Jetz *et al.* 2004). Viswanathan and Aarssen (2000) observed that current habitat availability explained the disparity between the number of biennial plant species and the number of annual and perennial plant species observed in a localized study. Life history strategies for plant species were linked to disturbance frequency to show that the availability of habitats with different disturbance frequencies could account for observed differences in the richness of each strategy type (biennial, annual or perennial).

The species pool hypothesis is supported by Hodgson's (1987) estimation that productive sites in England are currently more abundant than at any time since the last glaciation. If productive habitats had been relatively limited in England until recent times, few species would be adapted to the most productive sites and as such, the species pool for those sites could be limited providing an alternative explanation for the low diversity observed there. More recently, a meta-analysis of productivity-diversity studies found that high productivity sites were significantly less frequent than sites of intermediate productivity (Schamp *et al.* 2002). These results, however, do not rule out an underlying sampling bias shared by researchers who work on productivity-diversity issues. Sampling of high productivity sites may be limited today due to their extensive use for growing crops or other anthropogenic alterations that would preclude sampling. This may be responsible for a

current limitation in species available for immigration into a productive site, but may not limit the overall existence or historical opportunity for species adapted to such sites.

Contrary to Hodgson, Pärtel (2002) and Ewald (2003) have postulated that the historical availability of high *pH* soils across the Northern temperate zones has resulted in a large species pool adapted to high *pH* sites. Despite the current dearth of high productivity sites (i.e. nutrient-rich, high *pH* sites) in the Northern latitudes, evidence of a rich pool of species adapted to high *pH* sites may be linked to a historical bottleneck that favored calciphiles over the last glacial period (Ewald 2003). Results from non-glaciated sites in temperate North America do not support this hypothesis. Both local richness and species pool size were greatest at high *pH* sites (Peet *et al.* 2003). A large species pool adapted to high *pH* sites may result from plant species finding such sites more amenable due to their intrinsically high nutrient availability. At a local scale, studies have cited a correlation between habitat availability and species pool to explain areas of high productivity with low species diversity (e.g., Schamp *et al.* 2003 and Safford *et al.* 2001). These significant relationships between available habitat and diversity along the productivity gradient reinforce the idea that greater habitat availability allows for a larger species pool, which in turn increases the potential for greater local diversity. More comprehensive studies over larger areas would help to clarify these results.

The species pool may be influenced not only by the availability of habitat in time and space, but also by the relative potential for speciation within a region or phylogenetic group. For this reason, evolutionary factors such as the potential for adaptive radiations or allopolyploidy (Aarssen 2001), and the historical opportunity for reproductive isolation (Ricklefs and Schluter 1993) in a habitat, should be considered. One possibility is that

species may be more evolutionarily inclined to occur in intermediately productive habitats. This could result from a bias toward speciation in moderately productive locations derived from the tradeoffs between adapting to stressful low nutrient sites and more competitive nutrient rich sites. A bias toward speciation in the middle of the productivity gradient would also be expected if more selective pressures are present that result in speciation or if there is a different balance between speciation and extinction along the gradient (Vandermeulen *et al.* 2001). All these mechanisms could result in more species capable of occupying intermediate habitats without requiring evidence for a disproportionately larger area covered by intermediate habitats. A bias toward speciation within or species adaptation to moderately productive sites could lead to greater species diversity in moderately productive sites, thus in an evolutionary sense a validation of the species pool hypothesis does not preclude the humpbacked model (Aarssen and Schamp 2002).

Physical constraints on individuals found in productive sites may be responsible for reducing species diversity on the higher end of the production gradient via a sampling effect. In sites where increased productivity is manifested as an increase in the size of individuals (as opposed to an increase in the number of individuals over the same area), the presence of larger individuals could reduce the number of individuals contained within a local study site of fixed area (Zobel and Liira 1997). When fewer individuals are sampled, there is less likelihood of including as many species. Using computer models Aarssen and Schamp (2002) have demonstrated that the size constraints of species associated with productivity and disturbance gradients could reinforce or possibly contribute to the unimodal relationship observed between diversity and productivity. This supports Oksanen's (1996) suggestion that the observed pattern is not a result of "better competitors" *sensu* Grime, but of equal

competition that results in thinning (density-dependent mortality) which reduces the total number of individuals. As resources become more available along a fertility gradient individuals can become larger increasing the likelihood of density-dependent mortality as overall productivity (i.e. biomass per unit area) increases. Density-dependent mortality can reduce the number of individuals in a given sample area reducing the observed species diversity (Stevens and Carson 1999). Lower species diversity is a result of a sampling effect, instead of interspecific competition. In this scenario, the competitive interactions of individuals drive the loss of diversity along the productivity gradient. No significant interactions between species are expected and thus this is called the “no interaction” model (Oksanen 1996). When samples are assembled randomly from the same species pool, a sample with fewer individuals will on average exhibit less diversity than a sample with more individuals. These studies suggest that the hump-backed model may not be a product of competitive effects, but a result of how species assemble into local communities from the regional species pool.

The species pool effect

Beyond relating observed diversity to productivity of sites (Taylor *et al.* 2000, Grime 1979, Huston 1999, Wisheu and Keddy 1996), the species pool of a specific habitat may be used to explain local diversity regardless of habitat availability. This application of a species pool effect as a broadly used concept pre-dates the term itself. Hints of such an effect can be found in Stebbins’ museum hypothesis (1974), Shmida and Wilson’s (1985) ecological equivalency, and Ricklefs’ (1987) formulations on the contributions of regional processes to local community diversity. Aspects of a species pool effect are also detectable in much

earlier writings on such topics as seed availability and Clementsian community concepts. More recently, the species pool effect has been commonly addressed in three distinct ways: interpreting the effects of regional processes on local diversity; assessing whether a community is saturated with species; and relating the species pool to the process of community assembly (and especially supply-side ecology).

Assessing a regional species pool effect

Assessments of regional species pool effects tend to be wide-ranging studies, which often look for continental or intercontinental trends that may be a part of the fundamental evolutionary or ecological dynamic for the taxa of interest. A comprehensive survey of the regional species pool for an entire taxonomic group is untenable for most researchers, yet such a project would allow for the most comprehensive assessment of the factors that shape local and regional diversity. McPeck and Brown (2000) came close to achieving this in their thorough assay of nearly all damselfly taxa in North America. Natural history references, phylogenetic data and local observational data were interwoven to develop a schema for how different factors may have shaped the species pool. Both adaptive factors (predator avoidance) and non-adaptive factors (reproductive isolation due to genetic drift) were linked to the local diversities of different lakes. This work presents a clear picture of a species pool effect; macro-evolutionary processes at the regional scale are linked to local species richness. Although such thorough life history and phylogenetic information may not be available for larger taxonomic or functional groups, this project provides a good example of how different types of data can be used to assess the relative contributions of regional processes to local diversity. The most notable aspect of their approach is that the mechanisms associated with

the differential occurrence of species are specifically identified and potentially testable in a controlled setting.

An alternative to assessing an entire taxonomic or functional group for a region is to conduct a meta-analysis of how regional processes are linked to local diversity. Pärtel (2002) assessed the relationship between plant diversity and soil pH across six different continents. Diversity and pH were positively correlated when the evolutionary center for the flora was located in a high pH area and negatively correlated when the evolutionary center was located in a predominantly low pH area. This approach typifies how species pool-based hypotheses can be used in meta-analyses of great geographical extent. Similarly, intercontinental comparisons of species pools can be used to interpret the different evolutionary and historical factors that have shaped the regional pools over time, given the unique processes that act upon and within each continent (eg. Li and Adair 1994). Studies focusing on the regional pool of species allow for inquiries into how local diversity relates to the larger-scale processes that shape the regional biota (i.e., the species pool effect) and inter-regional or inter-continental comparisons that focus on the unique evolutionary or historical factors of each region or continent.

Local versus regional diversity, or searches for saturation

Terborgh and Faaborgh (1980) compared the local and regional diversity of Caribbean bird communities and concluded that the local island communities were saturated with species. Specifically, they showed that as regional diversity increased, local diversity increased initially, but then leveled off. When species assemblages are so niche-limited that adding additional species results in the requisite loss of existing species, the community is

considered to be saturated with species and local diversity will be unable to increase despite the availability or immigration of new species from the regional species pool (see Figure 2.3). A significant linear relationship between local and regional diversity would have been considered an indication of proportional sampling as expected from an unsaturated community (Loreau 2000). Terborgh and Faaborg interpreted the curvilinear local-regional richness relationship as a sign of species saturation. This use of the relationship between local and regional richness as a test of whether ecological interactions have resulted in niche-limitation draws from a rich ecological literature. [Charles Elton's (1950) idea of a "saturation point" and MacArthur and Levin's (1967) "limiting similarity" were early and influential expressions of these ideas.]

Many studies have reported findings of saturated and, more frequently, unsaturated communities based upon the linearity or non-linearity of the local-regional richness relationship (see reviews by Cornell 1999 and Srivastava 1999). This topic has also been addressed with respect to the ability of non-native or invasive species to establish themselves in native ecosystems. Most observational studies of the invasion literature suggest that communities are not saturated and demonstrate that higher diversity sites tend to support a greater number of non-native species (Longdale 1999 Stohlgren *et al.* 1999, see reviews by Sax and Gaines 2003, 2005). In contrast to the idea of a species-saturated community where all niches are occupied, scientists are beginning to consider the ecological ramifications of increased diversity because of species invasions (Sax and Gaines 2003).

Methodologically, there is much debate over the legitimacy of testing for saturation from local and regional richness. It has been suggested that results implying saturation may be confounded by the way researchers scale local and regional observations (Loreau 2000).

A number of methodological modifications have been prescribed to improve these analyses (Cresswell *et al.* 1995, Caley and Schluter 1997, Srivastava 1999). Approaches using null models (such as Monte-Carlo randomizations) to gauge the local-regional relationship may have more validity and allow for better hypothesis testing than simply assessing linearity (Pärtel *et al.* 1996, Fox *et al.* 2000, but see Ricklefs 2000). Evaluating community saturation from local and regional richness has been criticized in recent reviews for statistical problems that plague their interpretation (Srivastava 1999, Loreau 2000, Hugueny and Cornell 2000, Valone and Hoffman 2002). Overall, little direct evidence exists to support species saturation as an ecological process occurring in plant communities, while for animals the results are mixed (Cornell 1999).

The species pool and community assembly

The process by which individuals from the species pool populate community assemblages is the most direct way that the regional biota influences local diversity. Thus study of community assembly can aid our understanding of what factors limit local diversity at a site. Across multiple sites such patterns may elucidate “assembly rules” for a given habitat type. Assembly rules are testable hypotheses about patterns of co-occurrence that are often based upon the expected niche limitations and competitive hierarchies in a given habitat. Common assembly rules evoke such phenomena as guild proportionality (where the ratio of species, individuals or biomass associated with guilds or functional groups is consistently observed; Wilson and Watkins 1994) , or checkerboard patterns (where competing species seemingly occupy the same niche, but seldom coexist; Diamond 1975)

Focusing on traits of specific ecological or evolutionary significance may allow for a better understanding of how local interactions may limit diversity. Recently, Tofts and Silvertown (2000) used phylogenetically independent contrasts (PICs) to assess how the functional traits of species found at a study site differed from species in the regional pool not found in the site. Their results suggested that dispersal limitation was the most likely cause for the absence of species. A follow-up experiment took species that were in the species pool, but absent from the study site, and sowed their seeds (and in replicates transplanted individuals) into study plots where congeneric species were already present (Tofts and Silvertown 2002). Again, dispersal limitation was more limiting than competitive effects. The focus of these studies was to uncover the factors that shape community assembly but the results also shed light on a species pool effect.

The role of propagule availability in community dynamics is addressed for ecosystems under the umbrella of “supply-side ecology” (Roughgarden *et al.* 1987). While not a wholly new concept, the integration of propagule availability with the ecological modeling of local interactions provides for a more complete survey of the factors that determine local species assemblages (Underwood and Fairweather 1989). Interannual variability in propagules (such as masting events in trees or current oscillations in the transport of planktonic larvae) is correlated with changes in population structure that may be linked to changes in diversity and community structure over time (Connell and Green 2000). Supply-side ecology highlights this interface between the regional movement of individuals and the processes, that maintain a community. Species coexistence is the result of the two balancing forces: processes that open space in the community (predation and herbivory) and processes that close space (competition and recruitment) (Moore *et al.* 2004). Population-

level studies of immigration and establishment can provide insight into the way members of the species pool differentially gain membership in local communities.

Studying the process of community assembly can link the regional pool to ecosystem function (Foster *et al.* 2004), meta-community dynamics and the re-colonization of fragmented habitats (Butaye *et al.* 2002). In a more applied sense, interpreting how communities were assembled historically has been used as a means by which restoration ecologists may accurately reconstruct the species composition of a site (Zobel *et al.* 1998). Similarly, understanding the process of how natural communities have assembled themselves from the species pool should provide a basis for understanding how invasive species manage to insinuate themselves into native communities. Future work on community assembly should continue to explore the functional traits associated with species occurring in a given habitat type. Relating trait data to the species pool for a given habitat or comparing trait differences between the species pools of different habitats can add further insight into community assembly and should provide hypotheses about species' environmental preferences that can be tested experimentally.

Future directions for species pool approaches

Considerations for designing species pool studies

A number of authors have suggested that species pool-based hypotheses are by nature hard to test and are further complicated by the innate correlation of species pool size and local richness (Herben 2000, Wilson and Anderson 2001, Grace 2001, Leps 2001). While species pool concepts draw upon many ecological and evolutionary processes that are not readily quantifiable, testable hypotheses and models can be derived from these concepts.

Species pool-based hypotheses should be no more difficult to evaluate than other diversity hypotheses (Ericksson 1993) or ecological properties, such as inter-specific competition or limiting similarity. In practice, discrete and testable predictions can be derived from the application of species pool approaches alone or in conjunction with other models of community interaction (ex. Wisheu and Keddy 1996).

Calls for a reformulated set of hypotheses that would allow for more robust, quantifiable predictions of species pool effects (Srivistava 1999, Wilson and Anderson 2001, Zobel 2001) have been met by numerous suggestions as to how the species pool effect can be reframed in a testable manner (Zobel 1997, Zobel 2001, Schoolmaster 2001, Aarsen and Schamp 2002). Zobel (2001) responded by putting forth a “quasi-neutral concept of plant community” where it is suggested that species pool effects be compared amongst similar vegetation layers so that there is no asymmetric competition for light and on a per ramet or individual basis to avoid issues related to size. Zobel’s individualistic approach would sidestep the issue of appropriate plot size, one of the more common criticisms of studies invoking a species pool effect. Several recent studies have used a species per ramet measure of local diversity instead of species per unit area (Zobel and Liira 1997, Liira and Zobel 2000, Lundholm and Larson 2003)

Species per unit area cannot be compared to the observed species pool estimate to show a species pool effect (Herben 2000). As plot size increases or as more plots are averaged together, the observed contributions of regional effects become greater and the observed effects of biotic interactions are lessened (Grace 2001). Identifying the appropriate scales should be a priority for future species pool studies, but will vary on a case by case basis. Multi-scalar, individual-based, or nested approaches may contribute to better

addressing the scale at which to test for a species pool effect. If richness is determined at the smallest sample sizes by the size of individuals, and species interactions and species evenness and at the regional scale by the species pool, then multi-scalar studies could be employed to establish a scale at which the influences of these small-scale factors give way to the contributions of the species pool via more neutral processes.

The manner in which the species pool is estimated can have an impact on the results obtained and their significance to other species pool studies. Some authors have opted to construct species pools using multiple techniques producing several versions of the species pool, which are then each related to local richness patterns or processes. Recent comparisons of species pools have shown that different techniques may be used to build pools which nonetheless result in qualitatively similar relationships between local and regional richness (Winkler and Kampichlea 2000, Safford *et al.* 2001, Witman *et al.* 2004). Viewing the species pool as a fuzzy group where the threshold for membership is varied to provide both strict and loose versions may allow for an evaluation of how robust the observed species pool effect is. At the crux of such a technique will be the justification for why a stricter or looser version of the species pool is ecologically relevant to the hypothesis being tested.

One technique for estimating the regional species pool for communities was demonstrated by Pärtel *et al.* (1996) in which Ellenberg indicator values of different Estonian plant species were related to the observed environmental parameters of each Estonian plant community studied. Ellenberg indicator values provide approximations of environmental preferences for central European plant species, which, for Pärtel *et al.*, provided habitat criteria for delimiting species pools from the Estonian flora. Dupré (2000) explored the advantages of different pool building techniques including six variations on the technique of

Pärtel *et al.* and two pools constructed from the phytosociological literature for Swedish plant communities. Dupré suggested a comparison between a type-1 error and a type-2 error, characterized by the under-representation of locally occurring species in the regional species pool and the overestimation of species capable of occurring at a locality, respectively. The phytosociologically-derived pools were found to best represent the study sites while exhibiting minimal type-2 error.

Numerous techniques for constructing species pools have been suggested in the literature and the field would benefit from a thorough review and cross comparison of their relative strengths and weakness. The most common of these techniques can be categorized as pool-building from plot or sample data. A number of transformations, modeling programs and topic-specific techniques have been used to derive species pools from plot and sample data (Shurin 2000, Winkler and Kampichlea 2000, Safford *et al.* 2001, Butaye *et al.* 2002, Ewald 2002, Valone and Hoffman 2002, Heino *et al.* 2003, Peet *et al.* 2003, Witman *et al.* 2004). It is essential for any species pool approach that the estimation of the species pool incorporates realistic habitat criteria for the study area. For that reason, testing multiple species pool construction techniques on a known dataset may provide insight into what is the best approximation of the species pool for a given area and line of inquiry.

The relative contribution of the species pool

Given that local ecological interactions and regional processes are expected to have a combined effect on regional diversity (Auerbach and Shmida 1987), the best approach to the species pool hypothesis may be to assess the relative contributions of local and regional factors in a multivariate analysis (Grace 1999, 2001). Until recently, few actual case studies

had been conducted that assessed the relative contribution of the species pool to local richness. This may be due to the difficulties associated with species pool estimation and the innate autocorrelation between local richness values and the species pool (Pärtel and Zobel 1999, Grace *et al.* 2000). Safford *et al.* (2001) found the positive contribution of the pool of available species to local diversity to be twice as strong as the negative effects of increasing biomass. Similarly, Gough *et al.* (1994) found that the “potential richness” was most predictive of a site’s local richness across a heterogeneous habitat compared to biomass or environmental characteristics. When a less heterogeneous set of sites was examined, aboveground biomass was found to be more predictive than the species pool. It has been shown that even when biomass is found to be significantly correlated with local richness, only 25% of the overall variance is accounted for on average (Grace 1999). Such results suggest a more comprehensive approach to relating regional and local processes is needed.

The relative contribution of the species pool as an estimator of species availability has often been inferred by assessing its direct relationship to local diversity, although the processes connecting the two can be varied and indirect. Non-resource factors can differentially affect the species pool, biomass, and each one’s relationship with local diversity (Grace 2001). A multivariate approach can incorporate non-resource factors with local and regional diversity and other community properties in a quantifiable manner. Structural equation modeling (SEM) tests hypotheses in a framework that incorporates the relative contributions of factors such as biomass and environmental parameters. SEM is a process by which the relationships between quantifiable variables and latent variables are defined and measured. A model is structured so that variables are connected by direct and indirect pathways. A priori assumptions are built into a model, assessed, and modified or

removed, depending on how well their component variables account for the observed variance. SEM also produces quantifiable estimates of the strength of direct and indirect relationships that likely occur between factors of differing scales that are known to affect plant diversity, which allows for better hypothesis testing.

Modeling species pools using SEM techniques has shown explicitly how environmental factors affecting the species pool can account for more variability in local richness than the direct effects of environmental factors on local richness (Grace *et al.* 2000). The greatest potential from SEM and other multivariate approaches may be in the ability to develop a generalizable model that can be applied to multiple communities for comparative purposes. Such a model has been put forth by Grace and Pugsek (1997) and incorporates the effects of disturbance, abiotic factors, and biomass on richness, but the generality has not been fully confirmed (see Weiher *et al.* 2003). Regardless, the potential for a universal comparative model of the relative contributions of species pool, biomass, and an assortment of environmental factors on local richness has genuine promise. Multivariate techniques, such as SEM, enhance our ability to test hypotheses about the interrelatedness of direct and indirect factors that likely contribute to the observed relationships between the species pool and the local plant community.

Species pools along gradients

By estimating the change in a species pool along an environmental gradient, we gain insight into how and why richness changes with the environment. The observed pool of species along a gradient can be related to the realized niches of its component species. The collective responses of species to an environmental factor should drive the observed

relationship between the species pool and that factor. The variation in the species pool along a gradient will be indicative of how species are sorting out across the landscape with respect to that gradient. This has implications for the availability of niches along an environmental gradient. Using the observed environmental-breadth of species found in a species pool for a given community, a rough assay could be made of the niches that predominate in the community.

Building upon previous work along environmental gradients (specifically the “continuum concept” as modified by Austin and Smith, 1989), I suggest that characteristics of a species pool can be used to interpret the niche differences of its component species. If species have fundamental preferences along gradients that are derivative of their physiological limitations, we should expect to see such preferences reflected in the species pool along these gradients. For example, if most or all plant species share an optimal range for a measured resource, we might expect the species pool to exhibit greater number of species capable of occurring near this optimal range than on the periphery.

Estimation of a species pool along a soil pH gradient was utilized by Peet *et al.* (2003, see Figure 2.4) to test Pärtel’s supposition (2002) that species pools should reflect the soil pH of evolutionary centers around the world. Their results did not reflect Pärtel’s expected relationship between pH and diversity, but instead showed that potential richness and local richness for the region were greatest in more basic soils (Peet *et al.* 2003). This preference along the pH gradient was not being driven by high pH specialists and may indicate a physiological association with the increased availability of soil nutrients for plants at higher levels of pH (which for this regional sampling of plots was $\text{pH} > 4.7$.) Instead of a species pool effect, this richness pattern may simply reflect a physiological bias toward greater soil

nutrient availability. This interpretation is consistent with Pither and Aarssen (2005) who used similar techniques to test the species pool hypothesis for diatom richness with respect to the availability or commonness of different pH conditions for lakes in the northeastern United States. They found a significant relationship between the species observed at a given pH and the commonness of that pH across the region (Pither and Aarssen 2005).

Studying the response of species to environmental gradients is analogous to delineating the habitat of the realized niche (Austin 1985). A species-pool response curve could be constructed that would reflect the collective responses of its component species to an environmental gradient. This species pool response should embody features that reflect the collective realized niches of species pool members. The pattern associated with a species pool response curve may lend insight into the adaptations used by the species along the environmental gradient. The frequency of plant traits associated with specific adaptive characters can be evaluated across the species pool. The distribution of species with adaptive traits along the environmental gradient can be related to the overall response of the species pool along the gradient to evaluate hypotheses of how the niche space is divided up. Finally, experimental studies should be incorporated to demonstrate the link between adaptive traits and the partitioning of niche space along an environmental gradient.

Evaluating a species pool along an environmental gradient can only be useful for comparative studies if the sample of local observations is large enough and adequately represents the environmental variation observed across the study community. Additionally, we might expect to observe different trends for regional species pools along resource gradients versus regulator gradients (*sensu* Austin) as expected for its component species. Incorporating the trends of observed species occurrences (cumulatively as the pool of

available species for a given unit) along gradients with empirical knowledge of physiological preferences or limitations may provide a better understanding of how communities are shaped.

The observed and fundamental species pools

The distinction between the observed species pool and the potential, or fundamental, species pool is critical for the interpretation of experiments or studies (Weiher 1999, Grace 2001). The observed species pool is garnered from species observations collected across the community or region being studied, whereas the fundamental species pool includes the species capable of surviving in the environmental conditions associated with the community. The observed species pool is derived from actual observations of species occurring in the habitat (and by necessity occurring with other members of the species pool), whereas the fundamental pool is derived from information on the physiological tolerance of a species (which may come from observations outside of the target community or region, and often comes from experimental analyses). Weiher (1999) points out that the differences between the observed and fundamental species pools are somewhat representative of underlying realized niche and fundamental niche concepts. The observed pool would be expected to exhibit the limitations of species interactions, whereas the fundamental pool would be shaped by the historical and evolutionary factors of the region (Grace 2001). In communities where niche limitation is not considered a strong structuring force, one might expect the observed pool and the fundamental pool to be similar. In such a case, repeated sampling may show the observed pool to approach the fundamental pool over time.

In certain ecological communities such as grasslands for annual plants or migratory assemblages for birds, annual variation can result in different species composition at a single study site from year to year. Such variability may be an innate part of the community at the study site, but may not be directly attributable to any annual environmental variation or change in niche availability. This type of pattern may occur randomly. With respect to plant species, this phenomenon has been labeled the “carousel model” (van der Maarel and Sykes 1993). In essence, the carousel model suggests, “species move around the community and sooner or later reach every part of the community’s area”. Although in some cases this model may be hard to differentiate from inter-annual variation associated with resource availability or climate, the principle is important for interpreting and estimating species pools.

Species mobility will influence the observed richness in a sample, even for relatively sessile taxa like plants and corals. For a given study site, the aggregated richness observed over time may provide a realistic assessment of the fundamental species pool. This observed species pool could be used to back-check against previous interpretations of the fundamental pool capable of occupying that site. Understanding the temporal nature of a site’s species pool has implications for long-term conservation surveys and monitoring, especially with respect to metapopulation dynamics and habitat connectivity. By incorporating ecological time into species pool analyses, hypotheses made in the past can be tested against the accumulated species observed for a site (as long as temporal niche fluctuation is not a significant factor). It has been demonstrated that as species turnover at the smallest scales is incorporated into the total species diversity for a site, the sampling effect associated with the limitations of studying small-scale richness is reduced and the species pool is better

represented (Fridley *et al.* 2006). In this way, the observed pool becomes closer to the fundamental pool over time. A similar trend may be expected for the observed species pool as the extent over which it is derived increases.

Species interactions associated with niche limitation might be expected to exhibit the greatest impact on the observed species pool in highly localized and small-scale studies. If local interactions are most determinant of local patterns, this effect could be diluted as more samples over a larger range of the habitat are incorporated into observed richness. As the extent (over which the regional pool for a community type is estimated) approaches the full region, so too might the observed species pool approach the fundamental species pool for the region. Practically, this suggests that large-scale surveys may provide a mechanism for estimating the fundamental pool from the observed pool. This premise may be testable across well-studied regions such as central Europe where observed species pools of varying extents could be derived from sampling data and compared to the fundamental species pool as estimated from Ellenberg indicator values or the extensive phytosociological literature for the region.

Summary

The pool of available species for a plant community is shaped by the historical and evolutionary factors of the region. Species pools may represent regional influences when related to local species composition. In addition, relating regional diversity to local diversity can facilitate the detection of larger-scale patterns that are representative of larger-scale processes that can be influential to diversity at multiple scales. A number of species pool approaches for understanding local richness have been used in recent decades as the focus of

ecologists has shifted from studying strictly classical ecological interactions to the incorporation of more large-scale influences on local ecology. The *species pool hypothesis* is a well-developed concept that has received attention by researchers focusing on the specific relationship of how productivity relates to local diversity and whether there is a dearth of species capable of occupying high productivity sites due to limited habitat availability. The *species pool hypothesis* has inspired a great deal of debate over the relative effects of competition along a productivity gradient. Future work utilizing paleoecological references, historical habitat availability, and contemporary habitat availability may allow for a better understanding of whether the species pool for productive sites is limiting local diversity. More broadly, recent studies using a multitude of techniques have addressed richness at a variety of scales to assess whether a *species pool effect* might be observable.

Regional comparisons are improving our understanding of the relative contributions of large and small-scale influences on diversity. Meta-analyses and intercontinental studies using species pools, in particular, facilitate the study of historically or evolutionarily unique trends in diversity at the largest of scales. The use of local versus regional comparisons of diversity to identify species saturation, on the other hand, has not provided a strong body of evidence to support its utility, especially with respect to plant communities. Local-regional interactions have been addressed by developing a thorough understanding of how the pool of available species can be related to a target community or study site, via the process of community assembly. Continued work on assembly processes should focus on specific traits that are involved in a species' membership or exclusion from the local community. As larger trait databases become available, the process of community assembly should become more transparent. By linking plant trait data to occurrence patterns and environmental attributes,

plant ecologists will advance their understanding of assembly rules and allow for traditional concepts of guilds to be tested using phylogenetically or functionally similar species.

Beyond the established applications of species pool approaches to plant community diversity, a number of new approaches may contribute to plant ecology as a whole. The use of structural equation models allows the relative contribution of the species pool to be related to local diversity in direct and indirect ways that are quantifiable and potentially comparable between community types or regions. The use of SEMs may provide a repeatable method for integrating large-scale effects into local diversity models and improve hypothesis testing. Similarly, the analysis of a species pool along environmental gradients can reflect the underlying niche preferences of its component species. Analyzing species-pool response curves may provide a link between regional patterns of diversity and the shared adaptations that allow species to survive in similar habitats. Long-term surveys of plots, especially in habitats where species mobility is common (such as habitats with a large percentage of annual plants), may provide an estimate of the fundamental pool of species for a community or study site. This fundamental species pool might provide a test of the estimated species pool traditionally assigned to a study site. For these reasons species pool approaches should become a primary part of how ecological communities are studied.

TABLES

Table 2.1: Species pools defined

Definitions	
Species pool	Species that are capable of arriving and surviving at a given site
Range-limited pool	Species that are capable of dispersing to the study area in ecological time, regardless of the niche or habitat preferences of the species
Habitat-limited pool	Species in the region that are known to occur in the same habitat type as found in the study area or under the same environmental conditions

Table 2.2: Species pool construction methods

Species pool construction methods applied across the literature. Shading of the table varies according to the type of species pool that was produced.

Reference	Species pool type	Range-criteria	Habitat-criteria	Study organism
Species pools derived from species' proximity to the study area, despite habitat preferences				
Terborgh & Faaborg, 1980	Range-limited	All species on island	None	Birds
Kelt <i>et al.</i> 1995	Range-limited	Biogeographic regions	None	Small mammals
Rickleffs, 1987	Range-limited	All species on island	None	Birds
Bini <i>et al.</i> 2000	Range-limited	All species on continent	None	Viperid snakes
McPeck & Brown, 2000	Range-limited	Eastern North America	None	Enallagma damselflies
Species pools derived from previous ecological surveys of the habitat				
Kelt <i>et al.</i> 1995	Range-limited	Biogeographic regions	Ecological Literature	Small mammals
Tofts & Silvertown, 1999	Habitat-limited 1	50 km x 50 km survey	Ecological Literature	Broad-leaved species
Ewald, 2002	Habitat-limited 1	Biogeographic region	Ecological Literature	Vascular plants
Dupré <i>et al.</i> , 2002	Habitat-limited 1	Swedish forests	Ecological Literature	Vascular plants
Witman <i>et al.</i> , 2004	Habitat-limited 1	Biogeographic region	Ecological Literature	Benthic invertebrates
Species pools derived from species observed in the habitat surrounding the study site				
Duncan <i>et al.</i> 1998	Habitat-limited 2	Forest gap	All species observed within a gap	Vascular plants
Shurin, 2000	Habitat-	Samples within a	Water	Freshwater

	limited 2	region	column samples from lakes	crustacean zooplankton
Winkler & Kampichlea, 2000	Habitat-limited 2	Plot-derived species pool	Species totaled across plots by grassland	Collembola insects
Safford <i>et al.</i> , 2001	Habitat-limited 2	Plot-derived species pool	Species totaled across plots by alliance	Vascular plants
Butaye <i>et al.</i> , 2002	Habitat-limited 2	Species within a 1000m radius	Forest fragments	Vascular plants
Gering & Crist, 2002	Habitat-limited 2	Samples from a tree	Canopy insects	Beetles
Gering & Crist, 2002	Habitat-limited 2	Samples within a site	Canopy insects	Beetles
Gering & Crist, 2002	Habitat-limited 2	Samples within a stand	Canopy insects	Beetles
Gering & Crist, 2002	Habitat-limited 2	Samples within an ecoregion	Canopy insects	Beetles
Valone & Hoffman, 2002	Habitat-limited 2	Plot-derived species pool	Species totaled across all plots	Vascular plants
Heino <i>et al.</i> , 2003	Habitat-limited 2	Plot-derived species pool	Species totaled across samples by region	Macroinvertebrates
Lawes & Obiri, 2003	Habitat-limited 2	Forest gap	All species observed within a gap	Vascular plants
Foster <i>et al.</i> , 2004	Habitat-limited 2	All species observed within 2 km of study area	All species observed within 2 km of study site	Vascular plants
Witman <i>et al.</i> , 2004	Habitat-limited 2	Biogeographic region	Species totaled across plots by region	Benthic invertebrates

Species pools derived from environmental conditions associated with species occurring in the habitat across the region

Partel <i>et al.</i> , 1996	Habitat-limited 3	Estonian flora	Ellenberg indicator values	Vascular plants
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Butaye <i>et al.</i> , 2002	Habitat-limited 3	Species from across study area	Ellenberg indicator values	Vascular plants
Butaye <i>et al.</i> , 2002	Habitat-limited 3	Species within a 1000m radius	Ellenberg indicator values	Vascular plants
Dupré <i>et al.</i> , 2002	Habitat-limited 3	Swedish forests	Ellenberg indicator values	Vascular plants
Peet <i>et al.</i> , 2003	Habitat-limited 3	Plot-derived species pool	pH-groupings	Vascular plants
Pither & Aarssen, 2005	Habitat-limited 3	Plot-derived species pool	pH-groupings	Diatoms

Table 2.3: Species pool approaches

Definitions	
Species pool hypothesis	The availability of a habitat over time has shaped the pool of available species, which is responsible for modern patterns of diversity.
Species pool effect	Regional or historical processes that shaped the species pool determine local diversity.

FIGURES

Figure 2.1: Overview of the species pool concept

An overview of the local species pool is delimited from the regional flora and how it relates to locally observed species. Habitat criteria (yellow) specify a subset of species from across the region that exhibit tolerances of adaptations to the local environment; Range criteria (blue) specify the species capable of getting to the local study site. Local species pool is the intersection of these two sets of criteria, while the locally observed species are a subset of the local species pool that has passed through an ecological filter.

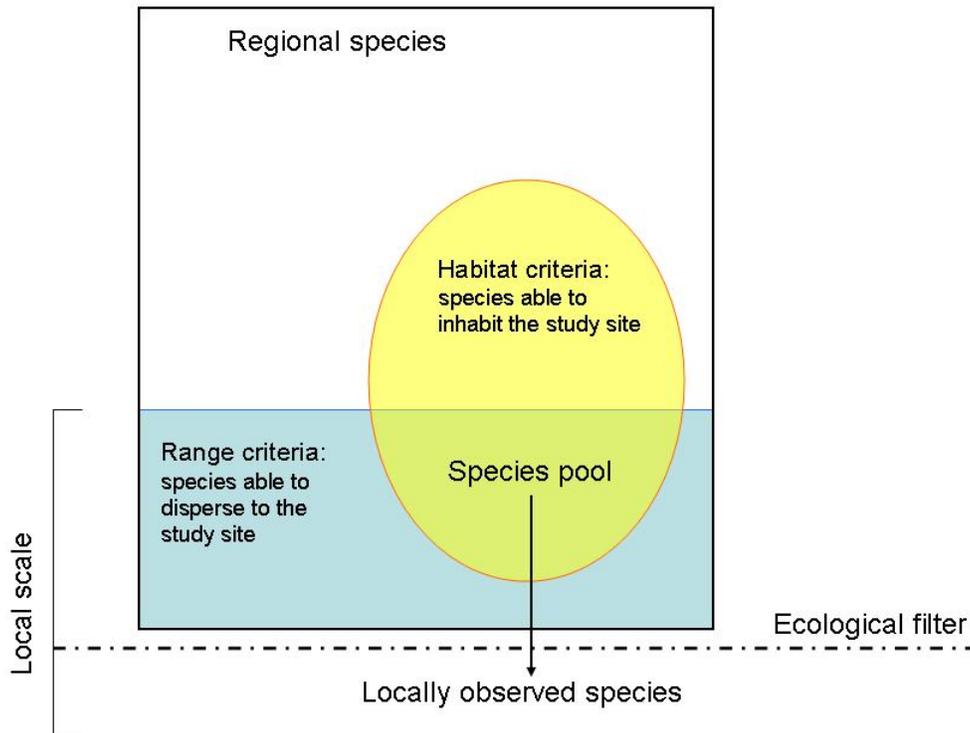


Figure 2.2: Hump-backed model of productivity and diversity

The generalized relationship for productivity and diversity exemplifying the hump-backed model.

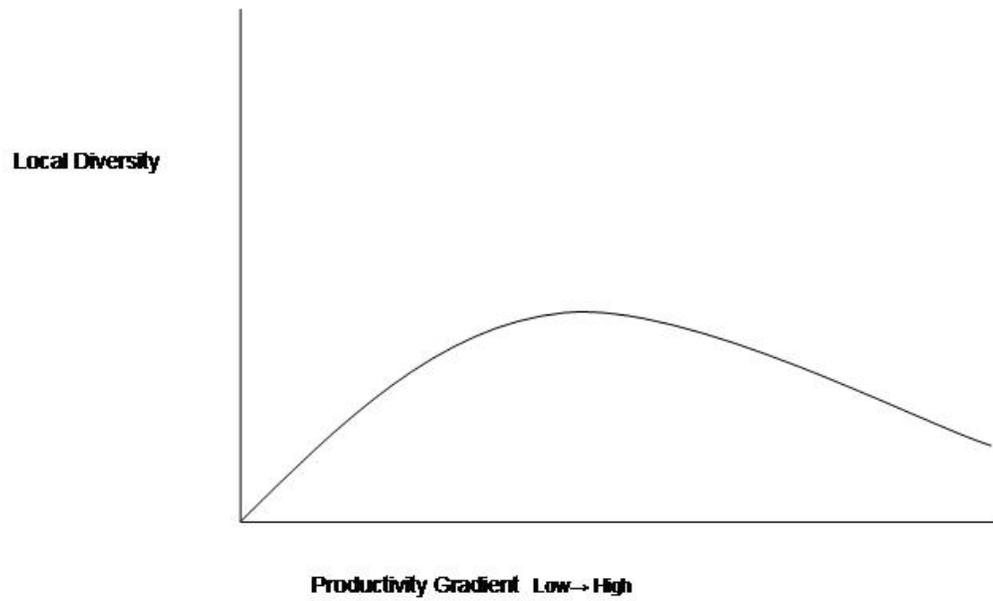


Figure 2.3: Proportional sampling from the species pool

The solid line represents a scenario where the local diversity is a proportional sample of the species pool. The dashed line shows the curvilinear relationship expected from species saturation.

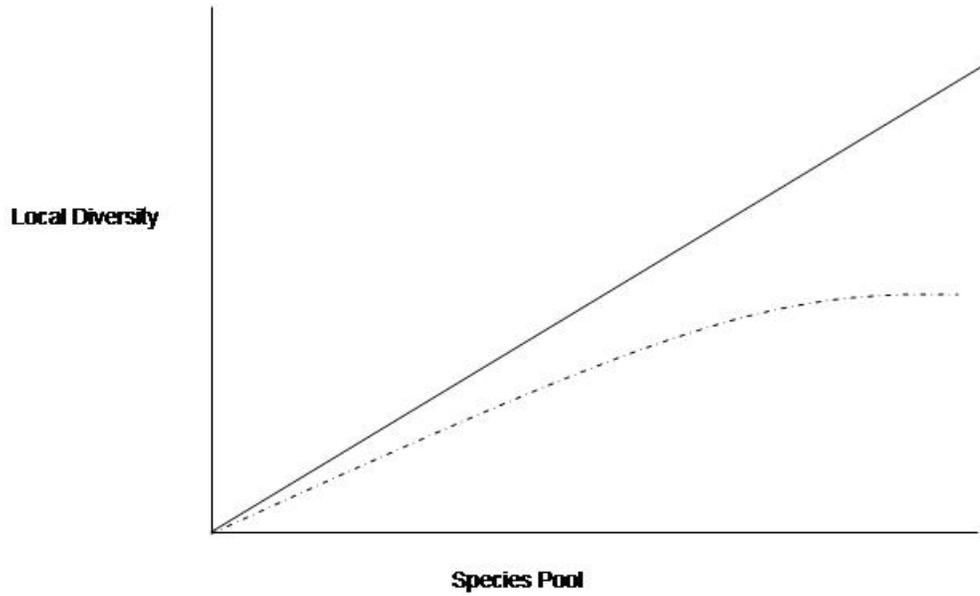
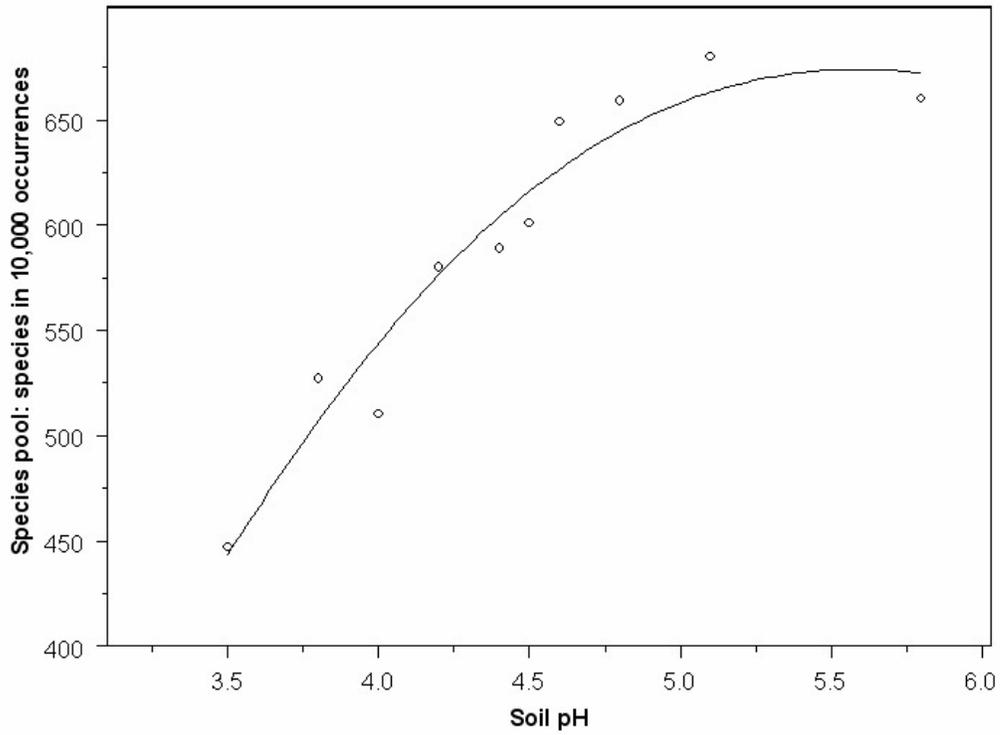


Figure 2.4: The species pool along a pH gradient

The pool of available species for montane forests of the Southern Blue Ridge region (Southeastern U.S.) derived from 100,000 species observations along a pH gradient.



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CHAPTER 3

ESTIMATING THE LOCAL SPECIES POOL

Introduction

Many phenomena observed in community, landscape and evolutionary ecology have been asserted to depend on the pool of species available at a given site. Local biotic interactions and stochastic variability in dispersal can contribute to the absence of species that might otherwise occupy the same site with essentially the same community at other times (Rickleffs 1987). The species pool represents the species within dispersal-distance of the site adapted to the site's ecological conditions. Attempts have been made to estimate the pool of available species from across a region that might populate a given habitat or study area (MacArthur and Wilson 1969, Diamond 1975, Keddy and Weiher 1999). Conceptually, all the species *capable* of occupying a site can be viewed as the species pool for that site. In practice, the determination of which species belong in a species pool is not an easy or straightforward process (Grace 2001).

Ecologists have commonly evoked the concept of the species pool in their studies of species saturation, community assembly and the effects of regional-scale processes on local diversity (see Chapter 2). These approaches have used species pool estimates as a means of linking the variation in large-scale species richness to locally-observed richness or environmental patterns. The application of species pool estimates to understanding plant diversity dynamics may be limited by the uncertainty surrounding the proper construction and evaluation of species pools (Grace 2001; Wilson & Anderson 2001). Different pool

building techniques can produce varied results which may be difficult to compare. A common template for devising species pools is needed to establish a framework for species pool studies and to facilitate comparisons between species pool estimates. Until comparisons between species pools can be made, studies relating species pools to local diversity patterns will be limited in their application to other regions and in their contribution to our understanding of ecological processes.

Local study sites will vary with respect to environmental heterogeneity and the species capable of occupying local sites should be expected to vary as well. Species presence (or absence) at a locality may be the result of how individual species respond to local variation in resource availability (Whittaker 1978). Species checklists and regional floras often do not take into account local variability in the habitat. When a regional flora or list is substituted for a species pool, species may be included despite having very limited ranges or very specific habitat preferences. Such species would be unlikely to occur at most study sites within the region, but would be predicted to occur in the species pool for all the sites. The best way to establish a species pool for a site would involve a series of transplant, introduction and seeding experiments to determine which regional species are capable of establishing and surviving at the site (Zobel 1998; Grace 2001). For most large-scale studies, these experimental techniques are not tenable. An effective non-experimental approach to estimating the species pool for a study site should take into account the fact that a species pool will vary across the landscape as the availability of suitable habitat varies.

Species pool estimates can be linked to individual study sites by assessing the suitability of the habitat with respect to all members of the regional flora within dispersal-distance of the site. This approach produces a continuous variation in the size of the

estimated species pool across the landscape that is reflective of both the availability of propagules and the environmental tolerances of the regional species. To estimate the species pool for a site, criteria for pool membership must be appropriate for the ecological question being addressed and explicitly linked to the ecological characteristics of these sites.

Two primary approaches have been used to assign species pools to localities within a region: the phytosociological approach and the ecological approach. Phytosociological approaches use patterns of species co-occurrence to construct species pools, while ecological approaches use information about how species respond to the environment to construct species pools. Phytosociological approaches assign individual species or groups of species to a site based upon patterns of species co-occurrence derived from community observations. Ecological approaches typically assign species to sites based upon known environmental tolerances of the individual species.

This paper uses a comparative method of species pool construction. Species pools were assigned to study sites and then related to the locally-observed species at each site. Ecological and phytosociological techniques of species pool estimation were used for sites across the region. Multiple sources of habitat and range criteria were combined to produce species pools for each site. A comprehensive overview of the methods used to build species pools is provided to demonstrate the strengths and weakness of using various combinations of pool building techniques and data sources.

Methods

Species pool construction from habitat and range criteria

The delineation of a species pool from the regional flora requires pool membership to be assessed for each species at each site. Criteria for species pool membership can be classified as habitat criteria or range criteria (see Chapter 2). Habitat criteria will reflect our understanding of the environmental conditions that determine plant species' occurrences. Knowledge of the preferred habitats for species is an essential part of predicting species occurrences and species pools (Pärtel and Zobel 1999).

Ecological approaches to species pool construction delineate appropriate habitat by comparing environmental conditions for a site to the environmental tolerances of each potential member of the species pool. Phytosociological approaches use patterns of species co-occurrence to define species pool membership. Whereas ecological approaches derive criteria for occupancy from the direct comparison of species to the known environment, phytosociological approaches link a potential species to other species that find a site inhabitable. The habitat criteria used in phytosociological approaches is indirect. Although ecological approaches to species pool building may be more direct, they are dependent upon choosing environment factors that are relevant to the species ability to occupy the site. In many cases there is limited or conflicting information of what factors determine site occupancy.

In most cases, range criteria should be combined with habitat criteria to produce a refined species pool for a study site. A range criterion may be excluded when a study is addressing how species pools vary across a region under the assumption of uniform species dispersal (e.g., neutral theory, Hubbell 2001); otherwise range criteria offer a useful way to filter out species that cannot get to a given site. In general, the ability of a plant species to disperse to a site may be just as deterministic of local richness as the suitability of the site's

habitat (Zobel *et al.* 2000; Foster 2001). The recent push to make natural history collections available on the web provides searchable sources containing records of species occurrences and ranges that can be used for documenting the distributions of species. Although natural history collections are a promising way to collect information on species distributions, researchers must be wary of the potential for taxonomic errors, sampling biases, and differences in current and historical species ranges (Graham *et al.* 2004). Observational data from natural history collections, horticultural studies, and archived plot surveys (such as those available through vegbank.org) may be combined to produce filters that encompass both the range and habitat criteria necessary to produce realistic estimates of the species pool.

The relative inclusiveness or exclusiveness of the species pool estimates being used should be quantified to assess the appropriateness of a species pool building technique. Dupré (2000) demonstrated that the overestimation and underestimation of species predicted to occur at a site based upon species pool estimates could be derived from the components of Sørensen's index of similarity. Unlike direct comparisons of regional richness values to local richness values, Dupré's error metrics take into account whether or not each predicted species occurrence is corroborated by a local observation.

Species pool estimates can be compared to local plot richness and evaluated for their underestimation of species (inability to predict locally occurring species; Dupré's error type-I) and their overestimation of species (overly predictive of what should occur at a site; Dupré's error type-II). Following Dupré (2000), error type-I and error type-II were calculated as:

Error Type-I = $(1 - c/A) \times 100$ = % of locally-observed species underestimated by the species pool

Error Type-II = $((B-c) / B) \times 100$ = % of predicted species overestimated by the species pool

where A = the number of species observed locally, B = the size of the species pool at a site (i.e. the number of species predicted to occur as at a site), c = number of species accurately predicted to occur at a site (i.e. number of species that are both predicted and observed at a site).

Type-I errors are a more important consideration when evaluating species pool estimates than type-II errors (Dupré 2000). A species pool estimate should contain all the species that occur at the site and other species that are currently absent, but nonetheless are still capable of occurring at the site. Type-II errors may be indicative of overestimating the species capable of occurring at the site, but will also include non-erroneous species predictions that are not borne out by the local observations due to the simple fact that not all species occur everywhere that they are capable of occurring all the time. To deal with this contradiction, innate to species pool construction, it is practical to focus on reducing the type-I error as much as possible. The sum of the type-I and type-II errors may also provide a useful gauge for balancing the tradeoffs between the underestimation and overestimation of species occurrences. This total error, as well as the type-I and type-II errors, can be used to interpret the relative effect of applying different species pool criteria across the same dataset. Dupre's metrics also facilitate comparisons to previously-evaluated techniques (such as Ewald 2002).

An ecological approach to woody species pool construction

A dataset was constructed with 1588 Carolina Vegetation Survey (CVS) plots from across North Carolina, South Carolina, Tennessee, Georgia and Florida. All plots were 0.1 ha in area (20 m x 50 m) and were collected using the methods of Peet *et al.* (1998). The woody species richness was derived from the plot records. The designation of “woody species” used in this study was derived from the species included in the USDA tree maps whose ranges intersected plot locations. Only trees and large shrubs were chosen for this

study so that species pools would be constructed for a single stratum of vegetation. A subset of plots dominated by *Pinus palustris*, longleaf pine (685 plots) and a subset of plots dominated by montane upland forest species (591 plots) were used for this study. Each subset was analyzed separately along with the full dataset as noted below.

Individual estimates of the *woody species pool* were built for each of the 1588 plots. A combination of range and habitat criteria was used to determine whether a tree species should be included in the woody species pool for a given plot. Range criteria were used to assess the ability of a species to get to a plot. Habitat criteria were used to assess the ability of the species to survive under the environmental conditions of the plot. A species had to meet both criteria to be considered a member of the species pool for a given plot. Nine different woody species pool estimates were derived for each plot using ecological habitat criteria. For each species pool estimate, one of three methods of estimating species ranges was linked to one of three methods of estimating species habitat preferences (Table 3.1).

Range criteria

Three methods of applying range criteria to species pool membership were used. The first method integrated distribution maps with plot locations to assign membership. For the second method species observations at the county scale were used to determine whether a species should be considered for a given plot location. The third method combined the information from the first two techniques to produce a more inclusive approach to assigning species pool membership for a site.

Tree map-derived range criteria

Digitized versions of 160 tree maps from the "Atlas of United States Trees" by Elbert L. Little, Jr were downloaded from the USGS website (U.S. Geological Survey, 1999). Only the tree maps that overlapped at least one plot location were included in the study. Although plot records note the occurrence and abundance of all plant species in each plot, this study only makes use of the woody flora that coincides with the 160 tree map species. Using ArcGIS software, plot locations were intersected with the ranges covered by each digitized tree map.

County record-derived range criteria

If the plot and tree species both occurred in a county, then the range criterion was met for that species and it was considered capable of dispersing to the plot. A presence/absence matrix was constructed for each plot based upon county records.

Combined range criteria

This method combines the available information from the two previous methods in an attempt to minimize the underestimation of species occurrences. Using this method plots have two opportunities to be included in a species range. If a plot falls into a species' range according to the digitized range map or based upon county records, the species is considered for species pool membership at that location. This method combines the generality of the range map technique with recorded observations that were made beyond that range's boundary.

Habitat criteria

After meeting the range criteria, each species had to also meet habitat criteria. Three methods of applying habitat criteria to species pool membership were used. A tree species was considered a member of the woody species pool for a plot, when the plot's soil *pH* and annual precipitation values both fell within the minimum and maximum observed *pH* and precipitation values of that species. Soil *pH* and precipitation exhibit strong correlations to plot-level species richness across the dataset (Chapter 4; Brown and Peet 2003; Peet *et al.* 2003). Soil *pH* and annual precipitation requirements were chosen because they are linked to plant nutrient availability, exhibit a strong correlation to species richness and could be obtained from multiple sources.

Each plot location was assigned an annual precipitation value from linking plot locations to a GIS coverage from the Daymet climate model (www.daymet.org). The Daymet modeled data, acquired as 1-km resolution GIS coverage of daily and annual meteorological data, were derived from 18 years (1980-1997) of weather station records and incorporated a digital elevation model. Every plot in the study had 1 or more soil samples collected from the A-horizon layer at the time it was surveyed. The soil *pH* and other chemical properties were measured from these samples. For plots with multiple soil samples, the average *pH* value was taken and assigned to the plot.

USDA habitat criteria

Minimum and maximum values of soil *pH* and annual precipitation were downloaded for each species from the United States Department of Agriculture's PLANTS database (Version 3.5; 12/2005). The database did not have information on 21 of the 160 tree species.

For these species, closely related taxa of the same region were used to approximate their environmental preferences.

CVS habitat criteria

The Carolina Vegetation Survey plot database was used to calculate the observed minimum and maximum values of soil *pH* and annual precipitation. For each of the 160 species, all plot occurrences in the database were queried to find the minimum and maximum observed values for each species.

Combined habitat criteria

This method combines the available information from the two previous methods in an attempt to minimize the underestimation of species occurrences. Species' habitat preferences were based upon the lowest minimum values and the highest maximum values (for soil *pH* and annual precipitation) assigned to a species, regardless of the information's source. The combined habitat criteria thus were more inclusive. USDA information can improve the observed minimum and maximum values for woody species that are under-sampled by the CVS. CVS observations can extend the known limits recorded by the USDA.

Woody species pool construction for longleaf pine forest and montane upland forest subsets

Subsets of plots were created representing the two most-sampled habitat types to investigate differences in species pool estimates assigned to different plant communities. Woody species pools were estimated for each of two subsets. A comparison was made

between the species pool estimates produced for the two habitat types to determine if the same pool-building technique performed equally well for both subsets. The longleaf pine forest dataset included 685 plots covering the southeastern Coastal Plain. The montane upland forest dataset included 591 plots from the southern Blue Ridge Mountains.

Combinations of range and habitat criteria were applied to the two subsets as described above for all plots. Each plot in a subset was assigned 9 woody species pool estimates (Table 3.1). Only ecologically-derived species pools were used in this comparison.

County-scale estimates of woody species pools the using species ranges

Scales greater than 0.1 ha were addressed by estimating species pools for entire counties. The potential woody richness of counties was derived by overlapping range maps onto a GIS coverage of the counties of North and South Carolina. A county by species presence/absence matrix was constructed where “1” values represented the intersection of a tree species’ range with a county. Counties outside of a tree species’ range were assigned a “0” value. Observed woody and total richness values were calculated from county records of plant species provided by the University of North Carolina Herbarium (NCU;). Only range criteria were used to estimate county-scale woody species pools because there was not an available source of data describing the environmental variation of counties. Range-derived species pool estimates for plots were constructed and compared to the county-scale species pool estimates.

A phytosociological approach to woody species pool construction

Species pools have also been constructed from patterns of species co-occurrence (Pärtel *et al.* 1996, Dupre 2000; 2002, Ewald 2003). Since the CVS dataset provides a large sample of species observations, the Beals smoothing transformation was used to convert presence/absence data to probabilities of species occurrences. Beals smoothing uses the known co-occurrences of a plant species with other plants found at a site to estimate the likelihood that it would also occur there (McCune and Grace 2002). The result is a plot-by-species matrix populated by probabilities of species occurrence. The probabilities for occurrences of woody plants in the CVS plots were derived by applying Beals smoothing to a matrix of all 2986 plants observed across the 1588 plots. By including the non-woody species in this process, maximal contextual information was applied to predicting species occurrences. This “smoothed” 1588×2986 matrix was reduced to a 1588×160 (plot by species) matrix. In order to construct species pools from the “smoothed” plot data a probabilistic threshold must be used to determine species pool membership for a given site (Ewald 2002). For example, one can assign membership to all species with a 10% or greater chance of occurrence at a site. A set of species pools with a 10% threshold can then be evaluated and compared to sets of species pools that were derived from 5% and 15% thresholds. For this study, 23 woody species pools were constructed using varying thresholds from 0.5%-95% (see Table 3.4). Range criteria were combined with the Beals-derived probabilities to produce 23 more woody species pools. If a species met the probabilistic threshold (from 0.5%-95%) for occurring in that plot and its range overlapped the plot location, then it was assigned membership in the species pool for that plot.

Application of observational, environmental criteria in species pool construction

Observational environmental data will be affected by site selection, human error and sample size. To account for potential anomalies in the observed environmental criteria, a series of environmental thresholds were applied to the environmental criteria derived from the CVS site data. For each species the total range of variation (difference between observed minima and maxima) was calculated for each environmental attribute. The minima and maxima were then increased and reduced respectively to shorten this range of variation. The data ranges were reduced on a scale from 0.5% to 95% similar to the probability thresholds that were applied to the physiological data. Species pools were then constructed with and without tree map range criteria to assess the reduction in error associated with reducing the range of the environmental criteria.

Comparing woody species pool estimates

Every set of species pool estimates (both ecologically- and phytosociologically-derived) was evaluated for type-I, type-II and total error. The type-I, type-II and total error were calculated for county-scale species pool estimates using county records for the “locally observed species”. These county-level errors were compared to error values calculated from range-derived estimates of woody species pools at the plot-level.

To evaluate species pools produced from multiple techniques, it is important to consider the type-I error, total error (type-I + type-II) and the species pool size. If two pool-building techniques exhibit relatively similar errors compared to local observations, it may be useful to assess the size of the species pool relative to the average number of species in a sample and the total regional flora. If the species pool estimate sums to less than the average number of locally observed species, it will not be very informative for interpreting species

absences. Similarly, if the estimated species pool includes nearly the entire regional flora, it will be limited in its comparisons to local richness.

Each set of plot-level species pool estimates was evaluated using the following formula:

$$SP = \frac{1}{4}(\text{Total Error}/200) + \frac{1}{4}(\text{Error Type-I}/100) + \frac{1}{4}(\text{Mean Local Richness}/\text{Pool Size}) + \frac{1}{4}(\text{Pool Size}/\text{Total Flora})$$

The SP formula accounts for the type-I error, total error, and the relative size of the species pool. SP scales between 0 and 1. A relatively low SP value indicates a pool with a relatively low type-I error value, and a relatively low total error. The formula for SP penalizes a pool for being “too big” (approaching the total flora of the region) or being “too small” (approaching the size of the mean local richness). The use of the SP statistic prevents the selection of an unreasonably large species pool when there are many habitat specialists in the regional flora. It also provides a succinct way to integrate the importance of minimizing type-I error, low total error and a reasonable pool size for comparison with local observations. SP was calculated for every set of plot-level species pool estimates, regardless of origin, and each set of species pools was ranked from lowest to highest SP value.

Results

Species pools are expected to exhibit greater type-II error than type-I error as a result of competitive exclusion, habitat availability or stochastic variation in the environment. Ecologically-derived species pools will be expected to exhibit type-II error due to interspecific interactions. If the ecological criteria for pool membership adequately represent the habitat preferences of the regional species, then differences between the pools and local observations may reflect the effects of competition on species occurrence.

Phytosociologically-derived species pools may exhibit type-II error as a result of unsuitable habitat instead of competition. Interspecific competition should have a greater influence on phytosociological habitat criteria than ecological habitat criteria. Stochastic variability in the environment may result in type-II error regardless of the pool-building technique.

Comparing ecologically-derived woody species pool estimates across all plots

Using ecological approaches, the species pool estimates for all 1588 plot locations tended to overestimate a larger percentage of species than they underestimated; as evidenced (Table 3.2). This is within the general expectations of ecologically-derived species pools and may allow for further analysis of indicators of interspecific competition. The amount of difference between the two error types varied across the 9 different pool-building techniques used. Comparisons of the type-I and type-II errors in Table 3.2 demonstrate the innate tradeoff that comes with estimating species pools. The best technique for minimizing the overestimation of species is not the best technique for minimizing the underestimation of species. In general all of the ecologically-based techniques had a considerably larger percentage of overestimation (average type-II error range of 76.16 – 83.07 across all plots). As discussed above, a species pool should not be penalized strictly for identifying species that might occur, but are not observed at a site. In fact this is one of the aspects of the species pool that is of most interest to ecologists: testing explanations for the observed differences between local and regional diversity.

The percentage of underestimated species varied greatly from one technique to the next (average type-I error range of 1.73-82.77 across all plots). In particular the USDA's habitat data did not facilitate good estimation of species pools (i.e. large type-I errors) across

the southeastern United States. Species pools constructed from the combined range criteria and CVS habitat criteria (Pool Comb-CVS and Pool Comb-Comb in Tables 3.1 & 3.2) exhibited the lowest type-I error, the lowest total errors, and the second and third lowest type-II errors. The next smallest total error and the second smallest type-I error were observed when woody species pools were estimated using CVS habitat criteria and tree maps to delineate range: Pool TM-CVS. When the CVS data is used to delineate habitat preferences, differences between the error values for pools derived mapped ranges and pools derived from mapped ranges and county records (Pool TM-CVS and Pool Comb-CVS, respectively), suggest that the addition of county record information as a part of the range criteria can decrease both the overestimation and underestimation of species.

Comparing ecologically-derived woody species pool estimates for different habitats

Across the longleaf pine and montane upland forest subsets of plots, the error values mirrored the results observed for the total dataset. The only major difference between the longleaf and montane forest subsets was the degree to which woody species were overestimated. Longleaf pine forest plots on average had a greater type-II error (85.4 - 93.81) than across the total dataset (76.16 – 83.07), while montane upland forest plots exhibited a lower type-II error (71.00-74.78; Table 3.2). . This disparity between the type-II errors may result from differences in woody species richness associated with each habitat. In general, longleaf pine forests harbor fewer large woody species than montane upland forests. In this study, the montane plots averaged 60.59 woody species whereas longleaf pine plots averaged 33.7 of the woody species addressed in these analyses. This difference may result

from frequent burns in longleaf habitats that suppress or keep out woody species which might otherwise meet the environmental requirements applied to the species pool.

Comparing range-based woody species pool estimates at different scales

When range maps are used to predict the potential woody richness at the scale of a county, the predictions exhibit considerably less underestimation and less overestimation (Figures 3.1-3.3; Table 3.3) than at the scale of a 0.1 ha plot. This result can be partially attributed to the increased heterogeneity that is often contained within a county's boundaries (mean county area = $1.4 \times 10^9 \text{ m}^2 = 1.4 \times 10^5 \text{ ha}$). The scale of the county is also greater than the scale at which one would expect to observe the effects of interspecific competition.

Unfortunately, there are few studies across the region that sample vegetation between 0.1 ha and $1.4 \times 10^5 \text{ ha}$ to provide an intermediate scale for estimating the species pool. In general the differences between the plot-scale estimates and county-scale estimates suggest that sampling areas $> 0.1 \text{ ha}$ may be useful for relating local species observation to predictions of species occurrence derived from range maps. A sampling effect may be responsible for these differences. Counties contain many more individuals than plots. This increases the likelihood that additional species from the regional flora will be observed. More observed species will produce lower type-II errors and lower total error for the species pool being assessed. The habitat heterogeneity and sampling effects associated with county-size study areas will obscure some patterns of competitive exclusion. Comparing how study sites nested within a county relate to species pools in different ways than the county does, may provide a means for investigating local competitive effects.

Woody species pool estimates derived from a phytosociological technique

Species pools for the 1588 plots that were produced using Beals smoothing technique (*a la* Ewald 2002) can be viewed along a continuum of more inclusive to more exclusive pools (Figure 3.4). When the cutoff for species pool membership is a very small probability of occurrence ($<.05$), a large percentage of the regional flora will be included in the species pool and the type-I error will be low (<1). As larger probabilities of species occurrence are used to build species pools, more species are excluded from the species pool for a given site until no species are predicted to occur there. Type-I errors increase as type-II errors decrease. Figure 3.4 shows the changes in type-I (ascending points), type-II (descending points) and total (connected points) errors associated with more stringent criteria for pool assignment. The lowest total error occurred when the species pool was made up of species with a 15% or greater probability of occurrence in a plot. This species pool had a total combined error of 78.63 with a type-I and type-II error of 15.29 and 63.34, respectively.

When range criteria derived from tree maps were combined with the smoothed habitat data, an even lower total error was observed. When the species pool was made up of species with a 25% or greater probability of occurrence in a plot, total error was reduced to 76.86, but type-I error was 27.72. The addition of the range criteria lowered type-II errors slightly more than it raised type-I errors (Figure 3.5). Figure 3.5 shows the differences between the observed errors from phytosociologically-derived species pools with and without range criteria. Although a lower total error is generally desirable, the high level of underestimation (large type-I error) of the phytosociologically-derived species pools with and without range criteria is a concern. Since most studies that use species pools as a means of relating regional diversity to local observation are interested in the differences associated with overestimation,

high levels of underestimation may create problems with analysis and interpretation. The primary assumption of a species pool is that locally-observed species are nested within the pool. The more this assumption is violated, the less useful the species pool will be for hypothesis testing.

Evaluating the application of observed environmental criteria in species pool construction

Observed environmental criteria were subjected to a series of reductions (thresholds) to minimize the ranges of environmental tolerance derived from species observations in the CVS database. When the ranges between environmental minima and maxima were reduced for the habitat criteria, there was an increase in type-I error that initially outpaced the decrease in type-II error (Table 3.5, Figure 3.6). Total error is lowest when no threshold has been applied, peaks at 65% reduction in the range of environmental tolerance and then becomes lower as the range of tolerance becomes prohibitively small. When species pool built with range and habitat criteria are compared on a scale of reduced environmental tolerance, the combined criteria produce less total error (Table 3.5, Figure 3.7). The addition of range to habitat criteria initially results in a small increase in type-I error, which is offset by a greater decrease in type-II error (Figure 3.7). Reducing the observed environmental tolerance could limit the over prediction of a species whose range was inflated by a single extreme observation, but there was no evidence that even a small reduction in the assigned environmental tolerance accomplished this. Pool TM-CVS with no reduction in its observed ranges of environmental tolerance performed better than any altered version.

Evaluating species pool estimates derived from both ecological and phytosociological methods

Previously, ecological approaches were found to be inferior to phytosociological approaches when compared using Dupré's error measures (Dupré 2000), but my results suggest that ecological approaches perform better. First, many of the phytosociologically-derived species pools are not practical for species pool analyses and can be eliminated if the minimum probability of occurrence used to generate the pool was too great to produce species pool estimates with an adequate number of potential species. As a simple cut off, species pools can be treated as invalid, when the number of woody species in the pool is less species rich than the average number of woody species in a plot. When the probabilistic threshold for species membership was above 35%, the mean species pool size for a plot was less than the 12.79 woody species found in a plot on average. Comparisons were made between 10 phytosociologically-derived species pools (0.5-30% threshold) with range criteria, 10 phytosociologically-derived species pools (0.5-30% threshold) without range criteria, and 9 ecologically-derived species pools using type-I error, total error, SP values and ranks (Table 3.6)

The species pools with the lowest total error were constructed from ecological methods utilizing CVS habitat information and mapped ranges or from phytosociological methods with a minimum probability of occurrence of 15%, or 25% when range criteria were included. When range criteria were derived from both tree maps and county records and then combined with habitat criteria derived from the CVS records or with habitat criteria from the CVS and USDA, type-I error was at its lowest (1.731). These two pools share the same type-I error, because the addition of USDA information was only applied to increase the known

environmental tolerances of species and thus could only add more species to the pool (see Methods). The phytosociologically-derived species pools exhibited their lowest total errors when a 15 to 25% likelihood of occurrence was used. At these thresholds, type-I error is relatively high (15.290-27.715) and pool sizes are relatively small (18.159-28.971). As noted above, the large type-I errors suggest that phytosociological pools may undermine the basic assumption of nestedness between local and regional richness. Thus we can conclude such pools are invalid; if the species pool under-predicts species richness at the site, how could it be an adequate estimate of what could be at the site?

When each set of species pool estimates was evaluated for a low type-I error, a low total error, a pool size greater than the mean local richness and a pool size less than the total flora, the ecologically-derived techniques that utilized CVS habitat information and mapped ranges were found to be optimal (Table 3.6). Species pools derived from those criteria or a combination including those criteria and are ranked 1-4 based upon their SP values (Pools: Comb-CVS, Comb-Comb, TM-Comb & TM-CVS, respectively). A minimum probability of occurrence of 5% produced the best species pool derived from Beals-transformed habitat data and the minimum of 2% produced the best species pool using both the phytosociological information and range maps (ranked 5th & 6th, respectively). Overall, the ecologically-derived pools outperformed the phytosociologically pools. Species pools that were devised based upon observed ecological preferences and mapped ranges best met the conditions of nestedness (low type-I error) without assigning nearly all species to each site (local pool size < regional flora).

Discussion

Techniques for comparing and evaluating species pool construction methods

The estimation of a species pool is a technique for linking species to a common locality based upon patterns of species occurrences or species responses from across the region. A set of procedures should be outlined for the general application of such a technique so that researchers can be more consistent. Guidelines for assigning membership in a species pool must be flexible enough to allow the user to logically follow a line of scientific inquiry; thus, species pool construction may be study-specific in nature. For example, a study investigating the possible effects of competitive exclusion on the maintenance of species ranges may require that species pools are derived solely from known habitat preferences. In such a study it would be beneficial to control for differences in ranges by assuming all species are capable of getting to every site. Species from the same pool (i.e. species sharing the same environmental requirements/tolerances) could then be grown together throughout the region to determine if competitive exclusion reduces fitness or if geographically-related factors lead to decreased species survival. Alternatively, species pools should be the product of our knowledge of both ranges and habitat preferences for species when ecologists attempt to determine the species capable of occupying a site in ecological time. If the species pool is to be used as an estimate of regional richness, criteria for species pool membership must reflect our understanding of how the environment and the distribution of species influence large-scale patterns of species occurrence (and the resulting species richness). Certain ecological processes are most observable at specific scales. When a species pool approach to hypothesis testing is being applied, the criteria for pool membership and the local scale for which the pool is being estimated should fit the scale at which the ecological process of interest are known to occur.

The construction of multiple species pools for the same site provides a useful means of evaluating pool-building techniques. This is achieved by varying the stringency of pool-building criteria or by comparing pool-building criteria derived from different sources. The differences between the species pools and locally-observed ecological attributes (such as richness, guild proportionality or environmental variance) can reveal insights into community assembly and the maintenance of ecological communities (e.g. Wilson 1999, Partel 2002, Goldberg *et al.* 2006). Dupre (2000) and Ewald (2002) have demonstrated different techniques for translating species co-occurrence patterns into phytosociologically-derived species pools. Ecologically-derived species pools were described by several studies that used Ellenberg indicator values as criteria for designating species pool membership (Pärtel *et al.* 1996; Dupré 2000; Butaye *et al.* 2002; Dupré *et al.* 2002). Ellenberg indicator values are based upon the responses of Central European plant species to light availability and soil fertility (Ellenberg *et al.* 1991). Other investigators have designated species pool membership using habitat preferences that were drawn from plot data (Safford *et al.* 2001; Ewald 2002; Valone and Hoffman 2002; Peet *et al.* 2003).

Dupré (2000) systematically compared multiple species pools derived from both ecological and phytosociological approaches. In her study of Swedish grasslands and forests, phytosociologically-derived species pools that were assigned to habitats based upon the regional floristic literature were considered to be superior to species pools derived from Ellenberg indicator values. Considering that these same pools would be later linked to the hump-backed model of richness and productivity (Dupré *et al.* 2002), an ecological pool might have been considered more appropriate than a pool built from phytosociological patterns that likely reflect past competitive interactions. As in this study Dupré concluded

that a pool-building method resulting in slightly higher type-I error may be superior if the pool size is not unrealistically large. Although this and other studies have explicitly addressed the habitat criteria used to derive species pools, the use of range criteria have been limited to inferences based upon species associations.

The comparison of species pool-building methods present here provides several new means by which species pool estimates can be produced and evaluated. Habitat and range criteria were combined to produce sets of species pool estimates that varied in inclusiveness and exclusiveness. In general there is a tradeoff between the inclusivity and exclusivity of species pools. For this reason, it is important that several species pool building-techniques be evaluated before conclusions are made about how a set of species pools relate to local species richness. A broad range of type-I and type-II error values was observed for species pool estimates of 0.1 ha plots located across the southeastern United States. Assessing the total error, combined type-I and type-II error, provides another metric for evaluating species pool estimates. While total error is closely related to Sorenson's index of similarity, it may be more useful for the comparison of species pools where one is evaluating the type-I and type-II errors. Across all of the species pool estimates in this study, the lowest total error values for a set of pools were associated with the lowest type-I errors. In addition to type-I and total error, it is also important that a species pool-building method produces an estimated species pool that is of a useful size. A species pool analysis of local or regional patterns becomes uninformative when the pool is smaller than local species numbers or approaches the size of the regional flora. Evaluating a set of species pool estimates with respect to type-I errors, total errors and pool size may be used as a general method for justifying the stringency of the

species pool criteria used. The SP metric provides a simple approach to assessing how well a set of species pool estimates meet these basic requirements.

Evaluation of species pool techniques

Across the entire dataset, one ecologically-derived set of species pool estimates consistently performed best. The low total error, low type-I error and low SP value suggest that the best ecological pool- building technique evaluated used CVS habitat criteria and a combination of county records and tree maps (Pool Comb-CVS in Tables 3.1, 3.2 & 3.5). When Dupré error values were applied to ecologically-derived pools across different habitat types, type-I error and total error exhibited minimal differences. The average type-II errors were significantly different between the two habitat types (“paired” $t = 16.0911$, $p\text{-value} = 0$). Observed differences in type-II error (overestimation) may reflect the greater likelihood for many hardwood species to be found in montane upland forests than in the coastal pinelands. The longleaf pine habitats of the southeastern Coastal Plain often have a frequent fire-interval (every 5 years or less) that inhibits the establishment of many hardwood species (Frost 2000). In general montane, upland forests burn less frequently and support a greater diversity (mean woody richness of 16.40 species in montane plots and 7.86 species in longleaf plots) and abundance (mean woody cover across all strata is 126.17% in montane plots and 37.04% in longleaf plots) of woody species than is typically found in longleaf pine forests.

Regardless of habitat type, using CVS habitat criteria with a combination of county records and tree maps to delineate range produced the least total error. In general, species pool estimates that used tree maps as a part of the range criteria exhibited significantly lower

type-I errors (9.89 percentage points less on average; p-value = .0001 in a paired t-test) with only slightly greater type-II errors (2.23 percentage points more on average). For the estimation of woody species pools in the southeastern United States tree range maps were effective range criteria. Similarly, habitat preferences that were assigned to species based upon the observed species occurrences throughout the CVS plot database were more effective habitat criteria for species pool membership than the habitat preferences reported by the USDA. Woody species pool estimates derived from the USDA habitat criteria had an average type-I error that was much greater (75.35 percentage points higher) and an average type-II error that was slightly more (3.23 percentage points higher) than the observed errors of CVS-derived species pool estimates. The combined habitat criteria produced species pools that were slightly more inclusive (greater type-II error), but were still very similar to the pools produced from the original CVS habitat criteria. Overall, ecological methods that used observed habitat preferences from the CVS database and range criteria from multiple sources (Pools F & I) did the best job of producing species pools that minimize underestimation while providing a reasonable number of species to compare to local richness (i.e. not too many or too few species to be informative).

Ewald (2002) used modified forms of Dupré's error type-I (underestimation of species) and error type-II (overestimation of species) formulas to evaluate species pools that were constructed using various levels of membership in his analysis of woody plots in the northwestern United States. He demonstrated that as species pools were modeled more restrictively, overestimation decreased but underestimation increased. This was different than Dupré's original observation for ecologically-derived species pool where underestimation varied by method, but overestimation was relatively high for most methods

of species pool construction. Dupré's phytosociological methods were more similar to what Ewald found. The results from the 9 different ecologically-derived techniques are very similar to what Dupré observed from species pools derived from Ellenberg Indicator values. Similarly, the phytosociologically-derived pools in this study mirror the results of Dupré and Ewald. Unlike the work of Dupré and Ewald, this study supports the use of ecological methods of species pool construction over the use of phytosociological methods. This may be related to the better performance of the CVS criteria over the USDA criteria for habitat suitability. The CVS data draws upon a thorough sampling of the study area, while USDA and Ellenberg values are more approximate values applied to the regional flora.

The Beals smoothing technique of pool construction provides a straightforward example of the aforementioned tradeoff between overestimating and underestimating species occurrences in the process of estimating the species pool for a site (Figures 3.4 & 3.5). While the average total error of the 15% probabilistic threshold species pool estimates was lower than any total error from the species pools produced from ecologically-derived habitat criteria, the type-I error was relatively high compared to pools made from other techniques. One problem with the Beals smoothing method of pool-building, is that type-I error will inevitably be reduced as the species pool approaches the total flora. This may lead to the false assumption that the "best" method of pool building will involve the most inclusive technique. If the minimum probability of occurrence is reduced to .01%, the type-I error will be less than 1, but the average species pool will contain 154/160 species. Such an inclusive approach may be no more informative than assuming all members of the regional flora can occur at all sites.

Applying the Beals smoothing technique alone can provide an infinite number of species pools to compare, but it provides little in the way of justification for discerning between pools. If a Beals smoothing technique is being used to assign a regional richness value to a site, then the pool should be evaluated based upon the type-I error, the total combined error and the relative size of the pool. Species pools built from Beals smoothing transformations may allow for the comparison of predicted regional richness to environmental differences from site to site, but this will merely be an inference based upon known species associations. If one is interested in how species diversity varies across environmental gradients it may be more productive to explicitly devise species pools along those gradients (e.g. Grace and Jutala 1999, Peet *et al* 2003). The application of phytosociological techniques may provide an interesting way to compare plant associations across large regions, but may not be appropriate for local estimations of the species pool when ecological methods are available.

Guidelines for selecting a species pool method

It is important to use a pool building technique that is relevant to the ecological question being addressed. If an analysis is testing a hypothesis about the relative effects of interspecific interactions shaping the relationship between local and regional diversity patterns, phytosociological data may be inappropriate. Phytosociological patterns may be the product of species assemblages that have already been filtered by local competitive interactions. On the other hand if an ecological analysis of species pool variation along environmental gradients is the focus of a study, then the use of phytosociologically-derived pools may be useful.

The comparison of ecologically-derived species pools may facilitate the testing of hypotheses of how species relate to their environment. Applying ecological information to the sorting of species into pools can be linked to explicit assumptions about how species relate to their environment. Differences in the relationship between the species pool and locally-observed species can be evaluated and compared for several different ecologically-derived sets of pools. These differences can then be compared to the different assumptions about how species relate to their environment that are explicit in the construction of each set of pools.

While other criteria (such as range limitations) can be combined with phytosociological information, the basic assumptions of why species are associated are numerous and can't be easily gauged. Species pools built from phytosociological techniques will reflect many of the local and regional effects that ecologists are attempting to investigate. By using known associations between plant species to build species pools, patterns of plants' responses to their environment may be obscured. The information in a phytosociologically-derived pool may provide an estimate of regional richness, but the differences among pools will be the results of multiple factors acting upon species separately. Phytosociological techniques attempt to model or replicate the species found at a site, while ecological techniques may be more useful for producing a pool of species capable of occupying a site.

When evaluating the type-I and type-II errors, one must keep in mind that the goal is not to eliminate all "error." It is important to remember that Dupré's type-II error is not necessarily the result of an erroneous prediction. If one were to reduce type-I and type-II errors to 0, the product would be an exact model of the observed local richness. There is an

important difference between modeling species richness and estimating the species pool for a site. As noted above, the species pool is used as an estimate of the species that may occupy a site, but rarely do all species occupy a site at the same time. Species richness models will be designed to mimic local richness, whereas species pool estimates may be most useful when they deviate from local richness. When a species pool estimate is produced, the designer must avoid the trap of trying to replicate the exact species found at a site. While a model that accurately predicts richness would be a useful tool unto itself, the species pool provides a useful foil to local richness or species' occurrence by illuminating the inaccuracies associated with our basic assumptions of what determines species' occurrences.

A well-designed species pool should accurately predict all species found at a site, while suggesting what other species are likely to occur there. Comparing the amount of "overestimation" of species for a site with variations in site attributes, patterns of co-occurrence and the criteria used to assign species pool membership can lend insight into how species actually relate to their environment. Although the species pool concept has been applied broadly, and may have untapped applications, ecologically-derived species pool estimates are most appropriate for addressing local variations across a landscape and are most explicit in their assumptions of how species are interacting with their environment.

Tables

Table 3.1: Species pools constructed from habitat and range criteria

Species pools were estimated using both habitat and range criteria. Habitat criteria were derived from the Carolina Vegetation Survey (CVS) database, the United States Department of Agriculture (USDA)-compiled habitat preferences, or a combination of both (Comb). Range criteria were determined from tree range maps (TM), county records (CR) or a combination of information from both sources (Comb).

Range Criteria	Tree map-derived range criteria	County record-derived range criteria	Combined range criteria
Habitat Criteria			
USDA habitat criteria	Pool TM-USDA	Pool CR-USDA	Pool Comb-USDA
CVS habitat criteria	Pool TM-CVS	Pool CR-CVS	Pool Comb-CVS
Combined habitat criteria	Pool TM-Comb	Pool CR-Comb	Pool Comb-Comb

Table 3.2: Error measurements for plot-level species pools using ecological habitat criteria

Mean type-I error (percent underestimation of locally-observed species), mean type-II error (percent overestimation of predicted species) and total error (sum of type-I & type-II) for species pool estimates of counties: all plots, longleaf forest plots and montane forest plots. Note the lowest errors for each dataset are highlighted. RM indicates that the range criteria were determined from species range maps. CR indicates that the range criteria were determined from county records. Habitat criteria were derived from either the Carolina Vegetation Survey (CVS) database or the United States Department of Agriculture (USDA)-compiled habitat preferences.

Dataset	Extent	Range	Habitat	N	Type I Error
All Plots	NC,SC,TN,GA,FL	TM	USDA	1588	76.12 ± 24.16
All Plots	NC,SC,TN,GA,FL	TM	CVS	1588	3.87 ± 6.80
All Plots	NC,SC	CR	USDA	1224	82.77 ± 19.29
All Plots	NC,SC	CR	CVS	1224	19.28 ± 17.39
All Plots	NC,SC	Comb	USDA	1224	78.25 ± 23.46
All Plots	NC,SC	Comb	CVS	1224	1.73 ± 4.26
All Plots	NC,SC	TM	Comb	1588	3.87 ± 6.80
All Plots	NC,SC	CR	Comb	1224	19.28 ± 17.39
All Plots	NC,SC	Comb	Comb	1224	1.73 ± 4.26
Longleaf	GA,NC,SC,FL	TM	USDA	685	74.04 ± 24.04
Longleaf	GA,NC,SC,FL	TM	CVS	685	1.57 ± 5.16
Longleaf	NC,SC	CR	USDA	363	85.44 ± 17.32
Longleaf	NC,SC	CR	CVS	363	15.19 ± 16.76
Longleaf	NC,SC	Comb	USDA	363	83.62 ± 18.87
Longleaf	NC,SC	Comb	CVS	363	0.57 ± 2.43
Longleaf	NC,SC	TM	Comb	685	1.57 ± 5.16
Longleaf	NC,SC	CR	Comb	363	15.19 ± 16.76
Longleaf	NC,SC	Comb	Comb	363	0.57 ± 2.43
Montane	NC,SC,TN	TM	USDA	591	87.44 ± 15.62
Montane	NC,SC,TN	TM	CVS	591	4.65 ± 5.18
Montane	NC,SC	CR	USDA	549	89.34 ± 12.56
Montane	NC,SC	CR	CVS	549	17.08 ± 13.83
Montane	NC,SC	Comb	USDA	549	86.37 ± 15.87
Montane	NC,SC	Comb	CVS	549	1.29 ± 3.17
Montane	NC,SC	TM	Comb	591	4.65 ± 5.18
Montane	NC,SC	CR	Comb	549	17.08 ± 13.83
Montane	NC,SC	Comb	Comb	549	1.29 ± 3.17

Table 3.2: Continued

Dataset	Extent	Range	Habitat	N	Type II Error
All Plots	NC,SC,TN,GA,FL	TM	USDA	1588	83.07 ± 18.12
All Plots	NC,SC,TN,GA,FL	TM	CVS	1588	80.17 ± 10.73
All Plots	NC,SC	CR	USDA	1224	80.22 ± 20.44
All Plots	NC,SC	CR	CVS	1224	76.16 ± 11.32
All Plots	NC,SC	Comb	USDA	1224	82.33 ± 18.57
All Plots	NC,SC	Comb	CVS	1224	78.94 ± 10.15
All Plots	NC,SC	TM	Comb	1588	81.22 ± 10.13
All Plots	NC,SC	CR	Comb	1224	77.37 ± 10.67
All Plots	NC,SC	Comb	Comb	1224	80.07 ± 9.39
Longleaf	GA,NC,SC,FL	TM	USDA	685	92.00 ± 7.67
Longleaf	GA,NC,SC,FL	TM	CVS	685	87.85 ± 5.48
Longleaf	NC,SC	CR	USDA	363	92.29 ± 9.00
Longleaf	NC,SC	CR	CVS	363	85.41 ± 6.43
Longleaf	NC,SC	Comb	USDA	363	93.81 ± 7.30
Longleaf	NC,SC	Comb	CVS	363	87.27 ± 5.41
Longleaf	NC,SC	TM	Comb	685	87.85 ± 5.48
Longleaf	NC,SC	CR	Comb	363	86.12 ± 6.20
Longleaf	NC,SC	Comb	Comb	363	87.95 ± 5.14
Montane	NC,SC,TN	TM	USDA	591	73.23 ± 23.94
Montane	NC,SC,TN	TM	CVS	591	73.51 ± 9.70
Montane	NC,SC	CR	USDA	549	72.36 ± 25.68
Montane	NC,SC	CR	CVS	549	71.00 ± 9.93
Montane	NC,SC	Comb	USDA	549	74.78 ± 22.93
Montane	NC,SC	Comb	CVS	549	74.63 ± 9.14
Montane	NC,SC	TM	Comb	591	74.27 ± 9.24
Montane	NC,SC	CR	Comb	549	71.72 ± 9.68
Montane	NC,SC	Comb	Comb	549	75.38 ± 8.70

Table 3.2: Continued

Dataset	Extent	Range	Habitat	N	Total Error
All Plots	NC,SC,TN,GA,FL	TM	USDA	1588	157.26 ± 32.35
All Plots	NC,SC,TN,GA,FL	TM	CVS	1588	84.05 ± 11.98
All Plots	NC,SC	CR	USDA	1224	160.97 ± 31.46
All Plots	NC,SC	CR	CVS	1224	95.18 ± 20.74
All Plots	NC,SC	Comb	USDA	1224	158.65 ± 33.14
All Plots	NC,SC	Comb	CVS	1224	80.67 ± 10.77
All Plots	NC,SC	TM	Comb	1588	85.09 ± 11.64
All Plots	NC,SC	CR	Comb	1224	96.65 ± 20.64
All Plots	NC,SC	Comb	Comb	1224	81.81 ± 10.30
Longleaf	GA,NC,SC,FL	TM	USDA	685	165.85 ± 29.03
Longleaf	GA,NC,SC,FL	TM	CVS	685	89.42 ± 7.64
Longleaf	NC,SC	CR	USDA	363	176.61 ± 24.20
Longleaf	NC,SC	CR	CVS	363	99.65 ± 16.20
Longleaf	NC,SC	Comb	USDA	363	177.19 ± 24.27
Longleaf	NC,SC	Comb	CVS	363	87.85 ± 5.84
Longleaf	NC,SC	TM	Comb	685	89.42 ± 7.64
Longleaf	NC,SC	CR	Comb	363	100.36 ± 16.03
Longleaf	NC,SC	Comb	Comb	363	88.52 ± 5.57
Montane	NC,SC,TN	TM	USDA	591	157.74 ± 30.75
Montane	NC,SC,TN	TM	CVS	591	78.17 ± 11.44
Montane	NC,SC	CR	USDA	549	159.49 ± 31.83
Montane	NC,SC	CR	CVS	549	88.08 ± 17.65
Montane	NC,SC	Comb	USDA	549	158.36 ± 30.25
Montane	NC,SC	Comb	CVS	549	75.92 ± 9.92
Montane	NC,SC	TM	Comb	591	78.92 ± 11.13
Montane	NC,SC	CR	Comb	549	88.81 ± 17.78
Montane	NC,SC	Comb	Comb	549	76.67 ± 9.63

Table 3.3: Comparing error measurements for plot-level and county-scale species pools
Mean type-I error (percent underestimation of locally-observed species), mean type-II error (percent overestimation of predicted species) and total error (sum of type-I & type-II) for range-derived woody species pools of counties: all plots, longleaf forest plots and montane forest plots.

Dataset	N	Type I Error	Type II Error	Total Error
County	146	2.01 ± 1.71	38.84 ± 14.52	40.85 ± 14.49
All Plots – TM	1588	3.87 ± 6.80	84.05 ± 8.03	87.92 ± 9.97
All Plots – CR	1224	19.28 ± 17.39	80.35 ± 8.72	99.37 ± 18.97
All Plots - Both	1224	1.73 ± 4.26	83.42 ± 7.13	85.15 ± 7.99
Longleaf - TM	685	1.57 ± 5.16	90.04 ± 4.41	91.61 ± 6.97
Longleaf - CR	363	15.19 ± 16.76	87.74 ± 5.42	101.98 ± 15.52
Longleaf - Both	363	0.57 ± 2.43	89.63 ± 4.22	90.20 ± 4.83
Montane - TM	591	4.65 ± 5.18	79.55 ± 6.63	84.21 ± 9.07
Montane - CR	549	17.08 ± 13.83	76.50 ± 7.67	93.58 ± 15.46
Montane - Both	549	1.29 ± 3.17	80.97 ± 5.89	82.26 ± 6.68

Table 3.4: Error measurements for plot-level species pools using phytosociological habitat criteria

Mean type-I, mean type-II error, and mean total error for species pools derived from Beals smoothing technique with varying smoothing thresholds and species pool derived from combining Beals smoothing with range maps (B&R).

Smoothing Threshold	Type I-B	Type I-B&R	Type II-B	Type II-B&R	Total-B	Total-B&R
95	100	100	0	0	100	100
90	98.90	98.90	0.00	0.00	98.90	98.90
85	95.44	95.44	0.54	0.54	95.98	95.98
80	91.92	91.92	2.14	2.14	94.06	94.06
75	89.63	89.63	4.85	4.85	94.48	94.48
70	87.30	87.30	7.92	7.90	95.22	95.20
65	82.73	82.74	10.39	10.11	93.12	92.85
60	77.25	77.28	13.31	12.52	90.57	89.80
55	71.37	71.43	17.25	15.78	88.61	87.20
50	64.34	64.47	22.70	20.38	87.04	84.84
45	56.30	56.57	28.68	25.70	84.98	82.27
40	48.77	49.33	35.21	31.75	83.98	81.08
35	41.46	42.30	41.02	37.41	82.49	79.71
30	33.97	35.01	46.32	42.72	80.29	77.73
25	26.45	27.72	52.38	49.15	78.83	76.86
20	20.77	22.37	58.19	55.16	78.97	77.53
15	15.29	17.55	63.34	60.23	78.63	77.78
10	10.86	13.67	69.45	66.26	80.31	79.93
5	8.13	11.32	77.65	73.59	85.78	84.91
3	6.36	9.60	81.83	76.97	88.19	86.57
2	4.72	7.99	84.34	78.82	89.06	86.81
1	3.43	6.70	87.38	81.15	90.81	87.85
0.5	3.30	6.59	89.28	82.56	92.57	89.15

Table 3.5: Changes in the observed error of species pools constructed with different environmental thresholds

Mean type-I, mean type-II error and mean total error for species pools derived from environmental observations with varying smoothing thresholds and species pool derived from combining environmental observations with range maps (TM-CVS).

Environmental Threshold	Type I- CVS	Type I- TM-CVS	Type II- CVS	Type II- TM-CVS	Total- CVS	Total- TM-CVS
95	99.59	99.61	12.03	6.63	111.62	106.24
90	98.88	98.92	24.08	17.37	122.96	116.30
85	97.58	97.68	32.43	25.41	130.01	123.08
80	95.27	95.45	41.65	33.80	136.92	129.25
75	92.84	93.09	48.69	39.93	141.53	133.03
70	89.86	90.23	56.72	48.70	146.58	138.92
65	85.20	85.69	62.71	54.95	147.91	140.64
60	79.76	80.38	65.43	58.58	145.19	138.96
55	73.39	74.24	68.72	61.78	142.10	136.02
50	66.23	67.37	71.44	64.33	137.67	131.70
45	58.67	60.10	74.15	66.41	132.82	126.51
40	50.76	52.46	77.16	68.91	127.91	121.38
35	42.50	44.50	79.90	71.53	122.40	116.03
30	35.09	37.44	81.47	73.98	116.56	111.41
25	27.24	29.83	82.53	75.44	109.77	105.27
20	18.56	21.39	83.41	76.73	101.97	98.11
15	11.17	14.22	84.25	77.54	95.42	91.75
10	6.55	9.79	84.92	78.33	91.47	88.12
3	3.67	7.15	85.97	79.65	89.64	86.80
2	2.61	6.19	86.33	80.03	88.94	86.22
1	2.01	5.63	86.45	80.15	88.46	85.79
0.5	1.47	5.15	86.47	80.18	87.94	85.34
0	0.00	3.87	86.40	80.17	86.40	84.05

Table 3.6: Evaluation of species pools using Dupre’s error metrics and SP values

Species Pool	Criteria	Type I Error	Type II Error	Total Error	Pool Size	SP Value	Rank
0.5	0.5	3.300	89.280	92.570	111.589	0.3269	21
1	1	3.430	87.380	90.810	94.352	0.3034	16
2	2	4.720	84.340	89.060	75.540	0.2834	13
3	3	6.360	81.830	88.190	64.567	0.2765	11
5	5	8.130	77.650	85.780	51.801	0.2702	5
10	10	10.860	69.450	80.310	36.645	0.2720	7
15	15	15.290	63.340	78.630	28.971	0.2921	15
20	20	20.770	58.190	78.970	23.781	0.3222	20
25	25	26.450	52.380	78.830	19.569	0.3586	23
30	30	33.970	46.320	80.290	15.602	0.4145	25
0.5 + TM	0.5 + TM	6.586	82.562	89.147	66.756	0.2800	12
1 + TM	1 + TM	6.697	81.153	87.849	61.007	0.2742	9
2 + TM	2 + TM	7.989	78.817	86.806	53.571	0.2718	6
3 + TM	3 + TM	9.600	76.972	86.572	48.656	0.2739	8
5 + TM	5 + TM	11.324	73.588	84.912	41.804	0.2762	10
10 + TM	10 + TM	13.671	66.259	79.930	31.947	0.2840	14
15 + TM	15 + TM	17.553	60.230	77.782	26.049	0.3045	17
20 + TM	20 + TM	22.375	55.155	77.530	21.832	0.3334	22
25 + TM	25 + TM	27.715	49.146	76.861	18.159	0.3698	24
30 + TM	30 + TM	35.013	42.716	77.728	14.562	0.4270	26
TM-USDA	TM-USDA	76.118	83.073	159.190	19.378	0.5845	27
TM-CVS	TM-CVS	3.874	80.172	84.046	63.353	0.2641	3
CR-USDA	CR-USDA	82.767	80.216	162.983	13.914	0.6621	29
CR-CVS	CR-CVS	19.280	76.164	95.444	49.056	0.3093	18
Comb-USDA	Comb-USDA	78.253	82.333	160.586	19.285	0.5922	28
Comb-CVS	Comb-CVS	1.731	78.940	80.671	68.047	0.2585	1
TM-Comb	TM-Comb	3.874	81.223	85.098	67.043	0.2685	4
CR-Comb	CR-Comb	19.280	77.371	96.651	51.650	0.3116	19
Comb-Comb	Comb-Comb	1.731	80.075	81.806	71.708	0.2632	2

FIGURES

Figure 3.1: Type-I error for range-based estimates of woody species pools.

Species pools for 0.1 ha plots were constructed from tree maps (TM), county records (CR), or both (Both). Species pools for counties were constructed from tree maps (County).

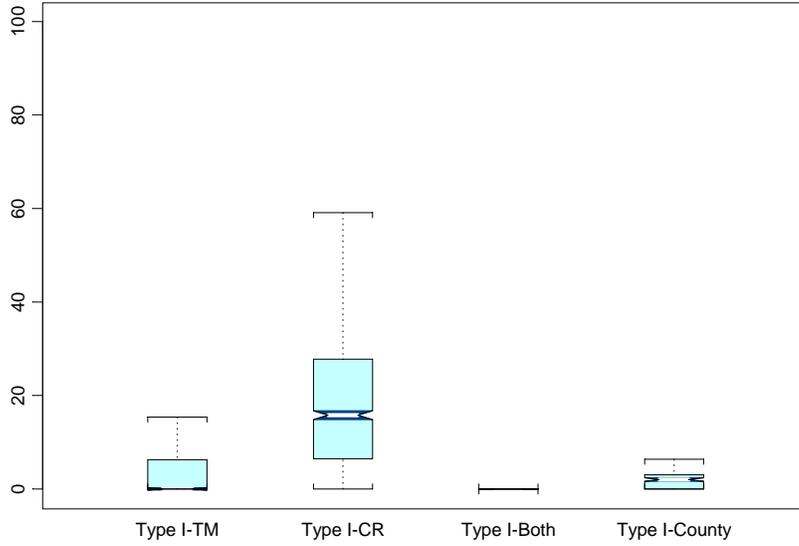


Figure 3.2: Type-II error for range-based estimates of woody species pools

Species pools for 0.1 ha plots were constructed from tree maps (TM), county records (CR), or both (Both). Species pools for counties were constructed from tree maps (County).

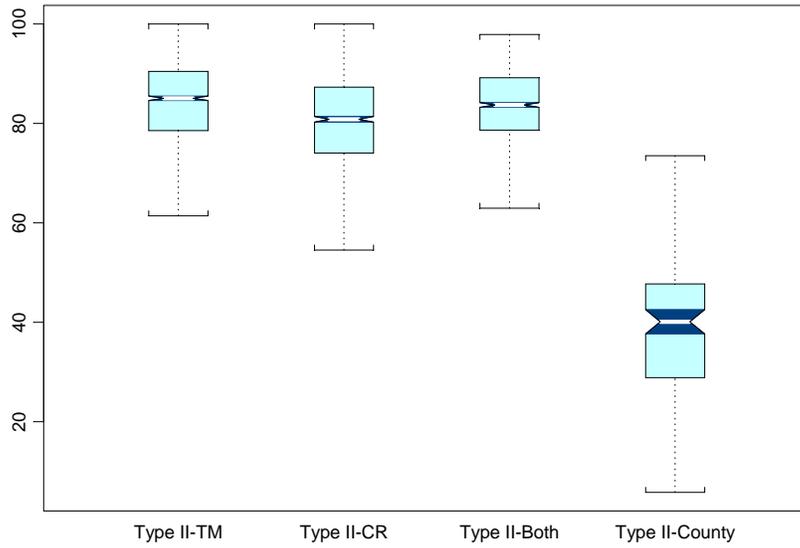


Figure 3.3: Total error for range-based estimates of woody species pools

Species pools for 0.1 ha plots were constructed from tree maps (TM), county records (CR), or both (Both). Species pools for counties were constructed from tree maps (County).

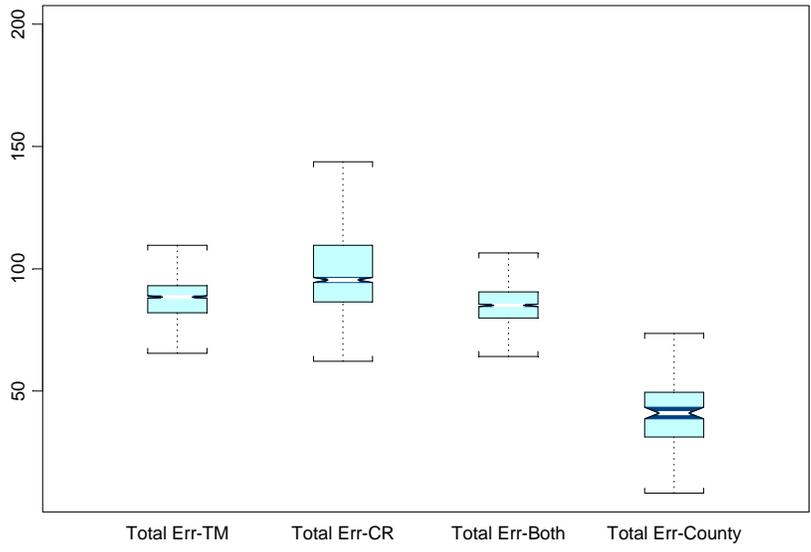


Figure 3.4: Tradeoff between type-I and type-II error for Beals-derived species pools
Type-I (ascending line, ○), type-II (descending line, □) and total error (connected line) for Beals-derived species pools

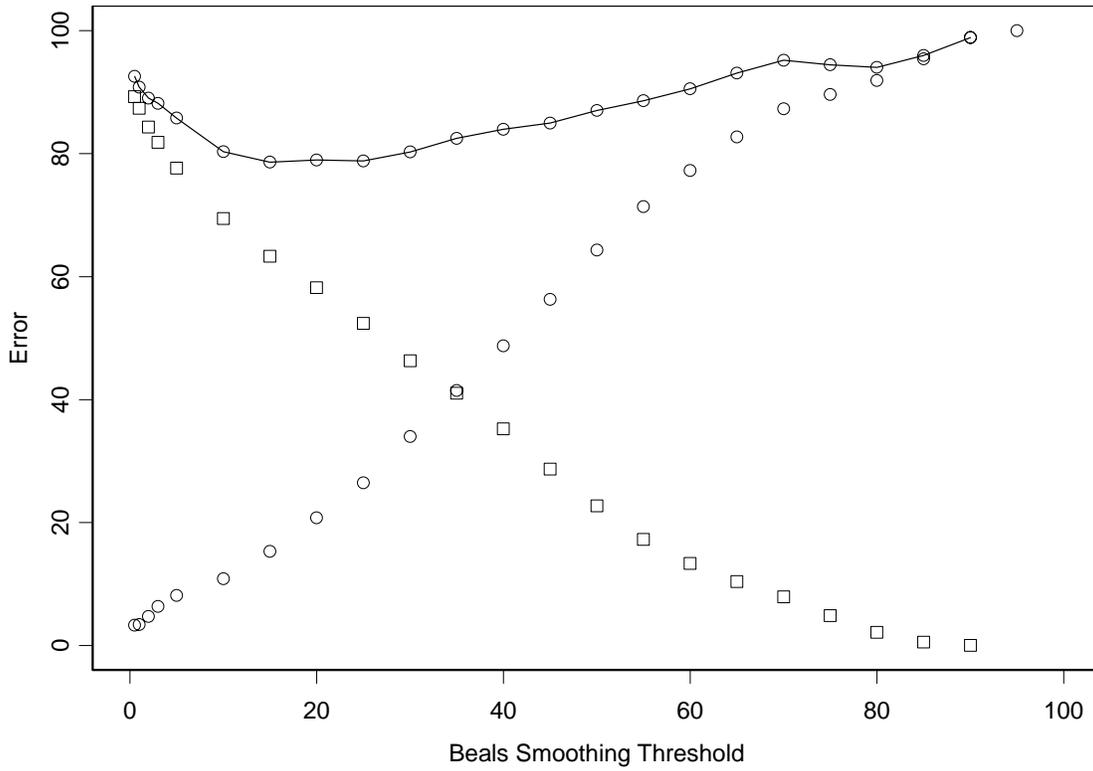


Figure 3.5: Effects of range criteria on Beals-derived species pools

Type-I (ascending line), type-II (descending line) and total error (connected line) for Beals-derived pools (\circ) and Beals-derived pools incorporating species' ranges (\triangle). The reference lines show the total error for species pools B (blue) and F (orange).

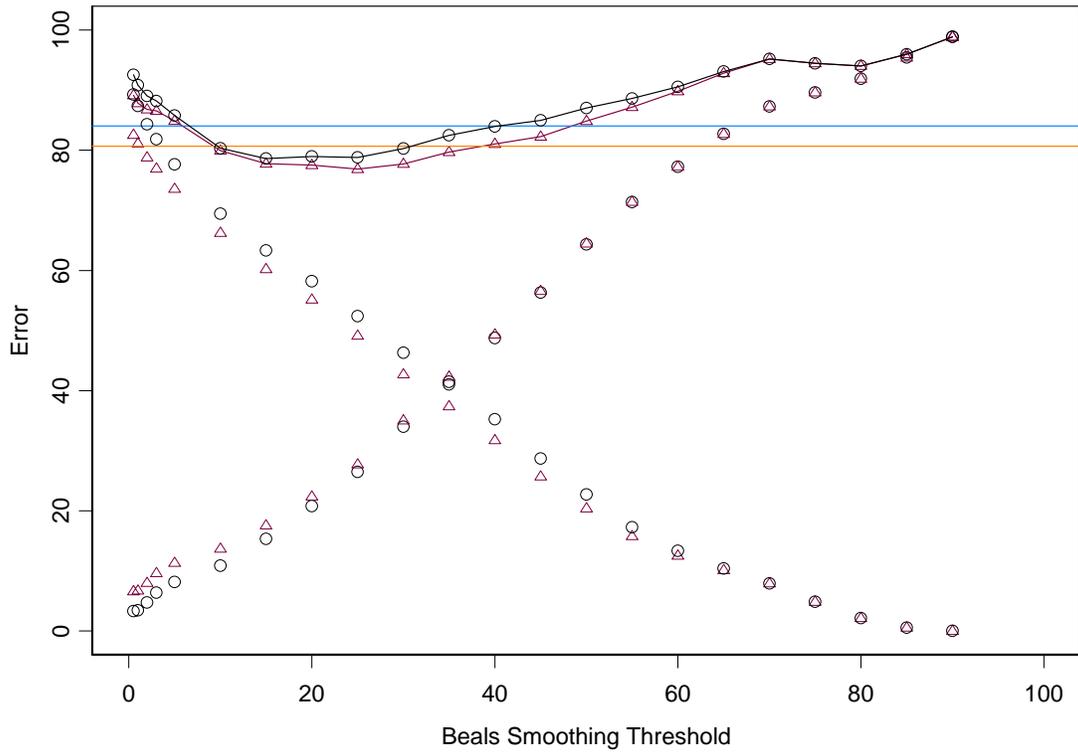


Figure 3.6: Changes in observed error of species pools constructed with different environmental thresholds

Type I (ascending line, \square), type-II (descending line, \circ) and total error (top line, \triangle) for species pools derived from species' range maps and observed environmental data with varying thresholds.

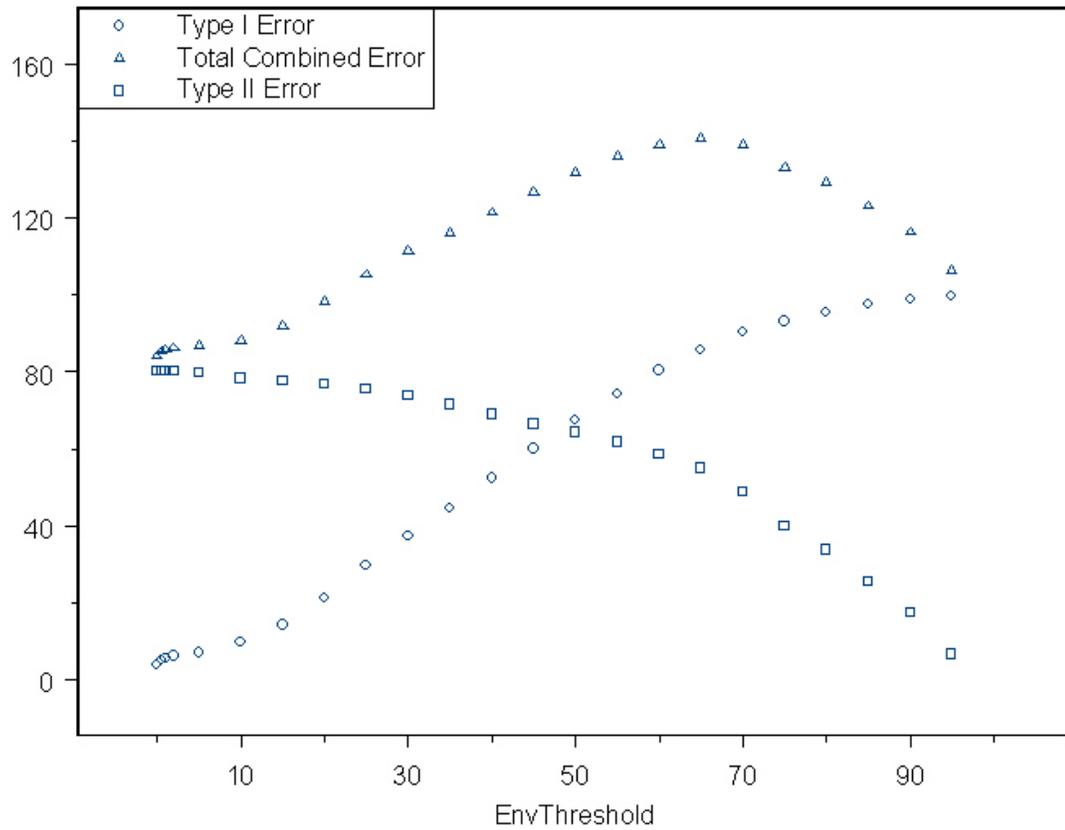
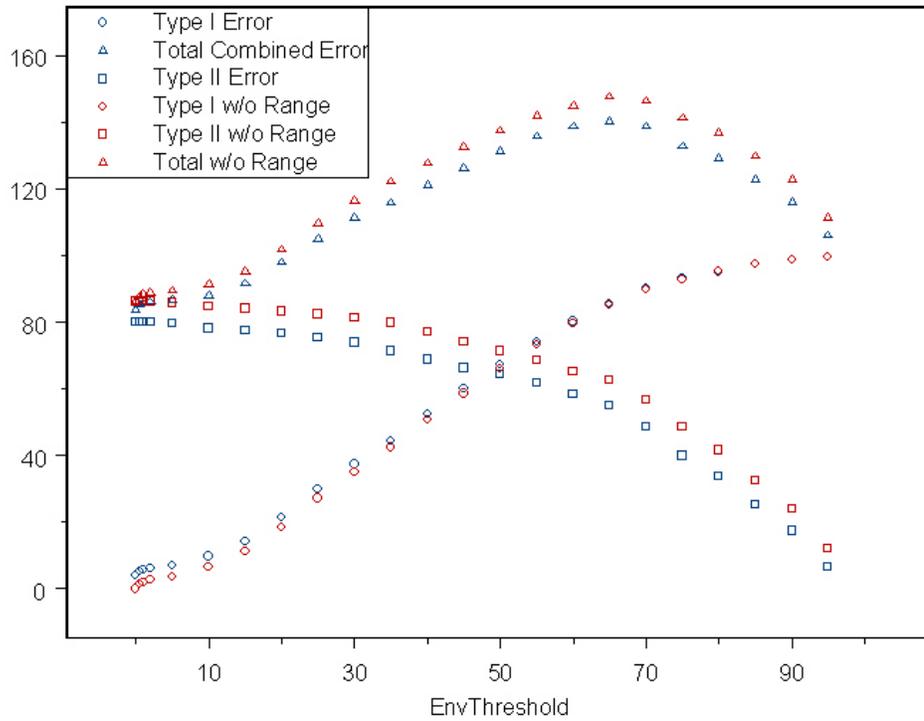


Figure 3.7: Effects of range criteria on species pools constructed with different environmental thresholds

Type-I (ascending line, \square), type-II (descending line, \circ) and total error (top line, \triangle) for species pools derived from species' range maps and observed environmental data with vary thresholds (blue). Species pools derived from observed environmental data without range criteria are also shown (red).



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CHAPTER 4

RELATING SPECIES POOL ESTIMATES TO LOCAL SPECIES RICHNESS: ADDRESSING SATURATION AND INVASION ACROSS THE LANDSCAPE

Introduction

The plant species capable of occupying a given study area can be viewed collectively as the species pool. Species pools are considered a suite of species that have been shaped by similar evolutionary or geological forces; species that co-occur in a particular region may be assigned to an entire region, or sub-region, and be referred to as the regional species pool. A pool of plant species can also be linked to a particular site within the region by assessing the suitability of abiotic site conditions for individual species found in the regional pool (Pärtel *et al.* 1996). Local species pools are then assigned across the landscape using ecological criteria to assess the potential for species occurrences. At the crux of the species pool concept is the potential to define the processes by which members of the regional species pool are winnowed down to a realized local plant assemblage. Local species pools provide a bridge between the regional species pool and local communities.

Comparisons of species pool estimates to local species richness have been used to test hypotheses of community assembly (Tofts *et al.* 2002, Mouquet *et al.* 2003). Biotic interactions may act as a filter selecting or restricting which species from the local species pool actually occupy a given site (Zobel 1997). It has been suggested that communities may become so saturated with species that competitive pressures from those species present will preclude further increases in the species richness of the community (Elton 1958). This idea

of “saturated” communities has been investigated at many scales using experimental and observational data, but remains a controversial topic. The question has taken on particular importance in discussions of the functional significance of biodiversity and the ability of communities to resist invasion of exotic species.

The effects of species saturation have been interpreted from regressions of local and regional richness (Figure 4.1; Terborgh and Faaborg 1980). Proponents of this approach argue that linear relationships are indicative of local communities that are proportional samples of the regional pool. Curvilinear relationships are interpreted as saturated communities (Figure 4.1: dotted line) where local richness is constrained by an upper limit of species diversity despite the availability of more potential occupants in that habitat. The introduction of non-native species by humans may provide modern ecologists the opportunity to test these assumptions.

The invasion of native plant communities by non-native plant species has been widely documented. Many researchers have suggested that species-rich assemblages should be more resistant to species invasion (Naeem *et al.* 2000, Stachowicz and Tilman 2005). Recent work has suggested that species-rich communities are capable of supporting a rich flora of both native and non-native species (Stohlgren 2003). If plant communities are saturated, then they should be resistant to invasive species. If instead, niches are available for colonization, then non-native species may be expected to respond positively to the same environmental attributes that are favorable for native plant species.

For plant assemblages across the southeastern United States, I assess the linearity of the relationship between local species richness and species pool. The correlation between native and non-native richness is used to test the hypothesis that plant communities with

more species are saturated and more resistant to new species than plant communities with fewer species.

Methods

Estimating the local species pool

Estimating the potential occupants of a regional flora for study sites requires a logical formula. Some authors have taken the approach that all species are equally likely to occupy any site within a region, and have then modeled the richness for local sites (Hubbell 2001). However, species pools can be derived from the known environmental tolerances of regional species (Pärtel *et al.* 1996, Dupré 2000). With this approach pool membership is judged by matching the abiotic characteristics of a site to the environmental preferences of species. Each site can then be assigned a species pool that is a unique product of the known needs and tolerances of the regional species to the site's actual conditions.

A dataset was constructed with 1349 plots from the Carolina Vegetation Survey (CVS) collected across North Carolina and South Carolina, plus adjacent counties in Tennessee and Georgia. Plots were surveyed according to the protocol of Peet *et al.* (1998). Species richness was measured at six scales (1000 m², 100 m², 10 m², 1 m², 0.1 m² and 0.01 m²). The total extent of each plot was 0.1 ha.

The species pool was estimated for each of the 1349 plots from across North Carolina, South Carolina, Tennessee and Georgia. Species pool estimates were built by comparing the observed environmental minima and maxima of the 2048 species present in these plots to the environmental conditions of each site. The environmental criteria for site suitability were chosen after an analysis of a nonmetric multidimensional scaling (NMS)

ordination of all 1349 plots indicated the factors which together best explained the distribution of taxa across the dataset. Soil pH, soil organic content, percentage of sand in the soil, average annual precipitation, and elevation were the environmental criteria used to determine site suitability for potential species pool members. Soil pH, soil organic content and the percentage of sand in the soil were derived from the analysis of one or more A-horizon soil samples collected for each plot. Soil samples were analyzed individually, but plots with multiple samples were assigned average values. Elevation and annual precipitation values were assigned to plot locations using GIS. Elevation was derived from a digital elevation model with 1 km² resolution provided to the public by the US Geological Survey's North America Hydro 1K project (http://edc.usgs.gov/products/elevation/gtopo30/hydro/na_dem.html). A GIS coverage of annual precipitation from the DayMet climate model was intersected with plot locations (www.DayMet.org). The DayMet model integrates locally-collected climatological data with satellite information to create a smoothed surface representing the 18-year average annual precipitation (1980-1997). The minimum and maximum values (for soil pH, soil organic content, percentage of sand in the soil, average annual precipitation, and elevation) were assigned to the 2048 species using over 200,000 species observations across the larger set of 4463 plots in the Carolina Vegetation Survey database.

Analysis

Local species richness was modeled with the species pool estimates across all plots using OLS regression with a single linear term and then with a 2nd order polynomial term. The linear and quadratic models were then evaluated based upon an F-test, AIC and

Mallow's " c_p ". The F-test was used to indicate whether the two modeling techniques were significantly different (i.e., whether a curvilinear fit was significantly different from a linear fit). AIC and Mallow's " c_p " were used to determine whether the linear or quadratic model was a "better" or more parsimonious explanation of the data. It has been suggested that when a community is saturated, a negative curvilinear relationship will be observed between local and regional richness. Since, AIC and Mallow's " c_p " were always in agreement only Mallow's " c_p " is reported.

A portion of the total dataset was divided into ecologically-classified subsets (<http://cvs.bio.unc.edu/vegetation.htm> 2003). The largest two subsets are examined in detail: pine-oak woodlands of the coastal plain and northern hardwood forests. The pine-oak woodlands designation includes several *Pinus palustris* dominated woodland types that may include *Quercus laevis*, *Q. margaretta*, *Q. incana*, *Q. hemispherica* or *Q. geminata*. The northern hardwood forests occur in the Southern Appalachian Mountains, primarily as beech gaps, birch-beech forests and high-elevation oak forests. The pine-oak woodlands and the northern hardwood forests were selected because they were the most comprehensively sampled subgroups in the study and comprise plant communities that are geographically, topographically and ecologically distinct from one another. For the processes of species invasion and species saturation, dispersal, disturbance and nutrient dynamics are of particular interest. Pine-oak woodlands exhibit more frequent fire-disturbance which alters nutrient dynamics and biomass accumulation. Northern hardwoods are found at higher elevations and may be expected to exhibit dispersal-limitation for some propagules. Both communities were primarily sampled from managed natural areas in the southeastern United States.

Analyses were conducted at the community-level using the same technique described above for all plots.

Native and non-native plant species designations were derived from the USDA PLANTS database at a state-by-state level. Native and non-native species richness were compared using regressions models. Linear and quadratic models were tested to assess the relationship.

To better address the invasive nature of non-native species, the 1000 m² analyses were also conducted on a set of plots (n=60) collected in forests bordering agricultural fields in North Carolina. Somewhat less than half of these plots began at the field margin and included forest edges, whereas the remainder was from nearby forest interiors. The comparison between local richness and species pool and the correlation between native and non-native species were conducted with and without these “edge” plots.

Results

Local versus regional richness relationship at 1000 m²

The relationship between observed plot richness at 1000 m² and the estimated species pool did not exhibit signs of saturation (Figure 4.2; Table 4.1). The quadratic model was not significantly different from the linear model (p-value = 0.199) and the linear model provides a more parsimonious explanation of the relationship than a curvilinear model (c_p of 767517.1 and 767715.2, respectively). Across the pine-oak woodlands (n=254) and the northern hardwood forests (n=160), the results were similar for 1000 m² species richness and the species pool. For both subsets the quadratic models were not significantly different from the linear models (Table 4.1) and neither indicated a negative curvilinear relationship. Contrary

to a saturated relationship, pine-oak woodlands data were better fit with a positive polynomial term indicating that local species richness was exhibiting greater influence from the species pool as the pool size increased (Figure 4.3). Northern hardwoods data exhibited the same overall patterns as the total dataset (Figure 4.4).

Local versus regional richness relationships at scales less than 1000 m²

The relationship between local species richness and the species pool changes as the scale at which richness is measured decreases (Figures 4.5.1-4.5.5). Across all plots the relationship becomes less linear and more J-shaped, indicating that the plots assigned the largest species pool estimates, were disproportionately richer in species than plots with smaller pool sizes. Across the pine-oak woodland plots the J-shaped relationship was observed at all scales (Figures 4.6.1-4.6.5), but was only found to be significantly different from a straight line when the plot size was 10 m² or less. The northern hardwood plot data exhibit linear relationships between local richness and the species pool estimates. The direction of this relationship changes as the scale of observation decreases. At the 0.01 m² scale the relationship is weakly negative (slope = -0.0001316779), despite being positive at larger scales. This suggests that the northern hardwood communities that are richest in species at the 1000 m² scale have large or well-spaced individuals. These results contrast the pine-oak woodlands where the richest sites at 1000 m² are also the richest sites at finer-scales of observation. This is may be a result of differences in the average size of individual plants within the two community types. Pine-oak woodlands support more graminoid and diminutive herb diversity while northern hardwood forests support a greater diversity of woody species and leafy forbs (see Chapter 3).

Native versus non-native species richness at 1000 m²

Native species richness and non-native species are correlated across all plots (Figure 4.8; $r^2 = .0393$; F-value = 14.71; p-value = 0.00015). This implies that sites that are suitable to support many native species will also support many non-native species. These results and the patterns described above both suggest that natural areas in the southeastern United States are not saturated with species.

Highly-disturbed habitats

When these analytical techniques are applied to disturbed sites, a different set of patterns is observed. The dataset of 60 forest plots neighboring agricultural fields from across North Carolina exhibit a different relationship between local richness and species pool estimates (Figure 4.9). These plots which are located in sites within close proximity to fertilizer and pesticide applications appear to be decoupled from the species pool relationship that is predominant across the natural areas of the region. There is a positive correlation between non-native and native plant species (Figure 4.10), although the average number of non-native species is much greater in these disturbed sites. When non-natives occur in natural areas there are on average 1.93 non-native species versus 8.66 non-native species observed at disturbed sites (Table 4.2). Although the results suggest that natural areas will support more native species and fewer non-native species, the sample of disturbed sites is relatively small and lacks the variety of habitats included across the natural areas that were sampled.

The disturbed sites were divided into “edge” plots and “forest” plots. Edge plots were located in areas that were periodically subjected to biomass removal (mowing or cutting back of brush) by land managers, while the forest plots were not directly affected by land management. Edge and forest plots exhibit similar linear relationships between native and non-native species as the entire set of disturbed plots, although the edge plots generally supported more non-native species (Figure 4.10; Table 4.2).

Discussion

The relationship between local species richness and species pool estimates observed across plots in the southeastern U.S. is not indicative of species saturation. Larger species pool estimates are consistently associated with greater species richness. There was no evidence of saturation, and when the relationship appeared nonlinear the trend was an upward bend rather than a decline with richness. This relationship directly contradicts the idea that communities may have an upper limit on local species richness due to local ecological processes.

At scales less than 1000 m² one might expect the local ecological processes associated with saturation to be most pronounced because of similar abiotic conditions and direct competitive interactions. There is a strong indication of saturation occurring at smaller scales. However, plots across the region exhibit a strong relationship between large species pool size and local richness, even at fine-scales. This is likely driven by the prevalence of species-rich longleaf pine communities such as the pine-oak woodlands presented here. Longleaf pine communities are frequently burned and can support very high small-scale diversity, especially amongst graminoids and small herbs. Northern hardwood forests are

characterized by more canopy cover, more accumulation of woody biomass, and larger individual plants. These factors may contribute to the deterioration of the positive local richness-species pool relationship as the scale of observation decreases.

The relationship between native and non-native richness as observed in natural and disturbed habitats (Figures 4.8 & 4.10) indicates that indeed the “rich are getting richer” (Stohlgren 2003); the species-rich areas are more prone to invasion, rather than less. However the question of whether natural species will continue to thrive in the presence of non-natives remains unanswered. In the short-term native species should continue to survive, but in the long-term non-natives may result in competitive exclusion driving down native diversity. The analyses of disturbed forest habitats along agricultural margins indicate that the effects of human land-use may be altering the fundamental relationship between local and regional processes. The results show that the relationship between species richness and abiotic factors (as represented by the species pool estimates) is different in anthropogenically disturbed sites with greater non-native species occurrences than in natural areas. This difference suggests that the processes by which plant species relate to their environment are altered by human disturbance and such disturbance may favor the establishment of non-native species. As site suitability becomes less connected to the regional species pool, the ecological and evolutionary processes that the regional flora has become adapted to may be irrevocably altered. The current influx and increase in non-native species is likely caused by these changes. Future plant assemblages are likely to become increasingly a product of anthropogenic activities rather than a local subset of the pool of species that originally evolved to survive in the region.

TABLES

Table 4.1: Comparison of linear and curvilinear models of local and regional richness
 Model-terms are in bold print to indicate the most parsimonious model selected using c_p . * indicates a significantly better fit for the model with p-value < 0.05; ** indicates significance with p-value < 0.005.

Plots	Scale	Model-terms	Sign	F-test	p-value	c_p
All	1000 m ²	Linear	+	1.651	0.199	767517.1
All	1000 m ²	Polynomial	+			767715.2
All	100 m ²	Linear	+	1.747	0.186	347492.3
All	100 m ²	Polynomial	+			347557.2
All	10 m ²	Linear	+	8.462	0.00368	105829.3
All	10 m ²	Polynomial**	+			105325.9
All	1 m ²	Linear	+	16.991	0.0000	38201.45
All	1 m ²	Polynomial**	+			37782.52
All	0.1 m ²	Linear	+	25.757	0.0000	10228.99
All	0.1 m ²	Polynomial**	+			10051.06
All	0.01 m ²	Linear	+	33.02	0.0000	1690.09
All	0.01 m ²	Polynomial**	+			1648.968
N. Hardwoods	1000 m ²	Linear	+	0.257	0.613	41208.31
N. Hardwoods	1000 m ²	Polynomial	+			41897.24
N. Hardwoods	100 m ²	Linear	+	0.305	0.581	18431.73
N. Hardwoods	100 m ²	Polynomial	+			18731.20
N. Hardwoods	10 m ²	Linear	+	0.016	0.900	5091.394
N. Hardwoods	10 m ²	Polynomial	+			5188.519
N. Hardwoods	1 m ²	Linear	+	0.007	0.931	1265.404
N. Hardwoods	1 m ²	Polynomial	-			1289.646
N. Hardwoods	0.1 m ²	Linear	+	0.606	0.438	205.9318
N. Hardwoods	0.1 m ²	Polynomial	-			208.7033
N. Hardwoods	0.01 m ²	Linear	-	0.105	0.746	31.90440
N. Hardwoods	0.01 m ²	Polynomial	-			32.51436
Pine-Oak	1000 m ²	Linear	+	2.381	0.124	139819.8
Pine-Oak	1000 m ²	Polynomial	+			139612.9

Pine-Oak	100 m ²	Linear	+	2.327	0.128	54906.17
Pine-Oak	100 m ²	Polynomial	+			54836.47
Pine-Oak	10 m ²	Linear	+	6.184	0.014	19648.41
Pine-Oak	10 m ²	Polynomial*	+			19333.66
Pine-Oak	1 m ²	Linear	+	8.212	0.005	7382.018
Pine-Oak	1 m ²	Polynomial*	+			7207.785
Pine-Oak	0.1 m ²	Linear	+	13.631	0.0003	1748.586
Pine-Oak	0.1 m ²	Polynomial**	+			1672.877
Pine-Oak	0.01 m ²	Linear	+	14.144	0.0002	305.5331
Pine-Oak	0.01 m ²	Polynomial**	+			291.4865

Table 4.2: Species richness across natural and anthropogenically-disturbed study sites

Mean total species richness, mean native species richness and mean non-native species richness for 1000 m² plots from natural areas and agricultural field margins. Edge plots were adjacent to the field. Forest plots were located >50 m from the field.

Study Sites	Mean Species Richness	Mean Native Species Richness	Mean Non-native Species Richness
Natural	68.30	66.37	1.93
Field margins	62.82	54.16	8.66
-Edge	65.26	53.52	11.74
-Forest	60.68	54.71	5.97

FIGURES

Figure 4.1: Proportional sampling and species saturation

Hypothesized relationship indicative of species saturation in a community. The full line indicates proportional sampling from the regional pool, while the dotted line is interpreted as local richness being constrained by species saturation.

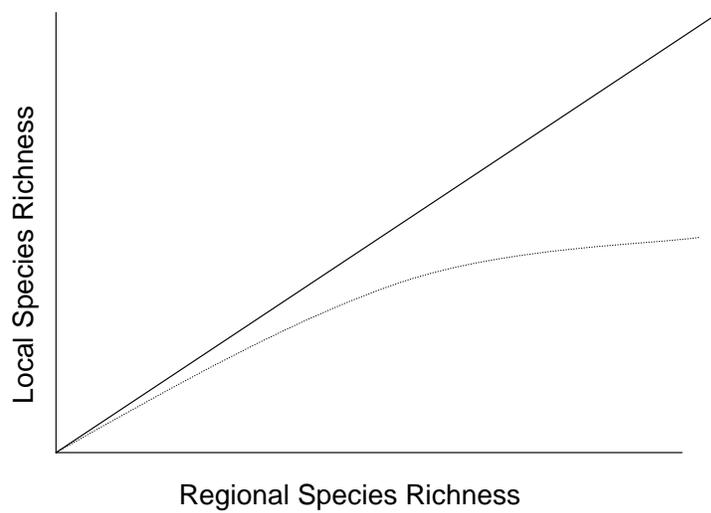


Figure 4.2: Species richness and species pool size across the southeastern U.S.

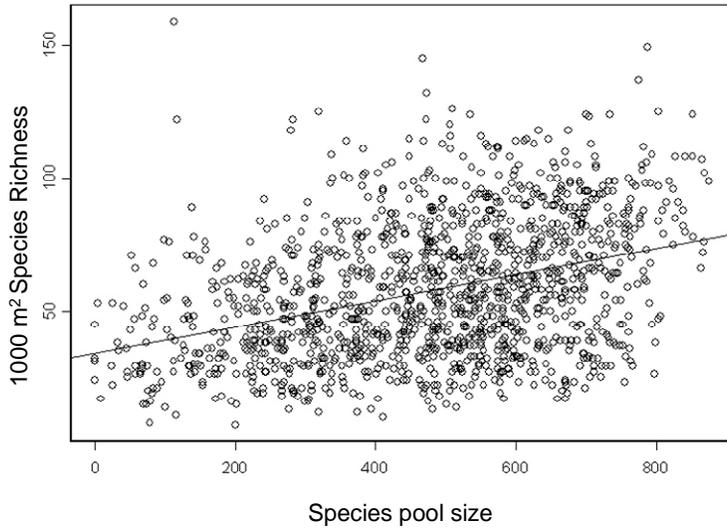


Figure 4.3: Species richness and species pool size of pine-oak woodlands across the southeastern U.S.

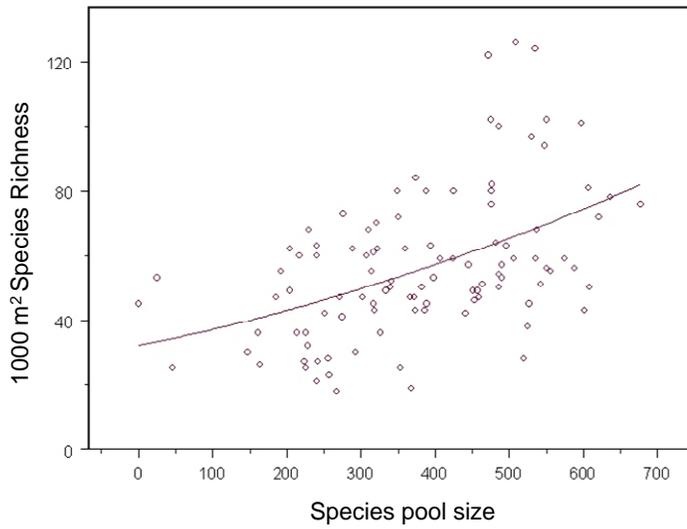
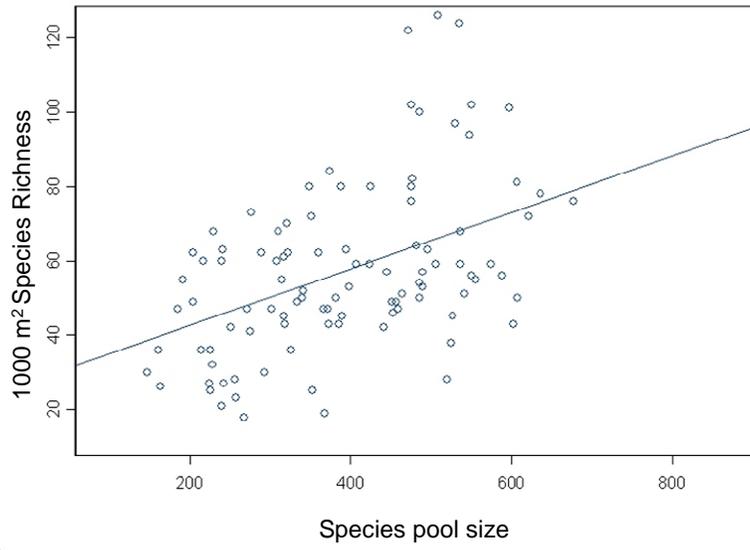


Figure 4.4: Species richness and species pool size of northern hardwood forests across the southeastern U.S.



Figures 4.5.1-4.5.5: Species richness and species pool size across the southeastern U.S. at multiple scales (100 m² - .01 m² plots)

Figure 4.5.1: Species richness and species pool size across the southeastern U.S. at 100 m²

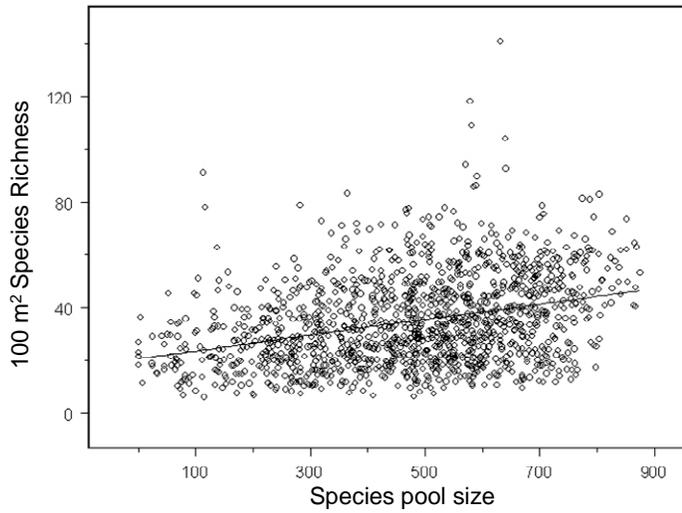


Figure 4.5.2: Species richness and species pool size across the southeastern U.S. at 10 m²

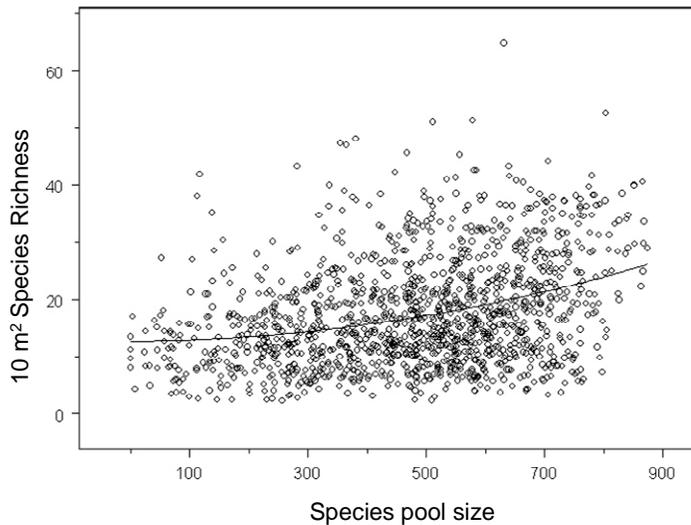


Figure 4.5.3: Species richness and species pool size across the southeastern U.S. at 1 m²

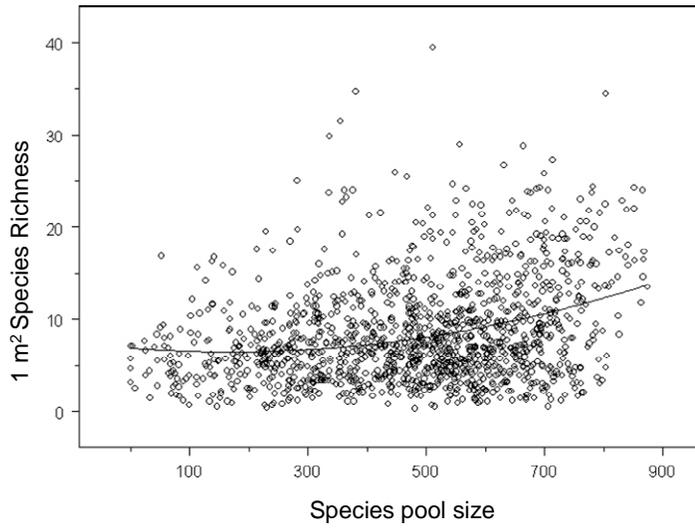


Figure 4.5.4: Species richness and species pool size across the southeastern U.S. at 0.1 m²

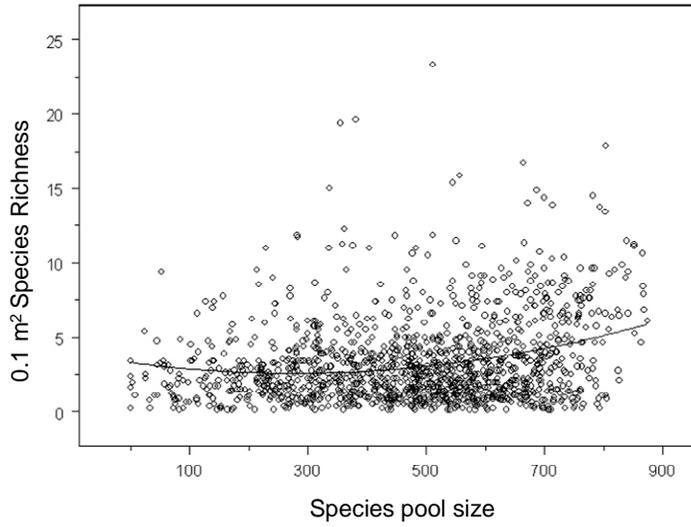
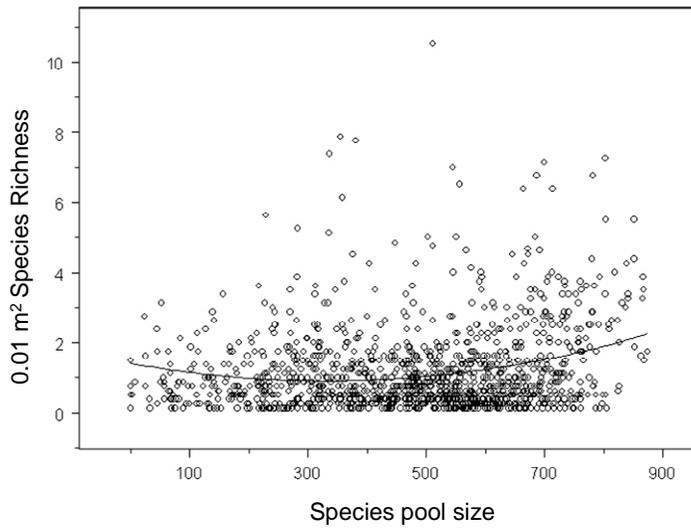


Figure 4.5.5: Species richness and species pool size across the southeastern U.S. at 0.01 m²



Figures 4.6.1 -4.6.5: Species richness and species pool size of pine-oak woodlands across the southeastern US at multiple scales (100 m² - .01 m² plots)

Figure 4.6.1: Species richness and species pool size of pine-oak woodlands across the southeastern US at 100 m²

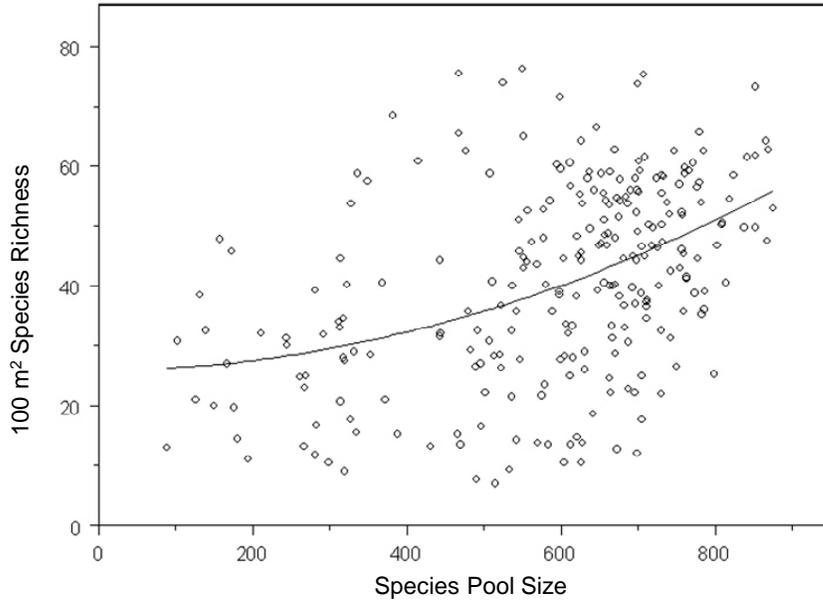


Figure 4.6.2: Species richness and species pool size of pine-oak woodlands across the southeastern US at 10 m²

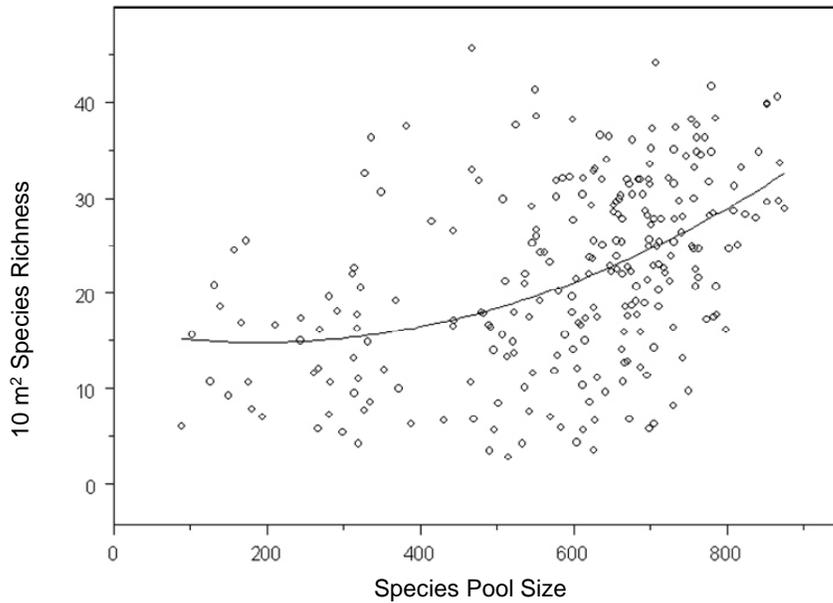


Figure 4.6.3: Species richness and species pool size of pine-oak woodlands across the southeastern US at 1 m²

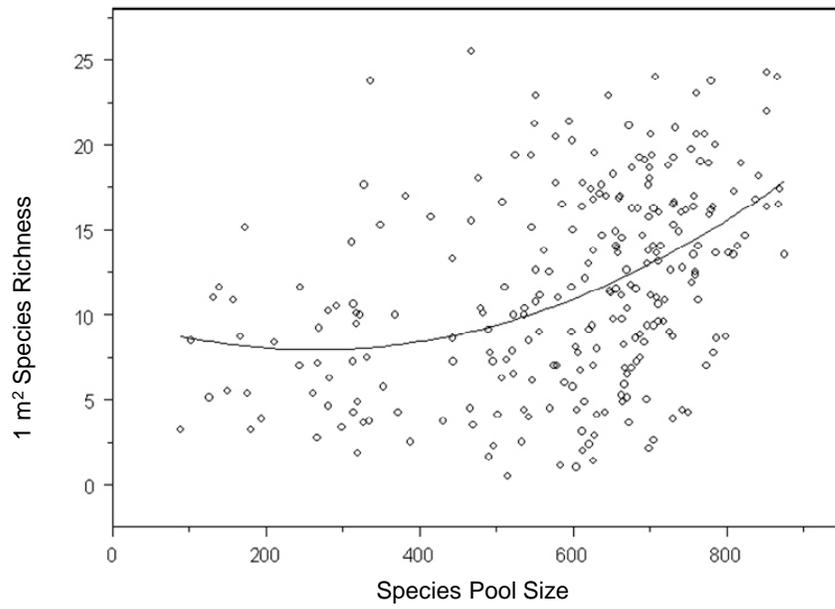


Figure 4.6.4: Species richness and species pool size of pine-oak woodlands across the southeastern US at 0.1 m²

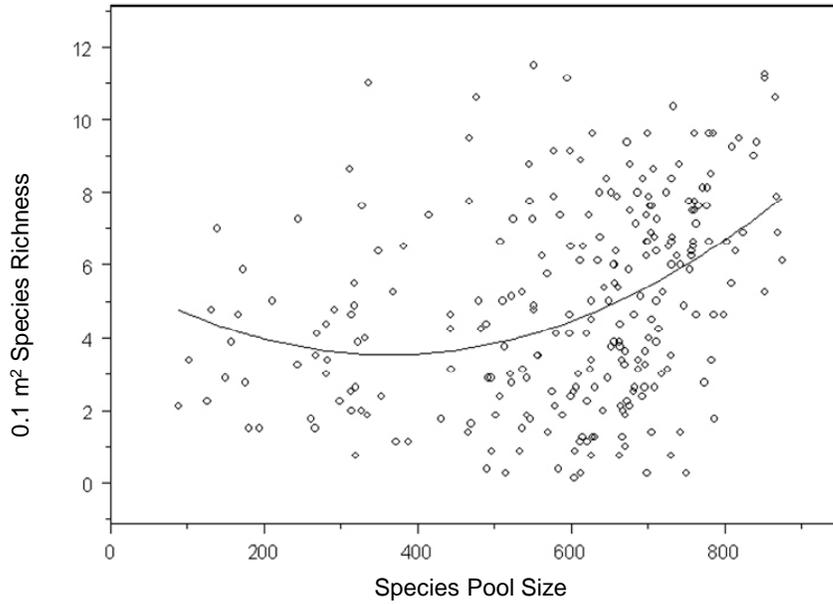
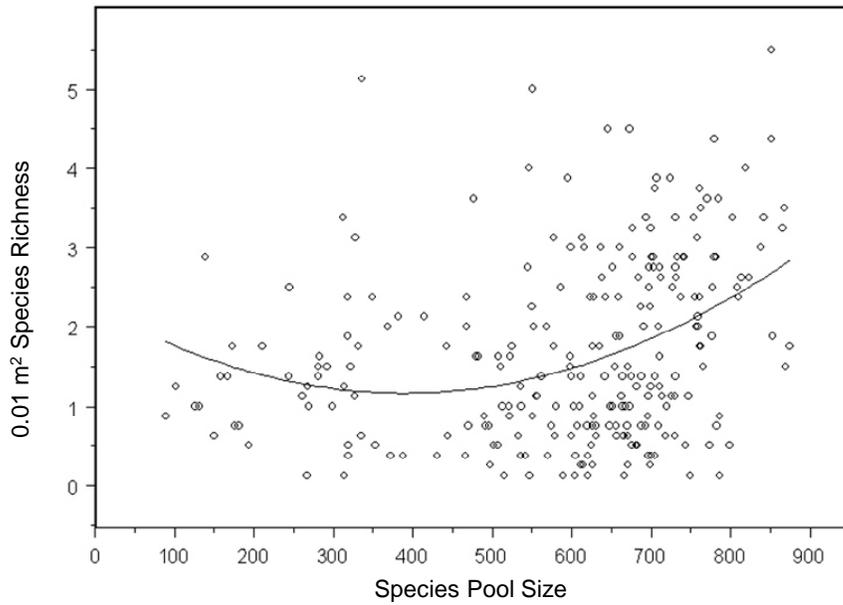


Figure 4.6.5: Species richness and species pool size of pine-oak woodlands across the southeastern US at 0.01 m²



Figures 4.7.1 -4.7.5: Species richness and species pool size of northern hardwood forests across the southeastern U.S. at multiple scales (100 m² - 0.01 m² plots)

Figure 4.7.1: Species richness and species pool size of northern hardwood forests across the southeastern U.S. at 100 m²

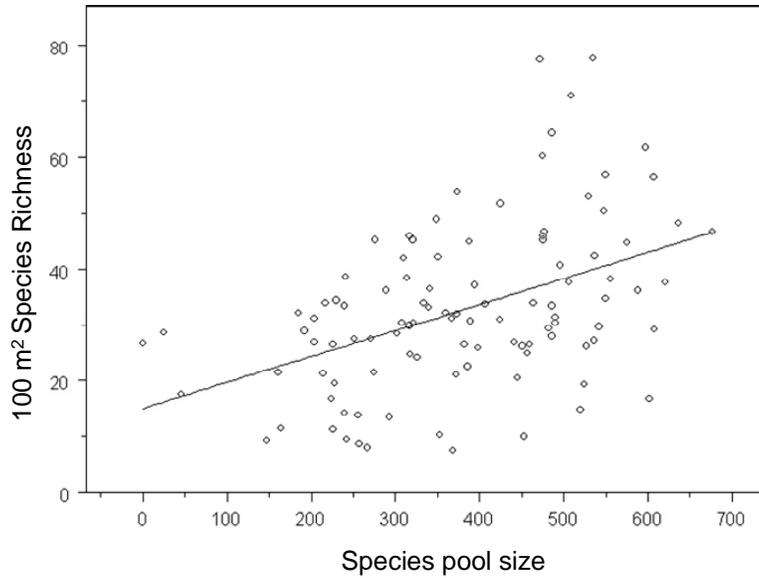


Figure 4.7.2: Species richness and species pool size of northern hardwood forests across the southeastern U.S. at 10 m²

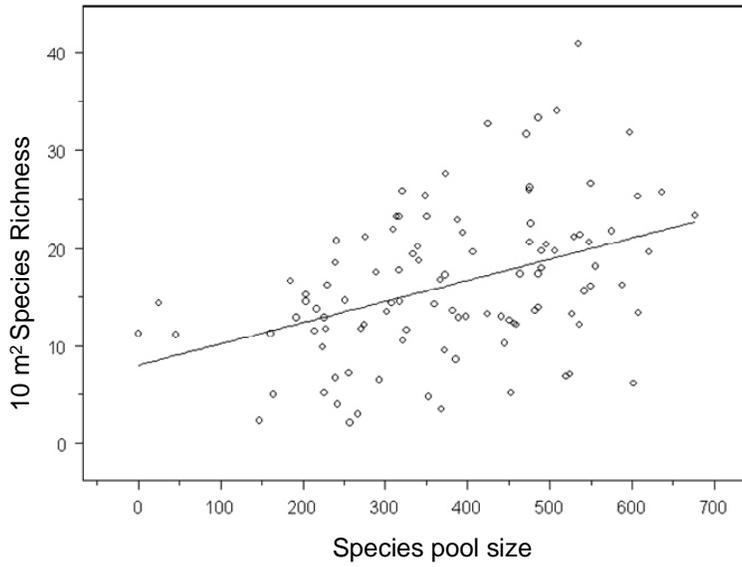


Figure 4.7.3: Species richness and species pool size of northern hardwood forests across the southeastern U.S. at 1 m²

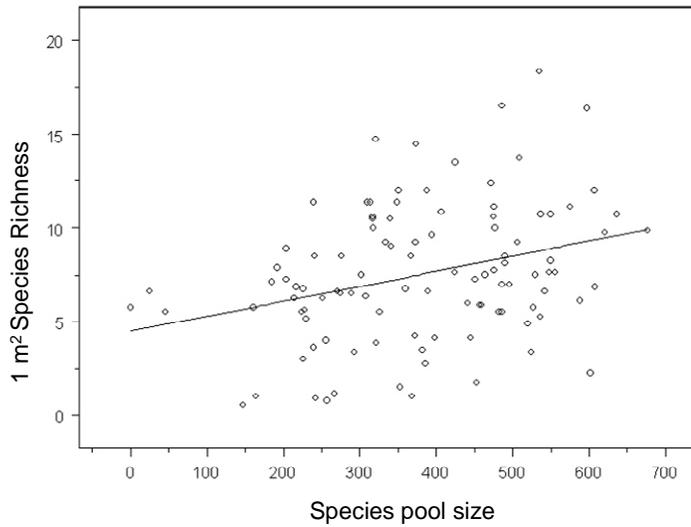


Figure 4.7.4: Species richness and species pool size of northern hardwood forests across the southeastern U.S. at 0.1 m²

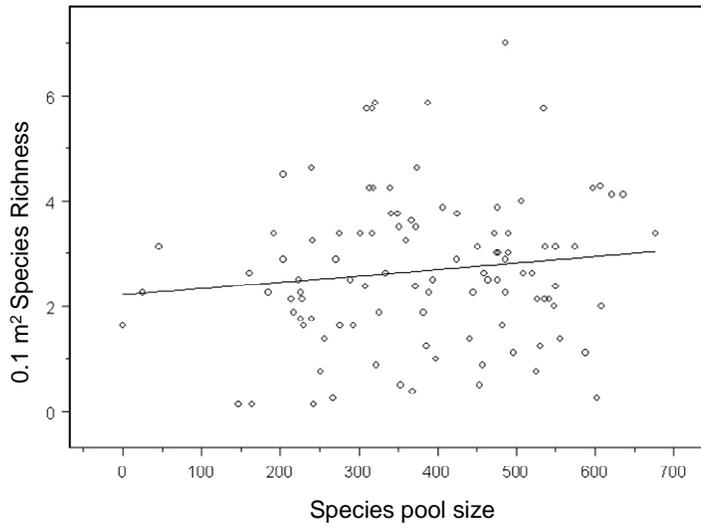


Figure 4.7.5: Species richness and species pool size of northern hardwood forests across the southeastern U.S. at 0.01 m²

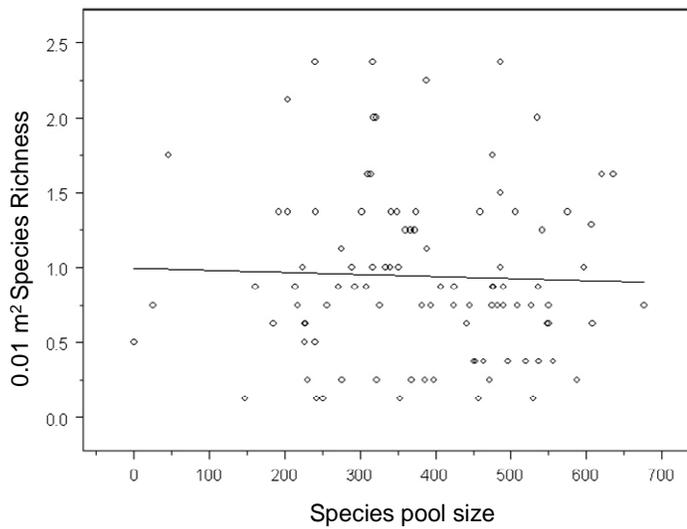


Figure 4.8: Non-native and native species richness across natural areas in the southeastern U.S.

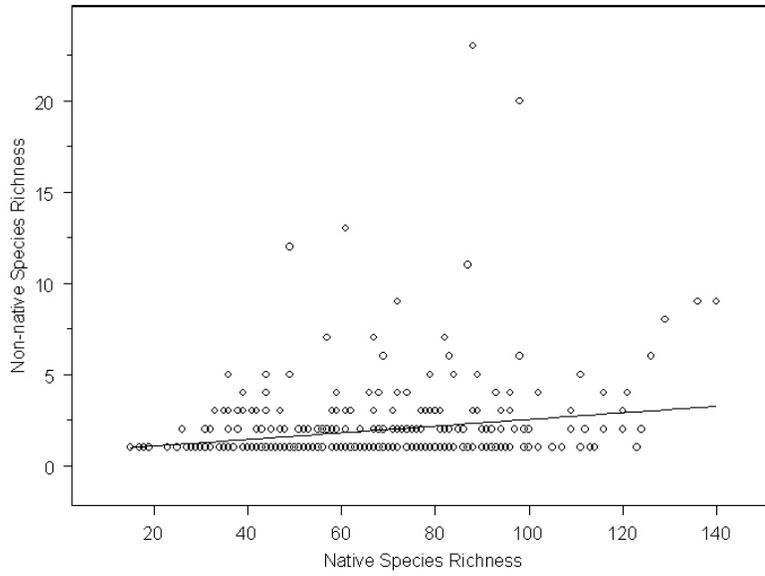


Figure 4.9: Species richness and species pool size across anthropogenically-disturbed areas in the southeastern U.S.

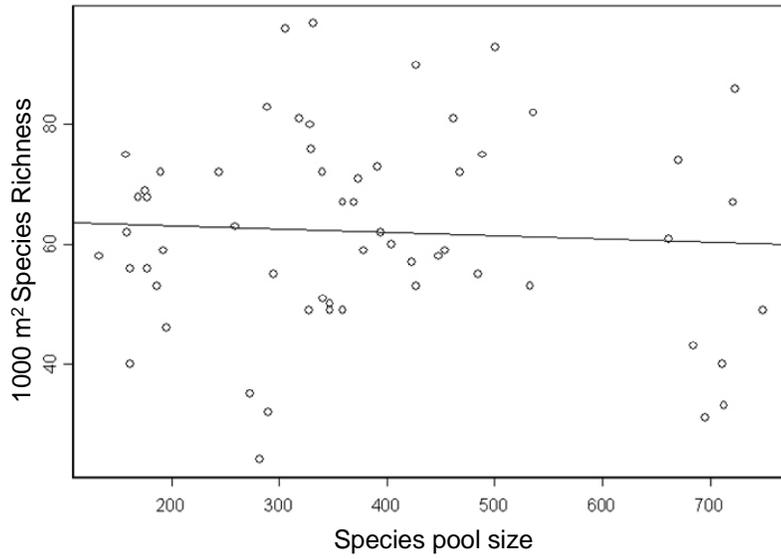
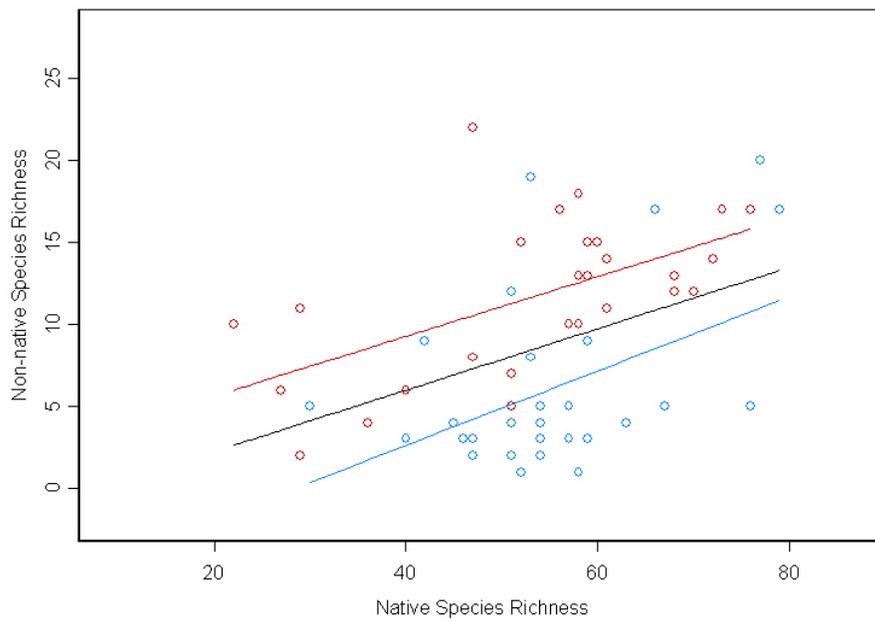


Figure 4.10: Non-native and native species richness across anthropogenically-disturbed areas in the southeastern U.S.

Non-native and native species in 1000 m² plots located across anthropogenically-disturbed areas in the southeastern United States. Black line indicates the total relationship of all plots. Blue line and points are representative of the forest plots while the red line and points are representative of the edge plots.



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CHAPTER 5

THE EVALUATION OF PRODUCTIVITY-DIVERSITY RELATIONSHIPS ACROSS TWO DISTINCT ECOLOGICAL COMMUNITIES USING LOCAL AND LANDSCAPE SCALE DATA

Introduction

A critical research objective for ecology is to provide useful models of how ecosystem function relates to species diversity (Keddy 2005). Anthropogenic effects such as climate change or habitat loss may have far reaching consequences for both plant species diversity and the regional and global functions that plant communities perform in maintaining the Earth's biosphere. The response of individual plants or species to the physiological effects of anthropogenic changes, such as increased CO₂ concentrations, can be modeled based on experimental and observational data, but predictions for plant communities or ecosystems may not directly scale up from these models (Geider *et al.* 2001). In order to address the long-term impacts of humans on the local, regional, and global environments, a greater understanding of how ecosystem functions (such as carbon sequestration and oxygen production) are linked to species diversity is needed.

Plant productivity is commonly related to species diversity to approximate how the functioning of an ecosystem is linked to its component species (Waide *et al.* 1999). Plant productivity may be defined as the amount of carbon fixed per unit area over a given time period (often g/m²yr). In some ecological systems, the actual biomass is harvested annually or seasonally to calculate the plant productivity. While this may work in systems dominated by herbaceous species, gauging the amount of productivity in mature forests has been

approached using other methods (such as the large-scale gas-exchange monitoring projects, remotely-sensed data, and regional or global climate models). For many studies, productivity or ecosystem function are inferred from other attributes at a study site such as soil nutrients (Ågren and Bosatto 1996), vegetation indices (leaf area index, LAI; normalized differential vegetation index, NDVI), or climatic attributes (precipitation, temperature) (Loustau *et al.* 2001). However, the observed relationship between a given estimator of ecosystem function and species diversity may vary with the method of estimation (Mittelbach *et al.* 2001, Groner and Novoplansky 2003).

The productivity-diversity relationship for plants has been studied across many different communities, but there is still much debate about how consistent the relationship is (Waide *et al.* 1999, Gross *et al.* 2000). Many authors have proposed that productivity-diversity relationships should be generalizable across habitat types. Grime's (1977) hump-backed model of productivity-diversity interactions is probably the most accepted of these generalizations (in which a unimodal pattern is observed with maximum diversity occurring at intermediate productivity values). The scale of observation may influence the observed relationship between productivity and diversity. (Oksanen 1996, Rapson *et al.* 1997, Chase and Leibold 2002). Estimates of productivity that exhibit high local variability, such as soil qualities, may exhibit different relationships with local diversity than large-scale indicators of productivity that have more gradual variation across the landscape, such as temperature or radiance.

Different productivity-diversity relationships can be produced when different aspects of ecosystem function are used to assess productivity. Several factors associated with productivity can be used to individually model the same set of diversity observations.

Modeled productivity-diversity relationships can then be compared using information criteria and correlation coefficients. Evaluating the relative fit of models derived from single estimators of productivity and combinations of those estimators can provide a better understanding of how the productivity-diversity relationship may be represented across a region. Applying the same modeling assay to richness patterns within specific habitat types or across different scales provides a test of the generality of productivity-diversity relationships.

The prevalence of a unimodal productivity-diversity relationship can be determined from a comprehensive modeling assay that draws upon several commonly used estimators of productivity. The standard expectation is that those estimators that are most closely related to small-scale harvestable biomass (as commonly used by Grime) will result in a unimodal or hump-shaped relationship. Since the scale at which productivity is estimated can alter the observed relationship between productivity and diversity, locally-observed (1000 m²) estimates of productivity should be compared to landscape-scale estimates. Local-scale environmental factors are expected to explain more of the variance in small-scale (< 1 m²) species diversity, whereas landscape-scale factors are expected to produce better (i.e. more explanatory) models of larger scale (1 m² - 1000 m²) species diversity. In this chapter I use a set of multi-scalar richness observations collected across the southeastern United States to evaluate the productivity-diversity relationship is evaluated with multiple surrogates of productivity.

Methods

Plant species observations

A 1662-plot dataset was constructed using 0.1-ha Carolina Vegetation Survey (CVS) plots in which species richness was recorded at the following scales: 0.01 m², 0.1 m², 1 m², 10 m², 100 m² and 1000 m². The total number of plant species observed was used to represent plant diversity at each scale. Each plot was sampled following the CVS protocol (Peet *et al.* 1998). Soil samples from each plot were collected, dried and then analyzed by Brookside Laboratories. When multiple soil samples were collected throughout the plot, the values of soil nutrient availability were averaged for the plot. All estimates of productivity were linked to plot locations, either through direct collection at the plot (local-scale estimates at 1000 m² resolution) or via remotely-sensing and modeling techniques (landscape-scale estimates at 1 km²)

Local-scale estimates of productivity:

Soil nutrients

Soil nutrient availability directly affects plant productivity (Ågren and Bosatto 1996, Schlesinger 1997). Cation exchange capacity, pH, calcium concentration, nitrogen availability and organic soil content were measured from one or more soil samples taken at each plot. Cation exchange capacity was reported in milliequivalents per 100 grams of soil. Nitrogen and organic soil content were reported as percentages. Calcium concentration was reported in parts per million. Calcium concentration was transformed by taking the cubed root of the observed values so that the range of transformed calcium concentration values would be similar to those of the other soil nutrients being modeled (approximately two orders of magnitude from minimum to maximum value).

Woody basal area

Diameter at breast height was recorded for every woody stem over 1.3 m tall in the study plots. Freedman (1983) demonstrated that the diameter of a plant was highly correlated with biomass ($r^2 = .997$, in a log-log comparison) for an individual plant. To approximate the standing biomass across a plot, diameter at breast height (dbh) measurements were converted to basal area measurements ($BA = \pi \times (\frac{1}{2} \text{ dbh})^2$) and tallied for each .1 ha plot. Woody basal area can be used to estimate the volume of standing biomass when multiplied times the height of the vegetation. Since information regarding stand height was not available for the majority of the plots in the study, woody volume was not estimated. In addition to its link with total woody biomass, woody basal area represents the total “footprint” of the largest individuals in a plot. This woody basal area excludes the rooting of all but a few epiphytic species found in the study area. Larger basal areas in a plot are likely associated with larger root systems and more intense belowground-competition for resources. Basal area in cm^2 was calculated for each plot and then transformed by deriving the cubed root.

Landscape-scale estimates of productivity:

Modeled climate data

Climate data was derived from GIS coverages of the DayMet climatological model (www.DayMet.org). The DayMet model uses elevation and weather station data collected across the United States from an 18-year period (1980-1997) to model daily and annual conditions on a smoothed landscape. Modeled values from a 1 km^2 -resolution coverage were intersected with plot locations. The average annual precipitation was assigned to each plot

location to provide a coarse measure of water availability. Precipitation has been linked to productivity when water is a limiting factor. Gillman and Wright (2006) warn that precipitation may give erroneous productivity-diversity results when water availability exceeds what is needed for maximal transpiration. For instance, production may decline in cool climates or at high altitudes when water is abundant but actual energy in the ecosystem is restricted by other factors. They conclude that precipitation should not be used as a surrogate when a monotonic relationship between precipitation and productivity would not be expected. For this analysis only the high-elevation montane plots fell into this category. The average daily radiance was assigned to each plot location to provide a measure of available light energy. Radiance provides a measure of the potential energy available to each site and which equates to potential productivity. The average minimum annual temperature was also derived from the DayMet modeled data for each plot location. Cold temperatures can act as a limiting factor to productivity by reducing microbial activity and nutrient uptake, restricting plant growth via photoinhibition and dehydration, and directly damaging or killing individuals through cold stress (Schulze *et al.* 2005).

Satellite data

The normalized vegetation differential index (NDVI) is a commonly used surrogate for plant productivity and biomass (Pettorelli *et al.* 2005). Using ArcGIS, coverages of processed Landsat spectral data were intersected with the UTM coordinates associated with each plot's location to assign Normalized Differential Vegetation Index (NDVI) values. NDVI values at 250 m² resolution were collected over 16-day intervals to avoid loss of data due to cloud cover. The 16-day NDVI values were then compiled over 7 intervals

encompassing the spring growth period (from late February to late May) for three different years. This growth period was chosen because studies have shown that correlations between NDVI and leaf area index (LAI) or the fraction of photosynthetically available radiation (fPAR) tend to fall off when LAI is at its maximum (Turner *et al.* 1999, Wang *et al.* 2005). The difference between the minimum NDVI value and the maximum NDVI value were calculated across the spring growth period for each year (2003-2005). This difference should be representative of the ANPP for each site (i.e. the annual net accumulation of biomass). The total NDVI observed for each site was also calculated. Total NDVI across all three spring growth periods was used to represent the cumulative production at a site.

Analysis

Plant species diversity was modeled using the following estimators of ecosystem function: woody basal area, pH, organic soil content, CEC, minimum annual temperature, annual precipitation, and available radiance. Linear models were constructed in which species richness was the response variable and one of these estimators of ecosystem function was used as the lone predictor variable. Quadratic models were also tested by comparing polynomial regression terms to linear regression terms. Ordinary least squares regression (OLS; following Gillman and Wright 2006) and generalized linear modeling with a Poisson error distribution (GLM; following Mittelbach *et al.* 2001) were both used to characterize the relationship between productivity and diversity. GLM results exhibited more and stronger correlations between variables than OLS results. As suggested by Gillman and Wright, GLM techniques were found to be more liberal than the OLS. Given current misgivings about the statistical assumptions implicit to each in biological analyses (Whittaker and Heegaard 2003,

Gillman and Wright 2006) only the more conservative OLS technique was used ($\alpha < 0.05$). Each model was evaluated using r^2 values and Akaike information criteria (AIC) to assess their relative strengths. AIC was chosen because it allows for an even comparison of regression models with different degrees of freedom and can facilitate a more parsimonious model selection (Burnham and Anderson 2002).

A “local” model and a “landscape” model were each constructed to evaluate the amount of variance explained by each set of productivity estimates. The local model used soil nutrient information and basal area data, collected in the plot, to predict species richness. The landscape model predicted species richness using remotely-sensed NDVI data and regionally modeled climate data. A “full” model was evaluated to determine the maximum amount of variance in species richness that could be explained from all of the productivity estimates as linear or quadratic terms. A stepwise approach using both forward and backward methods (stepAIC function in S/R programming applications) was used to determine which variables would be included in the multiple regression models (Venables and Ripley 1999). A “best” model produced from stepwise multiple regression was found for local, landscape and all variables. A montane upland forest subset and a longleaf pine woodland subset of the CVS data were used to model the productivity-diversity relationship across two geographically-distinct habitat types. Both subsets were evaluated using the same methods listed above for the entire dataset.

Results and Discussion

Ecosystem function and species richness across all plots

The relationships between species richness and local or landscape factors, used as surrogates for productivity produced an assortment of patterns that varied with scale and habitat type (Table 5.1). Across the entire regional dataset, woody basal area exhibited the strongest relationship with species richness ($r_{\text{adj}}^2 = 0.2629$); a negative or weakly U-shaped pattern at the 0.01 m^2 scale of observation (Figure 5.1.6). Since greater woody basal area may be associated with more canopy cover, greater individual root systems and a larger footprint of individual species, it is not surprising that small-scale diversity would be impacted. While competitive interactions associated with shading and nutrient acquisition are likely occurring, larger individuals alone may result in reduced small-scale species richness. For example: when a forest with many large individuals is sampled and a $10 \text{ cm} \times 10 \text{ cm}$ sub-plot falls on the base of a tree, the observed species richness may be reduced to 1. Oksanen's "no-interaction" model has demonstrated that larger individuals which are associated with the highest biomass observations reduce the number of individuals sampled (1996). In such cases, lower levels of observed richness may result from a sampling effect and not necessarily from competitive interactions. This may be the reason that small scale (0.1 m^2 - 1 m^2) richness across all plots was most affected by increasing biomass while the plot-level effect was relatively weak ($r_{\text{adj}}^2 = 0.0306$).

Species richness exhibited a unimodal relationship to $p\text{H}$ ($r_{\text{adj}}^2 = 0.1553$; Figures 5.2.1 & 5.2.2) at the 1000 and 100 m^2 scales across all plots. Greater $p\text{H}$ values and calcium concentrations are associated with the increased availability of soil nutrients and may be indicative of overall soil productivity. Species pool estimates in several regions including the southeastern United States have shown a strong preference of plant species for higher $p\text{H}$ (Peet *et al.* 2003). The species pool hypothesis would predict higher plant richness at higher

pH sites based upon the greater number of species evolved to occupy such sites. These unimodal patterns of richness across the *pH* gradient suggest that competition or other local interactions may limit species diversity on high *pH* sites. Unfortunately, the mid-upper range of *pH* is under-sampled precluding thorough testing of a species pool hypothesis across all plots.

Local and landscape indicators of ecosystem function do not exhibit two distinct relationships with species richness (Table 5.1). More importantly, landscape-scale factors linked to plot locations were not disconnected from local plot observations. The relationship between species richness and the difference in NDVI over the spring growing season paralleled the relationship between species richness and the locally-observed wood basal area. Both of these surrogates for biomass exhibit significant negative relationships with richness, although NDVI is more weakly correlated.

A warmer minimum temperature observed at a site is correlated with higher species richness especially at smaller scales (Table 5.1). This trend is indicative of a latitudinal effect and mirrors the effects of latitude on species richness (linear models of latitude on richness exhibit the following r^2 values at descending scales: 0.0767, 0.8714, 0.1254, 0.1626, 0.1660 and 0.1318). Since the southern most region of the survey area (the area with the highest minimum temperatures; central Florida) is made up of longleaf pine forests which are renowned for their high diversity at small-scales, habitat type is biasing this relationship as well.

No single-factor model explained as much variance in species richness as a combined model of all factors (Tables 5.2 & 5.3: Full Model). A slightly smaller model with slightly greater r^2 values was produced by the stepwise regression analysis (Tables 5.2 & 5.3: Best

Model). A combined model of local factors outperformed a combined model of landscape-scale factors regardless of whether it was the full model or the most parsimonious product of stepwise regression. No single local or landscape factor explained as much variance as their respective multiple regression models.

Ecosystem function and species richness across distinct habitats

Species richness across the longleaf pine habitat was most strongly related to soil nutrient availability (Table 5.1). A positive relationship between pH and large-scale species richness (1000 m² and 100 m²) was observed. At smaller scales the effects of nitrogen availability become more pronounced and pH becomes less influential. Nitrogen availability may be representative of the soil texture and its influence on nutrient retention. The amount of available nitrogen was positively correlated with the percentage of silt in the soil ($\text{Silt}\% = 28.81 + 0.340(\text{N})$, $p\text{-value}=0$, $r^2 = 0.180$), and negatively related to the percentage of sand in the soil ($\text{Sand}\% = 58.94 - 0.308(\text{N})$, $p\text{-value}=0$, $r^2 = 0.183$).

Woody basal area exerts a negative effect on small-scale richness. When woody biomass has accumulated at a site over time, the plant species diversity is reduced due to the shading out of small species and, possibly, the competition for other resources. Longleaf pine habitats frequently burn as a result of both management and lightning ignitions. Trends in small-scale diversity in longleaf pine forests are related to the cycling of nutrients and the removal of biomass associated with burns. Many small longleaf pine species (such as the Venus-fly trap; *Dionaea muscipula*) respond to this removal of live and dead biomass and the periodic availability of light and nutrients. In a frequently burned site (every 2-5 years), small scale richness will be high and woody biomass will be relative low.

Calcium, organic matter, minimum temperature, precipitation, and to a lesser extent nitrogen, CEC and NDVI differential, all elicit unimodal responses from species richness in longleaf pine habitats. Given that the richest longleaf pine sites are typically open and frequently burned, competitive exclusion would be expected to affect sites that have the resources to support continued biomass production in between disturbance events. When a longleaf pine habitat does not burn for several years the ground vegetation will crowd out some of the smaller, fire-adapted species (often slow-growing perennials or seed bank dwellers) that are most conspicuous post-burn. As more nutrients continue to be available in the soil over time, the larger plant species will respond with greater growth. This competitive dynamic may be responsible for some of the observed unimodal relationships. These factors may collectively result in a production gradient or a stress gradient akin to Grime's hump-backed model, although with shifts along the gradient following a burn.

The processes described by the hump-backed model may also be influencing species richness in the montane forest plots. Large-scale species richness exhibits a unimodal relationship with calcium concentrations and *pH* values from the soil. For plot observations at 1 to 1000 m², no other factors explain as much variance in montane forest species richness as calcium or *pH*. At smaller scales a positive relationship between species richness and *pH* continues, but the negative effects of basal area become significant. Based upon the effects of woody basal area and cumulative NDVI values on species richness at 1 m² and below, biomass appears to suppress species richness at smaller scales in montane forest plots.

Conclusions

Each of the factors of ecosystem function addressed in the study is linked to the concept of plant productivity in a different way. For this reason, it is not too surprising that there were varied results observed between and within factors when multiple scales and habitats were studied. In general the presence of woody biomass, as indicated by woody basal area, has a strong negative effect on small-scale ($< 1\text{m}^2$) richness throughout the southeastern United States. Whereas Schuster and Diekman (2005) found regression models of forest species richness based upon pH, calcium or standing biomass all described a similar amount of variance (adjusted $r^2 = 0.304\text{-}0.385$, with only C/N ratios accounting for more variance), these results demonstrate that varying the scale and habitat type can generate different productivity-diversity relationships. While calcium and pH may be indicative of nutrient rich soils and consequently linked to positive or unimodal richness patterns, soil nutrient dynamics will vary across habitats. Using nutrient productivity as a way of linking productivity to richness will need to take into account the physiological adaptations associated with the species assemblages that inhabit the study area.

If ecologists are to devise realistic models and theories for understanding how factors of ecosystem function collectively affect plant species diversity, then the models and theories must be robust enough to account for changes in scale (Levin 1992). A scale transition approach may provide a means by which the dynamics governing local species patterns can be scaled up to communities or even regions (Chesson *et al.* 2005). The scaling of biomass in comparison to soil nutrients has been found to be particularly complex based upon fractal analysis (Oline and Grant 2002). For this analysis, 1000 m^2 estimates of woody basal area

were used to represent standing biomass. Multi-scalar assessments of biomass may provide greater insight into the intricate relationship between species richness, biomass and other factors associated with plant productivity.

The multiple regression models presented above (Table 5.2) demonstrated that approximately 45% of the variance in species richness in longleaf pine habitats can be accounted for by these factors whereas only 26% was addressed by a single factor. A better approach to teasing apart the relative contributions of factors related to ecosystem function to species richness might involve a structural equation model or path analysis approach. The results of this analysis lay the ground work for a multivariate assessment of productivity and diversity in the Southeast in which the known pathways between factors are established and tested with respect to the interactions of other factors. Ultimately, singular approaches to estimating the effects of productivity on species diversity do not produce a consensus on the relationship. A combination of local and landscape-scale factors seems to work well for modeling richness. While nearly every factor in the full model was included in the most parsimonious model, it suggests that there is little or at least acceptable redundancy in the factors addressed in this study. Future models should be constructed to integrate local and landscape factors and account for differences in scale and habitat type. Only when the current variation in the relationship between diversity and ecosystem function is addressed can adequate models be produced that address how future changes in the environment will affect the productivity-diversity relationship.

TABLES

Table 5.1: The shape and r^2 value associated with simple regression models of productivity and diversity

Shapes and r^2 values for regression models: tBA = cubic root of basal area; tCa = cubic root of calcium concentration (ppm); CEC = cation exchange capacity; DiffNDVI = the difference in maximum and minimum NDVI values across a growing season (averaged from three different growing seasons); Temp = average annual minimum temperature; N = available nitrogen in the soil; Org = organic soil content; Precip = average annual precipitation; Rad = average daily radiance; TotalNDVI = cumulative NDVI over three growing seasons.

All Plots	tBA	tCa	CEC	Diff NDVI	Temp	N	Org	pH	Precip	Rad	Total NDVI
1000 m ²	Neg 0.0306	Uni 0.0379	NS	Neg 0.0056	Pos 0.0312	NS	Neg 0.0263	Uni 0.1553	NS	Pos 0.0615	NS
100 m ²	Neg 0.0505	Uni 0.0356 3	NS	Neg 0.0085	Pos 0.0421	NS	Neg 0.0287	Uni 0.1484	NS	Pos 0.0535	NS
10 m ²	Neg 0.0931	Uni 0.0192 7	NS	Neg 0.0147	Pos 0.0842	NS	Neg 0.0374	Uni 0.0988	NS	Pos 0.0445	NS
1 m ²	Neg 0.1658	Uni 0.0058	Neg 0.0037	Neg 0.0206	Pos 0.1391	NS	Neg 0.046	Uni 0.0422	Neg 0.0249	Pos 0.032	NS
0.1 m ²	Neg 0.2383	NS	Neg 0.0088	Neg 0.0279	Pos 0.1682	Neg 0.0488	U-shaped 0.0534	NS	Neg 0.0274	Pos 0.02	NS
0.01 m ²	U-shaped 0.2629	Neg 0.0042	Neg 0.0077	Neg 0.0261	Pos 0.1473	NS	U-shaped 0.0339	NS	Neg 0.0248	Pos 0.0096	NS

Table 5.1: Continued

Pine Forest	tBA	A	CEC	Diff NDVI	Temp	N	Org	pH	Precip	Rad	Total NDVI
1000 m ²	NS	Uni	NS	NS	Uni	Uni	Uni	Pos	Pos	Pos	NS
		0.1028			0.0796	0.0854	0.084	0.2159	0.0122	0.0681	
100 m ²	Neg	Uni	NS	NS	Uni	Uni	Uni	Pos	Pos	Pos	NS
	0.044	0.1017			0.0815	0.0966	0.0724	0.2021	0.0162	0.0562	
10 m ²	Neg	Uni	NS	NS	Uni	Pos	Uni	Pos	Uni	Pos	NS
	0.0913	0.1072			0.0823	0.1453	0.0897	0.1427	0.0208	0.0322	
1 m ²	Neg	Uni	NS	Uni	Uni	Pos	Uni	Pos	Uni	Pos	NS
	0.1653	0.098		0.0131	0.0616	0.2188	0.1164	0.0631	0.0322	0.0092	
0.1 m ²	Neg	Uni	Uni	Uni	Uni	Pos	Uni	Pos	Uni	NS	NS
	0.2383	0.0623	0.0353	0.0208	0.0361	0.2631	0.1069	0.0059	0.0432		
0.01 m ²	Neg	Uni	Uni	NS	Uni	Pos	Uni	NS	Uni	NS	NS
	0.2568	0.0418	0.0414		0.0238	0.2608	0.103		0.0455		

Table 5.1: Continued

Mt Forest	tBA	tCa	CEC	Diff NDVI	Temp	N	Org	pH	Precip	Rad	Total NDVI
1000 m ²	Neg	Uni	Uni	NS	Pos	Neg	Neg	Uni	NS	NS	Neg
	0.0425	0.1893	0.0002		0.0182	0.0231	0.0648	0.2966			0.0071
100 m ²	NS	Uni	Uni	NS	Pos	NS	Neg	Uni	NS	NS	Neg
		0.2013	-1E-04		0.0085		0.0632	0.3079			0.0133
10 m ²	NS	Uni	Uni	NS	NS	NS	Neg	Pos	NS	NS	Neg
		0.2024	0.0016				0.0509	0.2747			0.03
1 m ²	Neg	Uni	Uni	NS	NS	NS	Neg	Pos	Uni	NS	Neg
	0.1653	0.2013	0.004				0.0439	0.2407	0.0217		0.0463
0.1 m ²	U-shape d	Uni	Uni	NS	U-shape d	NS	Neg	Pos	Pos	NS	Neg
	0.2397	0.1643	0.0096		0.0181		0.0241	0.1708	0.0109		0.0446
0.01 m ²	U-shape d	Uni	Uni	NS	Neg	NS	NS	Pos	Pos	NS	Neg
	0.2633	0.1118	0.0083		0.0197			0.0835	0.007		0.0393

Table 5.2: R² values associated with multiple regression models of productivity and diversity

Regression Models	Full Dataset					
Scale	Plot r ²	100m ² r ²	10m ² r ²	1m ² r ²	.1m ² r ²	.01m ² r ²
Full Model	0.3039	0.3069	0.3123	0.3465	0.3786	0.3703
Best Model	0.3052	0.3071	0.3128	0.3464	0.3797	0.3713
Full Local Model	0.2541	0.2589	0.2560	0.2759	0.3082	0.3151
Best Local Model	0.2550	0.2587	0.2560	0.2759	0.3088	0.3166
Full Landscape Model	0.1122	0.1089	0.1328	0.1845	0.2204	0.1974
Best Landscape Model	0.1122	0.1089	0.1328	0.1845	0.2204	0.1974
Scale	Plot AIC	100m ² AIC	10m ² AIC	1m ² AIC	.1m ² AIC	.01m ² AIC
Full Model	15390.10	13653.10	11668.16	9843.94	7513.81	4574.64
Best Model	15383.05	13648.62	11666.16	9840.21	7502.96	4562.34
Full Local Model	15493.18	13752.49	11787.09	10002.43	7680.18	4702.62
Best Local Model	15489.23	13751.10	11787.09	10002.43	7676.85	4694.86
Full Landscape Model	15780.56	14056.89	12039.81	10198.14	7876.89	4964.11
Best Landscape Model	15780.56	14056.89	12039.81	10198.14	7876.89	4964.11
Regression Models	Longleaf Pine Forest Subset					
Scale	Plot r ²	100m ² r ²	10m ² r ²	1m ² r ²	.1m ² r ²	.01m ² r ²
Full Model	0.4437	0.4483	0.4603	0.4654	0.4478	0.4245
Best Model	0.4470	0.4507	0.4624	0.4675	0.4500	0.4244
Full Local Model	0.4155	0.4206	0.4309	0.4370	0.4234	0.3933
Best Local Model	0.4164	0.4195	0.4309	0.4370	0.4244	0.3947
Full Landscape Model	0.1432	0.1275	0.1184	0.1000	0.0937	0.1070
Best Landscape Model	0.1438	0.1284	0.1142	0.0978	0.0959	0.1069
Scale	Plot AIC	100m ² AIC	10m ² AIC	1m ² AIC	.1m ² AIC	.01m ² AIC
Full Model	6714.92	5976.50	5152.71	4428.01	3484.15	2258.72
Best Model	6701.79	5963.61	5141.12	4417.30	3469.53	2247.20
Full Local Model	6740.13	6001.29	5180.49	4454.86	3504.68	2286.38
Best Local Model	6737.00	5998.84	5180.49	4454.86	3501.36	2282.74
Full Landscape Model	7022.69	6303.90	5504.24	4801.86	3839.17	2572.02
Best Landscape Model	7020.17	6299.16	5503.83	4801.76	3835.40	2568.14
Regression Models	Montane Upland Forest Subset					
Scale	Plot r ²	100m ² r ²	10m ² r ²	1m ² r ²	.1m ² r ²	.01m ² r ²
Full Model	0.4155	0.4324	0.4260	0.4247	0.3623	0.2819
Best Model	0.4217	0.4367	0.4321	0.4294	0.3675	0.2863
Full Local Model	0.3831	0.4071	0.3982	0.3800	0.3006	0.2015
Best Local Model	0.3852	0.4090	0.4002	0.3801	0.3020	0.2004
Full Landscape Model	0.1444	0.1314	0.1152	0.1146	0.0980	0.0842
Best Landscape Model	0.1435	0.1309	0.1151	0.1136	0.0974	0.0869
Scale	Plot AIC	100m ² AIC	10m ² AIC	1m ² AIC	.1m ² AIC	.01m ² AIC
Full Model	5412.49	4736.48	3893.85	3047.00	2072.71	1013.47
Best Model	5395.57	4720.51	3876.02	3032.52	2058.26	998.28
Full Local Model	5432.81	4750.75	3910.25	3079.64	2115.76	1064.63
Best Local Model	5424.98	4746.87	3906.30	3075.63	2112.58	1061.55
Full Landscape Model	5624.21	4974.46	4136.11	3288.31	2264.15	1143.67
Best Landscape Model	5622.84	4972.81	4134.21	3287.00	2260.63	1139.99

Table 5.3: Multiple regression models used to assess the productivity-diversity relationship

Regression Models	Full Dataset
Full Model	Richness = pH + Org + DiffNDVI + tBA + Precip + tCa + TotalNDVI + CEC + Rad + N + Temp + pH ² + Org ² + DiffNDVI ² + tBA ² + Precip ² + tCa ² + TotalNDVI ² + CEC ² + Rad ² + N ² + Temp ²
Scale	Plot Level
Best Model	Richness = pH + Org + DiffNDVI + pH ² + tBA ² + Precip ² + tCa ² + TotalNDVI ² + CEC ² + Rad ² + N ² + Temp ²
Scale	100m ²
Best Model	Richness = pH + Org + Temp + DiffNDVI + pH ² + tBA ² + Precip ² + tCa ² + TotalNDVI ² + CEC ² + Rad ² + N ²
Scale	10m ²
Best Model	Richness = tBA + DiffNDVI + pH ² + tBA ² + Precip ² + tCa ² + TotalNDVI ² + CEC ² + Rad ² + N ² + Temp ² + Org ²
Scale	1m ²
Best Model	Richness = tBA + DiffNDVI + pH ² + tBA ² + Precip ² + tCa ² + TotalNDVI ² + Rad ² + N ² + Temp ² + Org ²
Scale	0.1m ²
Best Model	Richness = tBA + Temp + DiffNDVI + pH ² + Precip ² + TotalNDVI ² + Rad ² + N ² + Org ²
Scale	0.01m ²
Best Model	Richness = tBA + Temp + DiffNDVI + tBA ² + Precip ² + TotalNDVI ² + Rad ² + N ² + Org ²
Regression Models	Full Dataset-Landscape Models
Full Landscape Model	Richness = DiffNDVI + Precip + TotalNDVI + Rad + Temp + DiffNDVI ² + Precip ² + TotalNDVI ² + Rad ² + Temp ²
Scale	Plot Level
Best Landscape Model	Richness = Rad + Temp + DiffNDVI ² + Precip ² + TotalNDVI ² + Rad ²
Scale	100m ²
Best Landscape Model	Richness = Rad + Temp + DiffNDVI ² + Precip ² + TotalNDVI ² + Rad ²
Scale	10m ²
Best Landscape Model	Richness = Temp + DiffNDVI ² + Precip ² + TotalNDVI ² + Rad ² + Temp ²
Scale	1m ²
Best Landscape Model	Richness = Temp + DiffNDVI ² + Precip ² + TotalNDVI ² + Rad ² + Temp ²
Scale	0.1m ²
Best Landscape Model	Richness = Temp + DiffNDVI ² + Precip ² + TotalNDVI ² + Rad ² + Temp ²
Scale	0.01m ²
Best Landscape Model	Richness = Temp + DiffNDVI ² + Precip ² + TotalNDVI ² + Rad ² + Temp ²

Table 5.3: Continued

Regression Models	Full Dataset- Local Models
Full Local Model	Richness = pH + Org + tBA + tCa + CEC + N + pH ² + Org ² + tBA ² + tCa ² + CEC ² + N ²
Scale	Plot Level
Best Local Model	Richness = pH + N + pH ² + tBA ² + tCa ² + CEC ²
Scale	100m ²
Best Local Model	Richness = pH + N + pH ² + tBA ² + tCa ² + CEC ²
Scale	100m ²
Best Local Model	Richness = pH + pH ² + Org ² + tBA ² + tCa ² + CEC ² + N ²
Scale	1m ²
Best Local Model	Richness = pH + tCa + N + pH ² + Org ² + tBA ² + CEC ²
Scale	0.1m ²
Best Local Model	Richness = tBA + N + pH ² + Org ²
Scale	0.01m ²
Best Local Model	Richness = tBA + N + Org ² + tBA ²

FIGURES

Figures 5.1.1-5.1.6: The relationship between woody basal area and species richness at multiple spatial scales

Plant species richness and woody basal area at 6 scales (1000 m², 100 m², 10 m², 1 m², 0.1 m², 0.01 m²) across all 1662 plots. Note that the y-axis varies with the range of the species richness.

Figure 5.1.1: Plant species richness and woody basal area at 1000 m²

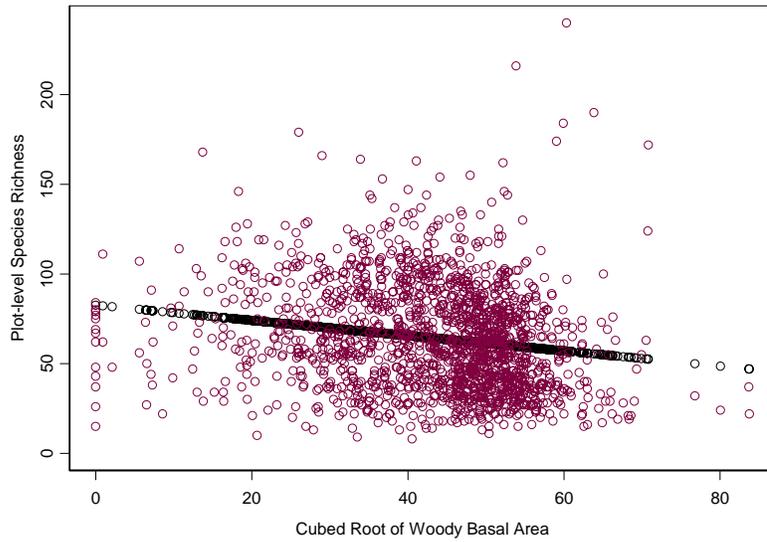


Figure 5.1.2: Plant species richness and woody basal area at 100 m²

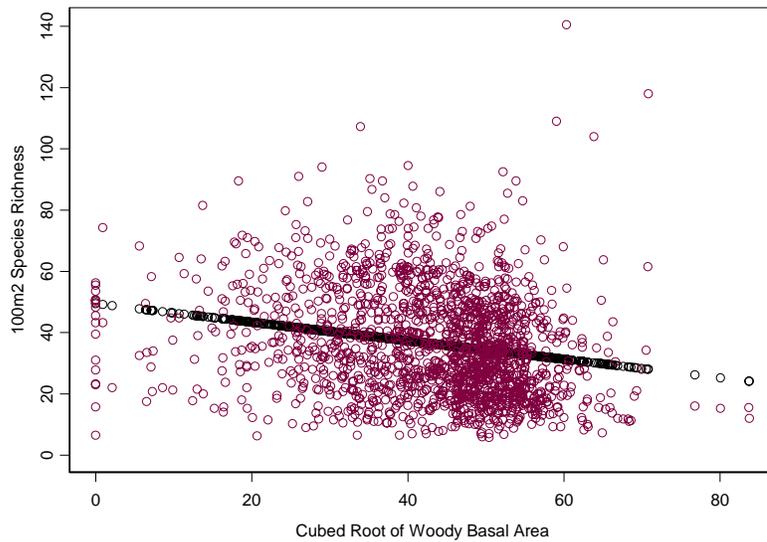


Figure 5.1.3: Plant species richness and woody basal area at 10 m²

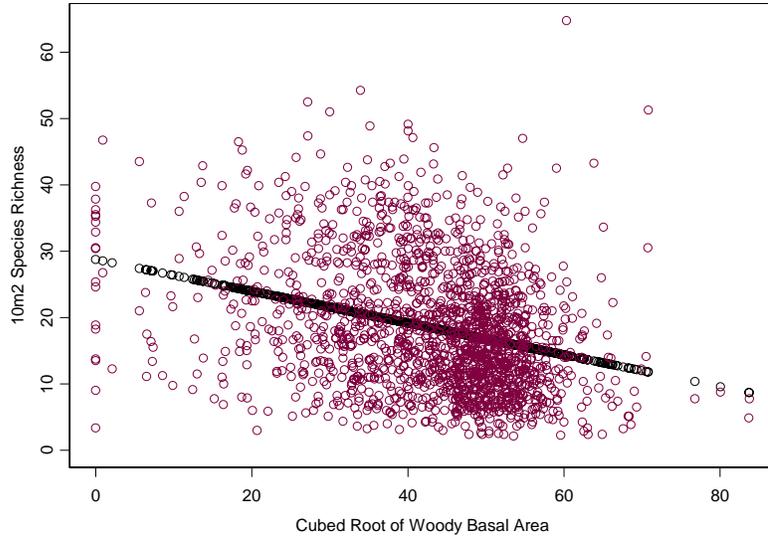


Figure 5.1.4: Plant species richness and woody basal area at 1 m²

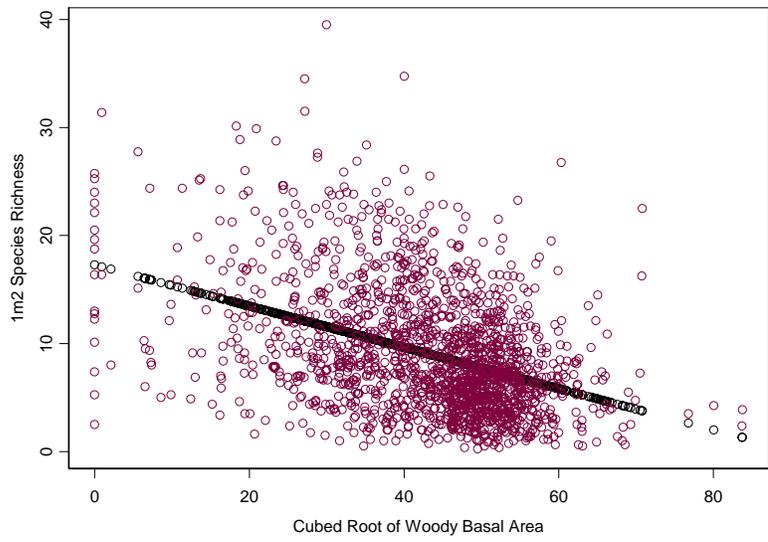


Figure 5.1.5: Plant species richness and woody basal area at 0.1 m²

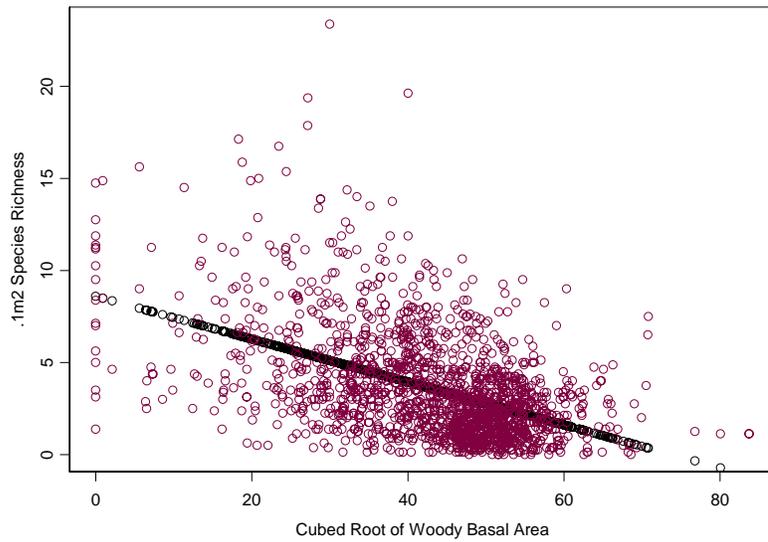
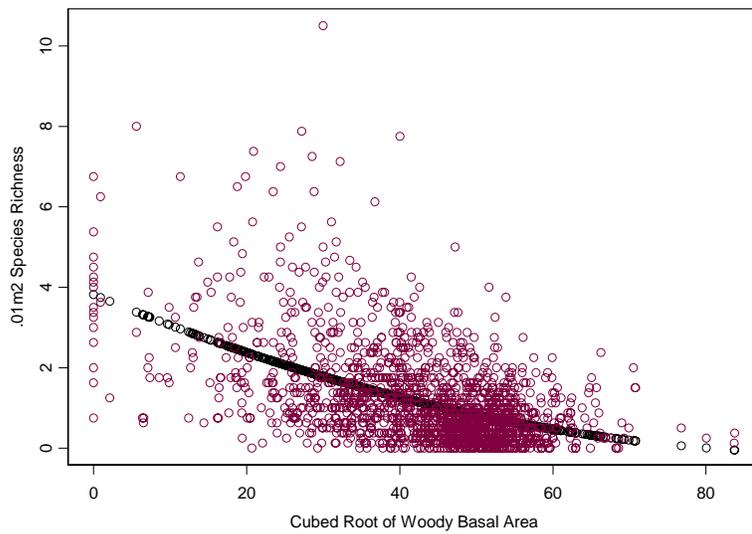


Figure 5.1.6: Plant species richness and woody basal area at 0.01 m²



Figures 5.2.1-5.2.6: Plant species richness and soil pH at 6 scales (1000 m², 100 m², 10 m², 1 m², 0.1 m², 0.01 m²) across all 1662 plots. Note that the y-axis varies with the range of the species richness.

Figure 5.2.1

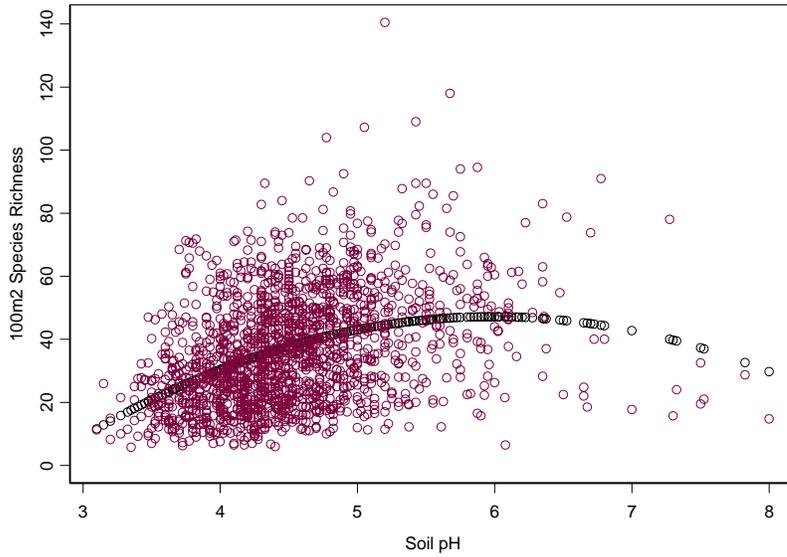


Figure 5.2.2

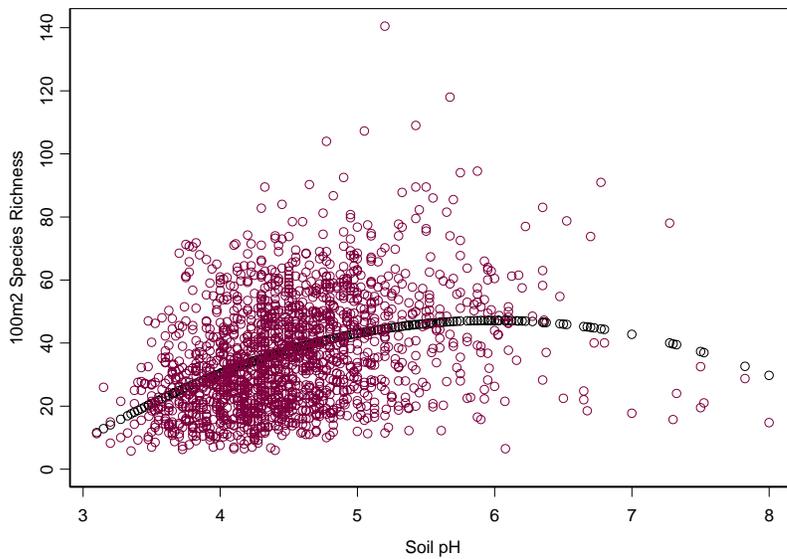


Figure 5.2.3

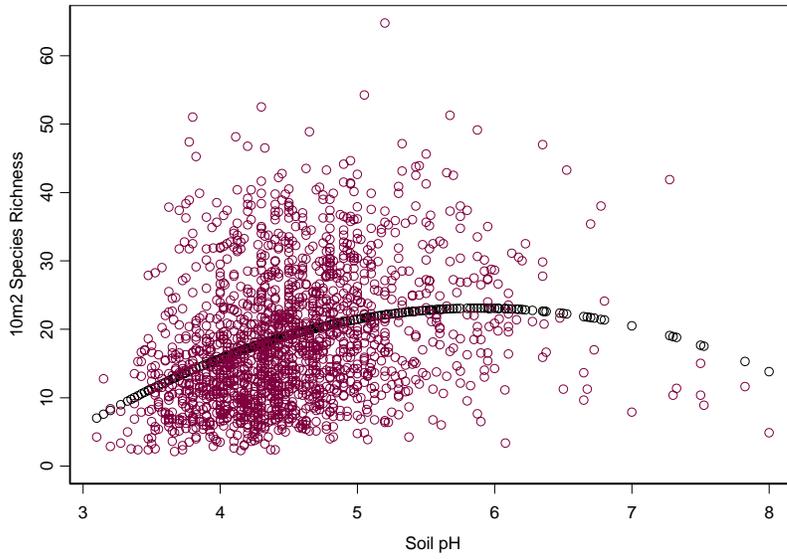


Figure 5.2.4

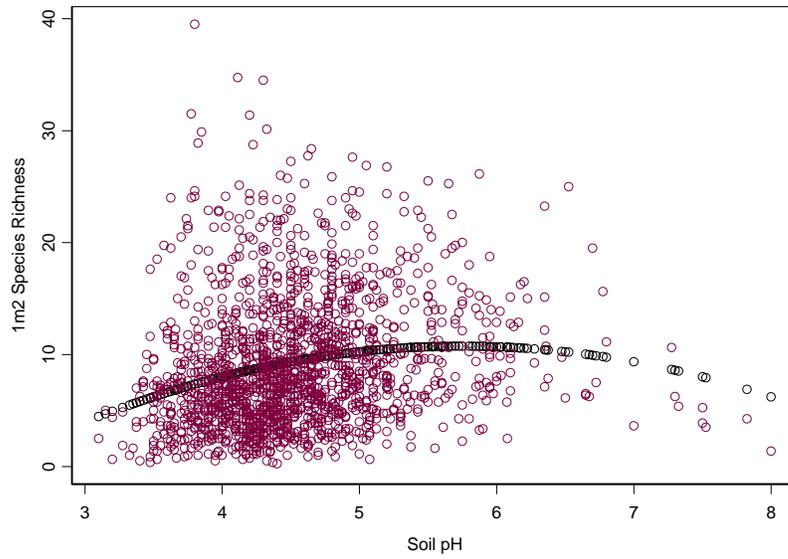


Figure 5.2.5

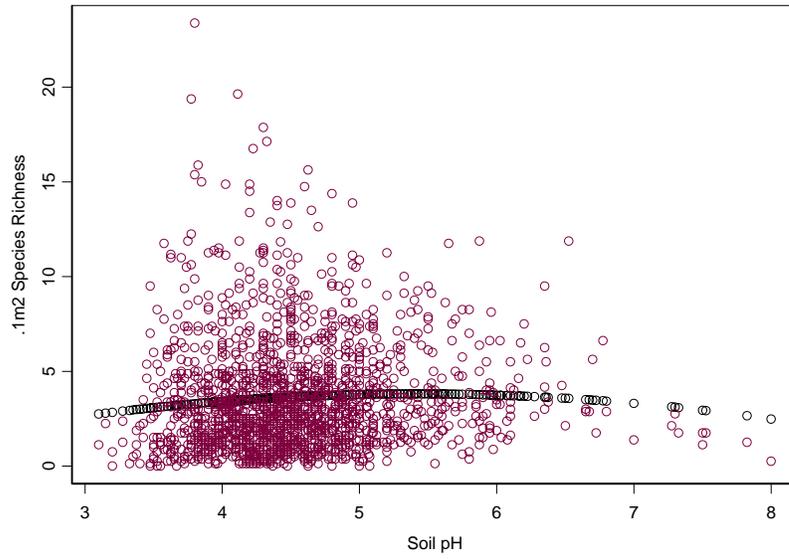
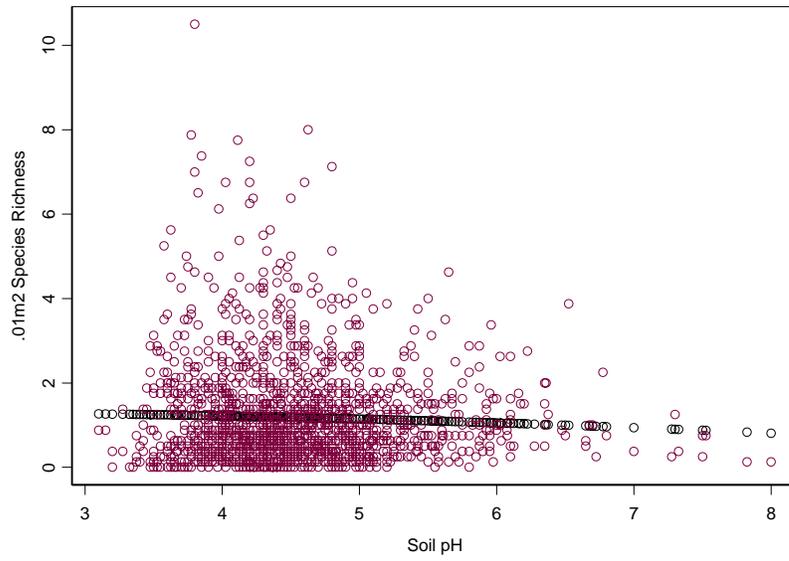


Figure 5.2.6: Plant species richness and woody basal area at 0.01 m²



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CHAPTER 6

MULTISCALAR APPROACHES TO PLANT DIVERSITY ACROSS THE SOUTHEASTERN UNITED STATES

The number of species that occur at a given site is more than merely a number. The species is a fundamental unit in the study of ecology and evolution. The presence of a plant species represents the ability to arrive at and occupy a location, or even a niche. Studying plant species diversity at a local site may provide insight into the shared or diversified processes which shape species distributions. Local patterns of co-existing plant species may be defined by local interactions such as competition (Tokeshi 1999) or stochastic variation (Fridley *et al.* 2006). Across a region, the occurrence of species may be the product of larger-scale processes: climate change, evolutionary events or long-distance dispersal. Reconciling the various patterns and processes that are related to plant species diversity at different scales is essential to the field of plant ecology.

Linking local and regional patterns of species diversity can facilitate the evaluation of the underlying processes that shape diversity at different scales (Rosenzweig 1995). While local species interactions are often studied at the local scale, relating regional richness to local richness can provide insight into how local interactions are influencing local richness. The group of species from across the region that may occupy a local site is the species pool. The environmental factors or ecological processes that result in a species absence from a site may be studied by comparing the species pool for a site (all the species that could be at the site) to the local richness (all the species that are at the site). The species pool, a subset of the

regional species, provides a conceptual link between the regional flora and local plant diversity

The estimation of a species pool from the regional flora has been approached using two types of data: ecological and phytosociological (Pärtel *et al.* 1996). These data may be used to interpret the suitability of local habitat for individual species. Habitat criteria, whether ecological or phytosociological, will often benefit from the addition of range criteria. Delimiting membership in the species pool can be achieved by using range and habitat criteria to support the likelihood that a species will be able to arrive at and survive at a site. Dupré (2000) demonstrated that Sorenson's index of similarity could be modified to evaluate the relationship between the species assigned membership in the species pool and the species that actually occur in the study area. Dupré's type-I and type-II error metrics assess the underestimation and overestimation of species that could occur across an area, given actual species occurrence data. Dupré's type-I error is associated with rejecting species pool membership for a species that actually occurs at the site. This may occur due to habitat or range criteria that are too stringent, although mass effect from a nearby source population could result in an unexpected species occupying a sub-optimal site at the time the site is surveyed. When the null hypothesis of species pool membership is accepted for a species that is not found at the site, this increases the type-II error metric (Figure 6.1). This is not a grievous error, because stochastic variation may contribute to a species being absent from a site that it is fully capable of occupying.

For local sites across the southeastern United States, species pools derived from ecological data performed better than pools from phytosociological data with respect to the Dupré metrics and their derivatives (Chapter 3). Phytosociological data is reflective of the

known co-occurrences of species. Since these co-occurrence patterns may already bare the imprint of local species interactions, phytosociological data should be avoided as species pool criteria when possible. Unfortunately, the availability of comprehensive information on the environmental tolerances of individual species is limited and few studies have been able to actually build species pools from ecological habitat criteria. Combining data from multiple sources may produce species pools that are more capable of predicting the plants able to occupy a site than the component datum

The ability for a plant to occupy a site might be prohibited if the niches are saturated with species. The most species rich sites may reflect an efficient partitioning of the niche space leaving no available resources for new species. While experimental work has demonstrated that certain species rich assemblages may be resistant to invasion, there has been limited support for species saturation from observational studies (Stohlgren 2003). When a community is saturated with species the relationship between local and regional richness may exhibit a curvilinear pattern where the richest areas or regions support proportionally fewer species (Terbourgh and Faaborgh 1980). Across the Southeast there was no sign of saturation when 0.1 ha plots were compared to species pool estimates, regardless of community type (Chapter 4). The relationship between native and non-native species at these sites was not indicative of a fortified species rich native habitat. Instead, the sites with the greatest diversity appear to be the sites most likely to harbor non-native species. This suggests that niches are not saturated and that the environmental conditions or resources which support a diverse native flora support a diverse non-native flora. The long-term effects of this relationship will be telling.

Across the U.S. over 5,000 introduced plant species have escaped into the wild and non-native weeds are reportedly invading 700,000 ha a year (Pimentel *et al.* 2000). While today the non-native and native species may actually be combining to increase plant diversity in species rich natural areas, the effects of competition brought by these new species with unique evolutionary lineages may be yet to come. In anthropogenically-disturbed sites the relationship between local species richness and the species pool does not exhibit the positive relationship found in natural areas. The species pool criteria that adequately represent native species may not be suited to the non-native species which are found in greater abundance at disturbed sites. The application of pesticides and fertilizers near the disturbed sites could provide another possible explanation for why the species pool-local richness relationship is decoupled. Reduction in herbivory or predation and the increased availability of nutrients could both alter the way species respond to their environment. If plant species are responding differently to environmental conditions then the ranges of environmental tolerances used to determine species pool membership will be inaccurate.

The way that plant species relate to local (< 0.1 ha) and landscape-scale (1 km²) factors can affect observed richness patterns at multiple scales. When productivity is related to diversity using different local or landscape-scale estimators, the resulting productivity-diversity relationship is different (Chapter 5). The most parsimonious models of the productivity-diversity relationship incorporate several estimators of productivity from the local and landscape-scale factors. When local and landscape-scale estimates of productivity are compared to richness at values of 1000 m² to 0.01 m², there is not a clear relationship between the scale of productivity estimate and the scale at which it affects richness. As the productivity-diversity relationship is calculated at scales below 1000 m², the relationship

changes as a result of how productivity is estimated, but not due the scale at which productivity was estimated.

Multiscalar approaches to plant species diversity are essential to understanding how ecological processes shape patterns of diversity. Using the species pool as an ecologically-relevant subset of the regional flora provides a tool for better understanding ecological factors affecting local species diversity at the local scale and beyond. By integrating local and regional-scale diversity into ecological studies there is the potential to uncover ecological relationships that might not be obvious at a single scale. Continued collection of richness and environmental data at multiple scales will lend itself to the construction of comprehensive diversity models capable of testing ecological theories at several scales.

FIGURES

Figure 6.1: Conceptual diagram of type-I and type-II error (*a la Dupré*)

H_0 = the species is a member of the species pool	True H_0 : Species occurs at the site	False H_0 : Species does not occur at the site
Reject the H_0	Type I Error	Correct
Do not reject the H_0	Correct	Type II Error

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