

PLANT FUNCTIONAL TRAITS AND COMMUNITY ASSEMBLY AND STRUCTURE

by

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(Under the Direction of Stephen P. Hubbell)

ABSTRACT

Understanding how plant species coexist and interact with their biotic and abiotic environment remains a key goal of community ecology. A growing knowledge of plant functional traits has led to their increasing use in studies of community assembly. This dissertation addresses questions of trait evolution and community assembly from both theoretical and empirical perspectives.

Using simulations, I explored the interacting impacts of species richness, habitat heterogeneity, multiple, linked traits, and varying levels of dispersal limitation on trait evolution and species persistence in an ecological community. Fine-scale habitat heterogeneity led to broad ecological equivalence and long-term species persistence, while the outcome of simulations with coarse-scale heterogeneity depended on other factors. These findings differ substantially from prior work, likely because we implemented the unique combination of spatially explicit interactions along with using a genetical model of trait evolution.

Most current work studies considering community assembly from the perspective of functional traits have been based on species mean trait values, minimizing the importance of intraspecific variation. In this study, I examined the structure of a temperate forest in detail with relation to five leaf functional traits. There is a strong intraspecific plastic response to light

availability in these traits, as well as substantial unexplained intraspecific and even within individual variation. This broad range of intraspecific trait values translates to strong interspecific overlap in trait values, suggesting most of the tree species within the studied forest share a common strategy with respect to these leaf functional traits. These results also call attention to the importance of considering individual-level variation in studies of community ecology. When these same traits are considered in a spatially explicit manner, there is some evidence supporting clustering of individuals with more similar traits than expected by chance, as well as many traits that appear randomly placed across the landscape. Combining the major temperate forest dataset with more limited data from a tropical forest, I attempted to address competing hypotheses of niche breadth and overlap in relation to the latitudinal gradient in species diversity. While data continues to be collected on this part of the project, initial analysis of the data suggests that some traits behave differently in the species-rich tropical forest than in the temperate system, but overall, niche breadth seems to be similar in the two systems.

INDEX WORDS: Community assembly, neutral theory, niche theory, limiting similarity, functional traits, functional ecology, community ecology, Barro Colorado Island, Panama, Belize, Thompson Mills Forest, functional equivalence, trait evolution

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DEDICATION

To my mother, Joyce A. Lake, and my wife, Julie L. Whiston

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

The origin and maintenance of species diversity remains a contentious and unresolved issue in understanding patterns of biodiversity (Wills *et al.* 2006; Wright 2002). The fundamental questions still remain – how do species make their living and coexist? Do species survive, as believed for years, through fine-scale niche differentiation, or, as more recently proposed, by sharing a common phenotype with their neighbors, giving no one species a strong upper hand? How is variation distributed among and within species? Do ontogeny or canopy position influence traits, or can a species (or individual) be well described by a single mean trait value? How is it that in species-rich tropical tree communities, hundreds of species can co-exist, while temperate forests only have at most a few dozen species of woody plants? This dissertation explores these questions using several different approaches.

Theories of community assembly

The advent of neutral theory in ecology (Hubbell 2001) has rekindled interest in the hypothesis of limiting similarity because it bears directly on the neutral-non-neutral debate. A central tenet of classical theory in community ecology is that coexistence requires that species exploit limiting resources differently from one another (Grinnell 1914 and 1917; Elton 1927; Gause 1934; Hutchinson 1957, 1959; MacArthur and Levins

1967; Tilman 1982). These classical theories posit that ecological communities are structured by competition. Despite decades of extensive and largely theoretical debate on this question, there are still relatively few empirical studies of within- and among-species distribution of variation in functional traits among coexisting species, particularly in plant communities. There are almost no tests of the hypothesis of limiting similarity in plant communities. However, a recent study of one plant community (Stubbs and Wilson 2004) found inconclusive evidence the authors claimed supported limiting similarity in some traits examined, but the study suffered from a lack of cross-community comparison, and substantial risk of type I error due to the large number of tests performed on the same dataset.

Under classical niche theory, as the number of species in a community goes up, either the total niche volume for the community must be larger, or else niches must become narrower to allow for coexistence of additional species. In modern terms, we can define niches in part by the collection of functional traits borne by the species. In species-rich tropical forest tree communities, hundreds of tree species co-occur within a relatively small area. Because of the importance of spatial structure in sessile plant communities, if functional trait differentiation is important to coexistence in these communities, then one should find greater trait differentiation of plants that grow in closer proximity to one another, i.e., as neighbors, than in random samples of these communities. Ecologists have argued that a fine partitioning of light and a greater range of light intensities in the tropics could help explain the higher tree diversity in tropical forests (e.g., Ricklefs 1977; Denslow 1980; Orians 1982). Schwilk and Ackerly (2005)

and Tilman (2004) argue, however, that limiting similarity and niche differentiation can and often will arise even with a significant role for stochasticity.

In contrast, Hubbell (2001) and colleagues argue that all this changes under strong dispersal and recruitment limitation. Dispersal and recruitment limitation mean that species fail to disperse to and/or recruit in all sites favorable to their survival and growth. Hubbell *et al.* (1999) found strong dispersal and recruitment limitation in a tree community in Panama, which they argued extensively delays competitive exclusion. In theoretical models, strong dispersal and recruitment limitation permits many species to coexist essentially indefinitely, even in the absence of limiting similarity (Hurtt and Pacala 1995). Hubbell (2006) has recently shown in model communities that under persistent dispersal and recruitment limitation, species can evolve functional equivalence easily and often, converging on traits adapting them to those environments that they most commonly experience over their evolutionary histories. He argues, for example, in shady, closed-canopy forests, a majority of species should evolve shade tolerance. Moreover, selection on trait character displacement may weaken in species-rich communities because pairwise encounter rates between any two species are low (Hubbell and Foster 1986). This hypothesis would predict opposite results from those of niche theory—namely, greater phenotypic divergence in a relatively species-poor temperate forest than in a species-rich tropical forest.

Weiher and Keddy (1995) offer another hypothesis, which they call environmental filtering. They suggest that plant species will tend to be filtered and sorted according to their respective environmental requirements, with the result that more similar species will occupy more similar habitats. The result should be a clustering of

individuals with similar requirements, and, presumably, similar functional traits. Because this theory operates independently of species richness, only habitat diversity at a given spatial scale should determine overall morphological differences among coexisting species.

Plant Functional Traits

Plant functional traits may be defined as “any attribute that has potentially significant influence on establishment, survival, and fitness and ... focus[ing] on those traits related to the ability to acquire, use, and conserve resources (Reich *et al.* 2003).” Capture of sunlight and the resulting assimilation of carbon are critical to the success of any plant. The morphological and physiological traits related to light capture certainly comprise a major component of those that affect a plant’s ability to acquire, use, and conserve resources, and unquestionably impact survival and fitness. Measuring variation in morphological and functional traits as a surrogate of niche has been a common practice since Hutchinson (1959) and Van Valen (1965), although that approach has mostly been applied to animal systems. The concept of limiting similarity was devised for morphological traits in animals (MacArthur and Levins 1967). Variation in morphological traits has also been used to measure niche space in plants, though much less frequently (Cody 1986; Wilson 1999; Stubbs and Wilson 2004). All these approaches assume that the measured morphological and functional traits have some adaptive significance to the species.

A comprehensive search of the literature has turned up only a single study of a plant community that used a similar approach to the one used here (Stubbs and Wilson

2004). This was a study of a sand dune community in New Zealand. The authors used a variety of plant morphological traits related to water, nutrient, and light acquisition to examine questions of limiting similarity among dune species. Of 670 tests performed, 54 showed significant results for limiting similarity, while three were significant in the direction of character convergence. Although the authors concluded that their study provided “the most convincing support for the theory of limiting similarity” in a plant community, over 90% of their statistical tests were non-significant, so Type I error may explain many of these supposedly significant results ($54/670 = 0.08$). The analysis was also static, and did not evaluate how variation in individual performance (survival, growth) correlated with trait variation, and did not consider relative degrees of limiting similarity in different communities. Further, their different approaches to testing these ideas did not produce robust results in terms of traits or species overlapping.

Several researchers have considered the distribution of leaf morphology either within or among communities, though most of the research was not couched in the theoretical background of community assembly. Some larger scale studies have shown some support for habitat filtering. Halloy and Mark (1996) found morphological convergence among species in similar alpine sites on different continents, and greater differences among sites of differing altitudes on the same continent than among similar sites on different continents. Schneider *et al.* (2003) found altitudinal gradients in some leaf morphological traits in Venezuelan forest communities, but few differences among stands of different ages, suggesting a limited role for habitat filtering for disturbance driven traits.

In contrast, some have found support for niche differentiation, particularly within specific genera. Cavender-Bares et al. (2004a, 2004b) concluded that Florida oak species were partitioning niche space finely in relation to habitat usage and functional traits. Davies (1998, 2001) showed that coexisting pioneer species in the tropical genus *Macaranga* were partitioning a continuum of niche-space in relation to photosynthetic traits, though the study focused more on mean species values than trait overlap.

Holscher *et al.* (2004) found that eight Asian pioneer species differed significantly from one another in leaf morphology, suggesting a continuum of trait values even within this functional class. Kappelle and Leal (1996) demonstrated that leaf nutrient levels decrease along a successional gradient, while leaf morphology is less impacted by successional status of the forest. Bragg and Westoby (2002) found that smaller-leaved understory species in a sclerophyllous forest tended to need higher light levels than larger-leaved species, while Ackerly and Donoghue (1998) found no such relationship among temperate species within the genus *Acer*.

Community Assembly from Functional Traits

Recent developments in functional ecology offer a promising approach to the problem of scaling attributes of individuals to community assembly and dynamics. Specifically, one must consider not just the species in a community, but the diversity of functional traits those species represent (Duarte *et al.* 1995; Diaz and Cabido 1997; Weiher *et al.* 1999; Lavorel and Garnier 2002; Chapin 2003; Diaz *et al.* 2004). Functional traits embody the mechanisms through which plants interact with their biotic and abiotic environment and reflect fundamental ‘niche axes’ which characterize the

leading dimensions by which plants differentiate from one another (Westoby *et al.* 2002). From this perspective, functional traits of plants entail multiple direct and indirect pathways, as well as feedbacks between structure and function, organisms and environment. The impact of functional traits on whole plant growth and survival is also well-established (i.e., Poorter and Bongers 2006; Laurence *et al.* 2006). However, a more generalized theory relating plant traits and the structure and dynamics of plant communities across diverse ecosystems has remained an elusive “Holy Grail” for plant community ecology (Lavorel and Garnier 2002). Shipley *et al.* (2006) have attempted built a predictive model of community assembly from functional traits using maximum entropy techniques, and used it rather successfully to predict community composition over a chronosequence of abandoned vineyards. However, the model has both problems of circularity and generality, having failed to accurately predict abundances in a more diverse temperate forest system (Lake *et al.*, in prep).

Key Questions

These efforts have left a number of fundamental questions that must be addressed both empirically and theoretically in order to move to a more general model of community assembly from plant functional traits. Specifically, we ask:

1. Is it appropriate to simply treat species as present or absent in a community when considering trait overlap and limiting similarity, or can a more complete picture be developed by considering abundance or other weighting factors?
2. Is it possible for ecological equivalence to evolve within a defined community, and if so, can equivalent or near equivalent species persist in the long term in such a

community?

3. How are trait values distributed within and among individuals and species in a temperate tree community?

4. How are traits distributed spatially among individuals in a temperate tree community, and what can that distribution tell us about the way ecological communities are assembled and structured?

5. Can the latitudinal gradient in species diversity be explained, at least in part, by increased specialization in a species-rich tropical forest system?

In attempting to answer each of these questions, we employ different methods to attempt to bring ecology a bit closer to that holy grail of understanding how ecological communities are assembled, of understanding why and how species are able to coexist, in spite of many apparent similarities.

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CHAPTER 2

COMMUNITY NICHE OVERLAP ESTIMATES: WEIGHTING FOR SPECIES IMPORTANCE IN A COMMUNITY¹

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Abstract

1. Recently proposed non-parametric measures of niche overlap for quantitative functional traits provide a new approach to questions of trait overlap among coexisting species (Mouillot *et al.* 2005). However, these community overlap indices weight all species as equally important in the community, regardless of their relative size, abundance or other impact on the community, which tends to overestimate the extent of community niche overlap.
2. To address fundamental questions of community assembly, particularly for communities of organisms varying in abundance or size, these measures can be extended to give a more complete picture of niche overlap in the community. In this research, we propose an extension to these new indices that allows weighting for community importance of species.
3. We explore the impact of different weighting methods on niche overlap estimates in a temperate forest tree community. Weighting by either species abundance or total basal area of a species, we re-estimate community niche overlap to be only about half of the community-level overlap obtained from the unweighted analysis (0.23-0.25 vs. 0.46). Although we found similar total community overlap from these two weighted approaches, the source of that overlap was different, and the similarity between these measures is coincidental.
4. These weighted indices and the application of appropriate measures of community importance provide another tool to further our understanding of community assembly.

Keywords: Kernel estimator, niche overlap, community assembly, functional traits

Introduction

Increasingly, the study of community ecology is focusing on the distribution of functional traits among species (McGill *et al.* 2006), examining the effect of traits not just on pairwise interactions among co-occurring species, but also looking at community-wide patterns. The fundamental question is the degree to which the assembly of particular communities is explicable in terms of functional traits of member and non-member species. In classical terminology, this question was framed in terms of the degree of niche overlap among member species; but this question can also be framed in terms of the similarity or dissimilarity of key functional traits involved in resource capture, environmental tolerance, and life history attributes, such as fecundity and colonizing ability. We know that simply considering pairwise competitive interactions cannot tell us what species will comprise a community or at what abundances. Nonetheless, until recently, there were few good quantitative tools to help us address questions of the species composition of entire communities.

Mouillot *et al.* (2005) have proposed a family of non-parametric indices to measure niche space and overlap based on quantitative functional traits. These indices provide a new tool for measuring both pairwise overlap and calculating a community index of niche overlap. The flexibility allowed by the continuous and non-parametric nature of these measures is a significant advance for quantitative measures of niche and for furthering understanding of community patterns of coexistence. These indices consider not only mean niche values, but also the variation around the mean, and the resulting trait overlap, with no prior assumptions of how trait variation is distributed.

Thus, we no longer need to force a fit of data to a particular pre-conceived statistical distribution to address questions of niche or trait overlap.

In the context of studying community assembly, however, such indices that calculate average niche overlap for a community do not yet capture some of the most important aspects of community structure—notably, the abundance or relative importance of each species in the community. The current Mouillot *et al.* (2005) method evaluates community niche overlap based on presence/absence data alone. It does not weight the importance of overlap by relative species abundance or relative biomass, even though some species might be orders of magnitude more abundant than other species. The result is that these indices weight rare species on a per capita basis much more heavily than common species in terms of the total amount of niche or trait space they occupy. This in turn skews the true picture of community niche structure. This problem arises in the Mouillot approach because the area under each species' niche breadth curve is normalized to unity. Few if any natural communities have an even distribution of species abundance or any other measure of importance; rather, most communities are dominated by a relatively few species, and many more are rare within the given community (ie, Hubbell 2001).

A key assumption behind the hypothesis that coexisting species exhibit limiting niche similarity and defining niches in terms of functional traits is that these traits affect the acquisition and use of limiting resources. Since functional traits are defined by Reich *et al.* (2003) as “any attribute that has potentially significant influence on establishment,

survival, and fitness....,” it is probable that, simply by definition, they should be closely related to classical niche axes for a species. If the distribution of functional traits among species reflect underlying differences in resource uptake and use (necessary if one is to study the question of limiting similarity of functional traits), then we must also consider the abundance (or some other measure of importance) of the species and therefore, their functional traits.

Relative species abundance provides one possible measure of the relative impact of a species in an ecological community. However, abundance is not the only or necessarily the best representation of the relative resource use of a given species. For example, in a forest tree community, adult individuals of a canopy species likely utilize many times the amount of resources of an individual of an understory species. In this case, biomass or a biomass surrogate such as a plant’s basal area or a scaleable linear measurement in animals, may be a better weighting factor. Or, perhaps, a measure such as importance values (an index of relative frequency, dominance, and density) would better describe a species’ resource use. These considerations lead us to propose some extensions to Mouillot *et al.*’s (2005) indices of community niche overlap that allow a more complete view of the distribution of resource use among species in a community.

Original niche metric described

As originally proposed (Mouillot *et al.* 2005), the index of niche overlap utilizes kernel estimators to describe the distribution of a continuous trait x , with n data points:

$$\hat{f}_h(x) = \frac{1}{n} \sum_{i=1}^n \frac{1}{h} K\left(\frac{x - X_i}{h}\right) \quad (1)$$

The standard normal density function K is used to represent each data point; note that using a normal density function here does not assume normality in the data, only in the error around a given datapoint (ie, Stine and Heyse 2001). Bandwidth, which controls the smoothness of the distribution, is represented by h . We chose to follow the lead of Mouillot *et al.* (2005) in selecting an estimator of bandwidth, $h = 1.06\sigma n^{-1/5}$, where σ represents the standard deviation of the dataset.

$$K\left(\frac{x - X_i}{h}\right) = \frac{e^{-\left(\frac{x - X_i}{h}\right)^2 / 2}}{\sqrt{2\pi}} \quad (2)$$

Next, pairwise overlap indices can be calculated for trait t for species i and j , estimated as the area under the lower of the two population density functions:

$$NO_{Kt}(i, j) = \int \min(f_{it}(x), f_{jt}(x)) dx \quad (3)$$

The authors of the original index go on to demonstrate methods for dealing with multiple traits, including discounting non-independent traits using correlation coefficients, producing NO_{Kw} , an estimate of niche overlap in many niche dimensions. They then extended this index to the full community by producing a community niche overlap estimator, $NO_{K,community}$:

$$NO_{K,community} = \frac{\sum_{i=1}^{S-1} \left(\sum_{j=i+1}^S NO_{Kw}(i, j) \right)}{\frac{S(S-1)}{2}} \quad (4)$$

Materials and methods

Niche overlap in a community

In the Mouillot *et al.* (2005) method the area under the niche curve (“kernel”) describing the frequency distribution of trait values over individuals of each species is normalized to unity. We suggest modifying this method by weighting the species kernels by the relative abundance of the species in the community. To make this modification, we simply multiply the kernels of each species by a relative weighting factor. These weights must sum to one. With no loss of generality, represent this weighting factor by g_i/G , where g_i represents the weight for species i , and G the sum of all g_i across all species in the community. Finally, multiply each species’ functional kernel by the total number of species in the community. This multiplication normalizes the total functional trait space in the community so that it sums to an integer equal to the number of species, S , but a sum that is now weighted by the relative importance of species in the community. This modification makes cross-community comparisons of niche overlap more meaningful and less sensitive to rare species effects that have little or no significance to community assembly. It also allows the user to adapt the overlap metrics to his or her own study system, and weight individuals according to the relevant metrics.

Specifically, the modified species level kernels in the community indices are given by kernel density:

$$\hat{f}_h(x) = S \frac{g_i}{G} \frac{1}{n} \sum_{i=1}^n \frac{1}{h} K\left(\frac{x - X_i}{h}\right) \quad (5)$$

Note that kernel densities produced by this model do not integrate to one, because species kernels are weighted by species importance. As a result, it is possible to calculate

pairwise overlap values in excess of 1.0, although the community-wide overlap index ought to never exceed 1. Therefore, this method is appropriate for assessing niche overlap at the community level, but not for pairwise species overlap calculations for across the range of a species (where relative abundances and biomass become less relevant). Results showing pairwise overlaps used in calculating the final community niche overlap index should thus be interpreted with extreme caution; they are better used to demonstrate the relative contributions of pairwise interactions to the community index than as a “stand-alone” metric.

Mathematically, the only change needed to the original work is in the initial calculation of population trait kernel estimators. By weighting these kernel estimators, we can then use already developed mathematical tools previously presented in Mouillot *et al.* (2005) to proceed in calculating community overlap estimates.

Temperate forest tree community

We illustrate the use of these modified indices, as well as why these modifications are important, by analyzing a dataset on leaf traits in a temperate tree community, and comparing three different approaches. The first utilizes an unweighted analysis of species, as described in Mouillot *et al.* (2005). The second weights species by relative abundance in the sample community, and the third utilizes stem basal area as a surrogate for biomass. For all three analyses, we use data from thirteen tree species sampled from a forest tree community at Thompson Mills Forest, Braselton, Georgia (See Table 1 for a list of species, their relative abundance, and basal areas in the study plot). Trait values

were sampled broadly from trees within three 0.4-ha. transect plots in the forest; however, the present analysis was restricted to a single 20x20 m quadrat at the base of a single transect to illustrate the impact of these weighting factors with a relatively simple system, and one that represents the likely area of among-individual interactions (see Hubbell *et al.* (2001), for example).

Analyses were restricted to a single trait, specific leaf area (SLA = one sided leaf surface area/leaf dry mass), measured according to standard procedures (Cornellisen *et al.* 2003), to make our methodological point. SLA is often associated with leaf level gas exchange, leaf lifespan as well as whole-plant growth rate (see Reich *et al.* 1999; Niinemets 2001; Wright *et al.* 2004). This paper is therefore not about the actual niche assembly of the tree community at Thompson Mills, but rather about the value of weighting community overlap indices by species importance. Further detailed analysis of community niche structure in this forest can be found in Lake (thesis chs. 4-5).

Results

Unweighted analysis

Specific leaf area (SLA) showed wide variation in cross-species overlap within the given community, ranging from 0 to 0.876 (Table 2 shows all unweighted pairwise overlaps). The species showing the least overlap with others is *Kalmia latifolia*, an evergreen understory shrub with very thick leaves. The SLA distribution of this species is very narrow, indicating strong similarity among the leaves sampled (fig. 1). Because of the narrow range of trait values, overlap was necessarily low with other species with

broader trait distributions. Canopy trees in general, particularly species in the genus *Quercus*, showed considerable overlap in their SLA distributions with one another, as did most sub-canopy species (i.e., *Acer leucoderme*, *Cornus florida*, *Crataegus* spp.). Community niche overlap was estimated at 0.46.

Weighted by abundance

When considering abundance, pairwise overlaps (Table 3) among the three most common species (*Acer leucoderme*, *Fagus grandifolia*, *Crataegus species*) accounted for much of the total community overlap. This is not a necessary result, because if species exhibited strong limiting similarity, the most common species should be segregated in functional trait space. Overall community niche overlap for SLA was estimated at 0.26.

Weighted by basal area

Not surprisingly, when using basal-area weighting, the community overlap index was driven by canopy tree individuals within the study area. Notably, area weighted pairwise overlap (Table 4) among the three species of *Quercus* and between *Fagus* and *Oxydendrum* were particularly high, while small individuals and understory species typically contributed relatively little to trait overlap simply because of their small size. Overall community niche overlap for SLA was 0.23.

Community level overlap estimation

Community overlap estimates varied widely (0.23-0.46) depending upon the species weighting system used. Unweighted overlap estimates as proposed by Mouillot

produced the highest (0.46) overlap, while weighting for a species' basal area produced the lowest estimate of trait overlap (0.23). This composite community mean, however, masks the variation in contribution of individual species pairs to overall niche overlap. Individual species pairs varied widely in their contribution to community-wide means of overlap depending on the weighting factors used.

Discussion

The aim of this paper is to illustrate the value of incorporating community importance of species in estimating overall community levels of niche overlap, particularly in communities where size or abundance vary widely. If we adopt a functional niche approach as proposed by Rosenfeld (2002) and followed in Mouillot *et al.* (2005), that is, use functional traits of a species as a surrogate for resource use, then it is valuable to consider more than simply the presence or absence of a species in a community. The abundance, biomass, or other measure of importance of species within a community is important to evaluating the relative exploitation of a given resource by those species. The unweighted estimators of niche overlap proposed by Mouillot *et al.* (2005) give equal weight to all species, and thus tend to inflate estimated niche overlap by over-emphasizing the contribution to niche overlap from rare species. When used to calculate community overlap estimates, the unweighted approach tacitly assumes that all species are utilizing a comparable total amount of resource, regardless of size, abundance, etc. The weighted overlap indices proposed here provide a more refined look at the resources or trait space used by individual species within a community.

This study also highlights the importance of selecting a weighting metric appropriate to the community being studied. Although both weighting methods (abundance, basal area) used here nearly halved the total community overlap index, the source of that overlap reduction is very different. Pairwise overlap between adult canopy trees dominated the overlap when weighting for total stem basal area, whereas highly abundant understory trees dominated the overlap indices when weighting for abundance. This point is well illustrated by considering two canopy tree species (*Nyssa sylvatica* and *Oxydendrum arboreum*), represented respectively in the study plot by a single sub-adult, the other by two adult individuals. When unweighted, the overlap between these two species is over 0.85; but overlap decreases considerably (to 0.26) when weighting by abundance, and even further when weighting by basal area (0.19) (See fig. 2). A similar pattern occurred in two highly divergent species—*Kalmia latifolia* and *Fagus grandifolia*. The SLA distribution of the two species overlap very little, but the effect of the changing relative importance is well illustrated by the changing relative areas under the distributions (fig. 1). Not surprisingly, when weighted for basal area (fig. 1C), the large canopy tree of *Fagus grandifolia* dominated the trait distribution, while the understory shrub, *Kalmia*, showed a very small distribution. While the overlap index is not much affected by this weighting (because of a lack of overlap to begin with), the overall distributions change markedly when weighting by importance measures is included instead of the unweighted analysis (fig. 1A).

We also must carefully consider the assumptions behind and limitations to these indices. While introducing a weighting factor provides a unique opportunity to consider

a species in the context of a particular local community, it also necessarily requires us to consider those traits within the context of the entire community. For example, if we were to consider pairwise trait overlap for two particular species separate from the broader community, but continued to use these weighting factors, the results would be biologically meaningless. In other words, this approach would be a poor choice for considering the trait overlap of two coexisting species; it is only meaningful with regard to the full community in which species have a particular abundance, biomass, etc. Consider the basal area-weighted pairwise overlap values for two understory tree species, *Cornus florida* and *Acer leucoderme*. In an unweighted analysis, their SLA overlaps 0.56—strong overlap, and hardly unexpected in these ecologically similar species. Because of their relatively small stature, however, these two species contribute relatively little to the basal area in the community, and therefore demonstrate “low pairwise overlap” of 0.19 when traits are weighted for basal area. This reminds us that we must regard the community-wide overlap metric as a measure of the total average overlap of the use of trait space, rather than as a summation of equal interspecific interactions.

Another limitation to consider is that these measures (comparable to those originally proposed by Mouillot *et al.* (2005) do not address one of the fundamental problems of species sorting into local communities from a metacommunity. It is possible that species are being competitively excluded from a community because they overlap too much in niche with other species. Equally plausible is the possibility that species are not arriving at a given local community due to dispersal limitation (ie, Hubbell *et al.* 1999). It may be possible to address this issue for rare, potentially transient species by

comparing the distributions for that species inside the study community to values for the species elsewhere, but this is not the primary purpose of these community niche metrics.

The development of weighted community niche overlap indices provides a new tool for studying the relative amount of niche overlap in various communities. It allows us to consider the relative use of trait space by each species within the community, while accounting for issues of abundance, biomass, and other measures of importance. Because of the flexibility of the metric and the weighting, these tools should be useful for a wide range of niche measures—both continuous and discrete—in a variety of ecological communities.

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Table 2.1. Species abundance and basal area within study quadrat.

Species	Abundance	Rel. Abund.	Basal Area (mm ²)	Rel. Basal Area
<i>Acer leucoderme</i>	21	0.42	50783.85	0.08002
<i>Acer rubrum</i>	1	0.02	314.16	0.00050
<i>Cornus florida</i>	3	0.06	9296.76	0.01465
<i>Crataegus sp.</i>	5	0.1	2335.77	0.00368
<i>Fagus grandifolia</i>	5	0.1	150024.40	0.23640
<i>Kalmia latifolia</i>	3	0.06	1665.83	0.00262
<i>Liriodendron tulipifera</i>	1	0.02	44862.73	0.07069
<i>Nyssa sylvatica</i>	1	0.02	9331.32	0.01470
<i>Oxydendrum arboreum</i>	2	0.04	54428.88	0.08577
<i>Quercus alba</i>	4	0.08	74421.97	0.11727
<i>Quercus nigra</i>	1	0.02	145220.12	0.22883
<i>Quercus rubra</i>	2	0.04	91233.42	0.14376
<i>Symplocos tinctoria</i>	1	0.02	706.86	0.00111

Table 2.2. Unweighted cross-species niche overlap, using kernel-based index as proposed by Mouillot et al (2005).

Species	A. <i>rubrum</i>	C. <i>florida</i>	<i>Crataegus</i> <i>sp.</i>	F. <i>grandifolia</i>	K. <i>latifolia</i>	L. <i>tulipifera</i>	N. <i>sylvatica</i>	O. <i>arboreum</i>	Q. <i>alba</i>	Q. <i>nigra</i>	Q. <i>rubra</i>	S. <i>tinctoria</i>
<i>Acer leucoderme</i>	0.324	0.558	0.621	0.688	0.001	0.722	0.811	0.852	0.422	0.122	0.330	0.641
<i>Acer rubrum</i>		0.443	0.560	0.240	0.125	0.504	0.431	0.356	0.675	0.489	0.796	0.610
<i>Cornus florida</i>			0.767	0.374	0.000	0.530	0.546	0.494	0.573	0.170	0.447	0.666
<i>Crataegus sp.</i>				0.039	0.014	0.579	0.586	0.556	0.585	0.291	0.545	0.717
<i>Fagus grandifolia</i>					0.000	0.696	0.749	0.732	0.308	0.074	0.242	0.509
<i>Kalmia latifolia</i>						0.157	0.020	0.031	0.307	0.567	0.235	0.042
<i>Liriodendron tulipifera</i>							0.819	0.810	0.587	0.341	0.520	0.740
<i>Nyssa sylvatica</i>								0.876	0.504	0.191	0.437	0.703
<i>Oxydendrum arboreum</i>									0.438	0.173	0.360	0.650
<i>Quercus alba</i>										0.549	0.780	0.700
<i>Quercus nigra</i>											0.624	0.283
<i>Quercus rubra</i>												0.610

Table 2.3. Weighted cross species niche overlap, using adapted index weighted for species abundance.

Species	A. <i>rubrum</i>	C. <i>florida</i>	<i>Crataegus</i> <i>sp.</i>	F. <i>grandifolia</i>	K. <i>latifolia</i>	L. <i>tulipifera</i>	N. <i>sylvatica</i>	O. <i>arboreum</i>	Q. <i>alba</i>	Q. <i>nigra</i>	Q. <i>rubra</i>	S. <i>tinctoria</i>
<i>Acer leucoderme</i>	0.246	0.788	1.266	1.198	0.034	0.207	0.26	0.494	0.737	0.129	0.392	0.257
<i>Acer rubrum</i>		0.197	0.242	0.132	0.041	0.114	0.113	0.148	0.259	0.128	0.259	0.159
<i>Cornus florida</i>			0.773	0.439	0.00278	0.144	0.177	0.29	0.532	0.0699	0.291	0.216
<i>Crataegus sp.</i>				0.509	0.0262	0.154	0.186	0.333	0.662	0.122	0.381	0.335
<i>Fagus grandifolia</i>					0.0029	0.193	0.253	0.48	0.375	0.045	0.199	0.226
<i>Kalmia latifolia</i>						0.029	0.0091	0.0223	0.308	0.166	0.145	0.016
<i>Liriodendron tulipifera</i>							0.198	0.216	0.168	0.0736	0.138	0.177
<i>Nyssa sylvatica</i>								0.263	0.172	0.0524	0.135	0.185
<i>Oxydendrum arboreum</i>									0.278	0.0772	0.193	0.238
<i>Quercus alba</i>										0.25	0.518	0.231
<i>Quercus nigra</i>											0.192	0.076
<i>Quercus rubra</i>												0.201

Table 2.4. Weighted cross species niche overlap, using adapted index weighted for total basal area for each species.

Species	A. <i>rubrum</i>	C. <i>florida</i>	<i>Crataegus</i> <i>sp.</i>	F. <i>grandifolia</i>	K. <i>latifolia</i>	L. <i>tulipifera</i>	N. <i>sylvatica</i>	O. <i>arboreum</i>	Q. <i>alba</i>	Q. <i>nigra</i>	Q. <i>rubra</i>	S. <i>tinctoria</i>
<i>Acer leucoderme</i>	0.0063	0.1919	0.0483	1.0414	0.0034	0.6290	0.1890	0.9481	0.5170	0.2125	0.4448	0.0144
<i>Acer rubrum</i>		0.0056	0.0061	0.0064	0.0011	0.0064	0.0064	0.0064	0.0064	0.0064	0.0064	0.0061
<i>Cornus florida</i>			0.0470	0.1919	0.0003	0.1919	0.1061	0.1919	0.1919	0.1080	0.1919	0.0127
<i>Crataegus sp.</i>				0.4828	0.0010	0.0483	0.0483	0.0483	0.0483	0.0465	0.0483	0.0124
<i>Fagus grandifolia</i>					0.0026	0.6651	0.1916	1.0345	0.7081	0.2393	0.5949	0.0146
<i>Kalmia latifolia</i>						0.0341	0.0038	0.0164	0.0344	0.0344	0.0344	0.0009
<i>Liriodendron tulipifera</i>							0.1929	0.7255	0.5243	0.3380	0.5912	0.0147
<i>Nyssa sylvatica</i>								0.1929	0.1447	0.1041	0.1383	0.0142
<i>Oxydendrum arboreum</i>									0.5419	0.2719	0.4821	0.0145
<i>Quercus alba</i>										0.9573	1.3206	0.0141
<i>Quercus nigra</i>											1.3599	0.0123
<i>Quercus rubra</i>												0.0134

Table 2.5. Community niche overlap estimates, based on weighting factor.

Weighting Factor	Overlap
Unweighted	0.464
Abundance	0.256
Total basal area	0.230

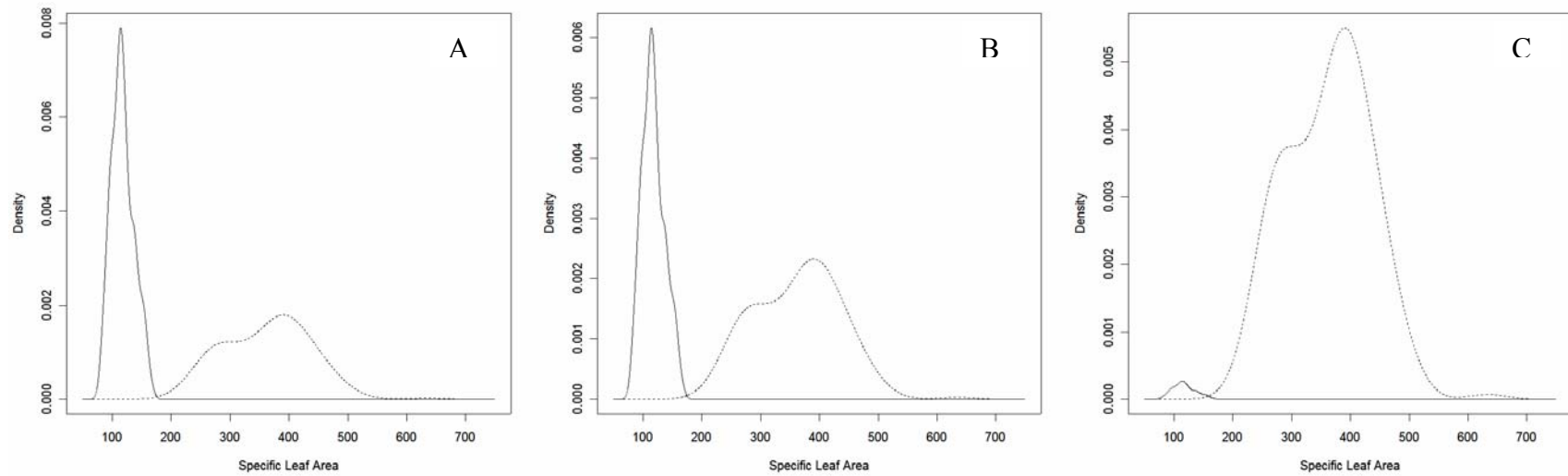


Figure 2.1. Overlap between the same two species, *Kalmia latifolia* (solid line) and *Fagus grandifolia* (dotted line), with three different weighting factors: (a) with unweighted kernel method, (b) weighted by abundance, and (c) weighted by total basal area.

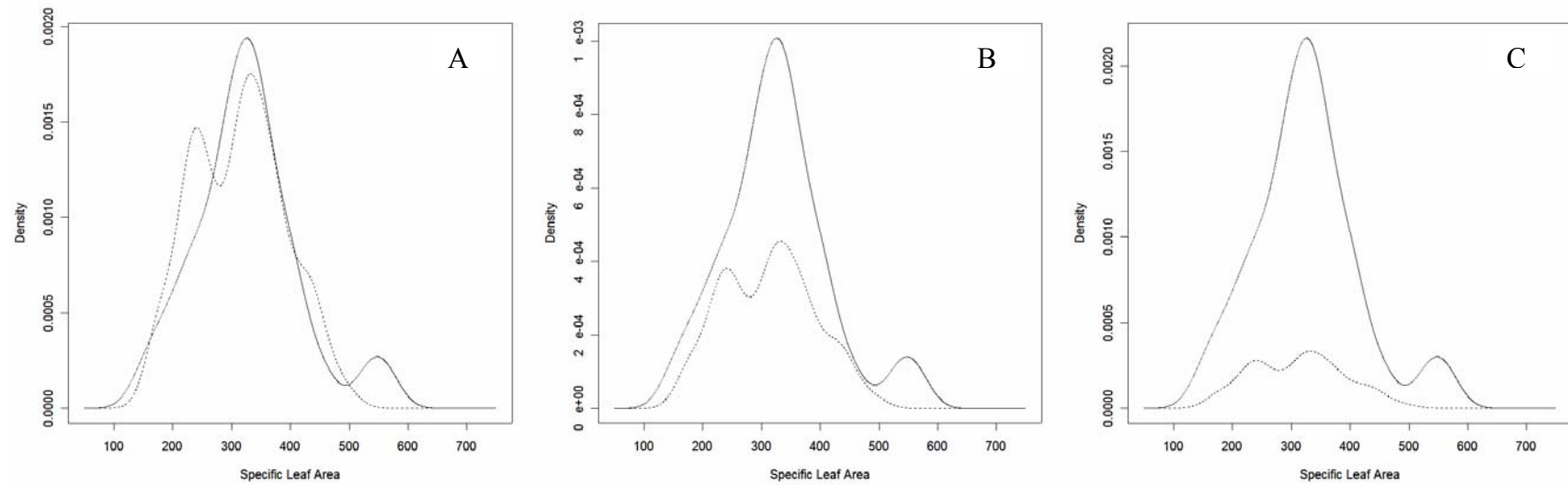


Figure 2.2. Overlap between the same two species, *Oxydendrum arboreum* (solid line) and *Nyssa sylvatica* (dotted line), with three different weighting factors: (a) with unweighted kernel method, (b) weighted by abundance, and (c) weighted by total basal area.

CHAPTER 3

EVOLUTION OF FUNCTIONAL EQUIVALENCE: EXPLORING THE IMPACT OF SPECIES DIVERSITY, MULTIPLE LINKED TRAITS, DISPERSAL LIMITATION, AND SPATIAL STRUCTURE ON TRAIT EVOLUTION IN A MULTI-SPECIES SIMULATION MODEL¹

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Abstract

Understanding how functional traits of species may evolve under varying ecological conditions directly addresses some of the fundamental mechanisms driving community assembly. Traditional ecological theory has posited that species that are too ecologically similar cannot coexist, and that competition should lead to niche differentiation or to extinction of one of the competing species. However, Hurtt and Pacala (1995) suggested that dispersal and recruitment limitation can severely retard competitive exclusion. Hubbell (2006) has shown circumstances that can lead to the evolution of functionally equivalent species that subsequently coexist, seemingly stably, for thousands of community turn-overs. Using simulations, we explore the interacting impacts of species richness, habitat heterogeneity, multiple, linked traits, and varying levels of dispersal limitation on trait evolution and community persistence. We find that fine-scale habitat heterogeneity always leads to broad ecological equivalence and long-term species persistence, while the outcome of simulations with coarse-scale heterogeneity depends on other factors. With weak dispersal limitation and no linkage, many species typically become extinct, and one or two species dominate most of trait and habitat space. With stronger dispersal limitation, and clumped initial species distribution, classical niche differentiation evolves, while random initial distribution of species leads to species displaying multiple ecotypes. So long as dispersal limitation is strong, most or all species persist for the duration of the simulations. These findings differ substantially from prior work, likely because we implemented the unique combination of spatially explicit interactions along with using a genetical model of trait evolution that more closely mimics “real world” plant reproduction.

Introduction

From the beginning of the study of community ecology in the 1880's, coexisting species have been assumed to require a limiting similarity in resource usage and functional traits such that greater similarity would lead one to competitively exclude another (Gause 1934; Hutchinson 1959; MacArthur and Levins 1967). In communities consisting of only a few species, particularly animal communities, this model seems well-supported both theoretically and empirically (e.g., Connell 1961; Werner and Hall 1976; Bengtsson 1989). Limiting similarity and competitive exclusion in spatially structured plant communities is much less well-documented, however, particularly when communities contain more than two or three species (i.e., Fowler 1981; Clatworthy and Harper 1962; but see Stubbs and Wilson 2004).

Recently, neutral theory has challenged this classical paradigm of community niche assembly (Hubbell 2001). By demonstrating strong fits to natural systems with a community model parameterized only with community size, migration rates, and speciation, neutral theory spurred ecologists to delve into the mechanisms resulting in observed community abundance patterns (e.g., Chave *et al.* 2002; Tilman 2004). Although most ecologists continue to invoke niche differences as driving community assembly (see Chase and Leibold 2003; McGill *et al.* 2006), Bell (2001) notes that the patterns predicted by neutral theory can be achieved either through a “strong version”, where species are truly ecologically equivalent, or, alternatively, that the patterns result from a “weak version”, where a combination of underlying mechanisms of relatively weak effect join to produce the observed patterns.

While equivalence in traits is not required for assumptions of neutrality to be upheld (only demographic equivalence is needed, so trait-driven, fitness equalizing trade-offs are not excluded), ecological equivalence in traits coupled with demographic equivalence provides perhaps the strongest evidence for neutral theory. Critiques of neutrality commonly arise from observations that “species are just different from one another”, and while this is true, much more seldom are these trait differences tied to demographic differentiation. While it is possible that stochastic effects or a variety of forces of relatively small effect simply swamp species-level fitness differences (Bell 2001; Hubbell 2001), making functional traits irrelevant to species’ success and leading to the patterns predicted under neutral theory, it is also possible that species are truly “doing the same thing”, at least to a first approximation, and that doing so may be the evolutionarily optimal strategy under certain ecological conditions. Indeed, while ecological equivalence among coexisting trophically similar species is highly controversial for most ecologists, and anathema to traditional views on community assembly, there are demonstrated circumstances under which close competitors (Hurtt and Pacala 1995) or ecologically equivalent species can persist for a very long time (Hurtt & Pacala 1995; Hubbell 2006).

However, most theoretical work has focused on mechanisms of trait divergence among species and coexistence through niche differentiation and tradeoffs (e.g., Tilman 1982; Lehmann and Tilman 1997; Chave *et al.* 2002), arguing that too similar of species would not arise, and if they did, evolutionary forces would either lead to selection for diversification, or to competitive exclusion. Rarely, if ever, has the evolution of traits within a broader ecological community comprised of many trophically similar species

been modeled, and then, it has usually focused on the evolution of trade offs (see Hubbell 2006). Indeed, Lehmann and Tilman (1997) specifically demonstrated that species would tend to evolve unique niches with regular spacing and little overlap in order to coexist. Their model allowed narrow phenotypic shifts in evolutionary time, and sympatric speciation, essentially packing the competition/colonization trade-off axis with species over hundreds of thousands of time steps. In this model community, coexistence was largely limited only by the size of the system. However, the nature of the assumptions on which this experiment was built virtually guaranteed the outcome. Because species were treated as monolithic entities following the species mean closely, most did not have the opportunity to evolve a generalist strategy; furthermore, by modeling trait evolution as incremental changes to phenotypic mean, it would be hardly surprising to find species differentiating into narrow niche space.

Although evolution of functional equivalence and persistence of equivalent species have seldom been modeled, there are a number of hypotheses suggesting circumstances that ought to favor either the evolution of equivalence, persistence of similar or identical species, or both. Perhaps most well-documented of these factors is the role of dispersal limitation in the context of species coexistence. Hurtt and Pacala (1995) demonstrated theoretically that strong and severe dispersal limitation could drastically slow the competitive exclusion of weaker competitors simply by preventing a given species from reaching all of its “ideal” sites.

Gravel *et al.* (2006), in pointing out the role of both niche and neutral processes in structuring communities, showed some circumstances that would tend to favor neutrality in community structure. These included increased neutrality with increasing species

richness (a result also predicted by Hubbell and Foster 1986), increased immigration from outside the local community, a more fine grained environment (results similar to those in Hubbell 2006), and longer local dispersal distances. This last result seems to contradict the work of Hurtt and Pacala (1995), where increasing dispersal limitation increased the persistence of similar species, but it is possible that the differences in grain of environment under consideration may have led to these divergent results. However, the authors again did not use a genetical model of trait evolution.

Hubbell (2006) demonstrated some circumstances under which functional equivalence could arise in a local community, although the model did not test the effects of many varying parameters. While showing that functional equivalence could evolve so long as the environment was fine-grained in nature, this study also found that a coarse-grained habitat could lead species to evolve and maintain widespread polymorphism for the selected trait.

In this paper, we fundamentally seek to answer the questions: 1) Are there realistic scenarios under which we would expect species in a community to evolve ecological equivalence; and 2) If so, can those ecologically equivalent species coexist? To more explicitly address those questions, we ask, do species exposed to a similar range of environmental conditions tend to converge on similar trait values and thus, ecological equivalence? Here, we further explore what ecological and species circumstances may lead to the evolution of various trait and niche structures in communities. Specifically, we explore: 1) the impact of fine- vs. coarse-grain spatial arrangement of habitat types; 2) the role of initial clumping or random distribution of species; 3) the importance of trait linkage; 4) the impact of varying degrees of dispersal limitation; and 5) the initial species

richness in a community. We use simulation-based modeling of the evolution of two traits, each governed by many genes of small effect, with selection for those traits driven by two habitat variables. We track trait evolution and the persistence of those species over many generations. To our knowledge, this is the first such study to incorporate multiple, linked traits, a genetical model of trait evolution, and spatially explicit, kernel-based dispersal limitation of varying strengths.

The Model

As in Hubbell (2006), we built on the initial model of Hurtt and Pacala (1995). With no loss of generality, we consider a community of 100,000 or 500,000 sites, or cells (which can be occupied by 10 and 50 species, respectively) with periodic boundary conditions to control for edge effects. Each cell is the site for a single individual, and is represented by two independent habitat values, each ranging from 0-40. To initialize, each cell was randomly (or, in later models, in a clustered fashion) assigned two independent habitat values ranging from 0-40, and a species number. Habitat variables were drawn from $\beta(5,2)$ and $\beta(2,5)$ distributions (which are mirrors of one another; see figure 1). Species were randomly sampled from a uniform abundance distribution, so starting abundances for all species were close to the total number of cells divided by number of species (about 10,000 in these simulations). In the first two scenarios, these species were initially randomly assigned to cells; in the third, conspecific individuals were clustered together.

The simultaneous evolution of two traits was studied, each modeled as a quantitative trait driven by additive genes of small effect for each trait (20 loci, diploid

organism, value of 0 or 1, so that the summation of all loci can result in genotype values from 0-40). These additive trait values were then used as a measure of “fit” to habitat variables—with each trait tied to its respective habitat. Linkage of these traits was modeled by weighting the probability of an allele in a given position “hitch-hiking” with the allele for the first trait. Linkage probabilities were either 0 (no linkage, random assortment) or 1 (complete linkage). Each individual was randomly assigned a genotype through repeated binomial sampling, $\text{mean}=0.5$, for each locus.

At each time step, all individuals were first mated, then killed and replaced, with complete turn-over of the community at each time step. Mating was established by selecting the nearest conspecific within a 100 cell distance in each direction; if no conspecific was found, the individual was selfed. Following pollination, a pool of 100 potential replacements for each cell was built by sampling from within the neighborhood. Dispersal limitation determined which potential parents from the prior generation could get offspring to the site, and was modeled as an exponential decay kernel with exponent levels of 0.1 and 1.0. From the pool of potential replacements, the site “winner” was selected by choosing the individual with the least total distance between genotype values and the habitat values for the cell in question.

Three main “starting scenarios” were run. The first scenario was with fine-scale (ie, uncorrelated) habitat levels and fully randomly distributed species. This scenario allowed all species to sample all habitats and to encounter all other species. Scenario 2 retained random initial species distributions, but added significant habitat autocorrelation, or “coarse-scale” habitat heterogeneity, with habitats following a full single cycle of increasing, then decreasing values along the linear habitat gradient. The second set of

habitat variables were offset by 0.125 of the length of the cycle so that the two habitat values were not strongly correlated with one another. This scenario still allowed species to fully sample available habitat. The third scenario used a clumped starting species distribution across coarse-scale habitats, leading species to only be able to sample one or a few habitats, particularly with strong dispersal limitation.

All simulations were run for 1000 turnovers; this proved more than adequate time for genotype frequencies and species abundance to stabilize in the community. Note that this does not equate to true “stable equilibrium” levels because of the stochastic nature of the simulations, merely a point where strong and ongoing directional trends in abundance and genotype was no longer occurring. Each model scenario and possible combination of linkage (0 or 1), number of species (10 or 50), and dispersal exponent (0.1 or 1.0) was run 10 times, each with a different initializing seed to ensure consistency of results. Because we typically began simulations with all species sharing a shared genotype distribution, we were concerned that any findings of evolved equivalence would simply be written off as “starting equivalence-ending equivalence”. Therefore, we also conducted a series of simulations with species’ means starting out evenly spaced over niche space (see fig. 2A for distribution).

We analyzed data from the simulations for longevity of species (number persisting after 1000 generations), as well as for a variety of trait characteristics. In addition to reporting the range of species mean trait values in simulations, we also calculated the standard deviations around the species means, and report the ranges found; this is one representation of the breadth of trait space used by the species present. We also report both the minimum and maximum pairwise Euclidean distances between

species means, as well as the range of overall mean Euclidean distances found in the simulations. Finally, we report the degree of niche overlap, following the methods proposed by Mouillot *et al.* (2005). For each species and trait, a trait distribution was calculated using a kernel estimator, and then calculating pairwise overlaps in trait space of coexisting species. Overlap is simply represented as the integral of the area under the species' respective kernel curves when overlaid on one another. From these pairwise overlaps, a community-wide overlap index is then calculated, simply by averaging these overlaps; comparably, multiple traits can be averaged for a multi-trait average overlap.

Results

Although this model was extensively modified from the basic approach of Hubbell (2006), we found qualitatively similar results to those presented earlier under all three scenarios, so long as strong dispersal limitation was maintained within the model. However, both explicit dispersal limitation and trait linkage produced a number of interesting interactions with the starting scenario, as did starting species numbers. Here, we outline the major findings for these three main scenarios.

Scenario 1: Fine scale habitat, no species clustering – Role of dispersal limitation, trait linkage, number of species

Under scenario 1, with fine-scale distribution of habitat and no initial species clumping, in no case did any species go extinct. These simulations consistently produced the most overall trait overlap, and the smallest differences among coexisting species. The lowest reported mean trait overlap within these scenarios was 0.39, while 0.20 was the highest reported in any other scenario. Overall trait evolution, however, differed

depending upon the number of species, dispersal limitation, and trait linkage. Increasing the number of species had relatively little overall effect on trait evolution and interacted little with other factors. The 50 species simulations tended to produce somewhat more trait overlap and slightly lower mean Euclidean distances between species than the 10 species scenario, which is not surprising given that the amount of niche space had not increased while the number of species did.

Strong dispersal limitation ($d = 1.0$) produced a narrower range of mean trait values for species, less distance between the means, and broader niched species than weak dispersal limitation ($d = 0.1$). Trait overlap was also higher in simulations with strong dispersal limitation (0.73-0.84) than weak dispersal limitation (0.39-0.61). Note the differences among the four sample scenarios in fig. 3. Trait linkage had no discernible effect on trait values under scenario 1.

Because we did find strong trait overlap and broad equivalence in these situations, we chose to address the potential critique of “starting similarity might lead to ending similarity”. In simulations with strongly niche-differentiated species, the species still evolved broad equivalence and overlap during the course of the simulation (see fig. 2B for results). Note that two species did go extinct almost immediately in this simulation; each of these species was initially specialized on a part of niche space for which there was essentially no available habitat. Therefore, their extinction is not surprising, and indeed confirms the strong selective environment to which all species in these simulations are exposed.

Scenario 2: Coarse-scale habitat, species not clustered – Role of dispersal limitation, trait linkage, and number of species

In the second scenario, with the habitat aggregated into a coarse-scale pattern and species initially distributed randomly across the landscape, species number, linkage and dispersal limitation all impact both species survival and trait distributions. Overall, this scenario consistently produces a suite of species with most or all species having multiple “ecotypes”, or trait peaks. Beyond this observation, however, these simulations produce the most variable and least predictable set of results, as well as the most complex set of interactions among factors.

Increasing the initial number of species from 10 to 50 decreases the percentage of species surviving 1000 generations (60-100% in 10 species system; 52.5-88% in 50 species). Higher initial species diversity results in species means ranging over a broader set of niche space, greater mean Euclidean distance among species, and, somewhat paradoxically, a broader range of species’ niche breadths. In spite of packing additional species into the same potential niche space, species trait overlap is also lower with higher starting numbers of species (0.04-0.06 vs. 0.08-0.20).

Trait linkage resulted in higher species survival, somewhat higher trait overlap, reduced Euclidean distances between species’ trait means, and a narrower range of mean trait values, at least in the low diversity scenario. Comparably, increasing dispersal limitation also increased species survival, but had little impact overall on trait evolution. However, there seem to be complex interactions when all three factors are considered in combination. Notice, in particular, the lower number of surviving species, broader range of species trait means and higher Euclidean distance between species in the unlinked, low

diversity scenario with little dispersal limitation. In terms of traits, the other three low-diversity scenarios are quite similar to one another. This pattern, however, does not exist within the higher diversity scenario.

With no trait linkage and low dispersal limitation ($d = 0.1$), about half of the initial species became extinct within 1000 generations, and one or a few species dominate the system. The most common species tend to occupy much of trait space, while those of middling abundance tend to be polymorphic for the traits, and rare species habitat specialists (fig. 4A). In contrast, strong dispersal limitation leads to high species persistence, and most species developed multiple ecotypes, a sort of polymorphic generalist strategy that develops quite rapidly and is stable for the long-term (fig. 4B).

Genetic linkage between the two traits serves as a surprising stabilizing mechanism in the absence of dispersal limitation. With weak dispersal limitation ($d = 0.1$), but full genetic linkage ($l = 1.0$), traits again were distributed into multiple ecotypes within most or all species (fig. 4C). Adding dispersal limitation ($d = 1.0$) changes abundances and patterns very little from the above scenario (fig. 4D).

Scenario 3: Coarse-scale habitat, species initially clumped – Role of dispersal limitation, trait linkage, number of species

The third scenario, with coarse-scale habitat and a clumped initial distribution of species led to a result most similar to classical “niche differentiation.” The starting species diversity, dispersal limitation and trait linkage had impact on species longevity and trait distributions. Consistently, this scenario produced relatively classically “niche differentiated” species within communities, with each species having a single trait peak

and with values distributed relatively narrowly around that value. It also was the scenario allowing the lowest overall percent persistence of species, ranging as low as 50%.

Increasing species numbers led overall to more species extinctions in spite of starting species with the same average population size in all scenarios (average persistence of 73-99% of species for 10 species vs. 45.6-77.4% for 50 species communities). Higher starting species number also resulted in species means ranging over a broader set of niche space, lower overall niche breadth, and, surprisingly, lower species trait overlap in spite of more species being packed into the same total niche space (0.03-0.05 vs. 0.08-0.17). Increasing dispersal limitation allowed additional species to persist, and tended to lead to more niche differentiated species with lower niche breadths and trait overlap. Comparably, trait linkage increased the number of species persisting. Again, there are complex interactions between these factors, leading to different survival patterns, in particular, with the high vs. low diversity simulations.

In scenarios with no trait linkage and low dispersal limitation ($d = 0.1$), many of the initial species disappear within 1000 turn-overs, and a few species dominate the system. The most common species tend to occupy much of trait space, while rarer species are more specialized, and, though trait means are quite widely dispersed, there is considerable overlap among species (Fig. 5A). When dispersal limitation is increased to $d = 1.0$, while maintaining no trait linkage, a classical scenario of niche differentiation emerges (fig. 5B). Species closely track habitat values, and species are able to coexist on similar habitat values so long as they (and the habitat values) are fairly well isolated in space.

Adding trait linkage produced surprising results, particularly in scenarios with weak dispersal limitation. In the low diversity scenario, when full linkage ($l=1.0$) is invoked with low dispersal limitation, species are able to disperse to multiple habitats in spite of their initially clustered situation (fig. 5C). This scenario led to convergence toward similar trait means among the different species. When strong dispersal limitation was added ($d = 1.0$), trait distributions were very similar to those seen without trait linkage (Fig. 5D).

Discussion

In these simulations, trait evolution has proven sensitive to a variety of both environmental and species-driven factors, but we have shown that under many circumstances, ecologically equivalent species can arise easily and persist indefinitely within an ecological community. Indeed, our results suggest that evolving equivalence is the route most frequently leading to the (relatively) stable coexistence of species over the long term. While some of our results were expected, a number of factors proved both surprising in their direct impacts and in the results of their interactions with other factors. These interactions are important to understanding the ultimate outcomes of our simulations.

Dispersal limitation

In terms of persistence in the community, dispersal limitation behaved quite consistently, regardless of other factors at work. Dispersal limitation serves as a strong stabilizing mechanism in communities, radically slowing rates of extinction, much as demonstrated by Hurtt and Pacala (1995). Interestingly, in simulations with fine scale

habitat distribution, dispersal limitation was unimportant for the number of species surviving to the completion of the simulations. In all of these simulations, no species became extinct, suggesting strong stabilization with a shared generalist phenotype. This scenario was the one with true ecological equivalence—in most cases, species showed widespread exploitation of most or all available habitat values, strong niche overlap and very similar mean trait values.

The impact of dispersal kernels on trait evolution, however, is more scenario-dependent. In scenario 1, wider dispersal led to somewhat more differentiation in trait means (not unlike a guild-structured community) than did limited dispersal. Greater dispersal distances cast genotypes and species more broadly into competition with each other, and thereby selected for weak niche differentiation. These results overall were in contrast to the increased equivalence Gravel *et al.* (2006) found in more freely dispersing simulations. Gravel’s relatively small (but not single celled) patch size, combined with dispersal distances likely led to these seemingly divergent results.

Trait Linkage

The impact of trait linkage also seems to be scenario dependent, with little visible effect in scenario 1, but stronger effects in 2 and 3, especially cases with little dispersal limitation, and particularly on species survival. Linkage consistently allowed additional species to persist throughout the simulations by slowing or preventing the evolution of an “ideal” genotype for a given site. Surprisingly, though, it favored more ecological equivalence, particularly in the absence of strong dispersal limitation in both coarse-scale habitat simulations—more of an ecotypic generalist approach when species are not

initially clumped. These probably result from a combination of sampling a wider range of habitats and the slowed evolution imposed by the linkage of traits.

Number of Species

Within scenario 1, overlap increased with number of species, supporting the idea that more species leads to a stronger shared common generalist strategy (Hubbell and Foster 1986). However, the overlap and shared strategy was high regardless of number of species, so it seems likely that a system with as few as ten species has enough unpredictability of neighborhood to promote diffuse pairwise selection and thus, ecological equivalence among coexisting species, so long as dispersal is limited and environmental factors are not highly autocorrelated.

In the other two scenarios, increasing the number of species increased the niche structure in the community. As species numbers increased, there was less trait overlap, trait means spanned a wider range of trait space, and in scenario 3, less variance around species' trait means. This suggests that individual species are specializing more on a particular habitat type as the number of species increases, in contrast with the expectations of Hubbell and Foster (1986) and Gravel *et al.* (2006). However, we only observed this result in the case when habitat is coarse-grained.

Fine vs. Coarse-Grained Habitat

Not surprisingly, the scale or grain of habitat has a profound impact on the evolution of functional traits within a community. More interestingly, it seems, whenever species are able to disperse to a wide variety of habitat conditions, they tend to evolve toward a generalist strategy. Note that even when species start out clustered in

coarse-grained habitat, so long as they are able to disperse widely, they continue to sample and adapt to a wide variety of ecological conditions (fig. 4A,C).

It may be argued that most habitat values will be coarse-grained in nature—where individuals and populations are not able to experience the full range of values. However, we would argue that many ecologically relevant plant traits in fact deal more with resources that are quite patchily distributed. Consider scenario 1, the fine scale habitat and lack of initial clustering of species. In the context of a forest community, light gaps are often much like this scenario—with particular light levels shown in only one or a few open sites (at least sites available to a mature individual) (ie, Denslow 1986) and with species not highly clumped, at least to a first approximation (Hubbell and Foster 1986). On the other hand, soil nutrients may provide an example of a more coarse-scale habitat factor (ie, Hubbell *et al.* in press; John *et al.* 2007), but even so, species clumping and dispersal limitation seldom prevent species from experiencing most of the diverse types of habitat available (as modeled in scenario 3).

Importance of Ecotypes within a Species

In a more dispersal limited scenario, individual species that experience selection from multiple habitat types (in a coarse-grained habitat matrix) tend to develop spatially segregated ecotypes that seldom disperse to populations of or mate with other conspecific ecotypes (fig. 2). This suggests that Levins (1968) was right in highlighting the importance of both environmental scale and degree of habitat differentiation in the persistence of multiple ecotypes within a species.

Role for individuals

While some authors (i.e., Rueffler et al 2006; Ackerly and Cornwell 2007) have begun to highlight the importance of considering the traits of individuals when considering ecological interactions, most work has focused mostly on trait means when considering species composition within a community (ie, Gravel *et al.* 2006; Lehmann and Tilman 1997). Our work suggests that considering trait means, or even mean and variance, is inadequate when considering how species are distributed within a community. After all, it is the individual that is interacting with both its biotic and abiotic environment, and traits at the level of that individual will determine its success or failure.

Reconciling niche and neutrality?

Recently, a number of authors have suggested possible methods of considering niche and neutral processes as extremes of a continuum of methods of structuring a community (ie, Adler *et al.* 2007; Gravel *et al.* 2006). The results presented here may provide insight to help us to reconcile the seemingly intractable differences between strongly niche and neutral world views. Some of the strongest evidence for classical niche processes driving plant communities comes from work in grasslands (i.e., Tilman 2004; Adler 2004), while Hubbell *et al.* (in press) provide strong evidence that these sorts of approaches have little or no predictive power in species rich tropical forest systems. It is worth noting that prairie plants, relative to their size, likely perceive a heavily spatially autocorrelated environment in terms of soil moisture and nutrients, and light levels are relatively constant across a landscape. In contrast, trees (particularly adult individuals, as

modeled here) likely perceive a much finer grained habitat relative to adult size. While we do not claim to capture all of the many complexities in an ecological community in this relatively simple model, it is worth noting that these results are, at a minimum, consistent with seemingly disparate empirical results observed in these plant communities.

Conclusion

In spite of repeated critiques of ecological equivalence and neutral theory as unrealistic, unlikely in nature, or even a virtual impossibility, ecological equivalence in relevant traits can evolve, and equivalent (or very similar) species can coexist for a very long time without directional change in either traits or abundance. The ecological conditions simulated are neither terribly unrealistic nor rare. Interactions among the grain of environmental variables, dispersal limitation, and trait linkage often produce surprising results. Perhaps most shocking to us was the prevalence of conditions that led to the evolution of either truly equivalent generalists or multiple ecotypes within a single species. Indeed, only in cases with coarse-grained habitat, clustered initial species distributions, and strong dispersal limitation did classical niche differentiation develop. These results suggest that we may frequently expect to find ecological equivalence, or at least ecotypic generalists, within spatially structured plant communities.

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Table 3.1. Summary statistics of trait values and species persistence based on all simulations, Scenario 1.

S	D	L	Range of Sp. Means, 10 runs, T1	Range of SD's within spp, high and low for 10 runs, T1	Range of Sp. Means, 10 runs, T2	Range of SD's within spp, high and low for 10 runs, T2	Range of average Euclidean distances among all species, 10 runs	Range of pairwise Euclid distances, all runs	T1 Overlap Range	T2 Overlap Range	Mean Trait Overlap Range, 10 runs	Mean # spp.	Range of # of Spp
10	0.1	0	18.35-35.84	1.87-7.62	4.22-22.25	1.86-8.16	8.33-10.51	0.37-21.28	0.37-0.49	0.34-0.56	0.39-0.50	10	10
10	0.1	1	17.34-36.00	1.77-7.07	3.78-21.73	1.40-6.37	8.24-10.28	0.33-21.47	0.38-0.55	0.39-0.53	0.41-0.53	10	10
10	1	0	23.15-33.20	3.83-7.55	7.28-17.91	4.29-7.69	2.55-5.14	0.15-10.17	0.74-0.84	0.70-0.83	0.73-0.82	10	10
10	1	1	24.27-32.74	3.87-7.61	6.95-14.55	3.76-7.61	1.69-3.97	0.20-8.71	0.76-0.84	0.73-0.86	0.75-0.84	10	10
50	0.1	0	18.63-35.93	2.13-8.95	4.60-21.28	2.12-9.06	5.60-6.74	0.02-18.66	0.56-0.62	0.57-0.62	0.58-0.61	50	50
50	0.1	1	18.35-35.60	1.96-8.89	3.86-21.00	1.91-8.92	5.51-6.24	0.10-18.86	0.57-0.64	0.57-0.63	0.59-0.61	50	50
50	1	0	26.39-31.28	4.94-7.62	8.69-14.05	4.86-7.33	1.42-1.71	0.01-4.94	0.83-0.84	0.83-0.85	0.83-0.84	50	50
50	1	1	26.18-31.79	4.83-7.64	8.12-14.17	4.92-7.52	1.45-1.74	0.02-5.58	0.82-0.84	0.82-0.84	0.83-0.84	50	50

Table 3.2. Summary statistics of trait values and species persistence based on all simulations, Scenario 2.

S	D	L	Range of Sp. Means, 10 runs, T1	Range of SD's within spp, high and low for 10 runs, T1	Range of Sp. Means, 10 runs, T2	Range of SD's within spp, high and low for 10 runs, T2	Range of average Euclidean distances among all species, 10 runs	Range of pairwise Euclid distances, all runs	T1 Overlap Range	T2 Overlap Range	Mean Trait Overlap Range, 10 runs	Mean # spp.	Range of # of Spp
10	0.1	0	8.04-38.81	0-8.45	2.79-30.49	0.00-9.08	8.71-14.71	0.57-33.30	0.06-0.16	0.07-0.16	0.08-0.14	7.6	6-9
10	0.1	1	20.11-37.96	0-10.71	3.00-22.44	0.00-9.73	4.65-8.32	0.30-20.23	0.12-0.19	0.12-0.21	0.13-0.20	9.8	9-10
10	1	0	17.74-39.14	0-10.41	3.71-23.44	0.00-12.03	4.74-10.09	0.36-24.21	0.10-0.14	0.10-0.13	0.10-0.13	9.9	9-10
10	1	1	19.76-34.27	1.78-9.27	3.64-20.69	1.63-8.87	4.04-6.14	0.20-15.33	0.13-0.17	0.16-0.20	0.15-0.18	10	10
50	0.1	0	4.79-40.00	0.00-12.85	0.96-35.32	0.00-12.00	9.77-12.64	0.00-39.11	0.04-0.06	0.04-0.06	0.04-0.06	28.5	21-35
50	0.1	1	4.71-40.00	0.00-11.16	0.00-35.24	0.00-11.94	9.28-10.74	0.12-36.42	0.04-0.06	0.046-0.055	0.04-0.05	40.4	37-43
50	1	0	3.08-40.00	0.00-11.86	0.58-37.06	0.00-12.74	9.33-14.51	0.07-42.38	0.03-0.05	0.03-0.05	0.04-0.05	35.3	31-39
50	1	1	8.59-40.00	0.00-13.06	0.93-36.97	0.00-14.77	9.27-11.66	0.14-38.83	0.04-0.05	0.04-0.05	0.04-0.05	41.9	40-44

Table 3.3. Summary statistics of trait values and species persistence based on all simulations, Scenario 3.

S	D	L	Range of Sp. Means, 10 runs, T1	Range of SD's within spp, high and low for 10 runs, T1	Range of Sp. Means, 10 runs, T2	Range of SD's within spp, high and low for 10 runs, T2	Range of average Euclidean distances among all species, 10 runs	Range of pairwise Euclid distances, all runs	T1 Overlap Range	T2 Overlap Range	Mean Trait Overlap Range, 10 runs	Mean # spp.	Range of # of Spp
10	0.1	0	4.78-37.65	0.00-9.40	1.05-33.60	0.00-11.06	10.97-16.78	1.03-38.04	0.04-0.13	0.07-0.12	0.07-0.13	7.3	5-8
10	0.1	1	16.00-39.56	0.00-8.44	2.10-22.40	0.00-9.78	7.22-10.45	0.32-25.67	0.10-0.15	0.14-0.19	0.13-0.17	9.5	8-10
10	1	0	16.26-38.51	0.00-4.70	1.51-38.00	0.00-4.53	11.17-15.87	0.44-37.72	0.08-0.13	0.06-0.09	0.08-0.13	9.1	8-10
10	1	1	14.92-39.25	0.00-4.31	2.04-23.69	0.00-4.65	11.37-12.66	2.50-26.13	0.08-0.12	0.09-0.13	0.09-0.12	9.9	9-10
50	0.1	0	4.70-40.00	0.00-4.85	0.98-30.13	0.00-5.36	10.90-13.36	0.26-36.43	0.04-0.05	0.04-0.07	0.04-0.05	22.8	20-25
50	0.1	1	8.06-40.00	0.00-4.67	0.00-31.91	0.00-6.06	10.98-12.77	0.06-36.66	0.04-0.05	0.04-0.05	0.04-0.05	36.1	33-41
50	1	0	3.00-40.00	0.00-2.91	0.00-28.45	0.00-3.41	12.28-13.72	0.05-37.71	0.03-0.04	0.037-0.041	0.037-0.040	27.9	23-32
50	1	1	11.09-40.00	0.00-3.23	0.00-28.69	0.00-2.88	11.88-12.56	0.04-31.80	0.03-0.04	0.03-0.04	0.03-0.04	38.7	35-44

Table 3.4. Summary of outcomes from simulations.

Scenario 1. Fine-Scale Habitat					
		10 Species		50 Species	
		<u>Linkage</u>		<u>Linkage</u>	
<u>Dispersal Limitation</u>		0	1	0	1
0.1	Moderate Equivalence		Moderate Equivalence	Moderate Equivalence	Moderate Equivalence
	All species persist		All species persist	All species persist	All species persist
1	Broad Equivalence		Broad Equivalence	Broad Equivalence	Broad Equivalence
	All species persist		All species persist	All species persist	All species persist
Scenario 2. Coarse-Scale Habitat, Random Individuals					
		10 Species		50 Species	
		<u>Linkage</u>		<u>Linkage</u>	
<u>Dispersal Limitation</u>		0	1	0	1
0.1	Mixed		Polymorphic generalist	Mixed	Polymorphic generalist
	Many species extinct		Most species persist	All species persist	Most species persist
1	Polymorphic generalist		Polymorphic generalist	Polymorphic generalist	Polymorphic generalist
	Most species persist		All species persist	Most species persist	Most species persist
Scenario 3. Coarse-Scale Habitat, Conspecifics Clumped					
		10 Species		50 Species	
		<u>Linkage</u>		<u>Linkage</u>	
<u>Dispersal Limitation</u>		0	1	0	1
0.1	Mixed		Polymorphic generalist	Mixed	Polymorphic generalist
	Many species extinct		Most species persist	Many species extinct	Most species persist
1	Niche Differentiation		Niche Differentiation	Niche Differentiation	Niche Differentiation
	Most species persist		Most species persist	Most species persist	Most species persist

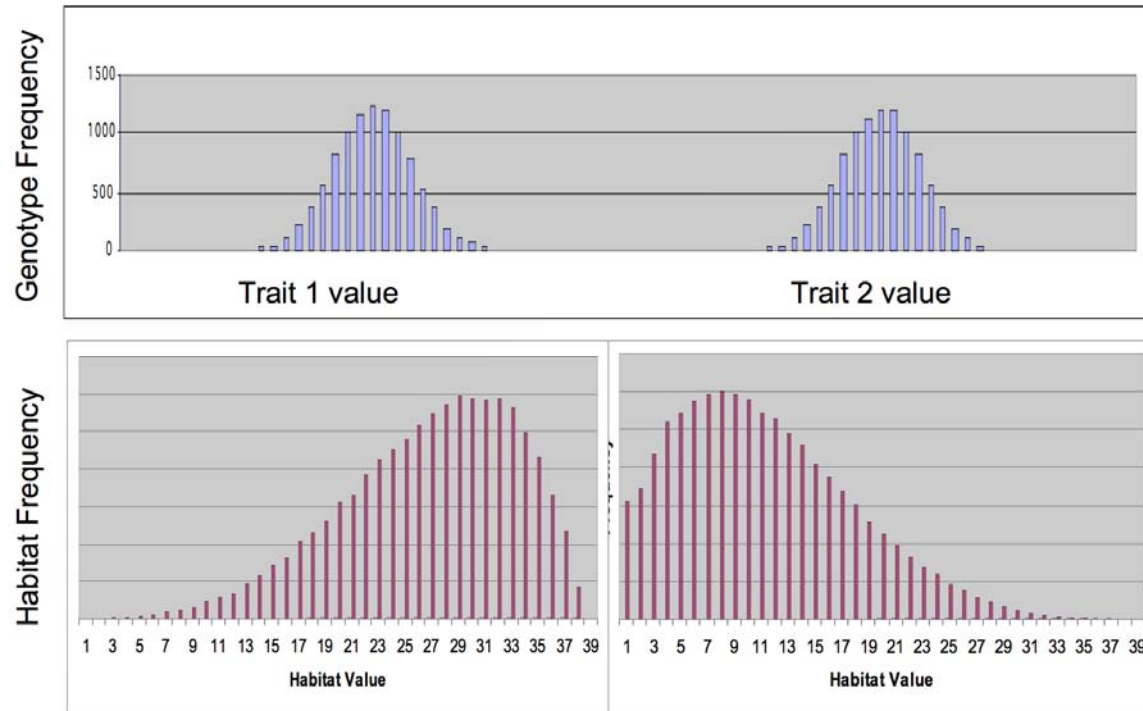


Figure 3.1. Initial conditions for all models. Above, a distribution of starting genotype frequencies for each trait are shown, based on repeated binomial sampling. Below, the distribution of habitat values, ranging from 0-40, drawn from Beta (2,5) and Beta (5,2) distributions, respectively.

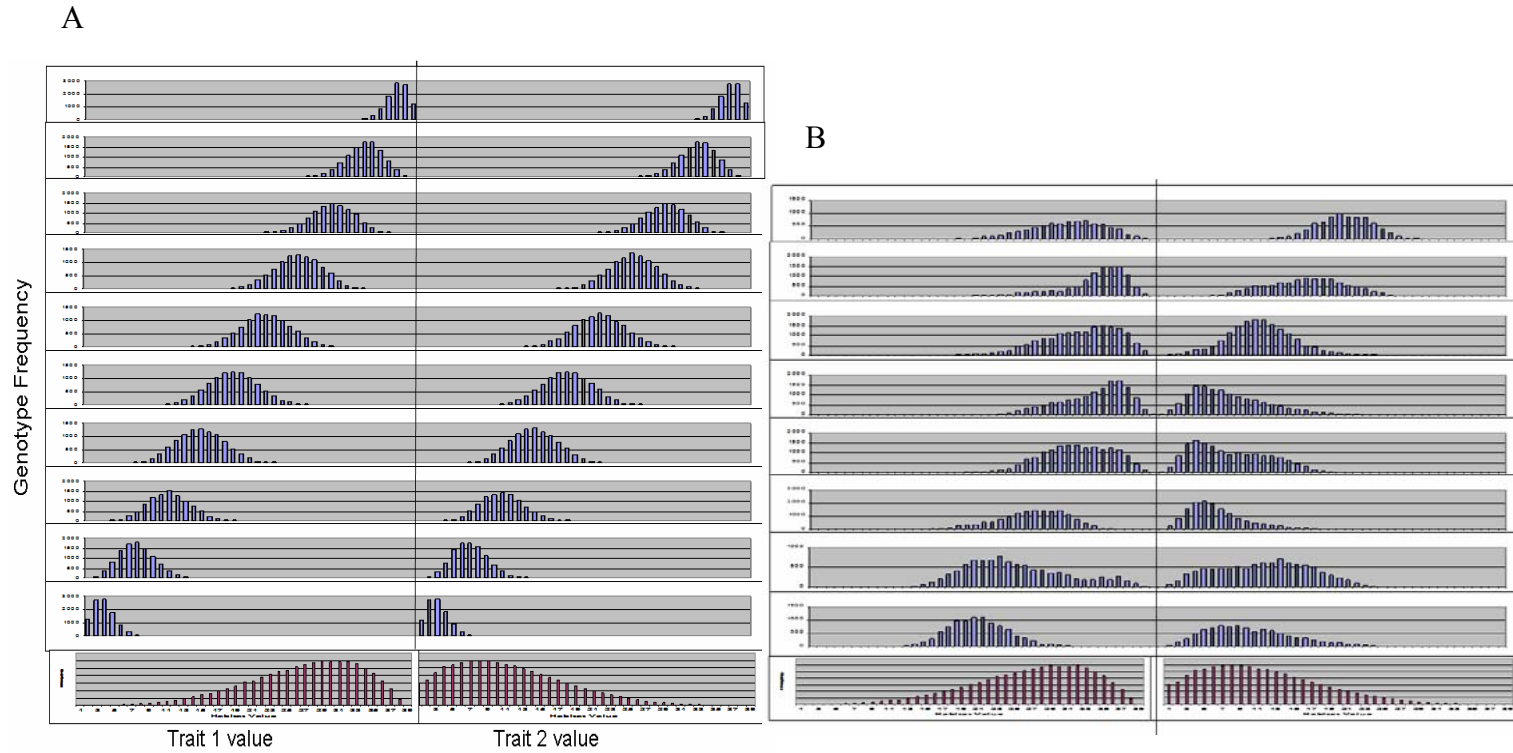


Figure 3.2. Results from starting species as non-equivalent. A. Starting conditions on left for trial simulation with species niche differentiated. B. Trait distributions after 1000 community turn-overs. Note the broad overlap and shared generalist approach of the species.

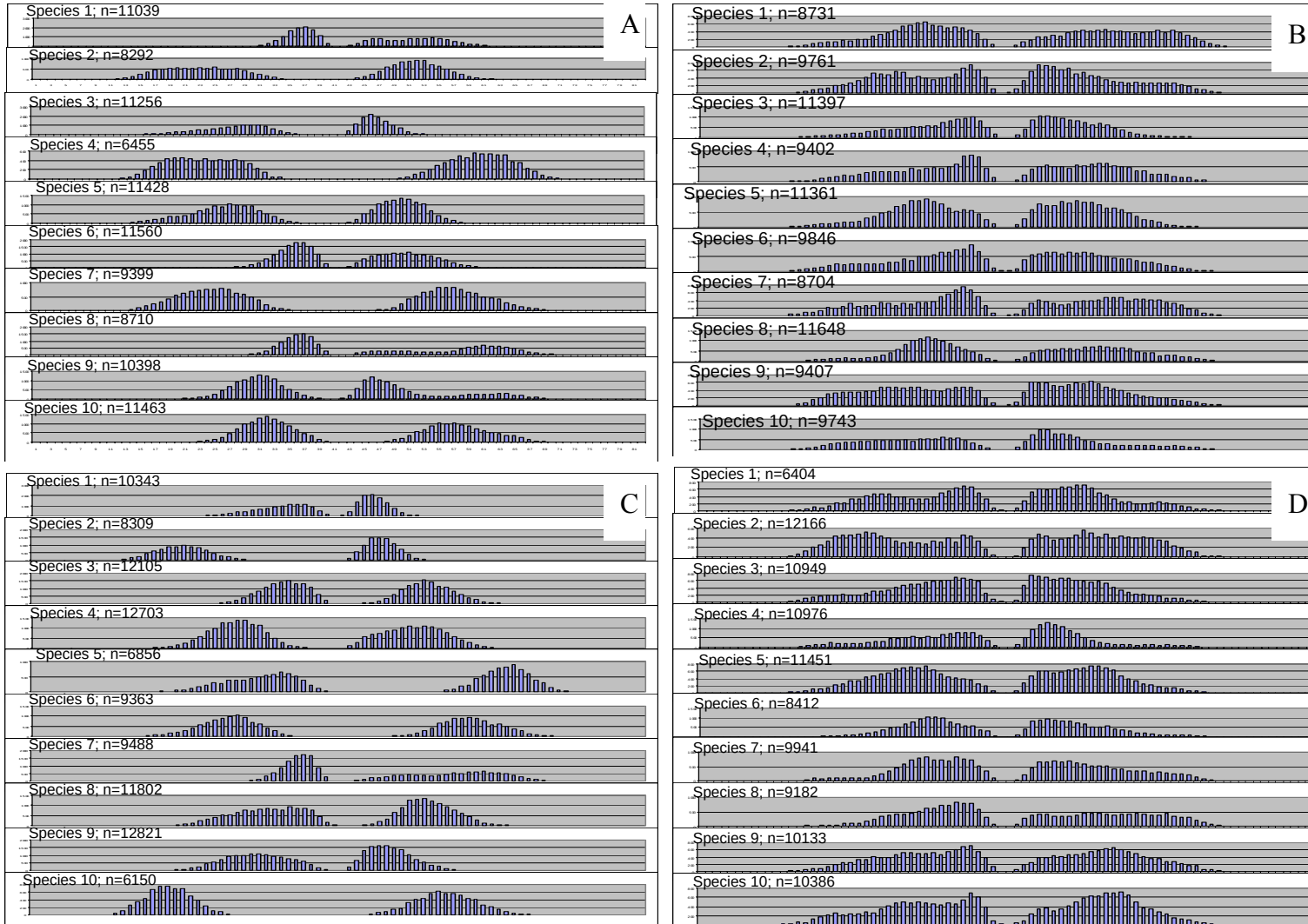


Figure 3.3. Sample species trait distributions resulting from low diversity simulation under scenario 1. A (upper left) with $d=0.1$, $l=0$; B (upper right) $d=1.0$, $l=0$; C (lower left) $d=0.1$, $l=1.0$; D (lower right) $d=1.0$; $l=1.0$.

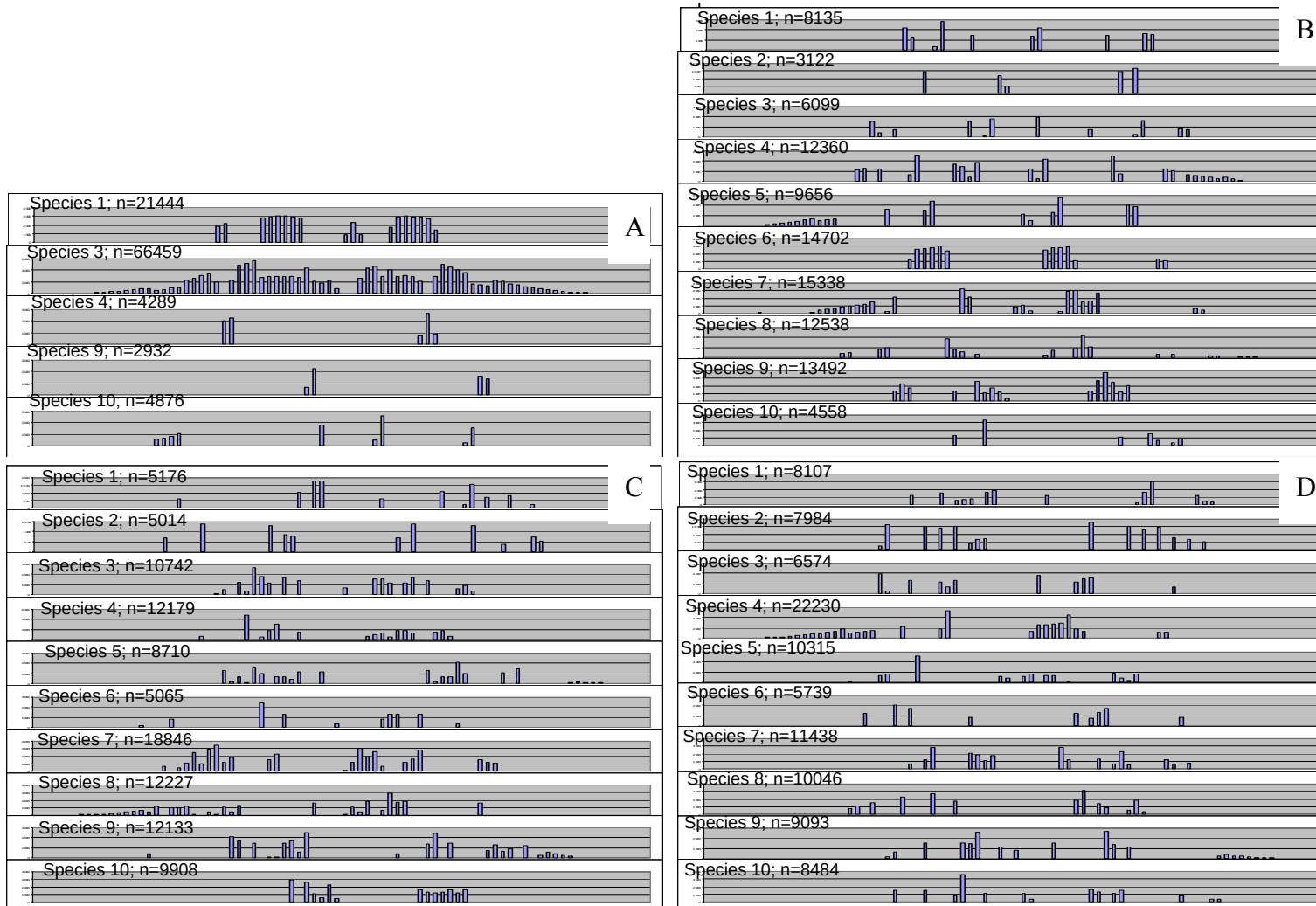


Figure 3.4. Sample species trait distributions resulting from low diversity simulation under scenario 2. A (upper left) with $d=0.1$, $l=0$; B (upper right) $d=1.0$, $l=0$; C (lower left) $d=0.1$, $l=1.0$; D (lower right) $d=1.0$, $l=1.0$.

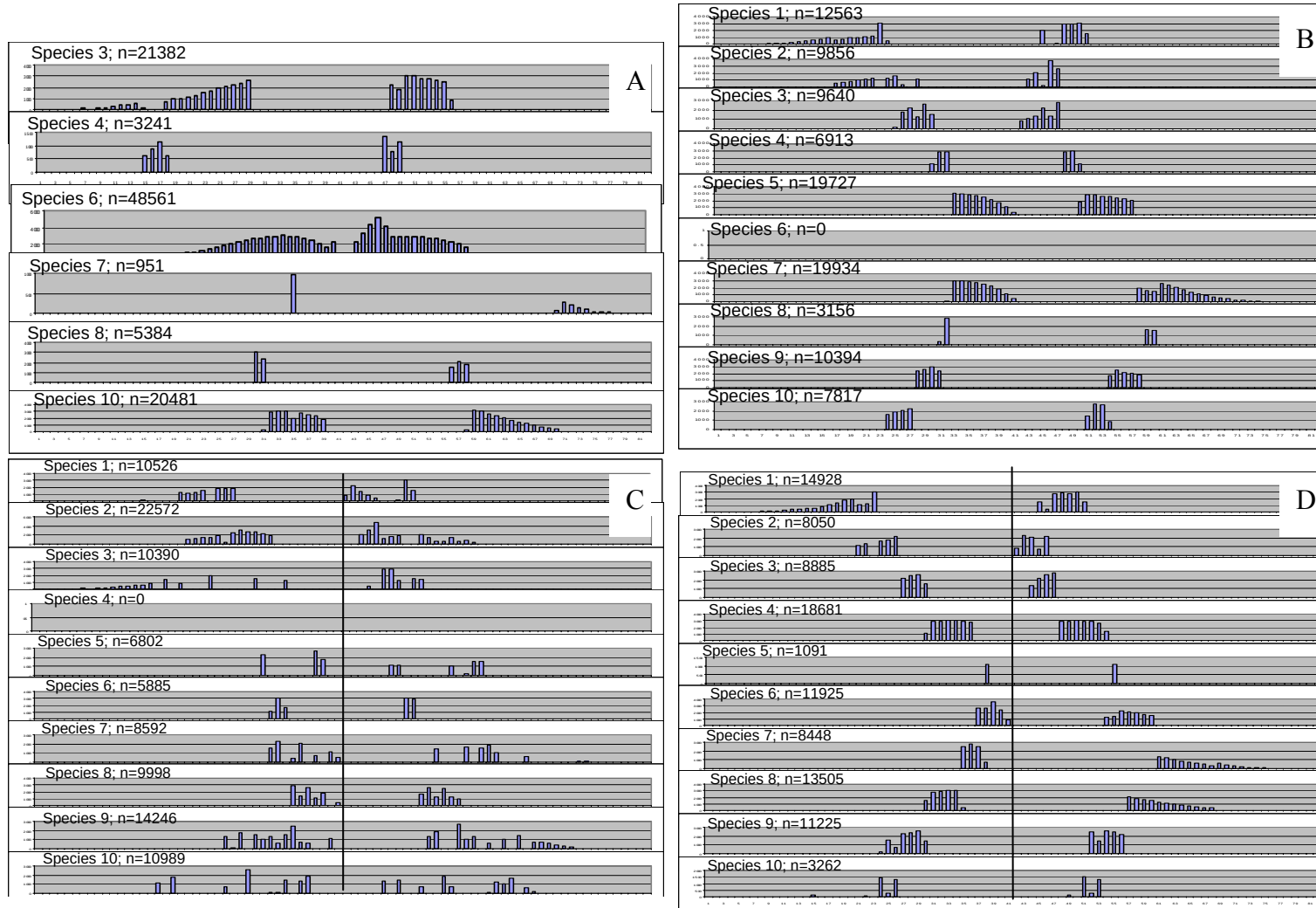


Figure 3.5. Sample species trait distributions resulting from low diversity simulation under scenario 3. A (upper left) with $d=0.1$, $l=0$; B (upper right) $d=1.0$, $l=0$; C (lower left) $d=0.1$, $l=1.0$; D (lower right) $d=1.0$; $l=1.0$.

CHAPTER 4

THE DISTRIBUTION OF VARIANCE IN LEAF FUNCTIONAL TRAITS IN A
TEMPERATE FOREST TREE COMMUNITY¹

¹Lake, J.K. and S.P. Hubbell. To be submitted to *Ecological Monographs*.

Abstract

When studying plant community assembly from the perspective of plant traits, ecologists have typically focused on species trait means, minimizing the importance of intraspecific variation, while most studies of plant adaptation have focused on intraspecific variation, but outside of the broader community context. Here, we examine the structure of a temperate forest in detail with relation to five leaf functional traits. We find the expected strong intraspecific plastic response to light availability, while still finding substantial unexplained intraspecific and even within individual variation in these traits. This broad range of intraspecific trait values translates to strong interspecific overlap in trait values, suggesting most of the tree species within the studied forest share a common generalist strategy with respect to these leaf functional traits. However, a strong sun-shade leaf continuum also suggests that, at least in part, ontogenetic niche shifts can be invoked, at least to explain some variance in leaf functional traits. Overall, these results also suggest that it will not be sufficient to treat individuals of a species as merely following the species' mean values, at least for the leaf functional traits studied here. This means that any predictive model of community composition from functional traits must, at the least, account for both ontogenetic variation in traits as well as unexplained variability.

Introduction

For centuries, taxonomists, natural historians, and ecologists have looked for, and found, differences among plant species. For taxonomists, this interspecific variation is key to describing and differentiating among species. Natural historians used the traits to relate the organism to its place in the world. And, ecologists have used the differences to attempt to explain species coexistence and interactions. More seldom has intraspecific variability been considered, particularly in an ecological context. As community ecologists turn to functional traits as a method for analyzing questions of community assembly and coexistence, however, it becomes more important to consider the distribution of relevant functional traits both within and among species. Most current work at the community level has focused on species mean trait values (ie, Wright *et al.* 2004; Stubbs and Wilson 2004; Shipley *et al.* 2006). While species means may well provide an adequate cross-taxon comparison in the context of trait evolution within a clade (i.e., Davies 1998; Cavender-Bares *et al.* 2004a), or even in considering global scale patterns of plant traits (Reich *et al.* 1997; Wright *et al.* 2004), if intraspecific variation is substantial, then species means are not a satisfactory representation of the traits of individuals in an ecological community.

Indeed, in reviewing the use of functional traits in community ecology, McGill *et al.* (2006) recognized this difficulty; however, they argue that only traits with significantly greater interspecific than intraspecific variation are preferable. In their maximum entropy model for prediction of community assembly from functional traits, Shipley *et al.* (2006) again argue that higher interspecific variability is important in selecting traits for analysis. While selecting such traits unquestionably simplifies

analyses and may well improve fits generated by the model, it runs the risk of ignoring ecologically important traits with higher intraspecific variability. Working from long-standing ecological observation and study, a group of ecologically important plant traits have been assembled as a baseline for consideration. While it is possible that high intraspecific variation in these traits may indicate their reduced ecological relevance, and therefore reduced selective pressure, it is also possible that such traits remain functionally relevant, but that plasticity or other intraspecific variability in the trait is simply a more adaptive strategy. The current body of evidence (i.e., Poorter and Bongers 2006; Wright et al 2004; Reich et al 2003) does support the selection of many of these traits, in particular, leaf area, specific leaf area, and leaf nitrogen concentration as relevant to the survival, growth, and overall strategy of species.

Levels of intraspecific variability can indeed inform us as to the forces structuring ecological communities, at least within the context of the traits studied. Following from the very definition of functional traits (Reich *et al.* 2003) as “any attribute that has potentially significant influence on establishment, survival, and fitness and ... focus[ing] on those traits related to the ability to acquire, use, and conserve resources,” these traits must necessarily be linked to the ecological niche of the given plant. Thus, functional traits embody mechanisms through which plants interact with their biotic and abiotic environment and reflect fundamental ‘niche axes’ along which plants may be differentiated from one another (Westoby *et al.* 2002). Comparably, functional trait variability can provide a measure of niche breadth and overlap for species.

We know there is at least a moderate degree of intraspecific variability and intracanalopy plasticity in leaf functional traits (Pearcy and Sims 1994; Lusk 2002; Sack *et al.* 2006). Many of these traits are leaf based traits, largely related to photosynthetic

carbon fixation, or the water or energy balance of individual leaves. Studies of this variation have predominantly focused on the well-documented, but somewhat less well-understood, difference between sun and shade leaves within single individuals (e.g., Sack *et al.* 2006). These differences typically include denser, smaller and more heavily lobed leaves in sun than shade (Percy and Sims 1994; Bond *et al.* 1999; Sack *et al.* 2006), although conflicting results have sometimes been reported (e.g., Niinemets and Kull 1994).

The degree of plasticity and variability found within a species has frequently been tied to the functional grouping of that species. Understory trees and shrubs are predicted to exhibit lower plasticity and variability than canopy tree species because they are exposed to fewer light environments throughout their lifetime (Percy and Sims 1994). Most studies also suggest that light-demanding gap tree species demonstrate higher plasticity in traits related to photosynthetic carbon gain than shade tolerant species (i.e., Valladares *et al.* 2000; Lusk 2002; Yamashita *et al.* 2002), but Yamashita *et al.* (2002) also found high plasticity in highly shade-tolerant species, though this plasticity resulted from leaf acclimation rather than leaf turnover. In that study, mid-successional species demonstrated the lowest overall plasticity in response.

To date, most studies have focused either on studies of multiple species under nearly identical conditions (i.e., Sack *et al.* 2006) or else of a group of related taxa within a broader ecological community (i.e., Davies *et al.* 2000, Cavender-Bares *et al.* 2004a; Valladares *et al.* 2000). Neither of these approaches focuses on trait variance within a full group of plants co-occurring within a single ecological community. At the community level, research has focused on species mean differences. Some researchers have found support for niche differentiation, particularly within specific genera. Cavender-Bares

et al. (2004a, 2004b) concluded that Florida oak species were partitioning niche space finely in relation to habitat usage and functional traits. Davies (1998, 2001) showed that coexisting pioneer species in the tropical genus *Macaranga* were partitioning a continuum of niche-space in relation to photosynthetic traits, though the study focused more on mean species values than trait overlap (see also Sterck *et al.* 2006). Holscher *et al.* (2004) found that eight Asian pioneer species differed significantly from one another in leaf morphology, suggesting a continuum of trait values even within this functional class. Kappelle and Leal (1996) demonstrated that leaf nutrient levels decrease along a successional gradient, while leaf morphology is less impacted by successional status of the forest. Bragg and Westoby (2002) found that smaller-leaved understory species in a sclerophyllous forest tended to need higher light levels than larger-leaved species, while Ackerly and Donoghue (1998) found no such relationship among temperate species within the genus *Acer*. However, all of these studies have focused predominantly on finding differences between species means, without considering explicitly the importance of individuals or of ontogenetic variation or plasticity within traits.

Within this study, we have selected five leaf traits upon which to focus: Specific Leaf Area (SLA), Leaf Size (or area), Leaf Nitrogen Content (N_{mass}), perimeter²: area ratio (p2a), and Leaf Shape Index (Length:Width ratio, LSI). Specific Leaf Area (SLA) is simply the surface area of a leaf divided by its mass. Because SLA is one of the strongest measures of a plant's photosynthetic investment, it should to be one of the best discriminants of niche position (mean), breadth (variance) and overlap. Reich *et al.* (2003, 1997) show that specific leaf area is a strong correlate of mass-based maximum photosynthetic (A_{max}) rate. Low values also tend to be associated with longer leaf lifespans, nutrient limited environments, sun leaves and high defensive investment. Across several species of tropical

trees, Poorter and Bongers (2006) have also shown that SLA is negatively related to whole-plant growth and negatively to survival. Leaf size is defined by Cornelissen *et al.* (2003) as the area of the leaf lamina or leaflets, *excluding* the petiole or rachis. It is a good indicator of photosynthetic surface, and impacts water and energy balance. Typically, sun leaves are smaller than shade leaves, although this pattern does not always hold (Sack *et al.* 2006). Leaf Nitrogen Concentration is highly correlated to mass-based maximum photosynthetic rates ($A_{\max}$). It provides insights into nutrient use and availability, and is correlated to leaf lifespan (Reich *et al.*, 1997). N_{mass} has been shown to correlate positively with growth, while N_{area} correlates with survival (Poorter and Bongers 2006). Perimeter²:Area Ratio (P^2A) is a measure of a leaf's lobing, with higher values showing greater departure from a circle, and thus higher lobing; increased lobing is associated with more strongly sun-exposed leaves (Talbert and Holch 1957), but this does not hold for all species of temperate trees (see Sack *et al.* 2006). Finally, leaf shape index (LSI), simply the length:width ratio of a leaf, was included in the analysis. This morphological trait, combined with P^2A and leaf size, is thought to be important to the energy balance of leaves (Rozendaal *et al.* 2006). Note that the functional/selective relevance of both P^2A and LSI are less well-documented in the literature; it is indeed quite possible that these traits are more free to drift interspecifically than others selected.

We have intentionally selected leaf functional traits as the focus of this study because of the role these traits clearly play in carbon fixation. Given that light is one of the most limiting resources in a closed-canopy forest community, and given the moderately well-documented growth-survival trade-off linked to tree demography, these resource axes and related traits seem a good place to look at how species vary in the way they make their livings. There is now strong evidence linking plant traits to individual plant performance,

including some work explicitly in a community setting (e.g., Poorter and Bongers 2006; Laurence *et al.* 2006; Davies 2001). At least some of these traits have also been demonstrated to affect local growth and survival (Poorter and Bongers 2006, for example), and to play an important role in the global functional trait spectrum (e.g., Reich *et al.* 1997; Wright *et al.* 2004).

Here, we set out to answer the fundamental question of how variability in leaf functional traits is partitioned within and among species. We quantify both interspecific and intraspecific variation in ecologically relevant leaf functional traits for all tree and shrub species within a temperate forest. Within species, we consider both plastic variation (within an individual) and broader inter-individual variation within a particular light environment and size class. By studying this variability, and its sources, we further the understanding of plant community structure in relation to leaf functional traits.

Materials and Methods

Site description

Thompson Mills Forest is a 135-ha. reserve located near Braselton, Georgia, in Jackson County, about 40 miles northeast of Atlanta in the Piedmont (34°7'39 N, 83°48'6 W). The site is composed of late-secondary oak-hickory forest, dominated by *Quercus* sp., *Carya* sp., *Liriodendron tulipifera*, and *Fagus grandifolia*. Average annual rainfall in this area is estimated at 141.7 cm, and mean annual temperature is 15.6 C (Georgia Automated Environmental Monitoring Network, Gainesville, GA). Three 20x200m sampling transects were established. The first runs along a northwest facing slope overlooking the Mulberry River; the second, along a southfacing slope overlooking Lee Creek; the third perpendicular to Lee Creek at a point upstream from the second,

rising along a gentle southeast facing slope (See fig. 1 for map of site, placement of transects). All are located in late-secondary forest areas with very limited or no recent human-based disturbance.

Sampling Methods

Within each transect, all stems >1 cm diameter at breast height (dbh, 1.4 m above the ground) were mapped, identified, and dbh was measured. Based on dbh and crown exposure, specimens were classified as adults or saplings, with cut-off size dependent on the species at hand (See table 1 for list of species and their abundance in the community.). For canopy trees, adulthood was equated with attaining a position within the main canopy of the forest, and thus having leaves exposed to full sunlight. For understory trees, evidence of reproductive ability or attaining a comparable size threshold was used to determine ontogenetic status. Shrub species were not subdivided into adult and sapling due to the already small stature of adult shrubs (ie, small dbh, etc.) and the lack of light structuring within their crowns. For all tree species (canopy and understory), up to a total of 24 specimens (12 adults, 12 saplings), as evenly spread as possible among and within transects, were selected for leaf sampling. In adults, three branchlets each from the sunniest position, and a strongly shaded position were collected and placed in water. Specimens were returned to the lab and rehydrated overnight. A total of six leaves from each canopy position were selected for analysis, two from each of the branchlets whenever possible. In the case of complex leaves, leaflets were treated as leaves, because they represent the photosynthetic unit for those plants. While size was not a factor in determining leaves sampled, we did select the most recently unfolded,

fully hardened leaves with the least amount of herbivory and epiphylls possible. Leaves were scanned on an Epson 1680 flatbed scanner, and analyzed using WinFOLIA 2005b Software. Subsequently, leaves were dried at 60C for at least 72 hours, then weighed on a Mettler balance.

Trait Analysis

Morphological traits were analyzed from scanned images using WinFOLIA software (leaf size), or from compounding data collected (P^2A , Leaf Shape Index, SLA). Leaf Nitrogen Content was analyzed by the Micro Dumas Analytical method, using a NA1500 C/H/N Elemental Analyzer. Dried leaf samples were ground using a ball mill, after bulking three leaves from a given canopy position. Specimens were processed in the University of Georgia analytical chemistry laboratory.

Statistical analyses

For each trait, mean and standard deviation was calculated for each species for sun and shade leaves separately for adults, and pooled for saplings. Overall pairwise correlations between traits were calculated. Nested or hierarchical analysis of variance (ANOVA's) were performed for each trait, setting species and canopy position/ontogeny as nested levels. From these ANOVA's, variance components were estimated for each level. All statistical analyses were carried out using the R statistical environment (R Core Development Team 2006).

For each species and trait, a trait distribution was calculated using a kernel estimator (see Mouillot *et al.* 2005). This method, which allows us to work with

continuous data without assuming a normal distribution of data, calculates a density function by assuming measurement error around each data point, and then using a smoothing function to estimate a distribution of all data for a given trait and population. These species (or population) kernels are then used to estimate pairwise overlaps in trait space of coexisting species. Overlap is simply represented as the integral of the area under the species' respective kernel curves when overlaid on one another. From these pairwise overlaps, a community-wide overlap index is then calculated, simply by averaging these overlaps. These overlap indices were calculated both while pooling all leaves sampled, and within each light exposure (sun-adult, shade-adult, and shade-sapling). Randomization tests on overlaps were performed to determine the impact of species identity on trait overlap. We held leaves constant on stems, and within canopy positions, but assigned species identity to individuals at random.

Results

Explanation of Variance

Using nested ANOVA's, we tested the hierarchical models to explain trait variation using species identity and canopy position/light exposure as predictor variables. In all cases, all levels of analysis were strongly statistically significant ($p < 0.0001$). We then calculated the percentage of variance explained by each level, finding in most cases a strong species signal, moderate signal for light, and a surprisingly large percentage of unexplained variation (see table 2). Notably, for three of the five traits tested (SLA, p_{2a} , and Leaf Area), unexplained variation exceeded both species and canopy position in their explanatory ability; in all cases, over 34% of the variance remained unexplained by these

variables. For specific leaf area, species identity and sun exposure explained comparable amounts of variance; for the remaining traits, species identity explained more of the variance than canopy position, with the strongest species-level effects in LNC and LSI. In both of these cases, canopy position explained very little of the variance in these traits (3.15 and 6.24%, respectively).

Variation among canopy positions: Effect of light levels

Once species was taken into account, leaves varied strongly in all tested leaf traits across canopy locations and ontogeny (Tables 3-7). Our results for SLA largely confirmed prior work—higher SLA, or thinner, less dense leaves in the shade than in sunny positions. Typically, there was little statistical difference between shade leaves of adult individuals and those of shaded saplings, but a few species did show a difference (*Carya spp.*, *Liquidamber styraciflua*, *Liriodendron tulipifera*, *Prunus serotina*, *Quercus alba*, *Q. rubra*, *Ulmus americana*), with saplings showing even higher SLA than shade leaves of adults. For leaf size, there is no discernible pattern that can be applied to all, or even most, species. Within each canopy class, extraordinary variability swamped most observed differences. However, *Morus rubra* and *Cercis canadensis*, both understory tree species, showed markedly smaller leaves in shade environment than sun.

Perimeter²:Area (p2a) ratios varied greatly among species, as well. Most species of oaks (*Quercus alba*, *Q. coccinea*, *Q. falcata*, *Q. rubra*) as well as *Liquidamber* showed greater p2a values, and therefore deeper lobing, in sun leaves than shade. Comparable to the findings of Sack *et al.* (2006), we found that species in genus *Acer* showed the opposite pattern—more lobed leaves in the shade than sun. Within *Liriodendron*, we found a more complex pattern that partially conflicts with Sack’s findings. Notably, p2a

is similar in sun leaves of adults, and shaded leaves of saplings, with lower, rather than higher, p2a in shade leaves of adults. This finding is puzzling, though it may be a result of the higher relative light environments that most saplings of this species require.

Leaf Shape Index (LSI), the leaf blade length:width ratio showed little discernible trend either within the group of species, or within any given species, suggesting that it is little affected by canopy position. Surprisingly, leaf nitrogen (N_{mass}) showed little overall response to canopy position, but a much stronger species level response.

Variation Among and Within Individuals

Within a single species, there is strong within and among individual variation for these traits, particularly SLA, even when controlling for canopy position. This is true for both canopy tree species (illustrated by *Quercus alba* in fig.) and for understory trees that experience a much reduced range of light environments over their ontogeny (illustrated by *Acer leucoderme* in fig. 2).

Correlation Among Traits

Generally, correlations among traits within this community were weak, with $r^2 < 0.08$ in all but one case (See table 8 for details). A moderately strong correlation (0.397) was found, as predicted, between LNC and SLA (see fig. 3), but the correlation was positive rather than negative, as found by Reich *et al.* (1997). It has been suggested that including sun, shade, and sapling leaves in a single dataset would confound the typically observed pattern (P.B. Reich, pers.comm.), but even when we split our dataset to only consider adult sun leaves, the correlation remained positive, and

moderately strong (0.359). The strong scatter, and relatively weak nature of virtually all trait correlations suggests that we can consider these traits as independent axes in community analyses.

Overlaps Among Species

Trait overlap among species for SLA is extraordinarily strong. Average overlap for species, when considering all leaves from all positions, is 0.482. When considering leaves from a single canopy position or age group (adult-sun, adult-shade, sapling), overlap fell slightly to 0.424, 0.392, 0.421, respectively, but these numbers still remain extraordinarily high for functional traits in coexisting species. Indeed, when we randomized the species identities of each individual, merely holding leaves within a given canopy position and on a given tree, in all cases, actual SLA overlap indices fell well within the values produced by the randomization tests (See fig. 4). Comparably, other traits fall within similar ranges, from 0.324-0.449 for LNC, 0.416-0.504 for Leaf Area, 0.402-0.443 for perimeter²:area ratio, and 0.287-0.386 for Leaf Shape Index (LSI). See table 9 for specifics. Importantly, there was no single leaf layer that consistently showed higher or lower overlap than others.

Discussion

Traits in community assembly

Our results suggest that these species of temperate trees are largely generalist species, at least with regard to these leaf functional traits. Intraspecific variability, even within a canopy position, is high enough to lead to broad trait overlap in all of these

functional traits, suggesting that species are not specializing within these leaf traits at the relatively fine spatial scale of this study. Even though species-level differences in the means of these traits are important in explaining the overall variance in traits, the trait spectrum for each species is sufficiently broad to produce strong interspecific trait overlap. Indeed, in predicting overlap values, species identity was unimportant, once canopy position and size class was accounted for. Such results make it highly unlikely to find support for limiting similarity within such a community.

It is clear that intracanopy plasticity and intra-individual variation in leaf functional traits as a function of light availability is high. Most of our results were consistent with the findings of earlier studies of the sun-shade leaf dichotomy; one notable exception was the lack of sizeable differences in LNC in sun vs. shade leaves. It is important to note, however, that even this well-documented ontogenetic and canopy-driven plasticity is not often factored into current studies of traits in ecological communities (e.g. Poorter and Bongers 2006; Shipley *et al.* 2006). It is clear that size matters, in some cases, as much species identity, to these leaf functional traits.

However, it is notable that this variability did not alone account for much of the variation within and among conspecific individuals. Clearly, this variability within individuals has the potential to have substantial impact on whole plant function. It will be difficult to scale plant function from leaf to tree to community given the amount of intra-canopy variability that remains unexplained in this type of study.

Comparably, the high trait variability among conspecific individuals, even when accounting for canopy position, will substantially impact community assembly and function. Even when we account for ontogeny and canopy position, we cannot explain

one-third to one-half of the variability among conspecifics in a single, narrowly delimited ecological community. This extraordinary variability within and among individuals argues strongly for trees as generalists—in part, responding through plasticity to the light environments to which they are exposed—but also as individuals with a unique genotype in a unique environment. Since trees clearly interact with one another and their environment as individuals, not as species, this variability becomes quite important to community interactions.

These findings suggest that it is ill-advised to represent these traits in species as a simple species mean for studies of community ecology, as recommended by McGill *et al.* (2006) and implemented by Shipley *et al.* (2006). In all ecological communities, it is individuals, not species, that are interacting with one another; within a spatially structured plant community, interactions of any given individual are governed by the particular neighborhood of that individual (e.g., Ahumada *et al.* 2004; Hubbell and Foster 1986; Hubbell *et al.* 2003). Given that a particular individual is likely only interacting with 10-20 other individuals at a particular time, to the extent that competition is driving selection, the selective environment of that focal individual is strongly driven by the traits of those –individual- neighbors, not the trait means of the species to which those neighbors belong. The well-documented ontogenetic and plastic response of plant traits (ie, Sack *et al.* 2006; Rozendaal *et al.* 2006) further suggests that, at least in tree communities, it ought to be possible to address some, but not all, of these complications by considering a size structured community. While this will undoubtedly help to address difficulties in building predictive trait-based models of community assembly, it still does

not capture or address the fundamentally high within and among individual variation we find within a single canopy position of a single individual.

Some proponents of a traits-based approach to community assembly suggest that traits for such studies should simply be selected based on a much higher degree of interspecific than intraspecific variability (i.e., McGill *et al.* 2006; Shipley *et al.* 2006). While this condition would produce a more convenient approach to predicting community assembly, it also assumes that it is those differentiated traits that are driving the observed species abundance patterns, and *a priori* invokes niche differentiation as the driving force in community assembly. While this approach may capture the mechanisms of community assembly quite successfully, it would exclude many of the traits long believed to be important to the ecology of tree communities—perhaps, most notably, those related to the capture of light resources. This leaves us to either ignore decades of work on plant functional traits (ie, Reich *et al* 1997; Reich *et al* 2003; Wright *et al* 2004), at least in terms of community assembly, or to reconsider approaches to predictive models of assembly to incorporate strong intraspecific variability.

Overall, this work shows that intracanopy as well as unexplained intra- and inter-individual variation in leaf traits is high, and will need to be factored into future efforts to predict community structure from plant functional traits. While we cannot conclude that these temperate tree species are generalists for all ecologically relevant traits, for the leaf functional traits measured, the strong interspecific trait overlap, combined with strong light-driven variability suggests that species are not specializing strongly on light gradients, at least as measured by these traits. It may be that the size asymmetric

competition inevitable in forest tree communities simply swamps any interspecific differences.

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Table 4.1. Count of species, adults and saplings, within sampling area.

Species	Adults	Saplings/Shrubs
<i>Acer leucoderme</i>	52	190
<i>Acer rubrum</i>	7	16
<i>Aesculus sylvatica</i>	0	9
<i>Amelanchier arborea</i>	0	2
<i>Carpinus caroliniana</i>	60	295
<i>Carya cordiformis</i>	4	12
<i>Carya ovalis</i>	5	17
<i>Carya tomentosa</i>	17	33
<i>Celtis laevigata</i>	6	12
<i>Celtis occidentalis</i>	1	9
<i>Celtis tenuifolia</i>	0	16
<i>Cercis canadensis</i>	5	1
<i>Cornus florida</i>	74	90
<i>Crataegus sp.1</i>	0	42
<i>Crataegus sp.2</i>	0	1
<i>Diospyros virginiana</i>	10	3
<i>Fagus grandifolia</i>	11	32
<i>Fraxinus pennsylvanica</i>	1	9
<i>Halesia caroliniana</i>	0	1
<i>Kalmia latifolia</i>	0	17
<i>Liquidamber styraciflua</i>	137	94
<i>Liriodendron tulipifera</i>	113	73
<i>Morus rubra</i>	6	4
<i>Nyssa sylvatica</i>	4	6
<i>Ostrya virginiana</i>	1	0
<i>Oxydendrum arboreum</i>	14	2
<i>Platanus occidentalis</i>	2	0
<i>Prunus serotina</i>	49	37
<i>Prunus umbellata</i>	0	4
<i>Quercus alba</i>	75	68
<i>Quercus coccinea</i>	3	0
<i>Quercus falcata</i>	7	10
<i>Quercus nigra</i>	111	102
<i>Quercus rubra</i>	14	17
<i>Quercus stellata</i>	2	8
<i>Rhododendron canescens</i>	0	7
<i>Sassafras albidum</i>	0	2
<i>Symplocos tinctoria</i>	0	3
<i>Tilia americana</i>	15	17
<i>Ulmus alata</i>	21	52
<i>Ulmus americana</i>	2	1
<i>Viburnum rufidulum</i>	0	7

Table 4.2. Percent of Variation in each trait explained by different levels, resulting from nested ANOVA: species identity, canopy position, and residual error. All levels were statistically significant ($p < 0.001$). Note that within this model, residual variation can arise from either within or among individual variation.

<u>Trait</u>	SLA	LNC	p2a	LSI	Leaf Area
<u>Source</u>					
Species	32.03	50.28	41.18	59.73	47.11
Sun/Shade/Sapling	31.3	3.15	15.05	6.24	4.94
Unexplained	36.67	46.56	43.77	34.02	47.95

Table 4.3. Species means and standard deviation for different canopy positions, Specific Leaf Area

Specific leaf area (SLA)		Mean +/- SD for canopy position, # inds, # lvs									
Species	# Adult Inds Sampled	# Sun lvs	Sun Leaf Mean	Sun SD	# Shade leaves	Shade leaf mean	Shade Leaf SD	# Sapling Inds Sampled	# Sapling lvs	Sapling Leaf mean	Sapling Leaf SD
<i>Acer leucoderme</i>	13	78	268.6309	48.77294	72	351.5356	45.10914	14	84	328.3536	53.60124
<i>Acer rubrum</i>	11	60	181.823	27.56172	66	210.2892	44.94198	15	90	235.1443	30.75812
<i>Aesculus sylvatica</i>	0	0	NA	NA	0	NA	NA	10	139	247.7713	37.12039
<i>Amelanchier arborea</i>	0	0	NA	NA	0	NA	NA	2	12	235.531	53.77976
<i>Carpinus caroliniana</i>	13	72	277.511	53.03192	78	329.4077	52.99439	13	78	333.2993	44.92806
<i>Carya cordiformis</i>	8	44	205.1768	35.60718	39	270.6434	27.52301	10	109	340.8522	56.06869
<i>Carya ovalis</i>	11	55	185.7942	24.70736	35	212.2543	35.27123	12	180	268.4343	44.20921
<i>Carya tomentosa</i>	10	174	194.8507	44.65359	156	266.0825	56.9388	14	308	298.9851	42.91961
<i>Celtis laevigata</i>	7	36	244.3576	59.92299	42	315.4493	62.00801	13	78	325.859	55.33702
<i>Celtis occidentalis</i>	1	6	267.8086	18.01791	6	314.8079	49.06475	11	66	317.4218	54.65919
<i>Celtis tenuifolia</i>	0	0	NA	NA	0	NA	NA	11	65	331.1267	65.58159
<i>Cercis canadensis</i>	7	42	277.9723	56.28567	31	330.4882	40.64735	1	6	299.7559	12.14643
<i>Cornus florida</i>	13	78	229.184	35.55862	78	256.5012	51.89105	11	66	277.0706	54.01505
<i>Crataegus sp.1</i>	0	0	NA	NA	0	NA	NA	18	120	257.145	47.08371
<i>Crataegus sp.2</i>	0	0	NA	NA	0	NA	NA	2	24	291.2402	26.45168
<i>Diospyros virginiana</i>	8	48	187.3388	37.17971	54	219.8498	59.82574	3	18	231.0634	32.67158
<i>Fagus grandifolia</i>	13	78	277.5037	46.75548	72	397.9051	54.45845	15	90	374.1957	57.06425
<i>Fraxinus pennsylvanica</i>	2	4	256.421	9.347267	22	335.9167	37.26133	7	173	298.3688	81.6177
<i>Halesia caroliniana</i>	0	0	NA	NA	0	NA	NA	1	12	459.14	30.98753
<i>Kalmia latifolia</i>	0	0	NA	NA	0	NA	NA	14	102	117.4934	19.04649
<i>Liquidambar styraciflua</i>	15	90	165.2325	60.50066	90	227.7028	78.4736	14	96	322.6126	75.5052
<i>Liriodendron tulipifera</i>	13	78	223.342	69.88192	82	276.5679	66.01009	12	72	383.5277	68.0298
<i>Morus rubra</i>	7	42	309.1989	100.9079	42	459.7583	143.4309	5	29	419.4649	82.7711
<i>Nyssa sylvatica</i>	5	24	234.0903	39.5955	30	366.0915	86.26629	7	42	319.1102	46.53312
<i>Ostrya virginiana</i>	1	6	226.3121	18.85448	6	256.5786	20.06597	0	0	NA	NA

<i>Oxydendrum arboreum</i>	12	72	291.9167	65.31476	72	353.9602	99.83765	2	12	365.5411	38.31016
<i>Platanus occidentalis</i>	2	12	208.74	43.37104	12	231.7098	35.34842	0	0	NA	NA
<i>Prunus serotina</i>	14	84	174.4463	43.50275	84	196.9549	28.75545	17	113	244.669	40.32729
<i>Prunus umbellata</i>	0	0	NA	NA	0	NA	NA	6	36	287.0871	40.07991
<i>Quercus alba</i>	17	102	159.1969	39.03515	92	227.2419	60.14931	12	71	264.6915	32.59776
<i>Quercus coccinea</i>	3	18	114.9013	38.12938	16	122.4392	24.51915	0	0	NA	NA
<i>Quercus falcata</i>	9	60	114.5675	23.84644	51	201.1467	52.52623	12	72	182.5418	35.31279
<i>Quercus nigra</i>	21	126	120.0757	25.68836	109	182.3661	32.33572	21	126	186.7108	34.66883
<i>Quercus rubra</i>	15	99	160.3244	34.65731	64	178.4683	37.5494	16	101	234.584	38.36594
<i>Quercus stellata</i>	2	12	156.921	12.5845	12	204.3056	13.28742	12	71	192.3051	29.84559
<i>Rhododendron canescens</i>	0	0	NA	NA	0	NA	NA	9	54	312.0817	37.05627
<i>Sassafrass albidum</i>	0	0	NA	NA	0	NA	NA	2	12	267.7857	39.41172
<i>Symplocos tinctoria</i>	0	0	NA	NA	0	NA	NA	4	30	278.9287	90.30062
<i>Tilia americana</i>	11	65	299.7838	57.89236	63	314.3374	72.63774	14	108	365.0808	71.83069
<i>Ulmus alata</i>	13	60	217.7354	31.95619	78	272.0506	74.06423	18	144	278.3756	44.23512
<i>Ulmus americana</i>	2	12	196.1324	54.07187	12	285.486	32.52101	1	6	384.2695	30.75123
<i>Viburnum rufidulum</i>	0	0	NA	NA	0	NA	NA	9	54	202.3074	23.27804

Table 4.4. Species means and standard deviation for different canopy positions, Leaf Size.

Species	Mean +/- SD for canopy position, # inds, # lvs										
	# Adult Inds Sampled	# Sun lvs	Sun Leaf Mean	Sun SD	# Shade lvs	Shade leaf mean	Shade Leaf SD	# Sapling Inds Sampled	# Sapling lvs	Sapling Leaf mean	Sapling Leaf SD
<i>Acer leucoderme</i>	13	78	30.56846	11.27213	72	26.84778	12.81891	14	84	23.75144	9.486291
<i>Acer rubrum</i>	11	60	38.96007	18.16135	66	40.22844	19.42595	15	90	38.53916	17.89524
<i>Aesculus sylvatica</i>	0	0			0			10	139	23.84435	10.78483
<i>Amelanchier arborea</i>	0	0			0			2	12	34.17298	7.353341
<i>Carpinus caroliniana</i>	13	72	16.06428	6.499894	78	13.96363	7.861039	13	78	15.10906	6.336846
<i>Carya cordiformis</i>	8	44	17.04733	10.52703	39	26.26619	18.09366	10	109	27.65477	20.92348
<i>Carya ovalis</i>	11	55	47.94604	27.27377	35	50.25994	29.02271	12	180	71.80588	52.44248
<i>Carya tomentosa</i>	10	174	44.66543	33.24352	156	47.12309	35.15694	14	308	40.23951	28.49249
<i>Celtis laevigata</i>	7	36	19.41613	6.902212	42	18.21593	12.13989	13	78	18.04804	8.187772
<i>Celtis occidentalis</i>	1	6	18.28893	5.672424	6	18.55003	5.168887	11	66	25.52941	12.5465
<i>Celtis tenuifolia</i>	0	0			0			11	65	13.75791	5.820809
<i>Cercis canadensis</i>	7	42	96.63797	82.94286	31	88.20329	54.80088	1	6	48.8969	26.06668
<i>Cornus florida</i>	13	78	45.4521	12.7792	78	43.03794	18.74696	11	66	42.94652	15.51658
<i>Crataegus sp.1</i>	0	0			0			18	120	10.64637	4.86606
<i>Crataegus sp.2</i>	0	0			0			2	24	53.02608	14.37974
<i>Diospyros virginiana</i>	8	48	37.49213	19.05356	54	40.43844	23.29956	3	18	32.56161	14.96574
<i>Fagus grandifolia</i>	13	78	50.04431	15.04965	72	38.48284	16.60644	15	90	42.67323	15.20404
<i>Fraxinus pennsylvanica</i>	2	4	25.4685	6.265876	22	39.26945	19.08487	7	173	43.53693	21.01387
<i>Halesia caroliniana</i>	0	0			0			1	12	53.79293	19.97286
<i>Kalmia latifolia</i>	0	0			0			14	102	14.64222	5.053044
<i>Liquidamber styraciflua</i>	15	90	54.97626	23.29085	90	49.65065	25.16564	14	96	35.53933	17.53619
<i>Liriodendron tulipifera</i>	13	78	92.00166	48.81698	82	100.023	52.9843	12	72	106.4453	49.91303
<i>Morus rubra</i>	7	42	206.0994	95.45601	42	131.5167	65.34004	5	29	106.0721	74.86587
<i>Nyssa sylvatica</i>	5	24	59.3939	12.69627	30	48.0367	26.68239	7	42	37.621	14.37366
<i>Ostrya virginiana</i>	1	6	36.60807	10.61803	6	39.84247	14.51073	0	0		

<i>Oxydendrum arboreum</i>	12	72	48.0354	15.84219	72	48.03705	18.28977	2	12	51.17373	22.31803
<i>Platanus occidentalis</i>	2	12	65.57417	33.19631	12	92.79203	65.11883	0	0		
<i>Prunus serotina</i>	14	84	21.70732	7.675255	84	20.15273	8.121449	17	113	19.41667	5.852402
<i>Prunus umbellata</i>	0	0			0			6	36	13.37976	4.183791
<i>Quercus alba</i>	17	102	51.67077	28.30624	92	69.15961	43.09291	12	71	55.84802	33.20616
<i>Quercus coccinea</i>	3	18	124.3786	48.17834	16	119.0085	68.86621	0	0		
<i>Quercus falcata</i>	9	60	70.11174	29.24406	51	61.74022	35.63151	12	72	66.31524	31.26076
<i>Quercus nigra</i>	21	126	15.44312	8.536488	109	20.13679	12.92189	21	126	22.46271	12.72685
<i>Quercus rubra</i>	15	99	94.50623	37.33838	64	100.2823	45.03106	16	101	116.3512	67.97442
<i>Quercus stellata</i>	2	12	113.3695	32.80362	12	92.32698	29.91245	12	71	108.4784	55.43497
<i>Rhododendron canescens</i>	0	0			0			9	54	14.11151	4.372057
<i>Sassafrass albidum</i>	0	0			0			2	12	70.77583	44.95784
<i>Symplocos tinctoria</i>	0	0			0			4	30	32.09939	9.89787
<i>Tilia americana</i>	11	65	67.14371	34.03376	63	68.5779	33.69911	14	108	48.03782	24.83066
<i>Ulmus alata</i>	13	60	14.65603	5.431416	78	15.46218	8.08096	18	144	14.31081	5.908738
<i>Ulmus americana</i>	2	12	26.13543	8.502084	12	19.05937	8.214681	1	6	27.39713	11.37189
<i>Viburnum rufidulum</i>	0	0			0			9	54	19.11806	8.61728

Table 4.5. Species means and standard deviation for different canopy positions, Leaf Nitrogen Concentration.

Leaf Nitrogen Content (LNC)			Mean +/- SD for canopy position, # inds, # lvs								
Species	# Adult Inds Sampled	# Sun lves	Sun Leaf Mean	Sun SD	# Shade lves	Shade leaf mean	Shade Leaf SD	# Sapling Inds Sampled	# Sapling lves	Sapling Leaf mean	Sapling Leaf SD
<i>Acer leucoderme</i>	13	78	2.2882	0.3061	72	2.2367	0.2017	14	84	2.2279	0.2063
<i>Acer rubrum</i>	11	60	1.915	0.2052	66	2.1572	0.6222	15	90	1.8567	0.2237
<i>Aesculus sylvatica</i>	0	0			0			10	139	2.1704	0.2559
<i>Amelanchier arborea</i>	0	0			0			2	12	1.925	0.1344
<i>Carpinus caroliniana</i>	13	72	2.1031	0.1805	78	2.1185	0.2068	13	78	2.0933	0.1977
<i>Carya cordiformis</i>	8	44	2.2017	0.1458	39	2.1525	0.2949	10	109	2.1647	0.4544
<i>Carya ovalis</i>	11	55	1.6907	0.1147	35	1.8338	0.2139	12	180	2.026	0.2607
<i>Carya tomentosa</i>	10	174	1.9753	0.3257	156	2.0692	0.2981	14	308	2.1289	0.3014
<i>Celtis laevigata</i>	7	36	2.8767	0.23	42	2.792	0.5222	13	78	3.3977	0.3701
<i>Celtis occidentalis</i>	1	6	3.175	0.0071	6	2.875	0.0071	11	66	3.1	0.5708
<i>Celtis tenuifolia</i>	0	0			0			11	65	3.0244	0.3507
<i>Cercis canadensis</i>	7	42	3.09	0.3967	31	2.635	0.7921	1	6	2.595	0.0071
<i>Cornus florida</i>	13	78	1.9154	0.212	78	1.8746	0.2776	11	66	1.8518	0.2226
<i>Crataegus sp.1</i>	0	0			0			18	120	1.965	0.2482
<i>Crataegus sp.2</i>	0	0			0			2	24	1.975	0.0071
<i>Diospyros virginiana</i>	8	48	2.3375	0.3017	54	2.2962	0.3389	3	18	2.0967	0.0851
<i>Fagus grandifolia</i>	13	78	2.265	0.2256	72	2.3117	0.1753	15	90	2.2507	0.1406
<i>Fraxinus pennsylvanica</i>	2	4	2.0925	0.2562	22	2.4575	0.4279	7	173	2.2429	0.3779
<i>Halesia caroliniana</i>	0	0			0			1	12	2.765	0.0778
<i>Kalmia latifolia</i>	0	0			0			14	102	1.37	0.1086
<i>Liquidamber styraciflua</i>	15	90	2.0073	0.2887	90	1.9407	0.3148	14	96	1.9446	0.2319
<i>Liriodendron tulipifera</i>	13	78	2.4127	0.2531	82	2.4882	0.5179	12	72	2.5975	0.2808
<i>Morus rubra</i>	7	42	3.134	0.4698	42	3.6017	0.3144	5	29	2.965	0.9604
<i>Nyssa sylvatica</i>	5	24	2.268	0.4149	30	2.17	0.2631	7	42	2.4557	0.823
<i>Ostrya virginiana</i>	1	6	1.795	0.0071	6	1.755	0.0071	0	0		
<i>Oxydendrum arboreum</i>	12	72	2.5018	0.3398	72	2.54	0.3217	2	12	3.2067	1.4931

<i>Platanus occidentalis</i>	2	12	2.01	0.1131	12	2.09	0.5091	0	0		
<i>Prunus serotina</i>	14	84	2.4531	0.4559	84	2.3869	0.3984	17	113	2.3089	0.2974
<i>Prunus umbellata</i>	0	0			0			6	36	2.506	0.1922
<i>Quercus alba</i>	17	102	2.2394	0.2308	92	2.24	0.2141	12	71	2.2933	0.1893
<i>Quercus coccinea</i>	3	18	2.27	0.2155	16	2.3233	0.3564	0	0		
<i>Quercus falcata</i>	9	60	2.064	0.3439	51	2.1289	0.2667	12	72	1.9145	0.2242
<i>Quercus nigra</i>	21	126	2.0929	0.2276	109	2.14	0.2051	21	126	2.0528	0.1992
<i>Quercus rubra</i>	15	99	2.3886	0.4073	64	2.163	0.2783	16	101	2.2812	0.2592
<i>Quercus stellata</i>	2	12	1.88	0.2121	12	1.8	0.0141	12	71	2.04	0.1374
<i>Rhododendron canescens</i>	0	0			0			9	54	1.8667	0.179
<i>Sassafras albidum</i>	0	0			0			2	12	2.86	0.0424
<i>Symplocos tinctoria</i>	0	0			0			4	30	2.47	0.3077
<i>Tilia americana</i>	11	65	2.7122	0.5794	63	2.8444	0.4491	14	108	2.6431	0.2681
<i>Ulmus alata</i>	13	60	2.5367	0.2677	78	2.5544	0.4112	18	144	2.5363	0.3522
<i>Ulmus americana</i>	2	12	2.18	0.0424	12	2.155	0.3465	1	6	2.915	0.0071
<i>Viburnum rufidulum</i>	0	0			0			9	54	1.4656	0.1148

Table 4.6. Species means and standard deviation for different canopy positions, Perimeter²: Area Ratio.

Perimeter ² :Area Ratio		Mean +/- SD for canopy position, # inds, # lves									
Species	# Adult Inds Sampled	# Sun lves	Sun Leaf Mean	Sun SD	# Shade lves	Shade leaf mean	Shade Leaf SD	# Sapling Inds Sampled	# Sapling lves	Sapling Leaf mean	Sapling Leaf SD
<i>Acer leucoderme</i>	13	78	39.78188	11.40727	72	47.97577	13.6138	14	84	44.35978	12.31673
<i>Acer rubrum</i>	11	60	33.6775	12.4485	66	37.62324	15.97667	15	90	36.80469	13.92407
<i>Aesculus sylvatica</i>	0	0			0			10	139	24.21291	4.790542
<i>Amelanchier arborea</i>	0	0			0			2	12	20.9635	2.220258
<i>Carpinus caroliniana</i>	13	72	23.38639	3.278872	78	22.46433	3.566124	13	78	23.49702	3.25598
<i>Carya cordiformis</i>	8	44	26.6445	6.396205	39	28.01208	9.902702	10	109	26.74064	10.61033
<i>Carya ovalis</i>	11	55	24.12514	6.750541	35	21.39696	4.799875	12	180	22.25048	11.93496
<i>Carya tomentosa</i>	10	174	22.35177	7.945753	156	20.68021	5.710802	14	308	20.81371	4.729258
<i>Celtis laevigata</i>	7	36	24.31206	6.05586	42	22.28166	3.949479	13	78	24.85292	3.989677
<i>Celtis occidentalis</i>	1	6	22.38558	2.31464	6	21.10448	2.218217	11	66	22.53837	2.977293
<i>Celtis tenuifolia</i>	0	0			0			11	65	21.25414	3.231013
<i>Cercis canadensis</i>	7	42	18.08087	3.543818	31	18.47583	4.494288	1	6	16.03936	0.8408
<i>Cornus florida</i>	13	78	19.2711	3.146441	78	20.59055	3.551524	11	66	19.72843	3.676043
<i>Crataegus sp.1</i>	0	0			0			18	120	33.54459	9.495336
<i>Crataegus sp.2</i>	0	0			0			2	24	21.93886	4.054995
<i>Diospyros virginiana</i>	8	48	20.77459	5.952695	54	21.4751	7.435799	3	18	18.30602	4.322299
<i>Fagus grandifolia</i>	13	78	22.04646	2.441437	72	21.22677	1.561836	15	90	20.05027	1.784177
<i>Fraxinus pennsylvanica</i>	2	4	19.33106	4.232547	22	22.54687	17.45418	7	173	21.15943	8.646284
<i>Halesia caroliniana</i>	0	0			0			1	12	17.00538	1.43729
<i>Kalmia latifolia</i>	0	0			0			14	102	18.71407	2.246125
<i>Liquidambar styraciflua</i>	15	90	51.39438	12.91264	90	42.46415	11.07587	14	96	32.80216	7.137664
<i>Liriodendron tulipifera</i>	13	78	42.32107	10.35628	82	37.24867	13.64882	12	72	45.96805	13.38809
<i>Morus rubra</i>	7	42	24.89091	5.415516	42	30.45833	13.39899	5	29	23.57268	5.45189
<i>Nyssa sylvatica</i>	5	24	17.09605	2.838827	30	18.11152	3.429164	7	42	19.87021	5.526185
<i>Ostrya virginiana</i>	1	6	32.966	5.642472	6	30.11671	3.429886	0	0		
<i>Oxydendrum arboreum</i>	12	72	20.21778	3.196316	72	19.9765	3.501095	2	12	16.57679	1.936345

<i>Platanus occidentalis</i>	2	12	28.8223	5.718781	12	32.66876	8.486809	0	0		
<i>Prunus serotina</i>	14	84	19.20407	3.057007	84	19.23361	3.250509	17	113	19.69341	3.32278
<i>Prunus umbellata</i>	0	0			0			6	36	24.90486	5.52011
<i>Quercus alba</i>	17	102	54.12245	27.0034	92	39.41947	19.60609	12	71	29.18381	5.5319
<i>Quercus coccinea</i>	3	18	91.80054	30.60839	16	59.56929	16.17263	0	0		
<i>Quercus falcata</i>	9	60	44.33285	15.03502	51	30.42989	10.53308	12	72	25.25068	7.804173
<i>Quercus nigra</i>	21	126	28.53525	6.025382	109	30.46326	7.8789	21	126	35.71964	11.01322
<i>Quercus rubra</i>	15	99	62.55388	21.69454	64	47.80943	16.36807	16	101	34.57793	12.1531
<i>Quercus stellata</i>	2	12	33.19105	5.675175	12	31.22153	8.462892	12	71	34.52339	9.70272
<i>Rhododendron canescens</i>	0	0			0			9	54	18.66759	3.034335
<i>Sassafras albidum</i>	0	0			0			2	12	22.07134	5.595912
<i>Symplocos tinctoria</i>	0	0			0			4	30	18.06523	1.747096
<i>Tilia americana</i>	11	65	24.50082	5.636739	63	23.97694	5.287989	14	108	24.55514	3.888587
<i>Ulmus alata</i>	13	60	26.7845	2.611607	78	27.89399	3.242554	18	144	27.24873	3.359083
<i>Ulmus americana</i>	2	12	34.44617	8.066142	12	32.02148	2.486001	1	6	27.62358	2.117315
<i>Viburnum rufidulum</i>	0	0			0			9	54	15.73212	1.686016

Table 4.7. Species means and standard deviation for different canopy positions, Leaf Shape Index.

Species	Mean +/- SD for canopy position, # inds, # lvs										
	# Adult Inds Sampled	# Sun lvs	Sun Leaf Mean	Sun SD	# Shade lvs	Shade leaf mean	Shade Leaf SD	# Sapling Inds Sampled	# Sapling lvs	Sapling Leaf mean	Sapling Leaf SD
<i>Acer leucoderme</i>	13	78	0.950827	0.082778	72	0.92355	0.113419	14	84	0.905816	0.094765
<i>Acer rubrum</i>	11	60	1.195228	0.1559	66	1.157242	0.176996	15	90	1.184322	0.185358
<i>Aesculus sylvatica</i>	0	0			0			10	139	2.460617	0.343378
<i>Amelanchier arborea</i>	0	0			0			2	12	1.786193	0.247912
<i>Carpinus caroliniana</i>	13	72	1.921593	0.215523	78	1.851878	0.260656	13	78	1.722578	0.15987
<i>Carya cordiformis</i>	8	44	2.713987	0.415355	39	2.238495	0.426035	10	109	2.208542	0.300523
<i>Carya ovalis</i>	11	55	2.10877	0.500844	35	1.99545	0.276942	12	180	1.953071	0.389997
<i>Carya tomentosa</i>	10	174	2.077291	0.372158	156	2.023115	0.321695	14	308	1.973177	0.284338
<i>Celtis laevigata</i>	7	36	2.116276	0.330182	42	1.874159	0.295615	13	78	2.114039	0.300483
<i>Celtis occidentalis</i>	1	6	1.942081	0.211842	6	1.713524	0.106608	11	66	1.781185	0.260612
<i>Celtis tenuifolia</i>	0	0			0			11	65	1.775124	0.209308
<i>Cercis canadensis</i>	7	42	0.963951	0.113395	31	0.899638	0.066314	1	6	0.982162	0.0707
<i>Cornus florida</i>	13	78	1.845304	0.230139	78	1.867106	0.28634	11	66	1.827429	0.25646
<i>Crataegus sp.1</i>	0	0			0			18	120	1.365041	0.307331
<i>Crataegus sp.2</i>	0	0			0			2	24	1.514465	0.171565
<i>Diospyros virginiana</i>	8	48	1.923479	0.327729	54	1.888818	0.371306	3	18	1.864402	0.240309
<i>Fagus grandifolia</i>	13	78	2.023751	0.193257	72	1.97932	0.169157	15	90	1.909282	0.15653
<i>Fraxinus pennsylvanica</i>	2	4	1.472804	0.131294	22	1.757787	0.339217	7	173	1.925995	0.340731
<i>Halesia caroliniana</i>	0	0			0			1	12	1.729532	0.202681
<i>Kalmia latifolia</i>	0	0			0			14	102	2.351754	0.280415
<i>Liquidambar styraciflua</i>	15	90	0.810238	0.089952	90	0.802752	0.083518	14	96	0.844846	0.074025
<i>Liriodendron tulipifera</i>	13	78	0.772996	0.147239	82	0.797	0.133712	12	72	0.722706	0.124272
<i>Morus rubra</i>	7	42	1.483542	0.187026	42	1.338021	0.182053	5	29	1.316942	0.1566
<i>Nyssa sylvatica</i>	5	24	1.923453	0.384433	30	1.932524	0.325351	7	42	1.982023	0.301804
<i>Ostrya virginiana</i>	1	6	2.506753	0.092177	6	2.150547	0.111168	0	0		

<i>Oxydendrum arboreum</i>	12	72	2.537847	0.431906	72	2.501493	0.43012	2	12	1.950733	0.246035
<i>Platanus occidentalis</i>	2	12	0.910844	0.126197	12	0.963775	0.133403	0	0		
<i>Prunus serotina</i>	14	84	2.249035	0.365112	84	2.208705	0.379669	17	113	2.268643	0.361888
<i>Prunus umbellata</i>	0	0			0			6	36	2.191637	0.342461
<i>Quercus alba</i>	17	102	1.713764	0.392522	92	1.743127	0.330333	12	71	1.809393	0.269363
<i>Quercus coccinea</i>	3	18	1.220372	0.182669	16	1.319135	0.185659	0	0		
<i>Quercus falcata</i>	9	60	1.755653	0.346146	51	1.970047	0.307382	12	72	1.803525	0.258348
<i>Quercus nigra</i>	21	126	2.512057	0.743839	109	3.082247	1.328326	21	126	3.863547	1.900629
<i>Quercus rubra</i>	15	99	1.406981	0.179604	64	1.415105	0.150778	16	101	1.486345	0.168936
<i>Quercus stellata</i>	2	12	1.499922	0.143443	12	1.462881	0.182303	12	71	1.441187	0.197485
<i>Rhododendron canescens</i>	0	0			0			9	54	2.171583	0.38494
<i>Sassafrass albidum</i>	0	0			0			2	12	1.865885	0.263472
<i>Symplocos tinctoria</i>	0	0			0			4	30	2.224987	0.212675
<i>Tilia americana</i>	11	65	1.247858	0.159157	63	1.220005	0.156113	14	108	1.295438	0.162461
<i>Ulmus alata</i>	13	60	2.404124	0.248495	78	2.325394	0.252903	18	144	2.416431	0.369989
<i>Ulmus americana</i>	2	12	2.070433	0.134219	12	2.31236	0.207427	1	6	2.002024	0.197998
<i>Viburnum rufidulum</i>	0	0			0			9	54	1.569031	0.18651

Table 4.8. Adjust r^2 values for pairwise correlative relationships between all traits. All reported are significant to $p < 0.001$, except for non-significant, reported NS.

	LNC	p2a	LSI	Leaf Area
SLA	0.1578	0.0499	0.01748	0.000732
LNC		NS	NS	0.02205
p2a			0.03355	0.06026
LSI				0.07788

Table 4.9. Mean trait overlaps for each trait for all leaves pooled, and for leaves in individual canopy positions.

Group		All	Adults-Sun Lves	Adults-Shade Lves	Saplings
Trait					
	Specific Leaf Area	0.482	0.424	0.392	0.421
	N mass	0.397	0.416	0.449	0.324
	Perimeter 2: Area	0.443	0.402	0.439	0.435
	Leaf Shape Index	0.371	0.287	0.315	0.386
	Leaf Area	0.456	0.416	0.504	0.469

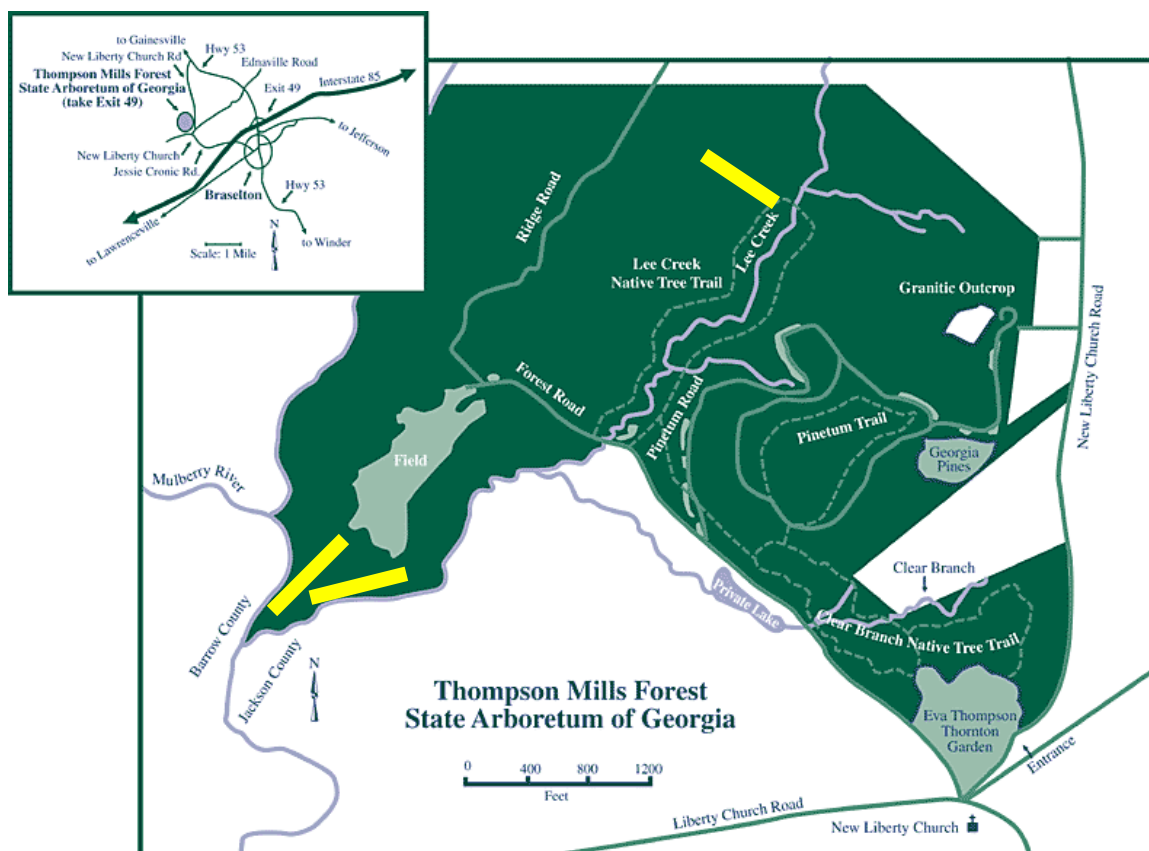


Figure 4.1. Map of Thompson Mills Forest and location of study transects. Map courtesy UGA Warnell School of Forest Resources.

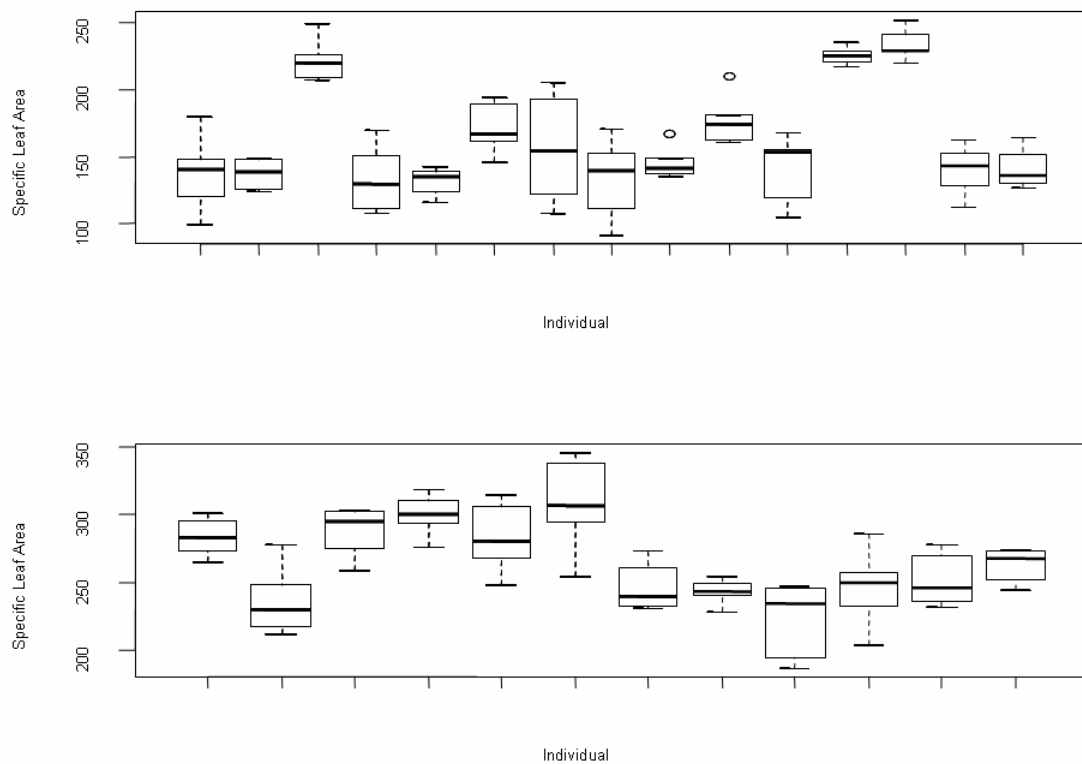


Figure 4.2. Boxplots of Specific Leaf Area (SLA) for *Quercus alba* individuals, each box representing leaves collected from a single individual tree, sun leaves of adults in top graph; sapling shade leaves below. Note the breadth of trait values within single individuals, as well as the lack of consistency among individuals.

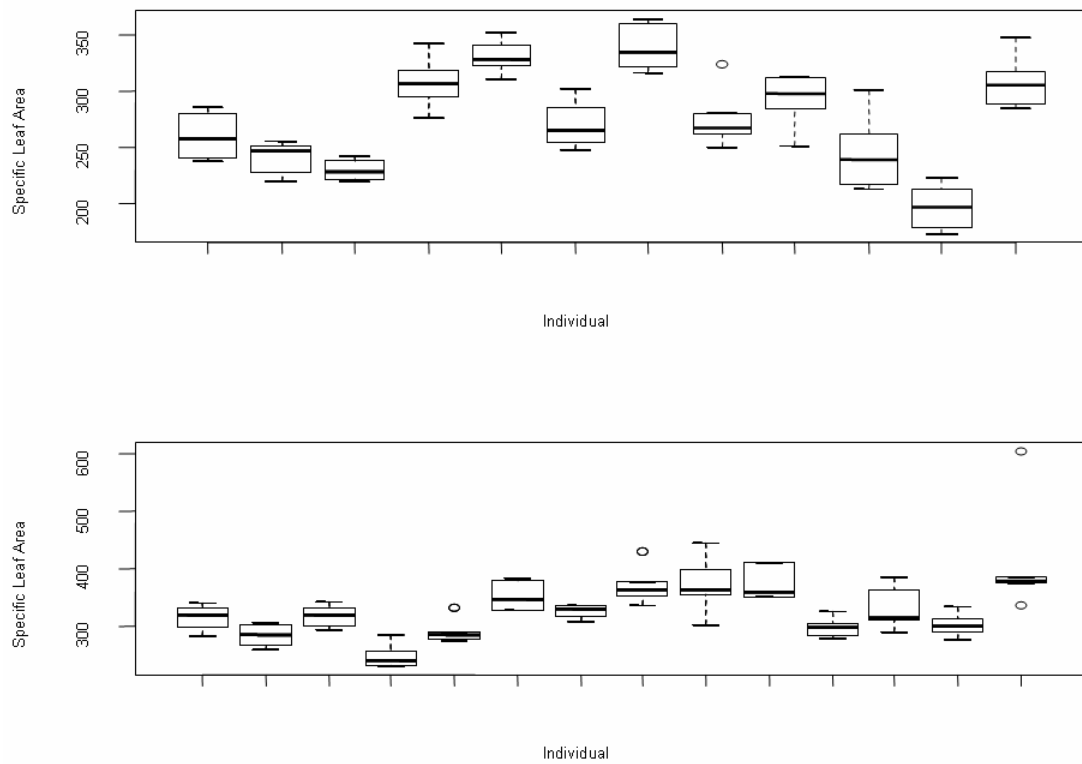


Figure 4.3. Boxplots of Specific Leaf Area (SLA) for *Acer leucoderme* (an understory tree) individuals, each box representing leaves collected from a single individual tree, sun leaves of adults in top graph; sapling shade leaves below. Again, note the breadth of trait values within single individuals, as well as the lack of consistency among individuals.

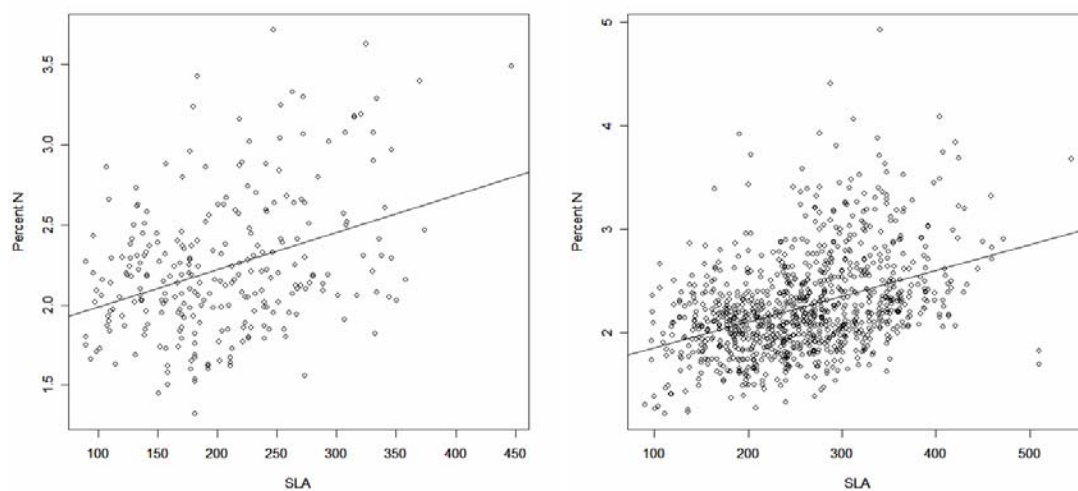


Figure 4.4. Correlation between Leaf Nitrogen Content (LNC) and Specific Leaf Area; adult sun leaves only on left; all leaves on right. Note wide scatter, but moderate positive correlation in both graphs.

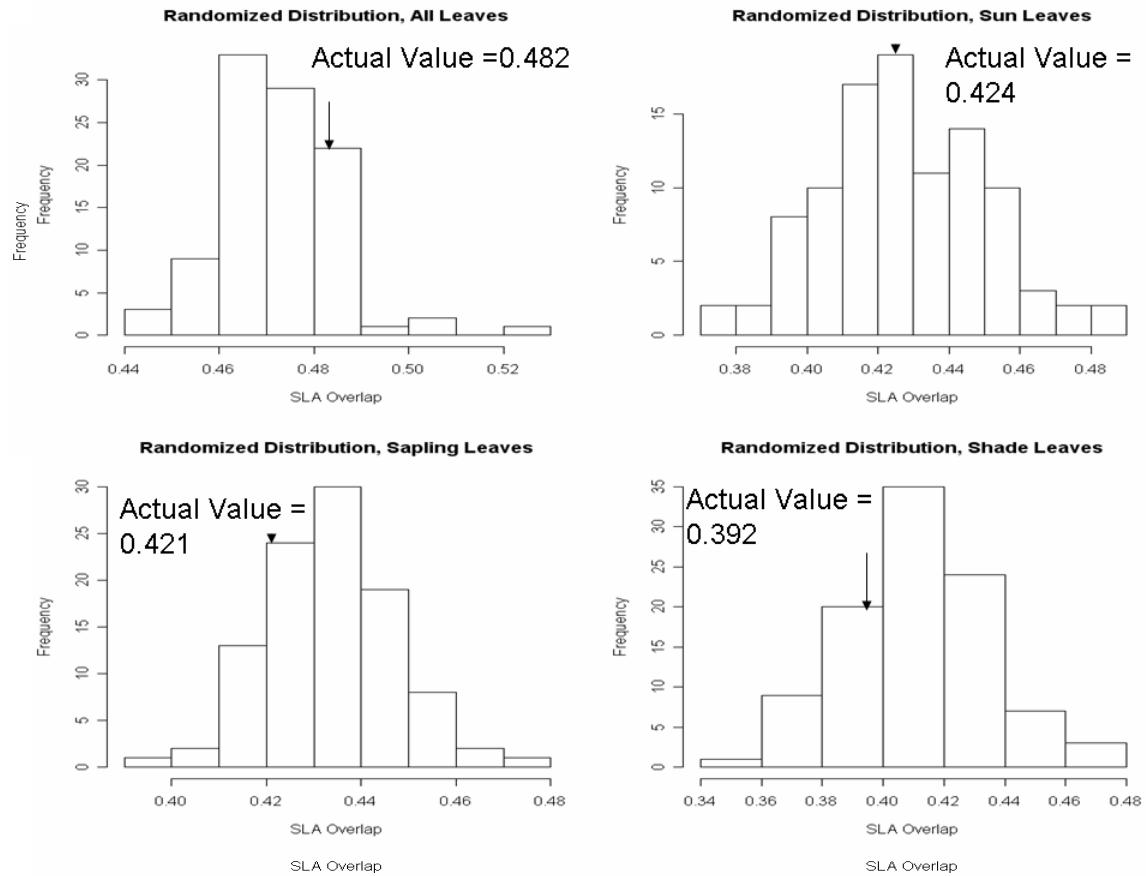


Figure 4.5. Distribution of 100 randomizations of species assignments to existing tree-leaf data. Note that observed trait overlap falls well within that expected to be generated if individuals were randomly assigned to species.

CHAPTER 5

SPATIAL DISTRIBUTION OF FUNCTIONAL TRAITS IN A TEMPERATE TREE
COMMUNITY¹

¹ Lake, J.K. and S.P. Hubbell. To be submitted to *Ecology Letters*.

Abstract

Three competing hypotheses of community assembly are tested using plant functional traits: limiting similarity, habitat filtering, and ecological equivalence/neutrality. The spatial distribution of trait overlap was used as a measure of similarity at the neighborhood level. We found no support for limiting similarity in our data, some support for habitat filtering, especially based on leaf nitrogen levels, and a largely random signal for these traits in most tested species.

Introduction

One of the most challenging ongoing problems in plant community ecology is that of species coexistence. Scores, or even hundreds, of species of woody plants commonly co-occur within a single hectare of tropical forests. Even in relatively species poor temperate forests, it is not uncommon to find 40 or more species of trees and shrubs in a comparable area. These observations have led to numerous hypotheses for mechanisms of coexistence (e.g., MacArthur and Levins 1967; Hubbell 2001; Weiher and Keddy 1995; Tilman 1982), but rigorous mechanistic tests of these hypotheses have remained relatively elusive. The advent of neutral theory in ecology (Hubbell 2001) has rekindled interest in hypotheses of community assembly because they bear directly on the neutral-non-neutral debate. However, developing a mechanistic, predictive theory of community assembly remains a “Holy Grail” of ecology (Lavorel and Garnier 2002).

Recently, there has been a renewed focus on plant functional traits as a driver of species coexistence (McGill *et al.* 2006). Because functional traits are defined as “any attribute that has potentially significant influence on establishment, survival, and fitness and ... focus[ing] on those traits related to the ability to acquire, use, and conserve resources (Reich *et al.* 2003)”, they ought to be a good measure of niche. And, although there is a long history of using morphological traits as a surrogate for niche in animal systems (i.e., Hutchinson 1967, Van Valen 1965), the idea has not been used on a wide-spread basis in plant communities until quite recently.

In the last few years, a series of studies have demonstrated a number of fundamental, globally applicable trade-offs (Reich *et al.* 1997; Wright *et al.* 2004) in plant functional traits, and particularly in leaf traits. These traits, associated with life history variation, appear fundamentally important to the way plants make their living (Wright *et al.* 2003). Poorter

and Bongers (2006) showed that leaf traits, in particular, are well correlated with plant performance in relation to particular crown exposure. In this research, we have chosen to focus on leaf traits, both because of their demonstrated importance in global patterns of plant diversity (ie, Wright *et al.* 2004) and also because of their central role in photosynthesis and respiration. Light has long been recognized as one of the most limiting resources in tropical forests, and indeed has been hypothesized to be one of the most finely partitioned resources in a tropical forest (i.e., Orians 1982, Ricklefs 1977, Denslow 1980). Of course, we do not imply that leaf traits represent every aspect of a species' niche space, but they certainly ought to be important to the way these species are surviving and coexisting.

Specifically, we have chosen five leaf traits upon which to focus. *Specific leaf area* (SLA, measured in cm^2/g) is one of the strongest measures of a plant's photosynthetic investment, and is a strong correlate of mass-based maximum photosynthetic rates (A_{max}). Low values tend to be associated with longer leaf lifespans, nutrient limited environments, and high defensive investment (Reich *et al.* 2003; Reich *et al.* 1997). Across several species of tropical trees, Poorter and Bongers (2006) have also shown that the SLA is positively related to whole-plant growth and negatively to survival, suggesting low investment in high turn-over, metabolically fast leaves in short-lived sun demanding plants. *Leaf size*, the area of leaf lamina or leaflets, excluding petiole or rachis, is a measure of actual photosynthetic surface, and is important to both water and energy balance (Cornelissen *et al.* 2003). *Leaf Nitrogen Content* (LNC) is highly correlated to mass-based maximum photosynthetic rates (A_{max}). It provides insights into nutrient use and availability, and is correlated to leaf lifespan (Reich *et al.*, 1997). N_{mass} has been shown to correlate positively with growth, while N_{area} correlates with survival (Poorter and Bongers 2006). *Carbon: Nitrogen ratios* (C:N Ratio) are indirectly tied to plant defense strategies. Higher

C:N ratios suggest a lack of nitrogen in the leaves, and the excess carbon is often invested in high carbon phenolic compounds for defense against herbivory (Sterner and Elser 2002). Finally, two leaf morphological traits, while less well understood ecologically, appear related to sun exposure and overall energy balance. *Perimeter²:Area ratio* provides a good measure of lobing, in essence providing the degree to which a leaf blade's shape diverges from a circle (Sack *et al.* 2006). *Leaf Shape Index (LSI)*, or the ratio of leaf length to width, provides another metric of a leaf's shape (Rozendaal *et al.* 2006).

Recently, several authors have begun to look to plant functional traits to assess questions of community assembly and structure (summarized in McGill *et al.* 2006). Shipley *et al.* (2006) have built a predictive model of community composition based on plant functional traits using maximum entropy methods. Stubbs and Wilson (2004) demonstrated a degree of limiting similarity in plant functional traits in a New Zealand dune community. Cornwell *et al.* (2006) used a combination of species with functional traits to demonstrate habitat filtering in small plots of California scrub forest communities using a convex hull volume method, and more recently, Ackerly and Cornwell (2007) used the same data to attempt to tease apart species' alpha and beta niche values for similar functional traits.

However, with the exception of the work of Ackerly and Cornwell (2007), all of these studies have assumed that interspecific variation is much stronger than intraspecific variability in these traits. Indeed, the success of Shipley *et al.* (2006)'s model depends on this assumption, and McGill *et al.* (2006) go so far as to argue that functional traits are only useful in community assembly if these assumptions are met. Yet, many of the traits used in this study show strong intraspecific variability. While this reality makes it more difficult to apply predictive models of community assembly, a vast literature has

demonstrated the importance of these traits to the ecology of species (ie, Reich *et al.* 1997; Wright *et al.* 2004). Therefore, this variability must be considered in any study of functional traits in the context of ecological communities.

Because spatial structure is inherent in sessile plant communities, an individual's biotic and abiotic environment is relatively easy to quantify. If functional trait differentiation is important to coexistence in these communities, then one should find greater trait differentiation of plants that grow in closer proximity to one another, i.e., as neighbors, than in random samples of these communities. A central tenet of classical theory in community ecology is that coexistence requires that species exploit limiting resources differently from one another (Grinnell 1914 and 1917; Elton 1927; Hutchinson 1957, 1959; MacArthur and Levins 1967; Tilman 1982). Gause (1934) invoked competitive exclusion as a process that ought to prevent too close of competitors from coexisting. Under classical niche theory, as the number of species in a community goes up, either the total niche volume for the community must be larger, or else niches must become narrower to allow for coexistence of additional species.

However, within plant communities, there is relatively little support for limiting similarity and competitive exclusion. Indeed, the asymmetric nature of plant competition and the spatial nature of their arrangement may reduce the importance of these forces. Nonetheless, within-taxon evidence from tropical gap plants (Davies *et al.* 2004) and within the genus *Quercus* (Cavendar-Bares *et al.* 2004a, 2004b) suggest that there may be differentiation of ecological traits within closely related species. Furthermore, Stubbs and Wilson (2004) found what they describe as the most compelling evidence for limiting similarity in plant communities in a study of dune species in New Zealand, although the

proportion of statistically significant tests showing such evidence was only around 8%, perhaps more the result of type I error than a real pattern. However, Ackerly and Cornwell (2007) also show a degree of differentiation among species in local plots of woody plant communities in California.

Weiher and Keddy (1995) offer another hypothesis, which they call environmental filtering. Plant species will tend to be filtered and sorted according to their respective environmental requirements, with the result that more similar species will occupy more similar habitats. The result should be a clustering of individuals with similar requirements, following the same spatial distribution as habitat availability. Although not typically tested in continually spatially explicit fashion, there is more evidence for habitat filtering (ie, Cornwell and Ackerly 2006; Harms *et al.* 2002) in plant communities.

In contrast, Hubbell (2001) and colleagues argue that all this changes under strong dispersal and recruitment limitation. Dispersal and recruitment limitation mean that species fail to disperse to and/or recruit in all sites favorable to their survival and growth. Hubbell *et al.* (1999) found strong dispersal and recruitment limitation in a tree community in Panama, which they argued extensively delays competitive exclusion. In theoretical models, strong dispersal and recruitment limitation permits many species to coexist essentially indefinitely, even in the absence of limiting similarity (Hurtt and Pacala 1995). Hubbell's neutral theory (2001) and the concept of ecological equivalence that has grown from the theory (ie, Hubbell 2006; Lake *et al.*, submitted) suggests that species share a common generalist approach. Some evidence relating plant occurrence to nutrient levels and ratios within a tropical forest suggests equivalence may be the norm,

at least within that system (Hubbell *et al.*, in press). If ecological equivalence is indeed driving community patterns, we would expect no spatial signal in plant traits.

In this paper, we test these three hypotheses using leaf functional traits. Each hypothesis has generated unique, specific predictions for the spatial distribution of functional traits within plant communities. While neutrality ought to produce a random distribution of ecologically relevant traits, limiting similarity would lead to overdispersion of mean trait values and reduced trait overlap at close spatial scales, decaying over additional space to a random pattern. In contrast, habitat filtering ought to lead to species with a shared strategy and shared requirements in close proximity, so mean trait values ought to be clustered at small spatial scales and there should be increased trait overlap, and concurrent with a change in habitat, there would be a change in species composition and ecologically-relevant traits.

Materials and Methods

Site description

Thompson Mills Forest is a 135-ha. reserve located near Braselton, Georgia, in Jackson County, about 40 miles northeast of Atlanta in the Piedmont (34°7'39 N, 83°48'6 W) . The site is composed of late-secondary oak-hickory forest, dominated by *Quercus* sp., *Carya* sp., *Liriodendron tulipifera*, and *Fagus grandifolia*. Average annual rainfall in this area is estimated at 141.7 cm, mean annual temperature is 15.6 C (Georgia Automated Environmental Monitoring Network, Gainesville, GA). Three 20x200m sampling transects were established. The first runs along a northwest facing slope overlooking the Mulberry River; the second, along a southfacing slope overlooking Lee

Creek; the third perpendicular to Lee Creek at a point upstream from the second, rising along a gentle southeast facing slope. All are located in late-secondary forest areas with very limited or no recent human-based disturbance.

Sampling Methods

Within each transect, all stems >1 cm diameter at breast height (dbh, 1.4 m above ground) were mapped, identified, and dbh was measured. Based on dbh and light availability, specimens were classified as adults or saplings, with cut-off size dependent on the species at hand. For all tree species (canopy and understory), up to a total of 24 specimens (12 adults, 12 saplings), as evenly spread as possible among and within transects, were selected for leaf sampling. In adults, three branchlets each from the sunniest position, and a strongly shaded position were collected and placed in water. When possible, branchlets were collected with pole pruners. However, sun leaves (and many shade leaves) of adult canopy trees were not accessible from the ground. For those specimens, we used a shotgun to bring down the branchlets with a ground spotter verifying canopy position. Specimens were returned to the lab and rehydrated overnight. A total of six leaves from each canopy position were selected for analysis, attempting to select two from each of the branchlets whenever possible. While size was not a factor in determining leaves sampled, we selected the most recently unfolded, fully hardened leaves with the least amount of herbivory and epiphylls possible. Leaves were scanned on an Epson 1680 flatbed scanner, and analyzed using WinFOLIA 2005b Software. Subsequently, leaves were dried at 60C for at least 72 hours, then weighed on a Mettler balance.

Trait Analysis

WinFOLIA automatically collects data on leaf area, perimeter, length and width, all used in subsequent analyses, usually as compound measures. Morphological traits were analyzed from scanned images using WinFOLIA software (leaf size), or from compounding data collected (P^2A , Leaf Shape Index, SLA). Leaf Nitrogen Content and C:N Ratio were analyzed by the Micro Dumas Analytical method, using a NA1500 C/H/N Elemental Analyzer. Dried leaf samples were ground using a ball mill, after bulking three leaves from a given canopy position. Specimens were processed in the University of Georgia analytical chemistry laboratory.

Statistical analyses

For these analyses, we focused primarily on SLA and LNC, the two traits most ecologically relevant to photosynthetic capacity and thus most likely to impact interspecific competition or species habitat affinities. For each species and trait, a trait distribution was calculated using a kernel estimator (see Mouillot *et al.* 2005). This method, which allows us to work with continuous data without assuming a normal distribution of data, calculates a density function by assuming measurement error around each data point, and then using a smoothing function to estimate a distribution of all data for a given trait and population. These species (or population) kernels are then used to estimate pairwise overlaps in trait space of coexisting species. Overlap is simply represented as the integral of the area under the species' respective kernel curves when

overlaid on one another. From these pairwise overlaps, a community-wide overlap index is then calculated, simply by averaging these overlaps.

In our first analysis, this community overlap index was calculated for nested “communities” of different sizes (0.04 ha, 0.1 ha, and 0.4 ha.), built from within the transects sampled. This approach followed traditional ecological methods of considering simply the presence or absence of a species within a given plot, or community. These overlap values were then regressed onto plot size.

Second, we considered an individual level spatial model, where the exact coordinates of each individual was used to calculate distances from every other individual within each transect. Saplings were separated from adults, and only values from sun leaves in adults were used for these analyses, in accordance with traditional approaches to functional ecology (Cornellisen *et al.* 2003). Trait overlap (as described above) was calculated for each individual pair in each transect, and then averaged at 5 m distance classes, both within species and size class, and subsequently, without regard to species. These analyses were run individually for each species and ontogenetic class, as well as pooled with all individuals. For each analysis, we also performed 100 community randomizations, maintaining size classes and overall abundance distributions, but randomly assigning species identities and their associated trait values to each individual. From these 100 randomizations, we recorded minimum and maximum overlap values at each distance class. All analyses were conducted using the R Statistical Environment (R Core Development Team 2006).

Results

When simply considering trait overlap as a function of community size, without regard to species abundances, we found no pattern in two of the three transects, and in the third, a significant negative association between trait overlap and plot size ($R^2 = 0.35$; $p=0.02$; see fig. 1) . For the third transect, this suggests decreasing species similarity/trait overlap as we sample a larger area; this pattern was not observed in either of the other sampling transects.

When all species were pooled, there were no departures from random expectations for overlap of SLA within any of the transects, illustrated here by transect 3 (see fig. 2). When performed by individual species and size class within each transect, there were seven out of 158 plots (4.4%) that showed any pattern outside of the randomization envelopes for SLA (See figs. 3 and 4). All seven showed greater overlap than expected by chance at small spatial scales, decreasing into the randomization envelopes within 15-25 m. With the exception of *Liquidamber styraciflua*, which demonstrated non-random patterns in overlap in transects 1 and 3, but not 2, the species demonstrating non-random patterns were not the same from one transect to the next.

For Leaf Nitrogen Content (LNC), the story is somewhat different. About 30% of the tests within Transect 1 showed greater trait overlap than expected by chance for LNC, although the pattern was often only distinguishable in one size class or the other, typically with a stronger signal in the sapling size class. Again, there was no evidence of limiting similarity (See fig. 5 for examples.)

Discussion

These spatial results strongly suggest a largely random distribution of plants in relation to specific leaf area across a landscape, and present a more mixed picture for leaf nitrogen. It is important to note, however, that LNC values often are driven in part by environmental availability, so it is possible that the patterns observed are being driven by environmental heterogeneity in soil nitrogen availability. Because we were unable to measure soil nitrogen levels, we are unable to test this idea directly. However, any environmental filter would be expected to operate over the lifespan of plants, so signals would be expected to become stronger in larger size classes (ie, older individuals that have already undergone selection); we observed exactly the opposite pattern.

In contrast to the strong evidence for limiting similarity found in a dune plant community (Stubbs and Wilson 2004), there is absolutely no evidence suggesting limiting similarity in these leaf functional traits in this temperate forest. While this finding is consistent with the overall paucity of evidence for limiting similarity in plant communities, it is somewhat surprising to find not a single species or size class showing any reduced overlap with near neighbors.

There was weak support in SLA overlap for habitat filtering, but as only seven of 158 (4.4%) tests showed a pattern departing from random, one could easily attribute these results to type I error. There was support, beyond that expected from type I error, for habitat filtering on the LNC trait, particularly within Transect 1, but the pattern was neither pervasive nor consistent among size classes. Furthermore, the lack of consistency in the species demonstrating this pattern among transects suggests that the process may not be pervasive in this tree community. Nonetheless, it is striking that all non-random

patterns found are consistent with habitat filtering, suggesting that this may be at least a weak force at work within the forest (or that it may be occurring more strongly at larger spatial scales than are tested with this 1.2 ha. study). Nonetheless, this is a process for which moderately strong support has been found, including at small spatial scales such as those presented in this study (ie, Cornwell and Ackerly 2006; Weiher and Keddy 1999). Perhaps most notable is that three species of relatively common understory shrub/small trees, *Kalmia*, *Rhododendron*, and *Crataegus* all demonstrated this pattern for both traits; this is perhaps not surprising, given the relatively narrow range of light environments these species are exposed to throughout their life.

It is surprising that the seemingly strong signal for habitat filtering found in one of the transects (see fig. 1) when species presence-absence data were used is not borne out in either the aggregated or species-level individual-driven analyses. It is likely that the individual-based approach provides a more thorough picture of the actual interactions at a community level than does a simple presence-absence matrix.

Overall, the high level of trait overlap, and the lack of a spatial signal in these leaf traits suggests a relatively random assembly process for forests at these spatial scales. The lack of spatial signal in most species' SLA overlaps is likely driven by the extraordinary variability of these traits in nature. Indeed, mean SLA overlaps among all species at the site were estimated at 0.482 (See chapter 4). While species means are subtly different from one another, these differences are often swamped by intraspecific variability, suggesting that trees function best as generalists. Given the wide range of light levels to which a given individual of a canopy tree is likely exposed over its lifetime, this strategy of high plasticity is not particularly surprising.

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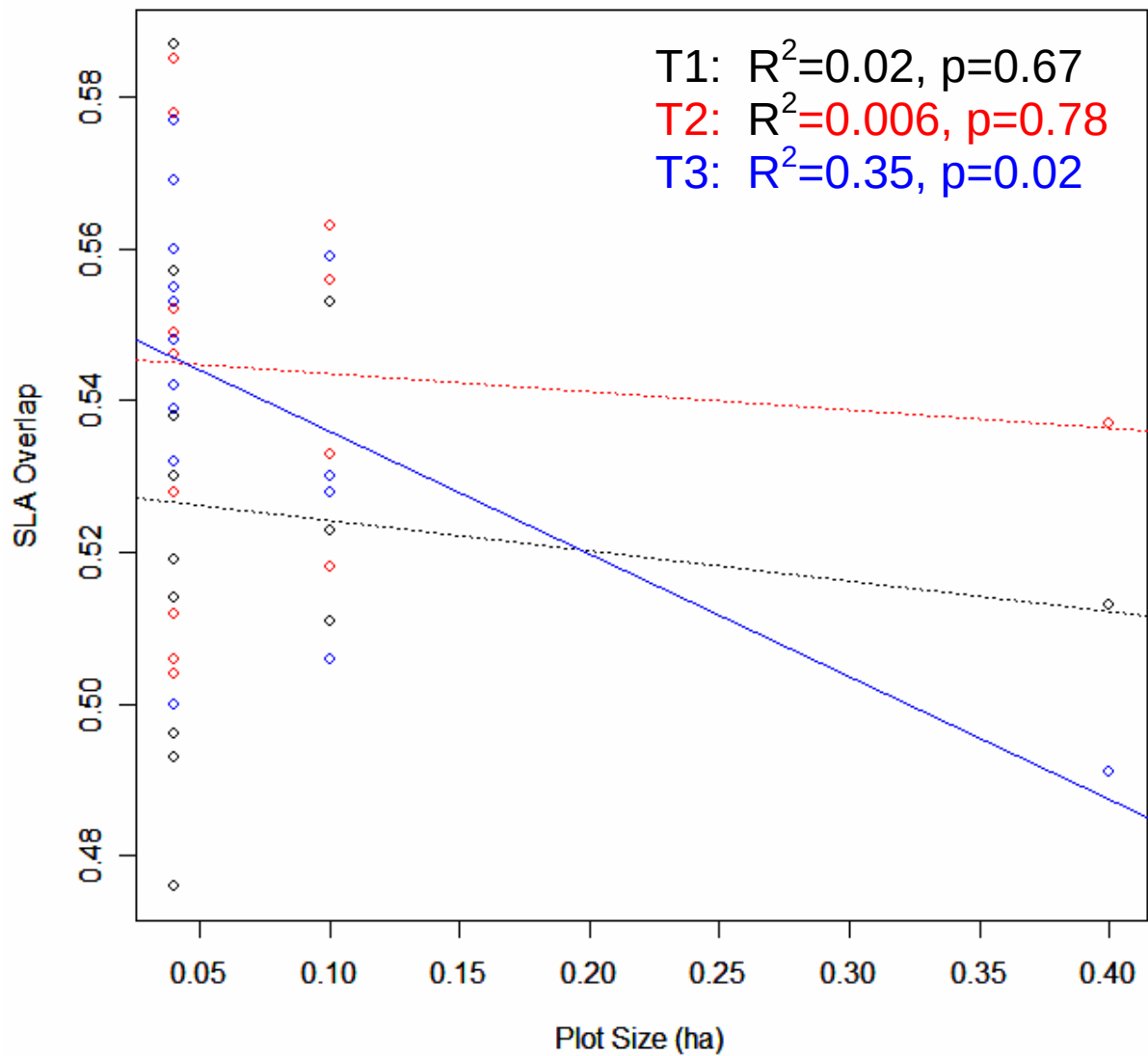


Figure 5.1. Overlap in specific leaf area as a function of plot size. Three sampling transects (T1, T2, T3) plotted separately. The smallest size represented by 10-20X20m quadrats within each transect; medium by 4-0.1 ha. subplots within each transect, and finally, by the overall transect. We would expect no slope and little explanatory power under neutral theory (as seen in T1 and T2); Transect 3 is consistent with habitat filtering.

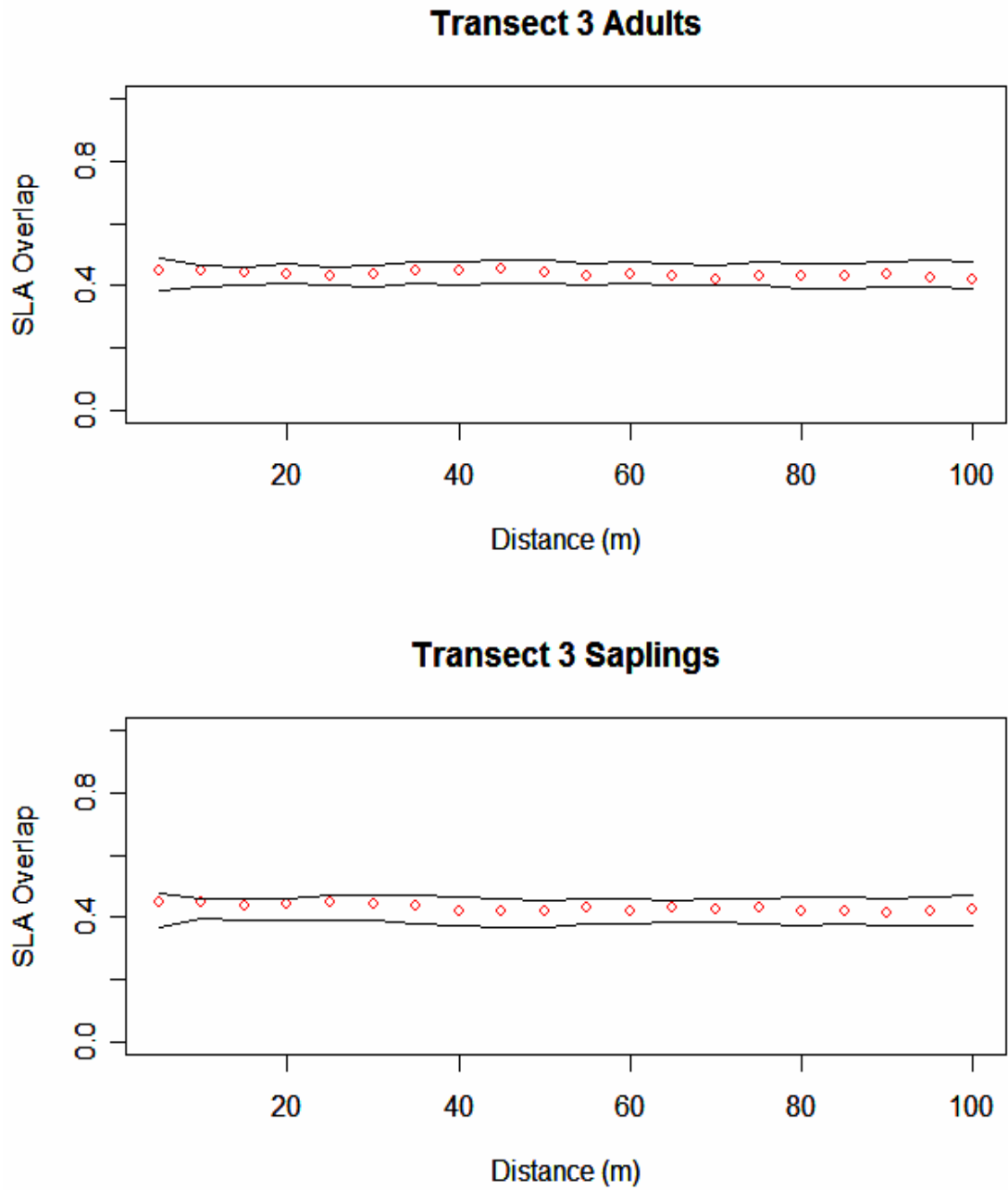


Figure 5.2. Pairwise overlap in specific leaf area (SLA) for all species pooled as a function of distance within transect 3. Data in red, black lines represent minimum and maximum values from 100 randomization tests.

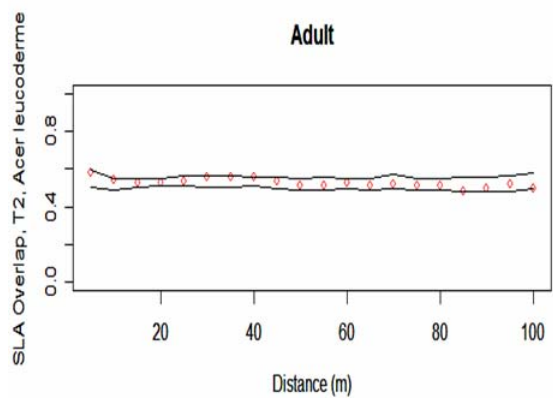
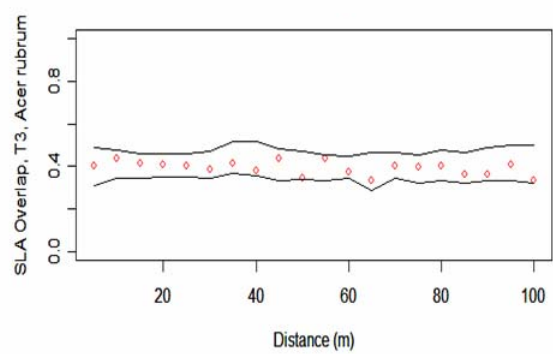
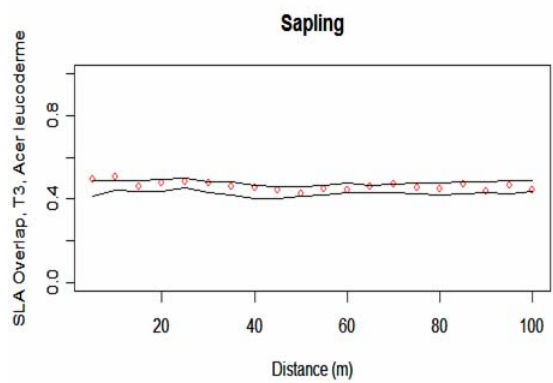
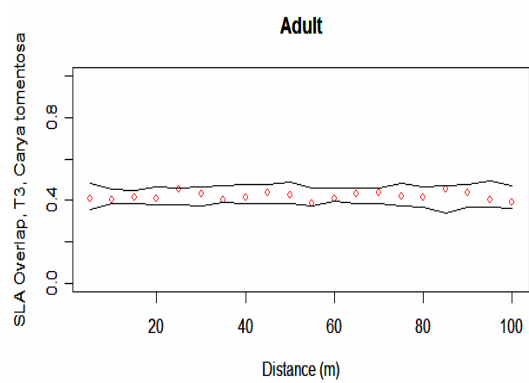
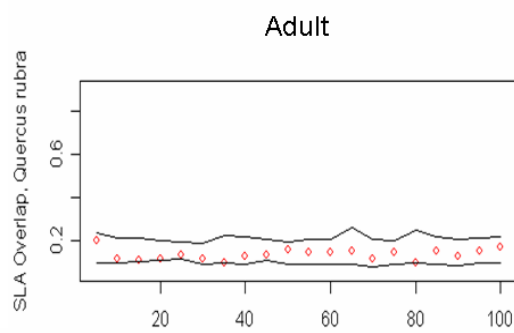
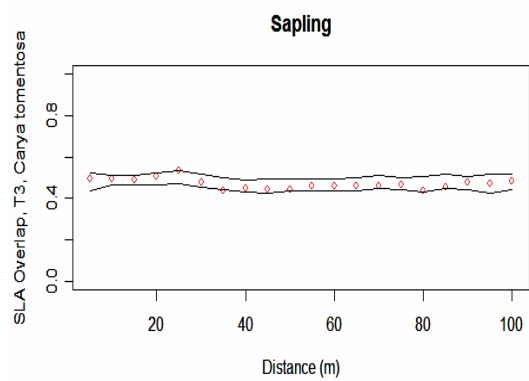
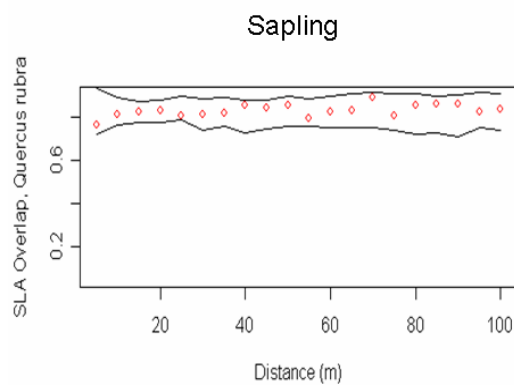


Figure 5.3. Spatial distribution of pairwise overlap in specific leaf area (SLA) for selected individual species, size classes, and individual transects. These seven plots reflect some of the most abundant species at Thompson Mills. Data in red, black lines represent minimum and maximum values from 100 randomization tests.

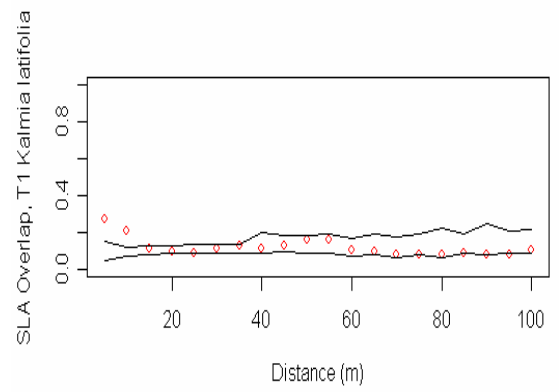
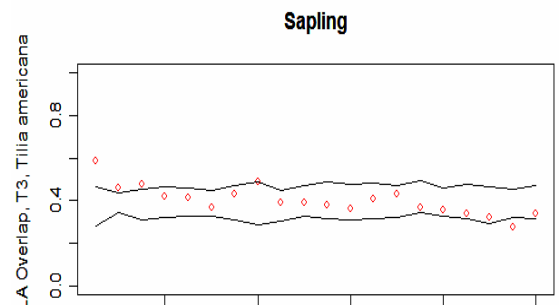
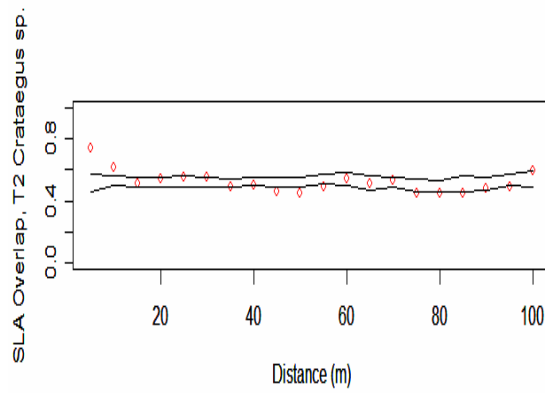
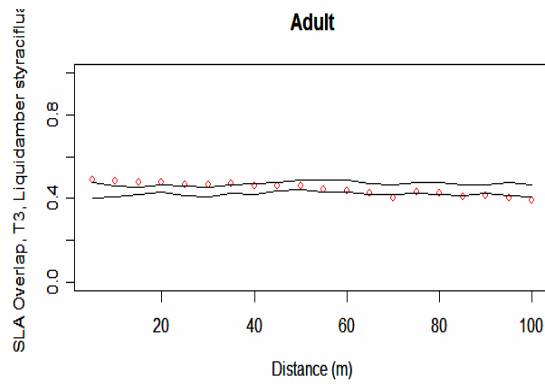
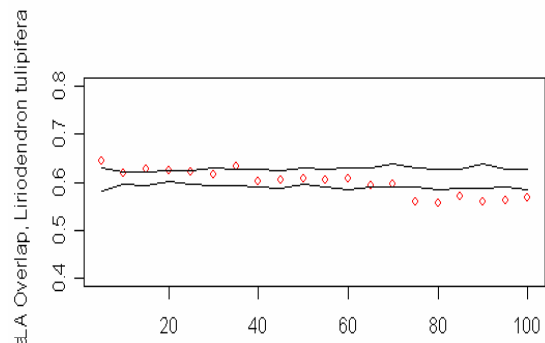


Figure 5.4. Spatial distribution of pairwise overlap in specific leaf area (SLA) for additional selected individual species, size classes, and individual transects. These eight plots reflect the only plots for which any non-random patterns were found. Data in red, black lines represent minimum and maximum values from 100 randomization tests.

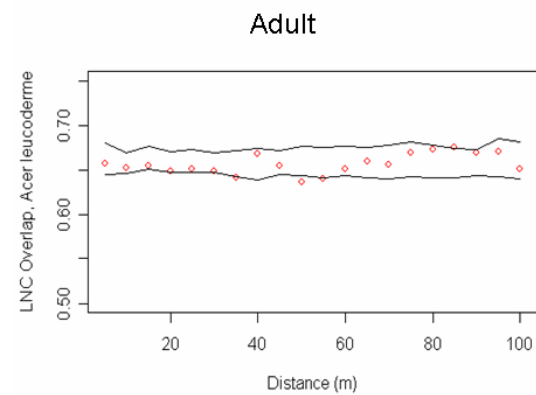
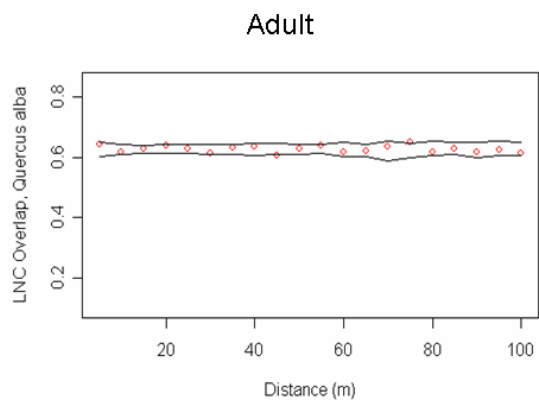
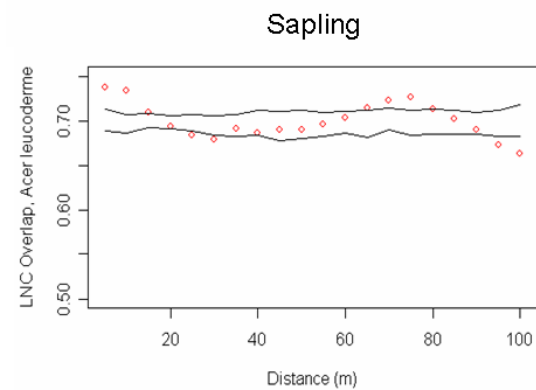
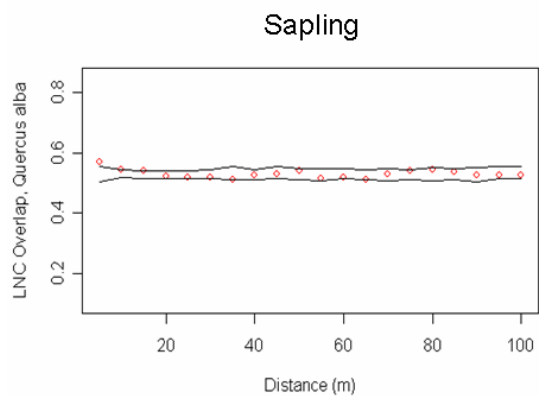
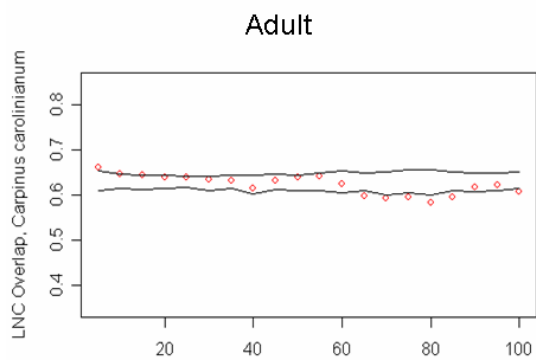
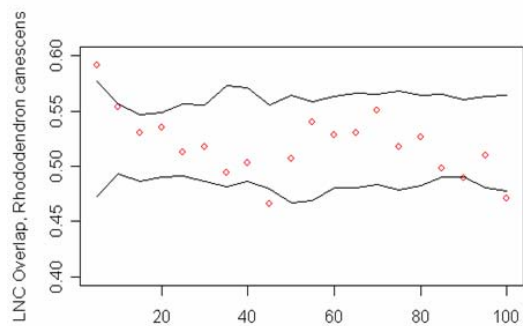
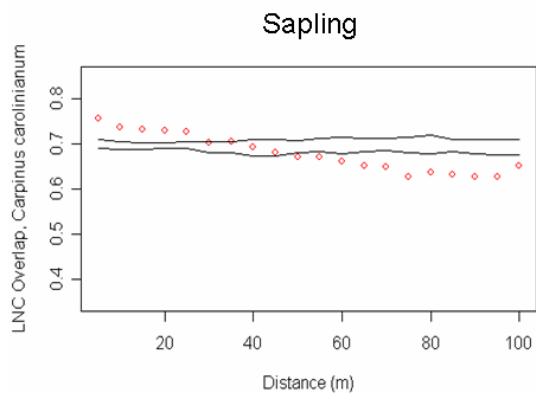
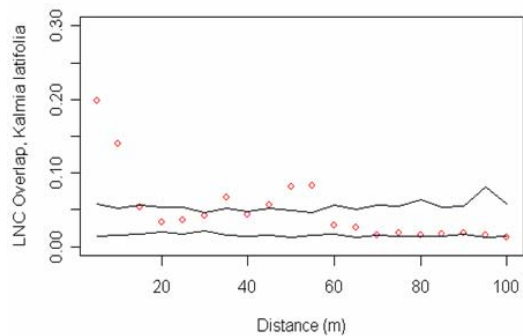


Figure 5.5. Spatial distribution of pairwise overlap in leaf nitrogen content (LNC) for selected individual species, size classes, and individual transects. These plots represent three common tree species and two shrub species from the site. Data in red, black lines represent minimum and maximum values from 100 randomization tests

CHAPTER 6

CAN THE DISTRIBUTION OF PLANT FUNCTIONAL TRAITS HELP EXPLAIN LATITUDINAL GRADIENTS IN SPECIES DIVERSITY?¹

¹Lake, J.K. & S.P. Hubbell. To be submitted to *Ecology Letters*.

Abstract

One of the great ongoing questions in community ecology is the latitudinal gradient in species diversity. While numerous authors have proposed literally hundreds of mechanisms that could drive existing patterns, few have rigorously tested potential mechanisms driving this pattern. We use plant functional traits to test two competing ideas used to explain the coexistence of so many species in tropical forests: 1. classical fine niche partitioning of light environment and gap space, and 2. increasing ecological equivalence in a shared generalist, shade-tolerant strategy. While initial findings of trait overlap suggest narrower niches and less trait overlap in tropical forests, when addressing smaller sample sizes from the tropical forest, we found little difference in niche/trait breadth between species in the two forests, suggesting little difference in the forces structuring leaf traits in forests with nearly an order of magnitude difference in species diversity.

Introduction

One of the most contentious, unresolved issues in understanding patterns of biodiversity is the strong latitudinal gradient in species diversity (Wills *et al.* 2006; Wright 2002; Pianka 1966). Although the current theoretical framework for the debate shifts over time, the fundamental questions still remains – how do so many species in tropical forests make their living and coexist? How is it that in species-rich tropical tree communities, hundreds of species can co-exist, while temperate forests only have at most a few dozen species of woody plants?

Central to classical theory in community ecology is the idea that coexistence requires species to exploit limiting resources differently from one another (Grinnell 1914 and 1917; Elton 1927; Hutchinson 1957, 1959; MacArthur and Levins 1967; Tilman 1982). Classical niche theory argues that as the number of species in a community increases, either the total niche volume for the community must be larger, or else niches must become narrower to allow for coexistence of additional species. Because of the extraordinarily high species diversity in the tropics, ecologists have long argued that these species must be finely partitioning niche space (ie, Dobzhansky 1950). Specifically, fine partitioning of light and a greater range of light intensities in the tropics could help explain the higher tree diversity in tropical forests (e.g., Ricklefs 1977; Denslow 1980; Orians 1982). Behind these hypotheses is the argument that species can finely partition varying light levels, largely created by the formation of gaps of various sizes, and the resulting gradient of light from center to gap edge, and into standing forest. However, this approach also depends upon strong and continual dispersal so that

propagules of a given species is in the “ideal” site at or very near the time of gap formation.

However, dispersal and recruitment limitation, meaning that species fail to disperse to or recruit in all sites favorable to their survival and growth, may limit the ability of species to finely partition niche space. Hubbell *et al.* (1999) found strong dispersal and recruitment limitation in a tree community in Panama, which they argued extensively delays competitive exclusion. In addition to a potentially strong role for dispersal limitation in preventing competitive exclusion, Hubbell and Foster (1986) argue that selection on trait character displacement may be extremely weak in species-rich communities because pairwise encounter rates between any two species are so low. This hypothesis would predict opposite results from those of niche theory—namely, greater phenotypic divergence in a relatively species-poor temperate forest than in a species-rich tropical forest.

Surprisingly, in spite of these richly testable predictions, there have not been any attempts to our knowledge to test these conflicting hypotheses along a latitudinal gradient. Within the context of this research, we focus on leaf functional traits because of their demonstrated role in photosynthetic carbon fixation and their fundamental relationship to shade tolerance/intolerance (Poorter and Bongers 2006; Wright et al 2004). Since most of the predictions for fine scale partitioning of resources in tropical forests centers around light levels and partitioning of gaps, these traits should show the strongest interspecific variability related to shade tolerance. Here, we ask the question of whether trait breadth and overlap is more, less, or comparable between species-rich tropical forests and relatively species-poor temperate systems.

Materials and Methods

Traits

Specifically, we have chosen five leaf traits upon which to focus. *Specific leaf area* (SLA, measured in cm²/g) is one of the strongest measures of a plant's photosynthetic investment, and is a strong correlate of mass-based maximum photosynthetic rates ($A_{\max}$). Low values tend to be associated with longer leaf lifespans, nutrient limited environments, and high defensive investment (Reich et al. 2003; Reich et al 1997). Across several species of tropical trees, Poorter and Bongers (2006) have also shown that the SLA is positively related to whole-plant growth and negatively to survival, suggesting low investment in high turn-over, metabolically fast leaves in short-lived sun demanding plants. *Leaf size*, the area of leaf lamina or leaflets, excluding petiole or rachis, is a measure of actual photosynthetic surface, and is important to both water and energy balance (Cornelissen et al 2003). *Leaf Nitrogen Content* (LNC) is highly correlated to mass-based maximum photosynthetic rates ($A_{\max}$). It provides insights into nutrient use and availability, and is correlated to leaf lifespan (Reich *et al.*, 1997). N_{mass} has been shown to correlate positively with growth, while N_{area} correlates with survival (Poorter and Bongers 2006). *Carbon: Nitrogen ratios* (C:N Ratio) are indirectly tied to plant defense strategies. Higher C:N ratios suggest a lack of nitrogen in the leaves, and the excess carbon is often invested in high carbon phenolic compounds for defense against herbivory (Sternner and Elser 2002). Finally, two leaf morphological traits, while less well understood ecologically, appear related to sun exposure and overall energy balance. *Perimeter²:Area ratio* provides a good measure of lobing, in essence providing the degree to which a leaf blade's shape diverges from a circle. *Leaf Shape Index (LSI)*, or the ratio of leaf length to width, provides another metric of a leaf's shape.

Site description: Temperate site

Thompson Mills Forest is a 135-ha. reserve located near Braselton, Georgia, in Jackson County, about 40 miles northeast of Atlanta in the Piedmont (34°7'39 N, 83°48'6 W) . The site is composed of late-secondary oak-hickory forest, dominated by *Quercus* sp., *Carya* sp., *Liriodendron tulipifera*, and *Fagus grandifolia*. Average annual rainfall in this area is estimated at 141.7 cm, mean annual temperature is 15.6 C (Georgia Automated Environmental Monitoring Network, Gainesville, GA). Three 20x200m sampling transects were established. The first runs along a northwest facing slope overlooking the Mulberry River; the second, along a southfacing slope overlooking Lee Creek; the third perpendicular to Lee Creek at a point upstream from the second, rising along a gentle southeast facing slope. All are located in late-secondary forest areas with very limited or no recent human-based disturbance.

Site Description: Tropical Site

Barro Colorado Island (BCI), Panama, is a 1600-ha. island in the Panama Canal composed of a seasonally moist tropical forest. A 50-ha Forest Dynamics Plot (FDP) is located within BCI. The FDP was established in 1980 by Hubbell and Foster (1983). All trees and shrubs within the plot over 1 cm dbh were tagged, mapped, measured, and identified between 1982 and 1983 (Hubbell and Foster 1983, Condit 1998). The plot has subsequently been recensused every five years through 2005. During the censuses, a total of 316 species have been identified, encompassing about 229,000 stems.

Sampling Methods – Temperate Forest

Within each transect, all stems >1 cm diameter at breast height (dbh, 1.4 m above ground) were mapped, identified, and dbh was measured. Based on dbh and light

availability, specimens were classified as adults or saplings, with cut-off size dependent on the species. For all tree species (canopy and understory), up to a total of 24 specimens (12 adults, 12 saplings), as evenly spread as possible among and within transects, were selected for leaf sampling. In adults, three branchlets each from the sunniest position, and a strongly shaded position were collected and placed in water. Specimens were returned to the lab and rehydrated overnight. A total of six leaves from each canopy position were selected for analysis, attempting to select two from each of the branchlets whenever possible. While size was not a factor in determining leaves sampled, we did select the most recently unfolded, fully hardened leaves with the least amount of herbivory and epiphylls possible. Leaves were scanned on an Epson 1680 flatbed scanner, and analyzed using WinFOLIA 2005b Software (CITE). Subsequently, leaves were dried at 60C for at least 72 hours, then weighed on a Mettler balance.

Sampling Methods – Tropical Forest

Within the BCI Forest Dynamics Project Plot, specimens were sampled from a range of 90 tree species, with 8-12 leaves sampled per individual, and, on average 2-3 individuals sampled per species. One species of understory tree, *Faramea occidentalis*, was sampled more intensively, including testing specimens in sun and shade environments. Leaves were collected, pressed, and dried in the field, and scanned dry using an Epson 1680 flatbed scanner, and analyzed using WinFOLIA 2005b Software. While there is shrinkage of leaves during the drying process, there is no expectation of disproportionate shrinkage (ie, that would substantially alter trait measurements), and Ackerly (2002) showed that there is typically no significant difference in ultimate trait values, whether using fresh or dried material for these analyses. Furthermore, because

we consistently used a wet or dry technique within a given community and are comparing traits only within those given communities, we further reduce any risk of confounding results by mixing fresh and dry material.

Trait Analysis

WinFOLIA automatically collects data on leaf area, perimeter, length and width, all used in subsequent analyses, usually as compound measures. Morphological traits were analyzed from scanned images using WinFOLIA software (leaf size), or from compounding data collected (P^2A , Leaf Shape Index, SLA).

Statistical analyses

For each species and trait, a trait distribution was calculated using a kernel estimator (see Mouillot *et al.* 2005). This method, which allows us to work with continuous data without assuming a normal distribution of data, calculates a density function by assuming measurement error around each data point, and then using a smoothing function to estimate a distribution of all data for a given trait and population. These species (or population) kernels are then used to estimate pairwise overlaps in trait space of coexisting species. Overlap is simply represented as the integral of the area under the species' respective kernel curves when overlaid on one another. From these pairwise overlaps, a community-wide overlap index is then calculated, simply by averaging these overlaps.

To determine the impact of sample size on trait breadth, log trait standard deviation was plotted vs. log sample size to get a sense of intraspecific variability. While each point represents the actual sample size of a species and its respective trait variance, thus masking any actual interspecific variability in trait breadth, it does provide a good sense of when

enough samples have been collected to reach a relatively good estimate of niche or trait breadth.

Results and Discussion

At first blush, the tropical forest community shows substantially lower interspecific community trait overlap than does the temperate forest for most traits (see table 1). These lower values would be strongly consistent with the idea of niche packing in tropical forest systems. The exception to this trend are the true leaf morphological metrics (p^2 ratio and LSI), which show moderately higher overlap in the tropical forest. Given the lower overall variability in leaf shape in tropical forest trees (e.g., Janzen 1975) due to few species with lobed leaves or marginal teeth, that the overlap would be higher in tropical tree communities is hardly surprising. The fact that these overlaps are not substantially higher is, in fact, the surprising result here.

However, because our sampling scheme was part of a pilot study, we therefore sampled relatively few leaves and individuals of most species in the tropical forest, providing a perhaps weak sample of the species. While our collection numbers were generally in line with sample sizes recommended by Cornellsen et al (2003), it appears that our sampling may not have adequately captured intraspecific variance in the traits sampled (see fig. 1). Indeed, the plots of trait variation (standard deviation) and sample size for the temperate and tropical forest seem to lie virtually on top of one another, suggesting our results are likely the result of low sample size.

While our data is currently insufficient to definitively answer the question of niche packing vs. ecological equivalence in more species-rich tropical systems, the astounding similarity of the two curves suggests there may be little difference in niche

breadth for species in temperate vs. tropical forests. If this similarity holds with more complete datasets, it would suggest that similar processes may be structuring both species-rich and species poor forests across the latitudinal gradient. Such a conclusion would suggest that neither strong specialization on specific parts of a light gradient through niche packing, nor increasing ecological equivalence through diffuse selective pressure in species-rich tropical systems are driving the latitudinal gradient in species diversity.

Fortunately, we should soon be able to better address the above questions. With a more complete field season in Panama, combined with the completion of analysis of two small plots in Belize (with approximately 80 and 95 species), we will have adequate sample sizes and a broader range of communities and species diversity levels to more rigorously address the central questions posed here.

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Table 6.1. Mean interspecific trait overlap for tree communities in a temperate forest in Georgia and tropical forest in Panama, based on preliminary data.

Group	#Spp	SLA Overlap	Leaf Area Overlap	p2a Ratio Overlap	LSI Overlap
Thompson Mills, GA	42	0.482	0.456	0.443	0.371
Barro Colorado Island, Panama	90	0.301	0.370	0.493	0.416

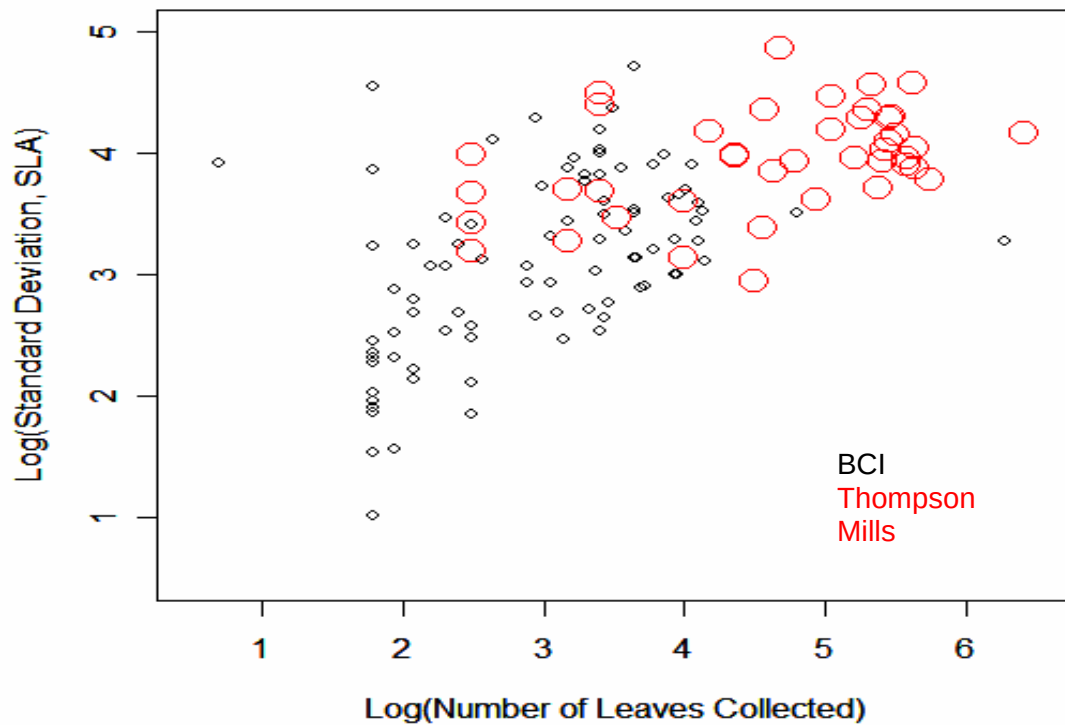


Figure 6.1. Plot of trait breadth (represented by standard deviation) vs. number of leaves collected for a given species at Thompson Mills (large red circles) and on Barro Colorado Island (small black diamonds). Note the broad overlap of the two data curves, and the relative flattening of the curve between 75-150 leaves collected/species.

CHAPTER 7
CONCLUDING REMARKS

In this body of research, we set out to test the role of plant functional traits in community assembly and structure. Plant functional traits have proven an interesting and potentially useful approach to niche structure, but we have shown that it will be important to treat these values carefully, to consider not only mean trait values, but also niche (or trait) breadth and overlap with other species, as well as among conspecific individuals of varying sizes and canopy exposure. We set out to answer five specific questions, each of which we address briefly.

1. Is it appropriate to simply treat species as present or absent in a community when considering trait overlap and limiting similarity, or can a more complete picture be developed by considering abundance or other weighting factors?

The appropriate niche metric is directly related to the questions a researcher is attempting to answer. If the goal is to compare species-level traits of species present in a given community, perhaps in contrast to excluded species, then it is not important or even appropriate to weight species for abundance, size, or any other factor. On the other hand, if a researcher is seeking to determine the way species are actually using the whole of trait space within a community, a weighted index may be crucially important to understanding the strength of interspecific interactions.

2. Is it possible for ecological equivalence to evolve within a defined community, and if so, can equivalent or near equivalent species persist in the long term in such a community?

We have shown that ecological equivalence can evolve easily and often, within the context of simulated communities, particularly when species are easily able to experience most or all of trait space—that is, having dispersal that greatly exceeds the grain of the environment. Coarse-grained environmental heterogeneity, but randomly distributed species leads to the evolution of multiple, spatially-segregated ecotypes within each species. Of our simulations, only a dispersal-limited, coarse-grained environment with species strongly clumped on the landscape led to traditional niche differentiation. Dispersal limitation, in particular, along with true ecological equivalence, provided the most consistent, stable long-term coexistence for species within our simulations.

3. How are traits distributed within and among individuals and species in a temperate tree community?

While we found some of the expected variation among species within a temperate tree community at Thompson Mills, GA, we also found strong intraspecific variation, driven in part by plastic response to the light environment. However, much unexplained intraspecific and intra-individual variation led to broad trait distributions that widely overlapped with co-occurring species. These results suggest an important role for canopy position and individual in determining a tree's functional trait spectrum, in addition to its species identity. Indeed, we report perhaps some of the highest niche overlap indices reported in the literature to date for the leaf functional traits within this community.

4. How are traits distributed spatially among individuals in a temperate tree

community, and what can that distribution tell us about the way ecological communities are assembled and structured?

There is little or no significant spatial structure in leaf functional traits in a temperate forest community. These results suggest that there is no role for limiting similarity in structuring these communities, and a weak role for habitat filtering at these spatial scales. Most observed patterns in trait overlap fell largely within values produced in randomization tests, suggesting that the broad trait overlaps reported in chapter 4 are indeed driving a largely random pattern of trait variation in the small spatial scales tested here.

5. Can the latitudinal gradient in species diversity be explained, at least in part, by increased specialization in a species-rich tropical forest system?

Our data are too preliminary to draw many conclusions about whether there is more or less niche differentiation in a highly diverse tropical forest than in a species-poor temperate community. However, our preliminary data suggest that niche, or trait, breadth within our more poorly sampled tropical forest may largely be a function of sample size, suggesting no role for latitude, and thus species diversity, in driving niche breadth. This contrasts with expectations of many researchers espousing either niche or neutral views of community assembly.

Overall, we have demonstrated a strong role for both equivalence and chance in driving community assembly, at least within the context of terrestrial forest communities. We have shown the need to consider not only species mean trait values, but to also look at actual individual-level variation, driven both by genetics and microhabitat. While current attempts to predict community assembly from functional traits are woefully inadequate in capturing this variation, it may be possible to incorporate enough variability within functional traits to build a more predictive model. Nonetheless, the generality and value of such models is called into doubt as the number of parameters begins to increase, calling into question the fundamental goal of predictive trait-based models of community assembly.

ERRATUM

DISSERTATION: PLANT FUNCTIONAL TRAITS AND COMMUNITY

ASSEMBLY AND STRUCTURE

BY JEFFREY K. LAKE

On pages 78-79, the correlation reported from the literature was incorrect; while explanatory power was lower in this research than in the literature, the correlation between LNC and SLA reported is, in both cases, positive.