ENVIRONMENTAL AND BIOTIC CONTROLS ON THE INVASION OF THE EXOTIC SHRUB *ELAEAGNUS UMBELLATA* IN A MICHIGAN FOREST

by

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ABSTRACT

Distinguishing the differences between invasive species and those of the invaded native community is important to understand both the mechanisms and the potential impacts of invasion. In this study, I ask how the effects of environmental and biotic factors on growth of fourteen native species in a southeast Michigan forest differ from the exotic shrub, *Elaeagnus umbellata*. Primarily focused on an understory woody plant community, I expect light availability to be a driving factor of growth. To test this hypothesis for the invasive shrub, I carried out a transplant experiment of seedlings of the invasive plant along light gradients. In a complementary analysis, I use growth data from forest censuses carried out five years apart to study how growth and invasibility of the exotic shrub species relate to the invaded community. From the experimental work, I found that seedling growth of the invasive shrub is strongly affected by soil water content and initial size, whereas light provides a marginal effect, contradicting common assumptions on how this species responds to resources. Results from the analysis of the census data show that the invasive shrub's adult growth is highly variable in response to environmental parameters, but is controlled by small-scale biotic interactions, like competition for space or limited resources. The model outcomes distinguish the growth of the invasive species from those of a native shade-intolerant tree and a native shade tolerant shrub in response to light availability. Predictions from the empirical model suggest an increased competitive ability under high light conditions of the invasive shrub over the native shrub (*Hamamelis virginiana*), but not over the shade-intolerant tree (*Sassafras albidum*). When

comparing these results to a community analysis of plant functional traits, I find similar results to the response to light; however, plant functional traits fail to reveal biotic controls noted in the demographic study. Ultimately, I conclude the spread of *Elaeagnus umbellata* is restricted by moisture and herbivory during early establishment and limited by proximity to taller individuals as an adult. However, despite the identification of controlling factors on the growth of *Elaeagnus umbellata*, it is still likely that functionally similar native species will experience negative impacts from the invasion event as the invasive shrub has a higher potential competitive ability than some of these species as measured by growth in the understory light environment.

ACKNOWLEDGMENTS

TABLE OF CONTENTS

INTRODUCTION

General Concepts Regarding Invasive Species

Invasive species are defined as exotic species that persist in an ecosystem to the detriment of the native community (Williamson and Fitter, 1996). With the continued introduction of alien species, evidence suggests invasive species present an ongoing threat to existing natural communities (Mack et al., 2000). The threat of invasive species to native ecosystems has been well documented along continental scales (e.g. Pimentel et al., 2000; Sakai et al., 2001; Vitousek et al. 1996); however, regional and local impacts are nearly impossible to predict from generalizations of current broad-scale invasions. Still, if we want to mitigate further losses in biodiversity and changes in ecosystem function we will need to understand the local scale processes that lead to successful introductions. This will require further testing of the mechanisms contributing to a species success in a novel habitat as well as their relative importance in relation to the native community in which they invade.

Previous studies have linked invasion mechanisms to general traits associated with colonizing potential (e.g. Rejmanek & Richardson, 1996) or some advantage for the uptake of resources (Theoharides & Dukes, 2007). The vast majority of these studies use multispecies datasets to compare invasive species with other invasive species or to compare invasive species with closely related non-invasive exotics or native species (Pyšek & Richardson, 2007; Diez et al, 2009). Others studies have considered the richness and functional diversity of the target community in

relation to potential invasion (e.g. Pokorny et al, 2005; Fargione & Tilman, 2005; Mwangi et al, 2007). A plethora of hypotheses have been proposed to explain invasiveness, notably empty niche hypothesis (Hierro, Maron, & Callaway, 2005), enemy release hypothesis (*reviewed by* Maron & Vila, 2001), novel weapons hypothesis (Callaway & Ridenour, 2004) and various fitness trade-off mechanisms (e.g. Richards et al, 2006; MacDougall, Gilbert, & Levine, 2009). In addition, many successful invasive species were selected by humans for their horticultural significance (Grotkopp, Erskin-Ogden, & Rejmanek, 2010). These species are likely to have a prolific propagule source from their widespread planting. Thus, if propagule availability is not an issue, one would expect distributions of the invaded range of these horticultural escapes to be primarily defined by environmental and biotic controls that they experience when establishing in natural habitats.

Some of these hypotheses are supported in specific cases, but remain poorly studied in a theoretical framework. For instance, consider the trade-offs of light-demanding ecological strategies in the context of the empty niche hypothesis and a traits-based approach. If we assume that all light levels are available in a forest, one might expect that any species with a higher photosynthetic capacity than that represented in the native community would occupy different trait space, suggesting a novel ecological strategy and therefore could potentially coexist in that plant community (Brym et al., *in review*; Wright et al., 2004). The higher photosynthetic capacity could give a growth advantage to the potential invader in relation to native plants in canopy gaps. However, due to physiological trade-offs, plants with high photosynthetic capacity and higher growth rates tend to experience lower survival rates under low light conditions than

plants with lower growth rates, such as those found in the forest understory (Bazzaz, 1979; Tilman, 1988; Wright *et al*., 2004). So the invasive shrub will likely be less competitive under those environmental conditions, unless it can somehow overcome these trade-offs. Therefore, a traits-based approach to predicting the dynamics of a species invasion into a local community, must consider both the ecological importance of measured traits and the natural history of the specific system to adequately address questions regarding a potential invasion event making a theoretical prediction difficult.

With this in mind, understanding the strategies of invasive species relative to the entire native community will be critical to be able to understand both the mechanisms and potential impact of invasion. In spite of the relevance of these comparisons, few studies of invasive species have taken a community-level approach to suggest species interactions. This thesis research seeks to better understand the natural history of a system and characterize the factors limiting growth of the alien species and its relationship with the native community. In particular, by combining growth data with environmental variables and biotic pressures, I intend to provide a more robust picture of the community dynamics of this system and the circumstances that lead to the invasion.

General Approach

When considering the dynamics of an invaded system and potential mechanisms by which an exotic plant species becomes established, we must first recognize mechanisms of plant

coexistence. It is likely that both stabilizing mechanisms (niche concept) and fitness equivalence (neutral theory) are acting on this system (Adler, HilleRisLambers, & Levine, 2007); however, determining the strength of these forces on the system is beyond the scope of the study. The niche concept, where species coexist by differentially utilizing limiting resources, motivates this study focusing on competition for light and other environmental resources (Hutchinson, 1957). In an understory forest, many potential factors can contribute to the coexistence or dominance of an introduced species. It is likely that the heterogeneity of light and nutrients will contribute to the coexistence of the species in an invaded system (e.g. Pacala & Tilman, 1994). In addition, various juvenile establishment strategies are also implicated in maintaining species coexistence in forest ecosystems, including early germination, fast initial growth, generalist habitat suitability, and high propagule pressure (Grubb, 1977; Kobe, 1999; Poorter, 2007). As these various invasion strategies exist, multiple life-history stages must be considered in obtaining a complete picture of the invasive species establishment and spread and the subsequent impact the exotic species will have on a native plant community.

The evaluation of community dynamics and competition requires some metric of success among populations. Early theoretical development strictly used number of individuals (N) within a population to describe community dynamics (Volterra, 1926; Gauss, 1934; Hutchinson, 1957). More recently, models of plant communities have considered differences in individual success by using relative growth rate, a standardized measure of biomass growth, to suggest community dynamics (Hunt, 1982; Tilman, 1988, Pacala & Tilman, 1994). Allometric relationships between biomass and other size metrics, like basal area and diameter, have been established that provide

for the evaluation of growth metrics based on non-destructive measurements of plants

(Westwood & Roberts, 1970; Enquist, Brown, & West, 1998). Relating these measurable

quantities among populations then allow us to suggest the interactions of species and community

dynamics. In general, more growth is attributed to superior individual success or competitive

ability.

For this thesis, I ask: "What are the driving factors that impact individual growth of *Elaeagnus*

umbellata?" A seedling transplant experiment was established to assess what environmental and

biological factors influence the establishment of this invasive species. However, simple

transplant experiments are small in scope and may not elucidate all-important interactions of the

invasive species with the native community. To complement the work on recruitment, data from

a forest census are explored in order to observe the demographic patterns of *E. umbellata*. The

census data also allows me to address the community scale patterns of the invasive species

interactions with the native forest community. With this, I pose this question: "Is the extent of

these effects similar between the invasive and the competing native species, or is *E. umbellata*

performing better than the local species?"

However, often demographic or growth data are unavailable to determine the impacts of invasive

species. Plant functional traits offer a novel and cost-effective alternate to studying species

interactions with the biotic and abiotic environment (Reich *et al*., 2003; McGill *et al*., 2006).

These traits often demonstrate significant differences among species that reflect various resource

use and life history strategies. This, in turn, reflects important fundamental niche axes along

which species are differentiated (Westoby *et al*., 2002; Violle & Jiang, 2009). For example, variation in certain leaf characteristics, including area, mass, and nitrogen content, reveal trade-offs involving photosynthetic carbon fixationamong plant species (Wright *et al*., 2004; Westoby & Wright, 2006). This continuum is recognized as the leaf economics spectrum [Figure 1]. Traits-based approaches have also been used to demonstrate high functional dissimilarity of successful invaders with the dominant plant species (Emery, 2007), as well as a high functional similarity among invasive species in distinct but similar regions or habitats (Kolar & Lodge, 2001; Lloret *et al*., 2005), and to identify traits that are more common among invasives than among natives (Williamson & Fitter, 1996; Rejmánek & Richardson, 1996; Grotkopp, Rejmánek, & Rost, 2002; Kyle & Leishman, 2009).

These studies often categorize species based on broad functional groups and rarely link functional traits to the biotic and abiotic filters (Pyšek & Richardson, 2007; Theoharides & Dukes, 2007). Here, I go one step farther and focus on comparisons of a single invasive species in relation to the entire native community. By combining the functional trait distributions of *E. umbellata* with those of each native species (Brym et al, *in review*) and the conclusions of the long-term forest census, I address the following question: "Do traits approximate the patterns described by a large demographic census?"

Target Species Description

Elaeagnus umbellata (autumn-olive) is a shade-intolerant shrub native to the sub-Himalayan regions of northern Pakistan, as well as China, India, Japan, and Korea (Ahmad, Sabir, & Zubair, 2006), where it occurs in open habitat. However, *E. umbellata* has been observed to be shade tolerant in introduced habitats (Orr, Rudgers, & Clay, 2005), persisting in both edge and interior conditions (Yates & Levia, 2004). *Elaeagnus* is widely established along roads, open spaces and forests in the eastern United States. It was first introduced to the US as a horticultural species from Japan in 1830 and was widely used in the 1940's for restoration of disturbed habitats (Black, Fordham, & Perkins-Veazie, 2005). A cultivated variety, "Cardinal," was established in 1963 for commercial use (Mehroff et al., 2003). Observation of *E. umbellata* in the forest understory remains inconsistent (e.g. Sanford, Harrington, & Fowness, 2003), although *E. umbellata* is found beneath the canopy in this study site suggesting some validity in the potential

Understory
5-30% Full Sun
Low Photosynthetic Capacity
Long Leaf Lifespan
Hamamelis virginiana

Edge/Gap
Intermediate

Open
>35% Full Sun
High Photosynthetic Capacity
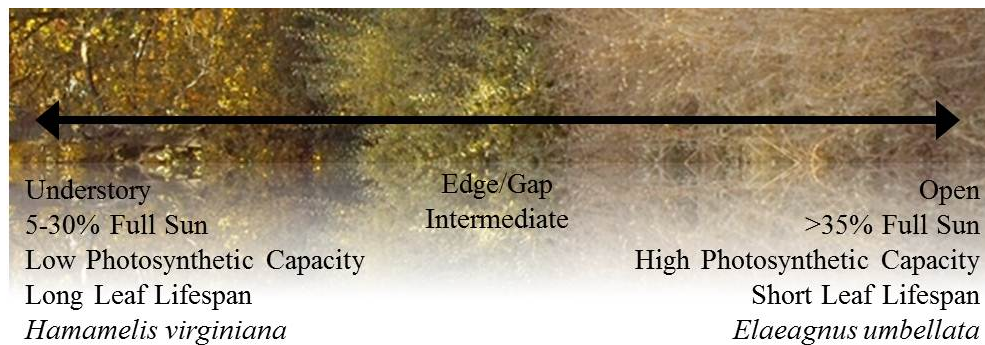Short Leaf Lifespan
Elaeagnus umbellata

Figure 1: A continuous trade-off axis of leaf functional traits along a gradient of light availability.

spread of invasion to the understory community. *Elaeagnus* tolerates a large variation of pH (4-8) and soil moisture availability ranging from drought to swampy conditions (Ahmad, Sabir, & Zubair, 2006). Morphological characteristics - leaf area, height, and diameter - vary significantly among its native ecotypes spanning a broad range of topography and microenvironments (Ahmad, Sabir, & Zubair, 2006). It is both allelopathic (Orr, Rudgers, & Clay, 2005) and nitrogen fixing (Pashke, Dawson, & David, 1989) and has been observed to sometimes persist in monotypic stands (Catling et al., 1997). Seeds are contained in nutrient rich fruits, which are dispersed by birds (LaFleur et al., 2007). A single plant can produce nearly 36 kg of fruit per year, which native occurring birds and small mammals readily eat, aiding in the dispersal and subsequent invasion of this species (Mehroff et al., 2003). Once established, *E. umbellata* has the ability to shade out its competitors or utilize chemical defenses to inhibit germination (Orr, Rudgers, & Clay, 2005; Brantley and Young, 2010).

Elaeagnus at the E.S. George Reserve

Elaeagnus was first observed at my study site, the E.S. George Reserve in the early 1980s (Evans, *pers. comm.*; Werner, *pers. comm.*). Although, most problematic in open habitats (Catling et al., 1997), it is now prolific not only in the open grasslands, but also along the roads and in forest edge habitat at the study site. We also find it persisting in the understory with 14 other native woody plant species in various life history stages. As with any closed canopy forest, we expect light availability to be a key driver of woody plant dynamics (Kobe et al., 1995;

Pacala et al., 1996; Finzi and Canham, 2000; Kobe, 2006), suggesting *E. umbellata* may have acquired some mechanism for persisting in a limited light environment. In a previous study, I characterized *E. umbellata* with an alternative growth strategy from the native understory woody plant community in the George Reserve and suggested the invasive shrub is released from direct competition with native species by "cheating" on established plant physiology trade-off axes (Brym et al., *in review*). The invasive shrub shows traits we would expect in an open habitat where it has a high photosynthetic capacity and short leaf lifespan [Figure 1]. Thus, we would not expect a shade-intolerant species, as *E. umbellata,* to be able to persist in a light-limited environment. The fact that *E. umbellata* is found in the forest understory at my site suggests that the exotic shrub has some mechanism to compensate for the low light availability.

Observationally, *E. umbellata* is a true invasive species, meaning that it has a detrimental effect on the native community, especially in the open grassland habitat; however, it is unclear as to the effects the invasive shrub has on the understory woody plant community. *Elaeagnus* severely limits light beneath its canopy restricting native recruitment (Brantley & Young, 2009). In addition, *E. umbellata* also produces secondary chemicals that limit seedling germination and growth (Orr, Rudgers, & Clay, 2005). It is possible that *E. umbellata* is an ecosystem engineer that creates conditions most favorable for its continued spread.

It is well understood that *E. umbellata* is a severe threat in open habitats (Catling et al., 1997). Thus, it is reasonable to expect that *E. umbellata* will spread throughout the remaining open habitats in the George Reserve [Figure 2]. A previous study at the E.S. George reserve attempted

to characterize the spectral signature of *E. umbellata* using advanced remote sensing techniques, with demonstrated success only in open habitats (Severtson, 2005). As this technique was unable to detect the species in understory environments and did not consider community dynamics, this study attempts to elucidate the dynamics of the invasion in the understory community. Specifically, I look at changes in the species' distribution between consecutive field censuses to assess potential patterns of the spread of *E. umbellata* under the forest canopy [Figure 3].

Patterns indicate that recruitment mainly takes place in areas with high light levels, and that adults survive once the canopy regenerates (e.g. de Villalobos, Vazquez, & Martin 2009), even if most reproductive adults are found in open spaces. Bird dispersal would act as the primary colonization mechanism of seeds to the understory. These understory aggregations could act as temporal sinks allowing advance regeneration of *E. umbellata* that would only prosper if the conditions were to become suitable (high light). Then, when a gap is created, *E. umbellata* is able to win the site through its advance regeneration, with an individual instantly present that can immediately grow fast and reproduce. With a critical mass of juvenile individuals, a thicket of *E. umbellata* can quickly form and then restrict regeneration of other species (Catling et al., 1997; Edgin & Ebinger, 2001).

To answer the questions stated above this research aims at describing the growth performance of *E. umbellata* relative to native species in a Michigan forest. I expect *E. umbellata* will respond most strongly to light availability, where some threshold value exists within the understory below which the shrub experiences a decline in growth, a proxy for competitive ability and

reproductive potential. Beyond this threshold of light availability, the invasive population may be

outcompeted by native species better adapted to the limited light environment. Observed

populations beyond that threshold would then only persist by source-sink dynamics and would

not be appropriately described as invasive in those native communities (Pulliam, 1988). Such

differentiation would help in the control of the invasion, as managers would know what

populations to target to optimize eradication and control efforts when resources are limited.
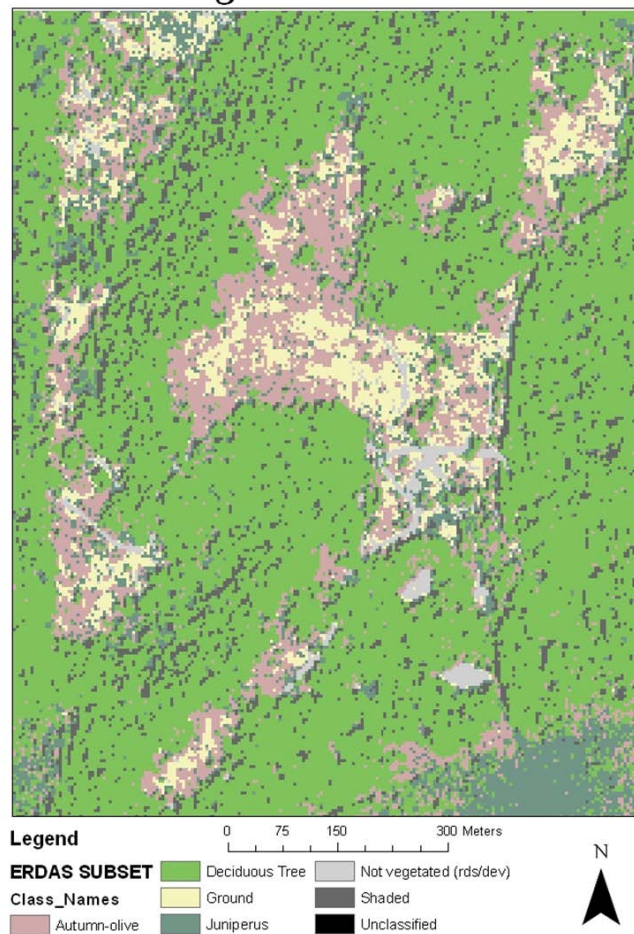
Figure 2: IKONOS image of a subset of the E.S. George Reserve identifying patches colonized by *E. umbellata* (rose; Severtson, 2005). Remaining open habitat is in tan.
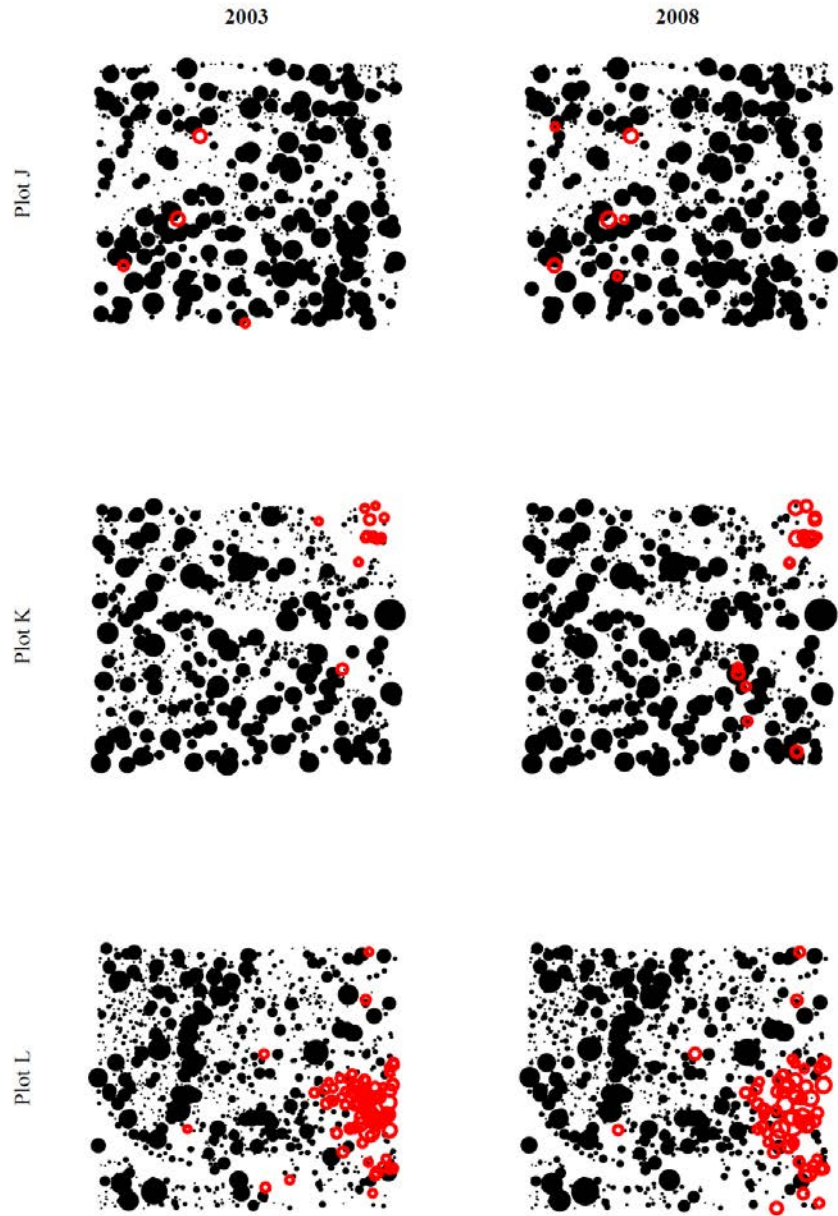
Figure 3: Spatial arrangement of a forest plot (1ha) at the E.S. George Reserve, demonstrating the presence and spread of *E. umbellata* in understory habitats. Black dots represent native species with their size relative to the circumference at breast height of the individual. Red open dots represent *E. umbellata* and a size 6 times the corresponding circumference. *Elaeagnus* is distributed mainly away from the largest of native trees in edge and open habitats.

Questions Addressed

What are the driving factors that impact individual growth of Elaeagnus umbellata?

A plant species potential to invade an established community is determined by the availability of suitable germination sites and the competitive ability of the individual (Grubb, 1977). Establishment and growth are directly impacted by the availability of light, water, and nutrients, (though nutrients are not directly measured in this study). Biotic factors will also affect the performance of an individual; in particular competition for those resources from the surrounding vegetation will have an effect on its growth capacity [Figure 4]. I address this question by first conducting a transplant experiment of *E. umbellata* seedlings along environmental gradients, and second, analyzing growth of adult individuals as a function of the resources and the surrounding neighborhood.

Is the extent of these effects similar between the invasive and the competing native species, or is E. umbellata performing better than the local species?

Comparing the growth rates of native species with respect to the invasive will provide a measure of the invasive's performance in the community. If the growth rates of *E. umbellata* in the understory of closed canopy forests are lower than those of the native species, the exotic shrub will have no competitive advantage and its understory populations are likely to act as sinks but not sources of propagules. Alternatively, if the growth rates of *E. umbellata* in the understory are

greater than those of the native community, the magnitude of the difference in growth rate would

offer insight into the invasive's competitive advantage. I have addressed this question by

comparing *E. umbellata* adult plant's growth rates with those of the most common species of the

native community in the forest understory.

Do leaf morphological and chemical traits approximate the patterns described by a large

demographic census?

Environmental and demographic data are not always available. In those cases plant functional

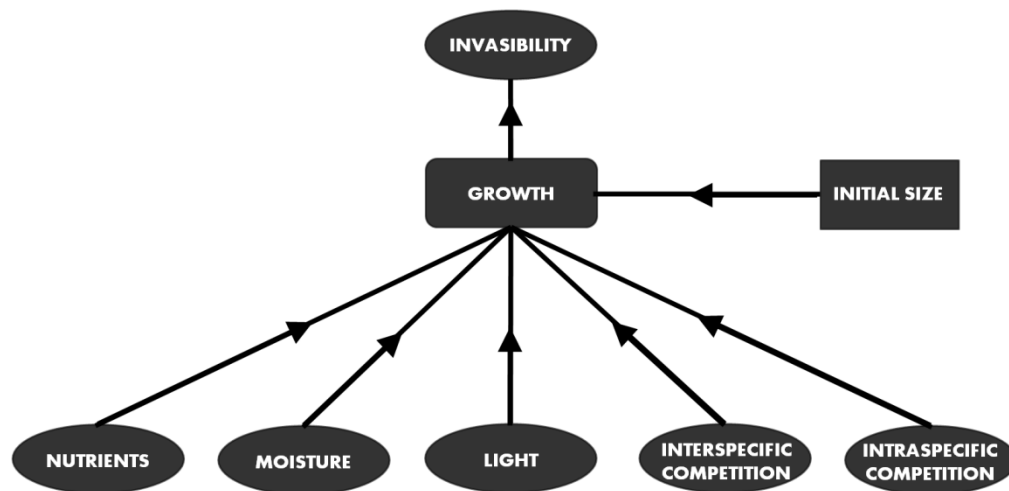traits could provide forest ecologists with a cost effective alternative for acquiring necessary

Figure 4: Conceptual diagram of the environmental and biotic factors influencing the establishment and growth of plant species.

information about a particular community. Moreover, determining the relationship of an invasive species' functional traits to those of the native community might reveal mechanisms of invasion or dynamics of the invaded system (Brym et al., *in review*). To evaluate the effectiveness of a traits-based approach, I compared conclusions based on leaf morphology and chemistry of woody plants in this community with the results derived from the above environmental and demographic data.

METHODS

Study Site Description

This research was conducted at the University of Michigan's E.S. George Reserve in Livingston County, MI (42° 27' 24.36" N, 84° 00' 40.03" W). The 525 hectare reserve is noted for its exceptional variety of environmental gradients for a Michigan forest, which allow researchers to establish sites among gradients in elevations (274.09m – 300.15m), slopes (7.33% - 52.51%), and aspects (22.9^{o} -179°,180° -346°). These environmental characteristics result in a high diversity of species and ample opportunities for ecological research. The reserve had been farmed prior to 1927, when it was designated as a game reserve. Within a few years, it was established as a University of Michigan wildlife sanctuary and research area with minimal human intervention. Observing the regeneration process from pastureland to forest is

exceptionally useful for the study of invasive species, as they tend to demonstrate characteristics of pioneer species in disturbed habitats.

Transplant Experiment

Experimental set up

In order to study the recruitment of *E. umbellata* seedlings under a variety of environmental conditions, I conducted a transplant experiment along a natural gradient of canopy cover and soil moisture. Four plots were established at the E.S. George Reserve: an open canopy and closed canopy plot, characterized by a wide range of light levels, at each of two elevations, with different soil water availability [Figure 5]. The plots were drawn along a 100-m transect following a gradient of canopy cover, or light availability, from east to west to match the path of the diurnal solar orbit. Within the plot, six rows were placed every 20 m along a southerly transect, each with six points separated by 3 m.

Seedling Transplants

Seeds of *E. umbellata* were purchased in the previous fruiting season, Fall 2009. Seeds came from natural populations collected in Ingham County, MI. To break dormancy, seeds were soaked in warm water for 24 hours on 2 February 2010 and then stratified at 5°C for 71 days,
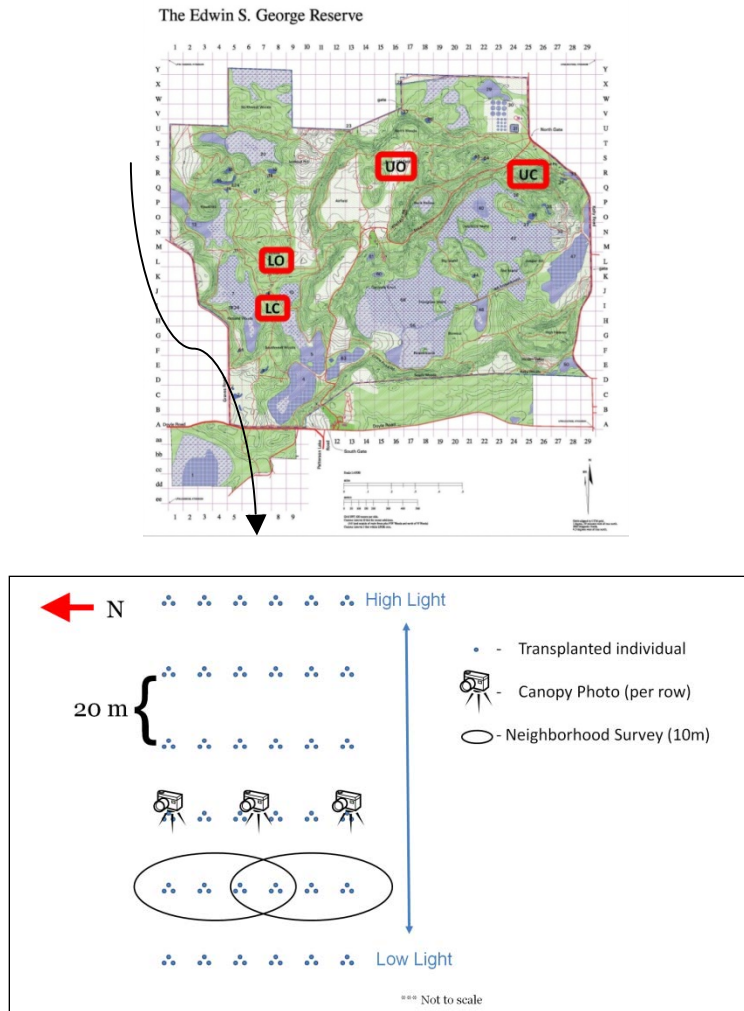
Figure 5: Map of E.S. George Reserve with designation for growth experiment plots (L – lower, U- upper, C-closed canopy, O-open canopy) and a diagram of the plot layout.

before planting them on 13 April 2010 in a controlled greenhouse for optimal growing conditions

at the Matthias Botanical Gardens. All seeds were placed in a medium sized plastic container (14

gallon roughneck Rubbermaid) filled about 25 cm with potting soil and perlite. The seedlings

were watered regularly. After being allowed to grow for seven weeks each seedling ($n = 432$)

was removed from the potting soil and excess soil removed from the roots. A mark was placed

on the stem at the former soil horizon and measured from this point to the branching point of the

terminal leaf. Flagging tape was tied around the stem for identification. The roots were then

grouped by transect row and placed in a moist paper towel within a Ziploc bag. Processed plants

remained in a cool dark room for one evening and planted the following day at the field site on

25 May 2010. I planted three individuals per point along each row in a standardized orientation.

Seedlings were visited periodically, every three weeks, throughout the summer and noted for

survival and foliar damage (herbivory, wilting, etc.). At the completion of the experiment, all

remaining seedlings (216) were measured for height, harvested and weighted for dry mass of

leaves, roots, and stems after at least a 72 hour air dry at 60°C.

Environmental Data

Light availability was quantified using canopy photographs (Anderson, 1964). Photographs were

taken using a digital camera (Sigma SD 14) with a 4.5-mm fisheye lens (Sigma EX DC HSM)

placed on a tripod 1 m above ground level. The lens was oriented flat to gravity using a bubble

level. Three photographs were taken for each row (north end, middle, south end). The

photographs were analyzed with a computer program (HemiView v2.1, Delta-T Devices)

outputting a global site factor (0.057 – 0.947), a measure of direct and indirect radiation reaching

the forest floor with values between 0 and 1 (full sun). Moisture data were gathered three times

throughout the summer using a soil moisture probe (Aquaterr 300 M). At each row and column,

the probe was placed approximately 10 cm into the ground in the middle of the three planted

seedlings. The value was recorded after equilibrium was reached or the meter display remained

constant for 5 seconds.

Model Development

I combined the environmental data and harvest data to analyze first year establishment as a function of the environmental conditions under which the seedlings grew. The final best-fit model is discussed below, but multiple submodels were tested [Table 1]. Bayesian approach was used in order to specify uncertainty in components of the model, process and variables (Gelman et al., 1995; Clark, 2005).

Harvested dry mass (*M*) was used as an output variable for growth success because it was readily measured from the collected seedlings and as only one growing season was conducted a relative measure of change in biomass is not possible. I modeled *M* for each individual *i* from a lognormal distribution (to ensure positive values), with mean μ and variance σ^2. μ was then estimated as a combination of fixed effects that included the variables contributing to the final harvested mass:

Likelihood:

$$(M_i) \sim \text{logNormal}\,(\mu_i, \sigma^2)$$

$$\mu_i = \alpha_0 + \alpha_1 * I_i + \alpha_2 * W_r + \alpha_3 * L_i$$

$$1/\sigma^2 \sim \text{Gamma}(0.01, 0.01)$$

α_0 is the intercept of baseline biomass; I represents the initial height [cm] of the harvested

individual i, as initial size may have influenced growth capacity and therefore final biomass.

Since a minimal number of moisture readings were taken during the length of the experiment and

precision of the soil moisture probe is low, I chose to average moisture level among rows, which

I have assumed had a relatively similar soil type and topography. I then estimated soil moisture

affecting each seedling by sampling it from a normal distribution with the mean being the

average of the moisture readings among the rows r and the variance found on those

measurements. The specific soil moisture value for each individual (W) was considered to be a

latent variable estimated from that individual's row r averaged soil moisture (six measurements

were taken at each row):

$$W_r \sim \text{Normal } (\overline{W_{row(i)}}, \sigma^2_{Wr})$$

L represents the light availability for individual i, as a percent visible sky as estimated by the

canopy photographs.

Table 1: Progression of submodels leading to predictions of harvested dry mass.

Submodel	Description
Model A	$\mu_i = \alpha_0 + \alpha_1 * I_i + \alpha_2 * W_i + \alpha_3 * L_i + \alpha_4 * J_i$
	Initial size (I), moisture per individual (W), light (L), number of neighborhood conspecific saplings (J)
Model B	$\mu_i = \alpha_1 * I_i + \alpha_2 * W_i + \alpha_3 * L_i + \alpha_4 * B_{10Ti} + \varphi_{plot} + \varphi_{row}$
	random effects (φ) for plot and row are added to this model along with the total neighborhood basal area in a 10 m radius (B_{10Ti}).

Model C $\mu_i = \alpha_1 * I_i + \alpha_2 * W_i + \alpha_3 * L_i + \alpha_4 * J_i + \varphi_{plot} + \varphi_{row}$

Similar to submodel B, but J_i replaces B_{10Ti}

Model D $\mu_i = \alpha_0 + \alpha_1 * I_i + \alpha_2 * W_r + \alpha_3 * L_i$

Linear model similar to submodel A, but moisture varies by row and J_i is removed. This model is described following as the best-fit model.

Alpha values were estimated from distributions with uninformative prior values:

$\alpha_{0-4} \sim$ Normal(0, 10 000), using a Monte Carlo Markov Chain sequence and a Gibbs sampler

(Gelfland et al., 1990; Gamerman, 1997). Uninformative priors were chosen to ensure posterior

distributions would reflect only the data. Models were run for at least 50,000 iterations to ensure

convergence and then run for an additional 30,000 iterations to estimate fixed effect parameter

(α) posterior mean values and variances. The models for above-ground mass and mass of roots

had a similar form to harvested dry mass, but were analyzed independently.

Model Selection

The model was written in OpenBUGS 3.1 (Speigelhalter et al., 2010). I tried model variations

that included only fixed effects, and other models with added random effects [φ] with respect to

plot and *row* [Table 1]. Data included in the sub-models but not in the best fit model are: W is the

soil moisture content measured for individual i (recall W in the model is an estimate of moisture

per row r), J is the total number of *E. umbellata* individuals < 3.18cm dbh counted in a 10 m

radius around individual i, B_{10T} is the total basal area of all individuals >3.18 cm dbh in a 10 m

radius around individual *i*. I compared the submodels and selected the one with the set of covariates that best fit the data by comparing the number of parameters included in the model (simpler models were preferred) and how the predicted values from the model and the observed values from the data for each model deviated from a 1:1 line (R^2). Fewer parameters were preferred over a slight increase in R^2.

Forest Census

Census data

The forest census data have been collected for ~22,000 individuals, in an area that covers 21 ha of mid- to late-secondary forest dominated by oak, maple, and hickory (Allen, Vandermeer, & Perfecto, 2009). Census data were gathered starting in 2003. All woody plants >3.18 cm dbh have been mapped, identified, tagged and tracked. The baseline survey was conducted in 2003 and the first follow-up in 2008 are included in this analysis.

Species Analyzed

The forest census includes 32 species of which 15 species were included in the final analysis. Only species with a sample size (*N*) of >30 individuals were used. The remaining species were categorized into two functional groups, understory shrubs and trees (color-coded blue in subsequent figures) and canopy trees (color-coded black in subsequent figures) [Table 2]. The

understory group was further categorized to recognize three target species, the invasive shrub that is the focus of this research *Elaeagnus umbellata* and two native species that are most related in habitat and growth strategy. *Sassafras albidum* is a native shade-intolerant tree (orange) with similar functional traits to *E. umbellata* (Brym et al, *in review*). *Hamamelis virginiana* is a native shade-tolerant shrub (green) that is perhaps the most direct competitor with *E. umbellata* in light-limited understory habitat. Predicted growth was evaluated for independently for all species following model selection and parameter generation.

Environmental Data

Slope (*S*), aspect (*a*), and elevation (*E*) layers developed by Severtson (2005) and the Livingston County Soils data (SEMCOG, 2010) were generated with the Spatial Analyst Tool in ArcMap to characterized the study area (ESRI, 2010). I matched the location of each individual with the environmental variables using layering of GIS data. Soil type (Boyer and Boyer-Ohtonen) did not vary greatly with relation to the biologically significant O and A horizons. Aspect (*a*), in degrees, was transformed (*A*) to values of -1 to 1 to reflect the effect aspect has on light availability and therefore growth of tree species. In the northern hemisphere the sun travels from east to west in the southern portion of the sky. Southern aspect (180°) was given a value of 1 and northern aspect (0°, 360°) was given a value of -1 with the following equation:

$$A = \cos\left(\frac{\pi a}{180}\right)$$

Slopes facing south are transformed to a positive value while slopes facing north are transformed

to a negative value to signify the relative greater light availability facing south.

Table 2: Species included in the final forest census analysis. Sample size, functional group and description of light requirements are listed (Barnes and Wagner, 2004).

Species	N	Group	Description
Elaeagnus umbellata	50	Understory	Shade-intolerant Invasive Shrub
Sassafras albidum	128	Understory	Shade-intolerant Native Tree *shade-tolerant as seedling
Hamamelis virginiana	77	Understory	Shade-tolerant Native Shrub
Cornus florida	62	Understory	Shade-tolerant Native Tree
Ostrya virginiana	3403	Understory	Shade-tolerant Native Tree
Amelanchier arborea	914	Understory	Shade-tolerant Native Tree
Fagus grandifolia	300	Canopy	Shade-tolerant Native Tree
Ulmus americana	209	Canopy	Shade-moderate Native Tree
Tilia americana	379	Canopy	Shade-tolerant Native Tree
Prunus serotina	3649	Canopy	Shade-intolerant Native Tree *shade-tolerant as juvenile
Quercus velutina	431	Canopy	Shade-moderate Native Tree
Carya glabra	622	Canopy	Shade-moderate Native Tree
Acer rubrum	86	Canopy	Shade-moderate Native Tree
Carya ovata	533	Canopy	Shade-moderate Native Tree
Quercus alba	1677	Canopy	Shade-moderate Native Tree

At the transplant experimental plots, a neighborhood survey was conducted on each row (north

end, south end) in which all stems >3.18 cm diameter at breast height (dbh) within a 10 m radius

were measured [Figure 5]. The 10 m radius was established using a laser range finder (Impulse

LR, Laser Technology, Inc.). Based on previous estimates of light using canopy photos and the

neighborhood survey [Figure 6], I evaluated the relationship between total basal area of all

individuals within a 10 m radius and light availability, using a simple linear model:

$$\psi_{Li} = a*\ln(B_{10i}) + b$$

ψ_{Li} is the value of light estimated from the canopy photos (Global Site Factor, it ranges from 0 to

1, being 1 full sun light), the biotic variable B_{10} represents the total basal area in a 10 m radius

around the point the canopy photo was taken for individual i. The estimates of the parameters

were a:-0.1631 and b: 1.7032, R^2=0.7383. For the census data I then estimated the light reaching

each plant as a function of its neighbors. Because there is uncertainty in my prediction of the

light environment I did not use that estimate directly but sampled it from a distribution:

$$Z_i \sim \text{Normal}(\psi_{Li}, 0.1)$$

$$\psi_{Li} = -0.1631*\ln(B_{10i}) + 1.7032$$
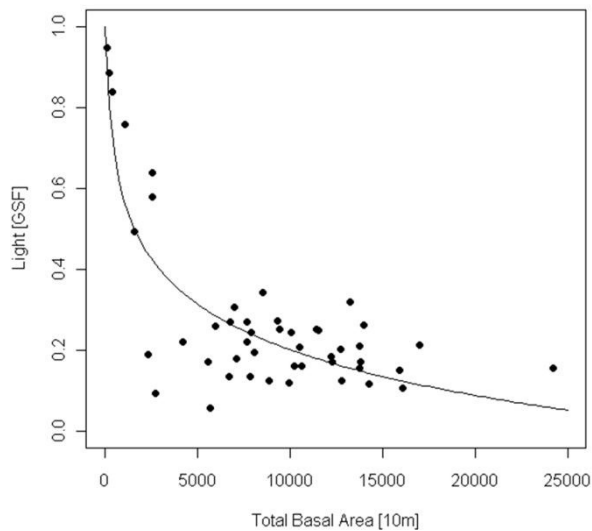
Figure 6: Relationship of total basal area for all individuals in a 10m radius and light [global solar fraction] (R^2=0.7383).

where *Z* represents the light available to individual *i* as a function of its neighborhood in a 10m radius. These calculations were made using the program R (R v2.11.1, R Foundation for Statistical Computing).

Model Development

I combined environmental variables established from GIS databases and neighborhood surveys conducted from the forest census data to construct an empirical model of relative growth rate of selected woody plant species. Figure 4a provides a diagrammatical representation of the best-fit model. A Bayesian approach was used in order to specify uncertainty in components of the model and its predictions, in this case the light environment.

The relative growth rate (G) for each individual i of species s has been established as growth in

circumference at breast height (g = trunk girth 2008 – trunk girth 2003) standardized by the

initial size (I = trunk girth 2003):

$$G = \frac{g}{I}$$

Notice here, relative growth rate is a function of circumference, not biomass as it was initially

derived (Hunt, 1982). As circumference can be directly related to biomass (i.e. Enquist, Brown,

& West, 1998), I assert this measurement can be used as an indicator of individual success and

therefore suggest dynamics of the community. Due to the error within circumference

measurements and the power-law relationship with biomass, I did not convert circumference to

biomass as I expected this calculation would introduce undue error into the evaluation of the

model. Individuals whose relative growth rate was less than or equal to zero were excluded from

the final analysis as these estimated rates are likely due to measurement error.

Relative growth rate is affected by a number of environmental [γ] and biotic [β] variables, as

well as initial size [α] [Figure 4a]. We used the natural log of G, $\ln(G)$, to ensure positive values
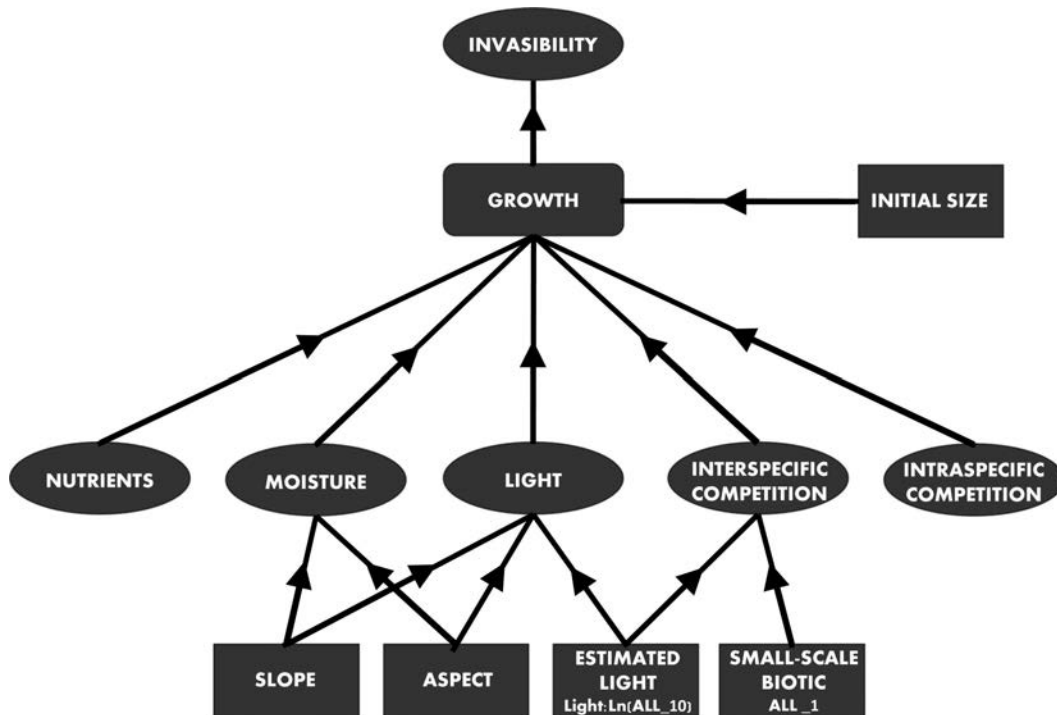
Figure 4a: Conceptual diagram of the environmental and biotic factors influencing the growth of plant species. Variables from the empirical model are included to connect data with the biological significance of the analysis. For predicting invasibility of the native understory community, the effect of light availability as a function of a 10 m neighborhood and the basal area of all individuals in a 1 m area were relevant variables. The remainder of the variables improved the predictability of the model as indirect variables.

of growth. The empirical model was constructed in the following way the natural log of relative growth of individual i of species s:

Likelihood:

$$\ln(G_{si}) \sim \text{Normal}(\chi_i, \sigma^2_s)$$

$$\chi_i = \alpha_s * I_i + \gamma_{1s} + \gamma_{2s} * S_i + \gamma_{3s} * A_i + \beta_{1s} * Z_i + \beta_{2s} * B_{1Ti}$$

$$1/\sigma^2_s \sim \text{Gamma}(0.01, 0.01)$$

I represents the initial size of the individual, and although growth rate is standardized, accounting

for initial size is still important as it may determine the plants position in the canopy and

therefore the light available to the individual. γ_{1s} represents the species specific intercept value

within the model. In earlier submodels [Table 3], *S* represents the slope of the terrain and is an

indication of the water available in the soil. *A* represents transformed aspect, the calculation

described above, and is an indication of the light intensity throughout the day. *Z* represents the

large-scale biotic interactions, estimated by the relationship of total basal area of stems in a 10 m

radius and light availability described above. B_{1T} represents the small-scale biotic interactions for

individual *i* and is calculated as the total basal area of all stems in a 1 m radius, a metric for the

crowding or competition from the closest surrounding individuals. Data values were standardized

to optimize convergence of the parameters. The prior parameters were estimated from

distributions with uninformative parameter values: $\alpha \sim$ Normal(0, 10 000),

$\beta_{1-2} \sim$ Normal(0, 10 000), $\gamma_{1-3} \sim$ Normal(0, 10 000), using a Monte Carlo Markov Chain sequence

and a Gibbs sampler (Gelfland et al., 1990; Gamerman, 1997). Models were run for at least

30,000 iterations to ensure convergence and then run for an additional 20,000 iterations to

estimate posterior mean parameter values.

Model Selection

The model was written in OpenBUGS 3.1 (Speigelhalter et al., 2010). I tried variations of the

model described above, using only environmental variables and then added levels of complexity

from the neighborhood surveys [Table 3]. Data included in the sub-models but not in the best fit

model are: γ_{ts} are intercept values for each of the soil types t found in the studied area for species

s, B_{20Ti} represents the total basal area of all species within a 20 m radius, B_{10Ci} represents the total

basal area of conspecific individuals within a 10 m radius, B_{5Ei} represents the total basal area of

E. umbellata in a 5 m radius. I compared the submodels and selected the one with the set of

covariates that best fit the data using deviance information criterion (DIC). DIC is a measure of a

model's predictability and deviance that is suited for a model with complex-sample size structure

and comparing models with various numbers of parameters (Burnham & Anderson, 2002).

Values of DIC estimate how well the model fits the data with the lowest value expressing the

best predictability.

Table 3: Progression of submodels leading to the final model used for growth predictions.

Submodel	Model Description
Submodel A	$\chi_i = \gamma_{ts} + \gamma_{5s}*M_i + \gamma_{6s}*A_i$
	Establish best predictive environmental variables
Submodel B	$\chi_i = \gamma_{ts} + \gamma_{5s}*M_i + \gamma_{6s}*A_i + \beta_{1s}*B_{20Ti} + \beta_{2s}*B_{10Ci} + \beta_{3s}*B_{5Ei}$
	Add best combination of neighborhood survey data
Submodel C	$\chi_i = \alpha_s*I + \gamma_{ts} + \gamma_{5s}*M_i + \gamma_{6s}*A_i + \beta_{1s}*B_{20Ti} + \beta_{2s}*B_{10Ci} + \beta_{3s}*B_{5Ei}$
	Add initial size of individuals
Submodel D	$\chi_i = \alpha_s*I + \gamma_{ts} + \gamma_{5s}*M_i + \gamma_{6s}*A_i + \beta_{1s}*Z_i + \beta_{2s}*B_{10Ci} + \beta_{3s}*B_{5Ei}$
	Incorporate light function of basal area for large-scale interactions
Submodel E	$\chi_i = \alpha_s*I + \gamma_{1s} + \gamma_{2s}*M_i + \gamma_{3s}*A_i + \beta_{1s}*Z_i + \beta_{2s}*B_{1Ti}$
	Remove Conspecific at 10 m *Elaeagnus* at 5 m and replaced with the single variable total basal area at 1 m. Simplified soil intercept to a single species specific intercept

Predicted Growth

Following the estimation of mean coefficients, growth predictions were generated independently for each species along a gradient of light availability as linked with neighborhood basal area. The natural log of predicted growth rate (P) was estimated for each species s for light availability Z_j (0.1-0.6):

$$\ln(P_{sj}) \sim \text{Normal}(\rho_j, \sigma^2_s)$$

$$\rho_j = \overline{\alpha}_s * \overline{I}_s + \overline{\gamma_{1s}} + \overline{\gamma_{2s}} * \overline{S}_s + \overline{\gamma_{3s}} * \overline{A}_s + \overline{\beta_{1s}} * Z_j + \overline{\beta_{2s}} * \overline{B_{1Ts}}$$

$$1/\sigma^2_s \sim \text{Gamma}(0.01, 0.01) * N_s$$

where average parameter values ($\overline{\alpha}_s, \overline{\gamma_{1s}}, \overline{\gamma_{2s}}, \overline{\gamma_{3s}}, \overline{\beta_{1s}}, \overline{\beta_{2s}}$) and data values ($\overline{I}_s, \overline{S}_s, \overline{A}_s, \overline{B_{1Ts}}$) are estimated for each species s and N is the total number of individuals sampled in species s.

RESULTS

Transplant Experiment

Model selection

After preliminary exploration of the data, an initial model was constructed to incorporate the biological aspects that seemed most relevant (initial size, moisture per individual, light, and number of neighborhood conspecific saplings). In additional models, I incorporated random effects and then treated soil moisture as a latent variable that needed to be estimated as part of the analysis. Each model produced predictions of harvested mass, which were compared to the observed values of harvest mass. This relationship was quantified by a linear regression with R^2 values reported [Table 4]. Submodel D was chosen for its improved R^2 value compared to submodel A and its relative simplicity to submodels B and C. Submodel D is comprised of all fixed-effect coefficients and incorporates variation by row using observed moisture data.

Environmental variables

The environmental variables that best predicted final mass were moisture (W) and light (L)

Table 4: Progression of submodels leading to predictions of harvested dry mass. R^2 values are reported for predicted *vs.* observed values of harvested mass.

Submodel	Description	R^2 Predicted vs. Observed
Model A	$\mu_i = \alpha_0 + \alpha_1 * I_i + \alpha_2 * W_i + \alpha_3 * L_i + \alpha_4 * J_i$	0.031
Model B	$\mu_i = \alpha_1 * I_i + \alpha_2 * W_i + \alpha_3 * L_i + \alpha_4 * B_{10Ti} + \varphi_{plot} + \varphi_{row}$	0.278
Model C	$\mu_i = \alpha_1 * I_i + \alpha_2 * W_i + \alpha_3 * L_i + \alpha_4 * J_i + \varphi_{plot} + \varphi_{row}$	0.272
Model D	$\mu_i = \alpha_0 + \alpha_1 * I_i + \alpha_2 * W_r + \alpha_3 * L_i$	0.270

 [Figure 7]. The parameter associated with moisture (α_2) was significantly positive for both above ground and root dry biomass and had the strongest effect on seedling growth [Table 5].

Significance was determined by the entire 95% credible interval of the posterior mean not including zero. The effect of light (α_3) on growth was slightly positive though not significant.

Biotic variables

The parameter associated with initial size (α_1) was significantly positive for both aboveground and root dry biomass. No other biotic variables were included in the final best-fit model.

Survival Data

Although complete analysis of survival data was not completed for this thesis, I observed that fewer of the individuals planted in the open habitat experienced mortality due to herbivory (26.2%) than those in a closed or gap habitat (84.3%) [Table 6]. Most of the individuals that died in the open habitat were listed as having wilted because of the lack of water.
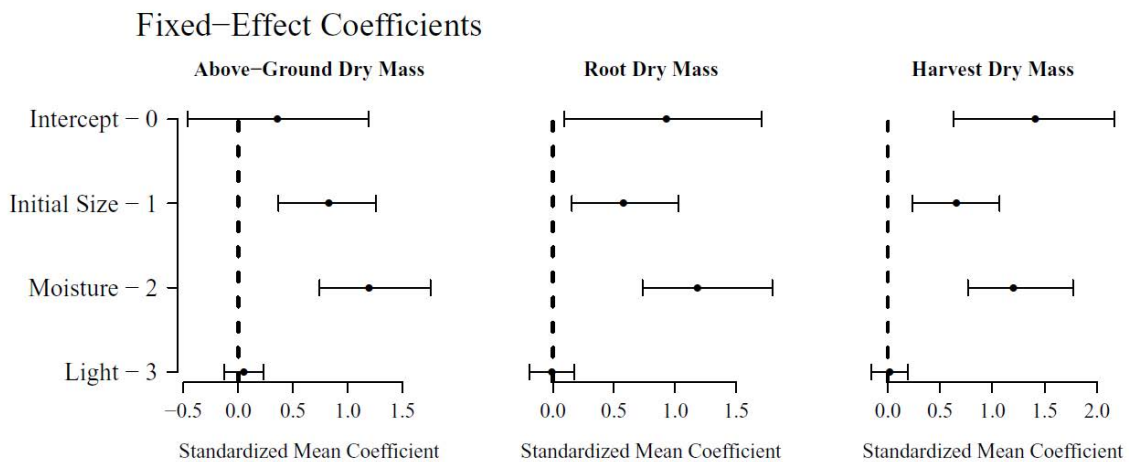

Fixed−Effect Coefficients

Figure 7: Results of the best fit model for the transplant experiment. Circles represent the posterior mean parameter value standardized by the mean value of the data. Whiskers represent the 95% credible intervals.

Table 5: Actual parameter values for the transplant experiment best-fit model, α_0: intercept, α_1: initial size, α_2: moisture, α_3: light.

Above-Ground Dry Mass

Parameter	Mean	St. Dev.	95% Credible Interval
α_0	0.3566	0.4191	-0.4625 - 1.1940
α_1	0.0149	0.0041	0.0066 - 0.0226
α_2	0.0422	0.0091	0.0262 - 0.0620
α_3	0.2816	0.5228	-0.7408 - 1.2880

Root Dry Mass

Parameter	Mean	St. Dev.	95% Credible Interval
α_0	0.9289	0.4099	0.0952 - 1.7050
α_1	0.0104	0.0040	0.0028 - 0.0185
α_2	0.0418	0.0094	0.0260 - 0.0634
α_3	-0.0435	0.5225	-1.0800 - 0.9705

Harvest Dry Mass

Parameter	Mean	St. Dev.	95% Credible Interval
α_0	1.4100	0.4066	0.6276 - 2.1640
α_1	0.0118	0.0038	0.0042 - 0.0193
α_2	0.0424	0.0091	0.0270 - 0.0626
α_3	0.0953	0.5048	-0.8950 - 1.0890

Table 6: Summary of cause of death for individuals in the transplant experiment. Open habitat is designated by >35% of total available light and closed or gap habitat by $\leq$ 35% available light.

Habitat	N	Deaths [%]	Deaths Due to Herbivory [%]
Open Habitat	60	70.0	26.2
Closed/Gap Habitat	372	42.7	84.3
All	432	46.5	72

Forest Census

Model selection

The final model used for growth predictions was determined based on the deviance information criterion (DIC) [Table 7]. The progression of models lowered the DIC while adding variables to the model, which is not surprising. However, as I refined the model to recognize limitations of the data, removing parameters, the DIC increased slightly. Conspecific basal area in a 10 m radius was removed because it was biologically redundant to the spatial scale at which I

Table 7: Progression of submodels leading to the final model used for growth predictions as evaluated by deviance information criterion (DIC).

Submodel	Model Description	DIC
Submodel A	$\chi_i = \gamma_{ts} + \gamma_{5s}*M_i + \gamma_{6s}*A_i$	29920
Submodel B	$\chi_i = \gamma_{ts} + \gamma_{5s}*M_i + \gamma_{6s}*A_i + \beta_{1s}*B_{20Ti} + \beta_{2s}*B_{10Ci} + \beta_{3s}*B_{5Ei}$	29530
Submodel C	$\chi_i = \alpha_s*I + \gamma_{ts} + \gamma_{5s}*M_i + \gamma_{6s}*A_i + \beta_{1s}*B_{20Ti} + \beta_{2s}*B_{10Ci} + \beta_{3s}*B_{5Ei}$	28860
Submodel D	$\chi_i = \alpha_s*I + \gamma_{ts} + \gamma_{5s}*M_i + \gamma_{6s}*A_i + \beta_{1s}*Z_i + \beta_{2s}*B_{10Ci} + \beta_{3s}*B_{5Ei}$	23310
Submodel E	$\chi_i = \alpha_s*I + \gamma_{1s} + \gamma_{2s}*M_i + \gamma_{3s}*A_i + \beta_{1s}*Z_i + \beta_{2s}*B_{1Ti}$	23710

evaluated light and had little effect in improving model predictions. Basal area for *E. umbellata* in a 5 m radius was removed as the majority of data demonstrated an absence of *E. umbellata* [Table 8]. The results of the model reflected this bias of data and had little effect in improving the model predictions. Submodel E was chosen for the final analysis. The variables included in the final empirical model are included in the graphical representation of the conceptual model [Figure 4a].

Environmental Variables

No environmental variable showed a significant effect on growth for the target species *E.*

umbellata [Figure 8]. A high variation in mean fixed-effect parameter values is observed for *E.*

Table 8: Presence of *E. umbellata*, average percent, around individuals of each species at three different radii.

Species	Presence of Invasive Stems		
	5m	10m	20m
Elaeagnus umbellata	68.8	77.9	93.5
Sassafras albidum	0.2	0.7	4.6
Hamamelis virginiana	0.1	1.1	6.7
Cornus florida	3.3	5.7	15.0
Ostrya virginiana	0.0	0.0	0.5
Amelanchier arborea	4.7	17.0	35.2
Fagus grandifolia	2.0	2.0	14.0
Ulmus americana	3.1	10.9	23.4
Tilia americana	0.0	0.0	6.5
Prunus serotina	2.2	7.4	20.7
Quercus velutina	7.2	16.1	30.4
Carya glabra	0.8	4.0	14.2
Acer rubrum	1.2	5.2	15.3
Carya ovata	1.2	5.8	20.9
Quercus alba	2.8	9.9	23.6

umbellata. The magnitude of variation of the mean parameter values is not consistent among

native species, but is less than *E. umbellata* in general. The posterior mean parameters of the

empirical model for the understory size class demonstrate the relative strength of effect each

variable has on the relative growth rate of a species and can be compared to suggest relative

effect on competitive ability [Table 9].

Biotic Variables

The effect of light as estimated by neighborhood basal area on growth for *E. umbellata* was slightly positive but not significant. The effect of light as estimated by neighborhood basal area on growth for *S. albidum* was slightly positive, while negative and significant for *H. virginiana* and all remaining understory species [Table 9, Figure 8]. *Elaeagnus* experienced the only significant negative effect from small-scale biotic interactions on growth [Table 9, Figure 8]. *Sassafras* and *H. virginiana* show a significant negative effect from initial size [Table 9, Figure 8]; however, *E. umbellata* has a mean coefficient value that is much lower than the native species and shows a larger credible interval which suggests a more variable response from initial size on relative growth.
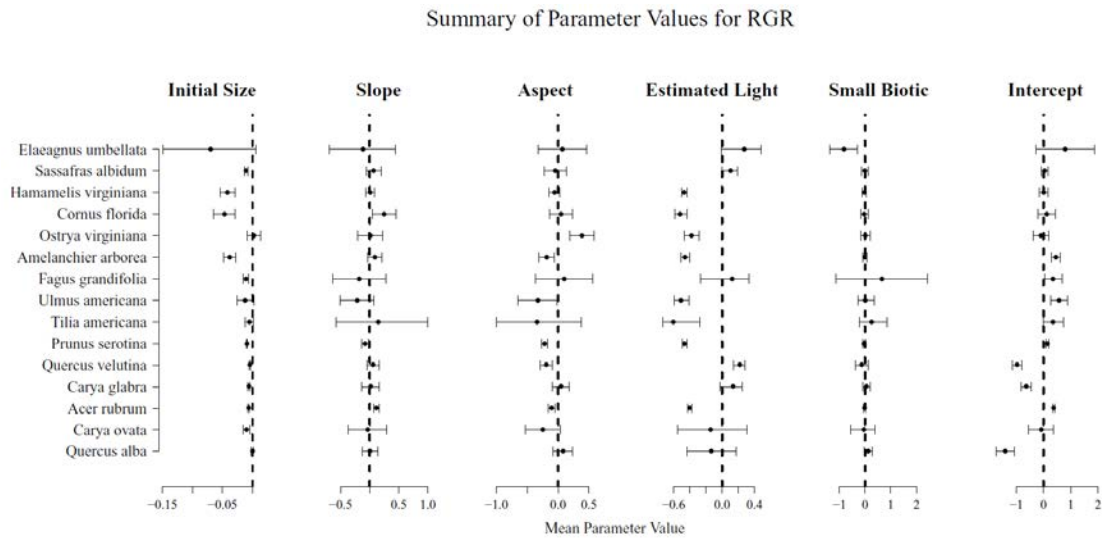

Figure 8: Posterior mean fixed effect coefficient values and 95% credible intervals of all analyzed species for the effect of initial size (α), slope (γ_1), aspect (γ_2), biotic large-scale (β_1), and biotic small-scale (β_2) on growth and the species specific intercept value.

Table 9: Mean values for fixed effect coefficient of all understory species. Standard deviation is included in parenthesis. The values are bolded if the 95% credible interval is entirely different from 0.

Variable	Parameter	E. umbellata	S. albidum	H.virginiana	C. florida	O.virginiana	A. arborea

Initial size	α	-0.070	**-0.011**	**-0.042**	**-0.047**	0.002	**-0.037**
		(0.039)	**(0.001)**	**(0.007)**	**(0.009)**	(0.006)	**(0.005)**
Slope	γ_2	-0.117	0.066	0.007	**0.246**	0.014	**0.089**
		(0.288)	(0.064)	(0.041)	**(0.101)**	(0.112)	**(0.060)**
Aspect	γ_3	0.070	-0.047	-0.058	0.049	**0.381**	**-0.186**
		(0.198)	(0.094)	(0.045)	(0.091)	**(0.104)**	**(0.065)**
Estimated Light	β_1	1.819	0.650	**-3.123**	**-3.444**	**-2.491**	**-3.051**
		(0.791)	(0.354)	**(0.124)**	**(0.277)**	**(0.334)**	**(0.180)**
Small Biotic	β_2	**-0.827**	-0.014	-0.032	-0.040	0.005	-0.016
		(0.278)	(0.069)	(0.039)	(0.073)	(0.095)	(0.044)
Intercept	γ_1	-1.515	-1.972	-1.076	-0.891	-1.349	**-0.664**
		(0.661)	(0.138)	(0.101)	(0.184)	(0.190)	**(0.093)**

Although the total basal area of all *E. umbellata* individuals was not included in the final model, the data support the fact that *E. umbellata* is often much closer to conspecific individuals than it is to any other species [Table 6]. Aside from itself, *E. umbellata* is most commonly found in the neighborhood of *Amelanchier arborea* and *Quercus velutina*.

DISCUSSION

Summary of Findings

I had originally predicted that light availability would explain the recruitment patterns of *Elaeagnus umbellata* and that the shrub would show a higher competitive ability in high light environments as it is generally characterized as a shade-intolerant species. However, this study suggests that the recruitment and growth of *E. umbellata* is mostly limited by moisture during early growth and that competitive ability as an adult mainly depends on the resulting light environment and biotic interactions at small scales. The transplant experiment demonstrates that seedling growth is greatest in intermediate canopy cover, most likely due to a sufficient level of moisture and, although to a lesser extent, light. I suggest this area is also potentially an ideal

location for recruitment as birds are the dispersal mechanism of seeds and perch in or near forest edges. As an adult, *E. umbellata* shows a greater growth rate than native species at ~35% available light, which corresponds with the intermediate canopy cover and edge habitat. In addition, is it in these edge and gap habitats where I predicted that *E. umbellata* is able to outcompete native species given the high photosynthetic capacity of its leaves and nitrogen fixing capabilities that were suggested from the study using leaf morphological and chemical traits (Brym et al., *in review*).

Transplant Experiment

Even though the experiment was only carried out for one growing season, the experimental design included sufficient variation along the environmental gradient to allow me to estimate the effects of those environmental variables on seedling growth. [Data for canopy cover ranged from 6% - 95% light availability with and primarily covered the range of understory light availability (mean: 18%, sd: 13%). Data for moisture ranged from 12.5% - 50% with a mean of 28% and a standard deviation of 8%.] Results show that soil moisture had the strongest impact on seedling growth during at least the first summer. Light was not correlated with moisture as might be expected from general landscape scale environmental gradients ($R^2 = 0.028$) and was not a significant factor on growth as was expected. This is contradictory to previous studies that demonstrate that light availability can explain a large percentage (21-79%) of variation in

seedling growth (Finzi & Canham, 2000; Kobe, 2006). In my case, the highest presence of *E. umbellata* seedlings (52 individuals / 314 m^2, data not presented) was observed in a closed canopy (13.5% total light) and *E. umbellata* seedlings were observed with as little light at 5.7%. No relationship was found between presence of *E. umbellata* seedlings and light availability (R^2 = 0.023, coefficient of determination, data not presented).

The additional finding from my transplants indicates that recruitment of *E. umbellata* is restricted within the deep understory environment (low light) by herbivory [Table 6]. A higher proportion of individuals died due to herbivory in a closed canopy environment than individuals in an open canopy environment where the main cause of mortality was lack of water. Of the individuals which died in the understory, I observed that often they were uprooted by small mammals or chewed at the stem by generalist herbivores. High herbivory pressure in this species may be related by the relatively high nitrogen content in the leaves of *E. umbellata* in relation to the native species (Brym et al, *in review*). This would suggest that recruitment of *E. umbellata* is limited in a high light environment by moisture and a low light environment by herbivory. This transplant experiment shows that there is a complex combination of factors that will define the optimal conditions for recruitment of this species.

Forest Census

The analysis of adult individual's growth produced unexpected results. *Elaeagnus* showed a relatively high variation on growth rates with respect to the environmental variables tested, but

did not demonstrate as strong a response to the light environments estimated as a function of

neighbor's basal area as I had hypothesized [Figure 8]. My estimation of the light availability did

not seem to have a strong effect on *E. umbellata* growth. It is possible additional factors are also

affecting *E. umbellata* growth rates or that the description of the light environment used here is

not a good representation of the light reaching the plants. Instead, the model seemed to uncover a

biotic control on growth of *E. umbellata* due to small-scale biotic interactions [Figure 8]. I

expect this is due in part to the theoretical dynamics posited by Adams, Purves, & Pacala (2007),

where plant coexistence is in part determined by resource competition for localized space and

light determined by the height structure of a forest. Although *E. umbellata* has the ability to drive

down understory light conditions (Brantley & Young, 2010), most of the potentially competing

native species are able to shade out the invasive shrub once gaining a height advantage.

This is supported by the general absence of *E. umbellata* individuals in the neighborhood of

native individuals, which suggests that *E. umbellata* has not established in areas with limited

light or space and that where *E. umbellata* has established is not dominated by other native

species [Table 8]. This suggests the possibility that intraspecific competition is less than

interspecific competition, as we observe an aggregation of *E. umbellata* in open and gap habitats

because it is otherwise outcompeted by native species in understory habitats. It is interesting to

note that *E. umbellata* is most often present near *Quercus velutina* and *Amelanchier arborea*,

canopy and understory species respectively, noted for their persistence in xeric soils and less

closed canopies (Barnes and Wagner, 2004). Therefore, although the best-fit model incorporates

two biotic terms separated by scale, the model demonstrates that ultimately the proximity and

magnitude of native forest species limits the growth of *E. umbellata*. Through my interpretation of the parameters, I suggest that competition for light is acting at a large scale to the advantage of *E. umbellata*, but only when competition for space is not limiting its growth and spread.

Cognizant of the limitations of this model, we might still consider species coexistence in forests using predictions from the data. As each parameter of an empirical model interact to some degree, it is not likely that a single parameter of a model predicting relative growth rate will directly demonstrate mechanisms of species coexistence. In order to discuss some of the implications of the model for the overall effects of *E. umbellata* on the native tree species, I estimated growth of all analyzed species along a gradient of light ("Light Environment"), mimicking the transition of habitat type from open grassland to shaded forest understory. As I am considering the dynamics of an understory tree community, light is likely to be the driving factor of species coexistence (Kobe et al., 1995; Pacala et al., 1996; Finzi and Canham, 2000; Kobe, 2006).

Elaeagnus (red) is projected onto a gradient of light to confirm the high variation and limited effect of light [Figure 9] along with the native shade-intolerant tree (*Sassafras albidum*, orange) and the native shade-tolerant shrub (*Hamamelis virginiana*, green). The mean predicted relative growth rate is the solid line, with the 95% predicted intervals in dotted lines. The understory light values can be considered from 0-30% global site factor and open habitat >35%, with gap and edge habitat in between. We see that as light increases, so does the variation within the predicted relative growth rate, reflecting the lack of data at high light levels. However, species with similar

sample sizes did not show that much variability in their responses, indicating that such plasticity in growth rates is probably due to the nature of the species and not just being an artifact of the distribution of the data. Perhaps, variation in traits associated with photosynthetic capacity can be attributed to some of *E. umballata*'s success in persisting under various light environments.

Despite the high variation of predicted growth for *E. umbellata,* I observe a divergence in ecological strategy in relation to light availability between the two target native species [Figure 9]. *Sassafras* has characteristics of a shade-intolerant tree experiencing a steady increase in relative growth rate with increasing light, whereas *H.virginiana* shows a decreased predicted growth rate as light increases even within the range of light values represented in the data. This is unlikely due to a decreased growth rate with increasing light, but perhaps a reflection of some other limiting resource (soil type, water availability) for *H. viriginiana* that becomes poorer along a light gradient. In fact, I would expect the predicted growth rate for *H. virginiana* to be relatively lower than *E. umbellata* as light increases because of the increased competitive ability of shade-intolerant species, but not less than its predicted growth rate with lower light availability.

Considering the native species in relation to the invasive shrub, I argue *E. umbellata* has an increased competitive ability over *H. virginiana*, but not *S. albidum*. By this, I suggest that the invasive shrub has a higher potential to grow faster than the native shrub after a certain light threshold and therefore has the advantage for competition for space and light. I also consider similar dynamics for the entire plant community [Figure 10].
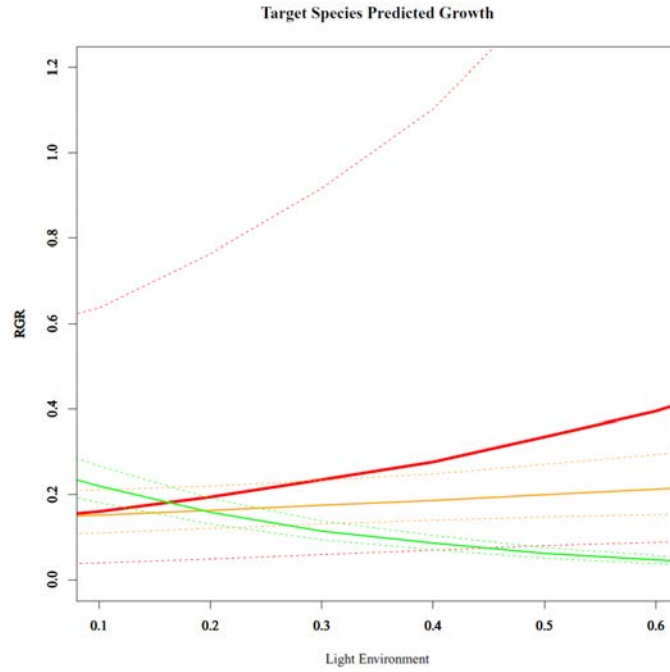
Target Species Predicted Growth

Figure 9: Predictions of relative growth rate over a gradient of light availability. Bold lines are the mean values with 95% credible interval shown in dotted lines. Red- *E. umbellata***, Orange –** *S. albidum***, Green –** *H. virginiana*
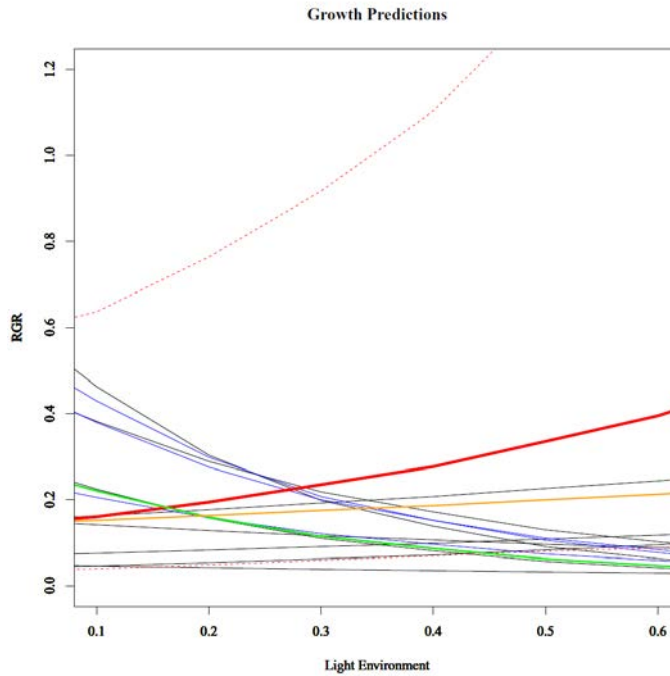
Growth Predictions

Figure 10: Predictions of mean relative growth rate over a gradient of light availability for the entire community. Red (dotted 95% predicted interval) and - *E. umbellata***, Orange –** *S. albidum***, Green –** *H. virginiana***, Blue – understory trees, Black – canopy trees.**

It is likely that various responses of relative growth rate to a gradient of light promote plant coexistence of this invaded understory (Koyhama, 1993). Considering the 95% predicted interval of *E. umbellata* growth rate, the invasive shrub may not experience a lower competitive ability than any of the native species, but it is likely that based on mean predicted growth rate, at least four understory and three canopy species experience a growth advantage at the low extreme of the light environment. It is possible that the low light levels will limit the growth and spread of the invasion in the understory. In a high light environment, *E. umbellata* has lower potential growth than at most four canopy species and a higher potential growth than all native understory species [Figure 10]. From understanding of the process of gap regeneration, I expect that canopy trees could have a long-term advantage over the invasive shrub in gap habitats, though these species are not observed to be in that high light environment and the growth predictions are extrapolations from the data. I suspect that increased propagule pressure of the invasive shrub permits it to be more prevalent in gap habitat, where it has a higher competitive ability than native understory species. However, ultimately, over large time scales native tree species would outcompete the shorter shrub for space as suggested earlier as a mechanism for forest coexistence (Grubb, 1977; Bazzaz, 1979; Adams, Purves, & Pacala, 2007).

Due to the controls shown in the model on *E. umbellata* by crowding and its relative advantage from growth in high light environments over native understory species, I posit that *E. umbellata* will coexist in this native understory community in relatively open habitats, gaps, or edges.

Elaeagnus appears to have some advantage of growth in early stages of development, evidenced by the inverse relationship of the effect of initial size on relative growth rate, which is a potential contributor to the plants success (Poorter, 2007). Some native understory species may be negatively impacted by the introduction of the invasive shrub, but I expect that the advantage that *E*. umbellata has growing at relatively high understory light levels will not be sufficient to drive native species out of the community.

Plant Functional Traits in Consideration of a Demographic Study

This thesis was motivated by work conducted during my undergraduate studies (Brym et al, *in review*). We considered the invasion of *E. umbellata* for a single hectare of the forest census data, where all species in the forest community were evaluated for plant functional traits. We observed morphological and chemical characteristics that describe trade-offs in the "Leaf Economic Spectrum" (Wright et al., 2004). We found that *E. umbellata* had a similarly high specific leaf area (SLA) to *S. albidum*, which is consistent with the general description of these two species as shade-intolerant (Kitajima, 1994; Westoby & Wright, 1999). However, *E. umbellata* had much higher leaf nitrogen content, an indirect measure of photosynthetic capacity, than the entire native understory community. Solely based on leaf morphological and chemical traits, we cited the empty niche hypothesis, positing that *E. umbellata* could have an increased competitive ability in open and gap habitat over shade-tolerant species, like *H. virginiana*, due to the higher relative growth rate in high light environments suggested by higher observed SLA and leaf nitrogen content. Following this conclusion, it was important to include a number of caveats

of using a traits-based approach and suggests confirmation of the method with demographic and environmental data.

This thesis research confirmed my hesitation to definitively claim *E. umbellata* would achieve some level of dominance in the forest understory from leaf functional traits. I was concerned that this theory did not consider the implication that a shade-intolerant species could outcompete a shade-tolerant species in a light limited environment, as introduced in the photosynthetic capacity scenario above. Although, the hypothesized relationships between leaf traits and community dynamics have been established for other communities (e.g., Kitajima, 1994; Westoby & Wright, 1999; Wright et al., 2004), demographic and natural history data, if available, are needed in order to yield definitive conclusions. In this system, it seems as though the empty niche hypothesis, in this case, will describe plant coexistence, but the notion of capitalizing on a high photosynthetic pathways without trade-offs with other biotic interactions is unfounded.

CONCLUSIONS

This study highlights the importance of considering the impacts of an invasive species in relation to the entire native community and utilizing demographic and environmental data to describe potential mechanisms of invasion. The initial hypothesis of this study, light limits the spread of *E. umbellata*, was not strongly supported by either the transplant experiment or the forest census

data. However, the study does support the idea that *E. umbellata* is out-competed in the understory by small-scale biotic interactions. Therefore, the characterization of *E. umbellata* as a shade-intolerant species is warranted, and some mechanisms are suggested from this study that limits the dominance of the invasive species in the forest understory.

The transplant experiment demonstrates that seedling recruitment is limited by moisture. It remains a possibility that herbivory, light availability, and dispersal restrict the movement of the invasive shrub to the deep understory. The forest census data suggests a strong negative effect on *E. umbellata* from the presence of native woody species, perhaps in relation to shading. The data does expose some increased competitive ability of the invasive species when compared to a native shade-tolerant shrub and native understory trees.

This study demonstrates that the range of *E. umbellata* is restricted within a forest understory habitat, confirming the edge habitat for optimal growth of the invasive shrub. Because of this conclusion, it would be most important to focus management on the woody encroachment of *E. umbellata* from edge habitat into threatened grasslands. New formed gaps may also pose an area of increased threat from *E. umbellata*. This study suggests that overall forest community dynamics may not be strongly affected by the inclusion of the invasive shrub, but some functional similar native species may be threatened by the invasion.

Some motion exists to incorporate *E. umbellata* into American agriculture for its increased lycopene content over a tomato and the ability to be intercropped and harvested mechanically

(Pashke, Dawson, & David, 1989; Black, Fordham, & Perkins Veazie, 2005). With the potential of the introduction of *E. umbellata* as a cash crop, much work remains to be done in order to sufficiently understand the ecology of this invasive species before the availability of its propagules significantly increases. With continued census of the E.S. George Reserve, it would be interesting to revisit the data to test the conclusions of this study. Also, understanding of the growth of *E. umbellata* between open habitats and the shaded understory would benefit from a tree ring analysis of yearly growth which could also serve to age the individuals in each of these habitats.

Although the extent of the invasion of *E. umbellata* is not as detrimental to understory woody plant populations as initially suggested, we must be diligent in recognizing the threat that this species poses to regeneration of gap habitats and grassland woody encroachment. Management is still necessary to limit the impacts this horticultural escape renders on native habitat.

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