

# Predicting forest structure, composition, and diversity

A synthesis of ecological theory and data

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The ultimate goal of community ecology is to understand how interactions among individuals, and between individuals and their environment, shape the distribution, abundance, and diversity of organisms. Understanding the diversity of organisms has been a perennial challenge in ecology because it involves an apparent paradox. The paradox in diversity is the discord between the clear richness of the natural world and simple experiments between paired species that have repeatedly shown competitive exclusion (Gauss 1934). There are numerous theories that suggest mechanisms that *may* drive community dynamics, and a vast array of experimental studies that show how a specific factor can affect a particular aspect of a community structure. However, it is often unclear which empirical factors and theoretical mechanisms are driving a system. While no one study can answer all questions, what I propose here is a synthesis that will shed new light on the dynamics of forest communities.

In my dissertation, I intend to address two questions in forest ecology:

- What mechanisms control the maintenance of species diversity?
- How do wind disturbance regimes affect forest composition, structure, and diversity?

I propose to investigate these questions using a combination of field studies, disturbance models, and a new forest simulator, **Adohi**. The forest simulator is the tool

that will tie together the results from the various field studies and disturbance models.

The goal is to use the model to understand diversity and disturbance in ways that would not be apparent from viewing the component parts independently.

Studies of forest succession, the directional change in vegetative communities over time, have strongly impacted both our thoughts about species coexistence in forests and our perception of recovery from natural disturbances, such as fire, blow down, and disease. Our classic ideas of forest succession are largely derived from studies of old fields (Oosting 1942, Keever 1950) and areas of primary succession (Cowles 1899). Early work by Clements (1936) introduced a strong sense of coherence and trajectory into successional change. While the most teleological aspects of classic successional theory have been dismissed, many ecologists still believe that the trajectory of succession is predictably driven by a few simple principles: such as fast-growing shade-intolerant species give way to slow-growing shade-tolerant species, and that shade-tolerant species are self replacing.

The intermediate disturbance hypothesis (Connell 1978) and theories of forest gap dynamics (Watt 1947, Whitmore 1989) have been proposed as possible mechanisms for species coexistence. Coexistence is possible because disturbance “resets” the community to an earlier successional stage, providing temporary habitat for early successional species, and creates a “mosaic” of successional stages on the landscape. However, evidence is building that forest gaps may not be working according to this model. Single-tree gaps may be insufficient to stimulate recruitment (Phillips and Shure 1990, Beckage et al. 2000, Vandermeer et al. 2000), while recruitment in multi-tree gaps may be dominated by understory trees and saplings that survive disturbance, rather than by “early successional” species (Runkle 1990, DeCoster 1996, Cooper-Ellis et al. 1999).

Furthermore, historical events may result in long-term changes in community composition that defy our archetype of succession (Christensen 1989, McLachlan et al. 2000). A clear challenge exists to incorporate observations such as these into our emerging understanding of the dynamics of forests.

The dynamics of forest communities are both slow and large scale, playing out over hundreds to tens of thousands of years and on the scale of hectares to continents, making direct experimental manipulation difficult. An alternative way to approach the dynamics of a population or a community is through a model. Models quantify our current understanding of a species' ecology and project them into the future. Models also allow researchers to run as many "experiments" as they desire, modifying the environment and the interactions between individuals in numerous ways. Models of the dynamics of forest tree communities, commonly referred to as "stand simulators" or "gap models," have influenced ecological research for 30 years (Botkin et al. 1972, Shugart and West 1977, Urban et al. 1991, Pacala et al. 1996). However, only recently have ecologists systematically designed field experiments to parameterize these models. Historically, forest models have not been demographically complete, focusing instead on adult life history stages, nor have they propagated measurement error and the inherent variability among individuals into the model output. I propose to develop a more demographically complete and statistically robust stand simulator parameterized from long-term field studies.

Traditionally, forest gap models have simulated gaps as occurring at the size of a single adult tree and distributed randomly in time and space (Sklar and Costanza 1991, Baker and Mladenoff 1999). Some forest simulators have considered disturbances with greater spatial extent and temporal structure but these models generally create

disturbances by arbitrarily removing large areas of adult trees with a static periodicity (e.g. Loehle 2000). Because disturbances are applied independently of age structure, species composition, or topography such models cannot address how these factors affect disturbance size, frequency, and location. The few models that have attempted to include autogenic aspects of disturbance have focused on fire (e.g. Miller and Urban 1999a, 1999b). By incorporating models of wind disturbance into **Adohi**, I will be in the unique position to explore the effects of wind disturbance on forest communities.

Understanding any disturbance regime requires that we characterize the disturbance itself (*intensity, spatial distribution, frequency*), the biotic impact of the disturbance (*severity*), and the biotic response to the disturbance (White and Pickett 1985). This translates into three specific goals of this study: characterize the wind itself, characterize the direct and indirect impacts of the wind (i.e. gap formation), and characterize the biotic response to gaps. The remainder of this proposal is divided into four sections that discuss the conceptual tasks involved:

- Wind disturbance regime characterization
- Impact of wind disturbance
- Characterizing gap recovery: the gap plots
- Development and analysis of forest model **Adohi**

Each section is further broken down into specific projects and analyses.

In conclusion, most hypotheses about the mechanisms that maintain diversity are plausible. Similarly, most researchers who study specific life history stages or species find effects that they believe could affect community structure and composition.

However, there has not been a systematic effort to synthesize the available data and theory to determine which processes and trade-offs are having a strong impact and which

are averaged over. One of the main objectives in this research project is to use **Adohi** to isolate mechanisms and processes that are believed to contribute to the maintenance of diversity. This will allow the assessment of which mechanisms are functioning in forest communities and what their relative strengths are. This is not an exploration of the forest model's parameter space, which is likely to demonstrate the potential importance of many mechanisms. Rather it is an effort, based on parameterization from field studies, to find where real communities lie in that parameter space and what mechanisms are driving those communities.

### **I. Wind disturbance regime characterization**

A simple hurricane model will be used to characterize the spatial and temporal distribution of hurricane wind events. This work expands the scope and methodology of important research by Boose et al. (1994, 2001) using the HURRECON model to characterize hurricane return intervals for New England. This analysis will make use of the NOAA HURDAT database (Jarvinen et al 1984, <http://www.aoml.noaa.gov/hrd>), which records the location, velocity, and wind speed of North Atlantic hurricanes since 1851. I have produced a computationally-efficient hurricane model based on HURRECON that will be used to reconstruct hurricane wind fields. These wind fields are assembled into maximum wind speed maps for each storm, which are then combined to generate maps of return interval across eastern North America.

Return interval estimates are strongly dependent upon overall hurricane activity, yet hurricane abundance and intensities are non-stationary in time. There is a short-term periodicity in hurricane frequency, a correlation between hurricane abundance and El Niño/Southern Oscillation (ENSO) events, as well as long-term trends in hurricane activity (Elsner et al 1999). In addition, general circulation models (GCMs) predict that

there may be an increase in hurricane intensity with an elevated CO<sub>2</sub> climate (Knutson et al 1998). To move beyond static return interval estimates, I will fit statistical models that summarize the distribution of local storm intensities, and can be driven by a historical hurricane time series or future scenarios for the distribution of hurricanes. This would allow for the estimation of how global hurricane trends translate into changes in local return interval.

Finally, I will compare wind intensity maps to wind damage maps. Damage maps will be generated based on tree damage assessments from the USFS Forest Inventory and Assessment (FIA) database (<http://www.srsfia.usfs.msstate.edu/scripts/ew.htm>). Storm damage will be compared to the wind intensity maps over the same period as the most recent FIA census.

## **II. Impact of wind disturbance**

Despite the prevalence of wind damage in many ecosystems, realistic models of wind disturbance have not been developed and the complex effects of wind disturbance remain under-explored. Numerous studies have shown that storm damage can vary with factors such as species, size, topographic exposure, tree mechanical properties, and stand age and composition (e.g. Putz et al. 1983, Foster 1988, Webb 1988, Foster and Boose 1992, DeCoster 1996, Rebertus et al 1997, Foster and Terborgh 1998, Hideyuki 2000, Canham et al. 2001). These factors generally behave in a predictable manner: damage increases with tree height and topographic exposure, and species with softer woods, typically the early successional species, are more susceptible to wind damage. Studies across many different forests generally have found damage to be **explainable** (*i.e.* a moderate amount of the variance in damage measurements can be accounted for using simple regression models). The challenge that remains is to make storm damage

**predictable.** Empirical studies that assess the impact of one particular storm at one particular place, and with wind speed generally unknown, are not generalizable to different intensities, locations, species, or wind profiles/stand structure. Single stand, single storm studies are also not in the position to explain differences among forest types in wind susceptibility.

At the individual scale, I will approach wind disturbance from a biomechanical perspective. Existing models of tree biomechanics (e.g. King 1986, Niklas 1992) suggest that tree mortality should increase with tree size, due to increased exposure to wind and decreased elasticity, but should vary between species based on the strength of the wood and the allometry of growth, thus predicting an autogenic component of wind disturbance. However, existing models are insufficient to move to damage risk assessment for individual plants. The main missing component is an estimate of the forces that winds exert on trees. I hypothesize that this force is a function of the vertical wind profile in the stand, the vertical distribution of foliage on the individual tree, and the drag coefficient of this foliage (Figure 1). It is now possible to use fluid dynamic approximations to estimate vertical wind profiles based on **stand level** foliage profiles (Katul and Albertson 1988, Katul *personal communication*), and individual and stand foliage profiles are themselves estimable based on allometric regressions or aerial surveys (e.g. LIDAR, digital videography). Estimates of foliage drag coefficients (Vogel 1989, 1996) will be made empirically in a wind tunnel at Duke. Another factor that is absent from biomechanical models of wind damage is an inclusion of belowground mechanics. I intend to estimate below ground forces based on allometric root distributions and soil mechanical properties, which vary spatially and with soil moisture content (Niklas 1992). Soil moisture content and rooting behavior should have a strong

effect on both disturbance susceptibility and the type of disturbance (e.g. snap vs. uproot).

I will validate this biomechanical model at the individual level using two sources of data. The first dataset consists of measurements of the torsional forces necessary to snap and uproot trees in Duke Forest and observations of the type of damage that resulted for different species and different sized trees. The second dataset is measurements of tree sway in natural wind conditions made at the Duke Forest hardwood eddy-covariance tower. At the stand level, the model can also be compared to observed storm damage censuses, such as those cited above or the Duke Forest damage from Hurricane Fran (Carpino 1998).

### **III. Characterizing gap recovery: the gap plots**

Small experimental gaps have shown that small gaps are insufficient to stimulate recruitment of tree seedlings (Beckage et al. 2000). In an effort to expand upon this research, an experimental gap study was initiated in 2000 to characterize the response of forest ecosystems to multi-tree blow down gaps. The study is repeated at two sites with the aim of mimicking wind-throw damage. The first site is the Coweeta Hydrological Laboratory LTER (<http://sparc.ecology.uga.edu>), a mixed hardwood forest in the Appalachian Mountains of western North Carolina. The second is the Duke Forest (<http://www.env.duke.edu/forest>), a mixed hardwood-pine forest in the Piedmont of central North Carolina. Both these sites have had active ecological research programs since the 1930's and thus have long-term climate records as well as background data on site history. The experimental gap plots aim to answer a number of ecological questions, such as what size gap is necessary to stimulate recruitment, and what life history stage dominates this recruitment. They also serve as a major source of data for the

parameterization of the forest simulator. It is important, though novel, to parameterize a gap model from data on gaps, as well as from closed canopy conditions, in order to capture the full range of conditions that plants may experience.

After collecting two years of pretreatment data, eighteen gaps were created in March 2002 by pulling down canopy trees within a given radius and leaving the snapped and uprooted trees in place (Figure 2). Research in the gaps is focused on understanding the complete demographic life history of the tree species in both forests: reproduction; dispersal; seed bank survival; seedling germination, growth, and survival; sapling growth and survival; and adult tree growth and survival. We have also collected data on the local environmental variables, such as understory light, soil moisture, and soil nutrients. The gap project builds upon numerous demographic studies in both sites, in particular the recent research in the Clark Lab (Clark et al. 1998, 1999a, 1999b, 2002, Beckage et al. 2000, HilleRisLambers et al. 2002, Wyckoff and Clark 2000, 2002).

The size of the experimental gap project necessitates the collaboration of multiple researchers. The demographic stages and environmental variables listed above, but not directly discussed below, are included in the doctoral research of I. Ibanez, M. Wolosin, S. LaDeau, and R. Parama. My personal projects within this experiment are focused on the following measurements: understory light, sapling demography, canopy gap closure rates, damaged tree demography, tree allometry, and site history.

Understory light has been measured using canopy photography annually at locations coincident with seed traps and seedling transects. Canopy photos are taken using a fish-eye lens at ~1.15m above the ground and analyzed with Hemiview software.

Sapling demography is being measured based on annual censuses of 10x10m sapling plots located both inside (1-2 plots/gap) and outside the gaps (2 plots/gap).

Within these plots, all trees between 0.5m and 2.0m in height are tagged, mapped, and measured (diameter, total height, height to last bud scar). In addition, the correlation between growth and survival is being explored for saplings and understory trees (<5cm DBH) by measuring annual growth rings from disks cut from sample live and dead individuals. Data will be analyzed by methods similar to Wyckoff and Clark (2000, 2002).

Canopy gap closure is being estimated using a number of complementary measurements. The first set of measurements are annual transects through each gap using laser point-quadrat sampling (Radtke and Bolstad 2001) to estimate foliage height distribution. The second set of measurements, for small gaps, is distance vectors from the center of the gap to the edge at 10-degree increments. The third set of measurements, for the large gaps, is the canopy radii in eight compass directions of overstory trees on the edge of the gaps.

The demographic rates of damaged trees are being estimated by censusing all pulled or damaged trees >10cm DBH for mortality, defined as a lack of live foliage over multiple years, and for stem sprouting. Initial censuses show clear differences between species in their post-gap mortality, suggesting that disturbance **resilience** (probability of damaged tree survival) may have an important roll in gap dynamics (FIGURE 3). The frequencies and types of indirect damage are also being censused. From this the risk of indirect (falling tree) damage to understory trees and saplings will be estimated.

The tree allometry study consists of measurements of the total height, height to base of canopy, and canopy radius of all the species in the plots over a range of diameters using the laser rangefinder. Allometric relations will be used in the forest model's light

submodel (below), in the wind biomechanics model (above), and by collaborators on the experimental gap project (e.g. in remote sensing).

Finally, site history is being assessed by a dendrochronology based on increment cores taken from all pulled trees and by an investigation into county and study site land records.

#### **IV. Development and analysis of forest model *Adohi***

##### *Model Development*

My first modeling objective is to develop a spatially explicit, demographically complete forest stand simulator. I have been developing this model, **Adohi**, in collaboration with S. Govindarajan, Dr. J. Clark, and Dr. P. Agarwal. **Adohi** will be parameterized from field data collected at Coweeta and Duke Forest, in particular data from the experimental gap plots, using hierarchical methods to allow for a more complete accounting of uncertainty (Clark et al. 2002). Hierarchical statistical methods permit models to account for intraspecific variation, allowing individuals in a population to draw parameters from a species-level distribution rather than all individuals being assigned identical parameters. **Adohi** will simulate forest dynamics on a continuous spatial landscape where individuals are discrete and assigned explicit coordinates. The model landscape, which we intend to be on the scale of ~1 km sq., will include topography, light, and heterogeneity in soil moisture and nutrients. Individuals will pass through all life history stages, from seed through adult, responding to the aforementioned environmental variables as well as competitive interactions between individuals and intra-specific variability (FIGURE 4). The model will also include a realistic sub-model of wind disturbance that incorporates the proposed research on characterizing hurricane regimes and gap-forming impacts. The forest simulator will be built on new spatial

computer algorithms, which I have helped to develop, that make such a large spatial model computationally feasible (Dietze *et al.*, *in prep*; Govindarajan *et al.*, *in prep*).

### *Wind disturbance analysis*

My second modeling objective is to analyze forest responses to wind disturbance and to changes in wind disturbance regime. A question that is vital to our understanding of how gaps function is: “What life history stage dominate gap recruitment?” The filling of wind-throw gaps may be driven by: 1) the horizontal ingrowth of the surrounding canopy, 2) surviving, but likely damaged, subcanopy trees, 3) sapling growth, 4) seedling growth, 5) seed bank recruitment, 6) seed rain recruitment, or 7) sprouting. This may vary with gap size and with the pre-disturbance vegetation. A related question is how much is post-disturbance vegetation similar to pre-disturbance vegetation? Do communities return to their pre-disturbance communities, get closer or farther from some “climax” composition, or change to some new composition?

Another set of questions surrounds the impact of altering the disturbance regime. For example, if we increased storm frequency or intensity, we might expect this to favor early succession species, such as pine, that would take advantage of the greater number of gaps. On the other hand, early successional species generally have both low resistance (high probability of damage) and low resilience (high probability of mortality once damaged). Increased disturbance may therefore favor more resistant species (e.g. *Carya* spp) but many of these are poor dispersers and may not be able to colonize large gaps. It is also possible that increased disturbance will favor species with good dispersal ability and intermediate resistance and resilience (e.g. *Acer rubrum*, *Liriodendron tulipifera*, *Liquidambar styraciflua*). This question is particularly relevant as global change is likely

to alter disturbance regimes, yet disturbance is generally ignored in most global change research.

### *Species Coexistence Analysis*

My third modeling objective is to isolate specific mechanisms in the model that are thought to affect community dynamics and species coexistence in order to determine what **processes** are important, and what processes need further study. This analysis will vary whole pathways that isolate specific hypotheses. These tests rely heavily on *neutral models*, which in this case are models in which interspecific differences are removed (Hubbell 2001). In the tests laid out below there are four different variants of each test: 1) the mechanism in question is removed from the full model, 2) interspecific differences in the mechanism are removed from the full model, 3) the mechanism is removed from the neutral model, and 4) interspecific differences in the mechanism are added to the neutral model. This pattern of tests aims at clarifying the role of a mechanism (e.g. long-distance dispersal) versus the role of interspecific life history trade-offs involving that mechanism (e.g. species differences in long-distance dispersal). In the following sections, I will review major coexistence hypotheses along with proposed tests. Coexistence mechanisms and their corresponding tests are summarized in Table 2. In these tests, change in diversity over time will be measured by species richness and basal area weighted Shannon-Weiner diversity.

Coexistence hypotheses can be divided into a number of groupings. One such division is the distinction between hypotheses that are “equalizing” and those that are “stabilizing” (Chesson 2000). Equalizing hypotheses don’t produce stable coexistence, but suggest that the smaller the fitness differences between species, the slower the community dynamics. In their ultimate form, Hubbell’s Neutral Theory (1979, 2001),

there are no differences between species and extinction may be sufficiently slow that diversity becomes merely a balance between speciation and extinction. I will test this by running the forest model with the appropriate neutral model, in which parameters are fit to the whole cross-species data set rather than to individual species. Henceforth, this parameter set is referred to as the null model.

Hubbell's neutral theory has been criticized for being sensitive to the assumption of competitive equivalence, such that small inequalities in species competitive abilities rapidly erode the ability of the effect to delay competitive exclusion (Zhang and Lin 1997). Therefore, I also intend to test the sensitivity of the neutral model to small interspecific differences in the light/growth relation.

Stabilizing hypotheses, which form the bulk of theory, invoke mechanisms that ultimately require some form of trade-off between life history traits. The oldest proposed mechanism is density dependence (Volterra 1926, Nicholson and Bailey 1935). Whether caused directly by competition, or indirectly by predation, herbivory, or disease, density-dependent mechanisms require that intraspecific density have a more negative impact on population growth than the density of other species. The Janzen-Connell hypothesis (Janzen 1970, Connell 1971) is essentially a specific case of density dependence, whereby herbivory and/or disease pressure on early life history stages is greatest near conspecific adult trees where density is greatest. In **Adohi**, there is density dependent mortality in the youngest life history stages (seed bank, first year seedlings, established seedlings). The importance of intraspecific and interspecific density-dependence will be assessed in a factorial set of tests involving no density-dependence, null density-dependence, and interspecific variation in the strength of density dependence (Table 2).

An additional test involves setting the intraspecific density-dependence equal to interspecific density-dependence.

Theories of resource competition (Tilman 1977,1982,1985) reach essentially the same conclusions as direct density-dependent competition, which is that intraspecific competition must exceed interspecific competition for stable coexistence. In **Adohi**, the only resource that trees compete for is light. I identify four different tests for the strength of light competition. The first is the removal of interspecific differences in canopy allometry, light extinction coefficient, and the light/growth relation. The second test of light competition is to remove light limitation in the understory by setting solar radiation to 100%. The third test is to remove the asymmetric (vertical) component of light competition, which is done by setting every individual to the same proportion of canopy area exposed. The fourth test is to remove light limitation in the canopy by setting exposed canopy area to its maximal value for all individuals.

One of the more interesting developments in ecological theory was the discovery that temporal variance itself could promote coexistence. Armstrong and McGehee (1980) and Levins (1979) both show that non-linearities in a species' response to a temporally varying factor can allow an inferior competitor to coexist with a superior competitor provided that there are times in which fluctuations allow their relative ranks to switch. A more intuitive variant of this idea is the storage effect (Warner and Chesson 1985), which shows that persistence is possible for inferior competitors so long as they have a resistant "storage" phase, due to adult longevity or seed banking, which allows them to survive through bad years and take advantage of rare good years. Implicit in the storage effect, and explicit in the nonlinearities model, is that species cannot be synchronized in their response (i.e. the more a "good year" is a beneficial for all species, the less it helps to

stabilize diversity). In contrast with the potentially stabilizing effects of environmental stochasticity, demographic stochasticity and intraspecific variation may exert a strong equalizing effect (Anderies and Beisner 2000)

The effects of temporal variance will be tested by a factorial combination of the presence or absence of environmental stochasticity, demographic stochasticity, and intraspecific variation in fecundity and growth rate. Further, these test runs will be repeated for fecundity alone, for growth rate alone, and for fecundity and growth rate simultaneously.

Testing the storage effect focuses on life history stages rather than on variances directly, removing, in turn and in combination, the effects of the seed bank, seedling/sapling bank, and adult longevity. The seed bank can simply be removed, while for seedling and sapling “banking” a maximum age can be set in each of these stages. For adult longevity, trees can be switched from being iteroparous to being semelparous, for example by having reproduction occurring only on the mean reproductive year. In this case, the same lifetime seed production would occur as in the normal model, it would just occur all in one year.

Recent research has shown that the inclusion of spatial interactions can also promote coexistence. One such mechanism is referred to as either recruitment limitation (Hurtt and Pacala 1995, Clark et al 1999) or the competition-colonization hypothesis (Hastings 1980, Tilman 1994). These models allow species to coexist by avoidance of competition; if a superior competitor is unable to disperse to an available site then whatever species is there will win by default. The inferior competitor in this model is assumed to have the trade-off of being a better disperser, and thus it is able to coexist as a “fugitive species.” Another spatial mechanism that can contribute to coexistence is mass

effect (Schmida and Ellner 1984), which is the complement to dispersal limitation. Mass effect is when the quantity of locally dispersed propagules or vegetative reproduction swamps out the propagules of other species, even if they are superior competitors, allowing the local species to hold a location over time. Finally, the effects of aggregation may slow the rate of competitive exclusion (Ghandi et al 1998)

The effects of recruitment limitation, mass effect, and aggregation are tested simultaneously because the first two mechanisms affect and are affected by aggregation. Testing these effects requires that we use four alternate dispersal kernels (**FIGURE 5**), which allow mass effect, dispersal limitation, neither, or both. Tests will use initial conditions with varying degrees of aggregation and the aggregation in each run will be measured using standard spatial statistics (e.g. Ripley's K) across time. An additional test is the inclusion of a constant seed source independent of species composition on the landscape. Besides being a complete elimination of dispersal limitation and mass effects, this test is also important for comparison with the predictions of classic forest simulations, which implemented dispersal in this manner.

Spatial arrangement can also assist the effects of temporal variability, for example if locations are not synchronous in their fluctuations. Metapopulation models have shown that if patches are moderately coupled by dispersal, but not synchronized in fluctuations, that the total population stability can increase (Murdoch et al. 1992). With too much coupling the metapopulation becomes one single population, which is less stable; with too little coupling, the metapopulation becomes two smaller independent populations, which are also less stable. To test this effect I will vary the spatial autocorrelation in environmental stochasticity.

All of the aforementioned spatial models assume that space is homogenous and any pattern is biologically generated. An additional way in which space can promote diversity is through the inherent spatial heterogeneity of a landscape. In this case all that is required for coexistence is that different species be specialized to the resources and/or conditions at a location. In other words ecological niches map to spatial locations. These effects will be assessed by running the model on various landscapes of varying topography, nutrient distributions, soil moisture, and temperature.

Some hypotheses specifically mention disturbance as an important agent in promoting coexistence. Most popular of these is the intermediate disturbance hypothesis (Connell 1978), which suggests that biodiversity is maximized at intermediate scales of disturbance size, frequency, and intensity. This hypothesis is largely an amalgamation of other mechanisms, adding transitory spatial heterogeneity onto a competition-colonization framework, making coexistence easier but convoluting how much of the effect is driven by niche heterogeneity versus dispersal limitation. Disturbances also introduce a number of life history challenges that often require trade-offs, and thus raise potential mechanisms for coexistence between species with different “solutions.” For example, species differences in resistance to disturbance have direct implications for what is the “optimal” life history strategy, and changes in disturbance regime can alter species dominance (Clark 1991a, 1991b, 1995, 1996). In this set of tests, the model will be run with varying distributions of storm frequency and using the four alternate kernels discussed above to control for dispersal effects (recruitment limitation, mass effect).

The forest model has sufficient flexibility that any of the above mechanisms could be acting. Similarly, it is likely that there is some part of parameter space where each of these mechanisms is driving the system. The big unanswered question is where are real

communities in this parameter space, and what mechanisms are important there? The challenge is to confront these numerous hypotheses with empirical data.

## V. Conclusions

A mathematical model is nothing more than a quantified working hypothesis. **Adohi** aims to synthesize the current hypotheses of how a forest behaves and confront these hypotheses with data. Thus, it aims to address the basic question of community ecology as a whole: how do interactions among individuals and with the abiotic environment control the distribution and abundance of organisms?

The proposed research will help advance research in a number of areas in ecology. I will produce the first realistic model of wind disturbance, integrating data across scales from the leaf to the continent. The experimental gaps will generate one of the most comprehensive data sets on forest gap dynamics and tree demography. This research will produce both the most demographically complete and statistically robust forest simulator to date. In conclusion, the research proposed here will provide new insight into the functioning of forest systems and the maintenance of diversity.

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<b>Hypothesis</b>	<b>Effect</b>	<b>Simulation</b>
Resource Competition	Interspp. differences	Allometry, light extinction constant, light/growth function
	Understory Limitation	Understory light = 1
	Canopy Location	All spp have same % of their max exposed canopy area
	Canopy Limitation	All spp have full canopy exposure
Density Dependence		$Interspecific \times Intraspecific + Combined$ <i>Density – Dependence Density – Dependence</i>
Neutral Theory		Complete Null
		Stability analysis of Null
Aggregation, Mass Effect, Recruitment Limitation		<i>Varying Initial Conditions</i> × <i>Varying Kernel</i>
Stochasticity		(Environmental Stochasticity) X (Demographic Stochasticity) X (Intraspecific Variation) X (Fecundity) X (Growth)
Storage	Seed Bank	No bank, null bank, full bank
	Seedling & Sapling Bank	Max age limit on time in each stage
	Adult	All repro in “mean reproductive” year
Intermediate Disturbance Hypothesis		$(Vary \ Storm \ Frequency) \times (Kernels)$
Spatial Synchrony		Vary spatial correlation in environmental stochasticity
Spatial Heterogeneity		Varying maps of topography, nutrients, moisture, temperature

Table 1: Diversity Hypotheses. F = “full” with intraspecific differences, N = “null” aggregate across species, 0 = effect removed completely

Figure 1: Outline of biomechanical modeling. A) Experimentally we can observe the overall relation between the diameter of a tree and the torque required to pull it over. On an individual tree basis we can observe the relationship between wind velocity and torque, and thus estimate the failure wind speed. B) Based on first principles we can approximate a tree as a cantilever beam (trunk) embedded in a non-rigid surface (soil). We can approximate the distributed force ( $F$ ) exerted on the trunk based on the wind speed profile, foliage profile, and leaf level drag coefficient. We can then compute the torque ( $M$ ) on the trunk. If we know the mechanical properties of the wood and the soil, we can then estimate the failure torque ( $M_{\max}$ ) for both the trunk (snapping) and the trunk/soil interface (uprooting) and thus back out the maximum wind speed the tree can sustain. By propagating uncertainty in this calculation we actually generate a posterior distribution of failure wind speeds, rather than an discrete failure point.

Figure 2: Experimental gap plots map

Figure 3: Damaged tree survival, Blackwood Division of Duke Forest. Proportion of stems (by taxonomic group) >10cm DBH that still had live foliage at the end of the growing season 2002 in Duke Forest following gap creation in March 2002. These estimates aggregate all damage types and both trees that were pulled or damaged by other trees. OXar = *Oxydendron arborium*, LItu = *Liriodendron tulipifera*, FRam = *Fraxinus americana*, ACru = *Acer rubrum*, COfl = *Cornus florida*, LIst = *Liquidambar styraciflua*, QUal = *Quercus alba*, QUru = combined red oaks.

Figure 4: Adohi life history stages

Figure 5: Alternate dispersal kernels

## Research Schedule

Summer 2000

Set up gap plots, map stands, begin light measurements

Fall 2000

Model: simple single stage, single spp model; Quad Tree vs Linked List

Spring 2001

Model: further develop simple model, work towards multispp/multistage

Summer 2001

Continue fieldwork, add sapling plots, allometric measurements

Fall 2001

Model: multispp/multistage implemented as spatial transition matrix

Light model developed outside simulator

HURRECON rewrite

Spring 2002

Model: Light model ported into forest model, growth model added.

Extensive work on algorithms, GUI implemented, draft documentation

Field experimental gaps put in, biomechanical measurements made.

Summer 2002

Continue fieldwork, add post-gap measurements

Fall 2002:

Complete initial version of forest model: light and demography

Prelims

Start "natural wind" biomechanics measurements

Spring 2003:

Model algorithm analysis w/ Sathish

Finish allometric analysis, write up.

Initial sapling growth/mortality analysis

Pull existing parameters together for model

Formalize what parameters require NEW experiments/measurements

Post-gap Cphoto analysis, light model parameterization

Summer 2003:

Continue fieldwork

New experiments as needed

Model runs: Null vs. full model, hierarchical vs. point estimate, simple forecasts

Fall 2003:

Biomechanics analysis  
Finish hurricane analysis  
Model: add abiotic heterogeneity (temp, precip, moisture) as needed

Spring 2004:

Model: add disturbance  
Write up biomechanics  
Write up disturbance regime  
Model: Diversity Hypothesis runs

Summer 2004:

Finish up field projects  
Model: Disturbance runs

Fall 2004:

Final analyses of field data  
Finish up model runs

Spring 2005:

Writing, defense, job hunting

# Figure 5

