

FACTORS AFFECTING THE
COMMUNITY INVASIBILITY OF TROPICAL DRY FORESTS
AND THE IMPLICATIONS FOR ECOLOGICAL RESTORATION

By

WESLEY RAY BROOKS

A Dissertation submitted to the
Graduate School-New Brunswick
Rutgers, The State University of New Jersey
in partial fulfillment of the requirements

for the degree of

Doctor of Philosophy

Graduate Program in Ecology & Evolution

written under the direction of

Dr. Rebecca C. Jordan

and approved by

New Brunswick, New Jersey

May 2013

ABSTRACT OF THE DISSERTATION

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Dissertation Director:

Rebecca C. Jordan

Biological invasions pose a serious threat to the provision of ecosystem goods and services, the conservation of rare species, and the natural capital of human economies. Understanding the factors that make communities more or less invulnerable is a particularly prominent and contentious area of ecological research today. In an age of rapid environmental change and constrained governmental budgets, the task of preserving natural areas, biodiversity, and ecosystem services as public resources is increasingly challenging. Yet, ecological restoration may provide the most efficient and cost-effective way to mitigate these challenges. While many comprehensive ecological restoration projects focus on exotic species control of particularly aggressive species, few restoration projects are informed by the results of invulnerability research.

I utilized both observational and experimental approaches to study invulnerability in tropical hardwood hammocks, a globally-imperiled tropical dry forest habitat that is also an excellent candidate community for restoration along its former range, including in metropolitan areas of South Florida. In Chapter 1, I surveyed the vascular flora of 13 tropical hardwood hammocks along the Miami Rock Ridge to determine which variables

best predicted observed patterns of exotic species richness at different spatial scales. In Chapter 2, using constructed mesocosms with tropical hardwood hammock woody seedlings, I measured the effects of species richness and plant density on community productivity. In Chapter 3, I tested the effects of native species richness, native plant density, and invader propagule pressure on tropical hardwood hammock seedling layer invasibility, and also explored whether there was a link between community productivity and invasibility. In Chapter 4, I introduce a new model of restoration designed to enhance local biodiversity levels within metropolitan areas while also improving prospects for regional biodiversity conservation, and apply this model to a tropical hardwood hammock restoration. In Chapter 5, I assessed the relative contributions of native outplantings and habitat management to changes in community composition and structure over time in a tropical hardwood hammock restoration. Finally, in Chapter 6, I gauged the effects of varying native species richness and density treatments of outplanted populations of tropical hardwood hammock species on exotic recruitment at this restoration site.

DEDICATION

To Mom, Dad, Kat, and Megan

Your love and support have guided, inspired, and enabled me to become the man I am today, and continues to serve as motivation to become the man I further aspire to be.

No words can describe how central you all are to my life and purpose,
but I promise to always try to convey my appreciation through all my actions
as a devoted son and husband.

ACKNOWLEDGEMENTS

First and foremost, I must acknowledge my advisor, Rebecca Jordan. Besides being a tireless advocate on my behalf, she is among the most insightful, thoughtful, and caring individuals I have ever known. I am proud to call her both a great mentor and a great friend. I would also like to thank the rest of my committee- Peter Morin, Julie Lockwood, Steven Handel, and Carol Horvitz- for their help in rounding this dissertation into form and providing many helpful suggestions along the course of my graduate career. Dave Howe has also been a major contributor to my success providing support and assistance and a sounding board for a wide variety of my scientific and nonscientific notions. Finally, Marsha Morin has been amazing and I am grateful for her kindness, advice, and tremendous resourcefulness in finding answers to all of my questions.

I am also thankful to the grad students who have passed through the Jordan and Lockwood labs during my tenure here at Rutgers who have been involved in the development and evaluation of my projects. I am especially grateful for the many wonderful friendships established during this period of my life, either through EcoGSA, the R*s, or through any other of the professional or extra-curricular activities in which I've been involved. These friendships and experiences were made possible, in part, by the relative financial security and support provided to me by The Graduate School- New Brunswick including graduate assistantships, teaching assistantships, the Bevier Fellowship, and Pre-dissertation, Fellowship, and Conference Travel awards. The professional staff of the Department of Ecology, Evolution, and Natural Resources and the Program in Science Learning helped manage all of these (sometimes overlapping) appointments. I am also thankful to the Graduate Program in Ecology & Evolution for

two Academic Excellence Fund Awards which contributed to this research. The Eagleton Institute of Politics also supported my non-Ecology interests and I would like to specifically acknowledge the wonderful assistance I received as a Governor's Executive Fellow from John Weingart, Pete McDonough, and Sarah Kozak. Additionally, I'd be remiss to not mention the strong support I received from Diana Martin and Barbara Bender while teaching General Biology labs.

I am also indebted to a long list of mentors from my undergraduate and secondary school years including Gary Dwyer, Susan Lozier, Stuart Pimm, and Jim Reynolds at Duke University, Brian Wuttke at Miami Killian Senior High, and Pam Wentworth at Glades Middle School. Additionally, I would like to thank my colleagues Betsy Kreakie, Jenn Possley, and Steve Woodmansee, who have been very supportive of my research in South Florida. I would also like to recognize the wonderful membership and employees of the Miami-Dade Chapter of the Florida Native Plant Society, the Key West Tropical Forest and Botanical Gardens, and Fairchild Tropical Gardens whom I have come to know over the years.

Finally, I wouldn't be where I am today without a long list of wonderful family and friends including my amazing wife Megan, Mom, Dad and Kat, Mema and Papa, Abuela, Abuelo and Margie, Brian, Jenny, and Landon, Nino, Nina, many amazing cousins, my goddaughter Stephanie, nieces and nephews Tyler, Maddie, Jack, and Eli, my new family in Michigan, Josh, Jeff, Eck, Egan, Zac, Matt, Christ, Alek and Ashley, Murph, Emily, and Mo, the best dog I could ever imagine sharing grad school with. Thank you all for your love, friendship, and support.

At the time of the publication of this dissertation the following chapters were in publication or review:

Brooks WR, JL Lockwood, & RC Jordan. 2013. Tropical paradox: a multi-scale analysis of the invasion paradox within Miami Rock Ridge tropical hardwood hammocks. *Biological Invasions* 15:921-930. (Chapter 1)

Brooks WR, & RC Jordan. *In review*. Species richness and plant density effects drive productivity in tropical dry forest seedling layers. Submitted to *Journal of Tropical Ecology*. (Chapter 2)

Brooks WR, & RC Jordan. 2013. Propagule pressure and native species richness drive invasibility in tropical dry forest seedling layers. *Perspectives in Plant Ecology, Evolution, and Systematics*. doi: 10.1016/j.ppees.2013.03.001 (Chapter 3)

Brooks WR, & RC Jordan. *In review*. A ‘novel natives’ model of restoration to enhance local, and conserve regional, biodiversity in metropolitan areas. Submitted to *Ecological Applications*. (Chapter 4)

Brooks WR, & RC Jordan. *In review*. Effects of habitat management and outplantings on restoration site community composition and structure. Submitted to *Restoration Ecology*. (Chapter 5)

Brooks WR, & RC Jordan. *In review*. Legacy effects dominate exotic recruitment patterns in a tropical dry forest restoration. Submitted to *Biological Invasions*. (Chapter 6)

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INTRODUCTION

Biological invasions pose a serious threat to precious ecosystem services, species biodiversity, and human economies (Mack et al. 2000; Pimentel et al. 2005). In the United States alone, major environmental and economic damages attributable to species invasions may reach nearly \$120 billion per year (Pimentel et al. 2005). Additionally, it is estimated that 49% of imperiled U.S. species are at risk because of competition with, or predation by, invasive species (Wilcove 1998). Increasing international economic integration means that floras and faunas are being exchanged intentionally and incidentally at greater rates each year (Lockwood et al. 2007). Species invasions, along with losses of native species as a result of anthropogenic disturbances, threaten the co-evolved relationships within biotic communities and the functioning of ecosystems- key factors to the provision of irreplaceable ecosystem goods and services for human use (Hooper et al. 2005; Loreau 2010).

The field of invasion ecology has largely centered on predicting what traits are particularly important for invasion success, and in following, what species will become invasive and under what circumstances (e.g., Ehrlich 1986; Williamson and Fitter 1996a, b). While lending some insights into the mechanisms of invasions and their impacts, this species-level focus has generally yielded only a diverse collection of case-studies which are relatively untenable for widespread predictive purposes (Orians 1986; Lodge 1993; Shao 2006). In response to this critique, a line of research has arisen in which site characteristics, be they abiotic or biotic factors, are studied for their potential to create windows in time and space for invasions (e.g., Orians 1986; Dethier and Hacker 2005;

Von Holle 2005). The concept of “invasibility” focuses on a community’s susceptibility to invasion by non-indigenous species (Ewel 1986).

The idea of site invasibility implies that every species has the potential to invade the right place at the right time depending on the biotic and abiotic characteristics that can serve to promote or hinder individual species invasions (Orians 1986; Simberloff 1986). Among these, physical habitat attributes have been shown to impact the success of invasions (e.g., Baker 1986; Byers 2002). Other factors like abiotic disturbance type, intensity, and frequency can also have consequences on the outcome of plant introductions and their potential spread and impacts on native communities (e.g., White and Jentsch 2004; Lockwood et al. 2007). Biotic factors such as the presence or absence of predators, dispersers, parasites, and disease, the density of competitors, and the availability of propagules at a site may all significantly affect the invasion potential of non-native introductions (e.g., Levine et al. 2004; Lockwood et al. 2007). Other community-level biotic properties including species richness and evenness have been surmised to play a role in the invasibility of a site, though they are believed to be more important in restricting abundance and spread than establishment per se (Levine et al. 2004; Lockwood et al. 2007). “Biotic resistance” remains one of the most prominent - and controversial - ideas in ecology today.

In “The Ecology of Invasions by Animals and Plants”, Elton (1958) first described the biotic resistance hypothesis. He noticed that roadsides and agricultural areas in Britain had higher numbers of weedy non-natives species than neighboring meadow communities. He attributed this difference to lower species richness in the invaded communities relative to the higher species richness of the un-invaded meadows.

He argued that introduced populations faced greater competition intensity in species-rich communities than species-poor communities and were, therefore, less likely to establish in richer communities. Since this idea was first proposed, various ecological studies have supported a negative relationship between species richness and invasibility (e.g., MacArthur 1970; May and MacArthur 1972; Moulton and Pimm 1983; Herbold and Moyle 1986; Case 1990; Case 1991; Law and Morton 1996; Tilman 1997; Stachowicz et al. 1999; Naeem et al. 2000; Hector et al. 2001; Kennedy et al. 2002; Fargione and Tilman 2005), while others contend that these community characteristics are actually positively-related (e.g., Robinson et al. 1995; Stohlgren et al. 1998; Stohlgren et al. 1999; Stohlgren et al. 2003; Howard et al. 2004). The role of community richness on invasibility remains a contentious focus of invasion ecology (e.g., Levine and D'Antonio 1999; Byers and Noonberg 2003; Bruno et al. 2005).

The conversion of natural habitats to human-dominated landscapes can result in much of the same negative ecological effects as species invasions (Moyle 1986; Lodge 1993; Stachowicz and Tilman 2005). Additionally, anthropogenic disturbance and species invasions can reinforce each other: habitat alterations and degradation can enhance the establishment and invasion success of non-native species while new species invasions can effectively shortcut the capacity of natural systems to regenerate or follow historical successional trajectories (e.g., Vitousek 1986; Randall et al. 1997; Simberloff and Von Holle 1999; Lockwood et al. 2007). Anthropogenically-disturbed communities often have lower native species richness, more non-native species, and reduced ecosystem function as compared to similar undisturbed communities (e.g., Ewel 1986; Moyle 1986; Smallwood 1994).

In fact, to improve ecosystem function and preserve biodiversity, most modern restoration efforts rely on invasive species management with a focus on control or eradication (Randall et al. 1997). However, especially in human-dominated landscapes, the removal of invasives does not often precipitate a community shift towards the structure and function of referential communities. This seems to indicate that biological invasions may be more likely to be the “passengers” of ecological change rather than the “drivers” (MacDougall and Turkington 2005). Given the potential link between community richness and invasibility (but see Hewitt and Huxel 2002), an effective restoration of community characteristics to species richness and evenness levels of reference sites via species reintroductions could significantly reduce the opportunities for invasions and their impacts on ecosystem functioning.

CHAPTER 1
TROPICAL PARADOX:
A MULTI-SCALE ANALYSIS OF THE INVASION PARADOX WITHIN
MIAMI ROCK RIDGE TROPICAL HARDWOOD HAMMOCKS

Abstract

The invasion paradox describes the scale dependence of native-exotic richness relationships (NERRs), where NERRs are negative at neighborhood scales and positive at landscape scales. However, a lack of tropical surveys and past failures to isolate potential confounding variables contribute to significant gaps in our understanding of the processes producing these patterns. We surveyed the vascular flora of 13 tropical hardwood hammocks for community characteristics (e.g., native and exotic species richness, vegetative cover) with a hierarchical sampling design. Using model selection, we determined which variables best predicted patterns of exotic species richness at each spatial scale of consideration. We found that native and exotic species richness were positively correlated at neighborhood scales, but negatively correlated at landscape scales. The latter result stands in stark opposition to the patterns published in the literature thus far. We found that natural disturbance history (as approximated by vegetative cover) was positively correlated with exotic species richness at intermediate and landscape scales only. Overall, hammock identity was the most important factor driving exotic species richness patterns at all spatial scales. Hammocks with highly-disturbed hydrologies, brought about by water management, had fewer native species and more exotic species than hammocks with more natural hydrological conditions. Our

results are among the first from examination of subtropical communities, and may support the hypothesis that tropical and subtropical communities are subject to more intense biotic interactions. However, given our unique sampling design, our results do not reject the hypothesis that environmental heterogeneity drives the relationship between native and exotic species richness patterns.

Key Words

Exotic; hierarchical modeling; model selection; species richness; vegetative communities

Introduction

It is well-known that native-exotic richness relationships (hereafter, NERRs) are scale-dependent, whereby the relationship is often negative at fine neighborhood scales and consistently positive at broad landscape scales (Herben et al. 2004; Fridley et al. 2007). A notable gap in the literature on NERRs is the lack of information from tropical communities (Fridley et al. 2007). A few analyses of exotic species richness were conducted at biogeographical scales comparing the number of established exotic species between tropical and temperate zones (Rejmanek 1996; Sax and Gaines 2005). These macro-scale results suggest a negative NERR, driven by an increase in native species and a decrease in exotic species relative to temperate regions (Fridley et al. 2007). To our knowledge, there are no published examples of subtropical NERRs that closely mimic the experimental and statistical designs of the numerous studies conducted in the temperate zone. Here, in our investigation of the patterns of naturalized exotic species richness across spatial scales within tropical hardwood hammocks of the Miami Rock Ridge in

South Florida, we submit one of the first examinations of NERRs conducted outside of temperate latitudes.

Fridley et al. (2007) outlined several factors that may address why tropical systems appear to be less invaded when compared to temperate ecosystems, and thus (when combined with greater native species richness) may contribute to the production of negative NERR patterns at large spatial scales. First, a general lack of human disturbance in intact tropical and subtropical habitats may limit the opportunities for non-native species to establish, especially relative to the often profound historical disturbances experienced within temperate ecosystems. Second, these regions generally have a relatively high incidence of weathered, nutrient-poor, and acidic soils. These soil types are generally associated with lower invasion rates. Third, the higher species richness typical of lower latitudinal communities relative to temperate communities could create more biotic interactions, and thereby limit the number of available niches for non-native species to occupy. Finally, the tropics and subtropics are relatively less connected to global sources of non-native species than are temperate zones and thus they receive less propagule and colonization pressure (*sensu* Lockwood et al. 2009).

Tropical hardwood hammocks are dense, evergreen, and naturally-discrete patches of tropical dry forest that occur on limestone outcrops characterized by limited development of endogenous shallow soils (Horvitz and Koop 2001; Armentano et al. 2003). These communities are mostly composed of West Indian and Neo-tropical plant species and feature a rich assemblage of ferns, orchids, and lianas (Tomlinson 2001). They are widespread in southern Florida, where they are vital to the conservation of nine federally-listed and 186 state-listed endangered plants and animals (USFWS 1999), but

can also be found throughout the Bahamian archipelago and Cuba (Tomlinson 2001; Gillespie 2006). Despite various conservation and management efforts, these communities suffer from a high invasion rate by a range of tropical ornamental and agricultural plants.

We explored how native and exotic species richness correlate across three distinct spatial scales within tropical hardwood hammocks. Our broadest scale is across a sampling of hammocks along the entire extent of the Miami Rock Ridge (landscape scale; approximately 60,000 ha in extent), our intermediate scale is across sampling transects within each of those hammocks, and our smallest scale is across 3 m x 5 m quadrats within those transects. At the quadrat and transect scales, we consider variables that reflect the disturbance history of each sampled site and the principle biotic interactions that are likely to pertain in this context. At the landscape scale we explicitly consider factors that are likely to influence potential differences in community composition and exotic richness across hammocks such as hammock area and surrounding human population density. Our sampling design is nested, which helps ensure that background environmental variables are relatively homogenous at the quadrat scale. However, our design moves from small (quadrats) to large (hammock) spatial extents and thus, the association between variables that likely co-vary with the richness of exotic and native species will tend to become stronger as the spatial distances between quadrats increase (e.g., Sandel and Corbin 2010).

Materials and Methods

We sampled thirteen tropical hardwood hammocks along the Miami Rock Ridge from North Miami to Long Pine Key, Everglades National Park (Figure 1). We conducted a floristic survey once at each hammock within an eight-month period spanning August 2007 to March 2008. We placed three 40 m transects within each hammock, where each transect included four evenly spaced 3 m x 5 m quadrats randomly set along each transect. Each transect start point was assigned by generating random pairs of latitudinal and longitudinal coordinates within the geographic extent of each hammock. Each transect was then assigned a randomly-generated geographic direction (0° – 359°) to run away from the start point. Prior to data collection, we used ArcGIS 9 and digital aerial photos (accessed as Digital Orthographic Quarter-Quads (LABINS 2007)) to ensure that each randomly-generated transect would (1) occur wholly within the hammock interior (i.e., no portion of the transect occurring within twenty meters of the hammock edge), and that (2) no two transects intersected. We used a Trimble GeoXM handheld GIS unit with sub-3 m accuracy to find each transect start point, and laid out transects with the aid of field tape and a compass. We used PVC pipe markers and rope to temporarily identify the boundaries of each quadrat during surveying.

Each quadrat was surveyed to provide insight into floristic community composition and structure. We identified and documented the occurrence of all plant species rooted in the quadrat, as well as those epiphytes occurring in the space above the quadrat. We utilized Wunderlin (1998), Nelson (2000), and Brown (2006) to identify plants. We estimated the vegetative cover of each quadrat categorically using Daubenmire cover classes (1: 0-5%, 2: 5-25%, 3: 25-50%, 4: 50-75%, 5: 75-95%, 6: 95-100%; see Elzinga et al. 1998) at ground (<1 m), subcanopy (1-4 m), and canopy (>4 m)

level heights above the forest floor. In forests, vegetative cover measurements provide insight into natural disturbance history. Woody plant density was recorded as the number of woody individuals greater than one meter in height. For each species rooted in the quadrat, we recorded woody basal area in cm^2 at breast height for all stems greater than 2.5 cm diameter-at-breast-height (DBH). To avoid boundary bias (see Elzinga et al. 1998) in our density and basal area metrics, in addition to those individuals completely within the plots, we counted all individuals occurring on the northernmost and easternmost boundaries of each quadrat (one 3 m side and one 5 m side), and omitted all individuals along the southernmost and westernmost boundaries.

Our goal was to compare the relationship between native and exotic species richness across three spatial scales, while controlling for confounding factors. Thus, we organized the data collected into three spatial categories: quadrat, transect, and hammock. The quadrat level is the smallest spatial scale we consider (15 m^2 per sampling unit; $N=156$). The transect level is intermediate in scale (60 m^2 per sampling unit), and was created by aggregating the information from the four quadrats embedded within each transect ($N=39$). Finally, we aggregate all information from each of the three transects within each hammock to generate the hammock-level dataset, our largest spatial scale under consideration (180 m^2 per sampling unit; $N=13$). .

We converted the canopy, subcanopy, and ground cover data from Daubenmire cover class values for each quadrat to the median percentiles from their representative ranges (i.e., 1= 2.5%, 2= 15%, 3= 37.5%, 4= 62.5%, 5= 85%, 6= 97.5%). This conversion formed quadrat-level canopy, subcanopy, and ground cover variables. We also created the following variable classes with the information from the floristic survey

data: native species richness, exotic species richness, and woody plant density and total basal area (both irrespective of native-exotic status). Our quadrat-level native and exotic species richness variables were taken directly from the species occurrence list of each quadrat. To produce our quadrat-level woody plant density and total basal area variables, we separately summed across all species the number of individuals greater than one meter in height, and the basal areas of all individuals greater than 2.5 cm DBH, respectively per quadrat.

All quadrat-level variables were tested for intercorrelation with a Pearson's correlation analysis in PASW Statistics GradPack 17.0.2 (2009). Canopy cover and subcanopy cover variables were highly correlated with an absolute value of the Pearson correlation coefficient greater than 0.80. As a result, we summed canopy and subcanopy cover values for each quadrat to yield a canopy-subcanopy cover variable that could range between 5% and 195%. We generated transect- and hammock-level canopy-subcanopy cover and ground cover variables by separately averaging the quadrat-level values of all nested quadrats for each transect and hammock, respectively. Transect- and hammock-level native species richness and exotic species richness were calculated from aggregated species occurrence lists of nested quadrats. Finally, we produced transect- and hammock-level woody plant density and total basal area by taking the sum of the density and basal area values of all nested quadrats within each transect and hammock, respectively. We tested for spatial autocorrelation of species richness values within our quadrat and transect levels, but found no evidence to support including spatial autocorrelation as a factor in our models (analyses not shown).

We also included hammock area and human population density as hammock-level variables for their potential to explain patterns of exotic species richness at large spatial scales. Hammock area was estimated using ArcGIS 9 and digital aerial photography (LABINS 2007), and recorded in m^2 . We recorded the human population density (persons mi^{-2} (persons 259 ha^{-1})) of the zip code for each hammock based on data from the 2000 US census.

Our models reflect the hierarchical nature of our dataset and explore the potential drivers of the patterns of exotic species richness at each spatial scale for which we had data. Thus, we set exotic species richness as our dependent variable in all models. Each of the quadrat, transect, and hammock levels have their own candidate set of models featuring all linear combinations of fixed effects including: (1) native species richness, woody plant density and basal area variables, (3) canopy-subcanopy cover and ground cover variables, (4) hammock area, and (5) human population density. Mature hammock communities have higher values of woody plant density and basal area. Hammocks with lower canopy-subcanopy cover and higher ground cover values suggest they have been impacted by more recent or intense natural disturbances than hammocks with higher canopy-subcanopy cover and lower ground cover values. Finally, we assume that hammocks in areas of higher human population density suffer from greater anthropogenic disturbance than those in areas of lower population density.

We designed our quadrat level global model as a three-level hierarchical model in which native species richness, woody plant density, basal area, canopy-subcanopy cover, and ground cover variables were first-level effects with quadrat data values, and hammock area and human population density variables were third-level effects with

hammock data values (Table 1). Additionally, we included a second-level random effect term for transect identity and a third-level random effect term for hammock identity in each quadrat model to account for the nested nature of the study design and dataset (Table 1). We designed our transect level global model as two-level hierarchical model in which native species richness, woody plant density, basal area, canopy-subcanopy cover, and ground cover variables were first-level effects with transect data values, and hammock area and human population density variables were second-level effects with hammock data values (Table 1). We included a second-level random effect term for hammock identity in each transect model to account for the nested nature of the study design and dataset (Table 1). In the same vein, we designed our hammock level global model as a one-level model with all fixed effect variables having hammock data values and no random effect terms (Table 1). Our approach to model construction yielded 127 models in the candidate set for model selection for each of our three scales of analysis.

We analyzed candidate sets of models in the Mixed Linear Models procedure in PASW Statistics GradPack 17.0.2 (2009). We generated AIC_c scores for each model and then ranked them in increasing order within each set. We considered models with $\Delta i < 2$ to have substantial support. Shared parameters in substantially supported models of the same candidate set were model-averaged. We calculated model weights and parameter effect sizes for these selected models. We used these methods separately to select and analyze the best-supported models from the candidate sets at each of the different spatial scales. By analyzing the supported models of naturalized exotic species richness at different scales using the same basic set of candidate models, we are able to directly

compare models within spatial scales while also indirectly comparing models between spatial scales.

Results

In all, we found 142 native species and 49 exotic species (see Appendix 1 for full list of species found). Table 2 presents mean, minimum, and maximum values for native and exotic species richness across spatial scales. Species accumulation data were compiled to ensure that our sampling was sufficient to capture variability in species richness across quadrats (see Appendix 2). Across the study area, most species were rare, and demonstrated clumped dispersion patterns. Of the natives, 92 species (64.8%) were found in 10 or fewer quadrats and only 12 species (8.5%) were found in more than 50 quadrats. Additionally, 49 native species (34.5%) were limited to only one of our surveyed hammocks while we noted only 30 native species (21.1%) occurring in more than six hammocks. *Ocotea coriacea* was the most commonly found native species, occurring in 133 quadrats (85.3%). *Bursera simaruba*, *Psychotria nervosa*, and *Quercus virginiana* were the most widely distributed natives; they were the only species that were found in each of our surveyed hammocks. Among the exotics, 42 species (85.7%) were found in 10 or fewer quadrats and only 2 species (4.1%) were found in more than 25 quadrats (*Oeceoclades maculata* in 44 quadrats, 28.2%; and *Schinus terebinthifolius* in 26 quadrats, 16.7%). Twenty-seven exotic species (55.1%) were found in only one of our surveyed hammocks while only *O. maculata* and *S. terebinthifolius* were found in more than five hammocks (10 each). Data for each hammock including hammock area, human

population density, species richness, cover, and other collected variables can be found in Appendix 3.

Our data only support the model with quadrat native species richness, transect identity, and hammock identity parameters as determinants of exotic species richness at the quadrat scale. The relative likelihood that this is the best model of the set considered was 64.3% (Table 3). This model explained 21.6% of the overall variation in exotic species richness (Table 3). Furthermore, we found that hammock identity explained the most variation in exotic species richness across quadrats with more than a 10x greater effect size than transect identity, and more than a 31x greater effect size than native species richness (Table 4). Nonetheless, our best model suggests that native species richness has a positive relationship with exotic species richness within quadrats (Figure 2(a)).

At our intermediate spatial scale two models were strongly supported by the data. Both models contain two parameters: transect canopy-subcanopy cover and hammock identity in one, and transect ground cover and hammock identity in the other. Together, the relative likelihood that one of these two models was the best of the set to predict transect exotic species richness was 51.0% (Table 3). The model featuring canopy-subcanopy cover had an R^2 value of 26.9% while the model featuring ground cover had an R^2 value of 24.6% (Table 3). In both models hammock identity has the greatest effect size; it is more than 140x more powerful in explaining variation in exotic species richness than canopy-subcanopy cover (Table 4). The calculated effect size of ground cover in the second-best model is inconsequential as its 95% Wald confidence interval overlaps zero

(Table 4). In the best model, transect canopy-subcanopy cover exhibits a negative correlation with exotic species richness.

Only the model that features native species richness and ground cover is strongly supported by our hammock-level dataset. The relative likelihood that this model is the best model of the set we considered was 55.2% (Table 3). This model, however, explains 63.8% of the overall variation in exotic species richness (Table 3). Additionally, we found that hammock native species richness is nearly 1.4x more powerful than hammock ground cover in explaining patterns of variation of exotic species richness at this spatial scale (Table 4). Native species richness is negatively (Figure 2(b)), while ground cover is positively, associated with exotic species richness (Table 4).

Discussion

Native-exotic richness relationships in Miami Rock Ridge tropical hardwood hammocks transition across spatial scales from being positive at the smallest scale to negative at the largest scale. Our results at the fine neighborhood scale, where nine hammocks featured positive relationships and four featured negative relationships, are in line with Fridley et al.'s (2007) assertion that fine scale NERRs are highly variable and not negative by rule. Meanwhile, our finding of a broad scale negative NERR is extraordinarily unusual relative to other previously published work (Herben et al. 2004; Fridley et al. 2007). We are aware of only one previous study of plant communities that has reported a negative NERR at broad landscape scales (in temperate oak savanna, Lilley and Vellend 2009); although there are several examples from some groups of temperate fauna (see Fridley et al. 2007). A previous meta-analysis of NERRs by Herben

et al. (2004) had concluded that no study with a mean sampling area greater than 30 m² reported a significant negative relationship for terrestrial plant communities.

At fine scales, our results may reflect the biotic acceptance hypothesis (Stohlgren et al. 2006; Fridley et al. 2007), and more particularly, the idea that some environments are ‘good sites’ that support more species (e.g., Brown and Peet 2003). Although these acceptance processes are most often invoked to explain positive NERRs at large scales, they can manifest at smaller scales in certain habitats (Fridley et al. 2007). Tropical hardwood hammocks have a complex and fine-scale mix of bare limestone, shallow organic soils, and thick leaf litter cover along the forest floor; improved plant germination, growth, and survival are more likely on bare soils as opposed to heavily leaf-littered soil or bare limestone. Thus, species richness of natives and exotics could be expected to correlate with the amount of optimal recruitment sites, and therefore produce a positive NERR at the local neighborhood scale. It should be noted, however, that merely the heterogeneity of substrate features could produce a positive NERR (Davies et al. 2005; but see Souza et al. 2011). In such a scenario, local sites with more substrate heterogeneity would hold more species of both native and exotic plant species of terrestrial, epiphytic, lithophytic, and saprophytic habits. Finally, another potential mechanism producing a positive NERR at fine scales in this system might be facilitation of exotics by native species (e.g., Bruno et al. 2003), perhaps involving the sharing of mycorrhizal networks (e.g., van der Heijden and Horton 2009).

At our broad landscape scale, hammocks that are rich in native species hold less exotic species than those with reduced native species. The most regularly invoked processes producing negative NERRs are biotic resistance and invasional meltdown

(Fridley et al. 2007). These processes, however, are unlikely to pertain here as our spatial grain at this scale is likely too large to capture true signatures of competition or facilitation. The possibility that our negative NERR is a statistical artifact of neutral processes (e.g., Fridley et al. 2004; Herben et al. 2004) is also unlikely given the large spatial scale in consideration. In addition, the number of individuals included in each of our sampling units is highly variable (hammock mean of 266 ± 95 , excluding all but >1 m tall woody plants) and greater than the relatively fixed and small (<200) communities of individuals proposed by Fridley et al. (2004) as being driven by neutral processes. Finally, these hammocks do not appear to be limited by the regional species pool; none of our sampling units turned up more than 10.5% of the total number of vascular plant species known from these communities in Miami-Dade County. Instead, we consider the possibility that our large-scale negative NERR is reflecting niche processes that are acting on native and exotic biodiversity in opposing ways. Differences in the community composition or the management or anthropogenic disturbance history of each hammock could represent a broad environmental gradient over which these niche processes are acting.

Hammock identity was consistently the most important parameter in all supported models and scales of analysis. We recognized that broad scale differences could influence our results, yet neither of the hammock-level factors we considered, hammock area and human population density, provided any explanatory power. Community composition patterns are also unlikely to correlate with patterns of exotic species richness, given the rare and patchy distribution of natives along our Miami Rock Ridge sites. However, the Central and South Florida Project of the 1950s and 1960s has created

a landscape-scale environmental gradient by impacting the natural hydrology of South Florida. In particular, the Miami Rock Ridge outside of Everglades National Park has experienced substantially lowered water tables as a result of the large system of canals and levees, as well as groundwater pumping for municipal usage (Gann et al. 2002). Congruent with these differences, we observed an average of about 37 native and 11 exotic species per hammock in those sites that have been relatively more affected by hydrological alterations as compared to an average of nearly 52 native and two exotic species for hammocks located in Everglades National Park. Exotic species appear to thrive in the hydrologically-disturbed hammocks at the expense of native species, though the exact mechanisms driving their exploitation of these hammocks remain unknown.

Effects of Natural Disturbances

Natural disturbance history also is a significant factor in predicting exotic species richness at intermediate and broad scales. Canopy-subcanopy cover is negatively correlated with exotic species richness, but only at intermediate scales. Our transect sampling is perhaps capturing the spatial dynamics of light gaps resulting from thunderstorm damage and tree mortality as a result of age and disease. It is likely that increases in light availability afforded by these gaps in an otherwise closed forest could result in increased opportunities for exotic establishment and spread.

Meanwhile at broad scales, the positive correlation between ground cover and exotic species richness is probably an historical effect of high intensity natural disturbances in this system (e.g., fire and hurricanes). Increased ground cover may remain for some time as a signature of these severe disturbance events in hammocks even

after the closure of the hammock canopy. Both fires and hurricanes release substantial nutrient loads and increase light availability over large, contiguous swaths of dry forest habitat (e.g., Dickinson et al. 2001; Van Bloem et al. 2005). This pulse of nutrients and light is likely to increase the amount of vegetative cover less than one meter in height in the form of mature tree basal resprouts, tropical lianas, and shade-intolerant herbaceous species (e.g., Horvitz and Koop 2001; Van Bloem et al. 2005). In particular, hammocks are known to be susceptible to invasion by exotic species following hurricanes (Horvitz and Koop 2001). Our ground cover levels are more likely to be the result of past hurricane disturbance than fire disturbance as none of our sampled sites have burned in the time since aerial photos became widely available for the region in the late 1930s.

Conclusions

Our striking finding of a broad scale, negative NERR in tropical hardwood hammocks along the Miami Rock Ridge may be the result of niche processes operating along an environmental gradient created by the anthropogenic disturbance of the natural hydrology of the Everglades. It should be noted, however, that the other systems prevalently used in previous examinations of NERRs (temperate forests and grasslands) - all of which reported positive NERRs at landscape scales - are also highly disturbed by human activities and, presumably, subject to similar niche processes. Clearly then, the manifestation of niche processes as a result of anthropogenic disturbance alone are not enough to determine the nature of the relationship between native and exotic richness.

As best as we can discern, our study differed from previous studies in two main ways. First, our study was carefully limited to within a single vegetative community.

Most other studies were limited only within a particular regional biome (e.g., the North American Great Plains). In these studies, the most common explanation for the broad-scale positive NERRs of other studies is environmental heterogeneity. If environmental heterogeneity is the driver of this pattern, then our negative NERR at broad-scales may be expected given the focus of our sampling to a single vegetative community. However, there is a chance that analyses of specific habitats may show negative NERRs at larger spatial scales because of more-tightly knit species interactions on the whole throughout these communities and the exclusion of ecotonal boundaries where weakened or transient species interactions may allow relatively greater exotic richness. In fact, Lilley and Vellend's (2009) finding of a negative NERR at their largest spatial scale (the only other study to show this result among plants), was reported from a study that was also limited to a single vegetative community (temperate oak savanna).

Second, our study is among the first reported from non-temperate systems. The wide variation in floristic composition between hammocks generally (e.g., Gillespie 2006; Reardon and Brooks 2009), and the rare distributions of native species in our surveys given our quadrat size and sampling scheme, appear to be consistent with reported diversity patterns in other tropical forests (e.g., Hubbell 1979). However, few of the factors limiting invasibility in tropical systems listed by Fridley et al. (2007) appear consistent as potential explanations for our results of a negative NERR. Tropical hardwood hammocks are impacted strongly by human disturbances; they have rich organic and mildly alkaline soils; and they certainly are exposed to a large supply of non-native propagules. The only explanation that may fit is that individuals in these communities may be intensely linked via biotic interactions to an extent not seen in

temperate communities. Additional testing of NERRs in tropical and subtropical regions, and both within and across individual communities, are necessary to confirm whether these methodological factors are underlying the differential outcomes between our study and others.

Acknowledgements

We are extremely grateful to M. Anderson Brooks, A. Brooks, L. Brooks, J. Fernandez, D. Howe, J. Klein, C. Rodriguez, J. Sadle, S. Thompson, J. Trimble, and S. Woodmansee for their contributions. We also thank C. Horvitz and P. Morin, as well as D. Simberloff, L. Wolfe, and four anonymous reviewers, for their thoughtful comments of earlier versions of the manuscript. Funding sources for this project were provided by a Pre-Dissertation Award from The Graduate School- New Brunswick and an Academic Excellence Fund Award from the Graduate Program in Ecology and Evolution at Rutgers University, as well as graduate support from USDA NRI 05-2221. Access and permits for field work were secured from the City of Miami Department of Parks and Recreation, Miami-Dade County Department of Parks and Recreation Natural Areas Management Division, Miami-Dade County Department of Environmental Resource Management, and Everglades National Park.

Table 1. Global models for quadrat, transect, and hammock levels of analysis including hierarchical model structure. Variables include native species richness (NSR), woody plant density (DEN), basal area (BA), canopy-subcanopy cover (CSC), ground cover (GC), hammock area (HA), human population density (HPD), random effect of transect (α), and random effect of hammock (β). The subscripts define the spatial scale of the data coded by the variable in question: quadrat (q), transect (t), and hammock (h).

Level of Analysis	First level effects	Second level effects	Third level effects
Quadrat	$NSR_q + DEN_q + BA_q + CSC_q + GC_q$	α	$HA_h + HPD_h + \beta$
Transect	$NSR_t + DEN_t + BA_t + CSC_t + GC_t$	$HA_h + HPD_h + \beta$	-
Hammock	$NSR_h + DEN_h + BA_h + CSC_h + GC_h$ $+ HA_h + HPD_h$	-	-

Table 2. Species richness data for quadrat, transect, and hammock levels.

	Quadrat			Transect			Hammock		
	Mean \pm SD	Min	Max	Mean \pm SD	Min	Max	Mean \pm SD	Min	Max
Native	14.0 \pm 6.0	3	28	25.6 \pm 8.0	11	43	41.5 \pm 11.0	25	61
Exotic	2.0 \pm 1.0	0	8	4.3 \pm 3.2	0	13	8.2 \pm 5.7	1	18

Table 3. Strongly supported models ($\Delta_i < 2$) for quadrat, transect, and hammock levels.

Δ_i is a relative measure of each model based on the “best model” (the model with the lowest AIC score) and w_i is the model weight, representing the probability that each model, *is in actuality*, the best model of the candidate set. We also include the percent of variation captured by each model. Variables include exotic species richness (*ESR*), native species richness (*NSR*), canopy-subcanopy cover (*CSC*), ground cover (*GC*), random effect of transect (α), and random effect of hammock (β). The subscripts define the spatial scale of the data coded by the variable in question: quadrat (*q*), transect (*t*), and hammock (*h*).

Dataset Level	Model	Δ_i	w_i	R^2
Quadrat	$ESR_q = NSR_q + \alpha + \beta$	0	0.6430	0.216
Transect	$ESR_t = CSC_t + \beta$	0	0.3695	0.269
	$ESR_t = GC_t + \beta$	1.938	0.1402	0.246
Hammock	$ESR_h = NSR_h + GC_h$	0	0.5515	0.638

Table 4. Parameter effect sizes of substantially supported models. Fixed effect parameters are designated with an asterisk (*), while random effect parameters are designated with a cross($^+$). Model parameters include hammock identity (β), transect identity (α), quadrat native species richness (NSR_q), transect ground cover (GC_t), transect canopy-subcanopy cover (CSC_t), hammock native species richness (NSR_h), and hammock ground cover (GC_h).

Dataset Level	Model Parameter	Estimate	95% Wald Confidence Interval	
			Lower Bound	Upper Bound
Quadrat	$^+ \beta$	1.6623	0.6562	4.2112
	$^+ \alpha$	0.1563	0.0399	0.6118
	* NSR_q	0.0530	0.0049	0.1011
Transect	$^+ \beta$	5.747	2.2539	14.6556
	* GC_t	0.0436	-0.0121	0.0994
	* CSC_t	-0.0409	-0.0767	-0.0052
Hammock	* NSR_h	-0.3114	-0.5302	-0.0926
	* GC_h	0.2253	0.0540	0.3967

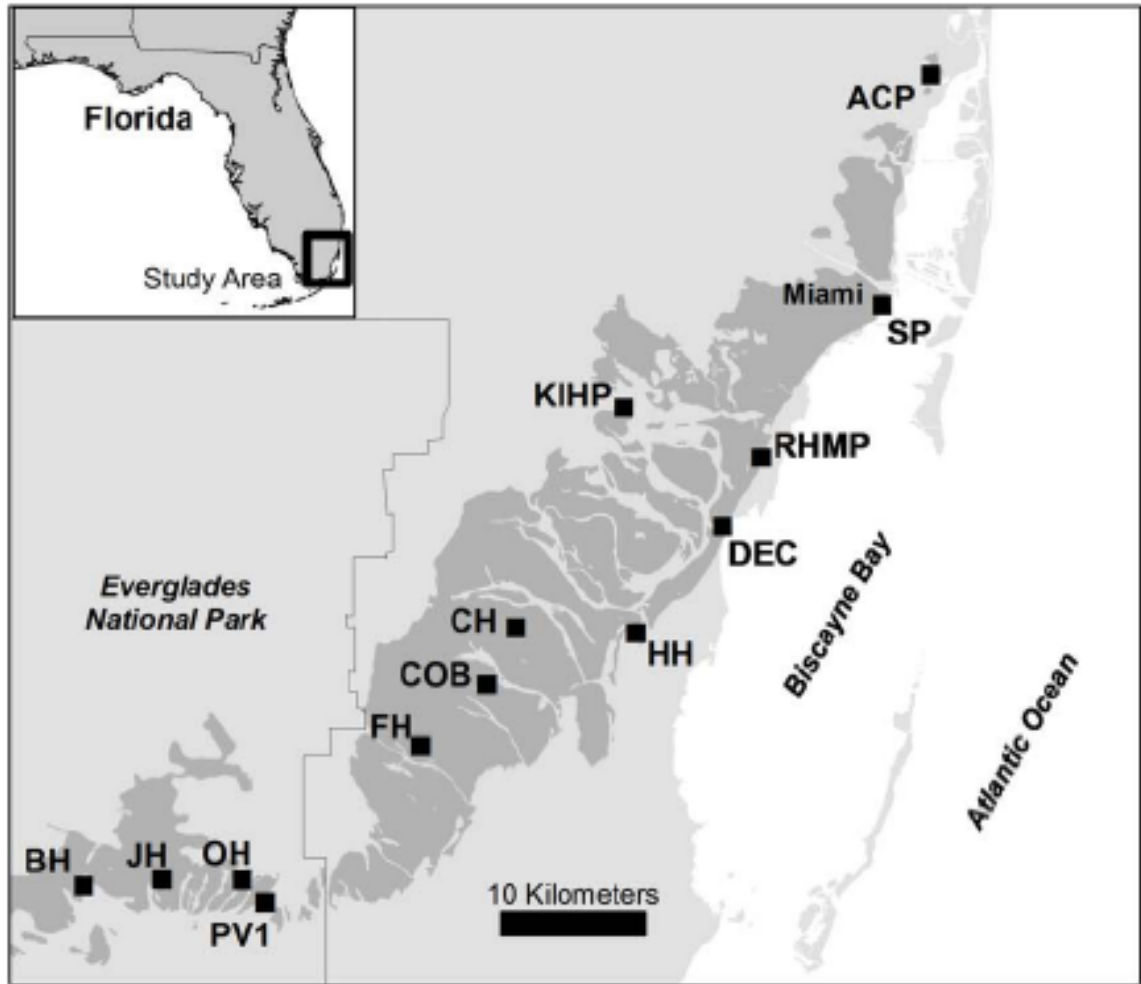


Figure 1. Map of hammock sites along Miami Rock Ridge (symbolized in dark gray) in study region. The boundary of Everglades National Park is indicated by the solid line. Hammock sites were Arch Creek Park (ACP), Bequaert Hammock (BH), Camp Owaissa Bauer (COB), Castellow Hammock (CH), Deering Estate at Cutler (DEC), Fuchs Hammock (FH), Harden Hammock (HH), Junk Hammock (JH), Kendall Indian Hammocks Park (KIHP), Osteen Hammock (OH), Palma Vista #1 (PV1), R. Hardy Matheson Preserve (RHMP), and Simpson Park (SP).

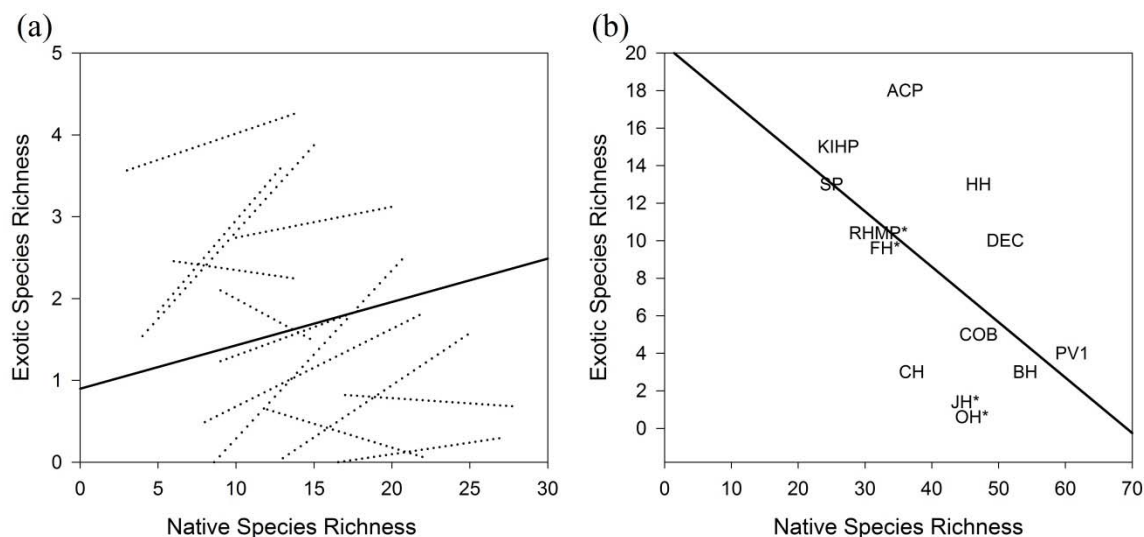


Figure 2. Native-exotic richness relationships in tropical hardwood hammocks at varying spatial scales. (a) Fine scale NERR across all quadrats (indicated by solid line). Dotted lines indicate NERRs of individual hammocks (using quadrat data). (b) Broad scale NERR across hammocks (indicated by solid line). Hammock sites were Arch Creek Park (ACP), Bequaert Hammock (BH), Camp Owaissa Bauer (COB), Castellow Hammock (CH), Deering Estate at Cutler (DEC), Fuchs Hammock (FH), Harden Hammock (HH), Junk Hammock (JH), Kendall Indian Hammocks Park (KIHP), Osteen Hammock (OH), Palma Vista #1 (PV1), R. Hardy Matheson Preserve (RHMP), and Simpson Park (SP). Hammock symbols marked with an asterisk (*) were offset slightly in graphical space to improve legibility.

CHAPTER 2

SPECIES RICHNESS AND PLANT DENSITY EFFECTS DRIVE PRODUCTIVITY IN TROPICAL DRY FOREST SEEDLING LAYERS

Abstract

The mechanisms controlling community productivity are poorly understood, especially in tropical forest systems. Woody seedlings, including 12 natives and *Ardisia elliptica*, a noxious invader, were grown in greenhouse mesocosms to mimic naturally-occurring seedling communities from tropical hardwood hammocks in South Florida's Everglades National Park. Biomass production by native seedling communities was assessed across different species richness, seedling density, and invader propagule pressure treatments. Species identity governed native monoculture productivity while an interaction between species richness and seedling density largely determined native polyculture productivity. Our model invader, *Ardisia elliptica*, had no significant impact on native biomass production. Most polycultures overyielded with facilitation via trait-independent complementarity effects being primarily responsible for this result; however, differing levels of species richness did not impact the magnitude of these effects. Instead, dominance effects demonstrated a positive relationship with species richness. Thus, the effects of facilitation on productivity may saturate at relatively low levels of species richness while sampling effects are primarily responsible for the differences in productivity among high vs. low diversity communities. These findings underscore the importance for conservation and restoration practitioners to encourage diverse and dense

native seedling layers to improve both productivity and resilience in the face of natural and anthropogenic disturbances.

Key Words

biodiversity effects; diversity-productivity relationship; mesocosm; monoculture; polyculture; seedling; South Florida; tropical dry forest; tropical hardwood hammock

Introduction

Primary productivity is an important component of ecosystem functioning, playing a considerable role in the delivery of many ecosystem services (Balvanera et al. 2006; Loreau 2010). Both species richness and plant density have been studied with regards to their role on plant community productivity. Several experiments have suggested that plant species richness is positively correlated with productivity (e.g., Marquard et al. 2009; Morin et al. 2011; van Ruijven and Berendse 2009; but see Fridley 2001; Huston et al. 2000). Yet, there remains a contentious debate regarding the predominant factor undergirding this positive diversity-productivity relationship: a direct effect of species richness (i.e., complementarity), or a sampling effect (i.e., dominance) (see Hooper et al. 2005; Wardle et al. 2000). Loreau and Hector (2001) proposed an “additive partition of biodiversity effects” that attempted to separate the relative contributions of the direct effects of species richness from those of sampling biases to community productivity. Fox (2005) refined this approach with his “tripartite partition”, allowing for enhanced interpretation of the potential underlying mechanisms contributing to observed changes in productivity. Along with species richness, plant density is also

receiving increasing attention within ecology (after decades of recognition in agricultural research) for its potential effects on community productivity (e.g., Polley et al. 2003; Stachová et al. *in press*).

Our understanding of the role of community properties such as diversity on primary productivity arises from studies mostly conducted with herbaceous species, either in artificial conditions or in grasslands (e.g., Balvanera et al. 2006; Mulder et al. 2001). A common criticism of these studies is that the effects on primary productivity revealed in these experiments may be specific to the system, or the plant life forms or species utilized. With regards to tropical forests, there is equivocal evidence, based on a small amount of data, to support diversity-productivity relationships (Cardinale et al. 2011). This is likely, in part, because of the large and long-lived nature of tropical woody species; studies that have addressed the impact of species richness on productivity in forests have typically done so by estimating biomass via modeling (e.g., Morin et al. 2011; Ruiz-Jaen and Potvin 2010).

Here, we work with tropical dry forest woody seedlings in an effort to broaden the contexts in which the mechanisms controlling productivity are studied. We focus on woody seedling communities to reduce research costs in terms of time and harvest effort in the collection of data derived from physical biomass. While not equivalent to studying mature forest systems directly, understanding productivity in the woody seedling layers of forests may still yield important insights into forest ecology, as survival and growth in this life-stage is determinative to the eventual structure and function of the mature forest communities that follow.

Tropical hardwood hammocks are natural, discrete “islands” of tropical dry forest habitat that occur on limestone outcrops throughout South Florida with analogs in the Bahamas and Cuba (Armentano et al. 2003; Gillespie 2006; Tomlinson 2001). These communities feature a rich assemblage of plants including ferns, orchids, lianas, and ~135 woody species, most with Caribbean affinities (Tomlinson 2001). Given the non-homogeneous nature of species richness and woody species occurrences throughout different hammocks in South Florida (Armentano et al. 2003; Brooks et al. 2013), these communities could serve as ideal models for testing the effects of diversity on ecosystem functioning.

In this manuscript, we explore the roles of native species richness, native plant density, and invader propagule pressure on native community primary productivity in artificially-assembled communities of 12 native woody tropical hardwood hammock seedlings from South Florida. These experimental mesocosm communities were used as part of an overarching study to explore how these factors simultaneously affect community productivity and invasibility (see Brooks and Jordan 2013, for our invasibility analysis). To serve as the model invader for this project, we chose a particularly noxious, and understudied species, *Ardisia elliptica*. *Ardisia elliptica* is a large shrub or small tree from Southeast Asia, and forms dense and extensive monocultures along these forests’ edges and understories (Langeland and Craddock Burks 1998). Specifically, we tested the notion that higher levels of native species richness and seedling density would contribute to increased productivity. Additionally, given *A. elliptica*’s assumed superior competitive abilities (see Horvitz et al. 1998) and the propensity of exotic species to

suppress native biomass (e.g., Maron and Marler 2008) we hypothesized that the addition of *A. elliptica* propagules would negatively affect native biomass production.

Methods

Seedling Cultivation and Mesocosm Construction

To ensure applicability to natural systems, we specifically selected the 12 native species and one invasive species used in this experiment to ensure that our mesocosm communities were likely to occur as real assemblages in nature given their (1) shared fruiting phenology and (2) documented presence in tropical hardwood hammocks of Everglades National Park (see Table 1 for species information). We collected seed from each native species on private lands with owner permission in Miami-Dade County, and from plantings along a major public transportation corridor in Monroe County, FL. All species are identified in this text as described in Wunderlin (1998). Fruit from *Ardisia elliptica* propagules was collected from Kendall Indian Hammocks Park in Miami-Dade County.

All germination, cultivation, and experimentation occurred in two adjoining bays in the Rutgers University Floriculture Greenhouse under a 50-percent shade cloth suspended near the ceiling. The facilities were temperature-controlled with a minimum of 20°C at night and maximum of 30°C during the day. Native seeds were planted in seedling liner plugs filled with Pro-Mix 'BX' + Mycorise Pro (Premier Tech Horticulture, Quakertown, PA), a general purpose, peat-based growing medium that is pH-adjusted with crushed limestone and inoculated with mycorrhizae.

All mesocosm communities were planted in plastic ‘half-flat’ trays, measuring 25.8cm wide and long by 6cm deep. This size was selected such that field-verified seedling densities could be utilized in each without major edge effects. Each half-flat was filled with Premier Pro-Mix ‘PGX’ (Premier Tech Horticulture, Quakertown, PA), a peat-based growing medium that is pH-adjusted with crushed limestone and designed for high-density growing applications. These conditions approximately replicate recruitment conditions and soil depth within the natural range for seedlings in tropical hardwood hammocks (Olmsted et al. 1990; W. R. Brooks, *pers. obs.*). Mesocosm soils were watered evenly every other day for the duration of the study. To avoid any potential microclimate or location effects, all mesocosms were randomly shuffled within the greenhouse bays each week. No fertilizer or soil amendments were added at any point during the study. Finally, three separate treatments of Neem Oil were applied evenly on all mesocosms over the course of our study as part of the Floriculture Greenhouse’s routine insect control efforts.

Experimental Design

We planted two types of mesocosms to assess the role of species richness and seedling density on community productivity: monocultures and polycultures. Monoculture mesocosms were planted to establish a baseline for species growth rates. Monoculture mesocosms consisted of plantings of six conspecific native seedlings. Eighteen monoculture mesocosms were planted for each of the 12 native species utilized in this experiment for a total of 216 mesocosms.

Polyculture mesocosms, meanwhile, were planted to assess the effects of species richness and seedling density on community productivity. Polyculture mesocosms were constructed based on a fully-crossed design of two levels of species richness (2, 5) and two levels of native seedling density (6, 12) with 36 replicates of each treatment. Because of our focus on the seedling community rather than individual species, the species composition and seedling abundances of these 144 mesocosms were randomized within the particular species richness and native seedling density treatment limits set for each mesocosm (see Appendix 4). For each mesocosm, we a priori assigned a specific ID number and randomized spatial configuration of each seedling community. The spatial configuration of each mesocosm was mapped to keep track of growth and mortality of individual seedlings (Figure 1). After planting, we allowed these communities to “grow in” for an initial 30 day period before the 180 day experimental period (a total of 210 days).

We then divided the mesocosms from each of our monoculture species blocks (3 subgroups of 6 replicates of each species) and polyculture species richness and seedling density treatments (3 subgroups of 12 replicates for each polyculture treatment) equally. Each subgroup of monoculture and polyculture mesocosms was treated with one of three *A. elliptica* propagule pressure treatments (zero, low, high). The ‘zero’ propagule pressure treatments simply consisted of native seedlings; no *A. elliptica* seeds were added to these mesocosms. Meanwhile, ‘low’ propagule pressure treatment mesocosms received a total of six *A. elliptica* seeds over the course of two introduction events (three seeds each on Day 31 and Day 121) added to their respective native seedling communities. Finally, ‘high’ propagule pressure treatment mesocosms received a total of

16 seeds over the course of 4 introduction events (four seeds each on Days 31, 61, 91, and 121), added to their respective native seedling communities. We sowed all *A. elliptica* seeds at a depth of 1cm and covered lightly with growing medium.

Data Collection

After 210 days, all experiments were terminated. Each mesocosm was matched according to its mesocosm map so that all native and invasive individuals could be identified, and at this time, we recorded any native seedling mortalities. To record above-ground biomass of native seedlings, we clipped individuals at the soil surface, including any remaining above-ground biomass from deceased individuals. Individual root systems of native seedlings were unable to be separated, thus, we alternately soaked and rinsed the whole soil and root mass from each mesocosm to remove as much substrate as possible without damaging roots. All samples were placed in a drying oven on site to dry for seven days at 70.5°C. Once removed from the drying oven, we immediately weighed samples and recorded the mass in grams.

We also calculated biodiversity effects for each low-density polyculture mesocosm as proposed by Fox (2005). Fox's partition retains Loreau and Hector's (2001) "complementarity effects" (as "trait-independent complementarity effects" (TICE)) but divides their "selection effects" into "dominance effects" (DE) and "trait-dependent complementarity effects" (TDCE). TICE captures changes in the average relative yield of species within a mixture, and are usually attributable to resource-partitioning or facilitation when positive, and inhibition when negative (Fox 2005; Loreau and Hector 2001). DE and TDCE, on the other hand, measure the extent to which species' specific

traits affect their productivity in a way that either impacts or has no impact, respectively, on the biomass production of species with different traits. We used native seedling above-ground biomass values in place of native total biomass because we could not effectively separate root systems of individual seedlings. Additionally, monoculture yield (M_i) values used in the calculation of these biodiversity effects were defined as the mean plot above-ground biomass of each species' *A. elliptica* propagule pressure 'zero'-level treatments; thus excluding any potential effects of *A. elliptica* on our reference values. Because each biodiversity effect calculation includes species-specific abundances or densities from within the community of interest, our randomized composition and abundance design does not affect our analyses.

Statistical Analyses

All statistical analyses were performed using PASW Statistics GradPack 17.0.2 (2009). Plot native above-ground biomass and below-ground biomass were highly-correlated both in monoculture and polyculture mesocosms ($\rho=0.891$ and $\rho=0.789$, respectively); therefore, we summed these measures of productivity into 'Total Native Biomass' for each mesocosm in both monoculture and polyculture analyses. To determine if there were differences in monoculture community productivity as a result of species effects or the addition of *A. elliptica* propagules we ran a GLM ANOVA with 'Total Native Biomass' as the response variable, and 'Propagule Pressure' and 'Species' as fully-fixed and fully-crossed factors using our monoculture dataset. Additionally, simultaneous Tukey's HSD tests were conducted to highlight any significant group differences within significant model effects. To test for differences in community

productivity in the polyculture mesocosms, we again ran a GLM ANOVA with ‘Total Native Biomass’ as the response variable, but with ‘Propagule Pressure’, ‘Native Seedling Density’, and ‘Native Species Richness’ as fully-fixed and fully-crossed factors using our polyculture dataset. Tukey’s HSD tests were conducted simultaneously to highlight any significant group differences within significant effects.

To test for differences in biodiversity effects, we ran a GLM MANOVA with ‘TICE’, ‘DE’, and ‘TDCE’ as the response variables, and ‘Native Species Richness’ as the independent variable among the low-density polycultures only. Finally, we also separately correlated the presence-absence and seedling density of individual species within plots to the ‘TICE’, ‘DE’, and ‘TDCE’ values derived from low-density polycultures to determine if particular species may have had a role in impacting productivity through particular biodiversity effects.

Results

In monoculture mesocosms, native biomass production was only significantly affected by native species identity (see Appendix 5). Mean productivity ranged widely between species from 4.25g per mesocosm plot for *Sideroxylon salicifolium* monocultures to 90.52g per mesocosm plot for *Ficus aurea* monocultures (Figure 2). In polyculture mesocosms, the interaction between native species richness and native seedling density determined native biomass production (see Appendix 6). The significance of this interaction effect was driven by the difference in mean productivity between low species richness mesocosms with six native seedlings (71.96g per plot) and those with 12 native seedlings (93.49g per plot)(Figure 3). Mean productivity between

high species richness mesocosms with native seedling densities of six and 12 (81.05g and 84.02g per plot, respectively) did not differ significantly from each other or the low species richness mesocosms (Figure 3). Finally, the addition of *A. elliptica* propagules (seeds) and their resultant germination and growth did not measurably impact monoculture or polyculture native biomass production (see Appendix 5 and Appendix 6).

In general, the productivity of seedling communities grown in low-density polycultures was greater than expected based on monoculture yields; 69 of 72 (95.8%) mesocosms overyielded (were more productive than predicted given the monoculture yields of their component species), and 37 of these (53.6%) did so transgressively (were more productive than the most productive monoculture among their component species). The presence of the legume species *Lysiloma latisiliquum* and/or *Piscidia piscipula*, however, was not associated with overyielding ($\chi^2_{(df=1, N=72)} = 0.971$, $p = 0.324$, for transgressive overyielding only; $\chi^2_{(df=1, N=72)} = 0.712$, $P = 0.399$, for transgressive and non-transgressive overyielding).

Biodiversity effects were significantly affected by native species richness in low-density polyculture mesocosms; however, this result was likely driven by a significant effect of native species richness on dominance effects (DE) only (see Appendix 7). Mean net biodiversity effects increased with the addition of native species in low-density polycultures from +17.58g per plot in mesocosms with two native species to +25.21g per plot in mesocosms with five native species (Figure 4). Meanwhile, mean DE increased by 114% when species richness increased from two native species (+4.13g per plot) to five native species (+8.82g per plot) in low-density polycultures (Figure 4). Nonetheless, trait-independent complementarity effects (TICE) and trait-dependent complementarity

effects (TDCE) were the largest and smallest determinants of productivity in these polycultures despite species richness levels, respectively (Figure 4).

We also found several significant correlations when assessing the relationships between individual biodiversity effects and the species represented within plots across our low-density polycultures (see Appendix 8). Most notably, *Citharexylum spinosum* seedling density was weakly negatively correlated and *F. aurea* presence/absence was weakly positively correlated with TICE (Appendix 8). *Ficus aurea* presence/absence and *Ocotea coriacea* presence/absence and seedling density were moderately positively correlated with mesocosm DE, while *Ilex krugiana* and *Zanthoxylum fagara* presence/absence were weakly positively correlated with mesocosm DE (Appendix 8). *Sideroxylon salicifolium* was negatively correlated, in terms of both presence/absence and seedling density, with mesocosm DE (Appendix 8). Additionally, *S. salicifolium* seedling density was negatively correlated with TDCE (Appendix 8).

Discussion

This research effort represents one of the first attempts to elucidate the mechanisms driving species richness and plant density effects among tropical dry forest communities of woody seedlings. We found that higher levels of native species richness and seedling density resulted in increased productivity of seedling communities, but found no evidence to suggest that the invasive shrub *Ardisia elliptica* had any impact on native biomass production even at relatively high introduction rates. Our polyculture results suggest that there is a significant interaction effect between native species richness and native seedling density that results in a strong increase in productivity at low species

richness levels and a negligible increase in productivity at high species richness levels with increasing seedling density.

We found evidence of substantial transgressive overyielding in our polyculture mesocosms, mostly as a result of strong trait-independent complementarity. Despite the importance of complementarity to the rates of overyielding we found in polycultures, further increases in species richness above two species did not significantly increase productivity through trait-independent complementarity effects, but instead were mainly as a result of increasing dominance effects. Taken together, this suggests that trait-independent complementarity effects may become saturated at extremely low levels of species richness (e.g., Roscher et al. 2007), and that dominance effects may become more important with increasing diversity. Thus, the effect of diversity on productivity is controlled by both complementarity and dominance simultaneously (Cardinale et al. 2011; Ruiz-Jaen and Potvin 2010). Given that complementarity and the relationship between biodiversity and productivity generally increase over time (e.g., Cardinale et al. 2011; Cardinale et al. 2007; Fargione et al. 2007), our results are likely somewhat conservative and would likely be strengthened had we further extended the relatively short duration of the experiment.

Overall, our findings regarding the positive relationship between diversity and productivity, in particular, are similar in nature to those reported for temperate herbaceous grassland communities using actual biomass (e.g., Fargione et al. 2007; Spehn et al. 2005; Tilman et al. 2001), and those reported for mature forests using models (e.g., Morin et al. 2011 (temperate); Ruiz-Jaen and Potvin 2010 (tropical)). With additional study in other untested systems and with different plant life forms and species,

the effects of species richness and plant density on primary productivity may prove to be highly generalizable across contexts.

Community Productivity

As stated above, we detected considerable overyielding and a high rate of transgressive overyielding within these polyculture mesocosms. Transgressive overyielding occurs when a mixture exceeds the production of its most productive component monoculture (Fridley 2001; Garnier et al. 1997), and has been found infrequently in similar studies (Cardinale et al. 2007; Cardinale et al. 2006; Hooper and Dukes 2004; but see Marquard et al. 2009). While it is widely accepted that the presence of nitrogen-fixing legumes within a mixture are often responsible for overyielding (e.g., Huston et al. 2000; Joliffe 1997), our results clearly demonstrate that overyielding is possible in the absence of legumes; more than half of our plots that transgressively (51.4%) and non-transgressively (65.6%) overyielded contained no legumes. Overyielding in the absence of legumes has been shown occasionally in other studies (e.g., Hooper and Dukes 2004; van Ruijven and Berendse 2003; van Ruijven and Berendse 2009).

We acknowledge that controlled greenhouse experiments may over-represent dominance effect relative to field experiments by limiting variation in soil depth and resource availability. In this case, while tropical hardwood hammock soil depths are highly variable (Olmsted et al. 1990), our experimental design relied on a single standardized soil depth that may have minimized differentiation in rooting depth (and potentially complementarity) among species within our experimental seedling

communities. This inherent limitation of variation and niche differentiation arising from artificial communities supports our contention that the complementarity values and positive diversity-productivity relationship found in our experiment may be more conservative than what one would expect to find in the field (i.e., Flombaum and Sala 2008).

Species Impacts on Productivity

Our experiment found no discernible effect of invasive *A. elliptica* seedlings on native seedling productivity, regardless of introduction pressure. This finding suggests that the establishment of *A. elliptica* monoculture stands in tropical hardwood hammocks does not appear to be the result of inhibitory mechanisms or of the consequences of direct competition with native seedlings. Rather, their success may be a result of their noted shade tolerance (Horvitz 1997), especially when compared to other tropical hardwood hammock species that, as evidenced by their entire distributions, seem to be more adapted to open forest and scrub (Tomlinson 2001).

Among native species, the two most productive species in our study, *Citharexylum spinosum* and *Ficus aurea*, featured significant correlations with biodiversity effects components within polyculture mesocosms. The seedling density of *C. spinosum* was negatively correlated with trait-independent complementarity effects suggesting that this species inhibited other species in mixture. This finding is corroborated by the fact that *C. spinosum* has been found to exhibit mild allelopathic inhibition (Fujii et al. 2004). Meanwhile, the presence of *F. aurea* was correlated with increased trait-independent complementarity effects. As a result of *F. aurea*'s rapid

growth and large leaves, individuals of this species apparently served as nurse plants, allowing for the enhanced productivity of the entire community, likely by decreasing soil moisture loss. Similar nurse plant effects have been detected in other studies of plant community productivity (see Fridley 2002; Fridley 2001; Spehn et al. 2005). Our finding of increased productivity under higher seedling densities may also be related to decreased soil moisture loss with increased cover.

Additionally, *F. aurea*, *Ilex krugiana*, *Ocotea coriacea*, and *Zanthoxylum fagara* presence/absence (and *O. coriacea* seedling density) all exhibited significant positive correlations with dominance effects. While *F. aurea* was the most productive species in monoculture, *I. krugiana*, *O. coriacea*, and *Z. fagara* were all among the bottom half of species utilized in this experiment in terms of monoculture productivity. Therefore we suggest that *F. aurea* is a strong competitor, while *I. krugiana*, *O. coriacea*, and *Z. fagara* are relatively weak competitors, with respect to our species pool.

Finally, we will not attempt to interpret the correlations between *Sideroxylon salicifolium* and dominance effects or trait-dependent complementarity effects which may have been a statistical artifact of an unusually high mortality rate in this species compared to all others in our study. For unknown reasons, the mortality rate of this species in monoculture and polyculture was 33.3% and 42.9%, respectively; no other species suffered mortality rates greater than 1% in monoculture or 5% in polyculture. Indeed, *S. salicifolium* mortalities comprised 92.3% of all mortalities in monoculture and 75.0% of all mortalities in polyculture.

Implications for Conservation, Restoration, and Management

Understanding the effects of species richness and plant density on woody seedling community productivity is especially important given that successful woody seedling assemblages grow to become the next generation of reproducing adults, impacting forest composition, structure, and function over the long-term. Therefore, our findings directly apply to the conservation of tropical hardwood hammocks in South Florida and other tropical dry forest communities. Our results suggest that the seedling layers of tropical hardwood hammocks will enjoy increased production with increased seedling density. Additionally, species mixes generally resulted in increased productivity relative to species monocultures. Consequently, tropical hardwood hammocks with species-rich and dense seedling layers may ultimately sustain higher and more consistent levels of primary productivity and increased resilience to canopy disturbances than those with species-poor and vacant seedling layers. Conservation managers should actively monitor tropical hardwood hammock seedling layers to identify the causes of diverse and dense native seedling layers in these communities, and actively promote those mechanisms as a long-term management strategy to minimize the impacts of natural and anthropogenic disturbances, including hurricanes, fire, and species invasions, on ecosystem functioning in these habitats. Additionally, restoration efforts may be improved by including species with higher reproductive rates in early plantings and ensuring that outplanted or *in situ*/extant populations of focus species are large enough to help overcome potential causes of recruitment limitation.

Acknowledgements

We are extremely grateful to M. Anderson Brooks, A. R. Brooks, A. W. Brooks, K. Brooks, L. Brooks, D. Howe, D. Mellor, M. Robson, M. Rojas, K. Ross, and the Rutgers Floriculture Greenhouse staff for their contributions to this effort. We also thank J. Lockwood and P. Morin for providing comments on an earlier version of this manuscript. Funding sources for this project were provided to WRB by a Pre-Dissertation Award from The Graduate School- New Brunswick and an Academic Excellence Fund Award from the Graduate Program in Ecology and Evolution at Rutgers University, as well as graduate support from USDA NRI 05-2221 and the New Jersey Agricultural Experiment Station.

Table 1. Species utilized in mesocosm experiments along with additional taxonomic, conservation, and native range information. ‘Status’ refers to the Institute for Regional Conservation’s regional ranking of a species’ conservation status in South Florida as described in Gann, Bradley and Woodmansee (2002) (with number of conservation areas in the region, out of a total of 434, where the species has been documented in parentheses (per Gann, Bradley and Woodmansee 2010)). ‘Native Range’ abbreviations for South Florida natives are as follows: The Bahamas including the Turks and Caicos (BA), Bermuda (BE), Central America (CE), Cuba (CU), peninsular Florida (FL), Hispaniola (HS), Jamaica including the Cayman Islands (JA), Lesser Antilles (LE), Mexico (MX), Northern South America including the Leeward Antilles (SA), Puerto Rico including the Virgin Islands (PR), and Texas (TX).

Species	Family	Status	Native Range
<i>Ardisia elliptica</i>	Myrsinaceae	Naturalized (76)	India, China, SE Asia
<i>Boussieria succulenta</i>	Boraginaceae	Rare (24)	BA, CU, HS, JA, LE, PR, SA
<i>Callicarpa americana</i>	Verbenaceae	Secure (141)	BA, BE, CU, FL, SE United States
<i>Capparis cynophallophora</i>	Capparaceae	Rare (45)	BA, CE, CU, FL, HS, JA, LE, MX, PR
<i>Citharexylum spinosum</i>	Verbenaceae	Rare (45)	BA, CU, FL, HS, JA, LE, SA, PR
<i>Ficus aurea</i>	Moraceae	Secure (193)	CE, CU, FL, HS, JA, MX, PR
<i>Guapira discolor</i>	Nyctaginaceae	Secure (69)	BA, CU, FL, HS, JA, LE, PR
<i>Ilex krugiana</i>	Aquifoliaceae	Rare (24)	BA, HS, PR
<i>Lysiloma latisiliquum</i>	Fabaceae	App. Secure (45)	BA, CE, CU, HS, JA, LE, MX, PR
<i>Ocotea coriacea</i>	Lauraceae	Secure (67)	BA, CE, CU, FL, HS, JA, LE, MX, PR
<i>Piscidia piscipula</i>	Fabaceae	Secure (55)	BA, CE, CU, FL, HS, JA, LE, MX, PR
<i>Sideroxylon salicifolium</i>	Sapotaceae	Secure (81)	BA, CE, CU, HS, JA, LE, MX, PR
<i>Zanthoxylum fagara</i>	Rutaceae	Secure (76)	BA, CE, CU, FL, HS, JA, LE, MX, PR, TX

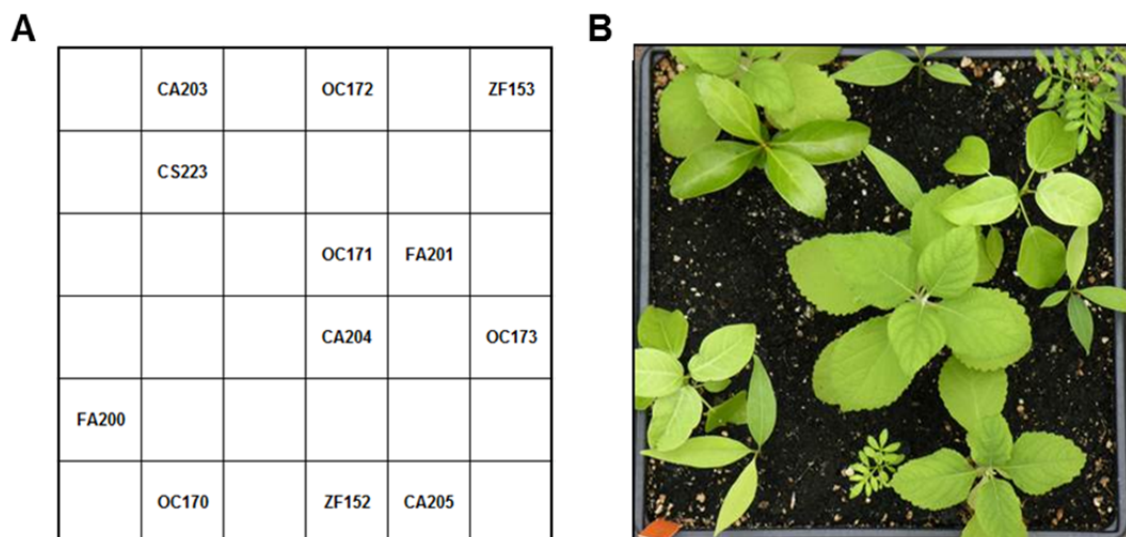


Figure 1. Mesocosm construction. (A) An example of a mesocosm map from mesocosm #328. The first two letters in the ID number designate species identity: CA- *Callicarpa americana*, CS- *Citharexylum spinosum*, FA- *Ficus aurea*, OC- *Ocotea coriacea*, ZF- *Zanthoxylum fagara*. (B) Photograph of mesocosm #328 from overhead 60 days after planting.

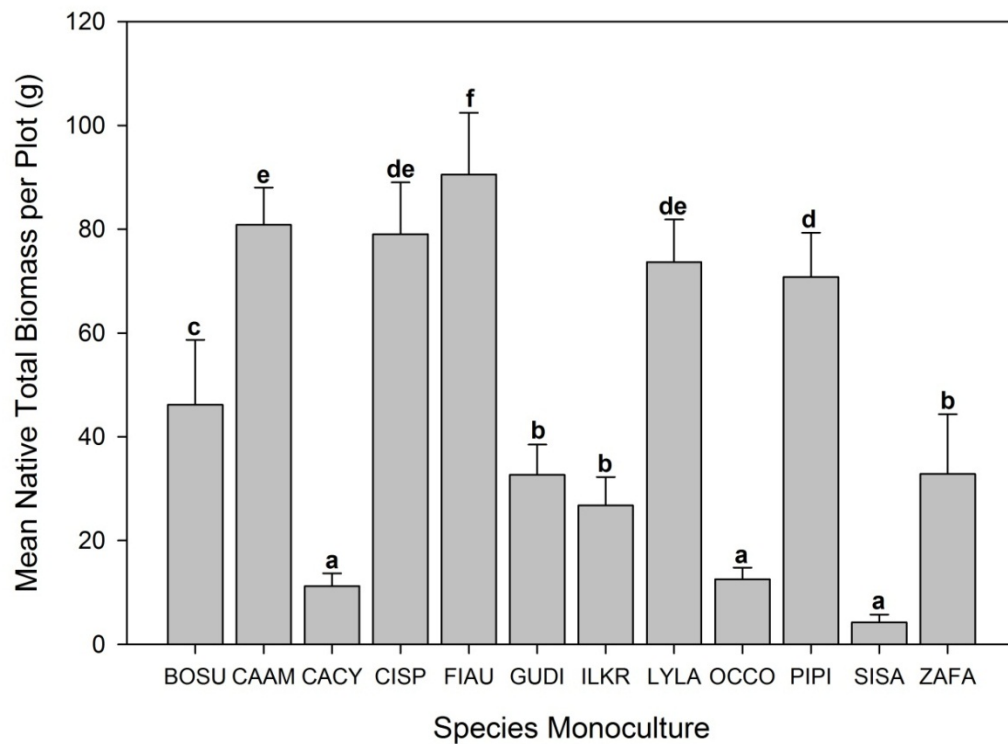


Figure 2. Monoculture mean native total biomass per plot by species. Letters above bars indicate significant differences between groups. Error bars represent standard deviations.

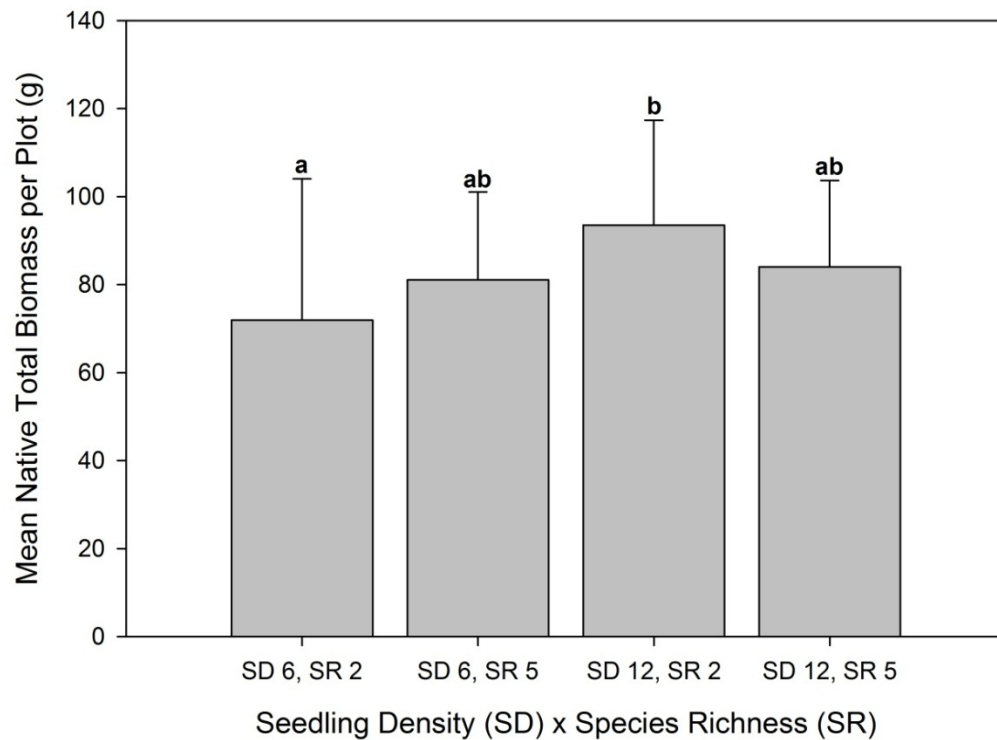


Figure 3. Mean native total biomass per plot by community treatment. Letters above bars indicate significant differences between groups. Error bars represent standard deviations.

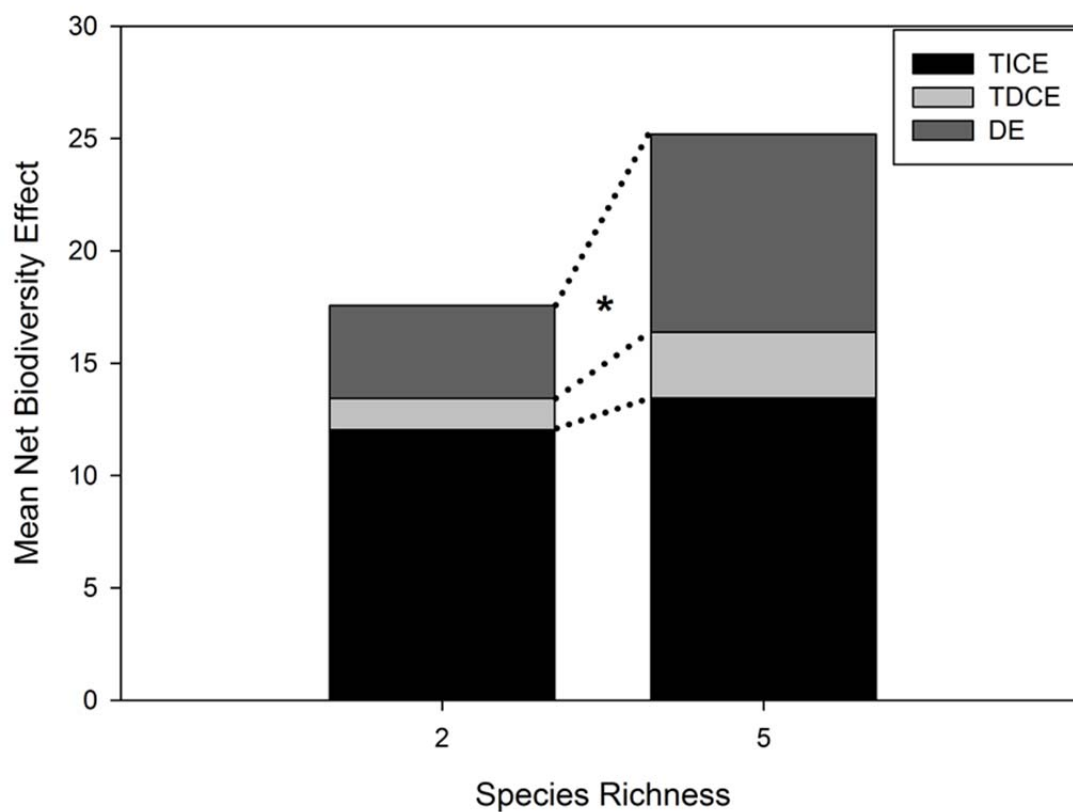


Figure 4. Effect of species richness on biodiversity effects. Asterisks denote significant differences in partitioned biodiversity effect components across species richness levels.

CHAPTER 3

PROPAGULE PRESSURE AND NATIVE SPECIES RICHNESS

EFFECTS DRIVE INVASIBILITY IN TROPICAL DRY FOREST SEEDLING LAYERS

Abstract

Understanding the factors that encourage or inhibit plant invasions is vital to focusing limited invasive control efforts within areas where they are most practical and cost-effective. To extend the range of contexts in which invasibility is studied and aid the development of practical strategies to limit damaging plant invasions, we set out to test the relative importance of native species richness, native seedling density, and invasive propagule pressure, on the invasibility of artificial assemblages of naturally-occurring tropical woody seedling communities. Our greenhouse mesocosms included a species pool of twelve trees and woody shrubs native to South Florida's tropical hardwood hammocks, and an increasingly prevalent noxious woody invader of this system, *Ardisia elliptica*. We found that invader propagule pressure was the single most important factor determining community invasibility. We also revealed a positive relationship between invasibility and native species richness in our polyculture mesocosms. Because *A. elliptica* biomass production significantly differed among different native monocultures and was not related to overyielding in native polycultures, we suggest that the effect of species richness on invasibility in this experiment was the result of sampling effects rather than a true effect of diversity.

Three broad findings hold potential for application in preventing and controlling plant invasions, especially in the seedling layers of tropical dry forests: (1) effective invasive control efforts will likely benefit from measures to minimize propagule pressure; (2) managers might do well to prioritize invasive monitoring and removal efforts on the most diverse habitats within a management region; and (3) while more data are necessary to further understand our finding of a lack of association between productivity and invasibility, management regimes aimed at maximizing primary productivity might not increase invasibility, and in fact, strategies for controlling invasive plants via the management of ecosystem productivity may be ineffective.

Key Words

biotic resistance; diversity; invasibility; productivity; propagule pressure; species richness

Introduction

Understanding the community factors that encourage or inhibit biological invasions is of preeminent importance to focusing invasive removal and mitigation efforts within areas where they are most practical and cost-effective (Levine et al. 2004). Many studies have focused on species richness as an important factor in the invasibility of a site or community, but the exact nature of the relationship between species richness and invasibility remains unclear (e.g., Byers and Noonberg 2003; Bruno et al. 2005; Hooper et al. 2005); in part, because of opposing results emerging from experiments of different styles and scales. Large-scale observational approaches tend to find a positive diversity-invasibility relationship while small scale experiments often reveal negative

relationships between species richness and invasibility (Fridley et al. 2007). A recent meta-analysis of biodiversity effects on ecosystem properties by Balvanera et al. (2006), however, seemed to indicate that on the whole, diversity increased resistance to invasion. Additionally, other factors including population densities (e.g., Von Holle and Simberloff 2005) and propagule pressure (e.g., Von Holle and Simberloff 2005; Colautti et al. 2006; Thomsen et al. 2006) have begun to be explored in various contexts, and cited as potentially important determinants of community invasibility.

Research aimed at clarifying the role of any one of these factors has often been inhibited by problematic experimental designs. In particular, the relationship between species richness and community invasibility is most often empirically tested with extremely limited species pools, often lacking monoculture treatments to discount individual species competitive abilities, prompting the possibility of confounded results because of sampling effects (Wardle 2001; Hooper et al. 2005). Another common criticism of these studies is that their results may be specific to the system, or the plant life forms or species utilized, given that much of this work to date has been conducted in a narrow suite of contexts (temperate grasslands, herbaceous communities, or agricultural systems (Balavanera et al. 2006)). Finally, few studies have attempted to assess the relative importance of multiple factors simultaneously (e.g., Von Holle and Simberloff 2005; Thomsen et al. 2006; Eschtruth and Battles 2009); thus, it has been difficult to identify practical management strategies to thwart biological invasions.

Tropical hardwood hammock communities occur as naturally-discrete “islands” of tropical dry forest habitat (Armentano et al. 2003) that occur on limestone outcrops throughout South Florida featuring diverse assemblages of plants including ferns,

orchids, lianas, and around 135 woody species, most with Caribbean affinities (Tomlinson, 2001). Despite extensive conservation and management efforts in South Florida, these communities are highly invaded by an assortment of tropical ornamental and agricultural plant species (Horvitz, 1997; Brooks et al. 2013). One such species, *Ardisia elliptica*, is a noxious shrub or small tree listed in Category I (the most severe class) of the Florida Exotic Pest Plant Council's Invasive Species List for its propensity to form dense monocultures in forest understories and exclude native species (Langeland and Craddock Burks 1998). It has successfully invaded forest ecosystems throughout Central and South Florida, the Caribbean, and Hawaii (Langeland and Craddock Burks, 1998). Given *A. elliptica*'s negative impacts and increasing prevalence in tropical hardwood hammocks in South Florida, including those of Everglades National Park, we chose it as our model invader.

In this manuscript we sought to determine the relative effects of native species richness, native seedling density, and invasive propagule pressure on community invasibility in constructed greenhouse mesocosms, utilizing woody seedlings from tropical hardwood hammocks of southern Florida in an effort to broaden the contexts in which the mechanisms controlling invasibility are studied. Specifically, by using woody seedlings we hope to be able to glean important information about invasibility in seedling communities and the competition between native and invasive seedlings that may prove determinative to the eventual structure and function of the mature forest communities that follow.

This manuscript also explores potential interactions between native productivity and invasibility in these woody seedling communities. Despite advances in our

knowledge of ecological processes and biodiversity patterns, there remains an urgent need to understand how exotic species introductions may impact ecosystem functioning (Hooper et al. 2005; Loreau 2010). Specifically, there has been considerable debate regarding the role of species richness, both in terms of its relationship with community productivity and invasibility (Tilman 1999; Hooper et al. 2005). However, only a few studies have sought to examine both sets of relationships concurrently (e.g., Hodgson et al. 2002; Beisner et al. 2006; Jiang et al. 2007), although only one study focused on plant communities (i.e., Jiang et al. 2007). More such investigations could provide important insights into how changes in species richness and abundance might impact ecosystem functioning and elucidate the specific mechanisms responsible (Tilman 1999; Hooper et al. 2005).

Methods

Mesocosm Construction

All experimentation occurred in two adjoining bays in the Rutgers University Floriculture Greenhouse under 50% shade cloth. The facilities were temperature-controlled with a daily 20°C minimum and 30°C maximum. All mesocosm communities were planted in plastic ‘half-flat’ trays, measuring 25.8cm wide and long by 6cm deep. Each half-flat was filled with Premier Pro-Mix ‘PGX’ (Premier Tech Horticulture, Quakertown, PA), a peat-based growing medium that is pH-adjusted with crushed limestone and designed for high-density growing applications. These conditions approximately replicate recruitment conditions and soil depth within the natural range for seedlings in tropical hardwood hammocks. Native seedlings of 12 tropical hardwood

hammock species were germinated and cultivated in the greenhouse from wild-collected seed for use in this experiment (see Appendix 9 for our phylogenetic, life history, and conservation information). These species were specifically chosen for use in this study on the basis of their (1) overlapping fruiting period and (2) presence in tropical hardwood hammocks of Everglades National Park. This assured that our mesocosm communities were representative of natural seedling layer assemblages in tropical hardwood hammocks of particularly high conservation value. All species are identified throughout this text as described in Wunderlin (1998).

Fruit of the invasive species, *A. elliptica*, were collected from Kendall Indian Hammocks Park in Miami-Dade County. *Ardisia elliptica* seeds were separated from depulped fruit, washed, and scarified in a small-meshed aluminum strainer. We dried and stored processed seeds in darkness at 12°C until their eventual planting in mesocosms (from six to ten months after storage). Of these, 216 seeds were utilized two months after storage to note germination times for planning our invasive propagule pressure treatments. We watered and observed these seeds for four months, noting that 93% and 98% of all *A. elliptica* seedlings that would eventually germinate did so by the 60- and 90-day marks, respectively.

Because each mesocosm was large enough to accommodate 36 seedling plugs, we imagined a grid of 36 available spaces over the surface of each mesocosm to be used for planning and identification purposes. All seedlings utilized were assigned a specific ID number and allotted a grid space randomly. We mapped the ID numbers and spatial configurations of all seedlings in each mesocosm to track growth and mortality of each seedling (see Figure 1). We also assigned specific ID numbers to the *A. elliptica* seeds

used in the experiment and randomly assigned them to available grid spaces so that their individual germination, growth, and mortality data could be monitored. This procedure also ensured that no seeds would be planted in the same grid space where seeds had been planted earlier in the experiment.

We planted all mesocosms to match the mesocosm maps we designed, and allowed native seedlings to “grow in” to their new communities for the first 30 days of our 210 day study. We watered mesocosms evenly every other day for the duration of the study following initial planting. We also randomly shuffled mesocosms within the greenhouse bays each week to avoid any potential microclimate or location effects on the results of our study. We added no additional fertilizer or soil amendments at any point during the study beyond what initially occurred in our soil mix. Finally, we evenly applied three separate treatments of Neem Oil on all mesocosms during a single evening in May, July, and September, to comply with the Floriculture Greenhouse’s routine insect control efforts.

Experimental Design

Our monoculture experiments were designed to use native seedlings as phytometers, assessing species growth rates and species’ relative competitive abilities against *A. elliptica* invaders. Monoculture experiments focused on two main factors:

- Native Species Identity (12 levels: one representing each species (See Appendix 9)), and
- Invader Propagule Pressure (three levels: zero, low, high).

Native species richness (one species) and density (six seedlings) levels were constant across all monoculture mesocosms. For the construction of each monoculture mesocosm, seedlings were directly transplanted in random arrangements from their original seedling liner plugs without disturbing their root systems. All factor levels were fully-crossed, and we created six replicate mesocosms per monoculture treatment, yielding a total of 216 mesocosms.

The propagule pressure factors represented the number of *A. elliptica* seeds that would be sown in each mesocosm. Mesocosms in ‘zero’ propagule pressure treatment groups received no invasive propagules throughout the duration of the experiment. Meanwhile, mesocosms in ‘low’ propagule pressure treatment groups received a total of six *A. elliptica* seeds over the course of two introduction events (three seeds each on Day 31 and Day 121). Finally, mesocosms in ‘high’ propagule pressure treatment groups received a total of 16 seeds over the course of four introduction events (four seeds each on Days 31, 61, 91, and 121). We sowed all *A. elliptica* seeds at a depth of 1cm and covered lightly with growing medium.

Polyculture experiments were designed to assess the effects of three main factors on community invasibility:

- Native Species Richness (two levels: two, five),
- Native Seedling Density (two levels: six, 12), and
- Invader Propagule Pressure (three levels: zero, low, high).

Once again, all factor levels were fully-crossed. We created 12 replicates per treatment for a total of 144 mesocosms. Native species composition and abundances were free to vary randomly within the framework of the factor levels assigned to each mesocosm (see

Appendix 10 for polyculture mesocosm species and seedling abundance information).

The invasive propagule pressure treatments for our polyculture experiments were conducted exactly as described above in the monoculture experiments.

To determine whether there were differences in germination rates between experimental introduction events for *A. elliptica*, and to tease apart mortalities from failed germinations in monoculture and polyculture experiments, we also separately planted and monitored 72 seeds of *A. elliptica* to serve as a control at the time of each planned experimental introduction event (Days 31, 61, 91, and 121); a total of 288 seeds. These seeds were sown in the same substrate and manner, and were watered similarly, to those utilized in our experiments except that they were each planted in individual seedling liner plugs. We recorded the number of seedlings that successfully germinated from each set of 72 seeds within 90 days of having been sown.

Data Collection

In this experiment, we define invasibility as the cumulative response of germination, survival, and biomass production of *A. elliptica* seedlings in our mesocosms. We measured germination and survival components of invasibility jointly as invader establishment rates. Additionally, we used two measures of invader biomass production to enable improved interpretation of *A. elliptica* invasibility data: total invader biomass production and individual invasive seedling growth.

At the conclusion of the experiment at 210 days we identified surviving invasive seedlings in each mesocosm where propagules had been introduced. Additionally, we noted failed germinations or mortalities by the absence of *A. elliptica* seedlings where

mesocosm maps indicated seeds had been sown. Our mesocosm invasive establishment rates were defined as the proportion of germinating/surviving invasive individuals over the total number of introduced propagules (seeds). Established *A. elliptica* seedlings were then gently removed from the mesocosm, after which we separated their respective above- and below-ground biomass. Samples were dried on-site in an oven for seven days at 70.5°C. We immediately weighed samples upon removal from the oven and recorded sample masses in grams.

We also recorded biomass production of native seedlings. We used native seedling above-ground biomass values rather than total biomass because we could not effectively separate the root systems of individual seedlings. We collected native seedling above-ground biomass by clipping individuals at the soil surface. Native above-ground biomass samples were dried and weighed in the same manner as *A. elliptica* biomass. As all seedlings were sown and grown from seed at the same time, we did not need to account for differences in initial seedling biomass relative to final biomass in our analysis.

We analyzed the potential for a relationship between native productivity and community invasibility in two ways: (1) comparing native and invasive biomass production across all mesocosms, and (2) comparing rates of native overyielding in a subset of polycultures with mean invasive seedling biomass production. To calculate native overyielding data, we used our native above-ground biomass dataset to calculate net biodiversity effects for our polyculture mesocosms, as established by Loreau and Hector (2001) and Fox (2005). Net biodiversity effects are a measure of the difference between the observed and expected yields of a polyculture based on the production of

individual species in monoculture and their relative abundances in polyculture assemblages (Loreau and Hector 2001). We limited our analysis to only our low density polycultures (those with six native seedlings) because our monoculture yield calculations were derived from our low density monocultures. Furthermore, we defined each native species' monoculture yield (M_i) value used in these calculations as the mean above-ground biomass from their six 'zero' propagule pressure treatment mesocosms.

Statistical Analyses

All statistical analyses were performed with the use of PASW Statistics GradPack 17.0.2 (2009). We used "0" and "1" to code for individual invader propagules that had failed to establish and those that successfully established, respectively. Though propagules were sown during four discrete events, we did not include 'Day Sown' in any germination models because there were no significant differences in 90-day germination rates by planting date among control propagules with 20, 26, 25, and 22 propagules germinating after being sown on Days 31, 61, 91, and 121, respectively (Pearson's Chi-square test: $\chi^2_{(df=3, N=93)} = 0.978$, $p = 0.806$). To assess if the establishment rate of *A. elliptica* propagules differed by the specific native species monocultures in which they were sown, we ran a binomial logistic GLM with 'Mesocosm' nested within 'Species' with data from our monoculture mesocosms. Similarly, to assess whether establishment rates differed by polyculture treatment, we ran a binomial GLM with 'Mesocosm' nested within 'Native Species Richness x Native Seedling Density' using *A. elliptica* germination/survival data from our polyculture mesocosms.

To assess the impact of community factors on total invader biomass in mesocosms, we ran two ANOVAs- one for our monocultures, and another for our polycultures. Our independent factors in full factorial fixed effects models included ‘Native Species’ (12 levels) and ‘Propagule Pressure’ (two levels) for monocultures, and ‘Native Seedling Density’, ‘Native Species Richness’, and ‘Propagule Pressure’ (all two-level factors) for polycultures. Tukey’s HSD tests were conducted simultaneously on ‘Native Species’ in the monoculture ANOVA to identify any significant group differences.

We also tested whether *A. elliptica* seedling growth was affected by community factors in monoculture and polyculture mesocosms and were interested in determining whether *A. elliptica* seedlings were differentially allocating biomass in response to the various factors we were testing. Thus, we checked *A. elliptica* seedling above- and below-ground biomass data for intercorrelation in both monoculture and polyculture mesocosms a priori. *Ardisia elliptica* above-ground biomass was moderately correlated with below-ground biomass in monocultures and polycultures ($\rho=0.642$ and $\rho=0.285$, respectively), and were utilized together in multivariate analyses. We restricted both analyses to invasive seedlings sown only on days 31 and 121 to avoid confounding our ‘Propagule Pressure’ and ‘Day Sown’ factors. For monocultures, we used a MANOVA with ‘AE Above-ground Biomass’ and ‘AE Below-ground Biomass’ as the response variables for individual *A. elliptica* seedlings with ‘Native Species’ (12 levels), ‘Propagule Pressure’ (two levels), and ‘Day Sown’ (two levels) as fully-fixed factors in a factorial design. For polycultures, we used a MANOVA with ‘AE Above-ground Biomass’ and ‘AE Below-ground Biomass’ as response variables for individual *A.*

elliptica seedlings, and ‘Native Species Richness’, ‘Native Seedling Density’, ‘Propagule Pressure’, and ‘Day Sown’, all two-level and fully-fixed factors in a factorial design.

Finally, we explored whether there was a relationship between native productivity and community invasibility in two ways. First, we used a linear regression to assess the relationship between total native biomass production and total invasive biomass production across all monoculture and polyculture mesocosms. Second, we explored whether there was a relationship between overyielding in native polycultures and invasive seedling growth. Once again, we were interested in determining whether individual *A. elliptica* seedlings were differentially allocating biomass in response to biodiversity effects. With data from all low native seedling density polyculture mesocosms with surviving *A. elliptica* seedlings at the end of our experiment, we ran separate linear regressions with ‘Mean AE Above-ground Seedling Biomass’ and ‘Mean AE Below-ground Seedling Biomass’ as the dependent variables and ‘Net Biodiversity Effects’ as the independent variable using a Bonferroni correction to hold the global- α level at 0.05.

Results

Invader Establishment

Across all mesocosms, *A. elliptica* establishment rates in monocultures (29.92%) were almost identical to those of polycultures (29.83%) and only slightly reduced from the control propagules planted several months earlier (32.29%). Establishment rates of invasive *A. elliptica* seeds were not significantly different across native species monocultures (Omnibus Likelihood Ratio Chi-square test: $\chi^2_{(df=143, N=1584)}=162.749$,

$p=0.124$). Similarly, we found no evidence that *A. elliptica* propagules established at different rates regardless of the native seedling density and native species richness treatments they were exposed to in polyculture mesocosms (Omnibus Likelihood Chi-square test: $\chi^2_{(df=95, N=1056)}=117.269, p=0.060$). In our polycultures, *Ardisia elliptica* establishment rates ranged from 24.6% in low seedling density and low species richness plots to 33.7% in high seedling density and high species richness plots.

Total Invader Biomass Production

Mesocosms exposed to high propagule pressure resulted in more *A. elliptica* total biomass than those exposed to low propagule pressure in both monocultures (7.02 g/plot vs. 2.35 g/plot) and polycultures (7.14 g/plot vs. 2.59 g/plot) (see Table 1 and Table 2, respectively). The identity of the native species monoculture in which invasive propagules were planted also significantly impacted total *A. elliptica* biomass production (Table 1); *A. elliptica* experienced increased productivity in *Ficus aurea* monocultures (6.74 g/plot) relative to its performance in monocultures of *Lysiloma latisiliquum* (3.72 g/plot), *Callicarpa americana* (3.61 g/plot), or *Sideroxylon salicifolium* (3.25 g/plot) (Figure 2A). Meanwhile, polyculture total invader biomass was also significantly affected by species richness mesocosms with two native species (4.15 g/plot) yielding less invasive biomass than those with five native species (5.57 g/plot) (Table 2; Figure 2B). Effect size calculations indicate that propagule pressure was the most powerful factor explaining variance in invasive biomass production in both analyses. Propagule pressure in monocultures (Partial- $\eta^2=0.597$) was nearly three times more powerful than native species (Partial- $\eta^2=0.211$), while in polycultures, propagule pressure (Partial-

$\eta^2=0.483$) was nearly six times more powerful than native species richness (Partial- $\eta^2=0.083$).

Individual Invasive Seedling Growth

Sowing date significantly affected *A. elliptica* above-ground biomass production but not below-ground biomass production in monoculture plots (Table 3). Mean invader above-ground biomass for seedlings sown on Day 31 was 0.74 g/seedling and 0.71 g/seedling for those sown on Day 121. Additionally, mean invader above-ground biomass was greatest when *A. elliptica* seedlings were grown amongst *C. americana* (0.67 g/seedling) and least when *A. elliptica* seedlings were grown amongst *Ilex krugiana* (0.78 g/seedling) (Figure 3A). Meanwhile, mean invader below-ground biomass was greatest when *A. elliptica* seedlings were grown amongst *Bouyeria succulenta* and *Guapira discolor* (0.75 g/seedling and 0.74 g/seedling, respectively) and least when *A. elliptica* seedlings were grown amongst *Ocotea coriacea* (0.63 g/seedling) (Figure 3A).

Among polycultures, the three-way interaction between native seedling density, propagule pressure, and day sown only significantly affected *A. elliptica* above-ground seedling biomass (Table 4); however, follow-up analyses could not statistically differentiate amongst treatment groups. Our inspection of interaction effect group means seemed to show that older *A. elliptica* seedlings (those sown on Day 31), on average, produced the most above-ground biomass when sown in mesocosms with higher conspecific densities (i.e., high propagule pressure) and lower heterospecific densities (i.e., low native seedling density), and produced the least above-ground biomass when sown in mesocosms with lower conspecific and heterospecific densities (low propagule

pressure and low native seedling density). On the other hand, above-ground biomass production by younger *A. elliptica* seedlings (those sown on Day 121), on average, was greatest when sown in mesocosms with higher conspecific and heterospecific densities, and least when sown in mesocosms with lower conspecific and higher heterospecific densities.

The two-way interactions between native species richness and propagule pressure, and native seedling density and native species richness, both only significantly affected *A. elliptica* below-ground seedling biomass in polycultures (Table 4). Mean invader below-ground seedling biomass was significantly greater in mesocosms treated with high native species richness and high propagule pressure (0.79 g/seedling) vs. all other treatment groupings (0.71-0.74 g/seedling) (Figure 4A). Conversely, mean invader below-ground seedling biomass was significantly reduced in mesocosms treated with low native seedling density and species richness (0.68 g/seedling) vs. all other treatment groupings (0.75-0.77 g/seedling) (Figure 4B).

Furthermore, while native seedling density and native species richness main effects both significantly affected invader below-ground biomass in polycultures, only native species richness significantly affected invader above-ground biomass (Table 4). Mean *A. elliptica* seedling below-ground biomass production increased with increasing native seedling density, from 0.73 g/seedling in mesocosms with six native seedlings to 0.76 g/seedling in those with 12 native seedlings. Additionally, increases in native species richness from two to five species also increased mean *A. elliptica* seedling biomass from 0.73 g/seedling to 0.76 g/seedling for above-ground tissue and from 0.72 g/seedling to 0.77 g/seedling for below-ground tissue (Figure 3B).

Finally, we found that polyculture productivity was not related to invasibility in either of the two ways we attempted to assess the relationship. Total native biomass production was not related to total invasive biomass production ($b=0.007$, $F_{(1, 239)}=1.172$, $p=0.280$, $R^2=0.005$). Additionally, native polyculture overyielding, as measured by net biodiversity effects, was not related with mean invader above-ground biomass production ($b=3.6 \times 10^{-6}$, $F_{(1, 44)} < 0.001$, $p=0.994$, $R^2 < 0.001$) or below-ground biomass production ($b=0.001$, $F_{(1, 44)}=0.975$, $p=0.329$, $R^2=0.022$).

Discussion

Based on our experiment, three broad findings hold potential for application in preventing and controlling plant invasions, especially in the seedling layers of tropical dry forests. First, because propagule pressure was the most powerful effect in our analyses of community invasibility (more so than native species richness or seedling density), effective invasive control efforts will likely benefit from measures to minimize the spread of propagules. Second, because more diverse plant communities may be more susceptible to invasion, managers might do well to prioritize invasive monitoring and removal efforts on the most diverse habitats within a management region. This recommendation neatly aligns with traditional conservation priorities that value the protection of species-rich habitats over species-poor ones. Finally, our study suggests that there may be no real relationship between native productivity and invasibility. While more data are necessary to further understand this lack of association, management regimes aimed at maximizing primary productivity may not impact invasibility.

Additionally, this may also suggest that strategies for controlling invasive plants through managing community or ecosystem productivity (i.e., Huston 2004) may be ineffective.

Community Invasibility

The lack of species or community effects on invader establishment suggests that early *A. elliptica* germination and survival must be almost entirely based on abiotic factors. However, in this study, we did find that propagule pressure and native species richness were both important factors contributing to the invasibility of tropical woody seedling communities. In particular, propagule pressure was the dominant factor determining the invasibility of native plant communities. These findings regarding propagule pressure further reinforces a growing body of research suggesting that propagule pressure may be the most fundamental factor in determining not only the success or failure of species introductions, but also the invasive potential of those species following establishment (e.g., Eschtruth and Battles 2009; Lockwood et al. 2009; Simberloff 2009).

Additionally, the positive relationship between invasibility and native species richness in this experiment runs counter to Elton's (1958) biotic resistance hypothesis and many recent experimental manipulations (e.g., Fargione and Tilman 2005; Beisner et al. 2006). However, a recent observational study in tropical hardwood hammocks in South Florida by Brooks et al. (2013) at fine scales echoes this experiment's findings of a positive diversity-invasibility relationship, as do the vast majority of large-scale observational studies (e.g., Brown and Peet 2003; Stohlgren et al. 2006). We suggest that the positive species richness effect on invasibility in our study is a sampling effect

rather than a true effect of diversity via complementarity. This is likely given that the invasibility of native species monocultures significantly differed by native species while *Ardisia elliptica* biomass production was not related to overyielding in native communities. Without evidence of a relationship between native community complementarity and invasibility, we would not be able to suggest the action of real diversity effects on invasibility unless polyculture invasibility exceeded, or was limited below, the maximum and minimum levels witnessed in native species monocultures, respectively. And in fact, while mean *A. elliptica* biomass per plot increased from the two to five native species richness polycultures, both group means fell well within the mean *A. elliptica* biomass per plot levels of the most invasible and least invasible native monoculture (Figure 2B).

Finally, productivity is often assumed to be positively related with invasibility as a result of observational studies of native-exotic richness relationships that promote the environmental favorability hypothesis as an explanation for the positive diversity-invasibility relationship they often reveal (Davies 2011). Yet, the few experimental manipulations that have sought to assess the relationship between productivity and invasibility have generally come to mixed conclusions. Hodgson et al. (2002) with bacteria and Jiang et al. (2007) with herbaceous plants, both found negative productivity-invasibility relationships, though when Hodgson's group controlled for dominance effects in their bacterial communities the negative relationship became weakly positive. On the other hand, Beisner et al.'s (2006) study of an invasive invertebrate in rockpools found increased invasibility with increased algal productivity. While more research on this topic is clearly needed, our finding of no relationship between productivity and

invasibility in woody tropical seedling layers along with the mixed results of other studies seems to suggest that any general relationship between these two community properties may either be highly context-dependent, or may simply be an experimental artifact (i.e., Hodgson et al. 2002).

Our monoculture and polyculture experiments allowed us to discern particular effects that impacted *A. elliptica* seedling growth. Additionally, the separation of *A. elliptica* above- and below-ground biomass in our analysis enabled us to understand how those factors impacted resource allocation by seedlings. In native monocultures, older *A. elliptica* seedlings produced more above-ground biomass than younger seedlings, but not root biomass. Additionally, while *A. elliptica* biomass production varied amongst different native competitors, invader above- and below-ground biomass generally varied similarly between different native monocultures.

Meanwhile, *A. elliptica* seedling biomass production in polycultures was affected by several factors including seedling age, invader density, native seedling density, and native species richness in complex and simple ways. Some of the simple effects we detected included the fact that *A. elliptica* seedlings responded to increased native seedling density by increasing below-ground biomass production. Moreover, invasive seedlings responded to increased native species richness by increasing both above- and below-ground biomass production. Interestingly, mean *A. elliptica* below-ground biomass per seedling in high species richness polycultures was the only measure to actually exceed the corresponding maximum mean *A. elliptica* biomass value from our monocultures (Figure 3B); in this case, *G. discolor* was the native monoculture with the greatest mean *A. elliptica* below-ground biomass per seedling in our experiment. This

particular result may have been bolstered by the interaction effect between species richness and propagule pressure whereby *A. elliptica* seedlings surrounded by more conspecifics (as a result of high propagule pressure) in high diversity polycultures were more productive than any other group. A similar conspecific facilitation effect where increased propagule pressure appeared to enhance mean *A. elliptica* seedling biomass productivity was evident in our inspection of treatment means of the significant three-way interaction effect of *A. elliptica* seedling age, invader density, and native seedling density.

Native species and community impacts on Ardisia elliptica

We were also particularly interested in several species-specific interactions, including the potential impacts of the legumes, *Lysiloma latisiliquum* and *Piscidia piscipula*, on invasibility. While both were associated with relatively high *A. elliptica* biomass in monoculture, they did not significantly augment invader productivity above levels of all other non-nitrogen fixing natives. This suggests that, at least in the context and duration of this experiment, the potential addition of soil nitrogen by legumes extended no measurable benefit to invasive seedlings. Another, native species of interest was *Citharexylum spinosum*. We found that *C. spinosum* inhibited productivity of the native communities constructed for this experiment (see Chapter 2), likely through allelopathic inhibition (i.e., Fujii et al. 2004). Yet, these inhibitory properties did not seem to affect *A. elliptica* productivity. In fact, invasive seedlings grew relatively well in *C. spinosum* monocultures as compared to other native species monocultures.

Overall, these findings illustrate what makes *Ardisia elliptica* such a well-regarded threat to tropical forest communities around the world. We found little evidence to suggest that *A. elliptica* significantly responded with large changes in establishment or growth to any interactions with the native species we utilized in this experiment, especially when sown in diverse native species mixtures. While this may be a reflection of the superior competitive abilities of *A. elliptica* proposed by Horvitz et al. (1998) relative to native tropical hardwood hammock species, it may instead reflect Levine et al.'s (2004) assertion that woody species, in general, may show less susceptibility to biotic resistance than other plant forms. Regardless, this apparent insensitivity to resource competition along with their potential for conspecific facilitation, when combined with their noted shade tolerance (Horvitz 1997), may portend why this species is frequently encountered in its introduced range growing in dense thickets to the exclusion of other species.

Acknowledgments

We are extremely grateful to M. Anderson Brooks, A. Brooks, K. Brooks, L. Brooks, W. Brooks, D. Howe, D. Mellor, M. Robson, M. Rojas, K. Ross, and the Rutgers Floriculture Greenhouse staff for their contributions to this effort. We also thank J. Lockwood and P. Morin for providing comments on an earlier version of this manuscript. Funding sources for this project were provided by a Pre-Dissertation Award from The Graduate School- New Brunswick and an Academic Excellence Fund Award from the Graduate Program in Ecology and Evolution at Rutgers University, as well as graduate support from USDA NRI 05-2221 and the New Jersey Agricultural Experiment Station.

Table 1. Native Monoculture Invasibility. ANOVA results for native monoculture total *A. elliptica* biomass by Propagule Pressure (PP), and Species (SP). Bolding indicates significant effects.

Source	df	SS	MS	F	P
Intercept	1	3165.234	3165.234	714.363	<0.001
PP	1	787.116	787.116	177.644	<0.001
SP	11	141.918	12.902	2.912	0.002
PP x SP	11	71.966	6.542	1.477	0.149
Error	120	531.702	4.431		
	144	4697.936			

Table 2. Native Polyculture Invasibility. ANOVA results for native polyculture total *A. elliptica* biomass by Propagule Pressure (PP), Native Seedling Density (SD), and Native Species Richness (SR). Bolding indicates significant effects.

Source	df	SS	MS	F	P
Intercept	1	2270.418	2270.418	13.463	<0.001
PP	1	498.217	498.217	82.133	<0.001
SD	1	4.520	4.520	0.745	0.390
SR	1	48.391	48.391	7.977	0.006
PP x SD	1	0.482	0.482	0.079	0.779
PP x SR	1	14.327	14.327	2.362	0.128
SD x SR	1	3.623	3.623	0.597	0.442
PP x SD x SR	1	2.096	2.096	0.346	0.558
Error	88	533.804	6.066		
	96	3375.877			

Table 3. Mean *Ardisia elliptica* Seedling Growth in Native Monocultures. MANOVA and ANOVA results for native monoculture mean *A. elliptica* above- and below-ground biomass by Day Sown (DS), Propagule Pressure (PP), and Native Species (SP). Bolding indicates significant effects.

Source	Wilks' Lambda			Univariate Test			Univariate Test		
	Multivariate Test			AE AG Biomass			AE BG Biomass		
	df	F	P	df	F	P	df	F	P
Intercept	2, 234	10039.7	<0.001	1, 235	16652.9	<0.001	1, 235	14524.2	<0.001
DS	2, 234	4.974	0.008	1, 235	9.187	0.003	1, 235	0.847	0.358
PP	2, 234	0.450	0.638	1, 235	0.012	0.911	1, 235	0.722	0.396
SP	22, 468	3.687	<0.001	11, 235	4.226	<0.001	11, 235	4.999	<0.001
DS x PP	2, 234	0.512	0.600	1, 235	0.021	0.886	1, 235	0.576	0.449
DS x SP	22, 468	0.627	0.906	11, 235	1.031	0.419	11, 235	0.544	0.872
PP x SP	22, 468	0.873	0.631	11, 235	1.156	0.319	11, 235	0.776	0.664
DS x PP x SP	20, 468	0.512	0.962	10, 235	0.463	0.912	10, 235	0.505	0.886

Table 4. Mean *Ardisia elliptica* Seedling Growth in Native Polycultures. MANOVA and ANOVA results for native polyculture mean *A. elliptica* above- and below-ground biomass by Day Sown (DS), Propagule Pressure (PP), Native Seedling Density (SD), and Native Species Richness (SR). Bolding indicates significant effects.

Source	Wilks' Lambda Multivariate Test			Univariate Test AE AG Biomass			Univariate Test AE BG Biomass		
	df	F	P	df	F	P	df	F	P
Intercept	2, 164	15363.0	<0.001	1, 165	19058.0	<0.001	1, 165	16763.3	<0.001
DS	2, 164	1.046	0.354	1, 165	0.481	0.489	1, 165	1.873	0.173
PP	2, 164	1.254	0.288	1, 165	1.551	0.215	1, 165	1.373	0.243
SD	2, 164	4.855	0.009	1, 165	0.439	0.509	1, 165	8.468	0.004
SR	2, 164	10.803	<0.001	1, 165	6.120	0.014	1, 165	18.451	<0.001
DS x PP	2, 164	0.004	0.996	1, 165	0.005	0.945	1, 165	0.004	0.949
DS x SD	2, 164	0.349	0.706	1, 165	0.008	0.930	1, 165	0.654	0.420
DS x SR	2, 164	0.110	0.896	1, 165	0.213	0.645	1, 165	<0.001	0.983
PP x SD	2, 164	2.371	0.097	1, 165	0.132	0.716	1, 165	4.771	0.030
PP x SR	2, 164	3.978	0.021	1, 165	2.830	0.094	1, 165	6.318	0.013
SD x SR	2, 164	5.463	0.005	1, 165	1.021	0.314	1, 165	10.747	0.001
DS x PP x SD	2, 164	3.771	0.025	1, 165	4.977	0.027	1, 165	1.538	0.217
DS x PP x SR	2, 164	1.623	0.200	1, 165	1.190	0.277	1, 165	2.549	0.112
DS x SD x SR	2, 164	0.661	0.518	1, 165	0.169	0.682	1, 165	0.997	0.319
PP x SD x SR	2, 164	1.807	0.167	1, 165	2.280	0.133	1, 165	0.826	0.365
DS x PP x SD x SR	2, 164	0.149	0.861	1, 165	0.063	0.802	1, 165	0.272	0.603

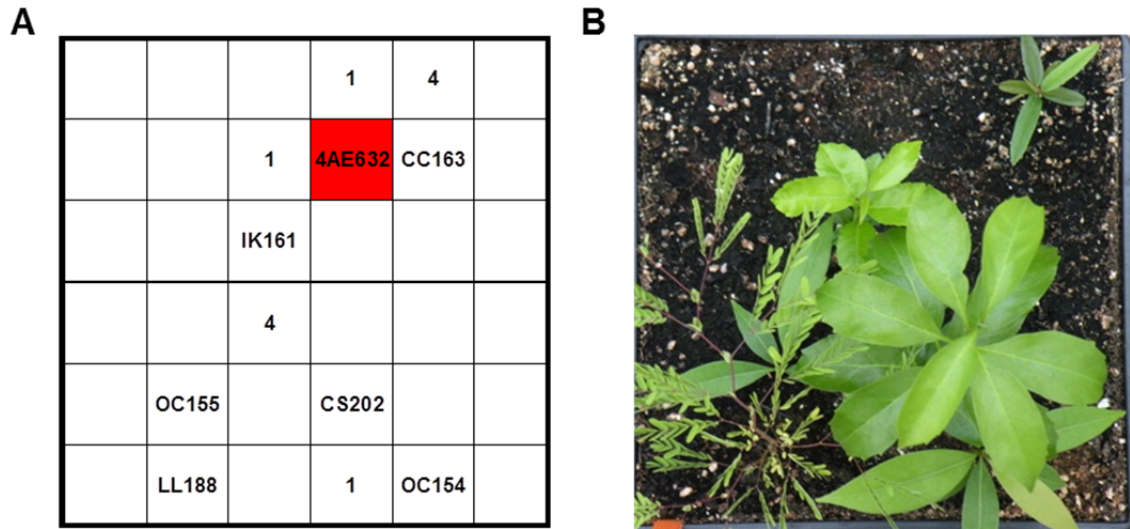


Figure 1. Mesocosm construction. (A) An example of the final mesocosm map from mesocosm #305. The first two letters in the ID number designate species identity: AE- *Ardisia elliptica*, CC- *Capparis cynophallophora*, CS- *Citharexylum spinosum*, IK- *Ilex krugiana*, LL- *Lysiloma latilisiquum*, OC- *Ocotea coriacea*. The “1”s and “4”s indicate where *A. elliptica* seeds were to be sown and from which cohort (1- Day 31, 4- Day 121). The colored square designates a germinated *A. elliptica* propagule. (B) Photograph of mesocosm #305 from overhead 60 days after planting.

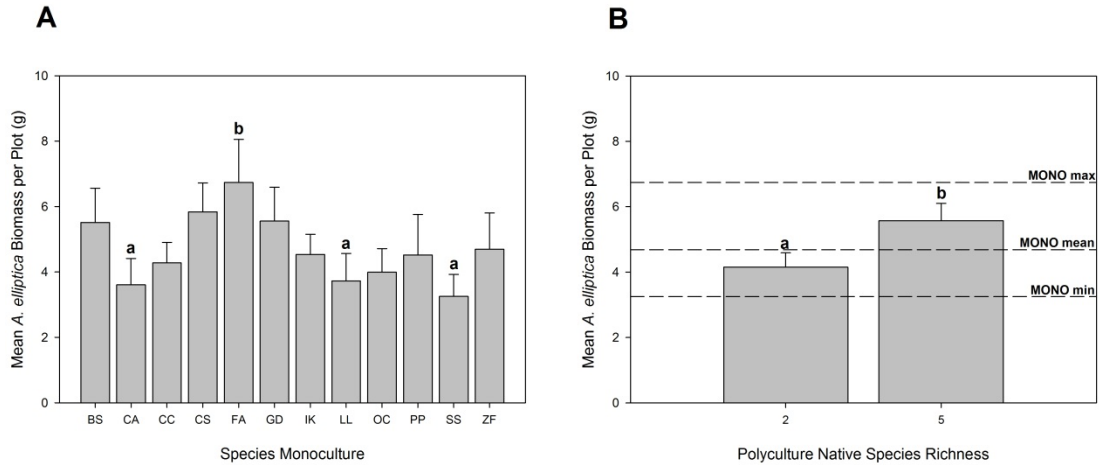


Figure 2. Mean *Ardisia elliptica* biomass per plot in native monoculture and polyculture mesocosms. Error bars represent mean standard errors. **(A)** Mean *Ardisia elliptica* biomass per plot by native species monoculture. Letters above bars indicate significant differences between groups; bars without letters represent groups that are not significantly different from any other. Two-letter native species abbreviations represent the first letter of genus and species names. **(B)** Mean *Ardisia elliptica* biomass per plot by polyculture native species richness. Letters above bars indicate significant differences between groups. To indicate the level of mean invader biomass across all monocultures, and of the most invasible, and least invasible native species monoculture groups, we included dashed lines labeled ‘MONO mean’, ‘MONO max’, and ‘MONO min’, respectively.

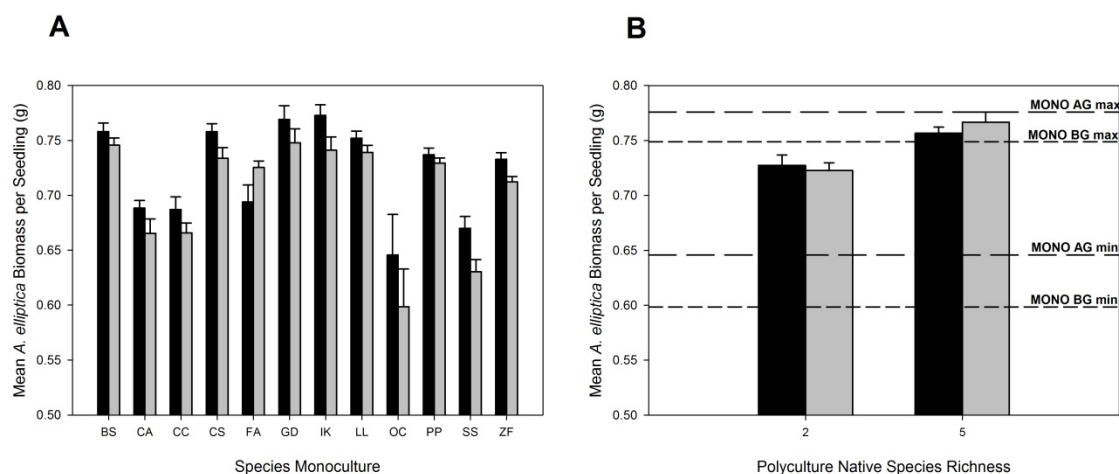


Figure 3. Mean *Ardisia elliptica* above- and below-ground biomass per seedling in native monoculture and polyculture mesocosms. Black bars represent above-ground biomass, while gray bars represent below-ground biomass. Error bars represent mean standard errors. **(A)** Mean *A. elliptica* above- and below-ground biomass per seedling by native species monoculture. Two-letter native species abbreviations represent the first letter of genus and species names. **(B)** Mean *A. elliptica* above- and below-ground biomass per seedling by polyculture native species richness. To indicate the highest and lowest levels of mean invader above-ground biomass among native species monoculture groups, we included long-dashed lines labeled ‘MONO AG max’ and ‘MONO AG min’, respectively. To indicate the highest and lowest levels of mean invader below-ground biomass among native species monoculture groups, we included short-dashed lines labeled ‘MONO BG max’ and ‘MONO BG min’, respectively.

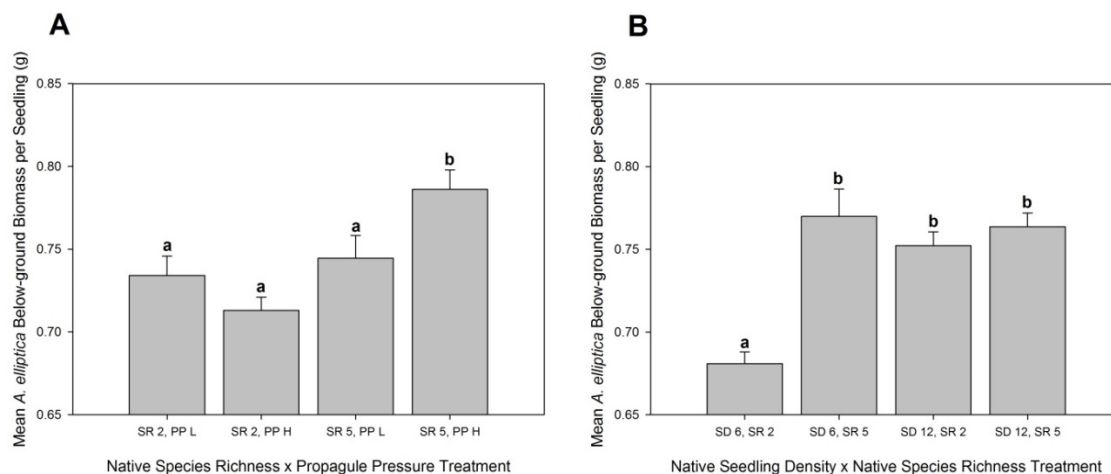


Figure 4. Significant interaction effects involving native species richness on mean *Ardisia elliptica* below-ground biomass per seedling in native polyculture mesocosms. Error bars represent mean standard errors. (A) Mean *A. elliptica* below-ground biomass per seedling by Native Species Richness x Propagule Pressure (SR x PP) treatments. Letters above bars indicate significant differences between groups. (B) Mean *A. elliptica* below-ground biomass per seedling by Native Seedling Density x Native Species Richness (SD x SR) treatments. Letters above bars indicate significant differences between groups.

CHAPTER 4

A ‘NOVEL NATIVES’ MODEL OF RESTORATION TO ENHANCE LOCAL, AND CONSERVE REGIONAL, BIODIVERSITY IN METROPOLITAN AREAS

Abstract

Conserving biodiversity is particularly difficult in metropolitan areas where anthropogenic disturbance, habitat fragmentation, and species invasions contribute to recruitment limitation among native species, altering successional trajectories and suppressing species richness. To guide outplanting species selection and habitat management for restoration projects in metropolitan areas where the restoration of historic abiotic processes and conditions are infeasible, we introduce a new model for restoration intended to enhance local, and conserve regional, biodiversity using ‘novel native’ species. We applied our model by outplanting 540 individuals of 26 tropical hardwood hammock species as part of our efforts to restore a diverse and resilient tropical dry forest community in South Florida on the site of historical wetlands that, following a series of complex and irreversible anthropogenic modifications, had since transitioned into a highly-invaded, low diversity, urban woodlot. To assess outplanting success, we measured individual survival, growth, and reproduction regularly since their introduction.

After two and a half years, our native outplantings experienced high survival, largely positive growth, and have begun to reproduce and recruit on the site, all at comparable rates to those reported in more traditional outplanting projects. The number of native species on the site increased by 61%, including the addition of eight state-listed

threatened or endangered species. Additionally, because 10 of our outplanted species have limited South Florida distributions, this restoration provides important new populations for the region-wide conservation of these species. This preliminary data suggests that our ‘novel natives’ restoration model may represent an important perspective and provide an additional option to restoration practitioners for improving the conservation of biodiversity within metropolitan areas and other sites where traditional restoration and outplanting models are too difficult or costly to implement.

Key Words

Biodiversity, conservation, Florida, outplanting, restoration, tropical dry forest, tropical hardwood hammock

Introduction

Conserving biodiversity is particularly difficult in metropolitan areas. These spaces are particularly vulnerable to the past and enduring effects of anthropogenic disturbance, habitat fragmentation, and species invasions; all of which contribute to limited recruitment of native species that delay or substantially alter natural successional trajectories and inhibit the recovery of biodiversity. To address these impacts and overcome recruitment limitation, restoration projects often reintroduce and expand native plant populations through active outplanting. Given the strong anthropogenic impacts on natural areas and public lands in metropolitan areas, the restoration of regionally-native communities on diminished sites must necessarily rely on outplanting. Reintroducing and expanding native plant populations through active

outplanting has been utilized in restoration practice for decades as a means to overcome recruitment limitations, speed up natural successional processes, and promote restoration of biodiversity and ecosystem function (e.g., Robinson and Handel 2000; Hartman and McCarthy 2004; Rey Benayas et al. 2008). In this manuscript, we introduce a new model for restoration geared to enhance local biodiversity and conserve regional biodiversity in metropolitan areas through the use of ‘novel native’ species outplantings.

Our model of restoration developed for metropolitan landscapes necessarily focuses on restoring native communities via “reallocation”, whereby the restoration of regional ecosystems that can be self-sustaining in these highly modified landscapes are prioritized over historical ecosystems that cannot feasibly be recreated (see Choi 2004). As such, we define ‘novel natives’ as those species that (1) are not extant on the site or area of interest, but (2) do occur as native components of the regional species pool, and (3) are likely to thrive given the modern prevailing abiotic conditions. By evaluating the contemporary abiotic conditions within these sites and introducing the historical plant communities of the region that best match those conditions, restoration practitioners and land managers can enhance local biodiversity and conserve regional biodiversity.

Because this restoration model disregards the identity of the most recent natural community to occupy the site, it may seem to result from a pessimistic view of traditional restoration goals. We must stress that we are in no way suggesting that rare and threatened communities that face long odds should be simply relinquished or even hastened to extinction. Rather, we believe that limited resources and the unique complexities associated with urban and suburban ecosystems require prioritizing the restoration of communities in ways that best preserve native plant populations, resist

invaders, promote resilience in the face of disturbances, and provide reliable ecosystem goods and services, all while minimizing the potential costs associated with ongoing and future management (see Moore et al. 1999). As such, we present this model as a means to augment the available options for restoration practitioners and land managers, not limit them.

In South Florida's vast metropolitan areas, our model would predominately favor replacing irreversibly-destroyed or diminishing wetlands and fire-dependent communities with tropical hardwood hammocks, an upland climax community. Tropical hardwood hammocks are dense, late-successional tropical dry forests, endemic to rocky limestone outcrops in southern Florida, the Bahamas, and Cuba (FNAI 1990; Armentano et al. 2003). They are classified as globally and state imperiled owing to their inherent rarity and the threat of extinction because of development and alteration of the hydrology of the Everglades ecoregion (FNAI 1990). Because these communities feature a rich assemblage of woody plants, ferns, orchids, and lianas with mostly Neo-tropical and Caribbean affinities (Tomlinson 2001), they are often targeted by local, state, and federal land preservation initiatives. Despite these measures, nearly 11% of the remaining tropical hardwood hammocks in South Florida were destroyed in just a 14-year period ending in 2003 (Kautz et al. 2007). Yet, these communities have also been touted as an ideal habitat for the restoration of disturbed sites within the urban and suburban environs of South Florida (Gann 2006).

We used our 'novel natives' restoration model to guide outplanting species selection and habitat management in combination with high diversity outplantings in our efforts to restore a diverse and resilient tropical dry forest community on the site of

historical wetlands that, following a series of complex and irreversible anthropogenic modifications, had since transitioned into a highly-invaded, low diversity, urban woodlot. Below, we present two and a half years of survival, growth, and reproduction data from our tropical hardwood hammock outplantings at Swamp Fern Experimental Hammock and discuss the efficacy of the ‘novel natives’ restoration model with regards to outplanting establishment and biodiversity conservation.

Methods

Site Description and History

Restoration efforts took place in Swamp Fern Experimental Hammock in Miami-Dade County, Florida, on a 1.125 ha plot of county-owned land approximately 20 km west-south-west of downtown Miami (25.693860 N, -80.380396 W) (Figure 1). Swamp Fern Experimental Hammock, established in 2009, was the result of a public-private partnership between Miami-Dade County and the Florida Native Plant Society in which local FNPS members took the lead in the management and monitoring of a county-owned and protected woodlot surrounded by suburban development and adjacent to another disturbed woodlot (Figure 1). Additionally, Kendall Indian Hammocks Park, a 44.5 ha mixed-use public park with approximately 16 ha of hardwood hammock habitat is located less than half a kilometer away (Figure 1).

Because the site is dominated by woody broad-leaved species, it is generally similar in appearance to the native tropical hardwood hammocks of the area. However, this site differs from representative tropical hardwood hammocks in several important ways including having (1) reduced native species richness, (2) increased non-native species richness, (3) decreased tree density and basal area, (4) increased vegetative cover

between 0-1m from ground level, and (5) decreased and patchier canopy cover (>4m in height) (see Chapter 5). Also, the native species composition of the site features a higher ratio of plants with North American distributions at the expense of those with decidedly Northern Caribbean and Tropical American distributions than other Miami Rock Ridge tropical hardwood hammocks (see Chapter 5; also see Reardon and Brooks 2009 for species distribution grouping definitions). And perhaps most importantly for the community's long-term prospects, few native species are well-represented among new recruits in the seedling layer (see Chapter 5).

Several lines of evidence suggest that this site historically supported a very different vegetative community. Geological evidence of surface waters flowing over the site (S. Woodmansee, *pers. comm.*), and the presence of several mature but non-recruiting facultative and obligate wetland species including *Clematis baldwinii*, *Ilex cassine*, *Quercus laurifolia*, and *Persea palustris* (see Chapter 5), indicates that this site was likely much wetter than today. Additionally, 1938 aerial photos (USDA 1938), and the extremely uncommon presence of *Serenoa repens* in a closed-canopied hammock (see Chapter 5) – as is the case on the site today – suggest that this site historically also exhibited sparse or no tree canopy.

The concomitant lowering of water tables and the exclusion of fire disturbance fueled by encroaching development in the early to mid-1900s likely led to the subsequent succession over several decades from a marl prairie or pine rockland community to a hardwood stand. Because the site occurred on the western edge of the Miami Rock Ridge, the only sources of woody colonizers were likely present in the surrounding marl prairie and wet pine rocklands, and the nearby hydric hammocks identified in aerial

photos, many of which would be ill-suited to xeric conditions. As water levels dropped, any mature hardwoods on site could continue to rely on taproots to reach the water table, however, only drought-tolerant woody species were able to sustain recruiting populations. Given the lack of intact upland habitat in the area as long ago as 1938 to supply propagules in this drying landscape, abundant vacant niches ensured little competition for the widely-dispersing invasive plants that did establish. The result is the species-poor and highly-invaded upland hammock-like community that exists today.

Outplanting Design and Monitoring

Individuals were planted in experimental arrangements in June 2009 as part of a larger effort to restore woody richness and vegetative structure to levels recorded in mature reference hammocks and to test whether restoration of these habitats increased biotic resistance to invasive recruitment (these projects are elaborated on in other manuscripts). Active management was carried out regularly as part of the ongoing restoration of the site and to encourage the health and survival of outplanting populations while suppressing the exotic plants already established on the site. Management actions included: (1) the removal of native palm fronds, vines, and dead native biomass in the lowest three meters of the forest that threatened to crowd out or cover outplantings, (2) the application of herbicide to surviving exotic woody shrubs and trees, (3) the removal of exotic herb, vine, and woody recruit biomass, and (4) the felling of standing dead biomass from herbicide-treated exotic trees when possible.

Overall, we outplanted 540 nursery-grown plants representing 26 woody tropical hardwood hammock species native to the Miami Rock Ridge across a 2,250 m²

experimental section of the site (see Table 1 for species details). These species were selected on the basis of being available in local native nurseries and, with the exception of a single seedling of *Ocotea coriacea*, being absent from Swamp Fern Experimental Hammock. This ‘locally-absent’ determination was supported by our initial floristic survey of the site conducted several months before restoration efforts commenced (see Chapter 5). We timed our plantings to coincide with South Florida’s wet season to improve establishment rates (see Trusty and Ober 2011), especially since no supplemental watering was planned nor carried out. Upon planting, individuals were fitted with a metal tag inscribed with a unique ID to facilitate monitoring.

Outplantings were monitored regularly to assess their survival, growth, and reproduction. Data were collected beginning with their initial planting at the site in June 2009 and continued every four months through June 2011 with an additional survey conducted in December 2011, for a total of eight data collection periods. During each data collection period we noted mortalities of any outplanted individuals. We measured growth by recording the height (in cm) of all surviving individuals and measured reproduction by noting any evidence of blooming or fruiting. We also recorded any evidence of animal disturbance (including holes dug around outplantings or individuals that had been knocked over or uprooted), herbivory, invasive Lobate Lac Scale (*Paratachardina pseudolobata*) infestation, and whether individuals appeared to be suffering from water stress at time of survey. Uprooted individuals were re-planted whereas individuals that had been knocked over without major harm to their root systems were left unaided to avoid further damage. Besides replanting uprooted individuals no other interventions were administered for any of the aforementioned conditions. Finally,

floristic inventories of the site were conducted regularly to assess restoration impact on community development (see Chapter 5 for details) during which time potential recruits were identified and counted.

Analysis

To assess outplanting survival, we tabulated the number of surviving individuals and mortalities by species as of the last monitoring survey (December 2011). All statistical analyses were conducted with PASW Statistics GradPack 17.0.2 (2009). We compared outplanting survival across species using a chi-square test for independence. We also compared survival rates across time to discern any temporal patterns in the data, and inspected whether there may have been an association between outplanting mortality and animal disturbance, herbivory, presence of scale insects, or water stress (the latter analyses were performed without the aid of statistics).

Additionally, we sought to assess differences in the growth of outplantings across time and by species. Including only individuals surviving to the last data collection period, we subtracted the height of each individual in each data collection period from its height in the subsequent data collection period. Because the last data collection period in December 2011 was six months later than the previous period (while all other observations took place four months apart), we divided differences in growth between data collection periods by the number of months between the respective set of observations. The result was a standardized dataset featuring seven growth rates (in cm per month) for each surviving outplanted individual. These data were analyzed in a repeated measures ANOVA featuring growth rate as the dependent variable and species

as the independent variable. Simultaneous contrasts between each pair of growth rates from consecutive periods and a Tukey's Honestly Significant Difference test of species groups were applied to enhance interpretation.

Finally, because outplanted populations that are not reproductive cannot be self-sustaining, we wanted to analyze the reproductive activity of outplanted individuals. We compared the rates of individuals budding or blooming and those fruiting across time and by species. Additionally, we recorded the presence and abundance of recruits of outplanted species. Because of the scarcity of positive data to this preliminary juncture, these analyses were conducted without the use of statistics.

Results

Outplanting Survival

Overall, 455 of the 540 (84.3%) outplanted individuals had survived throughout the duration of monitoring after two and a half years. All outplanted populations persisted to the last data collection period and most species exhibited high survivorship. Sixty percent of all outplanting mortalities occurred within the first two monitoring periods (34 by October 2009, and an additional 17 by February 2010). The number of mortalities then averaged 1.25 per month through June 2011 before doubling in the period between June 2011 and December 2011 to 2.5 mortalities per month. The Chi-square test for independence indicated a large and significant association between species and survival rates between June 2009 and December 2011 (Pearson's $\chi^2_{(25, 540)} = 185.969$, $P < 0.001$, Cramer's $V = 0.587$). Seventeen species had survival rates exceeding 90% including eight species with no mortalities (Table 2). Only three species had outplanting

survival rates under 50% (*Byrsonima lucida*- 40%, *Prunus myrtifolia*- 37.5%, and *Myrica cerifera*- 23.8% (Table 2). In fact, these three species contributed to 44.7% of all recorded mortalities over the first two and a half years after outplanting.

Our analysis of potential causes of mortality revealed that at least 15 mortalities (17.65%) were associated with water stress, 10 (11.76%) with animal disturbance, two (2.35%) with herbivory, and one (1.18%) with scale infestation. Mortalities as a result of water stress, in particular, are likely under-reported because of our limited data collection schedule. Overall, invasive Lobate Lac scale infestation was the most commonly recorded condition among our outplantings with 119 individuals (22.04%) at some point exhibiting active infestation. Water stress (19.07% of individuals) and herbivory (18.52%) were also problematic, with animal disturbance (7.41%) much less so.

We noted variation in these factors across time and by species. Animal disturbance was most prevalent immediately after planting (Appendix 11). Herbivory increased to its maximum levels in June and October 2010 and subsequently declined (Appendix 11). Similarly, the number of individuals infected by scale insects increased through October 2010 before declining dramatically (Appendix 11). Finally, water stress was highly variable, but peaked in October 2010 and June 2011 (Appendix 11). The species most commonly impacted by animal disturbance included *Krugiodendron ferreum* (28.57% of individuals) and *Exothea paniculata* (23.81% of individuals) (Appendix 12). *Hamelia patens* (100% of individuals) and *Zanthoxylum fagara* (71.43% of individuals) were disproportionately targeted by herbivores while invasive scale insects disproportionately infested *H. patens* (95.24% of individuals) and *Sideroxylon salicifolium* (90.48% of individuals) (Appendix 12). Finally, water stress was most

prominent among *Calyptranthes pallens* (61.90% of individuals) and *Guettarda scabra* (50.00% of individuals) (Appendix 12).

Outplanting Growth

Different outplanted species exhibited different patterns of growth over time (Figure 2). In general, the mean outplanting growth rate varied over time, but was positive between all monitoring periods except between October 2009 and February 2010, coinciding with the advent of the first dry season after planting (Figure 3a). There were also significant differences in growth rates by species (Figure 3b). In all, 20 species had positive growth rates over the length of monitoring compared to only six species with negative growth rates (Table 2).

Outplanting Reproduction

Overall, we recorded 51 outplanted individuals (9.44% of all individuals, representing nine species) flowering at some point from June 2009 through December 2011 (Appendix 13). Meanwhile, only 25 individuals (4.63% of all individuals, representing six species) were recorded fruiting at some point during the period in question (Appendix 13). The majority of flowering and fruiting occurred in June 2009 at the time of planting as a result of conditions individuals experienced in nursery cultivation, but both metrics were showing slight signs of increasing again in 2011 (Appendix 14). The woody shrubs or small trees *G. scabra* and *Tetrazygia bicolor* were the most prolific bloomers with 65.00% and 61.90% of individuals blooming at some point, respectively (Appendix 13). Meanwhile, *B. lucida* and *Ilex krugiana* were the

most prolific fruit producers with 40.00% and 38.10% of individuals fruiting at some point, respectively (Appendix 13); however, the fruiting activity of these species was not recorded again since the initial time of planting. We recorded both blooming and subsequent fruiting in individuals of only three species (*Erythrina herbacea*, *H. patens*, and *Randia aculeata*) during our monitoring, suggesting that these populations are the most likely to expand rapidly in the near future within Swamp Fern Experimental Hammock.

We also recorded the presence of recruits of three of the species that we outplanted on the site during our regular floristic inventories: *E. paniculata*, *O. coriacea*, and *S. salicifolium*. Because of unusual circumstances in each case, however, we are hesitant to entirely credit this recruitment to our outplantings outright. We found two new *O. coriacea* recruits after outplanting and recording fruiting in this species, including one recruit within a meter of an outplanted conspecific; however, there was already a single seedling of this species on site prior to introducing our outplantings. A single *E. paniculata* recruit was found within a meter of an outplanted conspecific, but, we did not observe any of our outplanted *E. paniculata* in bloom or fruiting. Finally, we documented a single recruit of *S. salicifolium*, also without documenting flowering or fruiting in outplantings of this species. Both *Ocotea coriacea* and *S. salicifolium* have been recorded in adjacent Kendall Indian Hammocks Park (~400 m away) and all three species are present in the yard of a local native plant enthusiast (~ 200 m away).

Discussion

The preliminary survival, growth, and reproduction data presented in this manuscript demonstrates the potential of the ‘novel natives’ model of restoration to enhance local, and conserve regional, biodiversity in metropolitan areas. In restoring native tropical dry forest woody plant populations on a former wetland site in South Florida, we found high rates of survival and largely positive growth rates among species that were not historically present on the site. The overall survival and growth of our outplantings provide strong indications that we successfully matched these species’ habitat needs with the current conditions present at Swamp Fern Experimental Hammock. After two and a half years, reproductive rates were not yet adequate to demonstrate the long-term sustainability of these populations, possibly reflecting a significant lag time for the majority of outplantings to reach reproductive maturity and/or recover adequate energy stores following establishment. A positive trend, however, towards increased flowering and fruiting was evident in recent monitoring periods.

Efficacy of ‘Novel Natives’ Model of Restoration on Outplanting Establishment

Few empirical studies have focused on the survival, growth, and reproduction of woody species outplantings used in community restoration projects. Additionally, tropical dry forest systems are vastly underrepresented in the restoration literature (Vieira and Scariot 2006). As a result, it was difficult to assemble a representative sampling of woody species outplanting experiments, let alone those from tropical dry forests. The four projects we found reporting results focused on outplanting survival, with only one reporting growth and reproduction rates. Survival rates varied considerably: ~34% survival for woody trees and shrubs across all year cohorts between one to seven years

after planting (tropical dry forest; Cordell et al. 2008); between 38%-67% survival for each of five species after eight months, including 21% overall mortality after the first month (tropical dry forest; Ammond et al. 2013); 92% survival after three years (temperate eucalypt woodland; Wilkins et al. 2003); and ~55%-95% survival, ~25%-60% annual growth rate for height, and ~2%-16% reproduction rates based on management treatments after 9 years (Mediterranean woodland; Rey Benayas and Camacho-Cruz 2004). The survival, growth, and reproduction rates from our ‘novel natives’ outplantings relate well to these other findings from more traditional restoration projects, especially outperforming the survival rates from tropical dry forests.

The majority of outplanting mortalities concentrated in a few species. Our experience, therefore, supports Jelinski et al.’s (2011) contention that targeting high-diversity vegetation is an appropriate, bet-hedging strategy, even over the short-term for outplanting establishment success. The timing of planting, coinciding with the wet season (Trusty and Ober 2011), and the presence of a moderate layer of canopy across most of the site may have contributed to lower rates of mortality than otherwise might be expected given the lack of supplemental watering (see Khurana and Singh 2001; Cordell 2008). Interestingly, however, species survival and growth rates of outplantings were not necessarily correlated. For example, all but one of the six species with negative mean growth rates exhibited high survival. Meanwhile, the two species with lowest survival rates exhibited positive mean growth over time, suggesting that surviving individuals were doing quite well. The six species with negative mean growth rates (*C. pallens*, *E. paniculata*, *G. scabra*, *I. krugiana*, *K. ferreum*, and *O. coriacea*), were disproportionately impacted by animal disturbance, herbivory, invasive scale infestation, and water stress.

These factors, often in some combination, rather than the suitability of the site itself, may have contributed to their negative mean growth rates to this point. Given the density dependence of biotic interactions, we believe that animal disturbance, herbivory, and invasive scale infestation rates, in particular, could be expected to increase in less diverse and more highly concentrated plantings than those we employed.

Efficacy of ‘Novel Natives’ Model of Restoration for Biodiversity Conservation

Two and a half years after outplanting and active management began, the site the number of native species on the site increased from 36 to 58 native species, including from 16 to 41 woody species (see Chapter 5). As such, this model has greatly enhanced local native, and especially woody, species richness. Additionally, we have increased the conservation value of Swamp Fern Experimental Hammock because eight of our outplanted species are state-listed as ‘Threatened’ or ‘Endangered’ - double the number of listed species on the site prior to restoration.

From a regional perspective, nine of the species we outplanted are considered ‘Rare’ (fewer than 100 occurrences within the region) by the Institute for Regional Conservation, *Tournefortia hirsutissima* was considered ‘Imperiled’ (six to 20 occurrences within the region), while the rest were considered ‘Secure’ in South Florida (Gann et al. 2012; see Table 1). As such, we have provided additional insurance against potential range contractions of those ‘Rare’ species while adding a new and significant population of *T. hirsutissima*. In fact, *T. hirsutissima* thrived in Swamp Fern Experimental Hammock, with the greatest mean growth rate of all outplantings. The success of this species is even more surprising given its conservation status and state-

listed ‘Endangered’ designation. Our results suggest it may be an excellent candidate for further reintroduction along the Miami Rock Ridge, especially as part of other tropical hardwood hammock restorations.

Additional support for our ‘novel natives’ model can be found in studies that have attempted to increase the range of endangered species. In one example from tropical dry forests, Kawelo et al. (2012) successfully reintroduced an endangered Hawaiian vine beyond its historic range into other likely suitable habitat. The authors contend that this approach has reduced the likelihood of a stochastic extinction event for this species. Our model simply extends this species conservation approach to the restoration of whole plant communities.

Conclusions and Future Directions

We have demonstrated that the ‘novel natives’ model of restoration can have equivalent, and in some cases, better outcomes, relative to more traditional outplanting projects, at least in the first three years since introduction. In situations where the restoration of historic abiotic processes and conditions are not feasible, the ‘novel natives’ model provides another potential restoration perspective lying somewhere between the extremes of doing nothing and doing the impossible. As such, this model may allow for better outcomes with respect to the local enhancement and regional conservation of biodiversity, and potentially at reduced management costs over the long-term than more traditional outplanting-based restoration models. We stress again, that this model is presented as an additional option to the perspectives and options currently available to restoration practitioners, and should not be taken to suggest that restoration

ecology should adopt a “wave the white flag” strategy and abandon critically-imperiled populations or communities because of long odds or large expense.

With continued monitoring in the future, we hope to further validate the success of our ‘novel natives’ restoration model, especially for metropolitan-based restoration projects. Future research should focus on the degree to which the ‘novel natives’ outplanting model vs. active habitat management alone leads to the restoration of desired community composition and structure. Another important focus for future research should consider whether restoration efforts utilizing the ‘novel natives’ model result in reduced community invasibility, and other causes of future management costs relative to traditional outplanting and restoration models. Finally, it is obvious that there is a dearth of scientific literature documenting the success or failure of outplanting projects, generally, but particularly with respect to woody species. This lack of data, especially of projects featuring multiple species simultaneously, makes the comparisons that allow for valuable abstraction between projects difficult, and reduces the opportunities to further develop testable hypotheses that integrate knowledge to the benefit of both basic and applied ecological research.

Acknowledgements

We are extremely grateful to the meaningful contributions of M. Anderson Brooks, A. Brooks, A.W. Brooks, K. Brooks, L. Brooks, D. Howe, J. Klein, J. Possley, S. Thompson, and S. Woodmansee. Funding sources for this project were provided by a Conservation Award from the Florida Native Plant Society, an Academic Excellence Fund Award from the Graduate Program in Ecology and Evolution at Rutgers University,

as well as graduate support from USDA NRI 05-2221. We also thank A. Leonard and the Miami-Dade County Chapter of the Florida Native Plant Society for their support of this project. J. Lawson of Silent Natives Nursery cultivated the native outplantings and S. Woodmansee of Pro Native Consulting provided invaluable input on species selection. Access and permits for field work were secured from the Miami-Dade County Department of Parks and Recreation Natural Areas Management Division.

Table 1. Outplanted species including number of individuals planted and size of outplantings. ‘Conservation Status’ refers to the Institute for Regional Conservation’s regional ranking of a species’ conservation status in South Florida at time of publication (see Gann et al. 2012; rankings described in Gann et al. (2002)). ‘Listed Status’ refers to legal protected status provided by the State of Florida. All species names follow Wunderlin (1998).

Species	Number Planted	Size	Conservation Status	Listed Status
<i>Ardisia escallonioides</i>	25	1 gal.	Secure	n/a
<i>Byrsonima lucida</i>	20	1 gal.	Rare	Threatened
<i>Calypttranthes pallens</i>	21	1 gal.	Rare	Threatened
<i>Chiococca alba</i>	20	liners	Secure	n/a
<i>Chrysophyllum oliviforme</i>	21	1 gal.	Rare	Threatened
<i>Citharexylum spinosum</i>	21	1 gal.	Rare	n/a
<i>Coccoloba diversifolia</i>	21	1 gal.	Secure	n/a
<i>Erythrina herbacea</i>	20	1 gal.	Secure	n/a
<i>Eugenia axillaris</i>	21	1 gal.	Secure	n/a
<i>Exothea paniculata</i>	21	1 gal.	Secure	n/a

<i>Guapira discolor</i>	20	1 gal.	Secure	n/a
<i>Guettarda scabra</i>	20	1 gal.	Secure	n/a
<i>Gymnanthes lucida</i>	21	1 gal.	Secure	n/a
<i>Hamelia patens</i>	21	1 gal.	Rare	n/a
<i>Ilex krugiana</i>	21	1 gal.	Rare	Threatened
<i>Krugiodendron ferreum</i>	21	1 gal.	Secure	n/a
<i>Myrcianthes fragrans</i>	21	1 gal.	Rare	Threatened
<i>Myrica cerifera</i>	21	1 gal.	Secure	n/a
<i>Ocotea coriacea</i>	21	1 gal.	Secure	n/a
<i>Prunus myrtifolia</i>	16	1 gal.	Rare	Threatened
<i>Randia aculeata</i>	21	1 gal.	Secure	n/a
<i>Sideroxylon salicifolium</i>	21	1 gal.	Secure	n/a
<i>Simarouba glauca</i>	21	1 gal.	Secure	n/a
<i>Tetrazygia bicolor</i>	21	1 gal.	Rare	Threatened
<i>Tournefortia hirsutissima</i>	21	3 gal.	Imperiled	Endangered
<i>Zanthoxylum fagara</i>	21	1 gal.	Secure	n/a

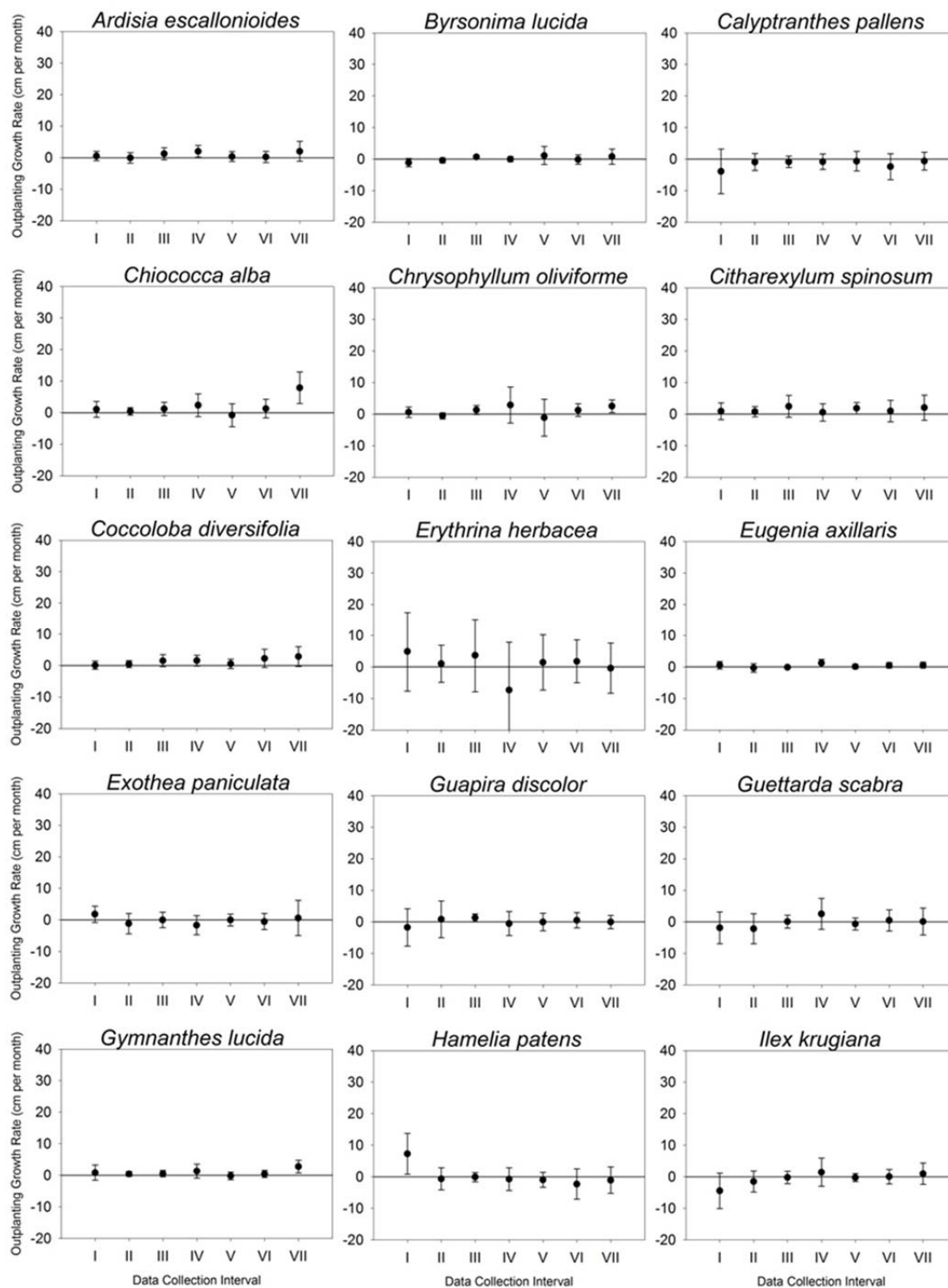
Table 2. Survival and growth rates of outplanted species. Survival is presented in % of outplanted individuals alive in December 2011. Growth rates are presented in cm per month as the mean rate of growth among all surviving outplanted individuals between June 2009 and December 2011. All species names follow Wunderlin (1998).

Species	Survival Rate	Mean
		Growth Rate (cm/month)
<i>Ardisia escallonioides</i>	96.0%	+0.92
<i>Byrsonima lucida</i>	40.0%	+0.15
<i>Calypttranthes pallens</i>	90.5%	-1.44
<i>Chiococca alba</i>	100%	+1.92
<i>Chrysophyllum oliviforme</i>	95.2%	+0.98
<i>Citharexylum spinosum</i>	95.2%	+1.37
<i>Coccoloba diversifolia</i>	100%	+1.31
<i>Erythrina herbacea</i>	85.0%	+0.71
<i>Eugenia axillaris</i>	100%	+0.35
<i>Exothea paniculata</i>	95.2%	-0.13

<i>Guapira discolor</i>	100%	+0.05
<i>Guettarda scabra</i>	60%	-0.21
<i>Gymnanthes lucida</i>	95.2%	+0.88
<i>Hamelia patens</i>	100%	+0.19
<i>Ilex krugiana</i>	76.2%	-0.58
<i>Krugiodendron ferreum</i>	76.2%	-0.13
<i>Myrcianthes fragrans</i>	100%	+0.59
<i>Myrica cerifera</i>	23.8%	+1.52
<i>Ocotea coriacea</i>	81.0%	-0.51
<i>Prunus myrtifolia</i>	37.5%	+0.50
<i>Randia aculeata</i>	100%	+1.04
<i>Sideroxylon salicifolium</i>	90.5%	+0.33
<i>Simarouba glauca</i>	90.5%	+0.56
<i>Tetrazygia bicolor</i>	95.2%	+0.19
<i>Tournefortia hirsutissima</i>	100%	+6.54
<i>Zanthoxylum fagara</i>	52.4%	+0.14



Figure 1. Aerial photographs of Swamp Fern Experimental Hammock in SW Miami-Dade County, FL in 1938 (left; USDA 1938) and 2011 (right; Google Earth 2011). The small polygon in each aerial designates the current extent of Swamp Fern Experimental Hammock, while the large polygon in each aerial designates the current extent of Kendall Indian Hammocks Park.



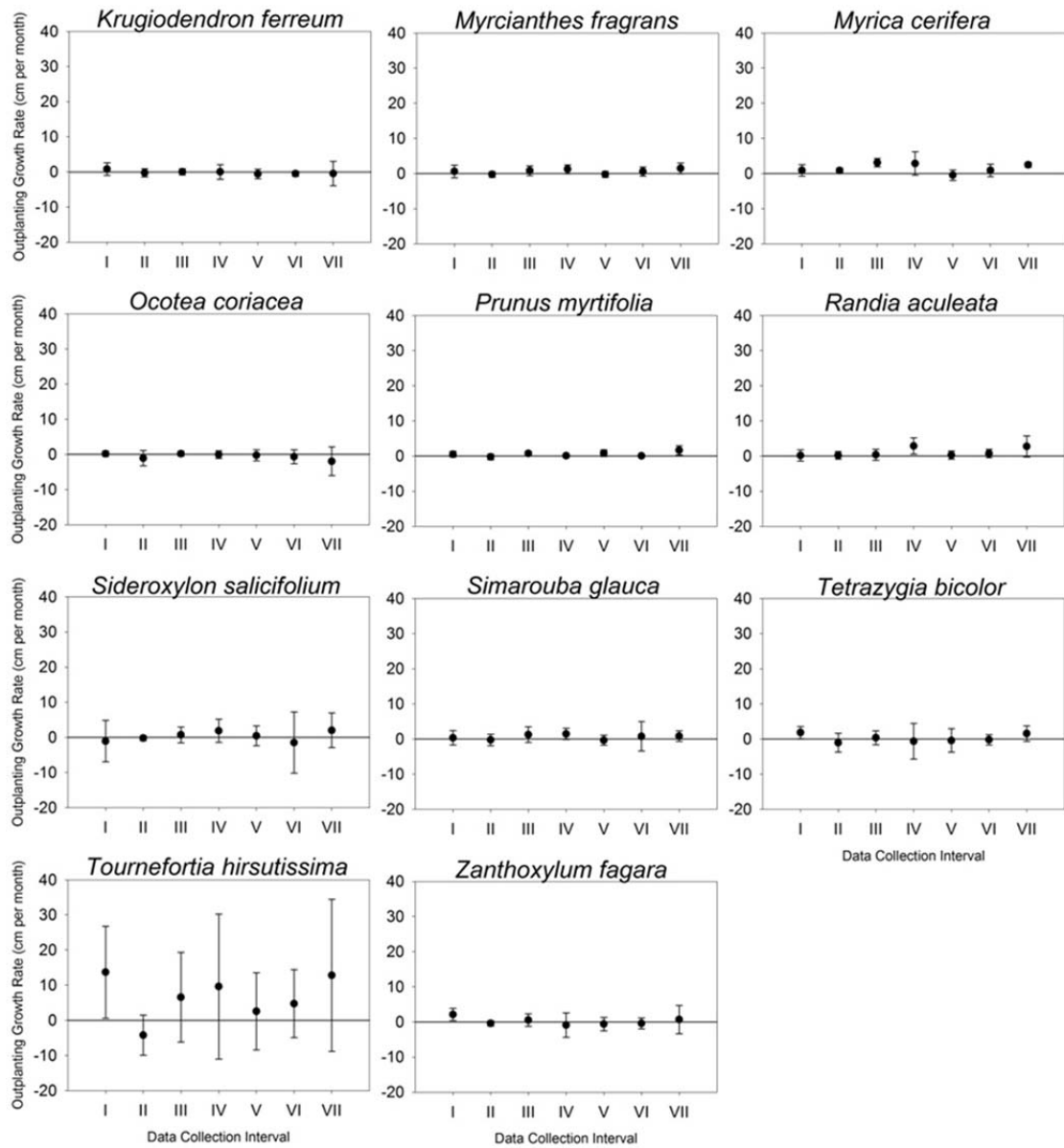


Figure 2. Mean outplanting growth rates over time by species. Error bars represent standard deviations. Data collection intervals include: I- Jun – Oct 2009; II- Oct 2009 – Feb 2010; III- Feb – Jun 2010; IV- Jun – Oct 2010; V- Oct 2010 – Feb 2011; VI- Feb – Jun 2011; and VII- Jun – Dec 2011.

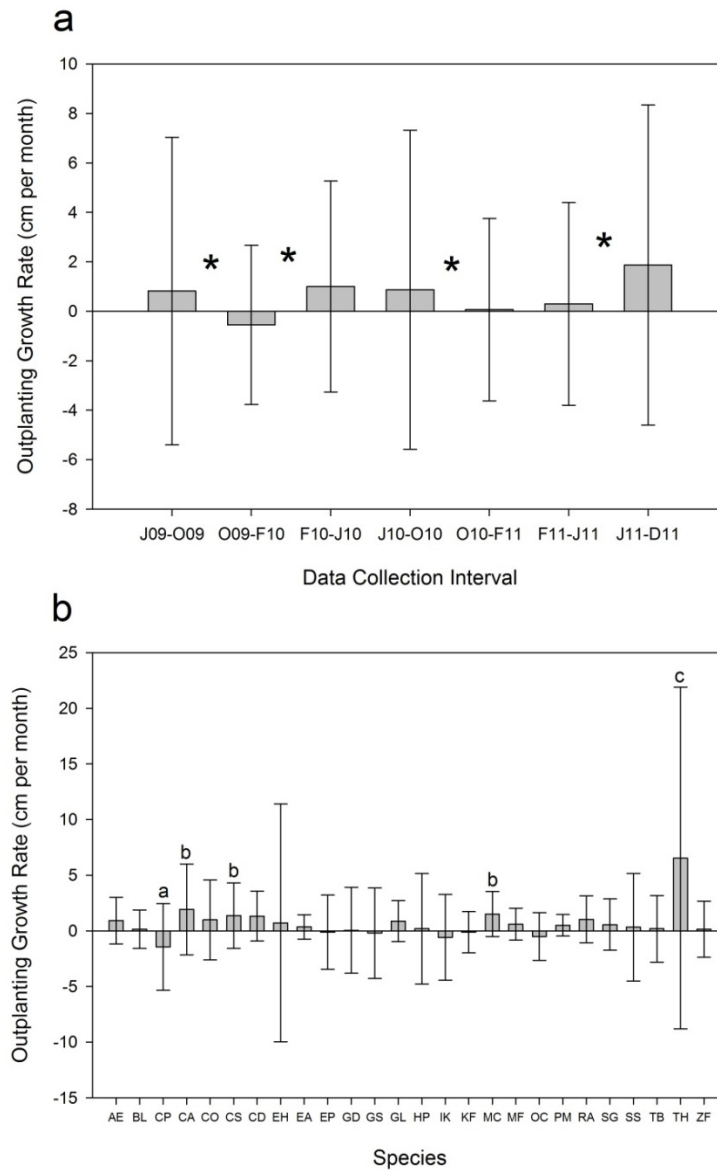


Figure 3. Outplanting growth rates. (a) Mean growth rates over time. Asterisks denote significant differences between consecutive observations. Error bars represent standard deviations. (b) Mean growth rates by species. Letters above bars indicate significant differences between groups (bars without letters indicate species with rates that were not significantly different from 'a' and 'b'). Error bars represent standard deviations. Species abbreviations represent the first letters of the genus and species names.

CHAPTER 5

EFFECTS OF HABITAT MANAGEMENT AND OUTPLANTINGS ON RESTORATION SITE COMMUNITY COMPOSITION AND STRUCTURE

Abstract

We sought to increase the conservation value and ecological resilience of a disturbed woodlot on protected land in suburban Miami-Dade County, Florida, by restoring a tropical hardwood hammock community. These efforts included adding 26 novel native tropical hardwood hammock species in different species richness and density treatments, and conducting regular habitat management actions including exotic biomass removal. We monitored a variety of community composition and structure variables to assess the success of our restoration efforts and the relative roles of habitat management vs. native outplantings in achieving those outcomes. Habitat management proved influential to changing community structure, while both habitat management and outplantings impacted changes in community composition, at least in the short-term. Habitat management and outplantings in combination, however, allowed us to successfully (1) increase the number of native species and decrease the number of exotic species, (2) increase the number of listed plant species on the site, and (3) alter the community composition and structure of the site from that of a highly disturbed woodlot to that of a typical Miami Rock Ridge tropical hardwood hammock. Our success in meeting these restoration goals in just two years is one such example where simple native outplanting and exotic control projects can produce large returns with minimal resources in the form of time, money, and manpower. Finally, the restoration of regrowth sites like

this one or other remnant habitats may prove an efficient and effective way to conserve biodiversity and basic ecosystem processes in close proximity metropolitan areas.

Key Words

exotics, Florida, monitoring, native species richness, principal components analysis, tropical hardwood hammock

Introduction

Exotic species control measures are often an integral part of comprehensive ecological restoration programs (Randall et al. 1997). Because of the sizable impacts of invasive exotics on habitat quality, exotic species control is an increasingly necessary component of habitat management, joining other measures including thinning young stands, reducing fuel loads, increasing the prevalence of snags, etc. Many conservation area managers spend the majority of their operating budgets on exotic species removal, leaving few resources for reinforcing native ecosystem components, including expanding rare and threatened populations and communities (D'Antonio and Meyerson 2002). However necessary, exotic species control alone is often insufficient to promote restoration of native systems because many non-native species are “passengers” rather than drivers of change (MacDougall and Turkington 2005). Even following exotic species control and other habitat management measures, native species and communities may remain diminished as a result of significant recruitment limitations.

One of the most common restoration strategies to overcome these recruitment limitations involves outplanting native populations (e.g., Hartman and McCarthy 2004;

Lamb et al. 2005; Rey Benayas et al. 2008). Outplantings may also be useful for increasing diversity, accelerating succession, and inhibiting species invasions (Hartman and McCarthy 2004). While both habitat management and outplanting strategies would ideally go hand-in-hand, conservation area managers and restoration practitioners often need to guide scarce resources where they will provide the most benefits. Yet, there is a lack of consideration as to whether habitat management (including exotic species removal) or outplanting native populations is a more effective strategy for restoring desired community composition and structure.

We used an experimental approach in our efforts to restore a species-rich tropical hardwood hammock that would exhibit increased resilience and conservation value at Swamp Fern Experimental Hammock (SFEH), previously the site of a highly invaded and low diversity urban woodlot. Tropical hardwood hammocks are characterized as discrete islands of tropical dry forest habitat composed of mixed tropical hardwoods on mesic, limestone substrate with rare or no fire (FNAI 1990; Armentano et al. 2003). Because of their unique mix of plant species and their geographic limitation to South Florida, the Bahamas, and Cuba, they are considered globally-imperiled communities (FNAI 1990; USFWS 1999), and have been touted as ideal habitats for restoration projects in metropolitan areas of South Florida because they can succeed on relatively small plots of land and are not fire-dependent (Gann 2006).

Our short-term restoration goals at SFEH included:

- Increasing native species richness and decreasing exotic species richness,
- Increasing the number of listed plant species on site, and

- Providing momentum for changing the community composition and structure towards that of a typical Miami Rock Ridge tropical hardwood hammock

In this manuscript, we document our progress towards meeting these goals and assess the relative contributions of habitat management vs. outplanting to that progress.

Additionally, we used outplantings in varying species richness and density levels to test the efficacy of experimental treatments in producing measurable changes in community composition and structure as a means to inform future restoration practice.

Methods

Site Description

Our restoration experiment utilized a 1.125 ha plot of county-owned land, protected from further development, approximately 20 km west-south-west of downtown (25.693910 N, -80.380305 W). It is bounded on the North and South by paved roads and on the East and West by developed lands. SFEH is in immediate proximity to another disturbed woodlot and to Kendall Indian Hammocks Park, a 44.5 ha park with approximately 16 ha of tropical hardwood hammock habitat. Appendix 15 features a short summary of historical changes at SFEH.

Floristic Surveys

In December of 2008, we laid out a grid of 150 adjoining 3 m x 5 m quadrats on an area extending 30 m by 75 m in the interior of SFEH (Appendix 16). The outermost quadrats along the perimeter of this grid, 58 in all, were set aside as “buffer quadrats”, physically separating the remaining 92 “interior quadrats” from untreated areas of the site

(Appendix 16). In March of 2009, we conducted our first survey of our interior and buffer quadrats to provide insight into floristic community composition and structure. We documented the occurrence and native status of all plant species rooted in the quadrat, as well as those epiphytes visible occurring in the vertical space above the quadrat, utilizing Wunderlin (1998), Nelson (2000), and Brown (2006) for plant identification. We categorically estimated the vegetative cover of each quadrat using Daubenmire cover classes (1: 0-5%, 2: 5-25%, 3: 25-50%, 4: 50-75%, 5: 75-95%, 6: 95-100%; see Elzinga et al. 1998) at ground (<1 m height), subcanopy (1-4 m height), and canopy (>4 m height) levels above the forest floor. For each species rooted in the quadrat, we recorded the number of woody individuals greater than one meter in height, and the basal area, in cm^2 , at breast height for all stems greater than 2.5 cm diameter-at-breast-height. To avoid boundary bias (see Elzinga et al. 1998), we included all individuals occurring on the northernmost and easternmost boundaries of each quadrat (one 3 m side and one 5 m side), and excluded all individuals along the southernmost and westernmost boundaries in our density and basal area metrics of each quadrat such that all individuals in the grid space were accounted for but none were double counted. These floristic surveys were later repeated every six months for interior quadrats only beginning in December 2009 through June 2011 (five total data collection periods including March 2009).

Prior to surveying SFEH we sought to obtain similar data from reference habitats. We conducted floristic surveys of thirteen tropical hardwood hammocks along the Miami Rock Ridge from North Miami to Long Pine Key, Everglades National Park between August 2007 and March 2008 (see Brooks et al. 2013 for details). We set four evenly-

spaced 3 m x 5 m quadrats (each quadrat five meters apart from the previous) along each of three 40 m transects within each hammock, each randomly generated and investigated for appropriateness using aerial photographs and GIS tools. We used PVC pipe markers and rope to temporarily identify the boundaries of each quadrat during surveying. We collected the same data utilizing the same methods from each reference quadrat as described above for SFEH interior quadrats, however, we did not resample reference hammock quadrats across time.

Outplanting Treatment Design

We utilized different outplanting treatments to assess the efficacy of different species richness (SR) and density (DEN) combinations on the community composition and structure of the restored hammock. As such, the 92 interior quadrats were managed for habitat quality and were randomly assigned to one of the following outplanting treatment groups (see Appendix 16):

- (1) 18 ‘high DEN x high SR’ quadrats to which we added two individuals of each of six species (12 total)
- (2) 18 ‘high DEN x low SR’ quadrats to which we added five individuals of each of two species (10 total)
- (3) 18 ‘low DEN x high SR’ quadrats to which we added one individual of each of six species (six total)
- (4) 18 ‘low DEN x low SR’ quadrats to which we added one individual of each of two species (two total)
- (5) 20 ‘control’ quadrats to which we added no additional individuals

Species selection was guided by our ‘novel natives’ model of restoration (see Chapter 4). This model relies on successfully matching native species from the regional species pool to the contemporary abiotic conditions they are likely to experience at the site rather than seeking to restore abiotic conditions and rely on passive recruitment (see Chapter 4). Twenty-six woody tropical hardwood hammock species native to the Miami Rock Ridge and available from local native nurseries were selected for outplanting (see Appendix 17). With the exception of *Ocotea coriacea*, for which a single seedling was found on site prior to restoration, all outplanted species were documented as absent from SFEH prior to restoration (see Appendix 17). The specific species outplanted in each experimental quadrat were randomly assigned from the available pool of 540 individuals of 26 native species. We planted individuals in June 2009 and relied solely on precipitation for outplanting establishment.

Habitat Management

As part of our plan to meet our restoration goals and facilitate our experiment, active management was carried out during the set of three to five days spent working on the site during each data collection period (10 periods from June 2009 through December 2011). Such actions may have included any of the following as needed within both buffer and interior quadrats, including:

- (1) manual removal of exotic herb and vine and woody seedling biomass (and small woody shrubs in June 2009 only),
- (2) application of herbicide to surviving exotic woody shrubs and trees,
- (3) felling of dead biomass from herbicide-treated exotic trees when possible,

- (4) felling of dead native biomass in the subcanopy layer (1-3 m height), and
- (5) removal of native palm fronds and vines in the subcanopy and sapling (<1 m height) layers that threatened to crowd out or cover outplanted individuals.

These actions were designed to suppress exotic plants already established within the experimental grid, limit the opportunity for aggressive exotic vines to climb into the existing canopy, and to encourage the health and survival of outplanting populations (see Appendix 18 for detailed exotic control information).

Statistical Analyses

We converted all canopy, subcanopy, and ground cover data collected from Daubenmire cover class values to the median percentiles from their representative ranges (i.e., 1= 2.5%, 2= 15%, 3= 37.5%, 4= 62.5%, 5= 85%, 6= 97.5%). These converted data formed our canopy, subcanopy, and ground cover variables. We also created variables representing native species richness, exotic species richness, and woody plant density and total basal area (both irrespective of native-exotic status), with the information from our floristic surveys. Our native and exotic species richness variables were taken directly from the species occurrence list from each quadrat. To develop our woody plant density and total basal area variables, we separately summed across all species the number of individuals greater than one meter in height, and the basal areas of all individuals greater than 2.5 cm diameter-at-breast-height, respectively per quadrat.

All statistics were analyzed with PASW Statistics GradPack 17.0.2 (2009). To test whether our experimental outplanting treatments impacted the community composition and structural characteristics of SFEH quadrats over the course of our

restoration, we utilized a series of independent repeated measures ANOVAs. Canopy cover, subcanopy cover, ground cover, woody plant density, total basal area, native species richness, and exotic species richness were set individually as dependent variables with outplanting treatment group identity as the independent factor in all analyses and applied a Bonferroni correction to maintain a global- α error rate of 0.05 ($p=0.007$ set as the cutoff for statistical significance for each test). Simultaneous contrasts between each pair of consecutive data collection periods and a Tukey's Honestly Significant Difference test of outplanting treatment groups were applied to each analysis to enhance interpretation.

We also assessed the degree to which these restoration efforts succeeded in changing the community composition and structure of SFEH to be more in line with reference sites. First, we created a dataset featuring canopy cover, subcanopy cover, ground cover, native species richness, exotic species richness, woody plant density, and total basal area variables for all reference quadrats and pre- and post-restoration observations of each SFEH interior quadrat (March 2009 and June 2011 data periods, respectively). We then ran a Principal Components Analysis. All components with eigenvalues exceeding one were retained and a varimax rotation was performed to enhance interpretation. Scores of retained principal components for reference and experimental quadrats were then entered as dependent observations in a MANOVA with hammock identity as the independent variable to assess differences between hammocks across principal components.

Results

Floristic Surveys

All species recorded in buffer and interior quadrats of SFEH are detailed in Appendix 17 and follow the nomenclature of Gann et al. (2012). In March 2009, in surveys including both buffer and interior quadrats, we found 36 native and 28 exotic species, of which only three natives and two exotics found in buffer quadrats were not also found in interior quadrats. Of the 33 native species found in interior quadrats, four were listed as protected species by the State of Florida: *Tillandsia balbisiana*, *Tillandsia fasciculata* var. *densispica*, *Tillandsia utriculata*, and *Zamia integrifolia*. Meanwhile, of the 26 exotic species found in interior quadrats, 14 were classified as Invasive (Category I) and three as Potentially Invasive (Category II) by the Florida Exotic Pest Plant Council (FLEPPC) (FLEPPC 2011).

By June 2011, the number of native species in the interior quadrats had increased to 58 and exotic species richness had fallen to 14. Besides the ‘novel natives’ we added as part of our outplantings, the ruderal herb *Bidens alba* var. *radiata* and the epiphytic fern *Phlebodium aureum* were new to SFEH interior quadrats. The addition of eight state-listed species via outplantings and the loss of two previously recorded epiphytic bromeliads (*T. balbisiana* and *T. utriculata*) brought the number of protected species in the experimental plots to 10. Among the exotic species, 13 species including three invasive and three potentially invasive FLEPPC-listed species were eliminated from interior quadrats, while *Cupaniopsis anacardioides*, another Category I invasive, was the only new exotic species recorded in June 2011 that wasn’t found in our initial floristic survey. Four other species (two native and two exotic) were documented after March 2009, but did not persist to be recorded in June 2011.

Relative to the initial floristic inventory, in June 2011 37 species were less widely distributed among interior quadrats, 15 species' distributions did not change, and 17 species (43 including those we outplanted) became more widely distributed. Our restoration efforts clearly benefitted native species at the expense of exotics; of the 37 species with declining distributions, only 13 (35.1%) were natives, while natives also made up 14 (82.4%) of the 17 species with increasing distributions. Furthermore, the 11 species with the greatest reductions in distribution from March 2009 to June 2011 were all exotics, while the eight species with greatest increases, excluding outplanted species, were natives.

Meanwhile, in our floristic surveys of reference hammocks, we found 142 native species and 49 exotic species (for full list of species reported, see Brooks et al. 2013). Native species distribution patterns were generally similar to our findings in SFEH; most species were rare with 92 (64.8%) of all natives and 42 (85.7%) of all exotics found in 10 or fewer quadrats (Brooks et al. 2013). *Ocotea coriacea* was the most commonly found native species, reported in 85.3% of reference quadrats, while *Bursera simaruba*, *Psychotria nervosa*, and *Quercus virginiana* were the only species that were found in each of our reference hammocks (Brooks et al. 2013). Of the species documented in the June 2011 survey of SFEH, 52 of 58 native species (including 25 of 26 of our outplanted species) and 9 of 14 exotic species were also documented in at least one of the reference hammock surveys.

Efficacy of Restoration Efforts

Our series of independent repeated measures ANOVAs detected significant changes amongst our community structure metrics. Canopy cover decreased initially and has since recovered and surpassed pre-restoration levels (Figure 1a; Appendix 19). Subcanopy cover has generally declined by half over the two years of observation (Figure 1b; Appendix 20). Meanwhile, ground cover in different outplanting treatments varied over time (Appendix 21). Ground cover decreased by nearly half to December 2010 before exhibiting a slight increase (Figure 1c). Additionally, quadrats with high density and high species richness outplantings had consistently greater ground cover levels than those with low density and low species richness outplantings (Figure 2). Like canopy cover, total basal area was initially reduced, but has since rebounded and exceeded pre-restoration levels (Figure 1d; Appendix 22). Lastly, we did not detect a significant change in woody plant density (Appendix 23).

All of our community composition variables (native species richness and exotic species richness) were significantly impacted in the restoration of SFEH. The native species richness of quadrats responded to different outplanting treatments in different ways over time (Appendix 24). In particular, high species richness treatment groups had significantly greater species richness levels than all other groups while low species richness treatment groups did not statistically differ from the control group (Figure 3a). Nevertheless, all outplanting treatments groups experienced increase in native species richness after restoration began (Figure 3b). After outplanting, the ranking of outplanting treatment groups by native species richness did not change over the course of the first two years of monitoring, though the low density and low species richness outplanting group had essentially fallen to control group levels of native species richness (Figure 3b).

On the whole, native species richness increased immediately after restoration began and peaked in June 2010 followed by a slow decline thereafter (Figure 4a). With respect to exotic species richness, there was no discernible effect of outplanting treatment (Appendix 25), but exotic species richness decreased substantially over time across the site (Figure 4b).

Principal components analysis revealed three components with eigenvalues exceeding one, explaining 30.65%, 19.61%, and 15.15% of the variance, respectively, for a cumulative total of 65.41%. Our rotated solution revealed all variables loading strongly on a single component with the exception of woody plant density and canopy cover which both loaded strongly on two components (Table 1). PC1 appeared to represent mainly community composition with native species richness and woody plant density loading positively, and exotic species richness loading negatively. PC2 appeared to represent community structure with woody plant density, subcanopy cover, and ground cover loading positively, and canopy cover loaded negatively. Finally, PC3 appeared to represent community maturity with total basal area and canopy cover loading positively.

Our MANOVA indicated significant differences between hammocks based on the principal component scores of each quadrat (Appendix 26). Specifically, there were significant differences between hammocks along PC1 (Figure 5a) and PC2 (Figure 5b), but not PC3 (Appendix 27). Our restoration efforts succeeded in altering the community composition (PC1) and community structure (PC2) characteristics of SFEH. Restoration efforts moved SFEH quadrats closer to reference quadrats in multi-dimensional space along PC1, but further from reference quadrats along PC2 relative to pre-restoration quadrats (Figures 6 and 7).

Discussion

In just two years we have succeeded in meeting all three of our short-term goals for the restoration of Swamp Fern Experimental Hammock (SFEH). We have increased the conservation value of SFEH by increasing the number of natives species by 61%, including adding seven state-listed threatened or endangered plant species, and reducing the number of exotics by half. Additionally, changes in the community composition of our interior quadrats with the addition of ‘novel native’ outplantings and the active removal of exotics contributed to SFEH becoming more representative of other Miami Rock Ridge tropical hardwood hammocks. However, outplanting treatments were not effective in measurably increasing woody plant density across the site. Meanwhile, our habitat management appeared responsible for shifting the community structure of SFEH to become more distinct from that of our reference sites. Therefore, if changes in community composition are preserved and habitat management is ended, SFEH should move quickly to be quite representative relative to other Miami Rock Ridge tropical hardwood hammocks.

Effects of Outplanting Treatments

The addition of ‘novel native’ species via outplantings did not necessarily result in statistically detectable increases in species richness across treatment groups. The addition of six species (via the high species richness addition treatments) successfully increased mean native species richness while the addition of two species (via the low species richness addition treatments) did not increase mean native species richness relative to control plots. Additionally, the persistence of species richness levels following

outplanting was not impacted by outplanting density. This result is likely attributable to the high survival of most outplanted species (see Chapter 4), but given that Robinson and Handel (2000) noted that woody plant diversity increased only slightly in the decade following their outplanting-based restoration, it could also be an artifact of the relatively short duration of this experiment to date (but see Ruiz-Jaén and Aide 2005).

The addition of novel native species, along with the simultaneous reduction in exotic species through habitat management, was also responsible for increasing the floristic similarity of SFEH quadrats to our reference hammocks; SFEH went from being floristically unique to being indistinguishable from Arch Creek Park, Fuchs, Harden, and Simpson Park hammocks. This is impressive considering that a restoration of Eucalypt woodlands in Australia found no clear evidence of a successful transition to reference vegetation and concluded that the development of restored species composition may take decades or more (Wilkins et al. 2003). With regards to tropical hardwood hammocks in South Florida, Brooks et al. (2013) surmised that differences in community composition were reflective of an anthropogenic disturbance gradient. If this is true, our outplanting efforts at SFEH have succeeded in concealing the lasting biotic legacy of anthropogenic disturbance at this site.

Outplantings did not seem to influence community structure variables with the possible exception of ground cover. We found a significant difference in ground cover between outplanting treatments, however, this pattern was evident among these quadrats prior to outplanting in March 2009 as well. Yet, given that most outplanting biomass was located in the first meter from the ground at planting, it is possible that the high density treatment quadrats maintained higher ground cover levels than low density and control

quadrats after June 2009 as a direct result of outplantings. Meanwhile, other studies have found an influence of outplantings on community structure. Ruiz-Jaén and Aide (2005) detected changes in vegetation height and herbaceous cover three years after outplanting seedlings while Wilkins et al. (2003) detected improved structural development and a reduction in ground cover in restoration sites 10 years after outplanting saplings.

Effects of Habitat Management

The majority of community structure measures were clearly impacted by habitat management as opposed to being affected by our outplanting treatments. Canopy cover, subcanopy cover, ground cover, total basal area, and exotic species richness all declined immediately and dramatically following the implementation of our exotic control efforts in June 2009. Once exotic control efforts began, extant native populations responded positively; canopy cover recovered by December 2010 and total basal area recovered and exceeded original levels by June 2011. Hughes et al. (2012) found similar and strong recovery responses of native biomass in tropical forests of American Samoa after the strategic elimination of the dominant invader of those forests. Additionally, after declining to a low in December 2010, ground cover levels began to increase, corresponding with the slow removal of persistent and prevalent exotic ferns and the increase in distribution and abundance of the native fern *Blechnum serrulatum* and grass *Oplismenus hirtellus*. There were also small increases in mean quadrat native species richness between October 2009 and June 2010 followed by small decreases thereafter that may have been associated with the changes in canopy cover brought about by exotic removal and native recovery.

Conclusions

Our pairing of habitat management and outplantings was critical in successfully meeting our short-term restoration goals within two years. Our experience at SFEH demonstrates that a simple outplanting project combined with modest habitat management can produce large returns with minimal resources in the form of time (~300 hours over two years), money (~\$3000, mostly for purchasing outplantings), and manpower (one to two persons at any given time), in contrast to the widely-held notion that restoration must be time-consuming and expensive (Holl et al. 2003). Habitat management proved to be more effective for manipulating community structure metrics than outplantings. Outplantings, meanwhile, provided a rapid way to impact community composition, although exotic control efforts associated with habitat management also played a role in changing the floristic character of the restoration site. Thus, habitat management was more influential to the results of our restoration efforts; however, we stress that these data represent only two years of monitoring. Further monitoring of outplanting treatment quadrats at SFEH will provide more data regarding the potential link between outplantings and ground cover levels, as well as the long-term potential impacts of outplantings on community structure.

Additionally, patterns of community compositional and structural recovery in SFEH may be associated with the fact that this site had already experienced years of natural regrowth prior to the commencement of restoration efforts. As such, other patches of regrowth or remnant vegetation in human-modified landscapes may represent the low-hanging fruit of restoration practice whereby managers can achieve restoration goals relatively quickly and inexpensively. The restoration of these sites through habitat

management and outplanting of appropriate species may prove an efficient and effective way to conserve biodiversity and basic ecosystem processes in close proximity metropolitan areas.

Implications for Practice

- Focusing habitat management and outplanting efforts on areas of remnant vegetation and regrowth may provide more “bang for the buck” in meeting conservation goals than “starting from scratch”.
- Recurring site monitoring and exotic control efforts can compensate for any opportunities for re-infestation or new invasions following the initial disturbance associated with restoration activities.
- Removing extant exotic biomass may be the single most effective tool for reducing sources of future invasive recruits and reshaping the trajectory of future community composition and structure.
- Haphazard additions of native species and individuals to a site may not necessarily lead to measurable increases in native species richness and plant density across the site.
- Scientific evidence and reasoning should be applied to every aspect of planning ecological restorations and implemented in combination with a long-term monitoring regime, not only to ensure better odds of restoration success, but also to collect and secure useful knowledge for future restoration endeavors.

Acknowledgments

We are extremely grateful to M. Anderson Brooks, A. Brooks, A.W. Brooks, K. Brooks, L. Brooks, D. Howe, J. Klein, J. Possley, S. Thompson, and S. Woodmansee for their contributions. Funding sources were provided by a Conservation Award from the Florida Native Plant Society, an Academic Excellence Fund Award from the Graduate Program in Ecology and Evolution at Rutgers University, and graduate support from USDA NRI 05-2221. We also thank A. Leonard and the Miami-Dade Chapter of FNPS for their support. J. Lawson of Silent Natives Nursery cultivated all outplantings and S. Woodmansee of Pro Native Consulting provided valuable input on species selection. Permission for work at Swamp Fern Experimental Hammock was secured from the Miami-Dade County Department of Parks and Recreation Natural Areas Management Division.

Table 1. Rotated component matrix for experimental and reference quadrat floristic and community data. Only strongly loading components are shown.

Variable	Loadings		
	PC1	PC2	PC3
Canopy Cover		-0.388	0.635
Subcanopy Cover		0.771	
Ground Cover		0.704	
Woody Plant Density	0.682	0.492	
Total Basal Area			0.804
Native Species Richness	0.842		
Exotic Species Richness	-0.784		

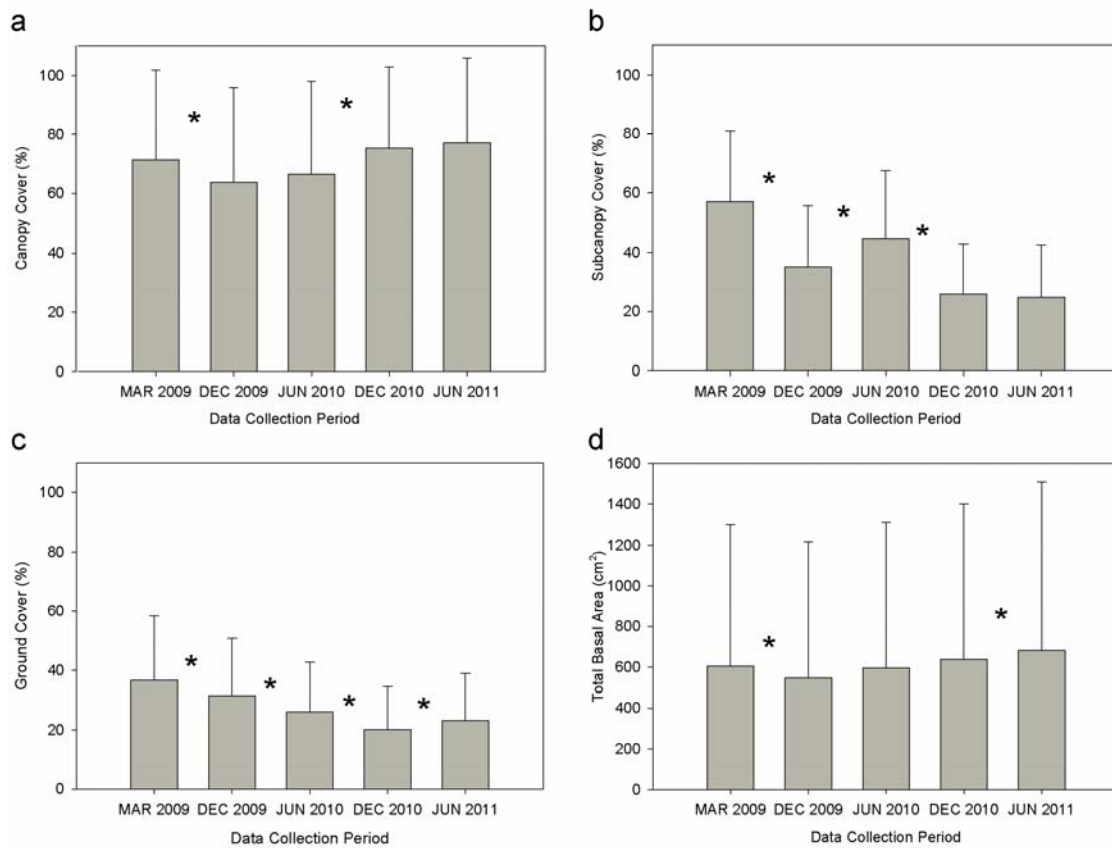


Figure 1. Significant changes in Swamp Fern Experimental Hammock community structure over time. Asterisks denote significant differences between consecutive observations. Error bars represent standard deviations. (a) Mean canopy cover of interior quadrats over time. (b) Mean subcanopy cover of interior quadrats over time. (c) Mean ground cover of interior quadrats over time. (d) Mean basal area of interior quadrats over time.

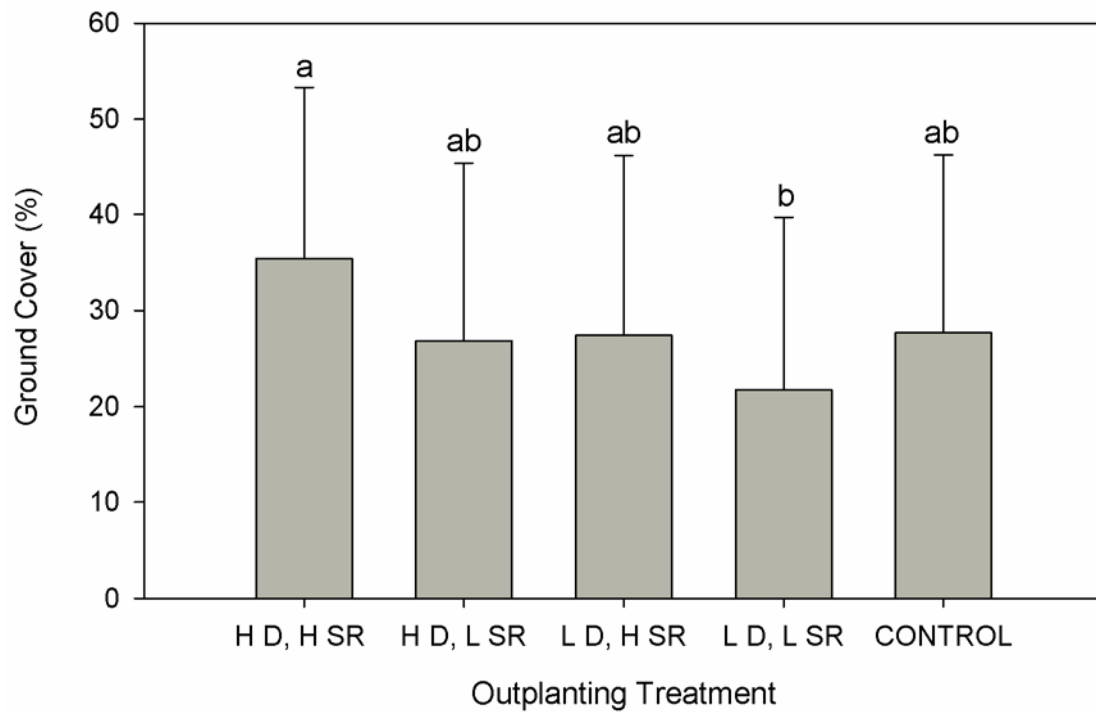


Figure 2. Mean ground cover of Swamp Fern Experimental Hammock interior quadrats by outplanting treatment. Letters above bars indicate significant differences between groups. Error bars represent standard deviations.

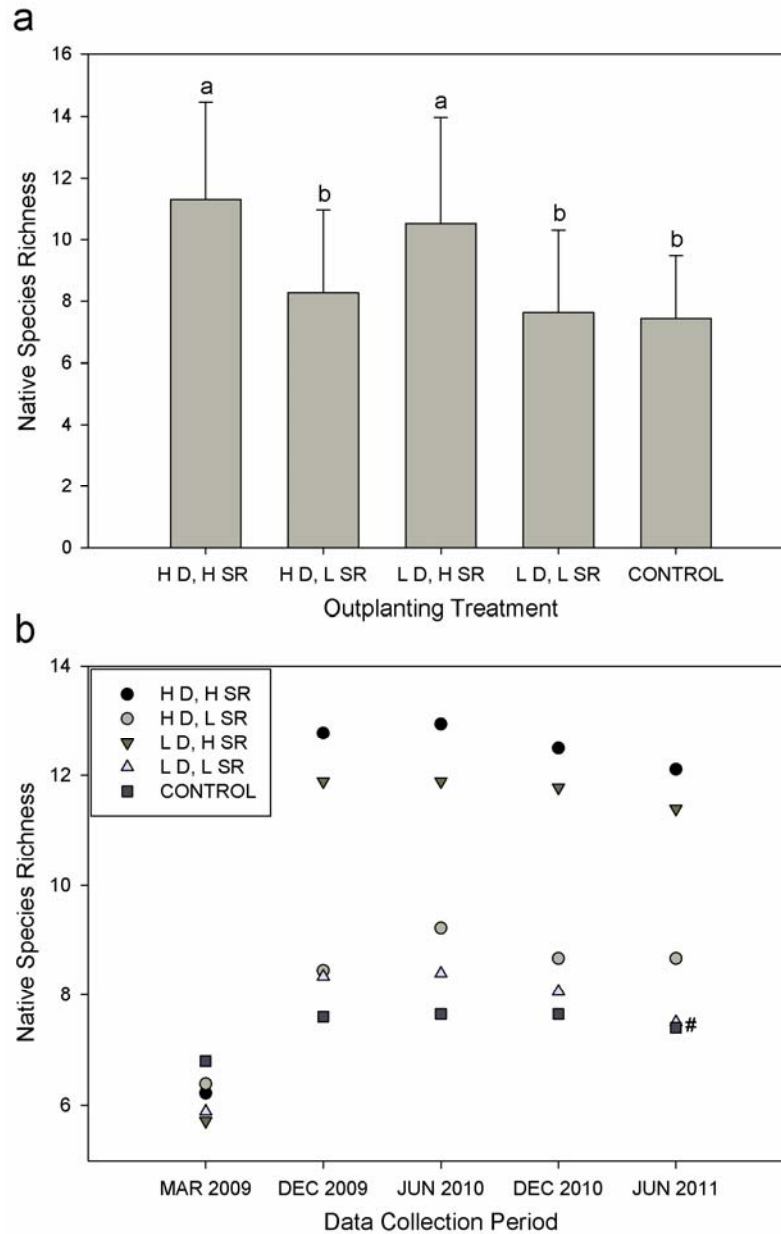


Figure 3. Mean native species richness of Swamp Fern Experimental Hammock interior quadrats. (a) Mean native species richness by outplanting treatment. Letters above bars indicate significant differences between groups. Error bars represent standard deviations. (b) Mean native species richness by outplanting treatment over time. A hashmark (#) indicates that symbols were offset slightly in graphical space to improve legibility.

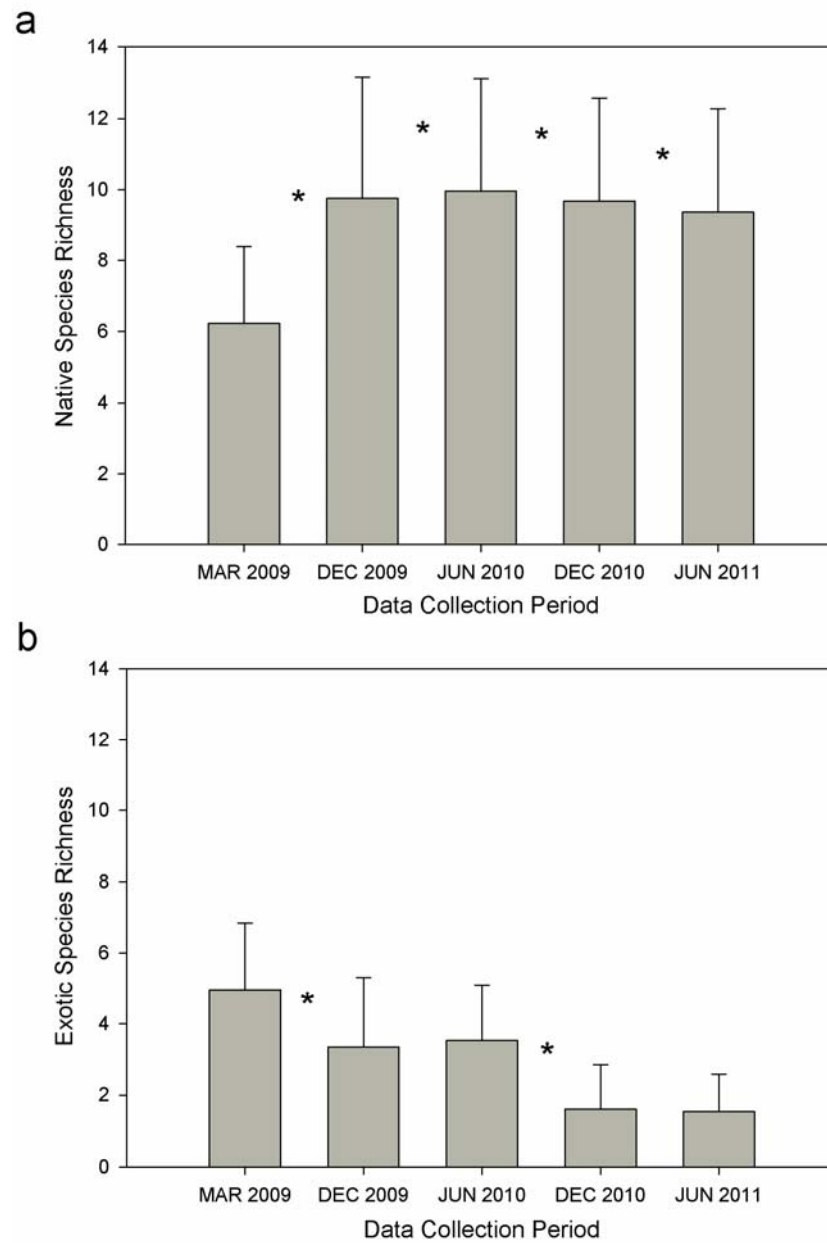


Figure 4. Species richness of Swamp Fern Experimental Hammock interior quadrats over time. Asterisks denote significant differences between consecutive observations. Error bars represent standard deviations. (a) Mean native species richness over time. (b) Mean exotic species richness over time.

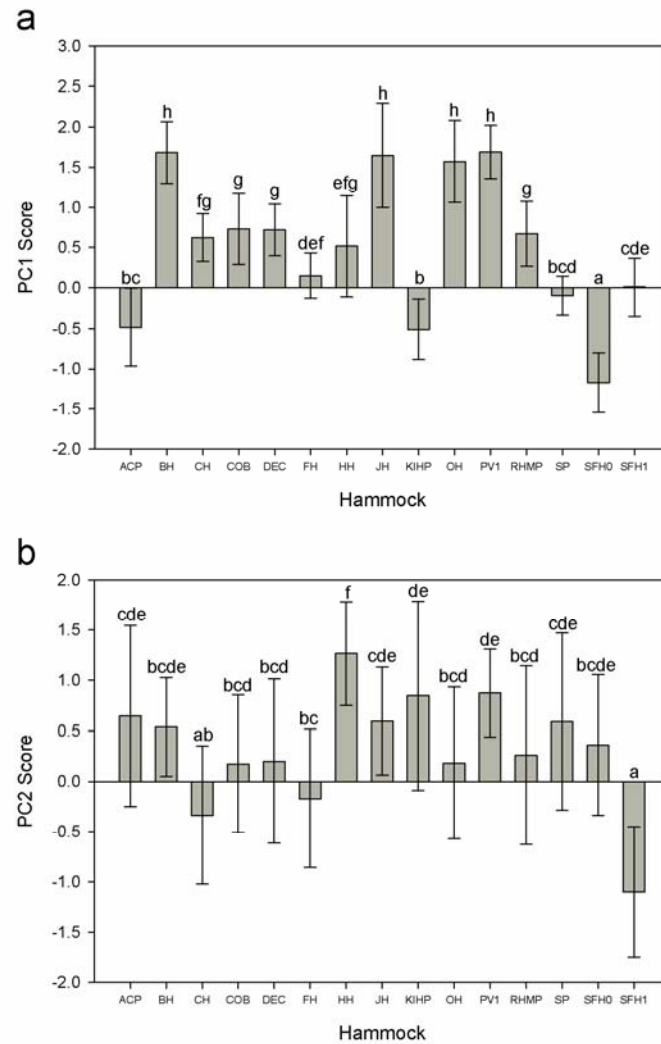


Figure 5. Mean principal component scores of hammocks. Hammocks include: Arch Creek Park (ACP), Bequaert Hammock (BH), Castellow Hammock (CH), Camp Owaissa Bauer (COB), Deering Estate at Cutler (DEC), Fuchs Hammock (FH), Harden Hammock (HH), Junk Hammock (JH), Kendall Indian Hammocks Park (KIHP), Osteen Hammock (OH), Palma Vista #1 (PV1), R. Hardy Matheson Preserve (RHMP), Simpson Park (SP), Swamp Fern Experimental Hammock before (SFH0) and after (SFH1) restoration efforts. Letters above bars indicate significant differences between groups. Error bars represent standard deviations. (a) PC1 scores by hammock. (b) PC2 scores by hammock.

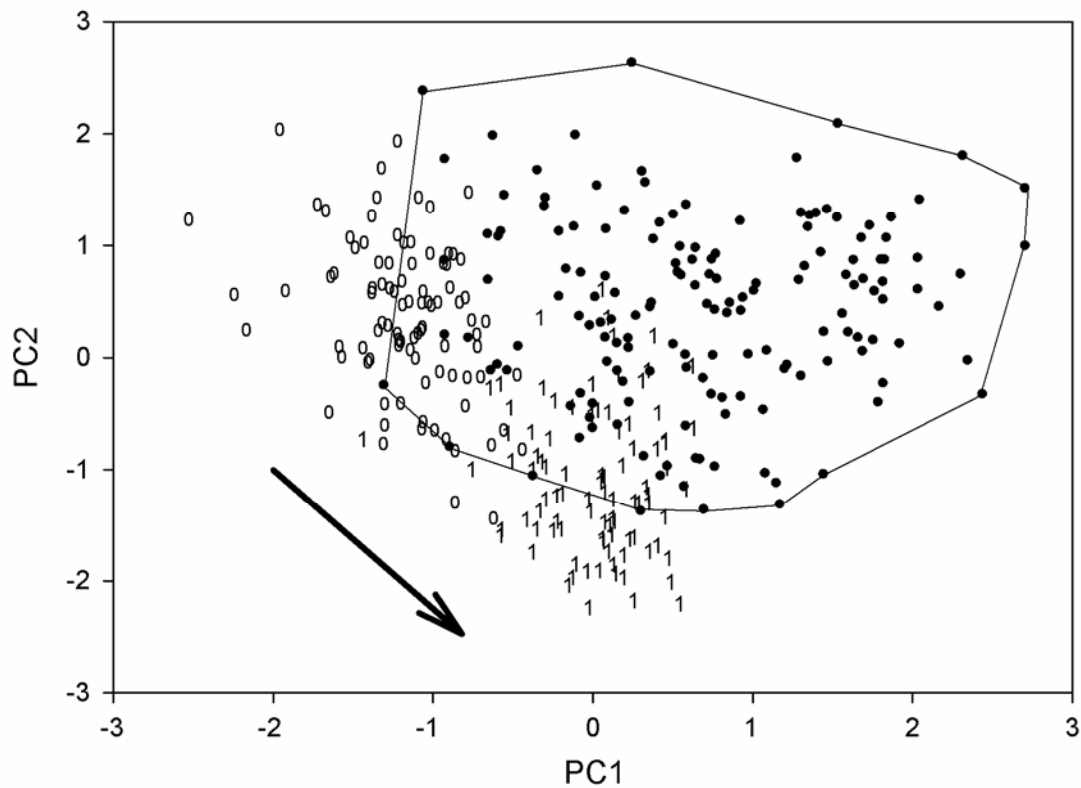


Figure 6. Score plot of hammock quadrats by PC1 and PC2. Circles represent individual reference hammock quadrats and are bounded by a solid line to represent the limits in variability of surveyed tropical hardwood hammocks. Each “0” represents an individual interior quadrat of Swamp Experimental Fern Hammock surveyed in March 2009. Each “1” represents an interior quadrat surveyed in June 2011. The bolded arrow represents the average spatial displacement of each quadrat between March 2009 and June 2011.



Figure 7. Photographs of quadrat #85 in Swamp Fern Experimental Hammock before (March 2009; left) and after restoration activities (June 2011; right).

CHAPTER 6

LEGACY EFFECTS DOMINATE EXOTIC RECRUITMENT PATTERNS IN A TROPICAL DRY FOREST RESTORATION

Abstract

Restoration practices are not often informed by the results of invasibility research, potentially compromising the efficacy and robustness of restoration efforts given the global trend in increased exotic species introductions. We tested the hypothesis that increasing the species richness and density of native woody trees and shrubs of a site would increase the recruitment of exotic woody seedlings during an active restoration of a tropical hardwood hammock community on protected lands in suburban Miami-Dade County, Florida, as has been demonstrated in Hawaiian tropical dry forests. Exotic woody seedling recruitment decreased greatly over time, though we did notice a slight, but statistically-significant, increase in both exotic woody seedling density and species richness entering the third year of the experiment. We were not able to detect an effect of outplanting native species richness and density treatments on exotic woody seedling recruitment. Instead, our results suggest that propagule pressure from reproductively-mature exotics present before restoration was the overwhelmingly dominant factor in exotic woody seedling recruitment on this site. These legacy effects decreased over time, such that after two years there were no consistent relationships between exotic woody seedling species richness or density and any of the community composition and structure variables we measured. We will continue to monitor our experimental plots in the future to observe the degree to which native recruits facilitate or compete with exotic recruits.

These results could define the extent to which outplantings can be utilized as effective tools for exotic plant limitation and control.

Key Words

exotic control; Florida; native species richness; outplanting; seedling; tropical hardwood hammock

Introduction

The role of native species richness in determining the invasibility of plant communities has been debated in ecology since the emergence of Elton's (1958) biotic resistance hypothesis. No scientific consensus on the issue has emerged as many observational studies have suggested a positive relationship between native and exotic species richness, while many empirical studies have suggested negative relationships between native and exotic species richness (e.g., Byers and Noonberg 2003; Levine et al. 2004; Bruno et al. 2005). Biotic resistance research has also increasingly focused on the role of density in mediating the biotic interactions in communities between natives and exotics, including competition and facilitation, that may also affect invasibility (e.g., Von Holle and Simberloff 2005; Thomsen et al. 2006; Brooks and Jordan 2013). Additionally, propagule pressure has been suggested to be the most influential element determining community invasibility (e.g., Von Holle and Simberloff 2005; Eschtruth and Battles 2009, Brooks and Jordan 2013), and serves as a confounding factor in most field experiments studying invasibility.

Restoration practices are not often informed by the results of invasibility research, potentially compromising the efficacy and robustness of restoration efforts given the global trend in increased exotic species introductions. A small number of recent studies have attempted to bridge this gap between the restoration and invasion ecology fields using planting or seeding to augment native species richness and population densities (e.g., Middleton et al. 2010; Questad et al. 2012; Oakley and Knox 2013). These experiments have emerged as a means to test the notion that replanting native plant populations may be a useful restoration strategy to limit further invasion following exotic removals (see Hartman and McCarthy 2004; Jelinski et al. 2011; Questad et al. 2012). Of these few studies, the majority concluded that increased native species richness through restoration plantings inhibits exotic plant invasions (e.g., Blumenthal et al. 2005; Middleton et al. 2010; Oakley and Knox 2013), however, one study from a Hawaiian tropical dry forest restoration found that woody outplantings alone may not be an effective defense against invasive plants (Questad et al. 2012). Instead, Questad et al. (2012) reported a positive relationship between native plant species richness and invasion rate after restoration plantings were established.

We were interested in assessing the efficacy of our own native outplanting treatments in limiting exotic woody recruitment as part of a larger investigation of a tropical hardwood hammock restoration within a disturbed and invaded woodlot in suburban Miami-Dade County, Florida. Tropical hardwood hammocks are semi-deciduous tropical dry forest communities, found on rocky limestone outcrops in southern Florida, the Bahamas, and Cuba (FNAI 1990; Armentano et al. 2003). South Florida's tropical hardwood hammocks feature rare assemblages of woody plants, ferns,

orchids, and lianas found nowhere else in the continental United States (Tomlinson 2001). Finally, these communities, especially those within the urban matrix of South Florida, seem particularly susceptible to species invasions (Ewel 1986; Horvitz et al. 1998).

Of particular interest to the restoration of tropical hardwood hammocks, previous studies have indicated unusual native-exotic richness relationship patterns within these communities. An observational study at multiple spatial scales found a positive relationship between native and exotic species richness at local scales, but an extremely rare negative relationship at landscape scales (Brooks et al. 2013). Additionally, an empirical study of tropical hardwood hammock seedlings in greenhouse mesocosms also indicated that species-rich native seedling communities were more invulnerable than species-poor ones (Brooks and Jordan 2013). Given these findings and those of Questad et al. (2012) from Hawaiian tropical dry forests, we tested the hypothesis that increasing the species richness and density of native woody trees and shrubs via restoration outplantings would increase the recruitment of exotic woody seedlings within our tropical hardwood hammock restoration site.

Methods

Site Description

This restoration project took place in suburban Miami-Dade County, Florida on a 1.125 ha plot of public land approximately 20 km west-south-west of the city of Miami (25.693910 N, -80.380305 W). Swamp Fern Experimental Hammock, as the site has been come to be called, is surrounded by fairly dense development though there is

another disturbed woodlot immediately to the North and a 44.5 ha county park with 16 ha of tropical hardwood hammock habitat less than a kilometer away to the East-Northeast.

Restoration and Experimental Design

We began by establishing 150 contiguous 3 m x 5 m quadrats extending 30 m by 75 m within the interior of Swamp Fern Experimental Hammock in December 2008 (Appendix 16). The outermost quadrats along the perimeter of our experimental grid were set aside as “buffer quadrats”, separating our 92 “interior quadrats” from the remainder of the site, which was left unrestored (Appendix 16). To promote the restoration of a resilient and diverse tropical hardwood hammock community within the interior quadrats of the experimental grid we engaged in both habitat management and the outplanting of native woody plant populations.

We began habitat management across the experimental grid in March of 2009. Our habitat management was designed to eliminate exotic plant species already established within the experimental grid and the limit opportunities for noxious exotic vines to blanket native canopy. (for detailed exotic control information see Chapter 5). We also were interested in managing abundant native palms and vines from impacting the establishment and survival of our native outplantings (described below), thus we cleared any vines away from outplantings and cut palm fronds that may have potentially smothered outplantings. Habitat management activities were conducted as needed over no more than five days a total of 10 times between March 2009 and June 2011.

With regards to our outplantings, species selection was informed by the ‘novel natives’ model of restoration (see Chapter 4). As such, we relied on making informed

choices to successfully match native species from the regional species pool that were not already present at the site to the contemporary abiotic conditions that they would be likely to experience at the site, as opposed to trying to restore historic abiotic conditions at the site and rely on passive recruitment (see Chapter 4). We selected 26 nursery-grown woody tropical hardwood hammock species native to the Miami Rock for outplanting (see Appendix 17). In all, 540 individuals were planted in June 2009 without any supplemental watering, relying solely on precipitation to promote successful establishment. Through December 2011, outplantings had demonstrated high survival (84.3%), and largely positive growth (see Chapter 4).

We utilized two levels of species richness and two levels of density to test the effect of outplantings on community invasibility by exotic woody seedlings. As such, one of five possible outplanting treatment groups was randomly assigned to each of the 92 interior quadrats (Table 1). Finally, the species used in each quadrat were randomly drawn from the available pool of 540 individuals of 26 native species.

Data Collection

To facilitate our analysis, we collected data from floristic surveys and from the manual pulling of exotic woody seedlings. In March of 2009, we conducted an initial survey of the experimental grid within Swamp Fern Experimental Hammock to evaluate floristic community composition and structure. In each quadrat, we noted the occurrence and native status of all terrestrial plant species, as well as the epiphytes visible in the vertical space above each quadrat. We referred to Wunderlin (1998), Nelson (2000), and Brown (2006) as needed for plant identification. Within each quadrat, we also estimated

the vegetative cover categorically using Daubenmire cover classes (1: 0-5%, 2: 5-25%, 3: 25-50%, 4: 50-75%, 5: 75-95%, 6: 95-100%; see Elzinga et al. 1998) at multiple levels above the forest floor including ground (<1 m), subcanopy (1-4 m), 1 canopy (>4 m) heights. Additionally, we documented the number of individuals greater than one meter in height, and the basal area in cm^2 at breast height for all stems greater than 2.5 cm diameter-at-breast-height, for all woody plants rooted in each quadrat. Per Elzinga et al. (1998), we included all individuals occurring on the northernmost and easternmost boundaries of each quadrat (one 3 m side and one 5 m side), and excluded all individuals along the southernmost and westernmost boundaries in our density and basal area metrics of each quadrat to avoid boundary bias in these measures. We repeated these floristic surveys every six months for interior quadrats only, beginning in December 2009 and ending June 2011 (a total of five data collection periods including the initial survey).

We measured exotic woody recruitment by identifying, removing, and counting all exotic woody seedlings that were present in each quadrat in December 2009, June 2010, December 2010, June 2011, and December 2011. All exotic woody seedlings present on the site in June 2009 were removed prior to outplanting our native populations. As such, all exotic woody seedlings collected in December of 2009 had recruited to the site or germinated from the seed bank only after introduction of restoration outplantings.

Statistical Analyses

All statistical analyses were conducted with PASW Statistics GradPack 17.0.2 (2009). To test whether our restoration outplanting treatments of varying species

richness and density affected exotic woody seedling recruitment over the length of our monitoring we utilized two independent repeated measures ANOVA. We used outplanting treatment group as our independent variable for both analyses and set 'Exotic Woody Seedling Density' and 'Exotic Woody Seedling Species Richness' as dependent variables in separate models. We used a Bonferroni correction to maintain a global- α level of 0.05 (cutoff for significance set at $p=0.025$). To enhance interpretation, simultaneous within-subjects contrasts between consecutive data periods and Tukey's Honestly Significant Difference Tests between outplanting treatment groups were used to identify significant differences in exotic woody recruitment across time and among restoration treatments, respectively.

Additionally, because of other restoration-related changes as a result of habitat management, we also conducted two correlation analyses to determine if there were other significant relationships that might help to explain exotic woody recruitment at our restoration site. In the first analysis, we sought to understand what floristic variables might be related to exotic woody seedling recruitment in each data collection period. To do so, we developed separate datasets for December 2009, June 2010, December 2010, and June 2011 data collection periods. Each dataset featured our measures of 'Exotic Woody Seedling Species Richness', 'Exotic Woody Seedling Density', 'Native Species Richness', 'Canopy Cover', 'Subcanopy Cover', 'Woody Plant Density', and 'Basal Area', all by individual quadrat. We ran a Pearson Product-Moment Correlation across each dataset focused on the relationships involving our exotic woody seedling species richness and density.

In the second correlation analysis, we sought to determine whether any of the initial floristic variables prior to restoration might be related to the cumulative exotic woody seedling recruitment observed since restoration. In this instance, we developed a dataset featuring initial floristic survey data from March 2009 with ‘Native Species Richness’, ‘Exotic Species Richness’, ‘Native Woody Species Richness’, ‘Exotic Woody Species Richness’, ‘Native Woody Plant Density’, ‘Exotic Woody Plant Density’, ‘Native Basal Area’, and ‘Exotic Basal Area’ as variables to describe each quadrat. We also developed ‘Total Exotic Woody Seedling Species Richness’ and ‘Total Exotic Woody Seedling Density’ variables by quadrat for this dataset as cumulative measures of exotic woody seedling species richness and density across all five exotic seedling removal periods beginning after the initial clearing of exotic seedling biomass in June 2009 through December 2011. Here, we ran a Pearson Product-Moment Correlation across the dataset focused on the relationships involving our total exotic woody seedling species richness and density variables.

Results

Swamp Fern Experimental Hammock Floristic Surveys

All species recorded in experimental quadrats of Swamp Fern Experimental Hammock from March 2009 through June 2011 are detailed in Appendix 17. In total, we documented 62 native species and 29 exotic species. Of these, 40 were woody natives while 15 were woody exotics. Over the course of the more than two and a half years of restoration efforts described in this manuscript, native species richness across the site nearly doubled, mainly through the addition of 26 novel native outplantings, and exotic

species richness was very nearly halved as a result of exotic control efforts (see Chapter 5). Additional information regarding pre-restoration floristic survey data by outplanting treatment group is detailed in Appendix 28 for native species and Appendix 29 for exotic species. Finally, floristic survey data organized by data period and outplanting treatment group is listed in Appendix 30.

Exotic Woody Seedling Recruitment

Exotic woody seedling density and exotic woody seedling species richness varied significantly across data periods, but not by outplanting treatment (Appendix 31 and 32, respectively). Mean exotic woody seedling recruitment data by data period and outplanting treatment group are detailed in Appendix 33. Significant decreases in exotic woody seedling density were documented between December 2009 and June 2011, followed by an increase in December 2011 (Figure 1). Similarly, exotic woody seedling species richness declined between June 2010 and June 2011, before increasing in December 2011 (Figure 2). In all we collected 4,874 exotic woody recruits of 13 species over two years within our 0.138 ha of interior quadrats (Table 2). This translates to approximately 14,128 exotic woody seedlings per hectare in annual recruitment at this site including dramatic reductions since restoration treatments began! These exotic woody seedling collections were dominated by recruits of the invasive woody shrub *Ardisia elliptica* - 3306 seedlings in all (67.8% of all exotic seedlings) (Table 2). Together with *Bischofia javanica* (13.5%) and *Schinus terebinthifolius* (11.3%), these three species made up almost 93% of all exotic woody recruits that we removed. On the

other hand, the total counts for five of the 13 exotic species we collected as recruits remained in single digits through December 2011 (Table 2).

We also attempted to understand potential relationships between exotic woody seedling recruitment and our floristic survey variables within quadrats across our restoration monitoring period. Significant correlations are listed in Table 3. We found that exotic woody seedling density and species richness were significantly positively correlated within quadrats across all data periods with the strength of correlation between these variables ranging between 0.456 and 0.706. Additionally, the number of correlations involving our exotic woody seedling recruitment variables with our floristic survey variables declined over time with five such relationships in December 2009, three in June 2010, and just one in each of December 2010 and June 2011. Only two sets of relationships retained significance over more than one data period: exotic woody seedling species richness was weakly positively correlated with native species richness from December 2009 through December 2010, and was also moderately correlated with canopy cover from December 2009 through June 2010. Interestingly, subcanopy cover was the only floristic survey variable negatively correlated with exotic woody seedling recruitment, including with exotic woody seedling density in December 2009 and with exotic woody seedling species richness in June 2010).

Finally, we sought to determine if pre-restoration floristic survey variables from March 2009 were related to cumulative exotic woody seedling recruitment within quadrats. Significant correlations between pre-restoration floristic survey variables and total exotic woody seedling recruitment are reported in Table 4. Total exotic woody seedling density and species richness were moderately positively correlated. Pre-

restoration exotic woody species richness was moderately positively correlated with both total exotic woody seedling species richness and density. In addition, pre-restoration exotic woody plant density was moderately positively correlated with total exotic woody seedling density and weakly positively correlated with total exotic woody seedling species richness. Finally, total exotic woody seedling species richness was also weakly positively correlated with pre-restoration native woody species richness.

Discussion

In this study, we tested the hypothesis that increasing the species richness and density of native woody trees and shrubs via restoration outplantings would increase the recruitment of exotic woody seedlings within Swamp Fern Experimental Hammock. While restoration outplantings succeeded in increasing native species richness, and exotic species control efforts successfully reduced exotic species richness (see Chapter 5), our analysis demonstrates clear changes in exotic woody seedling species recruitment patterns at this site in the two and a half years since restoration activities commenced. Notably, we documented a strong decline in exotic woody seedling species richness and density over time following restoration, but this decline was unrelated to native outplanting species richness and density treatments. This finding contrasts with several studies in grasslands and prairies reporting negative native-exotic richness relationships associated with restoration outplantings (Blumenthal et al. 2003; Bakker and Wilson 2004; Blumenthal et al. 2005; Middleton et al. 2010; Oakley and Knox 2013), and another study from a tropical dry forest restoration demonstrating increased invasibility associated with native outplantings (Questad et al. 2012). Instead, in our tropical dry

forest study, the legacy of pre-restoration exotic woody species richness and woody plant density was evident in exotic woody seedling recruitment patterns.

Patterns of Exotic Woody Seedling Recruitment

Total post-restoration exotic woody seedling recruitment within individual quadrats could largely be predicted on the basis of pre-restoration exotic woody species richness and exotic woody plant density. Thus, the seed rain from individual mature exotic trees and shrubs rooted within quadrats before exotic control and restoration outplantings was largely limited to falling to the ground directly below and around those plants. This result is further supported by negative correlations between subcanopy cover and both exotic woody seedling density (in December 2009) and exotic woody seedling species richness (in June 2010); quadrats with reduced subcanopy cover were those with high woody exotic plant densities before restoration, and thus, had higher propagule loads. Local propagule pressure was, therefore, the most important factor to the invasibility of individual quadrats, matching the findings of several recent reviews and research efforts (e.g., Lockwood et al. 2009; Simberloff 2009; Brooks and Jordan 2013).

Additionally, we found a positive relationship between exotic woody seedling species richness and seedling density across each data period. Thus, it appears that the same factor or set of factors promoting high exotic woody seedling density may also be promoting high species richness in this group (i.e., recruitment conditions, facilitation, generalist dispersers). Yet, both metrics responded to restoration activities at different rates initially. Exotic woody seedling density declined immediately between December 2009 and June 2010 whereas declines in exotic woody seedling species richness did not

materialize until between June 2010 and December 2010. The limitation of the persistence of propagules in the seed bank, through germination or death, may explain this trend. Interestingly, while remaining well below pre-restoration levels, both measures of exotic woody recruitment began to increase again between June 2011 and December 2011. This could reflect seasonal variation of propagule pressure that might be expected to fall off again between December 2011 and June 2012. Unfortunately, because we did not collect our suite of floristic survey variables in December of 2011, we are unable to determine if continuing changes in these metrics were related to this increase in exotic woody seedling recruitment.

In our correlation analyses we also discovered a trend of decreasing numbers of significant correlations between recruitment metrics and floristic survey variables over time. These diminishing relationships between exotic recruitment and community composition and structure may represent evidence that our successive exotic seedling removals have decoupled dispersal and seedling establishment from the other processes comprising invasibility. As such, our results suggest that community composition and structure in this system have little to no effect on exotic dispersal and seedling establishment patterns. However, the fact that we documented significant positive relationships between exotic woody seedling species richness and both native species richness and canopy cover over successive data periods early in our seedling collections may reflect these community composition and structure factors' potential effects on invasibility through later exotic establishment and growth processes.

Conclusions and Future Directions

In this system, while propagule pressure was the most important factor explaining exotic woody seedling recruitment, propagule loads were, in fact, the result of establishment and growth processes occurring before restoration that, based on correlation analyses, were likely positively associated with native species richness and canopy cover. These findings match the overall conclusions of a greenhouse study assessing the invasibility of tropical hardwood hammock seedling layers in which *Ardisia elliptica* germination and initial establishment was related to propagule pressure and unaffected by biotic factors, while biomass production was improved with increased native species richness (Brooks and Jordan 2013). Additionally, the incredibly short mean dispersal distances for exotic propagules in this system also suggests that small patches of tropical dry forest habitat in South Florida may not necessarily be more invulnerable than larger, contiguous habitats, and may have important implications for restoration and management of tropical dry forests fragments in South Florida and beyond.

Given these unique results when compared to other invasibility studies, we submit two potentially important caveats. First, given that *A. elliptica* dominated exotic woody seedling recruitment in this study, it is possible that the results presented in this paper may represent the dominant influence of this individual exotic species as opposed to the exotic community as a whole. Furthermore, our review of similar studies suggests that researchers may need to tread carefully in communicating the results of these types of experiments. In particular, because invasibility reflects the summative response of exotic dispersal, establishment, growth, and spread, ecologists need to be explicit about the exact process(es) being studied. Our experiment did not specifically test the invasibility

of restored tropical dry forest; rather, we focused on the recruitment and early establishment components of invasibility. Future invasibility research may be well served by addressing the individual processes associated with invasibility separately within an overarching experimental design to truly understand how these processes interact and as a means to unlock holistic and cost-effective control strategies.

Finally, given the relatively short time span since restoration represented by these results, further monitoring of Swamp Fern Experimental Hammock is necessary to determine the long-term effects of restoration efforts on exotic recruitment and community invasibility. Of particular interest is whether recruitment competition between native recruits of our outplanted native species might affect exotic recruitment, establishment, and growth. Specifically, we hope to be able to record how shifts in native:exotic propagule pressure ratios (as proposed by Horvitz 1997) might impact recruitment patterns that will ultimately determine the future composition and structure of this restored tropical dry forest. These results could further define the extent to which outplanted populations can be utilized as effective tools for exotic plant limitation and control.

Acknowledgements

We are extremely grateful to M. Anderson Brooks, A. Brooks, A.W. Brooks, K. Brooks, L. Brooks, D. Howe, J. Klein, J. Possley, S. Thompson, and S. Woodmansee for their contributions. Funding sources for this project were provided by a Conservation Award from the Florida Native Plant Society, an Academic Excellence Fund Award from the Graduate Program in Ecology and Evolution at Rutgers University, as well as

graduate support from USDA NRI 05-2221. We also thank A. Leonard and the Miami-Dade County Chapter of the Florida Native Plant Society for their support of this project. J. Lawson of Silent Natives Nursery cultivated the native outplantings and S. Woodmansee of Pro Native Consulting provided invaluable input on species selection. Access and permits for field work were secured from the Miami-Dade County Department of Parks and Recreation Natural Areas Management Division.

Table 1. Outplanting treatment design.

Outplanting Treatment	# of Quadrats	Added Species Richness	Density per Species Added	Total Outplantings per Quadrat
High DEN x High SR	18	6	2	12
High DEN x Low SR	18	2	5	10
Low DEN x High SR	18	6	1	6
Low DEN x Low SR	18	2	1	2
Control	20	0	0	0

Table 2. Exotic woody seedling recruitment across interior quadrats of experimental grid after initial clearing of exotics in June 2009 through December 2011. All species names follow Gann (2012). FLEPPC Status refers to invasive species as listed by the Florida Exotic Pest Plant Council (FLEPPC 2011).

Exotic Species	Total Seedlings Removed	FLEPPC Status
<i>Albizia lebbbeck</i>	8	Category I
<i>Ardisia elliptica</i>	3306	Category I
<i>Bischofia javanica</i>	656	Category I
<i>Carica papaya</i>	1	-
<i>Cupaniopsis anacardioides</i>	6	Category I
<i>Dyopsis lutescens</i>	52	-
<i>Eriobotrya japonica</i>	5	-
<i>Eugenia uniflora</i>	183	Category I
<i>Schefflera actinophylla</i>	38	Category I
<i>Schinus terebinthifolius</i>	551	Category I
<i>Senna pendula</i> var. <i>glabrata</i>	44	Category I
<i>Syzygium cumini</i>	23	Category I
<i>Urena lobata</i>	1	Category I

Table 3. Significant correlations for quadrat exotic woody seedling (EWS) recruitment and floristic survey variables by data period (N=92 for all comparisons).

Data Period	Variable 1	Variable 2	Pearson Correlation (ρ)	Significance (p)
December 2009		EWS Species Richness	0.606	<0.001
	EWS Density	Canopy Cover	0.280	0.007
		Subcanopy Cover	-0.248	0.017
		Canopy Cover	0.348	0.001
	EWS Species Richness	Ground Cover	0.271	0.009
		Native Species Richness	0.212	0.042
June 2010	EWS Seedling Density	EWS Species Richness	0.456	<0.001
		Canopy Cover	0.372	<0.001
	EWS Species Richness	Native Species Richness	0.217	0.038
		Subcanopy Cover	-0.217	0.037

December 2010	EWS Seedling Density	EWS Species Richness	0.706	<0.001
	EWS Species Richness	Native Species Richness	0.206	0.048
June 2011	EWS Seedling Density	EWS Species Richness	0.573	<0.001
		Native Species Richness	0.269	0.009

Table 4. Significant correlations for quadrat total exotic woody seedling (EWS; after June 2009 through December 2011) recruitment and pre-restoration (PR; March 2009) floristic survey variables (N=92 for all comparisons).

Variable 1	Variable 2	Pearson Correlation (ρ)	Significance (p)
Total EWS Density	PR Exotic Woody Plant Density	0.575	<0.001
	PR Exotic Woody Species Richness	0.335	0.001
	Total EWS Species Richness	0.468	<0.001
Total EWS Species Richness	PR Exotic Woody Plant Density	0.291	0.005
	PR Exotic Woody Species Richness	0.465	<0.001
	PR Native Woody Species Richness	0.246	0.018

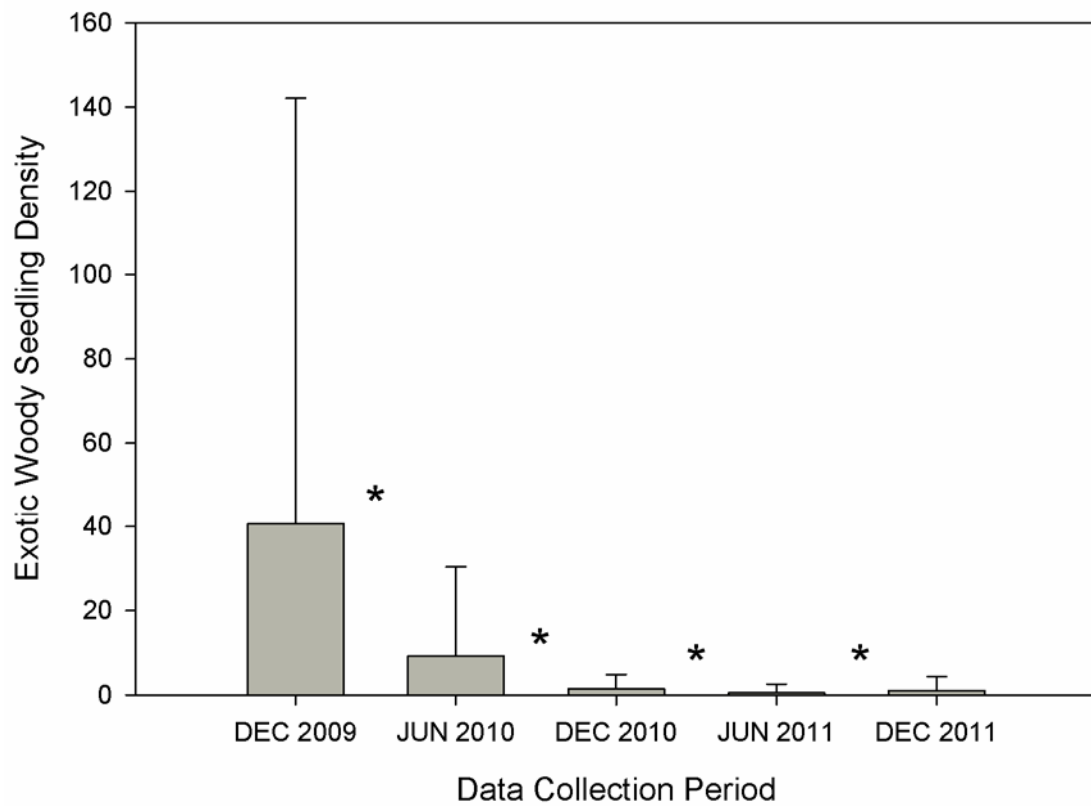


Figure 1. Mean exotic woody seedling density of interior quadrats over time. Asterisks denote significant differences between consecutive observations. Error bars represent standard deviations.

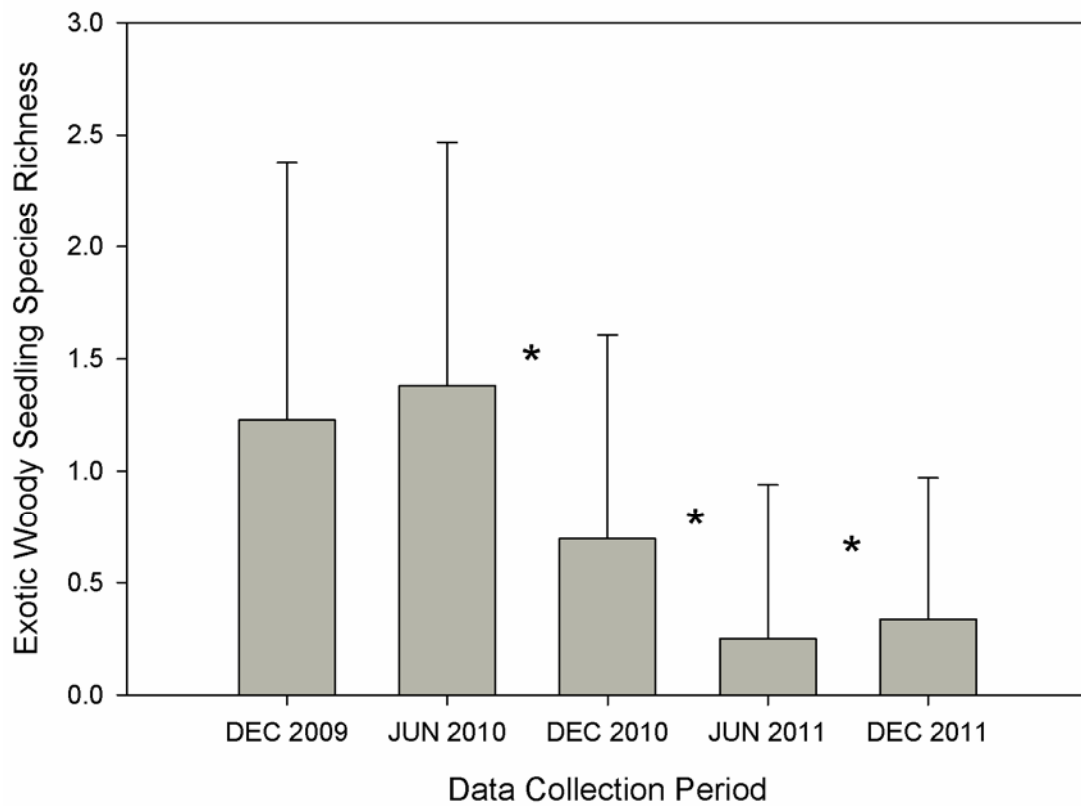


Figure 2. Mean exotic woody seedling species richness of interior quadrats over time. Asterisks denote significant differences between consecutive observations. Error bars represent standard deviations.

IMPLICATIONS

The early focus of invasion ecology to determine what species characteristics promote invasiveness may have contributed to the now widespread perception that natives and exotics were inherently different, and therefore, might respond to different factors (e.g., Williamson 1996a, b; Simberloff 1997). Instead, my research findings suggest that native and exotic species are responding to the same basic set of factors concurring with several other recent studies (e.g., Stohlgren et al. 2003; Souza et al. 2011). However, my research also suggests that there may be particular suites of factors that natives and exotics respond similarly to, and other factors to which they respond differently. In particular, natives and exotics both responded similarly to localized factors including soil water availability and potentially substrate availability or heterogeneity. On the other hand, natives and exotics responded in opposite ways to regional scale factors including anthropogenic and natural disturbance gradients.

My research also echoes other work suggesting that the primary factor determining invasibility is propagule pressure (e.g., Von Holle and Simberloff 2005; Eschtruth and Battles 2009; Lockwood et al. 2009; Simberloff 2009). In fact, the sum of my work indicates that there may be an interaction effect between recruitment and anthropogenic disturbance intensity that determines the overall native and exotic composition of communities. Exotic species are often disproportionately selected for their high recruitment potential while native species may suffer from recruitment limitation as a result of altered site characteristics including natural disturbance regimes, hydrology, substrate, etc. As a result, anthropogenic disturbance may favor exotics by promoting their enhanced recruitment at the expense of recruitment-limited natives.

The efforts reported here are among a growing set of research on tropical dry forest biodiversity conservation, restoration, and invasibility. The results of this research will have greater importance for tropical dry forests as these habitats are exposed to a greater range of exotics species as a result of augmented international trade in tropical regions in the future. The tropics have been surmised to have enhanced biotic resistance to invasions as a result of their higher levels of native species richness and more intense biotic interactions. However, I did not find evidence to support the biotic resistance hypothesis. In fact, tropical hardwood hammock plant communities do not appear to be structured by competition. Rather, our mesocosm experiments suggest that facilitation is a much more prominent mechanism structuring these communities. Therefore, tropical communities might actually exhibit greater invasibility than temperate communities if patterns of international trade were more equitable.

Finally, the success of the restoration efforts at Swamp Experimental Fern Hammock with minimal resources in the form of time, money, and manpower provides a model for managing disturbed habitats. Rather than trying to preserve native communities in sites where conditions have been irrevocably altered, restoring communities by outplanting species native to the regional pool that are better adapted to extant conditions may be more successful. Simultaneously removing exotics from the immediate site might enable a shift in propagule pressure ratios between natives and exotics thus promoting more natural and resilient communities. It is my hope that this research, in making additional progress towards resolving the nature of the factors affecting invasibility, may support the development of effective and economical restoration practices that seek to mitigate the negative impacts of species invasions,

protect biodiversity, and improve the provision of ecosystem goods and services, for current and future populations in South Florida and beyond.

APPENDICES

Appendix 1. Species found in floristic surveys including taxonomic information, habit, native and conservation status, and distribution among surveyed hammocks. ‘South Florida Status’ refers to the Institute for Regional Conservation’s regional ranking of a species’ conservation status in South Florida at time of publication (see Gann et al. 2012; rankings described in Gann et al. 2002). ‘Study Survey Distribution’ lists all hammocks where the species was found during our sampling. Study site hammocks included Arch Creek Park (ACP), Bequaert Hammock (BH), Castellow Hammock (CH), Camp Owaissa Bauer (COB), Deering Estate at Cutler (DEC), Fuchs Hammock (FH), Harden Hammock (HH), Junk Hammock (JH), Kendall Indian Hammocks Park (KIHP), Osteen Hammock (OH), Palma Vista #1 (PV1), R. Hardy Matheson Preserve (RHMP), and Simpson Park (SP).

Species	Family	Habit	South Florida Status	Study Survey Distribution
<i>Abrus precatorius</i>	Fabaceae	Vine	Not Native, Naturalized	ACP, DEC, KIHP
<i>Adenanthera pavonina</i>	Fabaceae	Tree	Not Native, Naturalized	SP
<i>Adiantum melanoleucum</i>	Pteridaceae	Herb	Critically Imperiled	HH
<i>Adiantum tenerum</i>	Pteridaceae	Herb	Imperiled	CO, OH

<i>Ampelopsis arborea</i>	Vitaceae	Vine	Secure	BH, PV1
<i>Anemia adiantifolia</i>	Anemiaceae	Herb	Apparently Secure	BH, HH, PV1
<i>Annona glabra</i>	Annonaceae	Tree	Secure	DEC
<i>Antigonon leptopus</i>	Polygonaceae	Vine	Not Native, Naturalized	ACP
<i>Ardisia elliptica</i>	Myrsinaceae	Shrub	Not Native, Naturalized	ACP, HH, KIHP, PV1
<i>Ardisia escallonioides</i>	Myrsinaceae	Shrub	Secure	BH, CH, COB, DEC, FH, JH, OH, PV1, RHMP
<i>Asplenium dentatum</i>	Aspleniaceae	Herb	Imperiled	DEC, RHMP
<i>Asplenium verecundum</i>	Aspleniaceae	Herb	Critically Imperiled	FH
<i>Baccharis glomeruliflora</i>	Asteraceae	Shrub	Secure	BH, DEC, KIHP, PV1
<i>Bidens alba</i> var. <i>radiata</i>	Asteraceae	Herb	Secure	ACP, KIHP
<i>Bischofia javanica</i>	Euphorbiaceae	Tree	Not Native, Naturalized	DEC, FH, HH, KIHP
<i>Blechnum serrulatum</i>	Blechnaceae	Herb	Secure	KIHP, PV1

<i>Bursera simarouba</i>	Burseraceae	Tree	Secure	ACP, BH, CH, COB, DEC, FH, HH, JH, KIHP, OH, PV1, RHMP, SP
<i>Callicarpa americana</i>	Verbenaceae	Shrub	Secure	ACP, DEC, HH, KIHP
<i>Calypttranthes pallens</i>	Myrtaceae	Tree	Rare	CH, COB, DEC, OH, PV1
<i>Calypttranthes zuzygium</i>	Myrtaceae	Tree	Imperiled	OH
<i>Campyloneurum phyllitidis</i>	Polypodiaceae	Herb	Rare	BH, JH, OH, PV1
<i>Canella winterana</i>	Canellaceae	Tree	Rare	PV1
<i>Carica papaya</i>	Caricaceae	Tree	Not Native, Naturalized	BH, COB, FH, RHMP, SP
<i>Caryota mitis</i>	Arecaceae	Tree	Not Native, Naturalized	FH, RHMP, SP
<i>Cayaponia americana</i>	Cucurbitaceae	Vine	Critically Imperiled	CH
<i>Celtis laevigata</i>	Ulmaceae	Tree	Apparently Secure	RHMP
<i>Chamaedorea seifrizii</i>	Arecaceae	Shrub	Not Native, Naturalized	FH

<i>Chiococca alba</i>	Rubiaceae	Shrub	Secure	ACP, BH, CH, COB, DEC, FH, HH, JH, KIHP, OH, PV1, RHMP
<i>Chromolaena odorata</i>	Asteraceae	Shrub	Secure	COB, DEC, HH
<i>Chrysobalanus icaco</i>	Chrysobalanaceae	Shrub	Secure	ACP, DEC, HH, JH, KIHP, PV1
<i>Chrysophyllum oliviforme</i>	Sapotaceae	Tree	Rare	BH, COB, HH, JH, OH, PV1
<i>Cissus verticillata</i>	Vitaceae	Vine	Secure	HH, SP
<i>Citharexylum spinosum</i>	Verbenaceae	Tree	Rare	CH, OH, PV1
<i>Citrus limon</i>	Rutaceae	Tree	Not Native, Naturalized	FH
<i>Clerodendron speciosissimum</i>	Verbenaceae	Shrub	Not Native, Naturalized	KIHP
<i>Coccoloba diversifolia</i>	Polygonaceae	Tree	Secure	ACP, CH, COB, DEC, FH, JH, OH, PV1, RHMP, SP
<i>Coccoloba uvifera</i>	Polygonaceae	Tree	Secure	HH
<i>Commelina diffusa</i>	Commelinaceae	Herb	Not Native, Naturalized	ACP
<i>Crassocephalum crepidioides</i>	Asteraceae	Herb	Not Native, Naturalized	HH

<i>Crossopetalum illicifolium</i>	Celastraceae	Shrub	Rare	DEC
<i>Ctenitis sloanei</i>	Dryopteridaceae	Herb	Imperiled	FH
<i>Cupaniopsis anacardioides</i>	Sapindaceae	Tree	Not Native, Naturalized	RHMP, SP
<i>Delonix regia</i>	Fabaceae	Tree	Not Native, Naturalized	ACP, SP
<i>Desmodium incanum</i>	Fabaceae	Herb	Secure	KIHP
<i>Dicanthelium commutatum</i>	Poaceae	Herb	Rare	BH, DEC, KIHP, PV1
<i>Dioscorea alata</i>	Dioscoreaceae	Vine	Not Native, Naturalized	RHMP
<i>Dioscorea bulbifera</i>	Dioscoreaceae	Vine	Not Native, Naturalized	DEC, KIHP
<i>Diospyros digyna</i>	Ebenaceae	Tree	Not Native, Naturalized	RHMP
<i>Drypetes lateriflora</i>	Euphorbiaceae	Tree	Rare	DEC, FH, RHMP
<i>Eltroplectris calcarata</i>	Orchidaceae	Herb	Critically Imperiled	OH
<i>Encyclia tampensis</i>	Orchidaceae	Herb	Secure	JH, OH, PV1
<i>Epidendrum nocturnum</i>	Orchidaceae	Herb	Imperiled	JH

<i>Epipremnum pinnatum</i> cv. <i>aurea</i>	Araceae	Vine	Not Native, Naturalized	SP
<i>Eriobotrya japonica</i>	Rosaceae	Tree	Not Native, Naturalized	COB, FH, KIHP, PV1
<i>Erythrina herbacea</i>	Fabaceae	Shrub	Secure	PV1
<i>Eugenia axillaris</i>	Myrtaceae	Tree	Secure	ACP, BH, CH, COB, DEC, FH, HH, JH, OH, PV1, RHMP, SP
<i>Eugenia confusa</i>	Myrtaceae	Tree	Imperiled	SP
<i>Eugenia foetida</i>	Myrtaceae	Tree	Secure	BH, COB, PV1
<i>Eugenia uniflora</i>	Myrtaceae	Tree	Not Native, Naturalized	KIHP, SP
<i>Eulophia alta</i>	Orchidaceae	Herb	Secure	FH
<i>Exothea paniculata</i>	Sapindaceae	Tree	Secure	BH, CH, COB, FH, JH, OH, PV1, SP
<i>Ficus aurea</i>	Moraceae	Tree	Secure	ACP, BH, CH, COB, DEC, FH, HH, JH, PV1, RHMP, SP
<i>Ficus citrifolia</i>	Moraceae	Tree	Secure	BH, COB, DEC, HH, JH, RHMP
<i>Ficus microcarpa</i>	Moraceae	Tree	Not Native, Naturalized	KIHP
<i>Forestiera segregata</i>	Oleaceae	Shrub	Secure	OH

<i>Galactia striata</i>	Fabaceae	Vine	Secure	BH, JH, OH, PV1
<i>Gouania lupuloides</i>	Rhamnaceae	Vine	Rare	COB, FH
<i>Guapira discolor</i>	Nyctaginaceae	Tree	Secure	CH, RHMP
<i>Guettarda scabra</i>	Rubiaceae	Tree	Secure	HH, JH, OH, PV1
<i>Gymnanthes lucida</i>	Euphorbiaceae	Tree	Secure	CH, OH, SP
<i>Habernaria floribunda</i>	Orchidaceae	Herb	Secure	BH
<i>Hamelia patens</i>	Rubiaceae	Shrub	Rare	ACP, COB, FH, HH, RHMP
<i>Heliotropium angiospermum</i>	Boraginaceae	Herb	Secure	ACP
<i>Ilex cassine</i>	Aquifoliaceae	Tree	Secure	BH, HH, KIHP, PV1
<i>Ilex krugiana</i>	Aquifoliaceae	Tree	Rare	CH, FH
<i>Ipomoea alba</i>	Convolvulaceae	Vine	Secure	BH, COB, DEC, FH, OH, PV1, SP
<i>Ipomoea indica</i> var. <i>acuminata</i>	Convolvulaceae	Vine	Secure	ACP, BH, COB
<i>Jasminum dichotomum</i>	Oleaceae	Vine	Not Native, Naturalized	HH, SP
<i>Jasminum fluminense</i>	Oleacea	Vine	Not Native, Naturalized	CH, COB, DEC, RHMP

<i>Kalanchoe pinnata</i>	Crassulaceae	Herb	Not Native, Naturalized	ACP
<i>Krugiodendron ferreum</i>	Rhamnaceae	Tree	Secure	CH, COB, DEC, RHMP, SP
<i>Lasiacis divaricata</i>	Poaceae	Herb	Apparently Secure	BH, COB, HH, JH, PV1, RHMP, SP
<i>Leiphaimos parasitica</i>	Gentianaceae	Herb	Imperiled	BH, OH
<i>Licaria triandra</i>	Lauraceae	Tree	Critically Imperiled	SP
<i>Lysiloma latisiliquum</i>	Fabaceae	Tree	Apparently Secure	BH, CH, COB, HH, JH, OH, PV1
<i>Macfadyena unguis-cati</i>	Bignoniaceae	Vine	Not Native, Naturalized	SP
<i>Mangifera indica</i>	Anacardiaceae	Tree	Not Native, Naturalized	FH
<i>Melothria pendula</i>	Cucurbitaceae	Vine	Secure	COB, DEC, HH, SP
<i>Metopium toxiferum</i>	Anacardiaceae	Tree	Secure	BH, COB, DEC, JH, OH, PV1
<i>Mikania cordifolia</i>	Asteraceae	Vine	Rare	COB, PV1
<i>Momordica balsamina</i>	Cucurbitaceae	Vine	Not Native, Naturalized	HH
<i>Momordica charantia</i>	Cucurbitaceae	Vine	Not Native, Naturalized	ACP, HH

<i>Morinda royoc</i>	Rubiaceae	Vine	Secure	BH, CH, HH, JH, KIHP, OH, PV1
<i>Myrcianthes fragrans</i>	Myrtaceae	Tree	Rare	BH, JH
<i>Myrica cerifera</i>	Myricaceae	Shrub	Secure	BH, PV1
<i>Myrsine cubana</i>	Myrsinaceae	Shrub	Secure	BH, DEC, HH, JH, KIHP, OH, PV1
<i>Nephrolepis biserrata</i>	Nephrolepidaceae	Herb	Rare	ACP
<i>Nephrolepis cordifolia</i>	Nephrolepidaceae	Herb	Not Native, Naturalized	ACP, DEC, KIHP
<i>Nephrolepis exaltata</i>	Nephrolepidaceae	Herb	Secure	BH, COB, DEC, HH, PV1
<i>Nephrolepis x averyi</i>	Nephrolepidaceae	Herb	Imperiled	KIHP
<i>Neyraudia reynaudiana</i>	Poaceae	Herb	Not Native, Naturalized	HH
<i>Ocotea coriacea</i>	Lauraceae	Tree	Secure	ACP, BH, CH, COB, DEC, FH, JH, OH, PV1, RHMP, SP
<i>Oeceoclades maculata</i>	Orchidaceae	Herb	Not Native, Naturalized	ACP, BH, CH, COB, FH, HH, KIHP, OH, PV1, RHMP
<i>Oncidium ensatum</i>	Orchidaceae	Herb	Critically Imperiled	JH

<i>Osplismenus hirtellus</i>	Poaceae	Herb	Apparently Secure	ACP, DEC, HH, KIHP, SP
<i>Oxalis corniculata</i>	Oxalidaceae	Herb	Secure	ACP, COB
<i>Panicum maximum</i>	Poaceae	Herb	Not Native, Naturalized	ACP
<i>Parthenocissus quinquefolia</i>	Vitaceae	Vine	Secure	ACP, BH, CH, COB, DEC, FH, HH, KIHP, PV1, RHMP, SP
<i>Paspalum caespitosum</i>	Poaceae	Herb	Secure	BH
<i>Passiflora pallens</i>	Passifloraceae	Vine	Imperiled	CH
<i>Passiflora sexflora</i>	Passifloraceae	Vine	Critically Imperiled	CH
<i>Passiflora suberosa</i>	Passifloraceae	Vine	Secure	BH, CH, COB, DEC, HH, JH, OH, PV1, RHMP
<i>Pennisetum purpureum</i>	Poaceae	Herb	Not Native, Naturalized	ACP
<i>Persea borbonia</i>	Lauraceae	Tree	Rare	ACP, PV1
<i>Petiveria alliacea</i>	Phytolaccaceae	Herb	Imperiled	ACP, RHMP
<i>Phlebodium aureum</i>	Polypodiaceae	Herb	Secure	PV1
<i>Phyllanthus amarus</i>	Euphorbiaceae	Herb	Not Native, Naturalized	ACP

<i>Picramnia pentandra</i>	Simaroubaceae	Tree	Critically Imperiled	SP
<i>Pilea microphylla</i>	Urticaceae	Herb	Secure	DEC, HH
<i>Piscidia piscipula</i>	Fabaceae	Tree	Secure	BH, SP
<i>Pisonia aculeata</i>	Nyctaginaceae	Vine	Secure	CH, COB, DEC, FH, HH, OH, PV1, RHMP, SP
<i>Pleopeltis polypodioides</i> var. <i>michauxiana</i>	Polypodiaceae	Herb	Secure	ACP, BH, COB, DEC, HH, JH, KIHP, OH
<i>Polyalthia suberosa</i>	Annonaceae	Tree	Not Native, Naturalized	RHMP, SP
<i>Polystachya concreta</i>	Orchidaceae	Herb	Rare	JH
<i>Ponthieva racemosa</i>	Orchidaceae	Herb	Imperiled	BH
<i>Prunus myrtifolia</i>	Rosaceae	Tree	Rare	CH, COB, DEC, FH, JH, OH, PV1
<i>Psilotum nudum</i>	Psilotaceae	Herb	Secure	BH, CH, DEC, FH, HH, KIHP, OH, RHMP
<i>Psychotria ligustrifolia</i>	Rubiaceae	Shrub	Imperiled	ACP

<i>Psychotria nervosa</i>	Rubiaceae	Shrub	Secure	ACP, BH, CH, COB, DEC, FH, JH, HH, KIHP, OH, PV1, RHMP, SP
<i>Psychotria sulzneri</i>	Rubiaceae	Shrub	Secure	CH, COB, DEC, FH, HH, KIHP, OH, PV1
<i>Pteridium aquilinum</i> var. <i>caudatum</i>	Dennstaedtiaceae	Herb	Secure	BH
<i>Pteris vittata</i>	Pteridaceae	Herb	Not Native, Naturalized	DEC, HH
<i>Pteris x delchampsii</i>	Pteridaceae	Herb	Not Native, Naturalized	HH
<i>Ptychosperma elegans</i>	Arecaceae	Tree	Not Native, Naturalized	SP
<i>Quercus virginiana</i>	Fagaceae	Tree	Secure	ACP, BH, CH, COB, DEC, FH, HH, JH, KIHP, OH, PV1, RHMP, SP
<i>Randia aculeata</i>	Rubiaceae	Shrub	Secure	BH, HH, JH, PV1
<i>Rivina humilis</i>	Phytolaccaceae	Herb	Secure	ACP, RHMP, SP
<i>Roystonea regia</i>	Arecaceae	Tree	Rare	ACP, DEC
<i>Sabal palmetto</i>	Arecaceae	Tree	Secure	ACP, BH, CH, COB, JH, HH, KIHP, OH, PV1, RHMP

<i>Sambucus canadensis</i>	Caprifoliaceae	Shrub	Secure	HH
<i>Sanseveria hyacithoides</i>	Agavaceae	Herb	Not Native, Naturalized	ACP
<i>Sarcostemma clausum</i>	Asclepiadaceae	Vine	Secure	BH
<i>Schaefferia frutescens</i>	Celastraceae	Shrub	Imperiled	BH
<i>Schefflera actinophylla</i>	Araliaceae	Tree	Not Native, Naturalized	FH, HH, KIHP
<i>Schinus terebinthifolius</i>	Anacardiaceae	Tree	Not Native, Naturalized	BH, CH, COB, DEC, HH, JH, KIHP, PV1, RHMP, SP
<i>Scleria lithosperma</i>	Cyperaceae	Herb	Imperiled	DEC
<i>Senna mexicana</i> <i>var. chapmanii</i>	Fabaceae	Shrub	Rare	CH
<i>Senna occidentalis</i>	Fabaceae	Herb	Not Native, Naturalized	ACP
<i>Serenoa repens</i>	Arecaceae	Shrub	Secure	HH, KIHP, PV1
<i>Sida rhombifolia</i>	Malvaceae	Herb	Secure	ACP
<i>Sideroxylon foetidissimum</i>	Sapotaceae	Tree	Secure	ACP, CH, COB, DEC, FH, JH, OH, RHMP, SP

<i>Sideroxylon salicifolium</i>	Sapotaceae	Tree	Secure	BH, CH, COB, DEC, HH, JH, OH, PV1
<i>Simarouba glauca</i>	Simaroubaceae	Tree	Secure	ACP, CH, COB, DEC, FH, JH, OH, PV1, RHMP, SP
<i>Smilax auriculata</i>	Smilacaceae	Vine	Secure	ACP, BH, COB, DEC, HH, JH, KIHP, OH, PV1, RHMP
<i>Smilax bona-nox</i>	Smilacaceae	Vine	Rare	BH, CH, DEC, FH, HH, JH, OH, PV1, RHMP
<i>Smilax laurifolia</i>	Smilacaceae	Vine	Secure	JH
<i>Solanum americanum</i>	Solanaceae	Herb	Secure	ACP
<i>Solanum diphyllum</i>	Solanaceae	Shrub	Not Native, Naturalized	ACP
<i>Solanum donianum</i>	Solanaceae	Shrub	Rare	DEC
<i>Solanum erianthum</i>	Solanaceae	Shrub	Rare	CH, COB, FH, SP
<i>Spiranthes costaricensis</i>	Orchidaceae	Herb	Critically Imperiled	OH
<i>Syagrus romanzoffiana</i>	Arecaceae	Tree	Not Native, Naturalized	DEC, HH, KIHP
<i>Syngonium podophyllum</i>	Araceae	Vine	Not Native, Naturalized	ACP, FH, KIHP

<i>Tectaria fimbriata</i>	Dryopteridaceae	Herb	Imperiled	COB, FH
<i>Tectaria heracleifolia</i>	Dryopteridaceae	Herb	Imperiled	COB, DEC, FH, HH
<i>Tetrazygia bicolor</i>	Melastomataceae	Shrub	Rare	COB, OH, PV1
<i>Thelypteris kunthii</i>	Thelypteridaceae	Herb	Secure	BH, COB, DEC, HH, PV1, RHMP
<i>Thelypteris reptans</i>	Thelypteridaceae	Herb	Imperiled	HH
<i>Thelypteris sclerophylla</i>	Thelypteridaceae	Herb	Critically Imperiled	HH
<i>Tillandsia balbisiana</i>	Bromeliaceae	Herb	Secure	JH, OH
<i>Tillandsia fasciculata</i> var. <i>densispica</i>	Bromeliaceae	Herb	Secure	BH, DEC, JH, OH, PV1
<i>Tillandsia flexuosa</i>	Bromeliaceae	Herb	Rare	PV1
<i>Tillandsia setacea</i>	Bromeliaceae	Herb	Secure	BH, JH, OH
<i>Tillandsia usneoides</i>	Bromeliaceae	Herb	Secure	ACP, RHMP
<i>Tillandsia utriculata</i>	Bromeliaceae	Herb	Secure	BH, JH
<i>Tillandsia variabilis</i>	Bromeliaceae	Herb	Rare	JH, OH

<i>Tournefortia hirsutissima</i>	Vitaceae	Vine	Imperiled	COB
<i>Toxicodendron radicans</i>	Anacardiaceae	Vine	Secure	ACP, BH, COB, DEC, FH, HH, JH, KIHP, PV1
<i>Trema micranthum</i>	Ulmaceae	Tree	Secure	ACP, DEC, PV1
<i>Triumfetta semitriloba</i>	Tiliaceae	Shrub	Not Native, Naturalized	KIHP
<i>Urena lobata</i>	Malvaceae	Tree	Not Native, Naturalized	ACP
<i>Urochloa subquadriflora</i>	Poaceae	Herb	Not Native, Naturalized	SP
<i>Verbesina virginica</i>	Asteraceae	Herb	Secure	ACP
<i>Vitis aestivalis</i>	Vitaceae	Vine	Imperiled	DEC
<i>Vitis cinerea</i> var. <i>floridana</i>	Vitaceae	Vine	Secure	BH, FH, HH, PV1
<i>Vitis rotundifolia</i>	Vitaceae	Vine	Secure	ACP, BH, CH, COB, DEC, FH, HH, JH, KIHP, OH, PV1, RHMP
<i>Vitis shuttleworthii</i>	Vitaceae	Vine	Rare	FH, PV1
<i>Vittaria lineata</i>	Vittariaceae	Herb	Secure	PV1
<i>Youngia japonica</i>	Asteraceae	Herb	Not Native, Naturalized	ACP, DEC, RHMP

<i>Zamia integrifolia</i>	Zamiaceae	Herb	Apparently Secure	BH, CH, DEC, HH, JH, PV1
<i>Zanthoxylum fagara</i>	Rutaceae	Tree	Secure	ACP, CH, DEC, HH, KIHP, RHMP

Appendix 2. Species accumulation across all quadrats in surveyed hammocks. Species richness values represent the mean number of species found after surveying x number of quadrats within a hammock. Values were obtained from the S_{obs} Mean metric through 250 sample order randomization runs for each hammock using EstimateS (Colwell 2006). Study site hammocks included Arch Creek Park (ACP), Bequaert Hammock (BH), Castellow Hammock (CH), Camp Owaissa Bauer (COB), Deering Estate at Cutler (DEC), Fuchs Hammock (FH), Harden Hammock (HH), Junk Hammock (JH), Kendall Indian Hammocks Park (KIHP), Osteen Hammock (OH), Palma Vista #1 (PV1), R. Hardy Matheson Preserve (RHMP), and Simpson Park (SP).

Hammock	# of Quadrats											Total SR
	1	2	3	4	5	6	7	8	9	10	11	
ACP	11.4	18.9	25.1	30.2	34.4	38.0	41.4	44.2	46.9	49.5	51.7	54
BH	23.0	32.4	38.3	42.6	45.6	48.0	50.0	51.8	53.3	54.7	55.9	57
CH	14.5	20.5	24.5	27.3	29.6	31.5	33.4	34.9	36.3	37.6	38.8	40
COB	15.5	23.1	28.4	32.6	36.3	39.4	42.1	44.5	46.7	48.6	50.3	52
DEC	16.7	25.9	33.3	38.6	42.9	46.4	49.7	52.5	54.9	57.3	59.2	61
FH	12.6	19.2	24.2	27.8	30.9	33.2	35.6	37.8	39.4	40.9	42.1	43
HH	18.0	27.0	33.1	37.8	41.7	45.0	48.1	51.2	54.0	56.5	58.9	61
JH	19.5	27.5	32	35.3	37.8	40.1	41.7	43.0	44.0	44.9	45.4	46
KIHP	10.9	16.9	21.2	24.4	27.5	29.9	32.3	34.2	36.2	38.0	39.6	41
OH	17.3	23.9	28.5	32.2	35.1	37.4	39.3	41.1	42.8	44.4	45.6	47
PV1	19.5	30.3	37.8	43.1	47.9	51.4	54.3	57.1	59.5	61.6	63.4	65
RHMP	13.6	19.5	24.1	27.7	30.6	33.2	35.4	37.3	38.8	40.0	41.1	42
SP	11.9	17.7	21.7	24.7	27.2	29.2	31.0	32.7	34.1	35.5	36.8	38

Appendix 3. Hammock data. Variables include hammock area (HA , in m^2), human population density (HPD , in persons mi^{-2}), mean quadrat canopy-subcanopy cover (CSC), mean quadrat ground cover (GC), mean quadrat basal area (BA , in cm^2), mean quadrat woody plant density (DEN , in plants $15m^{-2}$), total surveyed native species richness (NSR), total surveyed exotic species richness (ESR). Study site hammocks were Arch Creek Park (ACP), Bequaert Hammock (BH), Castellow Hammock (CH), Camp Owaissa Bauer (COB), Deering Estate at Cutler (DEC), Fuchs Hammock (FH), Harden Hammock (HH), Junk Hammock (JH), Kendall Indian Hammocks Park (KIHP), Osteen Hammock (OH), Palma Vista #1 (PV1), R. Hardy Matheson Preserve (RHMP), and Simpson Park (SP).

Hammock	HA	HPD	CSC	GC	BA	DEN	NSR	ESR
ACP	39,700	4182.5	96.0%	70.0%	1035.3	8.0	36	18
BH	113,640	21.4	125.4%	43.8%	331.7	23.8	54	3
CH	334,610	609	134.8%	22.5%	1322.7	17.9	37	3
COB	113,280	250.3	133.5%	30.2%	3489.375	15.4	47	5
DEC	450,660	4184.1	132.5%	36.3%	763.4	16.2	51	10
FH	107,270	1584.2	127.5%	21.5%	1159.4	15.1	33	10
HH	40,350	609	119.8%	59.8%	531.5	28.9	47	13
JH	34,390	21.4	153.3%	45.8%	603.2	27.6	45	1
KIHP	141,690	5958.3	155.0%	49.0%	812.1	20.7	26	15
OH	164,400	21.4	126.5%	34.0%	451.0	30.9	46	1
PV1	255,060	21.4	127.9%	44.0%	464.8	36.3	61	4
RHMP	44,750	2232.1	131.5%	29.2%	501.8	28.4	32	10
SP	36,830	8936.2	97.3%	44.0%	713.3	19.5	25	13

Appendix 4. Representation of native species planted in polyculture mesocosms by community treatment. The number of mesocosms in which each species were planted is reported by community treatment with the cumulative number of seedlings of each species planted in mesocosms reported in parentheses. Species are abbreviated by their four-letter species code, made up of the first two letters from each of their genus and species names.

Species	Low SD, Low SR	Low SD, High SR	High SD, Low SR	High SD, High SR	All Polycultures
BOSU	5 (13)	13 (15)	4 (29)	18 (50)	40 (107)
CAAM	6 (20)	19 (23)	7 (45)	18 (47)	50 (135)
CACY	7 (21)	12 (14)	4 (25)	16 (38)	39 (98)
CISP	7 (28)	21 (24)	9 (55)	16 (41)	53 (148)
FIAU	6 (17)	14 (16)	9 (54)	12 (31)	41 (118)
GUDI	6 (24)	16 (20)	8 (46)	18 (48)	48 (138)
ILKR	3 (5)	22 (30)	5 (35)	19 (43)	49 (113)
LYLA	6 (20)	11 (13)	9 (54)	16 (40)	42 (127)
OCCO	5 (16)	15 (22)	4 (22)	16 (36)	40 (96)
PIPI	8 (18)	16 (16)	4 (18)	8 (11)	36 (63)
SISA	11 (31)	10 (12)	4 (24)	9 (24)	34 (91)
ZAFA	2 (3)	11 (11)	5 (25)	13 (23)	31 (62)

Appendix 5. Monoculture mesocosm productivity. GLM ANOVA results for Monoculture Plot Native Total Biomass by Propagule Pressure (PP) and Species (SP). Significant effects are bolded.

Source	df	SS	MS	F	<i>P</i>
Intercept	1	472483.636	472483.636	7009.786	<0.001
PP	2	153.380	76.690	1.138	0.323
SP	11	188161.802	17105.618	253.780	<0.001
PP x SP	22	1306.995	59.409	0.881	0.619
Error	180	12132.618	67.403		
Total	216	674238.430			

Appendix 6. Polyculture mesocosm productivity. GLM ANOVA results for Polyculture Plot Native Total Biomass by Propagule Pressure (PP), Native Seedling Density (SD), and Native Species Richness (SR). Significant effects are bolded.

Source	df	SS	MS	F	<i>P</i>
Intercept	1	983187.928	983187.928	1695.381	<0.001
PP	2	2014.254	1007.127	1.737	0.180
SD	1	5403.475	5403.475	9.318	0.003
SR	1	1.342	1.342	0.002	0.962
PP x SD	2	1158.621	579.310	0.999	0.371
PP x SR	2	1464.467	732.234	1.263	0.286
SD x SR	1	3103.418	3103.418	5.351	0.022
PP x SD x SR	2	2142.044	1071.022	1.847	0.162
Error	132	76549.621	579.921		
Total	144	1075025.170			

Appendix 7. Biodiversity effects by species richness. GLM MANOVA results for trait-independent complementarity effects (TICE), dominance effects (DE), and trait-dependent complementarity effects (TDCE) by Native Species Richness (SR). Significant effects are bolded.

Source	Wilks' Lambda Multivariate Test	TICE Univariate Test	DE Univariate Test	TDCE Univariate Test
Intercept	df: 3, 68 F: 61.50 P: <0.001	df: 1, 70 F: 147.72 P: <0.001	df: 1, 70 F: 76.52 P: <0.001	df: 1, 70 F: 17.73 P: <0.001
SR	df: 3, 68 F: 3.30 P: 0.026	df: 1, 70 F: 35.45 P: 0.506	df: 1, 70 F: 10.04 P: 0.002	df: 1, 70 F: 2.22 P: 0.141

Appendix 8. Relationships between individual species and partitioned biodiversity effects components. Pearson correlation coefficient (ρ) results for significant relationships between individual species, represented by presence/absence (p/a) or seedling density (sd) data, and partitioned biodiversity effects in low-density polyculture mesocosms. Asterisks are used to represent the level of statistical significance of each relationship: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Species are abbreviated by their four-letter species code, made up of the first two letters from their genus and species names.

Species	TICE	DE	TDCE
CISP	-0.235* (sd)		
FIAU	0.263* (p/a)	0.432*** (p/a)	
ILKR		0.255* (p/a)	
OCCO		0.337** (p/a), 0.319** (sd)	
SISA		-0.324** (p/a), -0.296* (sd)	-0.298* (sd)
ZAFA		0.239* (p/a)	

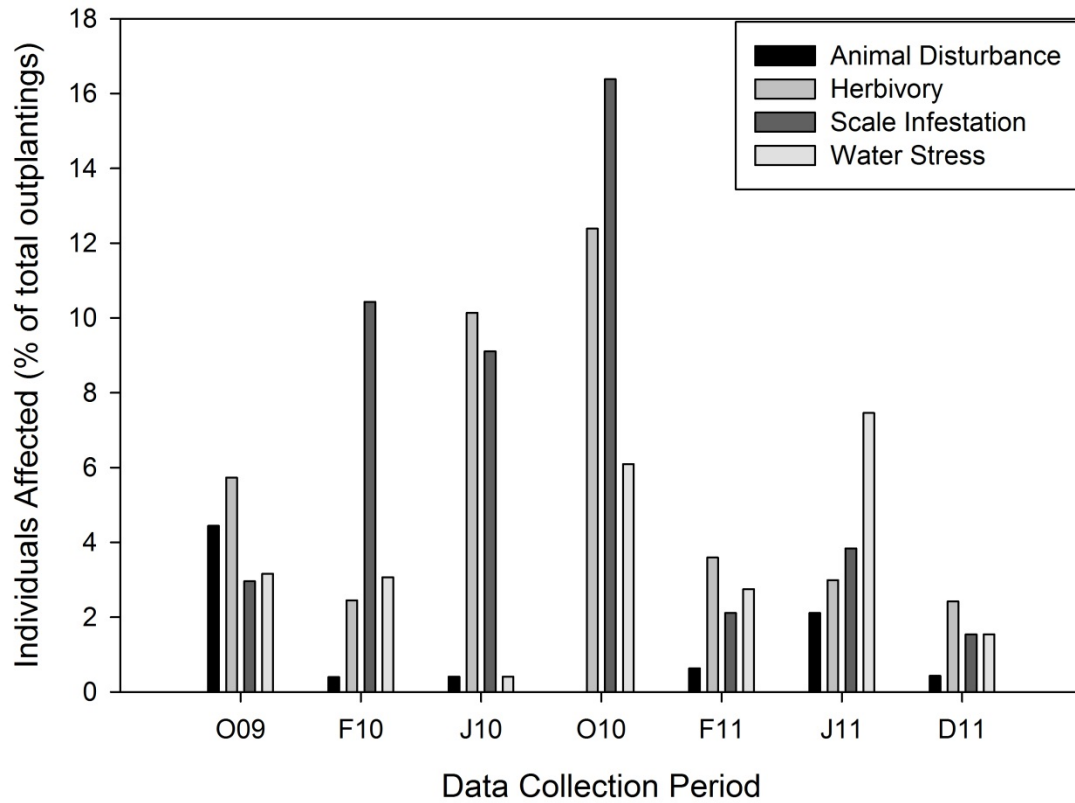
Appendix 9. Native species utilized in mesocosm experiments and other pertinent phylogenetic, life history, and conservation information. Species codes used in figures are included next to species names in parentheses. Habit, habitat component, and South Florida status information were obtained from the publicly-accessible Floristic Inventory of South Florida and Natives For Your Neighborhood online databases provided by the Institute for Regional Conservation and are available at www.regionalconservation.org.

Species	Family	Habit	Hammock Component	S. Florida Status
<i>Bourreria succulenta</i> (BS)	Boraginaceae	large shrub / small tree	sub-canopy and edge	rare
<i>Callicarpa americana</i> (CA)	Verbenaceae	shrub	edge and gap	secure
<i>Capparis cynophallophora</i> (CC)	Capparaceae	large shrub / small tree	sub-canopy and edge	rare
<i>Citharexylum spinosum</i> (CS)	Verbenaceae	small to medium tree	sub-canopy and edge	rare
<i>Ficus aurea</i> (FA)	Moraceae	large tree	canopy emergent	secure
<i>Guapira discolor</i> (GD)	Nyctaginaceae	large shrub / small tree	sub-canopy	secure
<i>Ilex krugiana</i> (IK)	Aquifoliaceae	medium tree	sub-canopy and canopy	rare
<i>Lysiloma latisiliquum</i> (LL)	Fabaceae	large tree	canopy	apparently secure
<i>Ocotea coriacea</i> (OC)	Lauraceae	medium tree	sub-canopy and canopy	secure
<i>Piscidia piscipulum</i> (PP)	Fabaceae	medium to large tree	canopy	secure
<i>Sideroxylon salicifolium</i> (SS)	Sapotaceae	medium tree	canopy	secure
<i>Zanthoxylum fagara</i> (ZF)	Rutaceae	large shrub / small tree	sub-canopy and edge	secure

Appendix 10. Native species utilized in mesocosm experiments along with abundance information by polyculture treatment factor level. Species codes used in figures are included next to species names in parentheses. The number of mesocosms in which species are represented is reported below with seedling abundances in parentheses.

Species	Native Seedling Density		Native Species Richness		Invader Propagule Pressure			Total
	Low	High	Low	High	Zero	Low	High	
<i>Bourreria succulenta</i> (BS)	18 (28)	22 (79)	9 (42)	31 (65)	12 (42)	13 (31)	15 (34)	40 (107)
<i>Callicarpa americana</i> (CA)	25 (43)	25 (92)	13 (65)	37 (70)	18 (45)	16 (55)	16 (35)	50 (135)
<i>Capparis cynophallophora</i> (CC)	19 (35)	20 (63)	11 (46)	28 (52)	11 (25)	11 (23)	17 (50)	39 (98)
<i>Citharexylum spinosum</i> (CS)	28 (52)	25 (96)	16 (83)	37 (65)	17 (47)	18 (57)	18 (44)	53 (148)
<i>Ficus aurea</i> (FA)	20 (33)	22 (85)	15 (71)	27 (47)	13 (39)	15 (45)	14 (34)	42 (118)
<i>Guapira discolor</i> (GD)	22 (44)	26 (94)	14 (70)	34 (68)	16 (56)	18 (41)	14 (41)	48 (138)
<i>Ilex krugiana</i> (IK)	25 (35)	24 (78)	8 (40)	41 (73)	12 (25)	18 (35)	19 (53)	49 (113)
<i>Lysiloma latisiliquum</i> (LL)	17 (33)	25 (94)	15 (74)	27 (53)	15 (45)	11 (22)	16 (49)	42 (127)
<i>Ocotea coriacea</i> (OC)	20 (38)	20 (58)	9 (38)	31 (58)	12 (25)	19 (51)	9 (20)	40 (96)
<i>Piscidia piscipulum</i> (PP)	24 (34)	12 (29)	12 (36)	24 (27)	14 (25)	11 (17)	11 (21)	36 (63)
<i>Sideroxylon salicifolium</i> (SS)	21 (43)	13 (48)	15 (55)	19 (36)	14 (25)	7 (25)	13 (41)	34 (91)
<i>Zanthoxylum fagara</i> (ZF)	13 (14)	18 (48)	7 (28)	24 (34)	14 (33)	11 (19)	6 (10)	31 (62)

Appendix 11. Percentage of outplantings impacted by animal disturbance, herbivory, scale infestation, and water stress over time.



Appendix 12. Percentage of outplantings impacted by animal disturbance, herbivory, scale infestation, and water stress at some time by species. All species names follow Wunderlin (1998).

Species	Rate of Animal Disturbance	Rate of Herbivory	Rate of Scale Infestation	Rate of Water Stress
<i>Ardisia escallonioides</i>	4.00%	20.00%	0%	36.00%
<i>Byrsonima lucida</i>	0%	5.00%	0%	10.00%
<i>Calyptranthes pallens</i>	9.52%	9.52%	61.90%	61.90%
<i>Chiococca alba</i>	5.00%	15.00%	5.00%	15.00%
<i>Chrysophyllum oliviforme</i>	0%	0%	0%	28.57%
<i>Citharexylum spinosum</i>	14.29%	9.52%	4.76%	38.10%
<i>Coccoloba diversifolia</i>	4.76%	38.10%	14.29%	14.29%
<i>Erythrina herbacea</i>	5.00%	10.00%	30.00%	5.00%
<i>Eugenia axillaris</i>	0%	0%	0%	14.29%
<i>Exothea paniculata</i>	23.81%	38.10%	66.67%	9.52%
<i>Guapira discolor</i>	5.00%	5.00%	25.00%	10.00%
<i>Guettarda scabra</i>	0%	10.00%	5.00%	50.00%

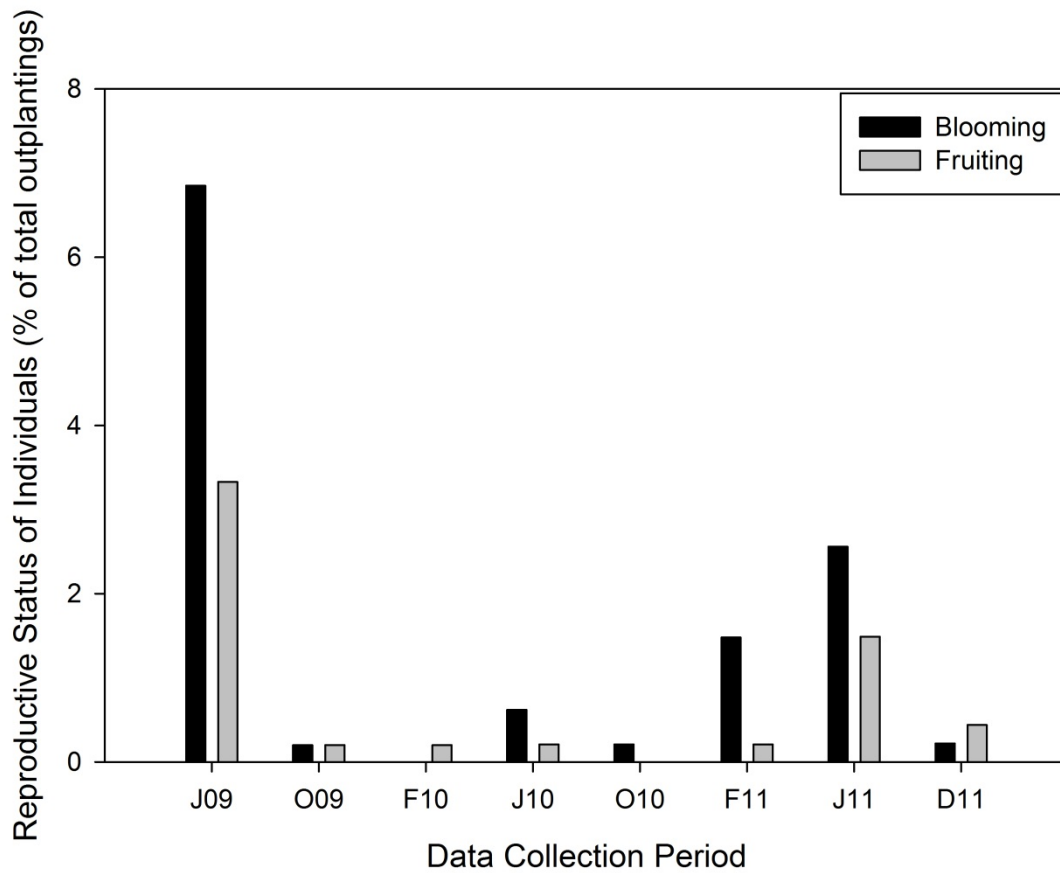
<i>Gymnanthes lucida</i>	9.52%	0%	4.76%	0%
<i>Hamelia patens</i>	4.76%	100%	95.24%	9.52%
<i>Ilex krugiana</i>	9.52%	9.52%	52.38%	33.33%
<i>Krugiodendron ferreum</i>	28.57%	42.86%	9.52%	14.29%
<i>Myrcianthes fragrans</i>	4.76%	4.76%	0%	23.81%
<i>Myrica cerifera</i>	19.05%	9.52%	0%	19.05%
<i>Ocotea coriacea</i>	0%	9.52%	9.52%	33.33%
<i>Prunus myrtifolia</i>	12.50%	0%	0%	18.75%
<i>Randia aculeata</i>	4.76%	0%	14.29%	0%
<i>Sideroxylon salicifolium</i>	9.52%	14.29%	90.48%	19.05%
<i>Simarouba glauca</i>	14.29%	0%	0%	4.76%
<i>Tetrazygia bicolor</i>	0%	23.81%	71.43%	14.29%
<i>Tournefortia hirsutissima</i>	4.76%	28.57%	4.76%	9.52%
<i>Zanthoxylum fagara</i>	0%	71.43%	4.76%	0%

Appendix 13. Percentage of outplantings blooming and fruiting by species. All species names follow Wunderlin (1998).

Species	Rate of Blooming	Rate of Fruiting
<i>Ardisia escallonioides</i>	0%	0%
<i>Byrsonima lucida</i>	0%	40.00%
<i>Calyptranthes pallens</i>	0%	0%
<i>Chiococca alba</i>	20.00%	0%
<i>Chrysophyllum oliviforme</i>	0%	0%
<i>Citharexylum spinosum</i>	14.29%	0%
<i>Coccoloba diversifolia</i>	0%	0%
<i>Erythrina herbacea</i>	35.00%	5.00%
<i>Eugenia axillaris</i>	0%	0%
<i>Exothea paniculata</i>	0%	0%
<i>Guapira discolor</i>	5.00%	0%
<i>Guettarda scabra</i>	65.00%	0%
<i>Gymnanthes lucida</i>	0%	0%

<i>Hamelia patens</i>	14.29%	14.29%
<i>Ilex krugiana</i>	0%	38.10%
<i>Krugiodendron ferreum</i>	0%	0%
<i>Myrcianthes fragrans</i>	0%	0%
<i>Myrica cerifera</i>	0%	0%
<i>Ocotea coriacea</i>	0%	4.76%
<i>Prunus myrtifolia</i>	0%	0%
<i>Randia aculeata</i>	28.57%	19.05%
<i>Sideroxylon salicifolium</i>	0%	0%
<i>Simarouba glauca</i>	0%	0%
<i>Tetrazygia bicolor</i>	61.90%	0%
<i>Tournefortia hirsutissima</i>	0%	0%
<i>Zanthoxylum fagara</i>	4.76%	0%

Appendix 14. Percentage of outplantings blooming and fruiting over time.



Appendix 15. Historical change at Swamp Fern Experimental Hammock.

Conditions at this site have changed dramatically within the last hundred years, and as a result, so have the plant communities (see Chapter 4). The entire character of the original vegetative community was lost with the logging, hydrological modifications, and fire suppression that accompanied urban development in this region. After these initial disturbances, this site was likely very quickly colonized by nearby hardwoods that had previously been excluded by frequent fires. While a few native drought-tolerant hardwoods have done reasonably well, hydric species only remain as small populations of mature, reproducing adults that are unable to successfully recruit, likely as a result of substantially lowered water tables (W. R. Brooks, *pers. obs.*). Additionally, SFEH has been overrun with exotic agricultural and ornamental species in recent decades that dominate the seedling and understory layers (W. R. Brooks, *pers. obs.*).

Appendix 17. Species found in floristic surveys of Swamp Fern Experimental Hammock interior and buffer quadrats. Distribution data refers to the number of interior quadrats in which each species was documented. ‘State Listed Status’ refers to state protected or prohibited status. FLEPPC I species are considered invasive while FLEPPC II species are considered potentially invasive (FLEPPC 2011). A hashmark (#) denotes a species found in buffer quadrats but not experimental quadrats in March 2009, a caret (^) denotes a species not recorded in any quadrat in March 2009, and an asterisk (*) denotes outplanted species introduced in June 2009. All nomenclature follows Gann et al. (2012).

Species	March 2009 Distribution	June 2011 Distribution	Change in Distribution	Native Status	State Listed Status
<i>Abrus precatorius</i>	12	1	-11	Exotic	FLEPPC I
<i>Acacia auriculiformis</i> #	0	0	0	Exotic	FLEPPC I
<i>Albizia lebbek</i>	3	0	-3	Exotic	FLEPPC I
<i>Ardisia elliptica</i>	67	7	-60	Exotic	FLEPPC I
<i>Ardisia escallonioides</i> *	0	16	16	Native	
<i>Bidens alba</i> <i>var. radiata</i> #	0	1	1	Native	
<i>Bischofia javanica</i>	1	0	-1	Exotic	FLEPPC I

<i>Blechnum serrulatum</i>	42	54	12	Native	
<i>Bursera simaruba</i>	3	4	1	Native	
<i>Byrsonima lucida</i> *	0	5	5	Native	Threatened
<i>Callicarpa americana</i>	9	9	0	Native	
<i>Calyptranthes pallens</i> *	0	9	9	Native	Threatened
<i>Carica papaya</i> ^	0	0	0	Exotic	
<i>Chamaesyce hypericifolia</i> ^	0	0	0	Native	
<i>Chiococca alba</i> *	0	11	11	Native	
<i>Chrysobalanus icaco</i>	17	10	-7	Native	
<i>Chrysophyllum oliviforme</i> *	0	9	9	Native	Threatened
<i>Citharexylum spinosum</i> *	0	10	10	Native	
<i>Clematis baldwinii</i>	4	9	5	Native	

<i>Coccoloba diversifolia</i> *	0	8	8	Native	
<i>Cupaniopsis anacardioides</i> ^	0	1	1	Exotic	FLEPPC I
<i>Cynodon dactylon</i>	1	0	-1	Exotic	
<i>Desmodium incanum</i>	9	3	-6	Native	
<i>Dioscorea bulbifera</i>	92	84	-8	Exotic	FLEPPC I
<i>Dypsis lutescens</i>	14	2	-12	Exotic	
<i>Eriobotrya japonica</i>	2	0	-2	Exotic	
<i>Erythrina herbacea</i> *	0	13	13	Native	
<i>Eugenia axillaris</i> *	0	12	12	Native	
<i>Eugenia uniflora</i>	18	4	-14	Exotic	FLEPPC I
<i>Exothea paniculata</i> *	0	11	11	Native	
<i>Ficus aurea</i>	3	4	1	Native	

<i>Guapira discolor*</i>	0	10	10	Native	
<i>Guettarda scabra*</i>	0	8	8	Native	
<i>Gymnanthes lucida*</i>	0	13	13	Native	
<i>Hamelia patens*</i>	0	9	9	Native	
<i>Ilex cassine</i>	2	1	-1	Native	
<i>Ilex krugiana*</i>	0	11	11	Native	Threatened
<i>Jasminum fluminense</i>	11	3	-8	Exotic	FLEPPC I
<i>Krugiodendron ferreum*</i>	0	11	11	Native	
<i>Mangifera indica</i>	5	0	-5	Exotic	
<i>Melothria pendula^</i>	0	0	0	Native	
<i>Morinda royoc</i>	10	9	-1	Native	
<i>Mucuna pruriens</i>	5	6	1	Exotic	
<i>Myrcianthes fragrans*</i>	0	11	11	Native	Threatened

<i>Myrica cerifera</i> *	0	4	4	Native	
<i>Myrsine cubana</i>	5	3	-2	Native	
<i>Nephrolepis cordifolia</i>	20	7	-13	Exotic	FLEPPC I
<i>Nephrolepis falcata furcans</i>	7	2	-5	Exotic	
<i>Nephrolepis multiflora</i>	89	12	-77	Exotic	FLEPPC I
<i>Neyraudia reynaudiana</i>	2	0	-2	Exotic	FLEPPC I
<i>Ocotea coriacea</i> *	1	15	14	Native	
<i>Oeceoclades maculata</i>	16	0	-16	Exotic	
<i>Oplismenus hirtellus</i>	15	28	13	Native	
<i>Parthenocissus quinquefolia</i>	16	22	6	Native	
<i>Passiflora suberosa</i>	11	14	3	Native	
<i>Persea palustris</i>	1	1	0	Native	
<i>Phlebodium aureum</i> ^	0	3	3	Native	

<i>Phytolacca americana</i> #	0	0	0	Native	
<i>Pinus elliottii</i> <i>var. densa</i>	4	4	0	Native	
<i>Prunus myrtifolia</i> *	0	6	6	Native	Threatened
<i>Psilotum nudum</i>	2	7	5	Native	
<i>Psychotria nervosa</i>	22	31	9	Native	
<i>Psychotria sulzneri</i>	1	1	0	Native	
<i>Pteris vittata</i> #	0	0	0	Exotic	FLEPPC II
<i>Quercus laurifolia</i>	3	3	0	Native	
<i>Quercus virginiana</i>	76	76	0	Native	
<i>Randia aculeata</i> *	0	11	11	Native	
<i>Sabal palmetto</i>	81	74	-7	Native	
<i>Schefflera actinophylla</i>	51	1	-50	Exotic	FLEPPC I
<i>Schinus terebinthefolius</i>	20	5	-15	Exotic	FLEPPC I

<i>Senna pendula</i> <i>var. glabrata</i>	2	3	1	Exotic	FLEPPC I
<i>Serenoa repens</i>	10	9	-1	Native	
<i>Sideroxylon</i> <i>salicifolium*</i>	0	12	12	Native	
<i>Simarouba</i> <i>glauca*</i>	0	9	9	Native	
<i>Smilax</i> <i>auriculata</i>	59	55	-4	Native	
<i>Smilax bona-</i> <i>nox</i>	7	6	-1	Native	
<i>Spermacoce</i> <i>verticillata</i>	1	0	-1	Exotic	
<i>Stenotaphrum</i> <i>secundatum</i>	2	0	-2	Exotic	
<i>Syagrus</i> <i>romanzoffiana</i>	4	0	-4	Exotic	FLEPPC II
<i>Syzygium</i> <i>cumini</i>	4	0	-4	Exotic	FLEPPC I
<i>Tetrazygia</i> <i>bicolor*</i>	0	10	10	Native	Threatened
<i>Tillandsia</i> <i>balbisiana</i>	1	0	-1	Native	Threatened

<i>Tillandsia fasciculata</i> var. <i>densispica</i>	7	5	-2	Native	Endangered
<i>Tillandsia recurvata</i>	14	19	5	Native	
<i>Tillandsia utriculata</i>	1	0	-1	Native	Endangered
<i>Tournefortia hirsutissima</i> *	0	10	10	Native	Endangered
<i>Toxicodendron radicans</i>	47	48	1	Native	
<i>Tradescantia spathacea</i>	2	0	-2	Exotic	FLEPPC II
<i>Trema micranthum</i> #	0	0	0	Native	
<i>Urena lobata</i>	0	0	0	Exotic	FLEPPC I
<i>Vitis rotundifolia</i>	83	84	1	Native	
<i>Vittaria lineata</i>	2	1	-1	Native	
<i>Wedelia trilobata</i>	6	0	-6	Exotic	FLEPPC II
<i>Zamia integrifolia</i>	3	3	0	Native	Commercially Exploited

<i>Zanthoxylum fagara*</i>	0	8	8	Native
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Appendix 18. Exotic species control measures undertaken in Swamp Fern Experimental Hammock.

	Removal Treatment			
	Mechanical Removal	Triclopyr (13.6%) Basal-bark Application	Glyphosate (1.2%) and Triclopyr (.1%)	
			Cut-stump Application	Foliar Application
<u>Trees and Shrubs</u>				
<i>Acacia auriculiformis</i>	X			
<i>Albizia lebbeck</i>		X		
<i>Ardisia elliptica</i>			X	
<i>Bischofia javanica</i>		X		
<i>Dyopsis lutescens</i>	X			
<i>Eriobotrya japonica</i>		X		
<i>Eugenia uniflora</i>		X		
<i>Mangifera indica</i>		X		

<i>Schefflera actinophylla</i>		X	
<i>Schinus terebinthefolius</i>		X	
<i>Senna pendula</i> <i>var. glabrata</i>	X		
<i>Syagrus romanzoffiana</i>	X		
<i>Syzygium cumini</i>		X	
<u>Vines</u>			
<i>Abrus precatorius</i>			X
<i>Dioscorea bulbifera</i>	X		X
<i>Jasminum fluminense</i>	X		
<i>Mucuna pruriens</i>	X		X
<u>Herbs</u>			
<i>Cynodon dactylon</i>	X		
<i>Nephrolepis cordifolia</i>	X		
<i>Nephrolepis falcata furcans</i>	X		

<i>Nephrolepis multiflora</i>	X		
<i>Neyraudia reynaudiana</i>	X		X
<i>Oeceoclades maculata</i>	X		
<i>Pteris vittata</i>	X		
<i>Spermacoce verticillata</i>	X		
<i>Stenotaphrum secundatum</i>	X		
<i>Tradescantia spathacea</i>	X		
<i>Wedelia trilobata</i>	X		

Appendix 19. Repeated measures ANOVA table for interior quadrat canopy cover by outplanting treatment. Cutoff for significance is $p=0.007$.

Source	df	Wilks' Lambda	F	<i>p</i>
Time x Outplanting Treatment	16, 257.262	0.730	1.745	0.039
Time	4, 84	0.510	20.181	<0.001

Appendix 20. Repeated measures ANOVA table for interior quadrat subcanopy cover by outplanting treatment. Cutoff for significance is $p=0.007$.

Source	df	Wilks' Lambda	F	<i>p</i>
Time x Outplanting Treatment	16, 257.262	0.858	0.827	0.654
Time	4, 84	0.272	56.320	<0.001

Appendix 21. Repeated measures ANOVA table for interior quadrat ground cover by outplanting treatment. Cutoff for significance is $p=0.007$.

Source	df	Wilks' Lambda	F	<i>p</i>
Time x Outplanting Treatment	16, 257.262	0.933	0.367	0.989
Time	4, 84	0.623	12.702	<0.001

Appendix 22. Repeated measures ANOVA table for interior quadrat total basal area by outplanting treatment. Cutoff for significance is $p=0.007$.

Source	df	Wilks' Lambda	F	<i>p</i>
Time x Outplanting Treatment	16, 257.262	0.770	1.437	0.124
Time	4, 84	0.786	5.717	<0.001

Appendix 23. Repeated measures ANOVA table for interior quadrat woody plant density by outplanting treatment. Cutoff for significance is $p=0.007$.

Source	df	Wilks' Lambda	F	<i>p</i>
Time x Outplanting Treatment	16, 257.262	0.709	1.918	0.019
Time	4, 84	0.855	3.575	0.010

Appendix 24. Repeated measures ANOVA table for interior quadrat native species richness by outplanting treatment. Cutoff for significance is $p=0.007$.

Source	df	Wilks' Lambda	F	<i>p</i>
Time x Outplanting Treatment	16, 257.262	0.236	9.718	<0.001
Time	4, 84	0.116	159.977	<0.001

Appendix 25. Repeated measures ANOVA table for interior quadrat exotic species richness by outplanting treatment. Cutoff for significance is $p=0.007$.

Source	df	Wilks' Lambda	F	<i>p</i>
Time x Outplanting Treatment	16, 257.262	0.873	0.729	0.764
Time	4, 84	0.186	92.008	<0.001

Appendix 26. MANOVA table for principal components scores by hammock.

Source	df	Wilks' Lambda	F	<i>p</i>
Intercept	3, 323	0.441	136.201	<0.001
Hammock	42, 958.938	0.064	34.754	<0.001

Appendix 27. Follow-up ANOVAs for principal components scores by hammock.

Source	PC1			PC2			PC3		
	df	F	<i>P</i>	df	F	<i>P</i>	df	F	<i>P</i>
Intercept	1	360.298	<0.001	1	45.459	<0.001	1	0.246	0.620
Hammock	14	288.629	<0.001	14	181.264	<0.001	14	21.082	0.095
Error	325			325			325		
Total	340			340			340		

Appendix 28. Interior quadrat mean and standard deviation data for pre-restoration (March 2009) floristic survey native variables by outplanting treatment. Outplanting treatment groups include: 1- high DEN x high SR, 2- high DEN x low SR, 3- low DEN x high SR, 4- low DEN x low SR, and 5- control. ‘Group’ refers to outplanting treatment group.

Group	Native Species Richness	Native Woody Species Richness	Native Woody Plant Density	Native Woody Basal Area
1	6.22 ± 1.99	2.33 ± 2.11	3.78 ± 2.18	415.99 ± 515.37
2	5.72 ± 1.71	2.39 ± 0.92	4.44 ± 2.73	335.14 ± 526.99
3	6.39 ± 2.66	2.89 ± 1.37	4.50 ± 1.95	741.86 ± 920.99
4	5.89 ± 2.35	2.39 ± 1.04	5.33 ± 3.38	693.28 ± 517.17
5	6.80 ± 2.07	2.85 ± 1.31	4.50 ± 2.70	543.59 ± 760.83

Appendix 29. Interior quadrat mean and standard deviation data for quadrat total exotic woody seedling (EWS; after June 2009 through December 2011) recruitment and pre-restoration (March 2009) floristic survey exotic variables by outplanting treatment.

Outplanting treatment groups include: 1- high DEN x high SR, 2- high DEN x low SR, 3- low DEN x high SR, 4- low DEN x low SR, and 5- control. ‘Group’ refers to outplanting treatment group, ‘Total EWS SR’ refers to Total Exotic Woody Seedling Species Richness, and ‘Total EWS DEN’ refers to Total Exotic Woody Seedling Density.

Group	Total EWS SR	Total EWS DEN	Exotic Species Richness	Exotic Woody Species Richness	Exotic Woody Plant Density	Exotic Woody Basal Area
1	2.89 ± 1.45	93.06 ± 186.34	5.22 ± 2.05	2.11 ± 1.41	3.11 ± 4.25	64.15 ± 124.93
2	2.50 ± 1.15	16.11 ± 16.44	4.50 ± 1.50	1.83 ± 1.34	1.33 ± 1.37	38.65 ± 67.71
3	2.83 ± 1.42	30.61 ± 37.52	5.00 ± 2.28	2.11 ± 1.18	1.67 ± 1.57	109.99 ± 294.90
4	2.72 ± 1.84	72.94 ± 127.24	4.67 ± 1.68	1.83 ± 1.15	2.00 ± 3.40	19.52 ± 47.73
5	2.40 ± 1.31	52.25 ± 107.18	5.35 ± 1.90	2.20 ± 1.15	1.95 ± 1.85	59.58 ± 88.27

Appendix 30. Interior quadrat mean and standard deviation data for floristic survey variables by data period and outplanting treatment from December 2009 through June 2011. Outplanting treatment groups include: 1- high DEN x high SR, 2- high DEN x low SR, 3- low DEN x high SR, 4- low DEN x low SR, and 5- control. ‘Group’ refers to outplanting treatment group, ‘EWS SR’ refers to Exotic Woody Seedling Species Richness, ‘EWS DEN’ refers to Exotic Woody Seedling Density, ‘NSR’ refers to Native Species Richness, ‘ESR’ refers to Exotic Species Richness, ‘CC’ refers to Canopy Cover, ‘SC’ refers to Subcanopy Cover, ‘GC’ refers to Ground Cover, ‘DEN’ refers to Woody Plant Density, and ‘BA’ refers to Woody Basal Area.

Data Period	Group	NSR	ESR	CC	SC	GC	DEN	BA
DEC 2009	1	12.8 ± 1.7	3.5 ± 2.1	57.2 ± 33.2	28.3 ± 20.4	38.1 ± 16.3	5.8 ± 2.9	409.7 ± 481.1
	2	11.9 ± 2.9	3.4 ± 1.6	63.8 ± 33.8	39.3 ± 18.9	33.5 ± 21.0	5.2 ± 2.7	362.9 ± 569.2
	3	8.4 ± 2.9	3.1 ± 1.9	72.2 ± 31.7	29.7 ± 18.9	28.1 ± 12.5	5.8 ± 3.2	771.1 ± 883.9
	4	8.3 ± 3.2	3.4 ± 2.0	62.4 ± 32.6	46.0 ± 24.3	29.0 ± 22.5	5.3 ± 3.1	697.8 ± 563.0
	5	7.6 ± 2.6	3.3 ± 2.2	63.5 ± 31.2	32.3 ± 16.8	29.3 ± 22.2	4.5 ± 2.9	500.0 ± 738.5

JUN 2010	1	12.9 ± 1.8	3.9 ± 1.1	61.7 ± 33.8	42.8 ± 24.7	32.9 ± 17.2	5.9 ± 2.9	503.0 ± 486.7
	2	11.9 ± 2.8	3.4 ± 1.3	61.8 ± 34.7	46.1 ± 20.0	26.3 ± 16.0	5.6 ± 2.5	396.8 ± 568.7
	3	9.2 ± 2.6	3.2 ± 2.0	78.2 ± 31.6	40.0 ± 26.0	25.8 ± 17.3	5.8 ± 3.5	781.1 ± 973.3
	4	8.4 ± 2.7	3.5 ± 1.9	61.3 ± 26.8	48.5 ± 21.8	17.4 ± 10.1	5.3 ± 3.4	817.4 ± 584.3
	5	7.7 ± 2.0	3.6 ± 1.4	69.4 ± 30.6	46.5 ± 22.1	27.6 ± 19.2	3.8 ± 1.9	491.4 ± 807.4
DEC 2010	1	12.5 ± 1.2	1.8 ± 1.3	69.0 ± 33.0	21.8 ± 16.1	27.5 ± 11.5	5.9 ± 2.7	509.1 ± 533.7
	2	11.8 ± 2.4	1.8 ± 1.5	71.0 ± 31.7	23.2 ± 18.5	21.3 ± 18.7	5.7 ± 2.6	419.4 ± 592.1
	3	8.7 ± 2.2	1.4 ± 0.9	79.7 ± 26.8	22.9 ± 14.1	21.0 ± 14.4	6.3 ± 3.6	933.5 ± 1067.4
	4	8.1 ± 2.5	1.2 ± 1.2	76.3 ± 22.3	34.9 ± 22.1	12.8 ± 8.4	4.8 ± 3.0	799.0 ± 566.7
	5	7.7 ± 2.0	1.8 ± 1.3	80.1 ± 24.4	26.3 ± 11.5	18.9 ± 14.4	4.0 ± 2.1	539.0 ± 851.7

	1	12.1 ± 2.2	1.9 ± 0.8	68.3 ± 36.0	24.9 ± 20.7	31.5 ± 15.6	6.5 ± 2.8	517.8 ± 538.4
	2	11.4 ± 2.4	1.2 ± 0.5	75.7 ± 29.9	26.4 ± 18.0	21.3 ± 15.1	5.6 ± 2.3	409.5 ± 565.9
JUN 2011	3	8.7 ± 2.5	1.0 ± 0.5	80.3 ± 30.5	19.7 ± 17.7	24.3 ± 20.0	6.4 ± 4.0	981.9 ± 1165.0
	4	7.4 ± 2.1	1.8 ± 1.7	82.9 ± 17.9	28.5 ± 19.1	14.9 ± 6.9	4.9 ± 3.0	934.0 ± 660.9
	5	7.5 ± 1.6	1.7 ± 1.0	78.4 ± 28.6	25.0 ± 13.3	24.0 ± 15.4	3.7 ± 2.1	580.8 ± 933.5

Appendix 31. Repeated measures ANOVA table for interior quadrat exotic woody seedling density by outplanting treatment. Cutoff for significance is $p=0.025$.

Source	df	Wilks' Lambda	F	<i>p</i>
Time x Restoration Treatment	16, 257.262	0.846	0.904	0.565
Time	4, 84	0.774	6.148	<0.001

Appendix 32. Repeated measures ANOVA table for interior quadrat exotic woody species richness by outplanting treatment. Cutoff for significance is $p=0.025$.

Source	df	Wilks' Lambda	F	<i>p</i>
Time x Restoration Treatment	16, 257.262	0.867	0.770	0.719
Time	4, 84	0.420	28.979	<0.001

Appendix 33. Interior quadrat mean and standard deviation data for exotic woody seedling recruitment by data period and outplanting treatment. Outplanting treatment groups include: 1- high DEN x high SR, 2- high DEN x low SR, 3- low DEN x high SR, 4- low DEN x low SR, and 5- control. ‘Group’ refers to outplanting treatment group.

Data Period	Group	Exotic Woody Seedling Species Richness	Exotic Woody Seedling Density
December 2009	1	1.33 ± 1.50	80.11 ± 173.01
	2	1.28 ± 1.23	9.94 ± 14.17
	3	1.17 ± 0.99	18.89 ± 32.70
	4	1.33 ± 1.08	55.80 ± 95.40
	5	1.05 ± 1.00	38.80 ± 100.75
June 2010	1	1.67 ± 1.03	10.72 ± 18.95
	2	1.28 ± 1.13	4.11 ± 6.26
	3	1.11 ± 1.13	8.56 ± 17.60
	4	1.56 ± 1.10	14.06 ± 37.94
	5	1.30 ± 1.08	8.60 ± 13.28

December 2010	1	0.83 ± 0.86	1.22 ± 1.77
	2	0.56 ± 0.92	0.78 ± 1.52
	3	0.89 ± 0.90	1.78 ± 3.54
	4	0.44 ± 0.92	1.33 ± 3.83
	5	0.75 ± 0.97	2.45 ± 4.66
June 2011	1	0.33 ± 0.59	0.44 ± 0.86
	2	0.11 ± 0.32	1.00 ± 4.00
	3	0.06 ± 0.24	0.06 ± 0.24
	4	0.50 ± 1.25	0.78 ± 1.93
	5	0.25 ± 0.55	0.45 ± 1.10
December 2011	1	0.28 ± 0.46	0.56 ± 1.04
	2	0.22 ± 0.43	0.28 ± 0.57
	3	0.44 ± 0.86	1.33 ± 3.80
	4	0.39 ± 0.70	0.94 ± 2.15
	5	0.35 ± 0.67	2.00 ± 5.76

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CURRICULUM VITAE

Education:

Ph.D. in Ecology and Evolution, Rutgers University, New Brunswick, NJ; May 2013
B.S. in Biology / B.A. in Political Science, Duke University, Durham, NC; May 2005

Academic/Professional Experience:

2012-2013. *Assistant to the Director*, Program in Science Learning, Rutgers University.
2012. *Lecturer*, Environmental Education, Rutgers University.
2011-2013. *Program Assistant*, Excellence in Mentoring Fellowship Program, Rutgers University.
2010. *Eagleton Placement*, National Center for Environmental Economics, U.S. Environmental Protection Agency, Washington, D.C.
2009-2010. *Governor's Executive Fellow*, Eagleton Institute of Politics, Rutgers University.
2009-2010. *President*, Ecology & Evolution Graduate Student Association, Rutgers University.
2007-2009. *Treasurer*, Ecology & Evolution Graduate Student Association, Rutgers University.
2006-2007. *Seminar Coordinator*, Ecology & Evolution Graduate Student Association, Rutgers University.
2006. *Field Technician*, Center for Remote Sensing and Spatial Analysis and Dept. of Ecology & Evolution, Cook College, Rutgers University.
2005. *Ecological Consultant*, Key West Tropical Forest & Botanical Garden, Key West, FL.
2002-2005. *Laboratory Technician*, Nicholas School of the Environment & Earth Sciences, Earth and Ocean Sciences Division Duke University, Durham, NC.

Peer-Reviewed Publications:

JORDAN RC, DELISI JR, BROOKS WR, GRAY SA, ALVARADO A, BERKOWITZ AR. *In press*. A collaborative model of science teacher professional development. International Journal of Modern Education Forum.
BROOKS WR, JORDAN RC. 2013 Propagule pressure and native species richness drive invasibility in tropical dry forest seedling layers. Perspectives in Plant Ecology, Evolution, and Systematics. doi: 10.1016/j.ppees.2013.03.001
BROOKS WR, NEWBOLD SC. 2013. Ecosystem damages in integrated assessment models (IAMs) of climate change. Working Paper #13-02. NCEE Working Paper Series.
BROOKS WR, LOCKWOOD JL, JORDAN RC. 2013. Tropical paradox: a multi-scale analysis of the invasion paradox within Miami Rock Ridge tropical hardwood hammocks. Biological Invasions **15**:921-930.
JORDAN RC, EHRENFELD JG, GRAY SA, BROOKS WR, HOWE DV, HMELO-SILVER CE. 2012. Chapter 11: Cognitive considerations in the development of citizen science projects. In: Dickinson JL, Bonney R (eds). Citizen Science: Public Collaboration in Environmental Research. Cornell University Press, Ithaca.

- JORDAN RC, BROOKS WR, HOWE DV, EHRENFELD JG. 2012. Evaluating performance of volunteers in mapping invasive plants in public conservation lands. *Environmental Management* **49**:425-434.
- JORDAN RC, HOWE DV, GRAY SA, BROOKS WR, EHRENFELD JG. 2011. Knowledge gain and behavioral change in citizen science programs. *Conservation Biology* **25**:1148-1154.
- BROOKS WR, JORDAN RC. 2010. Enhanced interspecific territoriality and the invasion success of the spotted tilapia (*Tilapia mariae*) in South Florida. *Biological Invasions* **12**:865-874.
- REARDON BJ, BROOKS WR. 2009. Vegetative community compositional gradients of tropical hardwood hammocks along the Florida Keys. *Biotropica* **41**:27-36.

Selected Presentations:

2012. Invited speaker for The Invasive Animals Cooperative Research Centre's Tilapia in Australia- State of Knowledge Forum. "Spotted Tilapia (*Tilapia mariae*) and Mozambique Tilapia (*Oreochromis mossambicus*) in the United States: invasive status, impacts, and control." Talk given May 16 in Brisbane, Australia.
2012. Invited lecturer for Dr. Ari Novy's Biology of Invasive Plants course at Rutgers University. "Invaded communities are ecological, too! Using the principles of community ecology to the advantage of restoration." Talk given March 5th in New Brunswick, NJ.
2011. Invited speaker for Dade Chapter of the Florida Native Plant Society Monthly Meeting. "Why the future may not quite look like the past: the science and art of ecological restoration." Talk given June 28th in Miami, FL.
2011. Invited leader for Dade Chapter of the Florida Native Plant Society Field Trip. "Kendall Indian Hammocks Park and Swamp Fern Hammock Experimental Restoration." Field trip led on June 25th in Miami, FL.
2010. Ecological Society of America Annual Meeting. "Testing the biotic resistance hypothesis across spatial scales: Evidence from tropical dry forests." Talk given August 4th in Pittsburgh, PA.
2009. Ecological Society of America Annual Meeting. "Effects of species richness, density, and propagule pressure on woody seedling community productivity and invasibility." Talk given August 5th in Albuquerque, NM.
2007. Ecological Society of America & Society for Ecological Restoration International Joint Annual Meeting. "Differential interspecific territoriality and the invasion of the Florida Everglades by the spotted tilapia, *Tilapia mariae*." Poster presented August 7th in San Jose, CA.

Selected Awards and Grants:

2011. ***Emerging Public Policy Leader***, American Institute for Biological Sciences.
2011. ***Excellence in Research Award***, The Graduate School- New Brunswick, Rutgers University.
2010. ***Louis Bevier Graduate Fellowship***, The Graduate School- New Brunswick, Rutgers University.
2009. ***Governor's Executive Fellowship***, Eagleton Institute of Politics, Rutgers University.

2008. *Academic Excellence Fund Award*, Graduate Program in Ecology & Evolution, Rutgers University.
2008. *Conservation Grant*, Florida Native Plant Society.
2007. *Pre-Dissertation Award*, The Graduate School- New Brunswick, Rutgers University.
2007. *Academic Excellence Fund Award*, Graduate Program in Ecology & Evolution, Rutgers University.
2005. *Graduate School Fellowship Award*, The Graduate School- New Brunswick, Rutgers University.

Professional Memberships:

Association for Tropical Biology & Conservation
 Ecological Society of America
 Florida Native Plant Society
 Society for Ecological Restoration International

Service:

Reviewer for *The American Midland Naturalist*; *Marine and Freshwater Research*