5-2016

Consequences of Fragment for Woody Plant Communities: A Study of Reservoir Islands

Danielle C. Zoellner
Clemson University, dzoelln@clemson.edu

Recommended Citation
Zoellner, Danielle C., "Consequences of Fragment for Woody Plant Communities: A Study of Reservoir Islands" (2016). *All Dissertations*. 1651.
https://tigerprints.clemson.edu/all_dissertations/1651

CONSEQUENCES OF FRAGMENTATION FOR WOODY PLANT COMMUNITIES: A STUDY OF RESERVOIR ISLANDS

A Dissertation
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy
Biological Sciences

---

by
Danielle C. Zoellner
May 2016

Accepted by:
Dr. Saara J. DeWalt, Committee Chair
Dr. Bryan Brown
Dr. Donald Hagan
Dr. John Hains
Dr. David Tonkyn

ABSTRACT

Forest fragmentation has been overwhelmingly cited as a major threat to the biodiversity and conservation of forested plant communities worldwide. Here I take a community- and species-specific approach to examine how species richness and composition respond to forest fragmentation. I conducted this research on a series of 35 small forested islands that were fragments of continuous forest created by impoundment of the Savannah River in the Southeastern Piedmont of the United States. I paired the islands with 10 mainland forest sites representing large remnant forest with only a single edge exposed along two reservoirs. Species richness was positively related to island area, as predicted by the species-area relationship, and islands in general had greater species richness than mainland sites because of an addition of liana and shrub species uncommon to oak-hickory forests. Due to the increase of lianas, shrubs and pioneer trees in small forested fragments I detected large differences in the plant communities that have developed on these sites over the last 40 to 70 years. In addition, it appears that islands will continue to diverge from mainland forest over time, likely degrading to the point that the species of oak-hickory forest may disappear and convert entirely to disturbance-tolerant early seral communities. Moreover, these fragments had invasive plants species that were less common in the more intact forest. I used a seedling outplanting experiment to determine if two of the more common, non-native woody invaders are likely to invade intact forest interior sites. Indeed, the non-native woody liana, *Lonicera japonica* appears to have the ability to not only survive, but also thrive under interior forest. In contrast, *Albizia julibrissin* does not appear to be a major threat to forest interiors unless there is a large canopy disturbance that increases light to seedlings. Finally, I used this study system to test whether species richness estimators provide accurate estimates and should continue to be used to examine important ecological patterns. I found that all 10 of the ones examined were so imprecise that none of them detected the true species-area relationship found across the forest fragments. Use of species richness estimators, in place of true richness, should therefore be used with extreme caution if the goal is to describe patterns in species richness across a set of sites. Overall, my dissertation highlights how much we still have yet to learn about generalities associated with forest fragmentation and species richness estimation techniques

ACKNOWLEDGMENTS

I have several people to thank for their support, contributions and insights over the years. I am what you might call the "non-traditional" PhD student since I did not even start my journey in graduate school until I was in my 30s. I did not realize that graduate school could even be an option for me for several years following graduation from Colorado State University with my B.S. in Natural Resource Management and Conservation Biology. After working for the Colorado Natural Heritage Program (CNHP) and the Colorado Department of Natural Resources (CDNR) seasonally for four years, I decided that it would be best to get back into legal secretary work in order to have a consistent pay check and health insurance. During this time I was lucky to work amazing people at CNHP, CDNR and the law office that constantly told me that I was selling myself short and that I would do well in graduate school. It took me a little while to believe them, and ultimately sitting in an office for 3 years was enough to get me moving on the idea of graduate school. I want to specifically thank Denis Culver and Gwen Kittel, two of the most intelligent and passionate women I know when it comes to conserving wetland and riparian areas out west. Without their influence I would have never started down this path. I also want to thank the attorneys and staff at the Law Offices of Griffith & Beach; not many law office employees would be sent off to graduate school to pursue a field totally unrelated law with a party and a bonus, and I feel very lucky to have been a part of their family. Everyone in that office was instrumental in supporting my decision to pursue graduate studies in South Carolina.

I received my M.Sc. Coastal Marine and Wetland Studies from Coastal Carolina University (CCU), and it was here that I realized that I truly enjoyed interacting with undergraduates. I thought teaching was going to be something I had to simply deal with to get through my degree and have assistantship income, but after getting over my initial terror I found that it was extremely fulfilling to watch when a "the light went on" for a student. It was also during my time at CCU that I had the privilege of working with several professors that influenced my path forward. I thank Kevin Godwin, Jim Luken, John Hutchens, and Keith Walters for their support and encouragement that made me realize that I was ready and able to take on the task of completing a PhD. I also want to give a special thanks to Kevin Godwin for his enlightening me on the K.I.S.S. principle, I still chant this mantra to myself on days I start spinning my wheels with statistical methods or doubting if my work is ready to submit.

At Clemson University, I am forever indebted to my advisor Saara DeWalt for her guidance, advice, support, and encouragement over the years. I am especially grateful that she has been so accommodating and supportive of allowing me to finish up my work from afar. I would also like to thank her for critically and meticulously reviewing my work and providing me with numerous opportunities for mentoring rising senior high school students and undergraduate students. Mentoring students has become a passion of mine that I continue to pursue. I also want to thank my other committee members, both past and present, at Clemson University – Bryan Brown (now at Virginia Tech), Donald

Hagan, John Hains, David Tonkyn, and Kalan Ickes – as they have challenged me and supported me throughout this journey.

I would also like to thank B. McGill, R. Glenn, K. M. Wallace, A. Grant, A. Slack, N. Brinton, B. Taylor, I. Park, C. Woods, S. Kelly, and V. James for help with my field work. Patrick McMillan helped with plant identification. I also thank the Army Corps of Engineers (USACOE) for logistical support, and Mike Marshall for use of his greenhouse space at Clemson University. I also greatly appreciate the financial support for my research through a National Research Initiative Grant no. 2006-55320-17251 from the USDA National Institute of Food and Agriculture Biology of Weedy and Invasive Species program, two Wade T. Batson Awards for Studies in Field Botany, the Summer Program for Research Interns funded through a grant from the Howard Hughes Medical Institute to the SC Life program at Clemson University, and the Calhoun Honors College of Clemson University.

I also want to give a special thanks to Kay Gross and Sieg Snapp from the Michigan State University Kellogg Biological Station. It is due to them that I was able to move back home to be close to my parents and work, while I completed this effort. Their guidance and support have been a driving force behind my persistence, and I look forward to continuing my journey at KBS.

Finally, I would like to thank my family and friends for all the love and support they have given me over the years. They often did not understand what I was talking about, but would listen shaking their heads in agreement and give me support when I was having an existential crisis. All the support, love, and laughter that my family and friends have given me throughout this challenge is how I was able to manage this process and ultimately finish up. And last but certainly not least, I would like to expressly thank my mom, Diane, my dad, Donald, and my husband, Shawn. They have provided endless support and made sure that I could continue to pursue this effort over the last three years. Shawn made sure the house was clean, laundry done, and our beautiful daughter, Leona, was happy and healthy while I was lost in the sea of my dissertation. Without all of you this would not have been possible.

TABLE OF CONTENTS

Page

LIST OF TABLES

Table Page

List of Tables (Continued)

List of Tables (Continued)

LIST OF FIGURES

List of Figures (Continued)

Figure Page

List of Figures (Continued)

Figure Page

List of Figures (Continued)

CHAPTER 1

INTRODUCTION

Forest fragmentation due to human development of the landscape is considered to be the leading threat to the conservation of forested communities and cause of biodiversity loss (Yates et al. 2004, Rodriguez-Loinaz et al. 2012). Fragmentation converts formerly contiguous areas of forest into smaller and more isolated patches of vegetation that experience a host of changes due to several interacting abiotic and biotic factors (Harper et al. 2005, Laurance et al. 2011). Forest fragmentation reduces the population size of forest species, interrupts dispersal patterns, and exposes previously protected forest interior (Harper et al. 2005, Laurance et al. 2011). All of these changes may impact the species composition and structure of woody plant forest communities (Tabarelli and Lopes 2008). In this dissertation, I examine how and why woody plant communities change in response to fragmentation. I use a natural experiment where former hilltops in southeastern Piedmont forests of the United States became forested island fragments with surrounding remnant mainland forest when the Savannah River was impounded for hydroelectric power.

Quantifying the effects of fragmentation

The study of forest fragmentation has historically taken one of three different approaches: those that quantify the impact of habitat reduction and isolation on organisms, those that study abiotic or biotic edge effects in fragments, and those that consider the impact of the surrounding matrix on organisms within fragments. Here, I examine the three approaches and describe why I chose to focus on fragment size and the importance of edge effects, while controlling for the impact of the surrounding matrix.

Initially, the equilibrium theory of island biogeography (ETIB) was a guiding model in the study of forest fragmentation. ETIB posits that small and more isolated islands will house a reduced number of species compared to larger, less isolated islands (MacArthur and Wilson 1967). Although ETIB exclusively considered oceanic islands that have been isolated from mainland habitats for millennia, ecologists rapidly adapted this theory to investigate species richness and diversity patterns of the vegetation, invertebrates, and mammals of recently created forest fragments (Laurance 2008). Using ETIB as a theoretical framework, small islands or fragments are thought to be relatively smaller "targets" for randomly dispersing propagules, which would lead to decreased species richness because the probability of a propagule landing in a habitat patch that is suitable for establishment and colonization is lower (Gilpin and Diamond 1976, Simberloff 1976, Lomolino 1990). Decreased species richness in small fragments may also be attributed to the vulnerability of species to stochastic extinction events wherein the smaller populations likely captured in a small fragment would have a greater probability of extinction compared to large populations that are assumed to exist in large fragments or continuous forests (Rosenzweig 1995). Increasing isolation is hypothesized to decrease species richness because fewer species have the ability to disperse long distances (MacArthur and Wilson 1967, Long et al. 2009). The interaction between size and isolation can give rise to various levels of species richness, but the largest and closest islands are predicted to house the largest number of species, while the smallest and furthest islands are expected to contain fewer species. For many mobile and relatively short-lived organisms, ETIB may be an appropriate theoretical framework to study and model species responses to habitat fragmentation, but it has become apparent that ETIB falls short when considering fragmentation impacts on immobile, long-lived woody vegetation associated with forests around the world (Kadmon and Allouche 2007, Laurance 2008, Villard and Metzger 2014).

One reason that ETIB has limited application to forest fragmentation theory is because the ETIB does not consider the influence of edge effects (Laurance 2008). Edge effects, or differences between the abiotic and biotic properties of forest edges and “intact” forest interior, may produce forest fragments that do not conform to the predictions of ETIB (Laurance 2008). Edge habitats often exhibit increased light levels, temperature, and wind speeds when compared to interior forest habitat, which may in turn be coupled with decreases in litter accumulation, soil moisture, and relative humidity, all of which can be variable even in fragments of similar size (Kapos et al. 1997, Gehlhausen et al. 2000, Feeley 2004, Laurance et al. 2007, Broadbent et al. 2008). Forest fragment edges are assumed to be inhospitable to remnant interior vegetation due to abiotic changes within fragment edges and therefore more likely to favor species adapted to the conditions associated with these habitats (McDonald and Urban 2006). Vegetation responses to fragmentation vary depending on the ability of remnant species to tolerate, survive, and reproduce in forest fragments, and these responses may be magnified or reduced in fragments with multiple edges in close proximity (Kuussaari et al. 2009, Porensky and Young 2013, Ibáñez et al. 2014).

Because different edge effects can vary widely on how deeply they penetrate into a forest fragment, studies have found that edge effects can be strengthened, weakened, or produce a completely different pattern when more than a single edge is impacting the population or community of interest (Porensky and Young 2013). Porensky and Young (2013) point out, correctly, that more studies in fragmented landscapes where the impact of multiple edges can be elucidated will be valuable as they were only able to identify 11 empirical studies that tried to tackle this problem and only five of these investigated forest vegetation responses. For instance, Harper et al. (2007) found that the edge effect for downed logs was intensified as edges in linear forest fragments between two clear cuts became closer, but that this effect was mitigated when the linear fragment was bounded on one side by a lake as opposed to another clear cut area. Similarly, corners of forest fragments in the in the Biological Dynamics of Forest Fragments Project (BDFFP) in the central Amazon of Brazil have higher mortality of canopy trees, lower basal area, greater density of understory vegetation, greater richness and altered species composition of pioneer tree species, and less richness and altered species composition of seedlings compared to plots at least 100 m from another edge, in large fragments, or continuous forest (Malcolm 1994, Benítez-Malvido and Martínez-Ramos 2003, Laurance et al. 2006, Porensky and Young 2013).

If remnant vegetation continues to survive and reproduce while new species colonize and proliferate due to edge effects, species richness in fragments may be greater compared to similar areas of continuous forest. At some point, remnant species may begin to go locally extinct, and species richness could "relax” to a new equilibrium over time. At such time, the fragment will have paid the “extinction debt”, which are the species currently in the community that are expected to go extinct following a disturbance such as habitat destruction or fragmentation, climate change, or invasion of exotic species (Kuussaari et al. 2009). Once this occurs, extinction and colonization rates are assumed to be stable and no further reductions in species richness are predicted (Tilman et al. 1994, Harper et al. 2005, Kuussaari et al. 2009). A portion of the extinction debt is often paid immediately, when a small habitat patch no longer contains all the species found in the large undisturbed habitat. The remaining extinction debt will then be paid over time based on the susceptibility of species in the community to the disturbance – this is called “relaxation time” (Kuussaari et al. 2009). Quantifying the extinction debt and relaxation times for fragmented communities continues to be a challenge for conservation biologists because biotic and abiotic edge effects can cause a gradual deterioration of habitat over time that is then coupled with varying ability of particular species to tolerate and survive conditions in the disturbed habitat (Kuussaari et al. 2009).

Demonstrated influence of the surrounding matrix on species and community response to fragmentation is also not incorporated into the predictions of ETIB because it is based on islands surrounded by an invariable matrix of water (Ibáñez et al. 2014, Villard and Metzger 2014). It has been found in several studies that differences in the surrounding matrix may have a large impact on how organisms respond to forest fragmentation (Prevedello and Vieira 2010). In addition, response to the composition of the surrounding matrix is often found to be species or life-form specific. For example, Öckinger et al. (2012) found that the richness of plants and butterflies was most negatively impacted in small patches of semi-natural grassland when surrounded by arable land, whereas richness of hoverflies and bees was most negatively impacted when the small patches were surrounded by forest. Nascimento et al. (2006) also found that significant differences in the composition of pioneer tree species depended on the dominant species present in the regrowth surrounding tropical forest fragments of BDFFP. As surrounding matrix can have a measurable impact on community composition and structure, studies that control for this factor may provide a unique perspective on the mechanisms at work in forest fragments since every fragment of interest would be surrounded by the same matrix.

A recent meta-analysis of over 200 journal articles aimed to discover universal patterns for vegetation response to habitat fragmentation, but instead found that they could be positive, negative, or both depending on the parameter measured and the species or community evaluated (Ibáñez et al. 2014). These results demonstrate how challenging it may be to draw widespread conclusions about how habitat fragmentation will impact species richness and community composition in plant communities. Ibáñez et al. (2014) go on to suggest that a more holistic approach that recognizes the vast interplay between abiotic factors, individual species responses, and community-level responses to human-induced fragmentation of the landscape is needed.

In my dissertation, I have employed a holistic approach to studying forest fragmentation. I controlled for the effect of the surrounding matrix and quantify the impact of forest fragmentation on oak-hickory forests of the Southeastern Piedmont physiographic region at level of the community and for particular species. I show how forest community composition and forest structure responds to fragmentation into small isolated patches by comparing small forested islands to nearby remnant mainland forest with only a single edge exposed.

Invasive species in forest fragments

Invasive species are often more common on edges than interior areas of fragments (Yates et al. 2004, Harper et al. 2005, Vilà and Ibáñez 2011, Dawson et al. 2015). For example, Yates et al. (2004) found that two of three plant species examined in fragmented forests of Illinois had lower abundance in forest interior, and the third species was present at similar abundances in both edge and interior plots. Similarly, Flory and Clay (2006) found that abundance for four of the seven exotic shrubs examined decreased in forest fragments dissected by roads as the distance from a road increased. Neither Yates et al. (2004) nor Flory and Clay (2006) were able to determine why those species were found primarily on fragment edges because their approach was purely observational.

Exotic, invasive plant species may be limited to edges because they are dispersal limited, are intolerant of the environmental conditions present under interior forest conditions, or are readily outcompeted in interior forest. Propagule pressure (seed deposition) may increase on edges if the surrounding landscape has a large proportion of invasive species, or if dispersal vectors preferentially choose edge habitat (Buckley et al. 2006, Cramer et al. 2007, Thomas and Moloney 2015). Alternatively, soil nutrients or light levels may be greater and herbivory or pathogen attack decreased on edges (Ries et al. 2004). Flory and Clay (2009) tried to distinguish these possibilities by examining germination, growth, and survival of out-planted seedlings of exotic and native woody species along edges and in interior sites of both young and mature temperate forest fragments in Indiana dissected by roads. They found that germination and survival of exotic species was not impacted by interior forest conditions, but that growth was enhanced near edges adjacent to roads. Thus, the exotic shrub species they examined may have been restricted to edges due to dispersal limitation, although subsequent growth may be reduced in forest interior (Flory and Clay 2009). As such, propagule pressure from the surrounding matrix or from edges to interior may have important consequences for the occurrence of exotic invasive species in the landscape (Thomas and Moloney 2015).

In my dissertation, I addressed whether non-native woody plant species have the ability to invade relatively undisturbed forest interior. In particular, I examined survival, growth, and herbivory on the edges and interiors of forested islands and remnant mainland forest for seedlings of two exotic woody plant species that appear to be habitat specialists in disturbed areas and along forest fragment edges.

Measuring species richness

Understanding the causes and consequences of species richness has long been a central theme in ecology and conservation biology (Colwell and Coddington 1994, Gotelli and Colwell 2001, Gotelli and Colwell 2011, Mori et al. 2013). Species richness is simply the number of species present within an area of interest. Despite a long history of ecological research, current researchers are still trying to understand the mechanisms that lead to differences in species richness. For instance, it has been recognized that species richness tends increase from the poles to the tropics for many taxonomic groups (Hillebrand 2004). Of course there have been several hypotheses put forth that attempt to explain this phenomenon, but little consensus has developed due to the wide variety of methods used and a paucity of global-scale data (Hillebrand 2004, Kerkhoff et al. 2014).

The species-area relationship (SAR) – the linear, positive relationship between the number of species and the size of the area in which they are found – has been found at so many spatial scales and across so many different study systems that it is considered one of the few laws of ecology (Lawton 1999). In particular, conservation biologists often use the SAR to identify potential biodiversity hotspots, predict species extinctions following habitat fragmentation, prioritize conservation sites, and guide management activities (Smith 2010). This is another area of active ecological research where there is still a considerable amount of debate over the mechanisms that produce the SAR. For example, ETIB proposed that the SAR results from an area-determined equilibrium between immigration and extinction on islands and island-like habitats (MacArthur and Wilson 1967, Harris 1984, Lomolino et al. 1989, Kadmon and Pulliam 1995, Brose 2003). In contrast, others have argued that the SAR is really linked to greater resource or habitat heterogeneity that are found in larger areas (Tilman and Pacala 1993, Rosenzweig 1995, Kadmon and Allouche 2007, Hortal et al. 2009). Regardless of the hypothesis being tested, species richness must be quantified accurately before one can effectively investigate how it may be responding to latitudinal, spatial, or environmental gradients.

What then is the best way to measure species richness? Thorough inventories of all species in an area of interest provide the most accurate measures of species richness, but they are often prohibitively time consuming and costly. Thus, species richness is often estimated for a larger area of interest using sample- or individual-based methods (Wei et al. 2010, Gotelli and Colwell 2011). Many species-richness estimators are non-parametric and use observed species richness and the number of species that occur rarely in a set of sampled individuals or samples (e.g., plots, traps; Colwell and Coddington 1994, Walther and Morand 1998, Walther and Moore 2005). Four of the more commonly used non-parametric methods for replicated, sample-based surveys are the coverage-based, Chao, jackknife, and bootstrap estimators (Heltshe and Forrester 1983, Chao 1984, Smith and van Belle 1984, Chao 1987, Colwell and Coddington 1994, Wei et al. 2010). These non-parametric estimators make no assumption regarding the shape of the species-abundance distribution, and all are thought to be relatively insensitive to unequal detection probabilities (i.e., differences in relative abundance; Gotelli and Colwell 2001, Magurran 2004). Increasingly, estimated species richness has replaced true richness when testing different hypotheses that explain patterns of species richness (e.g., Benítez-Malvido and Martínez-Ramos 2003, Paciencia and Prado 2005, Poulos et al. 2007, Page et al. 2010, Sánchez-González et al. 2010, Norfolk et al. 2015).

In my dissertation, I tested whether 10 species richness estimators provided estimates of species richness that were comparable to true richness in a set of small forest fragments. The small size of the fragments allowed for reliable measurement of true richness.

My study system

Forested reservoir islands, created by impounding rivers and isolating hilltops of continuous forest, provide a natural experimental system to explore how forest fragmentation may alter woody plant species structure and composition, examine exotic species performance in forest edges and interior, and test the ability of species richness estimators to provide accurate values for species richness. The spatial arrangement of reservoir islands and surrounding mainland forest is similar to that of fragments caused by residential and urban development and remaining, large remnant forest with only a single edge exposed (Fischer and Lindenmayer 2007). An advantage to studying forested communities in and along reservoirs is that forested reservoir islands and remnant mainland forest sites have well-defined edges and are nested in a consistent matrix of water (Watson 2002, Benchimol and Peres 2015). Having the same habitat at the edges of both small forested island fragments and large remnant mainland forest controls for confounding effects that variability in the immediate surrounding landscape may have on species composition (Lovei et al. 2006, Nascimento et al. 2006).

My dissertation research used recently created forested reservoir islands (i.e. < 70 years old) and remnant, mainland oak-hickory forest in the Southeastern US Piedmont ecoregion to answer several questions pertinent to forest fragmentation, exotic species invasion, and the use of species richness estimates in place of true richness values. I conducted this work on two reservoirs along the border of South Carolina and Georgia - Lake J. Strom Thurmond (288 km^2) and Lake Richard B. Russell (107.8 km^2), which were created for flood control and hydroelectric power along the Savannah River in 1954 and 1984, respectively. Impoundment created islands by isolating forested hilltops from what was once contiguous forest. Large areas of protected mainland forest occur in the landscape surrounding Lake Thurmond and Lake Russell (USACE 2013) and were used as representative areas of continuous forest with a single edge. I examined aerial photographs, topographic maps, field observations to identify forested islands that were not clear-cut prior to impoundment and were continuously isolated from mainland forest and other island fragments since the date of reservoir creation (see Chapter 2 for more details). I selected 13 islands in Lake Thurmond and 22 in Lake Russell for sampling (Fig. 2.1). Islands ranged in size from 0.08 ha – 2.47 ha and were 34.77 – 917.83 m from the closest mainland shore.

Testing predictions of ETIB

Before examining how fragmentation affects species composition, I wanted to test the predictions of MacArthur and Wilson's (1967) equilibrium theory of island biogeography (ETIB). Based on the ETIB and subsequent modifications for studying forest fragments (Laurance 2008b), smaller and more isolated fragments are predicted to have fewer plant species. Small fragments are thought to be relatively smaller "targets" for randomly dispersing propagules, which leads to lower colonization rates in smaller areas (Gilpin and Diamond 1976, Simberloff 1976, Lomolino 1990). Small fragments also tend to support smaller populations that are more likely to be lost due to stochastic extinction events (Rosenzweig 1995). Increased isolation of fragments is hypothesized to lead to lower species richness because fewer species disperse long distances and colonization rates therefore are lower than extinction rates (MacArthur and Wilson 1967, Kadmon and Pulliam 1995). I tested these more specific predictions by examining whether larger islands had a higher proportion of tree species that appear to be regenerating and a lower proportion that are at risk of local extinction. In addition, I tested whether islands closer to the mainland have a greater number of species that likely immigrated since fragmentation and have a greater proportion of species from the regional species pool (see Chapter 2 for details of these analyses).

I found a significant positive species-area relationship for the 35 forested islands surveyed, which was consistent across both lakes (Fig. 1.1). This relationship was mainly driven by tree species richness, as liana and shrub species richness was invariant to island size. I also detected a significant species-isolation relationship among our forested islands, but it was in the opposite direction of the relationship predicted by ETIB, with forested islands closer to the mainland having lower species richness than more isolated islands (Fig. 1.2). This relationship was only apparent when all species were considered together, as no relationship was detected between tree, shrub, or liana species and degree of isolation (Fig. 1.2).

Neither the proportion of regenerating (*R)* species nor those at risk of extinction (*De*) was related to island size as hypothesized (Fig. 1.4). Thus, the SAR does not appear to be driven by changes that have occurred after isolation – instead it is likely that larger fragments just passively encompass more individuals and therefore more species. In addition, the proportion of species that have likely immigrated since fragmentation was not related to degree of island isolation, and the most isolated islands housed the highest proportion of species from the regional tree species pool (Fig. 1.5). Again, active processes stemming from fragmentation and isolation do not appear to be affecting species richness per se.

Greater species richness and mean stem density on the most isolated islands may be due in part to deer utilizing islands that are closer to mainland forest. I observed deer scat on many of the less isolated islands, and on three occasions we discovered very young fawns bedded down under shrub cover. Deer browsing can have profound and lasting impacts on the composition and structure of forests (Horsley et al. 2003, Long et al. 2007, Bressette et al. 2012), and if deer are using the islands as nursery sites or regularly this may explain why the closest islands house fewer individuals at the plot-level and fewer species at both the island- and plot-level. For example, Rossell et al. (2005) found that seedlings of *Carya* species had been completely eliminated and *Quercus alba* seedlings had been significantly reduced in study plots without deer exclosures after just four years in Virginia oak-hickory forest. In another Virginia oak-hickory forest, Bressette et al. (2012) found that excluding deer over a period of 19 years led to significant increases in small tree and shrub stem densities. Future studies that quantify deer utilization of these forested islands may provide further insight on why this pattern emerged in both lakes.

Structure of the dissertation

The balance of my research examined community and species-specific changes resulting from forest fragmentation. In Chapter 2, I examine how species composition in these small forest fragments have changed over time and predict future changes. I explicitly test whether the difference in species composition is due to the extinction of canopy species in small fragments or colonization and proliferation of disturbance-tolerant species. In addition, I examine whether changes to forest structure and environmental conditions due to multiple, interacting edges may be contributing to changes in species composition.

In Chapter 3, I experimentally test whether a non-native pioneer tree and a non-native liana are primarily dispersal or environmentally limited in fragmented landscapes. Specifically, I test whether *Albizia julibrissin* (Fabaceae, mimosa tree) and *Lonicera japonica* (Caprifoliaceae, Japanese honeysuckle) are likely to invade interior forest if dispersal and germination barriers are overcome. This study grew out of the observations that *L. japonica* abundance was markedly lower away from edges in large tracts of forest and *A. julibrissin* was only found on edges of forest fragments.

In Chapter 4, I ask whether estimated species richness can be used reliably as a proxy for true richness. Here I use thorough survey data and plot-based sample data from the entire dataset of 35 small forested reservoir islands, and then a smaller subset of islands based on a more conservative sample completeness criterion, to explore whether species richness estimators produce values that can be used to inform management goals, prioritize conservation sites, or test ecological hypotheses. I determined the need for this study when I realized that estimated species richness was markedly different than the species richness values I obtained when thoroughly inventorying each island.

In Chapter 5, I summarize the overall conclusions and importance of this research and identify future research directions. In particular, I highlight the need for further studies that take a more integrated approach to how fragmentation impacts plant communities, compare the performance of non-native and native species in fragments and intact forests, and expand our understanding of how estimated species richness relates to true species richness.

REFERENCES

Benchimol, M. and C. A. Peres. 2015. Edge-mediated compositional and functional decay of tree assemblages in Amazonian forest islands after 26 years of isolation. Journal of Ecology **103**:408-420.

Benítez-Malvido, J. and M. Martínez-Ramos. 2003. Impact of forest fragmentation on understory plant species richness in Amazonia. Conservation Biology **17**:389-400.

Broadbent, E., G. Asner, M. Keller, D. Knapp, P. Oliveira, and J. Silva. 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. Biological Conservation **141**:1745-1757.

Brose, U. 2003. Island Biogeography of Temporary Wetland Carabid Beetle Communities. Journal of Biogeography **30**:879-888.

Buckley, Y. M., S. Anderson, C. P. Catterall, R. T. Corlett, T. Engel, C. R. Gosper, R. Nathan, D. M. Richardson, M. Setter, O. Spiegel, G. Vivian-Smith, F. A. Voigt, J. E. S. Weir, and D. A. Westcott. 2006. Management of plant invasions mediated by frugivore interactions. Journal of Applied Ecology **43**:848-857.

Chao, A. 1984. Non-parametric estimation of the number of classes in a population. Scandanavian Journal of Statistics **11**:265-270.

Chao, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. Biometrics **43**:783-791.

Colwell, R. K. and J. A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society of London B **345**:101-118.

Cramer, J. M., R. C. G. Mesquita, and G. Bruce Williamson. 2007. Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. Biological Conservation **137**:415-423.

Dawson, W., D. F. R. P. Burslem, and P. E. Hulme. 2015. Consistent effects of disturbance and forest edges on the invasion of a continental rain forest by alien plants. Biotropica **47**:27-37.

Feeley, K. J. 2004. The effects of forest fragmentation and increased edge exposure on leaf litter accumulation. Journal of Tropical Ecology **20**:709-712.

Fischer, J. and D. B. Lindenmayer. 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography **16**:265-280.

Flory, S. L. and K. Clay. 2009. Effects of roads and forest successional age on experimental plant invasions. Biological Conservation **142**:2531-2537.

Gehlhausen, S. M., M. W. Schwartz, and C. K. Augspurger. 2000. Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. Plant Ecology **147**:21-35.

Gilpin, M. E. and J. M. Diamond. 1976. Calculation of immigration and extinction curves from the species-area-distance relation. Proceedings of the National Academy of Sciences **73**:4130-4134.

Gotelli, N. J. and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters **4**:379-391.

Gotelli, N. J. and R. K. Colwell. 2011. Estimating species richness. Pages 39-54 *in* A. E. Magurran and B. J. McGill, editors. Biological Diversity: Frontiers In Measurement And Assessment. Oxford University Press, Oxford, UK.

Harper, K. A., S. E. MacDonald, P. J. Burton, J. Chen, K. D. Brosofske, S. C. Saunders, E. S. Euskirchen, D. Roberts, M. S. Jaiteh, and P.-A. Esseen. 2005. Edge influence on forest structure and composition in fragmented landscapes. Conservation Biology **19**:768-782.

Harper, K. A., L. Mascarua-Lopez, S. E. Macdonald, and P. Drapeau. 2007. Interaction of edge influence from multiple edges: examples from narrow corridors. Plant Ecology **192**:71-84.

Harris, L. D. 1984. The fragmented forest: island biogeography theory and the preservation of biotic diversity. University of Chicago Press, Chicago.

Heltshe, J. F. and N. E. Forrester. 1983. Estimating species richness using the Jackknife procedure. Biometrics **39**:1-11.

Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. American Naturalist **163**:192-211.

Hortal, J. n., KostasÂ A. Triantis, S. Meiri, E. ThÃ©bault, and S. Sfenthourakis. 2009. Island Species Richness Increases with Habitat Diversity. The American Naturalist **174**:E205-E217.

Ibáñez, I., D. S. W. Katz, D. Peltier, S. M. Wolf, and B. T. C. Barrie. 2014. Assessing the integrated effects of landscape fragmentation on plants and plant communities: the challenge of multiprocess-multiresponse dynamics. Journal of Ecology **102**:882-895.

Kadmon, R. and O. Allouche. 2007. Integrating the Effects of Area, Isolation, and Habitat Heterogeneity on Species Diversity: A Unification of Island Biogeography and Niche Theory. The American Naturalist **170**:443-454.

Kadmon, R. and H. R. Pulliam. 1995. Effects of isolation, logging and dispersal on woody-species richness of islands. Vegetatio **116**:63-68.

Kapos, V., E. Wandelli, J. L. Camargo, and G. Ganade. 1997. Edge-related changes in environment and plant responses due to forest fragmentation in central Amazonia. Pages 33-54 *in* W. F. Laurance and R. O. Bierregaard, editors. Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago.

Kerkhoff, A. J., P. E. Moriarty, and M. D. Weiser. 2014. The latitudinal species richness gradient in New World woody angiosperms is consistent with the tropical conservatism hypothesis. Proceedings of the National Academy of Sciences of the United States of America **111**:8125-8130.

Kuussaari, M., R. Bommarco, R. K. Heikkinen, A. Helm, J. Krauss, R. Lindborg, E. Öckinger, M. Pärtel, J. Pino, F. Rodà, C. Stefanescu, T. Teder, M. Zobel, and I. Steffan-Dewenter. 2009. Extinction debt: a challenge for biodiversity conservation. Trends in Ecology & Evolution **24**:564-571.

Laurance, W. 2008. Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory. Biological Conservation **141**:1731-1744.

Laurance, W. F., J. L. C. Camargo, R. C. C. Luizão, S. G. Laurance, S. L. Pimm, E. M. Bruna, P. C. Stouffer, G. Bruce Williamson, J. Benítez-Malvido, and H. L. Vasconcelos. 2011. The fate of Amazonian forest fragments: A 32-year investigation. Biological Conservation **144**:56-67.

Laurance, W. F., H. E. Nascimento, S. G. Laurance, A. Andrade, J. E. Ribeiro, J. P. Giraldo, T. E. Lovejoy, R. Condit, J. Chave, K. E. Harms, and S. D'Angelo. 2006. Rapid decay of tree-community composition in Amazonian forest fragments. Proc Natl Acad Sci U S A **103**:19010-19014.

Laurance, W. F., H. E. M. Nascimento, S. G. Laurance, A. Andrade, R. M. Ewers, K. E. Harms, R. C. C. Luizão, and J. E. Ribeiro. 2007. Habitat fragmentation, variable edge effects, and the lanscape-divergence hypothesis. PLoS One **2**:1-8.

Laurance, W. F., D. Pérez-Salicrup, P. Delamônica, P. M. Fearnside, S. D'Angelo, A. Jerozolinski, L. Pohl, and T. E. Lovejoy. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. Ecology **82**:105-116.

Lawton, J. H. 1999. Are there general laws in ecology? Oikos **84**:177-192.

Lomolino, M. V. 1990. The Target Area Hypothesis: The Influence of Island Area on Immigration Rates of Non-Volant Mammals. Oikos **57**:297-300.

Lomolino, M. V., J. H. Brown, and R. Davis. 1989. Island Biogeography of Montane Forest Mammals in the American Southwest. Ecology **70**:180-194.

Long, J. D., G. C. Trussell, and T. Elliman. 2009. Linking invasions and biogeography: Isolation differentially affects exotic and native plant diversity. Ecology **90**:863-868.

Lovei, G. L., T. Magura, B. Tothmeresz, and V. Kodobocz. 2006. The influence of matrix and edges on species richness patterns of ground beetles (Coleoptera: Carabidae) in habitat islands. Global Ecology and Biogeography **15**:283-289.

MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

Magurran, A. E. 2004. Measuring biological diversity. Blackwell Publishing, Oxford.

Malcolm, J. R. 1994. Edge Effects in Central Amazonian Forest Fragments. Ecology **75**:2438-2445.

McDonald, R. I. and D. L. Urban. 2006. Edge effects on species composition and exotic species abundance in the North Carolina Piedmont. Biological Invasions **8**:1049-1060.

Mori, A. S., T. A. Spies, K. Sudmeier-Rieux, and A. Andrade. 2013. Reframing ecosystem management in the era of climate change: issues and knowledge from forests. Biological Conservation **165**:115-127.

Nascimento, H. E. M., A. C. S. Andrade, J. L. C. Camargo, W. F. Laurance, S. G. Laurance, and J. E. L. Ribeiro. 2006. Effects of the surrounding matrix on tree recruitment in Amazonian forest fragments. Conservation Biology **20**:853-860.

Norfolk, O., A. Power, M. P. Eichhorn, and F. Gilbert. 2015. Migratory bird species benefit from traditional agricultural gardens in arid South Sinai. Journal of Arid Environments **114**:110-115.

Öckinger, E., R. Lindborg, N. E. Sjödin, and R. Bommarco. 2012. Landscape matrix modifies richness of plants and insects in grassland fragments. Ecography **35**:259-267.

Paciencia, M. L. B. and J. Prado. 2005. Effects of forest fragmentation on Pteridophyte diversity in a tropical rain forest in Brazil. Plant Ecology **180**:87-104.

Page, N. V., Q. Qureshi, G. S. Rawat, and C. G. Kushalappa. 2010. Plant diversity in sacred forest fragments of Western Ghats: a comparative study of four life forms. Plant Ecology **206**:237-250.

Porensky, L. M. and T. P. Young. 2013. Edge-effect interactions in fragmented and patchy landscapes. Conservation Biology **27**:509-519.

Poulos, H. M., A. H. Taylor, and R. M. Beaty. 2007. Environmental controls on dominance and diversity of woody plant species in a Madrean, Sky Island Ecosystem, Arizona, USA. Plant Ecology **193**:15-30.

Prevedello, J. A. and M. V. Vieira. 2010. Does the type of matrix matter? A quantitative review of the evidence. Biodiversity and Conservation **19**:1205-1223.

Ries, L., R. J. Fletcher, J. Battin, and T. D. Sisk. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. Annual Review of Ecology, Evolution and Systematics **35**:491-522.

Rodriguez-Loinaz, G., I. Amezaga, and M. Onaindia. 2012. Does forest fragmentation affect the same way all growth-forms? Journal of Environmental Management **94**:125-131.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, New York, New York.

Sánchez-González, A., E. Á. Zúñiga, and J. D. Tejero-Díez. 2010. Richness and distribution patterns of ferns and lycopods in Los Mármoles National Park, Hidalgo, Mexico. The Journal of the Torrey Botanical Society **137**:373-379.

Simberloff, D. S. 1976. Experimental zoogeography of islands: effects of island size. Ecology **57**:629-648.

Smith, A. B. 2010. Caution with curves: Caveats for using the species–area relationship in conservation. Biological Conservation **143**:555-564.

Smith, E. P. and G. van Belle. 1984. Nonparametric estimation of species richness. Biometrics **40**:119-129.

Tabarelli, M. and A. V. Lopes. 2008. Edge-effects drive tropical forest fragments towards an early-successional system. Biotropica **40**:657-661.

Thomas, S. and K. Moloney. 2015. Combining the effects of surrounding land-use and propagule pressure to predict the distribution of an invasive plant. Biological Invasions **17**:477-495.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature **371**:65-66.

Tilman, D. and S. Pacala. 1993. The maintenance of species richness in plant communities. Pages 13-25 *in* R. E. Ricklefs and D. Schluter, editors. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, IL.

Vilà, M. and I. Ibáñez. 2011. Plant invasions in the landscape. Landscape Ecology **26**:461-472.

Villard, M.-A. and J. P. Metzger. 2014. Beyond the fragmentation debate: a conceptual model to predict when habitat configuration really matters. Journal of Applied Ecology **51**:309-318.

Walther, B. A. and J. L. Moore. 2005. The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. Ecography **28**:815-829.

Walther, B. A. and S. Morand. 1998. Comparative performance of species richness estimation methods. Parasitology **116**:395-405.

Watson, D. M. 2002. A conceptual framework for studying species composition in fragments, islands and other patchy ecosystems. Journal of Biogeography **29**:823-834.

Wei, S.-g., L. Li, B. A. Walther, W.-h. Ye, Z.-l. Huang, H.-l. Cao, J.-Y. Lian, Z.-G. Wang, and Y.-Y. Chen. 2010. Comparative performance of species-richness estimators using data from a subtropical forest tree community. Ecological Research **25**:93-101.

Yates, E. D., D. F. Levia, and C. L. Williams. 2004. Recruitment of three non-native invasive plants into a fragmented forest in southern Illinois. Forest Ecology and Management **190**:119-130.

Fig. 1.1. Relationship between $\log_{10}$ island area (ha) and (A) total species richness ($R^2 = 0.27$, $p = 0.002$), (B) tree species richness ($R^2 = 0.38$, $p < 0.001$), (C) shrub species richness, and (D) liana species richness for all 35 islands. Islands in Lakes Russell and Lake Thurmond are indicated by dark grey and light grey circles, respectively. When a significant effect of lake was found, regression lines for Lake Russell and Lake Thurmond are solid and dashed, respectively.

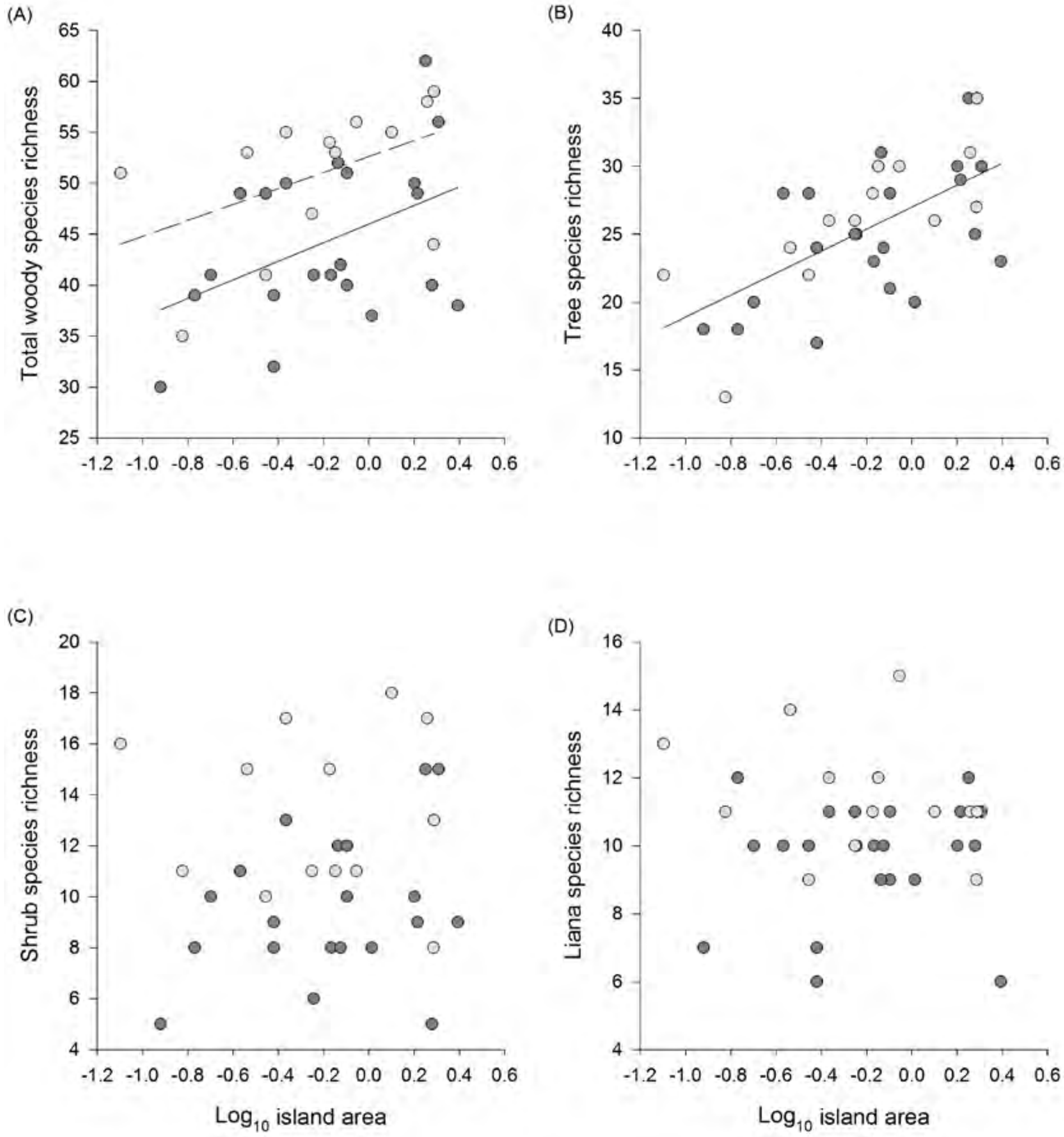


Fig. 1.2. Relationship between $\log_{10}$ distance from the mainland (m) and (A) total species richness ($R^2 = 0.18$, $p = 0.01$), (B) tree species richness, (C) shrub species richness ($R^2 = 0.30$, $p = 0.001$), and (D) liana species richness ($R^2 = 0.18$, $p = 0.02$) for all 35 islands. Islands in Lakes Russell and Lake Thurmond are indicated by dark grey and light grey circles, respectively.

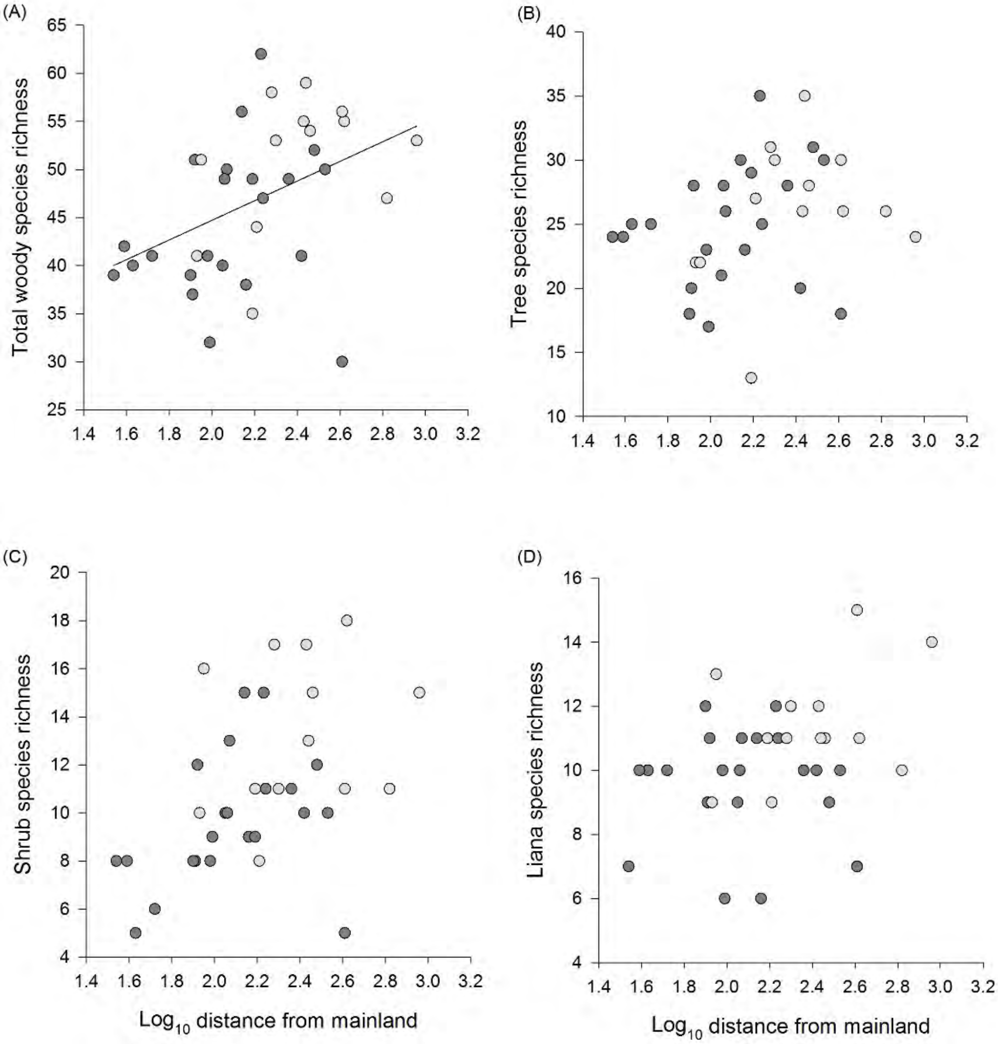


Fig. 1.3. Relationship between $\log_{10}$ island area (ha) and the proportion of regional (43 species) and within island tree species that are (A) regenerating (*R*), (B) at risk of extinction (*De*), and (C) have likely immigrated since the date of reservior construction (*I*) in Lake Russell. I also present (D) the proportion of tree species that could potentially colonize each site from the regional species pool (*Cc*).

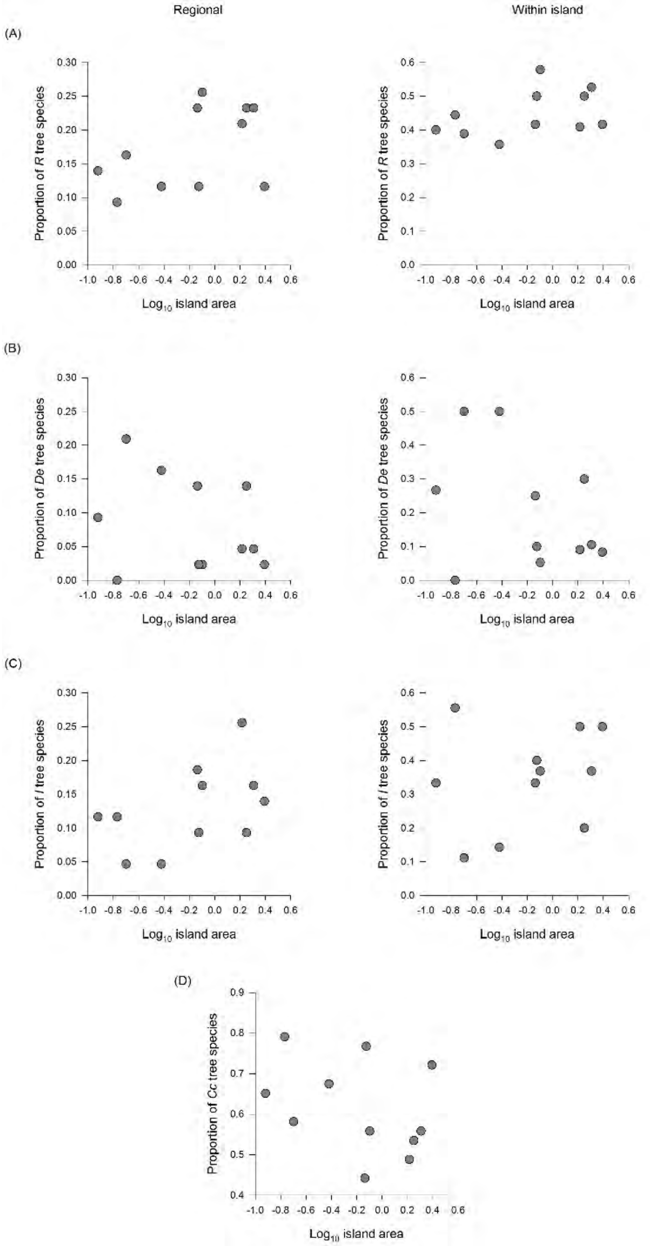
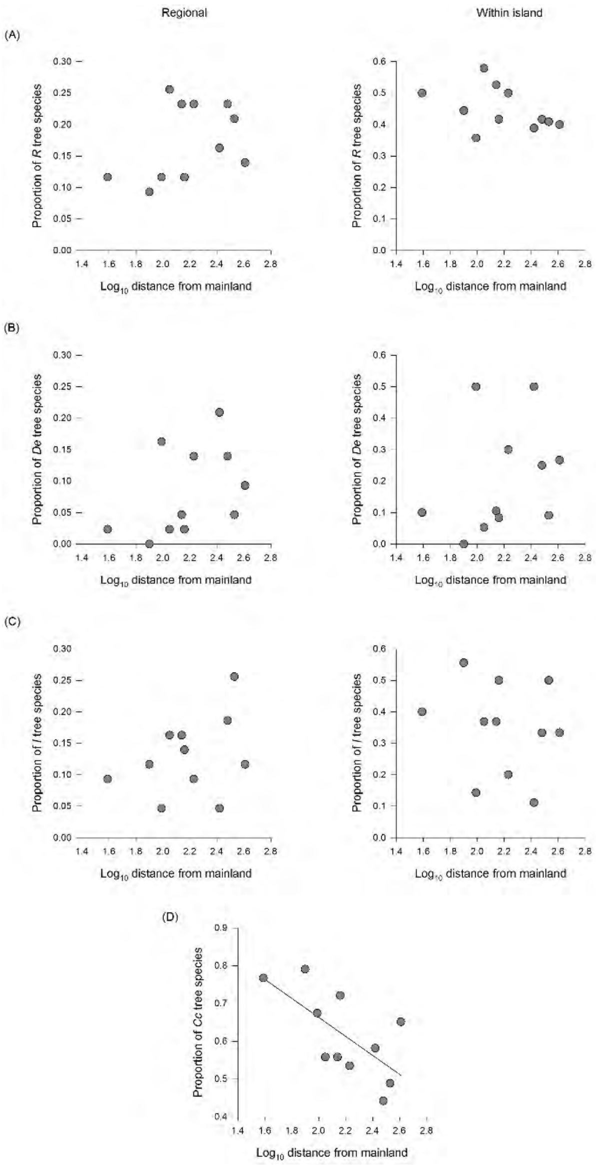


Fig. 1.4. Relationship between $\log_{10}$ distance from mainland and the proportion of regional (43 species) and within island tree species that are (A) regenerating (*R*), (B) at risk of extinction (*De*), and (C) have likely immigrated since the date of reservior construction (*I*) in Lake Russell. I also present (D) the proportion of tree species that could potentially colonize each site from the regional species pool (Cc; $R^2 = 0.46$, $p = 0.02$).



CHAPTER 2

DIVERGENCE IN FOREST FRAGMENTS RESULTS FROM ADDITION RATHER THAN DELETION OF WOODY PLANTS IN SOUTHEASTERN USA PIEDMONT FORESTS

INTRODUCTION

Forest fragmentation due to human development is considered to be a major threat to biodiversity and the conservation of forest communities worldwide (Wilcox and Murphy 1985, Yates et al. 2004, Haddad et al. 2015). Formerly contiguous areas of forest are rapidly being converted to a mosaic of forest fragments surrounded by a human-impacted non-forest matrix (Li et al. 2009, Wulder et al. 2009, Napton et al. 2010, Haddad et al. 2015). Within newly created fragments, forest vegetation experiences a host of changes including reduced available area, increased isolation, and shifts in environmental conditions (Ibáñez et al. 2014). The reduction in area can lead to smaller populations with greater risks of extinction, increased isolation may result in lower genetic exchange and barriers to dispersal, and edge effects may affect alter species interactions (Harper et al. 2005, Laurance et al. 2011, Vranckx et al. 2012, Ibáñez et al. 2014, Laurance et al. 2014). All of these changes associated with fragmentation may lead to a loss of species richness and changes in species composition; however, the effect of fragmentation on plant communities is unclear, with positive as well as negative effects being found in different systems (Ibáñez et al. 2014, Haddad et al. 2015). In particular, there is growing consensus that edge effects must be considered to fully appreciate the ecological impacts of fragmentation on species composition and, in turn, species richness (Debinski and Holt 2000, Laurance 2008, Koh et al. 2010, Ibáñez et al. 2014). With the number of forest fragments increasing and average fragment size simultaneously decreasing across the landscape (Griffith et al. 2003, Haddad et al. 2015), it is imperative to the conservation and management of forests to understand how woody plant communities respond to being fragmented into smaller and more isolated forest patches.

Species composition of small forest fragments often differs markedly from large forest fragments and intact forest interior (Harper et al. 2005, Laurance et al. 2011). These differences may result from the loss of canopy species unable to tolerate edge habitat, as well as the colonization and proliferation of disturbance-tolerant species that can thrive in edge environments because limiting resources have increased and competition was eliminated, or both (Laurance 2002, Harper et al. 2005, Hierro et al. 2006, Londré and Schnitzer 2006, McDonald and Urban 2006, Harper et al. 2007, Laurance 2008, Flory and Clay 2009, Fridley et al. 2009, LaPaix et al. 2012). Non-native, invasive woody plant species are also commonly found to be a substantial component of vegetation composition, particularly along forest fragment edges (Harper et al. 2005, McDonald and Urban 2006, Fridley et al. 2009). Even if fragments initially contain a representative sample of intact forest, species composition is likely to diverge from continuous forest as canopy species die and are replaced by species tolerant of the altered abiotic and biotic conditions in small fragments (Laurance 1991, Laurance et al. 2001, Laurance et al. 2006a, McDonald and Urban 2006, Flory and Clay 2009).

As the life-span of woody vegetation is relatively long compared to many other organisms, one might expect that young small forest fragments may not quickly pay their “extinction debt”, as canopy species continue to survive and new species colonize and proliferate due to edge effects (Tilman et al. 1994, Ewers and Didham 2006). Therefore, woody plant species richness may appear to be elevated in small fragments for a time before significant mortality and extinction occurs and species richness relaxes to a new equilibrium (MacArthur and Wilson 1967, Diamond 1972, Kuussaari et al. 2009). Integrating observation of the overstory, understory, and seedling layers in a forest system may provide unique insight on whether forest composition will likely degrade over time with the loss of overstory tree species and addition of tree species not typical of forest interior.

Many of the changes in species composition of fragments may be related to the addition of edge habitat and resulting structural and biological differences from forest interior. Compared to forest interior, forest edges generally have altered environmental conditions that impact species composition. In particular, forest edges frequently have higher light levels because of the removal of trees as well as subsequent mortality of canopy trees along the edge, which leads to further reduction of basal area and canopy height (Harper et al. 2005, Laurance et al. 2011). Higher light levels often lead to substantially lower soil moisture on edges (Harper et al. 2005, Laurance 2008), and as a result, species intolerant of dry conditions may be lost from edges. Changes in forest litter and soil quality may select for different suites of species than normally found in forested areas. Furthermore, multiple interacting edge effects in small fragments may produce habitat that is essentially functioning entirely as edge depending on how species respond to the abiotic and biotic changes that occur due to fragmentation (Fletcher 2005, Harper et al. 2007, Li et al. 2007, Laurance et al. 2011, Porensky 2011). The long-running Biological Dynamics of Forest Fragments Project (BDFFP) near Manaus, Brazil demonstrated that invasion of edges by species not typical of forest interior can be magnified in small fragments that have multiple edges in close proximity (Laurance et al. 2011). Harper et al. (2007) also found evidence for interaction between edges in close proximity in both deciduous and coniferous boreal forests, although this interaction appeared to be mediated when edges were near riparian areas.

Globally forests are in peril due to fragmentation, with the majority of forest fragments being less than 10 ha and nearly half of all forests in the world are within 500 m of an edge (Haddad et al. 2015). In the United States (US), the problem is even more severe, with half of all US forests located within 90 m of a forest edge, and the majority of intact forest relegated to public lands not available for agriculture or urban development (Riitters et al. 2012). Although the southeastern US Piedmont experienced a period of reforestation when large tracts of agricultural land were abandoned in the early 1900s, this region is currently experiencing an unprecedented conversion of these secondary forests to residential and urban development (Napton et al. 2010). London and Hill (2002) found a 30% increase in developed land from 1992 to 1997 and predicted that an additional 31 million acres will be converted to other uses by 2040. Forest conversion in the southeastern US Piedmont also ranked fourth out of 20 southeastern US regions examined (Napton et al. 2010). As the number of forest fragments has increased on the landscape, mean fragment size has declined by 12% since 1950 (Griffith et al. 2003). Despite demonstrated increases in forest fragmentation and decreased forest fragment size, we know relatively little about how fragmenting forests into small patches, which are likely experiencing multiple and interacting edge effects, impacts woody plant community structure and composition in southeastern US Piedmont secondary oak-hickory (*Quercus*-*Carya*) forests (but see Kadmon and Pulliam 1993, Fraver 1994, Kadmon 1995, Kadmon and Pulliam 1995, McDonald and Urban 2006, Fridley et al. 2009).

Forested reservoir islands, created by impounding rivers and isolating hilltops of continuous forest, provide an excellent natural experimental system to explore how forest fragmentation may alter woody plant species richness, structure, and composition (Benchimol and Peres 2015). The spatial arrangement of forested reservoir islands and surrounding mainland forest is similar to that of fragments caused by residential and urban development and remaining, large remnant forest with only a single edge exposed (Fischer and Lindenmayer 2007). This spatial configuration also allows for direct comparison of a large forest that is impacted by creation of only a single edge (mainland forest) with small forest fragments (islands) that likely are experiencing impacts from multiple, potentially interacting edge effects (Porensky and Young 2013). Other advantages to studying the response of forest communities to fragmentation in and along reservoirs is that fragmentation occurred at a specific and known time for all fragments under consideration, and forested islands and mainland forest sites have well-defined edges situated in a consistent matrix of water (Watson 2002, Benchimol and Peres 2015).

Having a single habitat (i.e., open water) along the edges of islands and mainland forest areas controls for confounding effects that variability in the surrounding matrix may have on plant species richness, composition, and structure (Lovei et al. 2006, Nascimento et al. 2006, Benchimol and Peres 2015).

We used a series of small forested islands and paired mainland forest sites to investigate how fragmentation impacts woody plant species richness, composition, forest structure, and environmental conditions in secondary oak-hickory forests in the southeastern US Piedmont. The reservoirs were created relatively recently (nearly 40-70 years ago), and therefore we predicted that differences between forested islands and mainland forest for forest structure and species composition would be related to a higher abundance of disturbance-tolerant native and non-native woody plant species rather than to a decline of typical overstory species associated with oak–hickory forest. We also predicted that species composition of the overstory, understory, and seedling layers would indicate that forested islands will likely continue to diverge from mainland forest as typical overstory species associated with *Quercus – Carya* forests fail to reproduce and disturbance-tolerant woody species become more dominant over time. We anticipated that these changes in species composition would be accompanied by structural and environmental differences between forested islands and mainland forest along transects from edge to interior.

METHODS

Study area

All study sites were located in Piedmont oak-hickory forests in and around Lake J. Strom Thurmond (Lake Thurmond) and Lake Richard B. Russell (Lake Russell) along the Savannah River between South Carolina and Georgia, US (Fig. 2.1). These sites are within the southeastern US Piedmont physiographic region, which is defined as the area from the Brevard Fall Line at the base of the Blue Ridge Mountains to the Sandhills Fall Line, which demarks the Coastal Plain to the east (Fairchilds and Trettin 2006). Currently, secondary forests of oak-hickory dominate undeveloped upland sites in the southeastern US Piedmont (Box 2015). This region is characterized by poor soils that range from deep clays to exposed bedrock (Richter et al. 2000, Fairchilds and Trettin 2006). Lake Thurmond (288 km^2) and Lake Russell (107.8 km^2) were created for flood control and hydroelectric power along the Savannah River in 1954 and 1984, respectively. Impoundment created islands of forest fragments by isolating forested hilltops from what was once contiguous forest. Large areas of protected mainland forest occur in the landscape surrounding Lake Thurmond (2775 ha of mainland forest) and Lake Russell (8332 ha of mainland forest) (USACE 2013). Mean annual rainfall along these reservoirs is 116.8 cm yr^{-1}, and average monthly temperature ranges from 9.4° to 23.9°C (SCSCO 2007).

Site selection

We examined aerial photographs and topographic maps, and used field observations to identify forested islands that were not clear-cut prior to impoundment, and were continuously isolated from mainland forest and other island fragments since the date of reservoir creation. Our sampling was limited to islands less than 3 ha in size as there were no larger islands that had been completely isolated since the date of reservoir construction, or were not greatly impacted by historic roads or settlement. Thirteen (13) islands fit these criteria in Lake Thurmond (Fig. 2.1). From the 62 islands that fit these criteria in Lake Russell, 22 were randomly selected for sampling (Fig. 2.1). Islands ranged in size from 0.08 ha – 2.47 ha and were 34.77 – 917.83 m from the closest mainland shore. We compared these 35 islands to 10 mainland forest sites located in protected areas along the shoreline of Lake Russell (5 sites) or Lake Thurmond (5 sites). Mainland sites were selected using a stratified random approach by placing random points in protected areas along the shoreline in GIS, then we examined aerial photographs and used field visits to ensure that selected mainland sites had not been highly disturbed during reservoir creation and were representative of oak-hickory forest in the region. As we were interested in how woody vegetation has responded to the influence of multiple edges on small forested islands as opposed to a single edge in large remnant forest, mainland forest sites were intentionally located in coves to eliminate influence from more than one edge in close proximity (< 100 m; Laurance et al. 2011).

Forested island species richness

To quantify total species richness on the forested islands, we conducted comprehensive inventories of all woody species on all 35 islands. We walked the entire area of each island from the edge to interior in concentric circles approximately 5 m wide and recorded the presence of all woody plant species that were ≥ 50 cm in height or length, in the case of lianas (Kadmon and Pulliam 1993). Three people were always used to complete these comprehensive surveys, with two people walking roughly 2.5 m from one another, and the third recording species occurrences and verifying that no species were missed. Plant species nomenclature follows Weakley (2006).

Island and mainland plot sampling

We sampled vegetation, forest structure, and environmental variables in plots running from the vegetated edge toward the approximate center of each island or forest interior of each mainland site between May and October in 2007, 2008, and 2009. Using ArcGIS (ESRI 2006), we randomly placed two transects per site, except at Lake Thurmond where only one transect per mainland site was sampled. Transects were oriented toward the center of each island or perpendicular to the shoreline for mainland sites. Centered along each transect, we censused vegetation within 4 m x 5 m (20-m^2) plots starting 2 m from the edge of vegetation. On the smallest islands, plots were also placed 8 m from the edge as well as in the center for a total of 5 plots per island. Additional plots were placed at 18 m on medium sized islands (7 plots per island); 18 and 30 m on the largest islands (9 plots per island); and 18, 30 and 50 m at mainland sites (5 plots per mainland transect). There were four islands that did not have a center plot because installing a center plot would have overlapped with plots at the ends of the two transects. We used ArcGIS (ESRI 2006) to quantify island area (ha), determine the distance of each island from the closest mainland forest (m), and describe how far each center plot was located from the closest island edge (m). A total of 314, 20-m^2 plots were measured with 239 plots on forested island fragments and 75 plots in mainland forest sites.

In each 20-m^2 plot, individual woody and semi-woody stems (i.e., trees, shrubs and lianas) $\geq$ 50 cm in length were tallied and identified to species. Lianas and shrubs were considered a single individual or stem if the base was rooted firmly in the ground and connection to other stems could not be confirmed. We used Weakley (2006) and the United States Forest Service Fire Effects Information System (USFS 2016) to assign species to the following categories: liana, shrub, pioneer tree, and non-pioneer tree. We also recorded the diameter at breast height (DBH) for all stems $\geq$ 1 cm DBH to calculate basal area per plot. Plots were pooled within each site for analysis of species composition.

Canopy height, basal area, litter mass, soil pH, and canopy openness

We quantified canopy height, basal area, litter mass, and soil pH for each sampling plot to determine how forest structure and soil properties differed along transects in each site type (island or mainland). Canopy height was quantified by measuring the height of the tallest woody stem in each plot, using either a meter tape for vegetation < 2 m tall or a laser range finder for vegetation ≥ 2 m tall (Impulse, Laser Tech, Inc., Englewood, CO). Total basal area for each plot was calculated by summing the individual basal area of all woody stems ≥ 1 cm DBH. For litter mass, we placed a 0.25 m^2 quadrat on two opposing corners of each plot and removed all litter above the mineral soil surface. Litter samples were bagged and dried at 60ºC until constant weight, and the final dry weight was averaged for each plot. Eight 2.54 cm x 10 cm soil cores were collected from each 0.25 m^2 quadrat, homogenized, passed through a 2mm sieve, and refrigerated until analysis of pH. Soil pH was quantified using 10 g of soil mixed with 10 ml of deionized water following the slurry method as described by McClean (1982), and measurement was made using a glass electrode pH meter standardized with pH 4 and pH 7. The two soil pH measurements were also averaged for each plot.

Between May and October 2010, we quantified canopy openness for a random subset of half the islands (n = 11) and for the 5 mainland sites in Lake Russell to determine if there were differences in light levels between the site types, or along transects from forest edge to interior. We measured the canopy openness using digital hemispherical photography and the Nikon CoolPix 4500 camera with Nikon FC-E8 fisheye lens mounted and leveled 60 cm above the center of each 20-m^2 plot. All photographs were taken before sunrise, after sunset, or on uniformly cloudy days to negate the impact of the solar disk on the calculation of canopy openness (Frazer et al. 2001). Images were imported into SideLook (Nobis and Hunziker 2005) and converted to pure black and white images before being analyzed for percentage of canopy openness using Gap Light Analyzer 2.0 (Frazer et al. 1999).

Expanded overstory and seedling sampling

Between May and October 2011, we expanded our vegetation sampling on the same subset of 11 islands and 5 mainland sites in Lake Russell (hereafter called Lake Russell subset) used to quantify canopy openness in order to examine patterns in overstory (> 5 cm DBH), understory (≥ 50 cm height to < 5 cm DBH), and seedling (10-50 cm height) composition. The 11 islands ranged in size from 0.12 ha – 2.47 ha, and were anywhere from 38.5 – 409.5 m from the closest mainland shore. On islands < 0.5 ha in size (n = 4), we recorded the species identity of every woody individual ≥ 5 cm DBH. On islands ≥ 0.5 ha (n = 7) and in the mainland sites, we constructed 10-m-wide belt transects centered on the previously established edge to interior transects, plus constructed a 10 m x 10 m^2 plot in the center of the island, and recorded the species identity of every woody individual ≥ 5 cm DBH. Woody individuals in the understory (≥ 50 cm height to < 5 cm DBH) were measured in the 20-m^2 plots as described above in *Island and mainland plot sampling*. Seedlings were counted and identified in a 1 m x 4-m^2 quadrat in the center of each 20-m^2 plot.

Analysis to determine differences between site types and to identify edge effects

We used general and linear mixed effects models to test whether there were effects of site type or distance from the edge on the following plot-level variables: species richness, total stem density, liana stem density, shrub stem density, pioneer tree stem density, basal area, canopy height, litter mass, soil pH, and percentage of canopy openness. As multiple plots were surveyed within a single site, we included site as a random effect in the analyses. For all count data, we modeled the Poisson distribution. All mixed effects analyses were conducted using R version 3.2.3 with the packages "lme4" v. 1.1-11 and "lmerTest" v. 2.0-30 and the functions 'glmer' for count data, 'lmer' for continuous data (R Development Core Team 2015). The t-tests for function 'lmer' use Satterthwaite approximations to calculate degrees of freedom. Generalized linear mixed models invoked by 'glmer' are fit by maximum likelihood (Laplace Approximation). We used the package "effects" v. 3.1-0 and the function 'effects' to visualize significant model effects ($p < 0.05$) in R (R Development Core Team 2015).

Analysis of species composition

We illustrated differences in species composition among sites on each lake and for the three forest layers in the Lake Russell subset, using three multivariate methods: non-metric multidimensional scaling (NMS) ordination, multiple response permutation procedure (MRPP), and indicator species analysis (ISA). All multivariate analyses were performed in PC ORD V. 6 (McCune and Mefford 2011). To reduce the influence of rare species on these analyses, we removed species that were present in less than 5% of the sites examined in the full data set (McCune and Grace 2002). All species captured in plots within sites in the Lake Russell subset occurred in more than 5% of the sites examined. We used the relative Sørensen (Bray-Curtis) distance for the NMS and MRPP analyses. For the NMS analyses, we used the automated "slow and thorough" setting in PC-ORD, which provides a random start and uses a Monte Carlo procedure with 250 runs of the real and randomized data to select the appropriate number of axes and minimize stress (McCune and Mefford 2011).

Multiple response permutation procedure (MRPP) was used to test for significant differences in species composition between site types (island and mainland) within and between the lakes (McCune and Grace 2002). Because MRPP analysis in PC-ORD (McCune and Mefford 2011) does not correct for multiple comparisons, we used the Bonferroni correction and set $\alpha = 0.008$ or $\alpha = 0.005$ for the MRPP analysis between the site types and lakes or between the site types and forest layers for the Lake Russell subset, respectively.

Indicator species analysis was used to identify species that had significantly higher frequency and abundance than expected by chance within a site type ($p < 0.10$) (Dufrêne and Legendre 1997, McCune and Grace 2002). Examination of correlations between species and NMS axes were used to determine whether significant indicator species for islands and mainland sites were also species that were strongly influencing the position of sites within the NMS ordinations. We highlighted positive and negative Pearson correlations (r) greater than 0.4 for species with NMS axes in the full dataset ($df = 43$, $p = 0.005$) or greater than 0.5 for the Lake Russell subset ($df = 14$, $p = 0.05$).

To explore how percentage canopy openness and soil pH are impacting site-level species composition in the Lake Russell subset, we reported Pearson correlations (r) of the mean percentage canopy openness and the mean soil pH for each site. Correlations of percentage canopy openness and soil pH with NMS axes greater than 0.5 for the Lake Russell subset ($df = 14$, $p = 0.05$) are highlighted.

Effects of area and isolation on tree species regeneration, risk of extinction, immigration, and colonization

We explored future effects of fragmentation on the tree community by determining, for each island and mainland site, which tree species appear to be regenerating, which are at risk of local extinction, which have likely immigrated since fragmentation, and which could colonize from the regional species pool in the future. We applied criteria used by Thijis et al. (2014) to the Lake Russell subset to classify tree species into these four categories. Regenerating tree species (R) were defined as tree species that were present in the overstory and the understory or seedling layer (or both) on the island or mainland site being analyzed (Thijs et al. 2014). Tree species at risk of local extinction (De) on an island or mainland site were defined as tree species that were present in the overstory but were not detected in either the understory or seedling layer (Thijs et al. 2014). Immigrant species (I) were those tree species that occurred in the understory or as seedlings on the island or mainland site, but did not have any overstory individuals present. These immigrant species likely colonized the island or mainland site since reservoir creation. Thijis et al. (2014) used the term recruitment credit (Cr) for these species. Potential colonizers (C_c) were those species that were not detected in any forest layer on any particular island or mainland site, but were present in the regional species pool.

For each island and mainland site, we calculated the proportion of the regional tree species pool that were classified as R, De, I, and Cc categories; and also the proportion of the local species pool (within site) that were classified as species in the *R*, *De*, and *I* categories. We defined the regional species pool as the 43 tree species that were encountered in our expanded overstory and seedling sampling on at least one of the 11 islands or 5 mainland forest sites. We defined the local species pool as the total number of tree species that were encountered on each island or mainland site, which ranged from 9 to 24 species on islands and 18 to 25 on mainland sites. We compared the proportion of species in each category on islands and mainland sites at both the local-level (within site *R*, *De*, and *I*,) and regional-level (*R*, *De*, *I*, and *Cc*) using t-tests.

RESULTS

During our comprehensive inventories of islands, we identified a total of 125 woody or semi-woody plant species that occurred across the 35 islands. Within the 314 plots sampled across 45 sites (35 islands and 10 mainland forest sites), we found 11,119 individuals and 98 species. Of the 98 species, 6 species were captured exclusively in plots in mainland forest, while 34 species occurred only in plots on forested islands. Based on our comprehensive island inventories, total woody plant species richness on islands ranged from 30 to 62 species. Islands in Lake Thurmond had an average of 5 more species per island than islands in Lake Russell (Chapter 1, Fig. 1.1). Mean total species richness of shrubs ($t = 3.63$, $p < 0.001$) and lianas ($t = 2.32$, $p = 0.006$), but not trees ($t = 1.22$, $p = 0.23$) was greater in Lake Thurmond than Lake Russell.

Large, scattered individuals of *Carya glabra*, *C. alba*, *Quercus rubra*, *Q. alba*, and *Pinus taeda* dominated the overstory on most forested islands and mainland forest

(Table 2.1). In mainland forest, small individuals of these same species were also prominent in the understory, along with *Cornus florida* and *Acer rubrum* (Table 2.1). On forested islands, we found that *Q. nigra*, *Juniperus virginiana*, *Ulmus alata*, *Diospyros virginiana*, and *Prunus serotina* were also common in the overstory, with smaller individuals of these same species in the understory, along with the native shrubs *Vaccinium arboreum* and *V. elliottii* (Table 2.1). *Vitis rotundifolia* and *Campsis radicans* were the most common lianas in mainland forest. In contrast, the most abundant liana species on forested islands were *Gelsemium sempervirens*, the non-native *Lonicera japonica*, *Smilax glauca*, and *S. bona-nox*. *Gelsemium sempervirens*, *U. alata*, and the non-native *L. japonica* were the most abundant woody species overall in this system, composing approximately 24% and 7% of all individuals sampled, respectively.

Stem density and species richness on islands and mainland sites in both lakes

Overall, the number of individuals captured in plots for all species was nearly two times greater on forested islands compared to mainland forest, and decreased from the edge to the interior in both site types (Fig. 2.2; Table 2.2). Lianas showed a trend for greater density on islands than mainland forest, but liana density was much more variable in mainland sites, and decreased in both site types as distance from the edge increased (Fig. 2.2; Table 2.2). Shrub density was nearly three times greater on forested islands, and density increased toward the center of islands but was similar from edge to interior forest in mainland forest. Density of individuals classified as pioneer tree species on forested islands was also nearly twice that found in mainland forest but there was no significant relationship with distance from the edge in either site type. The density of *L. japonica* individuals was greater on forested islands compared to mainland forest, but varied widely in abundance from edge to interior in both site types. Species richness per plot of all woody species on forested islands was also nearly double that found in mainland forest, and only exhibited a decrease from edge to interior in mainland forest (Fig. 2.4; Table 2.2).

Litter, forest structure, soil pH, and percent canopy openness

Litter mass, basal area, canopy height, soil pH, and percentage of canopy openness exhibited variable responses from edge to interior on forested islands and mainland forest (Fig. 2.3; Table 2.3). Litter mass increased from the edge to interior, and this pattern appeared to be driven primarily by forested islands, which had greater litter mass overall (Fig. 2.3; Table 2.3). Basal area was not significantly different between forested islands and mainland forest, and no difference was detected with increasing distance from the edge. In contrast, canopy height and soil pH increased and percentage of canopy openness decreased from the edge to interior but was not significantly affected by site type. Soil pH was quite variable and ranged widely from acidic soils typical for this region (pH = 4.0) to nearly neutral (pH = 6.9) on both islands and mainland sites (Fig. 2.3; Table 2.3).

Overall forest species composition on islands and mainland sites in both lakes

Of the 75 species retained for community analysis, only 1 species was exclusively found on mainland sites, while 17 species were only found on islands (Table 2.1). Forested islands and mainland forest differed in woody plant species composition as indicated by the separation of islands from mainland sites in the NMS ordination, primarily along Axis 1 (Fig. 2.4; 3-dimensional solution, stress = 13.9, variation explained = 80.7%). MRPP analysis of community composition indicated an overall difference between forested islands and mainland forest ($T = -8.26$, $A = 0.07$, $p < 0.001$). Pairwise comparisons between islands and mainland sites in the two lakes indicated that species composition between mainland forest in the two lakes did not differ, but forested island composition between the two lakes did differ (Table 2.4). Forested islands differed from mainland forest both within and between the two lakes (Table 2.4).

Indicator species analysis identified several species that contributed to compositional differences between forested islands and mainland forest, with the bulk of significant indicator species assigned to forested islands (Table 2.5). *Acer floridanum* and *Vitis rotundifolia* were noteworthy significant indicators of mainland forest. *Acer floridanum* was found only in Lake Russell, with mean stem density in mainland forest nearly double that found on islands (Table 2.1). While *V. rotundifolia*, a liana, occurred in both site types at relatively high densities, plots in mainland forest contained nearly three times the number of stems compared to island plots (Table 2.1). In addition, several species considered to be shade-intolerant and typically associated with disturbed areas were identified as significant indicator species for forested islands, namely: *G. sempervirens, J. virginiana,* the non-native liana *L. japonica, Pinus echinata, Prunus* *serotina, Rhus copallina, S. glauca*, and *U. alata*. Although many of the indicator species for islands were also found in mainland forest, they occurred at a much higher frequency and density on forested islands (Table 2.1). For example, the non-native liana *L. japonica*, and the native lianas *G. sempervirens*, and *S. glauca* were nearly 6 to 12 times more abundant per plot on islands when compared to mainland sites (Table 2.1). The abundance of disturbance-tolerant tree species *D. virginiana, J. virginiana*, and *U. alata* was also much higher in plots on forested islands (Table 2.1). The non-native shrub species *Elaeagnus pungens* was found in both site types, but had higher frequency of occurrence and much greater stem densities on islands compared to mainland sites (Table 2.1). The non-native tree species *Albizia julibrissin* was found in plots only on Lake Russell islands less than 0.6 ha in size (Table 2.1).

Overstory, understory, and seedling composition in Lake Russell

Forested islands and mainland forest in Lake Russell differed in woody plant species composition only for understory woody vegetation and seedlings as indicated by the separation of islands and mainland forest sites in the NMS ordinations and MRPP analysis (Fig. 2.5; Table 2.6). Additionally, pairwise comparisons between forest layers showed that the species composition of the three forest layers significantly differed for forested islands (Table 2.6). In mainland sites, the composition of the overstory differed from the understory and seedlings, but the latter two did not differ from each other.

Indicator species analysis identified several species that contributed to compositional differences between forested islands and mainland forest in Lake Russell, with the majority of significant indicator species assigned to mainland forest (Table 2.7). *Acer floridanum*, *Ostrya virginiana*, and *Q. alba* were significant indicators of mainland forest for all three forest layers, whereas *A. rubrum*, *C. alba*, and *Fagus grandifolia* were significant indicators for mainland forest overstory and seedlings (Table 2.7). On forested islands, we found that there were no significant indicator species for seedlings, though Pearson correlations with NMS axes indicated that *P. echinata*, *P. taeda*, *Prunus serotina*, and the non-native liana *L. japonica* were influencing island site positions along the NMS axes (Fig. 2.5). Several species were identified as significant indicators of the overstory and understory forest layers on islands, namely: *G. sempervirens*, *J. virginiana*, *P. echinata*, and *Q. nigra* (Table 2.7). Indicator species for islands and those that are differentiating islands from mainland forest along the NMS axes are known to be common in disturbed areas.

Mean percentage canopy openness and soil pH in Lake Russell sites were significantly correlated with NMS axes for each forest layer (Table 2.8). Soil pH was significantly and positively correlated with both Axis 1 for overstory vegetation and with Axis 2 for understory vegetation. Percentage canopy openness was significantly and positively correlated with Axis 3 for understory vegetation and with Axis 3 for seedling composition.

Predicted changes in forest composition

Our expanded overstory and seedling sampling on the mainland forest sites and subset of islands in Lake Russell captured a total of 43 tree species (i.e., regional species pool). Tree species richness ranged from 9 to 24 for the 11 forested islands, and all islands together captured 88% of the regional species pool. In the Lake Russell mainland forest sites, tree species richness ranged from 18 to 25, and the five sites captured 79% of the regional species pool. We identified only one island that had no local tree species at risk of extinction. On all other forested islands, we found that the proportion of local tree species regenerating ranged from 35% to 58%, the proportion of species at risk of extinction ranged from 5% to 50%, and the proportion of species that were thought to have immigrated to the island ranged from 10% to 55%. On the mainland sites we found that, locally, the proportion of tree species regenerating, at risk of extinction, or thought to have immigrated to the site was similar to that found on islands. Regionally, mainland sites captured a significantly greater proportion of the regional species pool (Cc; $t = -2.93$, $p < 0.03$), and a larger proportion of these were regenerating compared to islands (R; $t = 10.1$, $p = 0.006$). There were no differences between the site types for the proportion of immigrant or species at risk of extinction at the regional level.

DISCUSSION

Isolated forest fragments in this system are diverging from continuous forest through colonization and proliferation in shrub, liana, and pioneer tree species not common in oak-hickory forest. Tree species typical of this forest type appear to be surviving on the islands, at least for the time being. This persistence could be due either to the relatively recent creation of the fragments (40 to 70 years ago) or to the disturbance-tolerant nature of the canopy species associated with oak-hickory forests of the southeastern US (Cowden et al. 2014). Many of the tree species typically associated with this forest type occurred at similar frequencies and densities in both forested islands and mainland forest (*C. alba, C. glabra, Q. alba, Q. rubra, Q. velutina*, and *P. taeda*). However, changes in species composition are occurring, as more species are being added and pioneer trees, such as *J. virginiana*, *U. alata*, and *P. echinata*, are becoming more prominent in the overstory and understory on forested islands. In fact, forested islands supported, on average, at least four more species per plot than mainland forest and remained elevated across the entire island whereas there was significant decline in species richness per plot from edge to interior in mainland forest. Laurance et al. (2006a) found little difference in tree species richness between intact forest and edge plots or plots in fragments even though there were substantial changes in species composition. Greater species richness on forested islands than mainland forest likely resulted from the doubled stem density we found on islands compared to mainland forest. We attribute higher stem densities and species richness on islands to the creation of edge habitat through forest fragmentation, which has promoted the proliferation of liana, shrub, and pioneer tree species that are uncommon in relatively undisturbed, oak-hickory forests.

With the exception of lianas, we found that the number of individuals for all of these life-forms, as well as for the non-native liana *L. japonica,* were elevated well above the values we found in mainland forest and remained elevated across entire islands indicating that these biological edge effects are pervasive across small islands, in contrast to the distinct edge to interior pattern we found in mainland forests. Similarly, Londre and Schnitzer (2006) found that overall liana abundance in the deciduous temperate forests of Wisconsin substantially declined from forest fragment edge to interior. That *L. japonica* abundance was elevated across entire forested islands is not surprising, as Fridley et al. (2009) found that *L. japonica* abundance was higher on edges of a North Carolina Piedmont forest up to 70 m from the edge of an agricultural field. Edge effects for lianas and pioneer tree species were also demonstrated in the tropical forest of the BDFFP, where both richness and abundance of tropical liana and pioneer tree species were greater within 25 m of agricultural lands (Laurance et al. 2001, Laurance et al. 2006b), though we did not detect a decline in the density of pioneer trees on our small forested islands. We attribute the lack of steep declines with distance to the edge in shrub, pioneer tree, and *L. japonica* density on forested islands to compounded edge effects related to the small size of the islands and multiple edges in close proximity. Our largest island was less than 3 ha, and interior island plots were typically not more than 40-60 m from any edge. Laurance et al. (2011) also found that liana stem density and pioneer tree species in BDFFP were also shown to magnify as fragment size decreased and the number of fragment edges within 100 m increased. Thus, our fragments likely suffer from the influence of multiple edges (Harper et al. 2007, Laurance et al. 2011) and can be largely be considered entirely edge habitat.

Greater species richness in our forested islands may persist for several more decades, as the islands we sampled still have an "extinction debt" (Tilman et al. 1994) to pay due to the long-lived, disturbance-tolerant nature of the woody vegetation present. If canopy species fail to recruit and begin to go locally extinct, species richness may only then relax to an equilibrium point (Gonzalez et al. 2009), such that species richness on the islands becomes similar to the forested mainland sites or declines. Our analysis of the overstory, understory, and seedling composition of forested islands and mainland forest in Lake Russell predicts that the species composition of forested islands will indeed continue to diverge from mainland forest, and species richness may become more similar to mainland forest or decline over time as anywhere from 5% to 50% of the overstory tree species currently present on islands in Lake Russell are not represented in either the understory or seedling layers on islands.

Islands in Lake Thurmond, 30 years older than those in Lake Russell, appear to have diverged more from continuous forest in their species composition than the younger islands on Lake Russell. Islands on Lake Thurmond had a greater number of shrub and liana species than Lake Russell, and the species composition of islands in the two lakes differed significantly. In contrast, the mainland forests of the two lakes had similar numbers of species and species composition, suggesting that time since isolation is driving the changes in composition. Therefore, in the next 30 years we expect to see that forested islands in Lake Russell will continue to accumulate more shrub and liana species. If tree species continue to persist on islands in the two lakes, the differences in species composition and richness may disappear.

Edge effects in oak-hickory forest fragments

Despite a divergence in species composition between fragments and continuous forest in our system, the only environmental variable that differed between these site types, when accounting for distance from the forest edge, was litter mass. Litter mass markedly increased from edge to interior and was consistently greater on islands than on their mainland forest counterparts. It is unclear if the greater litter mass on islands was due to decreases in litter decomposition rates, or if greater stem density on islands means that more leaves and hence litter are produced (Ramalho et al. 2014). It is likely that increased stem density is providing a greater supply of litter on island fragments and may be considered largely a structural edge effect. However, lower soil moisture and relative humidity levels commonly associated with forest fragment edges (Matlack 1993, Broadbent et al. 2008) have also been shown to slow litter decomposition rates (Riutta et al. 2012). As litter depth has been shown to impact seedling composition in other systems (Benítez-Malvido 1998), long-term impacts of increased litter in these small fragments may impact seedling recruitment for overstory species associated with oak-hickory forests. For example, greater litter depth has been shown to inhibit germination for small-seeded species like *Liquidambar styraciflua* and reduce seedling growth for large-seeded species like *Quercus velutina* (Kostel-Hughes et al. 2005). Therefore, germination or growth of typical overstory tree species may be negatively affected in small forest fragments.

Soil pH significantly increased from edge to interior in both habitats, which was somewhat unexpected as the two other studies that measured this variable found the opposite pattern (Honnay et al. 2002, Alignier and Deconchat 2013). Both of those studies were conducted in landscapes where there was a large proportion of arable land as well as urban and residential development surrounding their fragments, and they concluded their results may have been due to nutrient influx from the surrounding landscape (Honnay et al. 2002, Alignier and Deconchat 2013). Our mainland forest and forested islands edges were located along water and nutrients are therefore not likely being deposited from agricultural areas in the surrounding matrix. The few nutrients being added to forested islands in the system are strictly from atmospheric deposition and the extant vegetation, which may be more nutrient rich in the interior of the fragments. Soils in this study system may weather and become more acidic over time (Schoenholtz et al. 2000, Farr et al. 2009). In addition, we found that mean soil pH for each site in the Lake Russell subset was significantly and positively correlated with NMS axes that consistently identified *J. virginiana* as a species that was contributing to the differences we see in species composition between forested island and mainland sites in Lake Russell. This result is likely due to the impact the *J. virginiana* has had on the soils, rather than how soil pH is affecting community composition. *Juniperus virginiana* is known to produce leaf litter that is extremely high in Ca which in turn can dramatically increase soil pH (Arend 1950) and which then impacts seedling and sapling communities in low nutrient habitats(Joy and Young 2002).

Canopy openness, our proxy for light availability, decreased from edge to interior in both site types. This result is similar to many other studies that have measured light availability along transects from forest edge to interior (e.g., Matlack 1993, Benitez-Malvido and Martinez-Ramos 2003, Londré and Schnitzer 2006, Flory and Clay 2009). That light availability on forested islands was not greater than that found in mainland forest was somewhat surprising, however, as we expected canopy openness to be higher on forested islands compared to mainland sites because island interiors were typically never further than 40 – 60 m from an island edge. Canopy openness has likely been influenced by the time since isolation, and it may be that light availability between the two habitats has become more similar over time as the vegetation has had nearly 40 years to respond and "edge closure" (Laurance et al. 2002) may have already occurred in these sites. A similar pattern was found in the BDFFP where woody vegetation exhibited edge closure as quickly as 1-5 years following fragmentation, and microenvironmental edge effects became more complex though did not disappear entirely (Kapos et al. 1997, Laurance et al. 2002). We also found that mean light levels on islands were significantly correlated with NMS axes that demonstrated compositional differences between forested islands and mainland forest in Lake Russell for the understory and seedling layers. This indicates that even though edge effects for light appear similar on islands and mainland sites, slight differences between the site types may be leading to large differences in composition. Furthermore, it may be that light levels from the edge to interior on forested islands and mainland forest have only recently become similar, and the difference in species composition reflects historic effects of overall greater canopy openness on islands compared to mainland forest.

Basal area and canopy height were similar between the two site types, and only canopy height increased with increasing distance from the edge. Our findings for canopy height are similar to several studies that have documented reductions in canopy height along forest edges (Harper et al. 2005). Basal area in our study system may have rapidly recovered to levels found in mainland forest because some woody species have likely benefitted from reduced competition and increased light when the forested islands were created nearly 40 and 70 years ago (Broadbent et al. 2008). Coupling our data for individual density and basal area, it appears that the increase in basal area on the edge results mostly from an increase in the number of smaller stems, rather than increases in basal area of persisting vegetation. This is also supported by the compositional data where *L. japonica*, shrub species, and pioneer tree species had greater abundance on forested islands and contributed to the separation of islands from mainland sites in the NMS.

Conclusion

Oak-hickory forest fragments in the Piedmont region of the southeastern US, even those as small as an American football field, have largely retained the canopy species found in mainland forests, at least for the time being. This persistence is due to an "extinction debt" (Tilman et al. 1994) that has not yet been paid by the long-lived, relatively disturbance-tolerant, woody species that were the focus of this study. However, the effects of fragmentation cannot be fully appreciated without explicit consideration of how edge effects contribute to forest community composition and structure (Harper et al. 2005, Koh et al. 2010). By sampling from the edge to interior of small forested islands and large mainland forest, we were able to demonstrate how forests in small fragments are affected by compounded edge effects and essentially function entirely as edge habitat for the non-native liana *L. japonica*, shrub and pioneer tree species and species richness on a per area basis, with concomitant changes in species composition primarily attributed to compositional differences in the understory. It is likely that the forested islands in our study will continue to diverge from mainland forest over time, and may ultimately degrade to the point that the forest community is made up entirely of disturbance-tolerant early seral species.

REFERENCES

Alignier, A. and M. Deconchat. 2013. Patterns of forest vegetation responses to edge effect as revealed by a continuous approach. Annals of Forest Science **70**:601-609.

Arend, J. L. 1950. Influence of fire and soil on distribution of eastern red cedar in the Ozarks. Journal of Forestry **48**:129-130.

Benchimol, M. and C. A. Peres. 2015. Edge-mediated compositional and functional decay of tree assemblages in Amazonian forest islands after 26 years of isolation. Journal of Ecology **103**:408-420.

Benítez-Malvido, J. 1998. Impact of forest fragmentation on seedling abundance in a tropical rain forest. Conservation Biology **12**:380-389.

Benitez-Malvido, J. and M. Martinez-Ramos. 2003. Influence of edge exposure on tree seedling species recruitment in tropical rain forest fragments. Biotropica **35**:530-541.

Box, E. O. 2015. Warm-temperate deciduous forests of eastern North America. Pages 225-255 *in* E. O. Box and K. Fujiwara, editors. Warm-Temperate Deciduous Forests around the Northern Hemisphere. Springer International Publishing.

Broadbent, E., G. Asner, M. Keller, D. Knapp, P. Oliveira, and J. Silva. 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. Biological Conservation **141**:1745-1757.

Cowden, M., J. Hart, and M. Buchanan. 2014. Canopy accession strategies and climate responses for three Carya species common in the Eastern Deciduous Forest. Trees **28**:223-235.

Debinski, D. M. and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology **14**:342-355.

Diamond, J. M. 1972. Biogeographic kinetics: estimation of relaxation times for avifaunas of Southwest Pacific Islands. Proceedings of the National Academy of Sciences **69**:3199-3203.

Dufrêne, M. and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs **67**:345-366.

ESRI. 2006. ArcGIS, Version 9.2. ESRI, Redlands, California.

Ewers, R. M. and R. K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews of the Cambridge Philosophical Society **81**:117-142.

Fairchilds, L. H. and C. C. Trettin. 2006. History and legacy of fire effects in the South Carolina piedmont and coastal regions. United States Department of Agriculture Forest Service, Southern Research Station, Asheville, North Carolina.

Farr, C., J. Skousen, P. Edwards, S. Connolly, and J. Sencindiver. 2009. Acid soil indicators in forest soils of the Cherry River Watershed, West Virginia. Environmental Monitoring and Assessment **158**:343-353.

Fischer, J. and D. B. Lindenmayer. 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography **16**:265-280.

Fletcher, R. J. 2005. Multiple edge effects and their implications in fragmented landscapes. Journal of Animal Ecology **74**:342-352.

Flory, S. L. and K. Clay. 2009. Effects of roads and forest successional age on experimental plant invasions. Biological Conservation **142**:2531-2537.

Fraver, S. 1994. Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke river basin, North Carolina. Conservation Biology **8**:822-832.

Frazer, G. W., C. D. Canham, and K. P. Lertzman. 1999. Gap Light Analyzer (GLA): Users Manual and Program Documentation. Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.

Frazer, G. W., R. A. Fournier, J. A. Trofymow, and R. J. Hall. 2001. A comparison of digital and film fisheye photography for analysis of forest canopy structure and gap light transmission. Agricultural and Forest Meteorology **109**:249-263.

Fridley, J. D., A. R. Senft, and R. K. Peet. 2009. Vegetation structure of field margins and adjacent forests in agricultural landscapes of the North Carolina piedmont. Castanea **74**:327-339.

Gonzalez, M., M. Deconchat, and G. Balent. 2009. Woody plant composition of forest layers: the importance of environmental conditions and spatial configuration. Plant Ecology **201**:305-318.

Griffith, J. A., S. V. Stehman, and T. R. Loveland. 2003. Landscape trends in Mid-Atlantic and Southeastern United States Ecoregions. Environmental Management **32**:572-588.

Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, W. M. Cook, E. I. Damschen, R. M. Ewers, B. L. Foster, C. N. Jenkins, A. J. King, W. F. Laurance, D. J. Levey, C. R. Margules, B. A. Melbourne, A. O. Nicholls, J. L. Orrock, D.-X. Song, and J. R. Townshend. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances **1**.

Harper, K. A., S. E. MacDonald, P. J. Burton, J. Chen, K. D. Brosofske, S. C. Saunders, E. S. Euskirchen, D. Roberts, M. S. Jaiteh, and P.-A. Esseen. 2005. Edge influence on forest structure and composition in fragmented landscapes. Conservation Biology **19**:768-782.

Harper, K. A., L. Mascarua-Lopez, S. E. Macdonald, and P. Drapeau. 2007. Interaction of edge influence from multiple edges: examples from narrow corridors. Plant Ecology **192**:71-84.

Hierro, J. L., D. Villarreal, O. Eren, J. M. Graham, and R. M. Callaway. 2006. Disturbance facilitates invasion: the effects are stronger abroad than at home. American Naturalist **168**:144-156.

Honnay, O., K. Verheyen, and M. Hermy. 2002. Permeability of ancient forest edges for weedy plant species invasion. Forest Ecology and Management **161**:109-122.

Ibáñez, I., D. S. W. Katz, D. Peltier, S. M. Wolf, and B. T. C. Barrie. 2014. Assessing the integrated effects of landscape fragmentation on plants and plant communities: the challenge of multiprocess-multiresponse dynamics. Journal of Ecology **102**:882-895.

Joy, D. A. and D. R. Young. 2002. Promotion of mid-successional seedling recruitment and establishment by Juniperus virginiana in a coastal environment. Plant Ecology **160**:125-135.

Kadmon, R. 1995. Nested species subsets and geographic isolation: a case study. Ecology **76**:458-465.

Kadmon, R. and H. R. Pulliam. 1993. Island biogeography - effect of geographical isolation on species composition. Ecology **74**:977-981.

Kadmon, R. and H. R. Pulliam. 1995. Effects of isolation, logging and dispersal on woody-species richness of islands. Vegetatio **116**:63-68.

Kapos, V., E. Wandelli, J. L. Camargo, and G. Ganade. 1997. Edge-related changes in environment and plant responses due to forest fragmentation in central Amazonia. Pages 33-54 *in* W. F. Laurance and R. O. Bierregaard, editors. Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago.

Koh, L. P., T. M. Lee, N. S. Sodhi, and J. Ghazoul. 2010. An overhaul of the species–area approach for predicting biodiversity loss: incorporating matrix and edge effects. Journal of Applied Ecology **47**:1063-1070.

Kostel-Hughes, F., T. P. Young, and J. D. Wehr. 2005. Effects of leaf litter depth on the emergence and seedling growth of deciduous forest tree species in relation toseed size. The Journal of the Torrey Botanical Society **132**:50-61.

Kuussaari, M., R. Bommarco, R. K. Heikkinen, A. Helm, J. Krauss, R. Lindborg, E. Öckinger, M. Pärtel, J. Pino, F. Rodà, C. Stefanescu, T. Teder, M. Zobel, and I. Steffan-Dewenter. 2009. Extinction debt: a challenge for biodiversity conservation. Trends in Ecology & Evolution **24**:564-571.

LaPaix, R., K. Harper, and B. Freedman. 2012. Patterns of exotic plants in relation to anthropogenic edges within urban forest remnants. Applied Vegetation Science **15**:525-535.

Laurance, W. F. 1991. Edge effects in tropical forest fragments: application of a model for the design of nature reserves. Biological Conservation **57**:205-219.

Laurance, W. F. 2002. Hyperdynamism in fragmented habitats. Journal of Vegetation Science **13**:595-602.

Laurance, W. F. 2008. Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. Biological Conservation **141**:1731-1744.

Laurance, W. F., A. S. Andrade, A. Magrach, J. L. C. Camargo, M. Campbell, P. M. Fearnside, W. Edwards, J. J. Valsko, T. E. Lovejoy, and S. G. Laurance. 2014.

Apparent environmental synergism drives the dynamics of Amazonian forest fragments. Ecology **95**:3018-3026.

Laurance, W. F., J. L. C. Camargo, R. C. C. Luizão, S. G. Laurance, S. L. Pimm, E. M. Bruna, P. C. Stouffer, G. Bruce Williamson, J. Benítez-Malvido, and H. L. Vasconcelos. 2011. The fate of Amazonian forest fragments: A 32-year investigation. Biological Conservation **144**:56-67.

Laurance, W. F., T. E. Lovejoy, H. L. Vasconcelos, E. M. Bruna, R. K. Didham, P. C. Stouffer, C. Gascon, R. O. Bierregaard, S. G. Laurance, and E. Sampaio. 2002. Ecosystem decay of Amazonian forest fragments: A 22-year investigation. Conservation Biology **16**:605-618.

Laurance, W. F., H. E. M. Nascimento, S. G. Laurance, A. Andrade, J. Ribeiro, J. P. Giraldo, T. E. Lovejoy, R. Condit, J. Chave, K. E. Harms, and S. D'Angelo. 2006a. Rapid decay of tree-community composition in Amazonian forest fragments. Proceedings of the National Academy of Sciences **103**:19010-19014.

Laurance, W. F., H. E. M. Nascimento, S. G. Laurance, A. C. Andrade, P. M. Fearnside, J. E. L. Ribeiro, and R. L. Capretz. 2006b. Rain forest fragmentation and the proliferation of successional trees. Ecology **87**:469-482.

Laurance, W. F., D. Pérez-Salicrup, P. Delamônica, P. M. Fearnside, S. D'Angelo, A. Jerozolinski, L. Pohl, and T. E. Lovejoy. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. Ecology **82**:105-116.

Li, M. S., C. Q. Huang, Z. L. Zhu, H. Shi, H. Lu, and S. K. Peng. 2009. Assessing rates of forest change and fragmentation in Alabama, USA, using the vegetation change tracker model. Forest Ecology and Management **257**:1480-1488.

Li, Q. L., J. Q. Chen, B. Song, J. J. LaCroix, M. K. Bresee, and J. A. Radmacher. 2007. Areas influenced by multiple edges and their implications in fragmented landscapes. Forest Ecology and Management **242**:99-107.

London, J. B. and N. L. Hill. 2002. Land conversion in South Carolina: state makes the Top 10 list. Jim Self Center on the Future, Clemson, South Carolina.

Londré, R. A. and S. A. Schnitzer. 2006. The distribution of lianas and their change in abundance in temperate forests over the past 45 years. Ecology **87**:2973-2978.

Lovei, G. L., T. Magura, B. Tothmeresz, and V. Kodobocz. 2006. The influence of matrix and edges on species richness patterns of ground beetles (Coleoptera: Carabidae) in habitat islands. Global Ecology and Biogeography **15**:283-289.

MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

Matlack, G. R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. Biological Conservation **66**:185-194.

McCune, B. and J. B. Grace. 2002. Analysis of ecological communities. MjM Software, Gleneden Beach, Oregon.

McCune, B. and M. J. Mefford. 2011. PC-ORD. Multivariate analysis of ecological data. MjM Software Design, Glendon Beach, Oregon.

McDonald, R. I. and D. L. Urban. 2006. Edge effects on species composition and exotic species abundance in the North Carolina Piedmont. Biological Invasions **8**:1049-1060.

Mclean, E. O. 1982. Soil pH and lime requirements. Methods of Soil Analysis, Part 2. Chemical and Microbiological PropertiesAg. Monograph No. 9, 2nd edition. Soil Science Society of America, Madison, Wisconson, USA.

Napton, D. E., R. F. Auch, R. Headley, and J. L. Taylor. 2010. Land changes and their driving forces in the Southeastern United States. Regional Environmental Change **10**:37-53.

Nascimento, H. E. M., A. C. S. Andrade, J. L. C. Camargo, W. F. Laurance, S. G. Laurance, and J. E. L. Ribeiro. 2006. Effects of the surrounding matrix on tree recruitment in Amazonian forest fragments. Conservation Biology **20**:853-860.

Nobis, M. and U. Hunziker. 2005. Automatic thresholding for hemispherical canopy-photographs based on edge detection. Agricultural and Forest Meteorology **128**:243-250.

Porensky, L. M. 2011. When edges meet: interacting edge effects in an African savanna. Journal of Ecology **99**:923-934.

Porensky, L. M. and T. P. Young. 2013. Edge-effect interactions in fragmented and patchy landscapes. Conservation Biology **27**:509-519.

R Development Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available at URL: http://www.R-project.org.

Ramalho, C. E., E. Laliberte, P. Poot, and R. J. Hobbs. 2014. Complex effects of fragmentation on remnant woodland plant communities of a rapidly urbanizing biodiversity hotspot. Ecology **95**:2466-2478.

Richter, D. D., D. Markewitz, P. R. Heine, V. Jin, J. Raikes, K. Tian, and C. G. Wells. 2000. Legacies of agriculture and forest regrowth in the nitrogen of old field soils. Forest Ecology and Management **138**:233-248.

Riitters, K. H., J. W. Coulston, and J. D. Wickham. 2012. Fragmentation of forest communities in the eastern United States. Forest Ecology and Management **263**:85-93.

Riutta, T., E. M. Slade, D. P. Bebber, M. E. Taylor, Y. Malhi, P. Riordan, D. W. Macdonald, and M. D. Morecroft. 2012. Experimental evidence for the interacting effects of forest edge, moisture and soil macrofauna on leaf litter decomposition. Soil Biology & Biochemistry **49**:124-131.

Schoenholtz, S. H., H. V. Miegroet, and J. A. Burger. 2000. A review of chemical and physical properties as indicators of forest soil quality: challenges and opportunities. Forest Ecology and Management **138**:335-356.

SCSCO. 2007. Historic climate data. South Carolina State Climate Office. http://www.dnr.sc.gov/climate/sco/ClimateData/sc_historical_climate_data.php.

Thijs, K. W., R. Aerts, W. Musila, M. Siljander, E. Matthysen, L. Lens, P. Pellikka, H. Gulinck, and B. Muys. 2014. Potential tree species extinction, colonization and recruitment in Afromontane forest relicts. Basic and Applied Ecology **15**:288-296.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature **371**:65-66.

USACE. 2013. Corps Lakes on the Savannah River.*in* S. D. US Army Corps of Engineers, editor. US Army Corps of Engineers.

USFS. 2016. USFS Fire Effects Information System. USFS.

Vranckx, G. U. Y., H. Jacquemyn, B. Muys, and O. Honnay. 2012. Meta-analysis of susceptibility of woody plants to loss of genetic diversity through habitat fragmentation. Conservation Biology **26**:228-237.

Watson, D. M. 2002. A conceptual framework for studying species composition in fragments, islands and other patchy ecosystems. Journal of Biogeography **29**:823-834.

Weakley, A. B. 2006. Flora of the Carolinas and Virginia. University of North Carolina, Chapel Hill, North Carolina.

Wilcox, B. A. and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. The American Naturalist **125**:879-887.

Wulder, M. A., J. C. White, M. E. Andrew, N. E. Seitz, and N. C. Coops. 2009. Forest fragmentation, structure, and age characteristics as a legacy of forest management. Forest Ecology and Management **258**:1938-1949.

Yates, E. D., D. F. Levia, and C. L. Williams. 2004. Recruitment of three non-native invasive plants into a fragmented forest in southern Illinois. Forest Ecology and Management **190**:119-130.

TABLES

Table 2.1. Frequency and mean stem density per 20-m^2 for the 75 species retained for community analysis in Lake Thurmond and Lake Russell on islands (239 plots) and mainland (75 plots) sites. Pioneer trees are indicated with the superscript “P” under growth form. Species found only in Lake Russell or Lake Thurmond are indicated with the superscripts “R” and “T” respectively.

Species	Frequency		Mean stem density per plot		Growth Form
	I	ML	I	ML	
Acer floridanum^R	0.004	0.05	0.003	0.12	Tree
Acer leucoderme^R	0.03	0.10	0.06	0.15	Tree
Acer rubrum	0.18	0.24	0.47	1.15	Tree^P
Albizia julibrissin^R	0.04	0	0.06	0	Non-native tree^P
Amelanchier arborea	0.06	0.01	0.08	0.01	Shrub
Aralia spinosa^T	0.04	0	0.12	0	Tree^P
Asimina triloba	0.02	0.03	0.03	0.03	Shrub
Baccharis halimifolia^T	0.04	0	0.08	0	Shrub
Berchemia scandens^T	0.02	0	0.03	0	Liana
Betula nigra	0.008	0	0.007	0	Tree
Bignonia capreolata	0.03	0	0.26	0	Liana
Callicarpa americana	0.03	0.01	0.03	0.03	Shrub
Campsis radicans	0.05	0.06	0.13	3.12	Liana
Carya alba	0.19	0.09	0.34	0.12	Tree
Carya glabra	0.24	0.33	0.34	0.67	Tree
Ceanothus americanus^T	0.02	0	0.03	0	Shrub
Celtis tenuifolia	0.06	0.01	0.15	0.01	Shrub
Cephalanthus occidentalis^T	0.004	0.04	0.02	0.11	Shrub
Cercis canadensis	0.08	0	0.15	0	Tree^P
Clinopodium georgianum	0.008	0.01	0.007	0.01	Sub-shrub
Cocculus caroliniana	0.04	0	0.13	0	Liana
Cornus florida	0.07	0.11	0.17	0.21	Tree
Crataegus sp. 1	0.04	0.03	0.05	0.03	Shrub

Crataegus sp. 2	0.14	0	0.23	0	Shrub
Diospyros virginiana	0.21	0.04	0.41	0.07	Tree
Elaeagnus pungens^{R}	0.03	0.01	0.24	0.01	Non-native shrub
Euonymus americanus	0.07	0.03	0.42	0.04	Shrub
Fraxinus americana	0.03	0.08	0.03	0.09	Tree
Gelsemium sempervirens	0.56	0.16	10.84	1.84	Liana
Hypericum hypericoides	0.08	0.05	0.13	0.25	Sub-shrub
Ilex decidua	0.03	0.01	0.22	0.01	Shrub
Ilex opaca	0.03	0.01	0.03	0.01	Tree
Juniperus virginiana	0.53	0.21	2.07	0.44	Tree^{P}
Liquidambar styraciflua	0.31	0.31	1.24	1.51	Tree
Lonicera japonica	0.33	0.13	3.03	0.52	Non-native liana
Lonicera sempervirens	0.08	0	0.18	0	Liana
Matelea carolinensis	0	0.03	0	0.45	Liana
Morus rubra^{R}	0.03	0.01	0.04	0.01	Tree^{P}
Myrica cerifera^{T}	0.09	0.01	0.60	0.01	Shrub
Nyssa sylvatica	0.09	0.05	0.31	0.07	Tree
Ostrya virginiana	0.12	0.19	0.52	0.52	Tree
Oxydendrum arboreum^{R}	0.02	0.03	0.10	0.03	Tree
Parthenocissus quinquefolia	0.04	0.03	0.10	0.04	Liana
Passiflora incarnata^{R}	0.01	0	0.02	0	Liana
Pinus echinata	0.19	0.01	0.36	0.01	Tree^{P}
Pinus taeda	0.36	0.29	1.37	0.53	Tree^{P}
Pinus virginiana	0.05	0	0.08	0	Tree^{P}
Prunus serotina	0.21	0.03	0.42	0.04	Tree^{P}
Prunus umbellata	0.04	0	0.14	0	Tree
Quercus alba	0.13	0.19	0.18	0.35	Tree
Quercus falcata	0.09	0.01	0.10	0.01	Tree
Quercus marilandica^{R}	0.01	0.01	0.02	0.01	Tree
Quercus nigra	0.27	0.09	0.54	0.27	Tree
Quercus phellos	0.07	0.08	0.11	0.09	Tree
Quercua rubra	0.02	0.07	0.03	0.12	Tree
Quercus stellata	0.24	0.17	0.54	0.27	Tree
Quercus velutina	0.15	0.11	0.23	0.20	Tree
Rhus copallina	0.13	0.01	0.33	0.01	Tree^{P}
Rhus glabra	0.03	0	0.04	0	Tree^{P}
Rubus argutus	0.06	0.01	0.39	0.07	Liana
Sassafras albidum	0.02	0	0.03	0	Tree^{P}
Smilax bona-nox	0.38	0.17	1.72	0.69	Liana

Smilax glauca	0.40	0.09	1.65	0.12	Liana
Smilax rotundifolia	0.04	0.03	0.15	0.03	Liana
Smilax smallii[T]	0.03	0.01	0.10	0.08	Liana
Toxicodendron radicans	0.10	0.05	0.28	0.07	Liana
Ulmus alata	0.56	0.32	3.08	0.70	Tree[P]
Ulmus rubra[R]	0.008	0.01	0.007	0.01	Tree
Vaccinium arboreum	0.18	0.09	0.99	0.25	Shrub
Vaccinium elliottii	0.19	0.10	0.79	0.24	Shrub
Vaccinium pallidum	0.13	0.02	0.40	0.03	Sub-shrub
Vaccinium stamineum[T]	0.02	0	0.08	0	Shrub
Viburnum prunifolium	0.05	0.01	0.29	0.01	Shrub
Viburnum rufidulum[T]	0.02	0	0.10	0	Shrub
Vitis rotundifolia	0.41	0.61	1.72	5.04	Liana

Table 2.2. General linear mixed effects model results for fixed effects of site type (island or mainland) and distance from edge on individual density for all species, lianas, shrubs, pioneer trees, and the non-native liana *Lonicera japonica*, as well as for total species richness. Significant effects ($p < 0.05$) are in bold font.

Source	All species		Lianas		Shrubs		Pioneer trees		*Lonicera japonica*		Species richness	
	z	*p*	*z*	*p*	*z*	*p*	*z*	*p*	*z*	*p*	*z*	*p*
Type	-3.11	**<0.001**	-1.87	0.06	-3.64	**<0.001**	-3.98	**<0.001**	-2.33	**0.02**	-2.96	**0.003**
Distance	-6.19	**<0.001**	-9.36	**<0.001**	2.82	**0.004**	-0.70	0.48	-0.70	0.48	0.91	0.36
T*D	-2.64	**<0.001**	2.09	**0.03**	-1.70	0.09	-1.28	0.20	-1.28	0.20	-2.44	**0.01**

Table 2.3. Results of linear mixed effects models for effects of site type (island or mainland) and distance from edge on litter mass, basal area, canopy height, soil pH, and percentage of canopy openness. Significant effects ($p < 0.05$) are in bold.

Source	Litter mass (g)		Basal area (m^2 $plot^{-1}$)		Canopy height (m)		Soil pH		% canopy openness	
	t	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*
Type (T)	-1.06	0.29	-0.39	0.69	0.26	0.79	-0.30	0.76	-1.13	0.27
Distance (D)	4.41	**<0.001**	0.85	0.39	2.67	**0.003**	2.31	**0.02**	-2.50	**0.01**
T*D	-2.33	**0.02**	1.29	0.20	0.90	0.37	0.97	0.97	0.43	0.66

Table 2.4. Multiple response permutation procedure (MRPP) results for differences between woody and semi-woody plant species composition on Lake Russell and Lake Thurmond islands and mainland sites. Relative Sørensen (Bray-Curtis) distance was used on a matrix of species abundance data for each site. The test statistic (*T*) and the chance-corrected within group agreement (*A*) are presented for each analysis. We applied the Bonferroni correction for multiple comparisons and set $\alpha = 0.008$ for this analysis.

Lake	Site type	Average within group distance	*T*	*A*	*p*
Lake Russell	Mainland	0.56	-0.96	0.02	0.16
Lake Thurmond	Mainland	0.77			
Lake Russell	Island	0.67	-4.22	0.03	**0.002**
Lake Thurmond	Island	0.64			
Lake Russell	Island		-4.74	0.04	**<0.001**
Lake Thurmond	Mainland				
Lake Thurmond	Island		-6.96	0.11	**<0.001**
Lake Russell	Mainland				
Lake Russell	Island		-6.69	0.05	**<0.001**
Lake Russell	Mainland				
Lake Thurmond	Island		-3.22	0.04	**0.007**
Lake Thurmond	Mainland				

Table 2.5. Species identified as significant indicator species ($p < 0.10$) for each site type (island or mainland) and their Pearson correlations (r) with NMS axes in Figure 1. Correlations greater than ± 0.400 are indicated in bold font.

Site Type	Species	Axis 1	Axis 2	Axis 3
Island	*Cratageous* sp. 2*	-0.262	-0.383	0.076
	Diospyros virginiana	**-0.414**	-0.244	-0.221
	Gelsemium sempervirens	-0.384	**-0.423**	**-0.629**
	Juniperus virginiana	**-0.469**	-0.240	-0.235
	Lonicera japonica	**-0.500**	-0.279	0.115
	Pinus echinata	-0.228	-0.210	-0.042
	Prunus serotina	-0.378	-0.171	-0.287
	Quercus nigra	0.098	-0.297	0.087
	Rhus copallina	-0.173	-0.143	0.129
	Smilax bona-nox	**-0.500**	-0.202	-0.387
	Smilax glauca	**-0.447**	-0.259	-0.169
	Ulmus alata	-0.042	**-0.455**	0.018
Mainland	*Acer floridanum*	0.131	0.273	-0.048
	Acer rubrum	0.007	0.231	-0.262
	*Matelea carolinensis**	-0.045	0.060	0.020
	Quercus rubra	0.103	0.296	-0.254
	Vitis rotundifolia	-0.107	**0.648**	-0.199

*Species that occurred only in a single site type.

Table 2.6. Multiple response permutation procedure (MRPP) results for differences between overstory (≥ 5 cm DBH), understory (≥ 50 cm HT and < 5 cm DBH), and seedling (≥ 10 cm and < 50 cm HT) woody and semi-woody plant species composition on Lake Russell islands and mainland sites. Relative Sørensen (Bray-Curtis) distance was used on a matrix of species abundance data for each forest layer. The overall test was significant (T = -13.16, A = 0.15, p < 0.001). The test statistic (T) and the chance-corrected within group agreement (A) are presented for each analysis. We applied the Bonferroni correction for multiple comparisons and set α = 0.005 for this analysis. DBH = diameter at breast height. HT = height (or length in the case of lianas).

Within forest layer	Site type	Average within group distance	*T*	*A*	*p*
Overstory	Island Mainland	0.66 0.66	-2.93	0.07	0.015
Understory	Island Mainland	0.64 0.57	-5.22	0.08	**<0.001**
Seedlings	Island Mainland	0.77 0.54	-4.57	0.07	**<0.001**
Within site type			*T*	*A*	*p*
Overstory *Understory*	Island		-5.34	0.07	**<0.001**
Overstory *Seedlings*	Island		-8.63	0.11	**<0.001**
Understory *Seedlings*	Island		-3.89	0.04	**0.002**

Overstory *Understory*	Mainland	-3.19	0.08	**0.003**
Overstory *Seedlings*	Mainland	-4.25	0.14	**0.002**
Understory *Seedlings*	Mainland	-3.17	0.09	**0.007**

Table 2.7. Species identified as significant indicator species ($p < 0.10$) for each site type (island or mainland) within each forest layer (overstory, understory, seedlings) using indicator species analysis (McCune and Grace 2002), and their Pearson correlations (r) with NMS axes in Fig. 2.7. Correlations greater than 0.5 are indicated in bold. DBH = diameter at breast height. HT = height (or length in the case of lianas).

Forest Layer and Site Type	Species	Axis 1	Axis 2	Axis 3
Overstory (> 5 cm DBH)				
Island	*Juniperus virginiana*	**0.626**	0.157	0.292
	Pinus echinata	0.076	**0.583**	-0.004
	Quercus nigra	0.158	0.439	0.346
Mainland	*Acer floridanum*	-0.395	-0.384	-0.040
	Acer leucoderme	**-0.569**	-0.376	0.339
	Acer rubrum	**-0.506**	**-0.542**	0.208
	Carya alba	**-0.554**	**-0.509**	0.117
	*Carya ovata**	-0.449	-0.129	-0.102
	Fagus grandifolia	-0.441	**-0.580**	0.175
	Fraxinus americana	0.004	-0.291	-0.182
	Liriodendron tulipifera	**-0.725**	-0.446	0.337
	Ostrya virginiana	-0.435	-0.135	0.318
	Quercus alba	**-0.592**	-0.486	0.055
Understory (> 50 cm HT to 5 cm DBH)				
Island	*Cratageous sp. 2*	0.224	**-0.698**	0.272
	Gelsemium sempervirons	0.105	-0.050	0.477
	Juniperus virginiana	-0.009	0.391	0.354
Mainland	*Acer floridanum**	0.087	0.191	-0.217
	Cornus florida	-0.342	-0.128	**-0.692**
	Liquidambar styraciflua	0.127	-0.142	**-0.692**
	Matelea carolinensis	0.082	0.052	-0.223
	Ostrya virginiana	-0.013	0.006	**-0.581**

	Quercus alba	-0.392	0.238	-0.363
	Toxicodenron radicans	-0.142	0.181	-0.339
	Viburnum prunifolium	0.070	0.206	-0.097
Seedlings (10-50 cm HT)				
Island	None			
Mainland	*Acer floridanum*			
	Acer rubrum	-0.165	0.067	**-0.580**
	*Bignonia capreolata**	0.146	0.132	-0.392
	Carya alba	-0.195	-0.003	**-0.547**
	*Carya glabra**	0.042	0.110	-0.485
	Dioscorea villosa	0.230	0.126	-0.286
	Fraxinus americana	0.213	0.121	-0.226
	Nyssa sylvatica	-0.229	-0.029	**-0.604**
	*Ostrya virginiana**	-0.038	0.122	-0.416
	*Parthenocissus quinquefolia**	0.273	0.135	-0.252
	*Quercus alba**	-0.244	0.107	**-0.562**
	Quercus rubra	0.089	0.074	**-0.557**
	Quercus velutina	0.003	0.023	-0.370
	Smilax glauca	-0.310	-0.105	**-0.802**
	Toxicodenron radicans	0.043	0.090	-0.301
	Vitis rotundifolia	-0.053	-0.056	**-0.752**

*Species that occurred only in a single site type.

Table 2.8. Pearson correlations (*r*) between mean values for percentage of canopy openness and soil pH for each forested island and mainland forest site with NMS axes for each forest layer. Numbers in "( )" are the percent variation explained by the axis. Correlations greater than 0.5 are indicated in bold.

Forest layer and NMS axis	% canopy openness	Soil pH
Overstory (> 5 cm DBH)		
Axis 1 (37.9)	0.472	**0.512**
Axis 2 (33.9)	0.435	-0.492
Axis 3 (15.0)	-0.390	0.109
Understory (> 50 cm HT to 5 cm DBH)		
Axis 1 (5.5)	0.333	-0.156
Axis 2 (24.8)	-0.005	**0.747**
Axis 3 (59.5)	**0.625**	0.094
Seedlings (10-50 cm HT)		
Axis 1 (14.1)	-0.240	**0.575**
Axis 2 (34.6)	0.270	0.278
Axis 3 (37.4)	**0.540**	0.288

FIGURES

Fig. 2.1. Aerial photographs with the location of islands and mainland sites in Lake Russell (left) and Lake Thurmond (right) along the border of South Carolina and Georgia. Island sizes and mainland sites are indicated by the following symbols: islands 0.08 - 0.43 ha = Δ, islands 0.56 - 0.88 ha = O, islands 1.03 - 2.47 ha = ×, and mainland sites = ▭ . Please note that symbols are much larger than actual sites in order to illustrate site position at this scale.

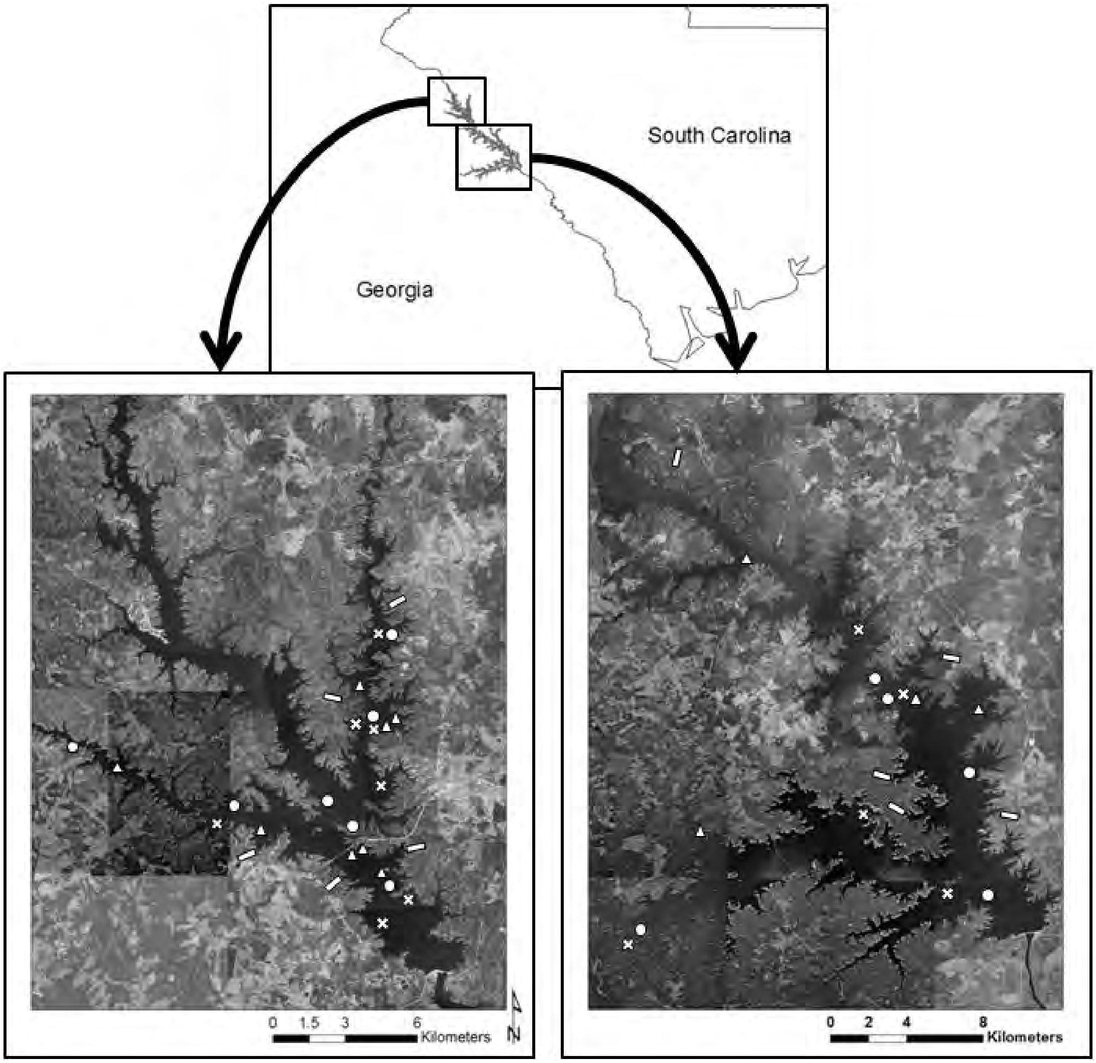


Fig. 2.2. Predicted number of individuals per 20-m^2 plot for (A) all species together, (B) lianas, (C) shrubs, (D) pioneer trees, (E) the non-native liana *Lonicera japonica*, and (F) species richness on island and mainland sites in Lake Russell and Lake Thurmond. Grey shading indicates the 95% confidence interval around each predicted line. Significant model effects for site type (T) and distance from edge (D), or their interaction (T*D) are indicated in bold font for each panel where appropriate (Table 2.4).

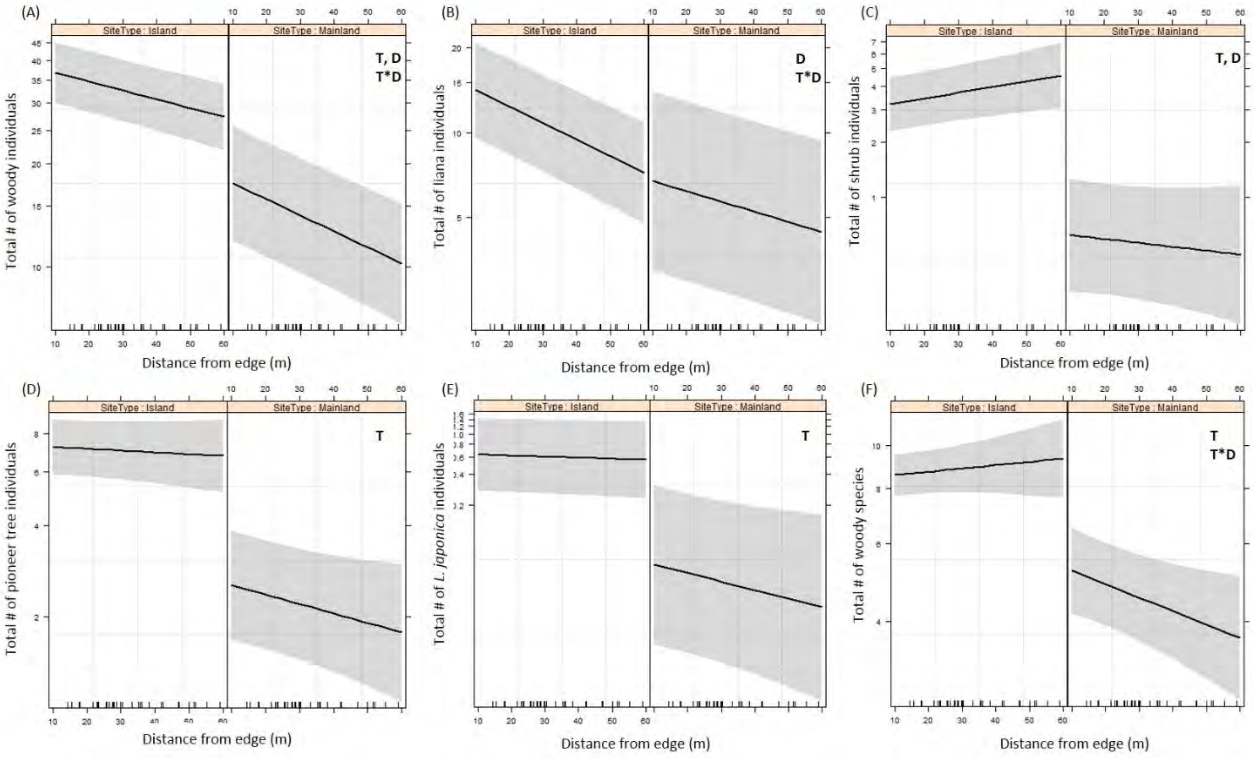


Fig. 2.3. Predicted (A) litter mass, (B) basal area, (C) canopy height, (D) soil pH, and (E) percent canopy openness on island and mainland sites in Lake Russell and Lake Thurmond. Grey shading indicates the 95% confidence interval around each predicted line. Significant model effects for site type (T) and distance from edge (D), or their interaction (T*D) are indicated in bold for each panel where appropriate (Table 2.5).

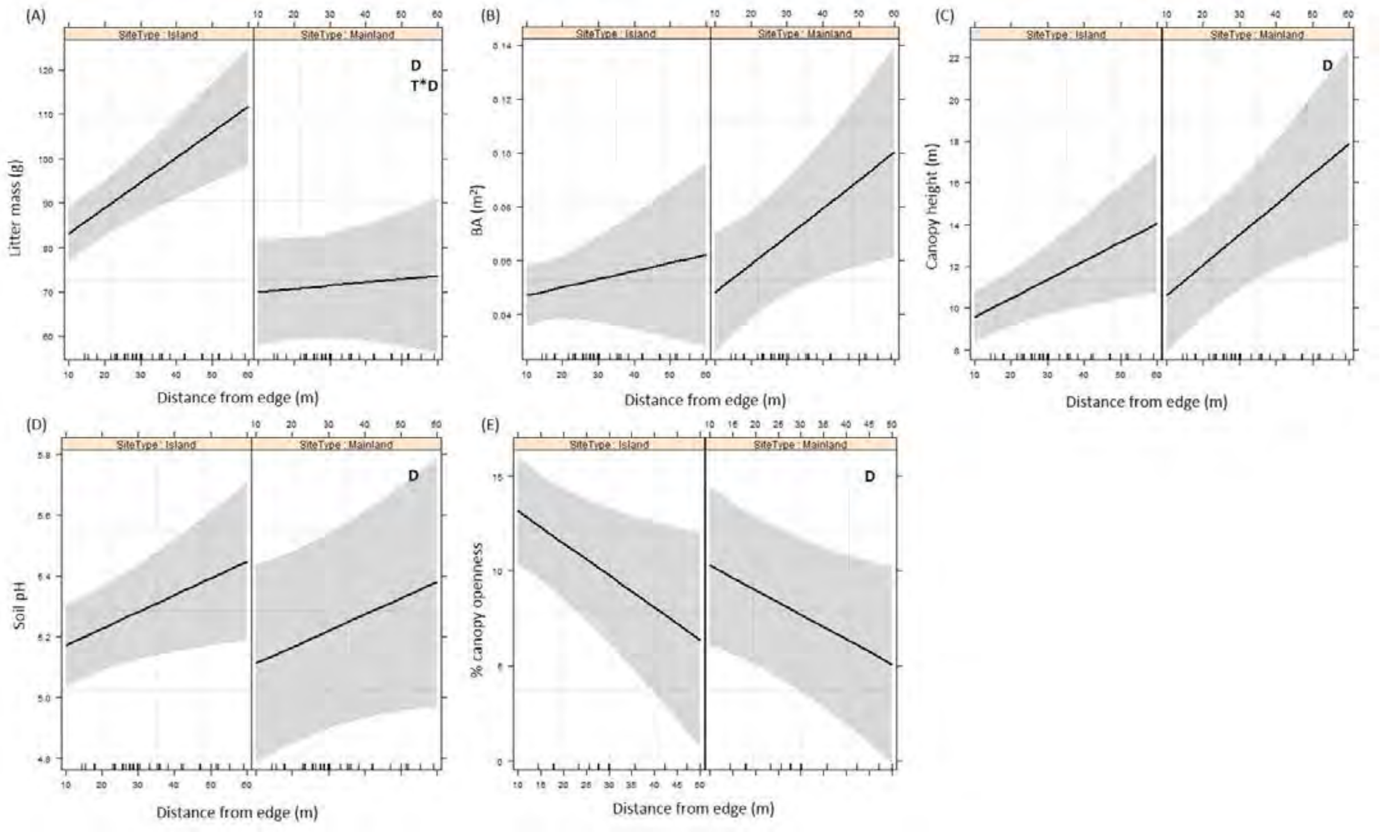


Fig. 2.4. NMS using relative Sørensen (Bray-Curtis) distance measure on a matrix of the 75 species that occurred in more than 15 of the 20-m^2 plots in Lake Russell and Lake Thurmond (stress =13.9, total variation explained = 80.7%). Species with significant Pearson correlations (*r* > ± 0.4) with NMS axes are indicated on the appropriate positive or negative axes, respectively. Islands and mainland sites are represented by grey circles and black squares, respectively.

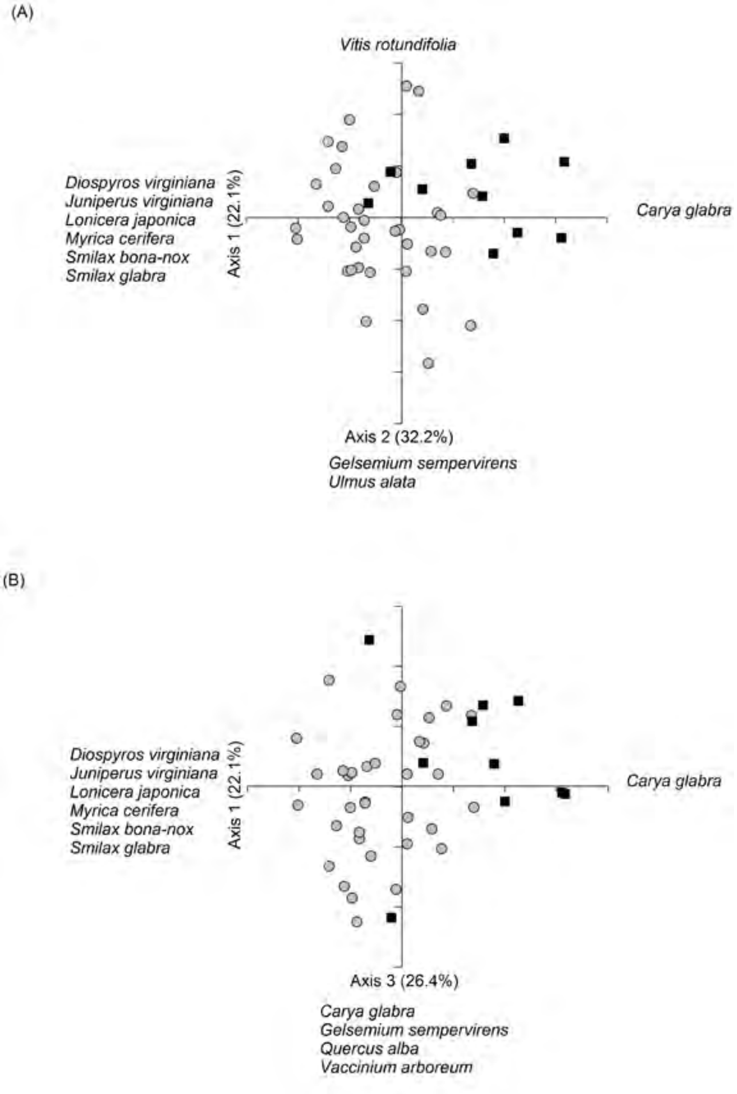
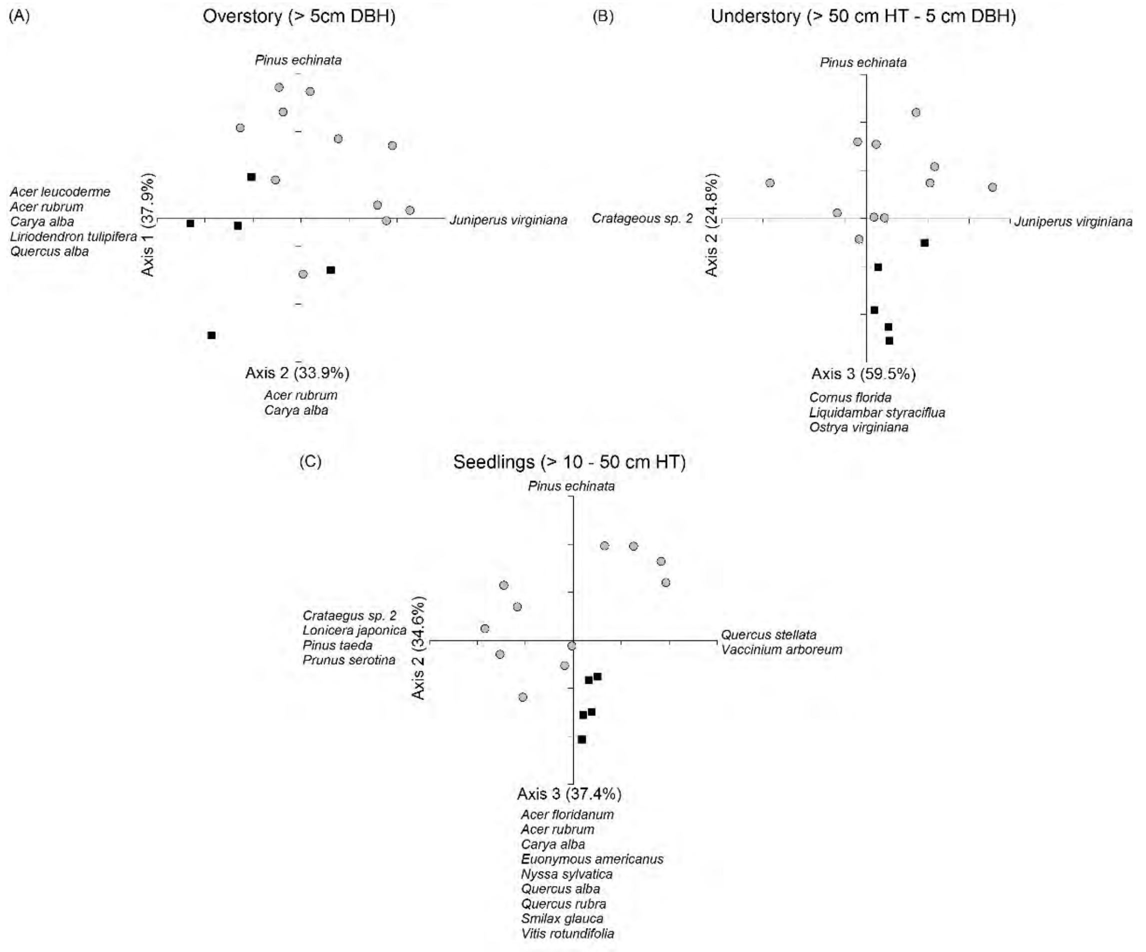


Fig. 2.5. NMS using the relative Sørensen (Bray-Curtis) distance measure for all species that were sampled in the (A) overstory (> 5 cm DBH; stress =6.94, total variation explained = 86.8%), (B) understory (>50 cm HT and <5 cm DBH; stress =8.97, total variation explained = 89.8%), and (C) seedlings (10 – 50 cm HT; stress =9.52, total variation explained = 86.4%) in the subset of 11 islands and the 5 mainlands sites in Lake Russell. Species with significant Pearson correlations (*r* > ± 0.5) with NMS axes are indicated on the appropriate positive or negative axes, respectively. Islands and mainland sites are represented by grey circles and black squares, respectively. DBH = diameter at breast height. HT = height (or length in the case of lianas).



CHAPTER 3

INVASIVENESS OF TWO NON-NATIVE WOODY SPECIES IN SOUTHEASTERN US FOREST FRAGMENTS

INTRODUCTION

Habitat fragmentation and species invasions have been cited as two of the most important drivers of biodiversity loss and ecosystem degradation (Mack et al. 2000, Pimentel et al. 2000, Flory and Clay 2009). These two factors may act not only independently but also synergistically, as species invasions often are associated with habitat fragmentation. In particular, many non-native, invasive plant species tend to proliferate on edges of forest fragments (Harper et al. 2005, Flory and Clay 2006, Vilà and Ibáñez 2011). However, we do not yet fully understand whether they occur primarily on forest edges simply because their propagules have not dispersed to interior forest (i.e., dispersal limitation) or because they cannot establish, survive, and grow under the environmental conditions typically associated with undisturbed interior forest (i.e., environmental limitation).

The question of whether non-native plant species are primarily dispersal or environmentally limited is a basic one in community ecology and has important implications for invasive species management and conservation. If dispersal limitation (Tilman 1997) is the only reason non-native species are found on fragment edges, only sufficient propagule pressure would be needed for invasion of undisturbed interior forest and invasive species should eventually take hold within interior forest. Non-native plant species that are commonly dispersed by wind, or by organisms known to make use of edge and interior forest habitat, will likely be dispersed from edges to interior forest sites on a relatively short timescale. In contrast, non-native species that are gravity dispersed will travel only centimeters to meters from the reproductive plant (Vittoz and Engler 2008) and might take decades or centuries to invade forest interior even if they are well suited to the environmental conditions present. If non-native plant species can grow and reproduce in environmental conditions typical of intact forest interior, then management of plant invasions would need to focus on removing propagule sources. Environmental limitation could also restrict non-native species to forest edges because they may not have the ability to germinate and proliferate under the environmental conditions typically associated with interior forest. If environmental limitation controls non-native species occurrence in forest interiors, then management could simply concentrate on preservation of interior forest conditions, which is potentially a less expensive option than eradication of propagule sources.

Two species that are common non-native, woody invaders of forest fragments in the southeastern United States (US) are *Albizia julibrissin* Durazz. (Fabaceae, mimosa/silk tree) and *Lonicera japonica* Thunb. (Caprifoliaceae, Japanese honeysuckle) (Schierenbeck 2004, Chang et al. 2011). Both species are listed as “severe threats to the structure and functioning of native habitats” in South Carolina (Clemson Universty Cooperative Extension 2009), and as “invasive species of concern” in Georgia (Evans et al. 2006).

Albizia julibrissin is a small to medium-sized tree native to Asia and it is thought to have been initially introduced to the southeastern US for horticultural purposes by way of Andre Michaux's Charleston, South Carolina nursery in 1785 (Cothran 2004). This species appears to have been offered for sale in catalogues as early as 1808 and was found to be naturalized in South Carolina forests in 1976 (Gettman 1976). We do not know of any studies that document the ecological impacts of *A. julibrissin* invasion, but anecdotal accounts of negative impacts on native plant communities are common in regional guides to invasive flora (USFS 2016). Despite its listing as an invasive species in Kentucky, Tennessee, South Carolina, Georgia, Alabama, and Florida (Bargeron et al. 2008), *A. julibrissin* is still sold online and at nurseries across the US. This species is also being actively investigated as a potential agroforestry species to be used as animal fodder in the Coastal Plain of the southeastern US (Pitman 2008, Yiakoulaki et al. 2014), with Yiakoulaki et al. (2014) stating "mimosa trees in pastures can enhance the nutritive value of diet of suckling goat kids consuming forage of low to moderate nutritive value." In an observational study, we found that *A. julibrissin* only occurred in plots located on small (< 0.6 ha) forested reservoir islands located along the South Carolina-Georgia border of the southeastern US (Chapter 2; Table 2.1) and was sometimes observed along the shoreline of mainland forest (D. Zoellner, *personal observation*). Overall, it was not an abundant component of vegetation on forested reservoir islands and was completely lacking in sampled mainland forest sites. In Illinois, it also appears to primarily occur in open sites and forest edges (McClain et al. 2012).

Lonicera japonica, a semi-evergreen liana, was introduced to the southeastern US in the 1800s for ornamental gardening and was historically planted in natural areas for deer browse (Blair 1982, Schierenbeck 2004). This liana is known to be particularly abundant in small forest fragments, along the edges of large fragments, and in disturbed areas (Merriam 2003, Yates et al. 2004, Honu and Gibson 2006). *Lonicera japonica* can reduce species diversity in oak-hickory forest (Davison and Richard 1982); negatively impact the occurrence of particular herbaceous plant species as succession proceeds in old fields (Myster and Pickett 1992); and have significant negative effects on photosynthetic rates, nitrogen use, and biomass allocation on a common native host tree, *Liquidambar styraciflua* L. (Hamamelidaceae, sweet gum) (Dillenburg et al. 1993a, b). We found *L. japonica* to be the third most abundant species on forested reservoir islands, and it was most abundant within 30 m of island edges (Chapter 2). Although *L. japonica* appears to be somewhat shade-tolerant (Blair 1982, Baars and Kelly 1996, Schierenbeck 2004), it is unclear whether this species can survive and reproduce over the long-term in the environmental conditions associated with undisturbed forest interior.

The level of leaf herbivory on both of these species may be quite low if natural enemies are less abundant or have less effect on *A. julibrissin* and *L. japonica* compared to native species, as is hypothesized by the Enemy Release Hypothesis (Keane and Crawley 2002). Although *A. julibrissin* has been in North America since the late 1700s, we could not find any published studies quantifying the level of leaf herbivory on this species. In contrast, *L. japonica* has been demonstrated to have significantly lower rates of leaf herbivory, and a larger compensatory growth response to leaf herbivory, when compared to its native congener *L. sempervirens* L. (Caprifoliaceae, coral honeysuckle; Schierenbeck et al. 1994). Herbivore damage may also be influenced by fragment size and proximity to forest fragment edges as generalist herbivores are thought to thrive in forest edges due to favorable microenvironmental conditions and edge-induced increases in food quality and quantity (Wirth et al. 2008). However, like many other abiotic and biotic properties measured in forest fragments, levels of leaf herbivory do not appear to be consistently higher or lower in edges or interiors of fragments, or when fragments are compared to non-fragmented forest (Rao et al. 2001, Benítez-Malvido et al. 2005, Ibáñez et al. 2014).

Several studies have found that species restricted to edges are correlated with environmental factors that differ between forest edges and interior (Flory and Clay 2006, Honu and Gibson 2006, Fridley et al. 2009), but these studies are observational and do not adequately address whether the observed pattern is due to dispersal or environmental limitation. To address this pattern, experiments that transplant species in the edges and interiors of small forest fragments and edges and interiors of large remnant forest, and also couple plant performance measures with habitat and environmental measures will help give insight to whether non-native species can be expected to invade interior forest.

Here we use this type of outplant experiment to address the question of whether *A. julibrissin* and *L. japonica* will proliferate under interior forest conditions if dispersal and establishment barriers are overcome. Specifically, we tested whether seedlings of these species are environmentally limited, and as such, restricted to particular habitats in a forest-fragment landscape. We investigated survival, growth, and herbivore damage of outplanted seedlings on both forested islands and mainland forest sites because we wanted to determine whether the species performed similarly in small forest fragments with multiple edges (islands) versus large forests with only a single edge (mainland forest). Based on our previous observations and other studies (Schierenbeck and Marshall 1993), we predicted that *L. japonica* would have higher survival and growth on edges than interior forest sites, but would still survive in the shaded forest interior over the study period. We also predicted that *A. julibrissin* survival and growth would be highest on edges, but we expected that it would not grow and survive in forest interior because this species appears shade-intolerant (Koepke-Hill et al. 2012; Chapter 2). Determining whether *A. julibrissin* and *L. japonica* are primarily dispersal or environmentally limited will provide important insight on the management of these two non-native species by providing guidance on whether aggressive management of propagule sources is a worthwhile effort in order to control invasion of forest interior by these two species.

METHODS

Site description and selection

We located sites in and along Lake Richard B. Russell (Lake Russell), a reservoir that was created for hydroelectric power along the Savannah River between South Carolina and Georgia in 1984 (Chapter 2). Lake Russell is located in the Southeastern Piedmont physiographic region of the southeastern US and is characterized by rolling hills and poor soils that range from deep clays to exposed bedrock (Chapter 2; Richter et al. 2000, Fairchilds and Trettin 2006). Reservoir impoundment created forested islands by isolating forested hilltops from what was once contiguous forest. We confirmed that all sites selected for study were not logged immediately prior to impoundment and had never been inundated. Mean annual rainfall is 116.8 cm yr^{-1}, and average monthly temperature ranges from 9.4° to 23.9°C (SCSCO 2007).

We randomly selected a subset of nine forested islands that ranged in size from 0.12–2.47 ha, and used all five mainland forest sites that were previously sampled for woody plant species composition and forest structural variables between May and September of 2007 and 2008 (Fig. 3.1; Chapter 2). We planted seedlings in blocks located on the edge and interior of each forested island and mainland forest site selected for study.

Experimental outplanting

We collected seeds for both species from sites surrounding Lake Russell between October and December 2007. Seed pods were collected from eight individuals of *A. julibrissin*, and intact seeds were removed from dried pods and stored in brown paper envelopes at room temperature. Seeds were fully randomized and covered with 98°C water and allowed to sit in the water for a period of approximately 24 hours prior to planting (Fordham 1965, 1968). On 10 July 2008, we filled Cone-tainers™ (RLC7 – Stuewe and Sons, Corvallis, Oregon) to the top rim with a germination potting soil mix (Fafard Superfine Germinating Mix), and one *A. julibrissin* seed was placed approximately 1 cm below the soil surface of each container and then covered lightly with the germination potting soil mix.

Berries from 11 individuals of *L. japonica* were collected and seeds were extracted, cleaned, dried, and stored in brown paper envelopes at room temperature.

Lonicera japonica seeds were cold stratified at 5°C for 37 days and fully randomized prior to planting (Hidayati et al. 2000). On 7 July 2008, we filled Cone-tainers© (RLC7–Stuewe and Sons, Corvallis, Oregon) to the top rim with a germination potting soil mix (Fafard Superfine Germinating Mix), and three *L. japonica* seeds were sown on the surface of the soil of each container and then covered lightly with the germination potting soil mix. If more than one *L. japonica* seed germinated in a container, we haphazardly removed individuals so that there was only one individual per container.

All flats were placed in a growth chamber at 25°C under 24-hour full-spectrum florescent lighting for germination. Once > 90% of seeds had germinated, the light cycle was reduced to 16 hours of light and 8 hours of darkness. Plants were moved to an outdoor location at the Clemson University Greenhouse Complex in October 2008 to allow for acclimation to the local climate prior to outplanting in the field. All seedlings were planted in the field in mid-January 2009.

Outplanting blocks consisted of five replicate seedlings of each species planted 30 cm apart. One outplanting block mistakenly contained 6 individuals of *A. julibrissin* and 4 individuals of *L. japonica.* At all five mainland forest sites, we placed an outplanting block at 2 m ("edge" blocks) and another 50 m from the forest edge ("interior" blocks), each offset by 5 m to the left of the transect previously surveyed for vegetation composition (Chapter 2). On the nine forested islands, we placed an outplanting block at 2 m from the island edge (edge block), offset by 5 m to the left for each of two transects established in our previous study of vegetation composition (Fig. 3.2; Chapter 2). We also placed two outplanting blocks in the center of each forested island fragment spaced

10 m apart (interior blocks; Fig. 3.2). Each *L. japonica* was provided with a 1 m wooden dowel for climbing. In total, 231 *A. julibrissin* and 229 *L. japonica* individuals were outplanted in 46 outplanting blocks (5 mainland edge, 5 mainland interior, 18 island edge, 18 island interior). Outplants were surveyed approximately two weeks later for mortality, and two individuals were replaced. Initial height was measured immediately after planting, and it was not significantly different among outplanting blocks, treatments for site type (island or mainland), or position (edge or interior).

Following initial planting, outplants were surveyed at the beginning (May/June) and end (Oct/Nov) of each growing season in 2009, 2010, and 2011 for survival, plant height to the nearest cm, and leaf herbivory. For *L. japonica* individuals, we measured the length of all stems and then summed them for a single measure of that we call height here for simplicity. We quantified leaf herbivory by recording the total number of leaves, the number of leaves with signs of herbivory, and also a visual estimate of the percentage of herbivory on each leaf in 5% increments. We then used these measures to calculate two variables: the percentage of leaves with signs of herbivory and the average percentage of herbivore damage per leaf for each plant. Quantification of leaf herbivory was conducted by a single person (DCZ) to ensure consistency.

In November 2011, approximately three years after outplanting, we completed final measurements and harvested above-ground biomass by clipping stems at the soil surface for all living individuals. Harvested plants were dried at 60ºC until constant weight. Relative growth rates (RGR; mm mm^{-1} day^{-1}) were calculated using the difference between the natural log of the final height and the natural log of the initial height divided by the number of days between the first and last measurement on living plants. Following harvest for above-ground biomass, we ensured that all remaining below-ground plant parts were excavated and completely removed.

Habitat conditions and environmental variables

We characterized environmental conditions for edge and interior outplanting blocks by measuring canopy height, basal area, litter mass, light, soil moisture, various soil nutrient concentrations, air temperature, and vapor pressure deficit. Canopy height, basal area, and litter mass were measured in vegetation plots located adjacent to each outplanting block. Methods for measuring these variables can be found in Chapter 2. All other measurements were made in or adjacent to the outplanting blocks, and the methods are described below.

The percentage of canopy openness was quantified using digital hemispherical photography and the Nikon CoolPix 4500 camera with Nikon FC-E8 fisheye lens mounted and leveled 60 cm above the outplanting block for edge and mainland interior positions and between the blocks located at the center of each island for island interior positions. All photographs were taken before sunrise, after sunset, or on uniformly cloudy days to negate the impact of the solar disk on the calculation of percentage of canopy openness (Frazer et al. 2001). Images were imported into SideLook (Nobis and Hunziker 2005) and converted to pure black and white images before being analyzed for canopy openness using Gap Light Analyzer 2.0 (Frazer et al. 1999).

To determine soil moisture content, pH, and nutrient concentrations, we collected eight 2.54-cm diameter soil cores taken to a depth of 10 cm from 0.25-m^2 quadrats that were located within 1 m of each edge outplanting block or between the two interior blocks located at the center of each island. All soil samples were collected on 17 June 2010, approximately 24 hours following a rain event of approximately 2.5 cm of precipitation. These samples were homogenized prior to analysis. We determined soil moisture content gravimetrically using 10 g of wet soil that was dried at 60ºC until constant weight, and present soil moisture content as the percentage of wet soil mass that was attributed to water (Klute 1986). A higher soil moisture content generally indicates greater soil moisture retention and water holding capacity (Klute 1986). Remaining soil was placed in soil sample bags and submitted to Clemson Agricultural Extension Service for analysis of soil pH and extractable nutrients (P, K, Ca, Mg, Zn) using the Mehlich-1 extraction method and ICP analysis (see the Clemson Agricultural Services website for detailed soil analysis methods). All soil nutrient concentrations are expressed as kg ha^{-1}.

We measured air temperature and relative humidity on the five mainland forest sites and a random sub-set of five forested islands using LogTag© temperature and relative humidity loggers. Loggers were deployed within 50 cm of the outplanting blocks for edge blocks and the interior blocks of mainland sites, but we placed loggers between the two center outplanting blocks on island interiors. Loggers recorded temperature and relative humidity every 5 min from 30 August 2010 until 15 September 2010. We then calculated the five-day average maximum temperature and relative humidity for the period of 9-13 September 2010 as these were five consecutively cloud-free days at all sites. We used these temperature and relative humidity measurements to calculate the vapor pressure deficit (VPD) in kilopascals (kPa) for each outplanting block.

Data Analysis

We examined how survival for *A. julibrissin* and *L. japonica* differed between site types (T; mainland or island) and outplanting block positions (P; edge or interior) using a generalized linear mixed effects model with a binomial error distribution. We used a linear mixed effect model and a Gaussian error distribution to examine how the continuous variables of RGR, plant height, above-ground biomass, percentage of leaves with herbivory, and percentage of herbivore damage per leaf differed between site types and positions. For all plant performance measures, the fixed effects were site type and position, whereas site identity and outplanting block were designated as random effects to account for multiple outplanting blocks in a single site and multiple individuals within an outplanting block.

We analyzed the outplanting block-level measurements of canopy height, basal area, litter mass, percentage of canopy openness, percent soil moisture content, VPD, soil pH, and soil nutrients (P, K, Ca, Mg, and Zn) using linear mixed effects models with a Gaussian error distribution, fixed effects of site type and position, and the random effect of site identity. We then used Tukey's HSD post-hoc test for multiple comparisons when the T*P interaction was significant in order to examine differences among all site type and position combinations.

To explore how abiotic variables that were found to be significantly different between site types or positions were related to survival of individual plants (i.e., percentage of canopy openness, Mg concentration, and Zn concentration), we used hierarchical generalized linear mixed effects modeling with the binomial distribution and included site identity and outplanting block as random effects. We selected the best-fit model by comparing each model's Akaike information criterion corrected for finite sample sizes (AICc). The models with the lowest AICc values and a ΔAICc < 2.0 were considered to have the most support.

All analyses were conducted using R version 3.2.3 with the packages lme4 v. 1.1-11 and lmerTest v. 2.0-30 and the functions 'glmer' for survival, 'lmer' for environmental data and leaf herbivory, and 'lsmeans' for testing for differences among the four site and outplanting block locations when either the T, P, or T*P fixed effects were significant (R Development Core Team 2015). We used AICcmodavg v. 2.0-1 and the function 'aictab' to select the best fit model in our set of hierarchical models for survival (R Development Core Team 2015). The t-tests for function 'lmer' use Satterthwaite approximations to calculate degrees of freedom. Generalized linear mixed models invoked by 'glmer' are fit by maximum likelihood (Laplace approximation).

RESULTS

Environmental conditions

Overall, forested island and mainland forest sites were environmentally very similar (Tables 3.1 and 3.2). Only Mg concentrations were significantly higher on forested islands than mainland forest sites (Table 3.1). However, edges and interior positions differed significantly; edge positions had lower canopy height, less litter mass, greater canopy openness, and lower Zn concentration than interior positions (Tables 3.1 and 3.2; Fig. 3.2). The effect of position only differed by site type for canopy height, with the difference in canopy height between interior and edge positions being much more pronounced on mainland forest sites (Table 3.1; Fig. 3.2).

Outplant survival, growth and leaf herbivory

Overall, seedlings of *A. julibrissin* exhibited 79% mortality over the three-year study period, whereas *L. japonica* seedlings had only 65% mortality. Mortality occurred throughout the three years but was concentrated during the first sampling period specifically for *A. julibrissin* (Fig. 3.3). Survival and final biomass of *A. julibrissin* was greater on edges compared to interiors of both forested islands and mainland forest sites, but RGR and plant height of *A. julibrissin* did not differ by site type or position (Table 3.3; Fig. 3.4). *Lonicera japonica* survival and biomass did not differ among site types or outplanting block positions, but this species had lower RGR and plant height on edges of both mainland forest sites and forested islands (Table 3.3; Fig. 3.4). Lower RGR and plant height on edges was due to stem die-back, and outplants of *L. japonica* on edges were actually shorter at the end of the experiment than at the beginning (i.e., negative RGR).

Leaf herbivory on *L. japonica* was relatively low with an average of nearly 20% of leaves showing signs of herbivory, in contrast to *A. julibrissin* which had an overall average of 74% of leaves showing signs of herbivory. The percentage of leaves showing evidence of herbivory and the average percentage of herbivory per leaf on *A. julibrissin* were lower on mainland sites, but there were no differences between positions for these indicators of leaf herbivory (Table 3.3; Fig. 3.5). Leaf herbivory was extremely variable across the outplanting blocks. In addition, only four individuals of *A. julibrissin* survived to the end of the study period on mainland edges, and there was no evidence of leaf herbivory on them. Herbivore damage on *L. japonica* was similar between edges and interiors on mainland forest sites and forested islands (Table 3.3; Fig. 3.5).

Environmental variables impact on survival

The top two models explaining survivorship included species and canopy openness (Table 3.4). Of the abiotic environmental variables that differed between site types and positions (i.e., canopy openness, Mg, and Zn), only canopy openness had a significant effect on survival (Table 3.4). Predicted survival increased with increasing canopy openness for both species, but *L. japonica* had consistently higher predicted survival than *A. julibrissin* along the entire gradient of canopy openness (Fig. 3.6).

DISCUSSION

Environmental differences between edges and interiors of forests were apparent in our study system, but islands and mainland sites overall were similar. Edge sites generally had lower canopy height, less litter, and greater canopy openness. In addition, survival and growth of the two invasive species were only related to their position relative to the edge. Even though our fragments (small forested islands and remnant mainland forest) differed dramatically in size, each species responded similarly in both habitats.

In this three-year experimental outplanting study, we found that both *A. julibrissin* and *L. japonica* appear to be environmentally limited by low light levels associated with forest interior. Canopy openness in forest interior never exceeded 10%, and while the majority of outplants for both species did not survive under these light conditions, some interior outplanting blocks had one to three individuals that survived the entire duration of this study, indicating that they may also be partly dispersal limited in this system. This result is troublesome as new populations for some species may need only a single, or a few, individuals to begin invasion of a new habitat. Pardini and Hamrick (2008) observed that some of their study populations of *A. julibrissin* in Georgia, USA were founded by single individuals, which indicates that this is a possibility. Whether populations of *L. japonica* can be founded by just a single individual is unclear. Survival of both of these species in forest interiors over a period of nearly three years indicates that they may have the ability to invade relatively undisturbed forest interior if dispersal and establishment barriers are overcome. However, proliferation in the understory is unlikely to occur unless a canopy gap is created.

Albizia julibrissin

More than three-quarters of outplanted *A. julibrissin* seedlings died by the end of our study period and the bulk of mortality was concentrated in forested island interiors. In addition, survival of outplanted seedlings of *A. julibrissin* and canopy openness were positively related, indicating that forest fragments with higher light levels are likely to be more invasible by this species. Loewenstein and Loewenstein (2005) reported that *A. julibrissin* was found in riparian forests in 6 of the 15 watersheds they sampled. This non-native tree is considered a pioneer species both in its native (Okubo et al. 2005) and invasive range indicating that this species is likely rather shade-intolerant, but no studies to date have rigorously quantified this characteristic for *A. julibrissin*. Although we measured individuals over a longer period of time than any other study of this species to date, we cannot determine if the last of the surviving individuals in the lowest light conditions would ultimately have survived and become reproductive individuals in the future. As *A. julibrissin* is still continually introduced to the US landscape as a horticultural species, this species may then have the potential to invade shaded forest interior in the future, particularly if increased shade tolerance is selected for in horticultural varieties.

Despite relatively harsh conditions associated with drought during the study period (see below), biomass for *A. julibrissin* was greatest on edges. Plant height did not differ between outplanting block positions, and thus the greater biomass likely results from larger diameter stems or greater leaf mass on fragment edges. We conjecture that seedlings may have had greater height and RGR on forest fragment edges as well if there had not been a drought. Even in drought, it appears that *A. julibrissin* is able to cope with the hot and dry conditions frequently reported on forest fragment edges (Harper et al. 2005). Ares et al. (2009) investigated *A. julibrissin* for agroforestry applications and also found that this species appears to tolerate limited access to water and nutrients. Nevertheless, *A. julibrissin* is most likely to proliferate in forest fragments that have high soil moisture and light levels.

The mean percentage of leaves exhibiting signs of herbivory and the percent herbivory per leaf for *A. julibrissin* was significantly lower in mainland forest sites compared to forested island fragments. Potential herbivores may be concentrated in small, forest fragments, and therefore plants on islands may have been more easily detected by herbivores than in mainland forest sites where relatively few surviving individuals were spread among four of the five sites (Rossetti et al. 2014). Results from studies of leaf herbivory on plants in forest fragments are mixed with regard to how fragmentation impacts herbivory, with herbivory increasing or decreasing in forest fragments, or from edge to interior, compared to intact forest depending on the focal species examined (Ibáñez et al. 2014).

To our knowledge, our study is the first to quantify herbivore damage to leaves in *A. julibrissin*, which appears relatively high for a non-native species, signifying that this species has either acquired generalist leaf herbivores in its introduced range or leaf herbivores from its native range have migrated to the US. Indeed, three non-native insects that are specialists on *A. julibrissin* in its native range have been detected in this region within the last 10 years: the wood boring beetle *Agrilus subrobustus* Saunders; the seed predator beetle, *Bruchidius terrenus* (Sharp); and the psyllid *Acizza jamatonica* (Kuwayama) (Ulyshen and Miller 2007, Hoebeke et al. 2009). Therefore, herbivory may help mitigate establishment and proliferation of this species in forest fragments.

Lonicera japonica

Approximately a third of the outplanted *Lonicera japonica* seedlings survived until the end of the three-year experiment. Seedlings had a similar chance of survival no matter whether plots were located on islands or mainland sites, edges, or interiors. Although predicted survival increased as canopy openness increased, *L. japonica* mortality in outplanting blocks with less than 10% canopy openness was not complete (Fig. 3.6). If dispersal and germination barriers are overcome, *L. japonica* appears to tolerate canopy closure similar to that found in undisturbed forest interior, as has been found previously in a study of forest fragments in Illinois (Gehlhausen et al. 2000). Indeed, *L. japonica* can be found in forested understory, although typically at relatively low abundance (Chapter 2; Yates et al. 2004). Schierenbeck and Marshall (1993) found that *L. japonica* out-performed the native *L. sempervirens* with regard to photosynthetic rates and net carbon gain in secondary forest understory, and partially attributed this to the observation that *L. japonica* retains its old leaves as new leaves are forming. While photosynthetic rates are reduced during leaf turnover in this species, *L. japonica* does have the ability to take advantage of increased canopy openness during the winter months in deciduous forests (Schierenbeck and Marshall 1993). All of these attributes may combine to make this species effectively more shade tolerant than *A. julibrissin* and would explain why *L. japonica* showed no difference among site types or outplanting block position for survival or final aboveground biomass.

Relative growth rates for *L. japonica* were significantly affected by plot position but not in the way that we expected. Plants on edges of islands and mainland sites had lower (and even negative) RGR and achieved shorter heights than in forest interior locations. Many individuals in edge habitats suffered stem die-back and regrowth during the study period, and negative relative growth rates for *L. japonica* likely reflect harsh conditions associated with forest fragment edges during these drought years. Our study occurred during a period of time that was uncharacteristically dry in the region, with "abnormally dry" to "extreme" drought conditions for much of the growing season over the entire study period (NDMC 2013). It appears that forest interiors acted as a buffer against drought conditions and desiccation for *L. japonica*, which is in agreement with observational studies that have found *L. japonica* to be limited by insufficient soil moisture (Schierenbeck 2004). Had this study occurred during a period of time when precipitation was near normal levels, we may have observed a different trend, with RGR, height, and biomass elevated on edges compared to forest interior.

Leaf herbivory on *L. japonica* was relatively low compared to that of *A. julibrissin.* Schierenbeck at al. (1994) found that *L. japonica* had significantly lower rates of both insect and mammal herbivory than its native congener *L. sempervirens*.

Although *L. japonica* is more closely related to the native *L. sempervirens* than other native lianas, this native species of honeysuckle was not common in our study system (Chapter 2). It would be more informative to know how *L. japonica* fairs relative to other more common native liana species in the region, such as *Gelsemium sempervirens* (L.) W.T. Aiton (Loganiaceae, yellow jessamine). If herbivory is lower on *L. japonica* than native lianas, enemy release may partly explain why this species has become such a frequent and abundant member of edge and disturbed communities, and also appears in low densities in forest interior (Chapter 2; Merriam 2003, Beans et al. 2012).

Conclusion

Both of these species can still be acquired for horticultural purposes, and *A. julibrissin* is being actively investigated for agroforestry applications in the US. Though our study demonstrates that *L. japonica* has a higher potential to proliferate in forest interior compared to *A. julibrissin*, both species may invade interior forest particularly following disturbance events such as treefalls in forest interior. It will be imperative to fully evaluate their potential invasiveness at every life stage, including interior forest habitats.

Future studies investigating whether *A. julibrissin* and *L. japonica* have the ability to germinate and, in the long-term, reproduce under interior forest conditions would be valuable to fully address the threat of invasion by these two species for undisturbed intact forest interior. Since *L. japonica* survival was relatively high even in shaded forest interior, managers should certainly consider methods that will control propagule flow to forest interior (e.g., removal of nearby seed sources), while control of *A. julibrissin* can likely concentrate on limiting anthropogenic disturbance in forest interior. Large canopy disturbances are expected to stimulate the invasion for both of these species given adequate propagule pressure, and therefore the only way to ensure that these species do not invade forest fragments or intact forests is to remove seed sources.

REFERENCES

Ares, A., D. Burner, and D. Brauer. 2009. Soil phosphorus and water effects on growth, nutrient and carbohydrate concentrations, δ13C, and nodulation of mimosa (*Albizia julibrissin* Durz.) on a highly weathered soil. Agroforestry Systems **76**:317-325.

Baars, R. and D. Kelly. 1996. Survival and growth responses of native and introduced vines in New Zealand to light availability. New Zealand Journal of Botany **34**:389-400.

Bargeron, C. T., C. R. Minteer, C. W. Evans, D. J. Moorhead, G. K. Douce, and R. C. Reardon. 2008. Invasive Plants of the United States DVD-ROM: Identification, Biology and Control. USDA Forest Service. Pages FHTET-08-11 Forest Health Technology Enterprise Team, Morgantown, WV, USA.

Beans, C. M., F. F. Kilkenny, and L. F. Galloway. 2012. Climate suitability and human influences combined explain the range expansion of an invasive horticultural plant. Biological Invasions **14**:2067-2078.

Benítez-Malvido, J., M. Martínez-Ramos, J. L. C. Camargo, and I. D. K. Ferraz. 2005. Responses of seedling transplants to environmental variations in contrasting habitats of Central Amazonia. Journal of Tropical Ecology **21**:397-406.

Blair, R. M. 1982. Growth and non-structural carbohydrate content of southern browse species as influenced by light-intensity. Journal of Range Management **35**:756-760.

Chang, S. M., E. Gonzales, E. Pardini, and J. L. Hamrick. 2011. Encounters of old foes on a new battle ground for an invasive tree, *Albizia julibrissin* Durazz (Fabaceae). Biological Invasions **13**:1043-1053.

Clemson Universty Cooperative Extension. 2009. Invasive Plant Pest Species of South Carolina. Clemson Universty Cooperative Extension, Clemson, South Carolina, USA.

Cothran, J. R. 2004. Treasured Ornamentals of Southern Gardens – Michaux's Lasting Legacy. Castanea **69**:149-157.

Davison, S. E. and T. T. F. Richard. 1982. Herb and Shrub Dynamics in a Mature Oak Forest: A Thirty-Year Study. Bulletin of the Torrey Botanical Club **109**:64-73.

Dillenburg, L. R., D. F. Whigham, A. H. Teramura, and I. N. Forseth. 1993a. Effects of vine competition on the availability of light, water, and nitrogen to a tree host *Liquidambar styraciflua*. American Journal of Botany **80**:244-252.

Dillenburg, L. R., D. F. Whigham, A. H. Teramura, and I. N. Forseth. 1993b. Effects of below- and aboveground competition from the vines *Lonicera japonica* and

Parthenocissus quinquefolia on the growth of the tree host *Liquidambar styraciflua*. Oecologia **93**:48-54.

Evans, C. W., C. T. Bargeron, D. J. Moorehead, and G. K. Douce. 2006. Invasive Plants of Georgia's Forests: Identification and Control. Georgia Forestry Commission, University of Georgia, Athens, GA, USA.

Fairchilds, L. H. and C. C. Trettin. 2006. History and legacy of fire effects in the South Carolina piedmont and coastal regions. United States Department of Agriculture Forest Service, Southern Research Station, Asheville, North Carolina.

Flory, S. L. and K. Clay. 2006. Invasive shrub distribution varies with distance to roads and stand age in eastern deciduous forests in Indiana, USA. Plant Ecology **184**:131-141.

Flory, S. L. and K. Clay. 2009. Effects of roads and forest successional age on experimental plant invasions. Biological Conservation **142**:2531-2537.

Fordham, A. J. 1965. Germination of woody legume seeds with impermeable seed coats. Arnoldia **25**:1-8.

Fordham, A. J. 1968. Propagation of *Albizia julibrissin*. Arnoldia **28**:35-40.

Frazer, G. W., C. D. Canham, and K. P. Lertzman. 1999. Gap Light Analyzer (GLA): Users Manual and Program Documentation. Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.

Frazer, G. W., R. A. Fournier, J. A. Trofymow, and R. J. Hall. 2001. A comparison of digital and film fisheye photography for analysis of forest canopy structure and gap light transmission. Agricultural and Forest Meteorology **109**:249-263.

Fridley, J. D., A. R. Senft, and R. K. Peet. 2009. Vegetation structure of field margins and adjacent forests in agricultural landscapes of the North Carolina piedmont. Castanea **74**:327-339.

Gehlhausen, S. M., M. W. Schwartz, and C. K. Augspurger. 2000. Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. Plant Ecology **147**:21-35.

Gettman, R., W. 1976. Plants New to South Carolina and Oconee County, from the Andrew Pickens Division of Sumter National Forest. Castanea **41**:356-360.

Harper, K. A., S. E. MacDonald, P. J. Burton, J. Chen, K. D. Brosofske, S. C. Saunders, E. S. Euskirchen, D. Roberts, M. S. Jaiteh, and P.-A. Esseen. 2005. Edge influence on forest structure and composition in fragmented landscapes. Conservation Biology **19**:768-782.

Hidayati, S. N., J. M. Baskin, and C. C. Baskin. 2000. Dormancy-breaking and germination requirements of seeds of four *Lonicera* species (Caprifoliaceae) with underdeveloped spatulate embryos. Seed Science Research **10**:459-469.

Hoebeke, E. R., A. G. Wheeler, J. M. Kingsolver, and D. L. Stephan. 2009. First North American records of the east palearctic seed beetle *Bruchidius terrenus* (Coleoptera: Chrysomelidae: Bruchinae), a specialist on mimosa (*Albizia julibrissin*, Fabaceae). The Florida Entomologist **92**:434-440.

Honu, Y. A. K. and D. J. Gibson. 2006. Microhabitat factors and the distribution of exotic species across forest edges in temperate deciduous forest of southern Illinois, USA. Journal of the Torrey Botanical Society **133**:255-266.

Ibáñez, I., D. S. W. Katz, D. Peltier, S. M. Wolf, and B. T. C. Barrie. 2014. Assessing the integrated effects of landscape fragmentation on plants and plant communities: the challenge of multiprocess-multiresponse dynamics. Journal of Ecology **102**:882-895.

Keane, R. M. and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution **17**:164-170.

Klute, E. A. 1986. Methods of Soil Analysis: Part 1 - Physical and Mineralogical Methods. American Society of Agronomy-Soil Science Society of America, Madison, Wisconson, USA.

Koepke-Hill, R. M., G. R. Armel, J. T. Brosnan, G. K. Breeden, J. J. Vargas, and T. C. Mueller. 2012. Control of silk tree (*Albizia julibrissin*) with Aminocyclopyrachlor and other herbicides. Weed Science **60**:345-349.

Loewenstein, N. and E. Loewenstein. 2005. Non-native plants in the understory of riparian forests across a land use gradient in the Southeast. Urban Ecosystems **8**:79-91.

Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications **10**:689-710.

Merriam, R. W. 2003. The abundance, distribution and edge associations of six non-indigenous, harmful plants across North Carolina. Journal of the Torrey Botanical Society **130**:283-291.

Myster, R. W. and S. T. A. Pickett. 1992. Dynamics of associations between plants in 10 old fields during 31 years of succession. Journal of Ecology **80**:291-302.

National Drought Mitigation Center (NDMC). 2013. United States Drought Monitor. National Drought Mitigation Center (NDMC), the U.S. Department of Agriculture (USDA) and the National Oceanic and Atmospheric Association (NOAA). Available at URL: http://droughtmonitor.unl.edu/.

Nobis, M. and U. Hunziker. 2005. Automatic thresholding for hemispherical canopy-photographs based on edge detection. Agricultural and Forest Meteorology **128**:243-250.

Okubo, S., A. Kamiyama, Y. Kitagawa, S. Yamada, A. Palijon, and K. Takeuchi. 2005. Management and micro-scale landform determine the ground flora of secondary woodlands and their verges in the Tama Hills of Tokyo, Japan. Biodiversity and Conservation **14**:2137-2157.

Pardini, E. A. and J. L. Hamrick. 2008. Inferring recruitment history from spatial genetic structure within populations of the colonizing tree *Albizia julibrissin* (Fabaceae). Molecular Ecology **17**:2865-2879.

Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. Bioscience **50**:53-65.

Pitman, W. D. 2008. Establishment and regrowth responses of *Albizia julibrissin* on Louisiana USA coastal plain soils. Agroforestry Systems **74**:259-266.

R Development Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available at URL: http://www.R-project.org.

Rao, M., J. Terborgh, and P. Nunez. 2001. Increased herbivory in forest isolates: Implications for plant community structure and composition. Conservation Biology **15**:624-633.

Richter, D. D., D. Markewitz, P. R. Heine, V. Jin, J. Raikes, K. Tian, and C. G. Wells. 2000. Legacies of agriculture and forest regrowth in the nitrogen of old field soils. Forest Ecology and Management **138**:233-248.

Rossetti, M. R., E. Gonzalez, A. Salvo, and G. Valladares. 2014. Not all in the same boat: trends and mechanisms in herbivory responses to forest fragmentation differ among insect guilds. Arthropod-Plant Interactions **8**:593-603.

Schierenbeck, K. A. 2004. Japanese honeysuckle (*Lonicera japonica*) as an invasive species; history, ecology, and context. Critical Reviews in Plant Sciences **23**:391-400.

Schierenbeck, K. A., R. N. Mack, and R. R. Sharitz. 1994. Effects of herbivory on growth and biomass allocation in native and introduced species of *Lonicera*. Ecology **75**:1661-1672.

Schierenbeck, K. A. and J. D. Marshall. 1993. Seasonal and diurnal patterns of photosynthetic gas-exchange for *Lonicera sempervirens* and *L. japonica* (Caprifoliaceae). American Journal of Botany **80**:1292-1299.

SCSCO. 2007. Historic climate data. South Carolina State Climate Office. http://www.dnr.sc.gov/climate/sco/ClimateData/sc_historical_climate_data.php.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology **78**:81-92.

Ulyshen, M. D. and D. R. Miller. 2007. First record of *Acizzia jamatonica* (Hemiptera: Psyllidae) in North America: Friend or foe? The Florida Entomologist **90**:573-573.

USFS. 2016. USFS Fire Effects Information System. USFS.

Vilà, M. and I. Ibáñez. 2011. Plant invasions in the landscape. Landscape Ecology **26**:461-472.

Vittoz, P. and R. Engler. 2008. Seed dispersal distances: a typology based on dispersal modes and plant traits. Botanica Helvetica **117**:109-124.

Wirth, R., S. T. Meyer, I. R. Leal, and M. Tabarelli. 2008. Plant herbivore interactions at the forest edge. Pages 423-448 *in* U. Lüttge, W. Beyschlag, and J. Murata, editors. Progress in Botany. Springer-Verlag, Berlin, Germany.

Yates, E. D., D. F. Levia, and C. L. Williams. 2004. Recruitment of three non-native invasive plants into a fragmented forest in southern Illinois. Forest Ecology and Management **190**:119-130.

Yiakoulaki, M. D., A. L. Goetsch, G. D. Detweiler, and T. Sahlu. 2014. Effects of creep grazing and stocking rate on forage selection and nutritive value of the diet for meat goat does and kids on grass/forb pasture. Small Ruminant Research **117**:119-123.

TABLES

Table 3.1. Linear mixed model results for the effects of site type (T; island or mainland) and outplanting block position (P; edge or interior) on canopy height, basal area, litter, percentage of canopy openness, soil moisture content expressed as a percentage of dry soil mass, and vapor pressure deficit (VPD).

Source	Canopy height (m)		Basal area (m^2 $plot^{-1}$)		Litter (g)		% canopy openness		% soil moisture		VPD (pKa)	
	t	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*
Type	-0.73	0.47	-0.24	0.81	-0.42	0.68	-1.22	0.23	1.62	0.10	-1.52	0.14
Position	2.46	**0.02**	1.56	0.13	2.43	**0.02**	-3.70	<**0.01**	1.57	0.13	-1.29	0.21
T*P	2.61	**0.02**	-0.91	0.37	-1.23	0.23	0.90	0.38	-1.12	0.28	0.48	0.63

Table 3.2. Linear mixed effect model results for the fixed effects of site type (T; island or mainland) and outplanting block position (P; edge or interior) on soil pH and concentrations of P, K, Ca, Mg, and Zn. Means (± SE) for each treatment combination are also presented (ME = mainland edge, MI = mainland interior, IE = island edge, II = island interior).

Source	Soil pH		P (kg ha^{-1})		K (kg ha^{-1})		Ca (kg ha^{-1})		Mg (kg ha^{-1})		Zn (kg ha^{-1})	
	t	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*
Type	-0.95	0.35	-1.49	0.15	0.08	0.93	-1.76	0.09	-2.17	**0.04**	-0.79	0.43
Position	1.40	0.17	-0.82	0.42	-0.55	0.58	0.63	0.53	-0.65	0.52	3.16	**<0.01**
T*P	0.47	0.64	0.70	0.49	0.59	0.56	1.14	0.26	1.59	0.12	-0.34	0.74
ME	4.86 (0.15)		7.39 (0.57)		97.44 (27.25)		597.63 (143.16)		169.79 (33.97)		3.05 (0.42)	
MI	5.28 (0.20)		9.41 (1.15)		115.14 (16.20)		1536.42 (354.44)		337.57 (48.35)		4.64 (0.75)	
IE	5.15 (0.11)		16.49 (3.68)		110.57 (8.54)		1905.49 (312.12)		440.35 (64.35)		3.66 (0.33)	
II	5.41 (0.30)		12.94 (2.50)		111.75 (19.32)		2123.27 (669.50)		392.37 (85.87)		5.65 (0.65)	

Table 3.3. Generalized linear and linear mixed effects model (glmer and lmer) results for the fixed effects of site type (T; island or mainland) and plot position (P; edge or interior) on survival, relative growth rate (RGR), height, aboveground biomass, proportion of leaves with herbivory and percent herbivory per leaf for *Albizia julibrissin* and *Lonicera japonica*.

Source	Survival		RGR (mm day^{-1})		Height (cm)		Biomass (g)		Proportion of leaves with herbivory		% herbivory per leaf	
	z	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*T*	*p*	*t*	*p*
Albizia julibrissin												
Type	-0.98	0.32	0.33	0.75	-0.06	0.95	-1.12	0.27	-2.90	**<0.01**	-2.00	**0.05**
Position	-2.53	**0.01**	0.81	0.42	0.72	0.48	-2.37	**0.02**	1.40	0.18	0.14	0.88
T*P	1.74	0.08	-0.06	0.95	-0.33	0.75	0.98	0.33	1.74	0.10	0.53	0.60
Lonicera japonica												
Type	-1.05	0.30	-0.05	0.96	0.11	0.91	-0.96	0.35	-0.48	0.63	-0.53	0.59
Position	-0.93	0.35	2.43	**0.02**	2.33	**0.03**	0.69	0.49	-1.00	0.33	0.11	0.91
T*P	0.14	0.88	0.71	0.49	0.33	0.74	0.03	0.97	0.85	0.40	0.31	0.75

Table 3.4 AICc, ΔAICc, and AICc weight for hierarchical models used to evaluate the impact of measured abiotic variables that differed by site type or outplanting block position on survival of *A. julibrissin* and *L. japonica* (i.e., percentage of canopy openness, Mg, and Zn). All models include random effects for site identity and outplanting block to account for multiple outplanting blocks within a site and multiple individuals within an outplanting block. PCO = percentage of canopy openness; Spp = species; Mg = concentration of Mg in soil; Zn = concentration of Zn in soil.

Model	AICc	ΔAICc	AICc weight
Spp+PCO	505.09	0.00	0.52
Spp+PCO+Spp*PCO	505.96	0.87	0.34
Spp+PCO+Mg+Zn+Spp*PCO+Spp*Mg+Spp*Zn+PCO*Zn+PCO*Mg+Mg*Zn	508.46	3.37	0.10
Spp+PCO+Zn+Spp*PCO+Spp*Zn+PCO*Zn	510.42	5.33	0.04
PCO	516.44	11.35	0.00
Spp	518.21	13.12	0.00
PCO+Mg+Zn+PCO*Zn+PCO*Mg+Mg*Zn	518.39	13.30	0.00
PCO+Zn+PCO*Zn	519.41	14.32	0.00
Mg	531.10	26.01	0.00
Zn	531.68	26.59	0.00

FIGURES

Fig. 3.1: Aerial photograph of Lake Russell (left) with island and mainland experimental sites highlighted and the physiographic regions of South Carolina with the study location (right). Symbols denote the location of outplanting sites but are much larger than the actual size so that they are visible at this scale.

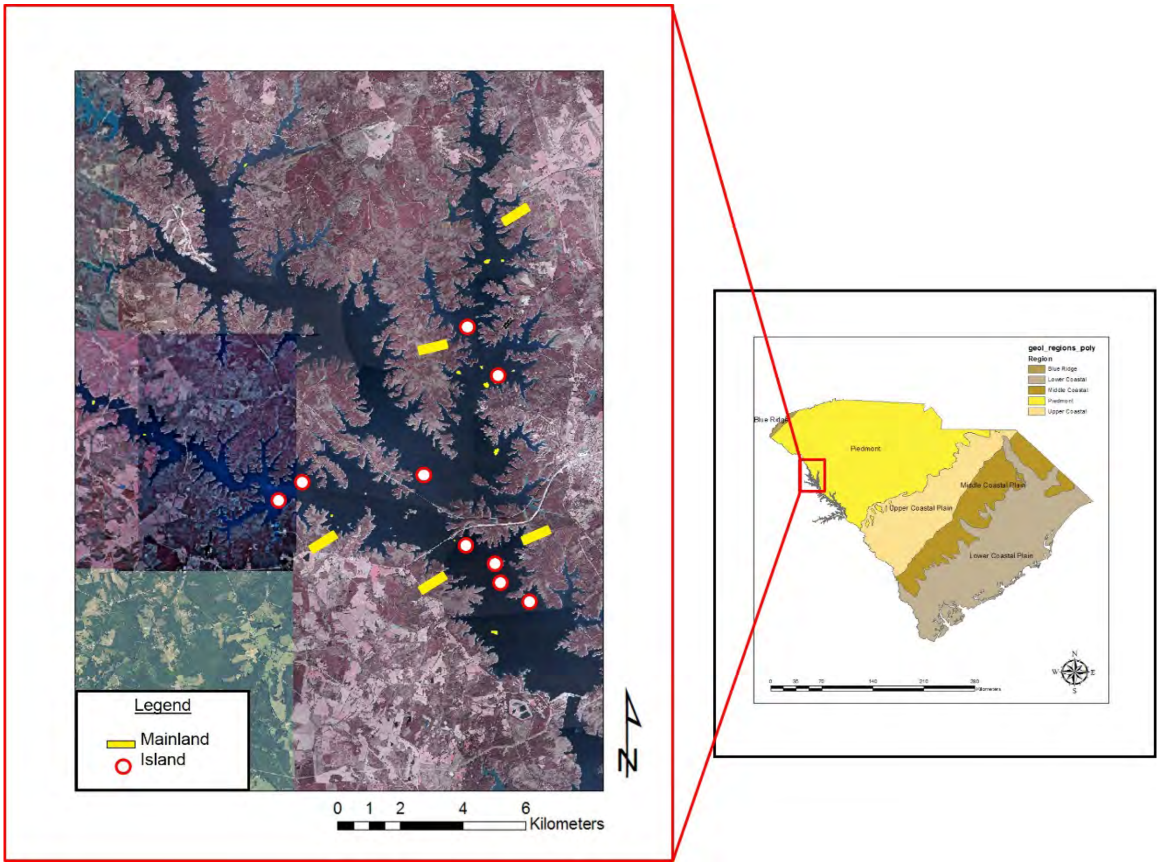


Fig. 3.2. Mean (± SE) habitat conditions including (A) canopy height, (B) basal area, (C) litter mass, (D) percentage of canopy openness, (E) soil moisture content expressed as a percentage of dry soil mass, and (F) vapor pressure deficit (VPD) at the outplanting sites on edges and interiors of forested island fragments and mainland forest sites in Lake Russell, SC/GA. Significant effects ($p < 0.05$) of site type (T), position (P), or their interaction (T*P) are indicated in bold for each panel where appropriate. Means with different letters are significantly different using Tukey's HSD ($p < 0.05$).

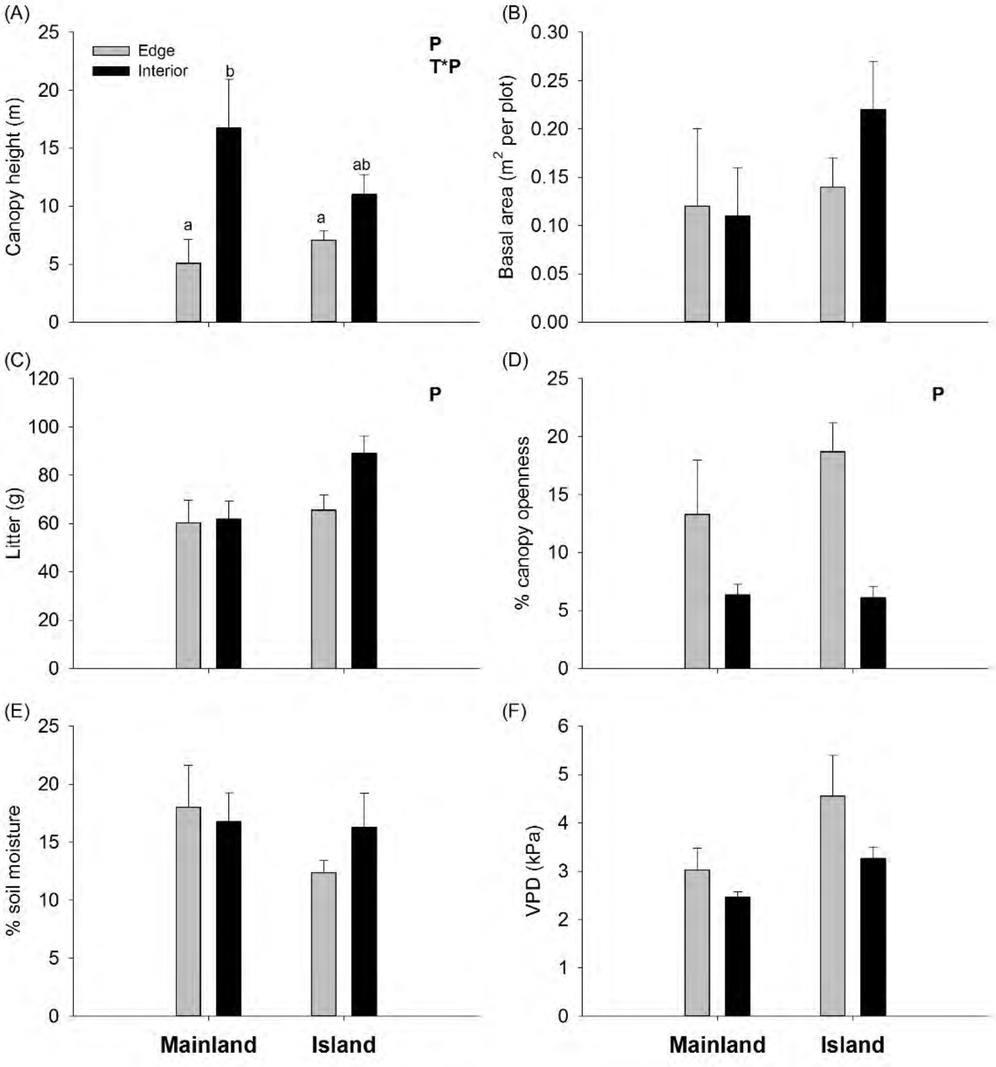


Fig. 3.3. Survival curves over the entire study period from January 2009 through November 2011 for *A. julibrissin* and *L. japonica* out-planted on edges and interiors of forested island fragments and mainland forest sites in Lake Russell, SC/GA.

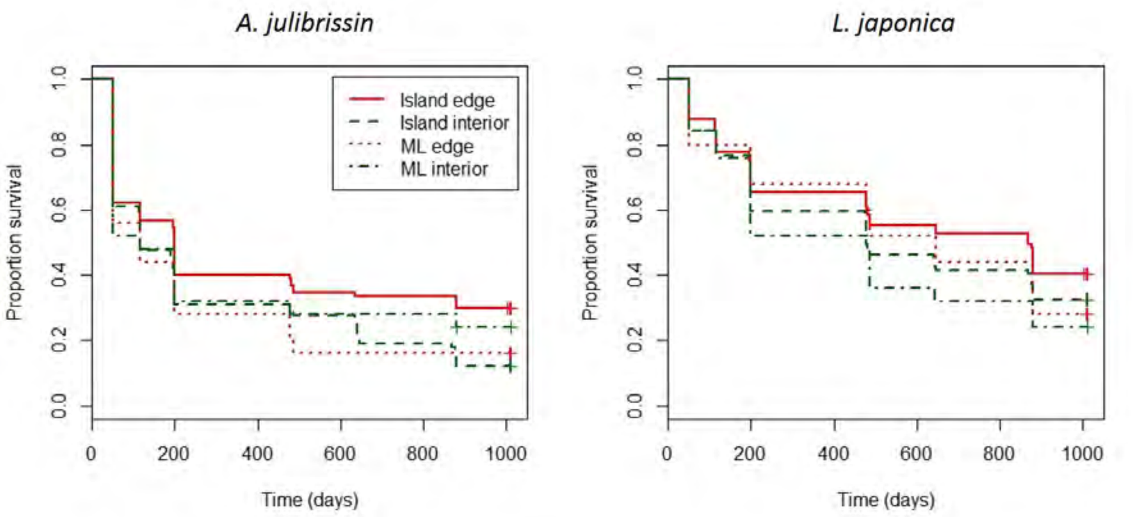


Fig. 3.4. Mean (± SE) for individual (A) survival, (B) relative growth rate (RGR), (C) height, and (D) above-ground biomass for *A. julibrissin* and *L. japonica* outplanted on edges and interiors of forested island fragments and mainland forest sites in Lake Russell, SC/GA. Significant effects ($p < 0.05$) of site type (T), position (P), or their interaction (T*P) are indicated in bold for each panel where appropriate.

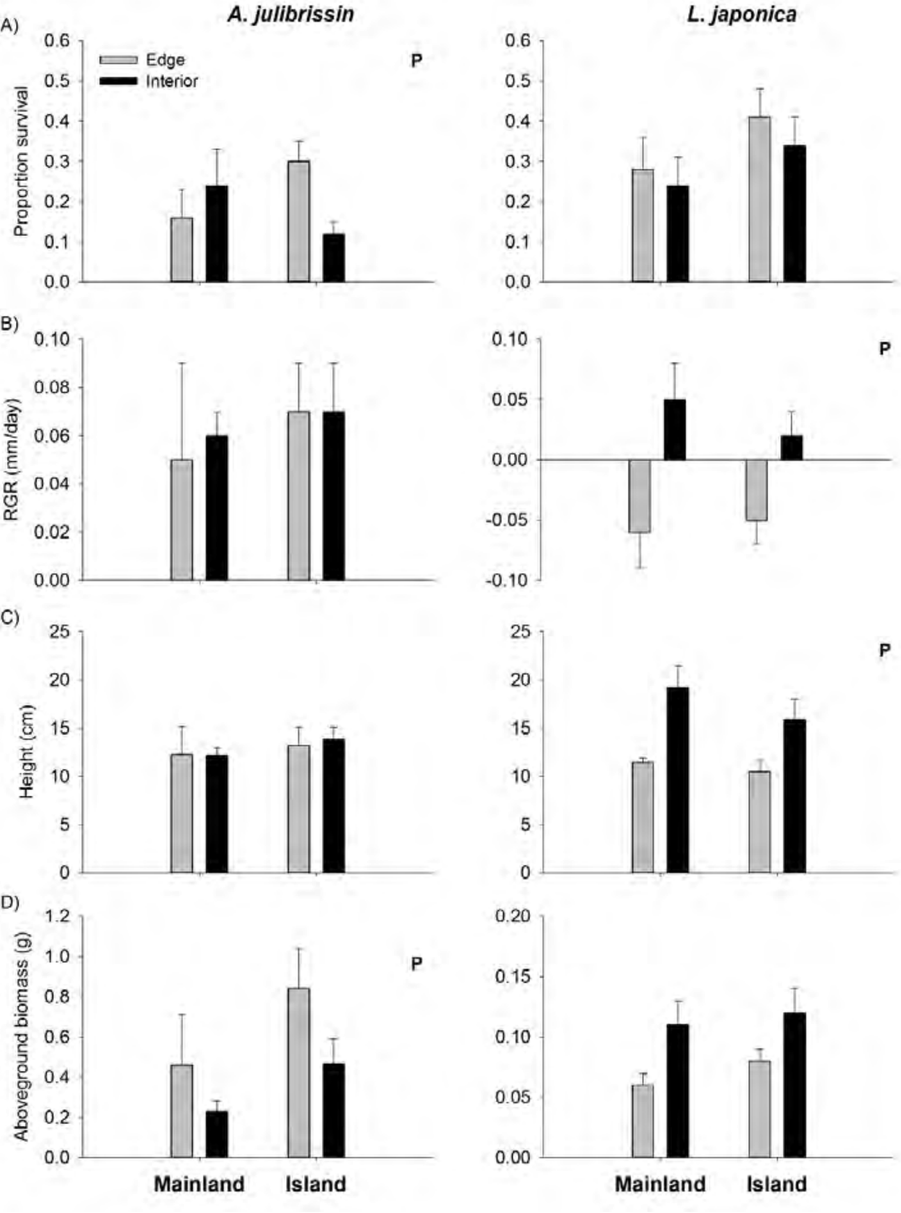


Fig. 3.5. Mean (± SE) (A) percentage of leaves with herbivory and (B) percentage of herbivore damage per leaf for *A. julibrissin* and *L. japonica* outplanted on edges and interiors of forested island fragments and mainland forest sites in Lake Russell, SC/GA. Significant effects ($p < 0.05$) of site type (T), position (P), or their interaction (T*P) are indicated in bold for each panel when appropriate.

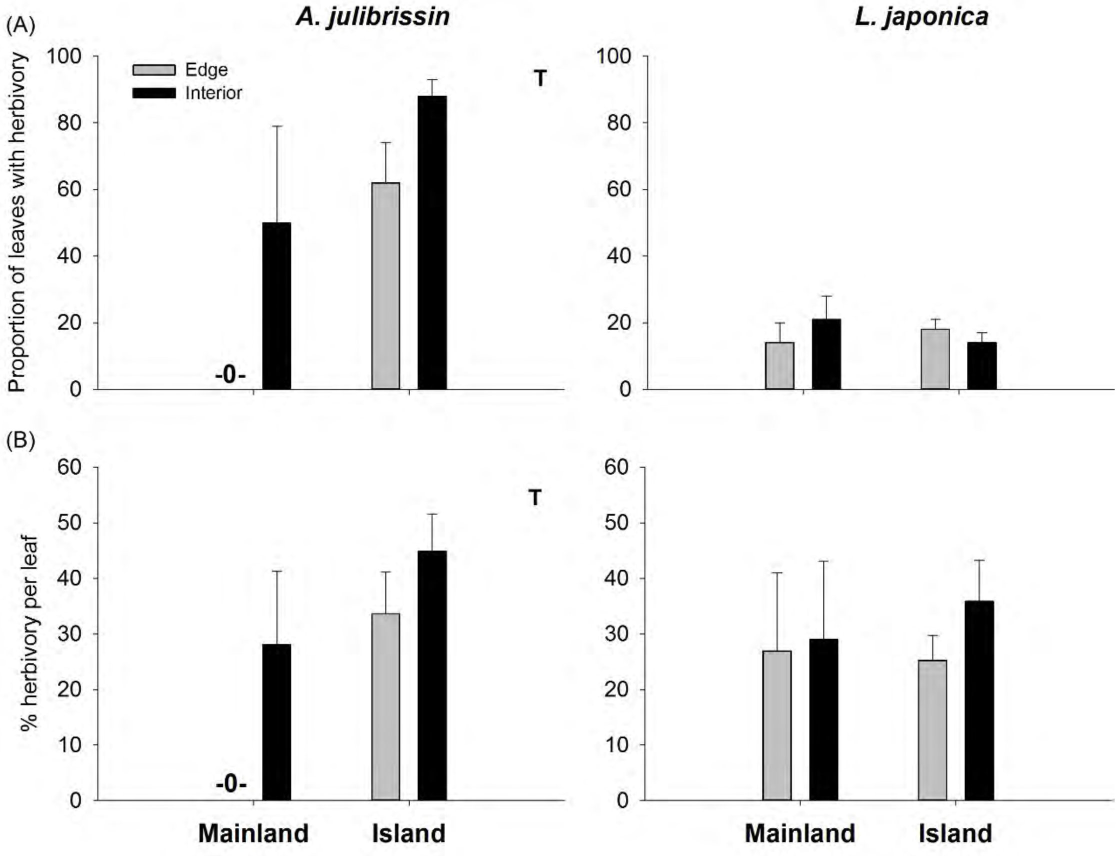
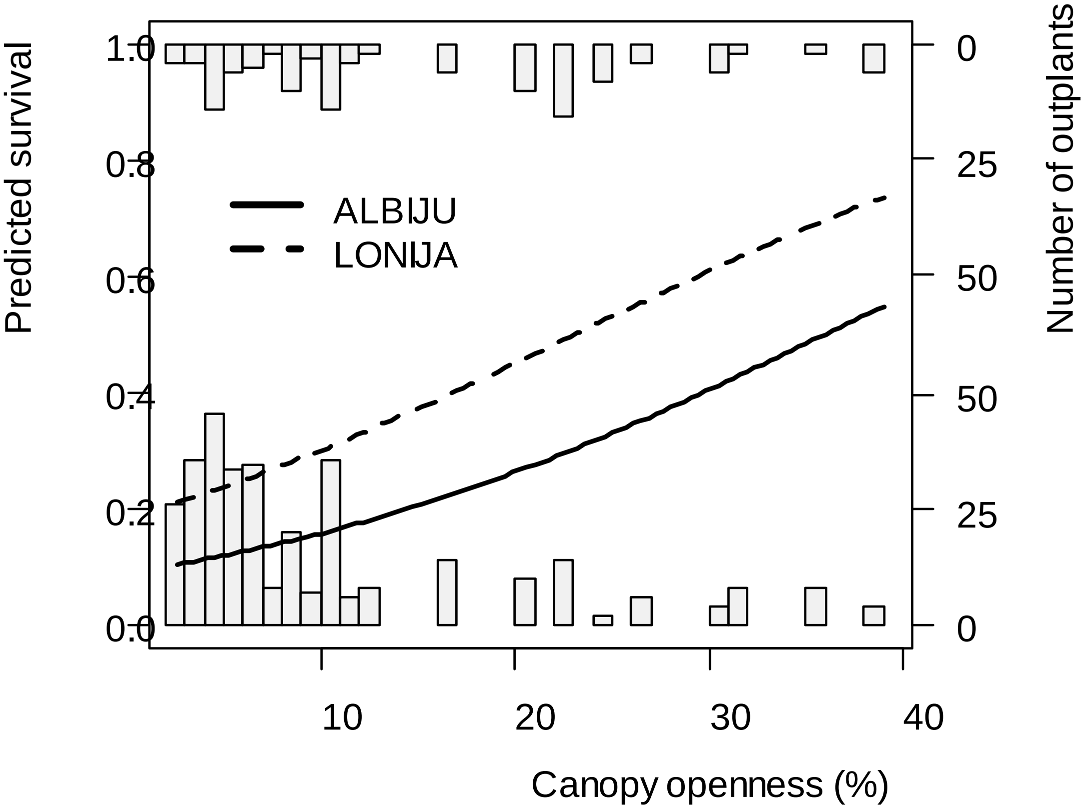


Fig. 3.6. Predicted probability survival for outplanted *A. julibrissin* (ALBIJU) and *L. japonica* (LONIJA) over 3 years in relation to percentage of canopy openness on islands and mainland sites at Lake Russell, SC/GA. The predicted probabilities are from parameter estimates from the best-fitting model. The histogram represents the actual number of seedlings that died (y=0) or survived (y=1) in the range of canopy openness values plotted on the x-axis. Longer bars represent a greater number of outplants that were found in that range of canopy openness.



CHAPTER 4

USE OF SPECIES RICHNESS ESTIMATORS OBSCURES PATTERNS IN SPECIES RICHNESS: AN EXAMPLE USING ISOLATED FOREST FRAGMENTS

INTRODUCTION

Understanding the causes and consequences of species richness has long been a central theme in ecology and conservation biology (Colwell and Coddington 1994, Gotelli and Colwell 2001, Gotelli and Colwell 2011, Mori et al. 2013), but species richness must be measured accurately to describe patterns and identify processes that are thought to maintain diversity. Comprehensive inventories of all species in an area of interest provide the most accurate measures of species richness, but they are often prohibitively time consuming and costly. Thus, species richness is often estimated, using one or more of several sample- or individual-based methods (Wei et al. 2010, Gotelli and Colwell 2011). In fact, estimated species richness, rather than measured richness, is commonly used to explore mechanisms that generate and maintain species diversity (e.g., Benítez-Malvido and Martínez-Ramos 2003, Paciencia and Prado 2005, Poulos et al. 2007, Page et al. 2010, Sánchez-González et al. 2010, Russo et al. 2015) and to conduct conservation planning (Fleishman et al. 2006). Therefore, it is important to validate widely used methods of species richness estimation.

The most widely used estimation techniques include sample- or individual-based methods based on parametric rarefaction or non-parametric techniques (Magurran and McGill 2011). Species estimation based on rarefaction is essentially a statistical interpolation method based on an assumed species abundance distribution that allows the user to “thin” a reference sample down to a common number of individuals or samples by randomly drawing random subsets of individuals (or samples) in order to standardize the comparison of diversity between two reference samples or regions where sampling intensity may have differed (Gotelli and Chao 2013). Gotelli and Colwell (Gotelli and Colwell 2011) point out that, in their experience, classic rarefaction species richness estimation methods typically perform poorly when fewer than 20 individuals or samples are measured, and studies have found that non-parametric richness estimators consistently outperform parametric rarefaction methods (Walther and Morand 1998, Walther and Moore 2005). Non-parametric methods are thought to perform better than rarefaction techniques because they make no assumption regarding the shape of the species-abundance distribution and are relatively insensitive to unequal detection probabilities across species (Gotelli and Colwell 2001, Magurran 2004, Magurran and McGill 2011).

Non-parametric techniques estimate how many species should occur in the site of interest by adding a correction factor based on the number of species that occur rarely in a set of sampled individuals or samples to the observed species richness (Colwell and Coddington 1994, Walther and Morand 1998, Walther and Moore 2005, Gotelli and Colwell 2011, Magurran and McGill 2011, Gotelli and Chao 2013). Estimators based on species incidence rather than abundance are preferred when it is difficult to determine whether plants represent distinct genetic individuals (Chiarucci et al. 2003, Gotelli and Colwell 2011, Gotelli and Chao 2013). Non-parametric estimators for replicated, sample-based surveys using incidence data include the Incidence-based Coverage (ICE), Chao 2 (Chao2), Jackknife 1 (Jack1), Jackknife 2 (Jack2), and Bootstrap estimators; and their analogues for use with abundance data are the Abundance-based Coverage (ACE), and Chao 1 (Chao1) estimators (Heltshe and Forrester 1983, Chao 1984, Smith and van Belle 1984, Chao 1987, Colwell and Coddington 1994, Chao et al. 2000, Walther and Moore 2005, Wei et al. 2010). Newer methods in richness estimation include an estimator that extrapolates the rarefaction curve and users can extrapolate up to three times beyond the smallest number of observed individuals or number of samples (S*est*; Colwell et al. 2012). In addition, Chiu et al. (2014) have recently improved on the Chao1 and Chao2 estimators by exanding the information the estimators take into account up to the number of species that occur as tripletons and quadrupletons, or in the case of incidence-based methods, species that occur in three and four plots (iChao1 and iChao2).

Species richness estimators are typically evaluated using measures of bias, precision, and accuracy based on a set of quantitative definitions put forth in Walther and Moore (2005). Bias is generally defined as the average over- or underestimate of species richness in relation to the true value (Walther and Moore 2005). Precision is then defined as the variance of the over- or underestimate of species richness across all samples or sites for each estimator (Walther and Moore 2005). Accuracy is influenced by both bias and precision. Mathematically, it is defined as the non-directional distance of the estimated value from the true value and is expressed as either the absolute value of estimator bias or the square of estimator bias (Walther and Moore 2005). Species richness estimators are often found to be negatively biased (Gotelli and Colwell 2001), but they may still be useful for ecological inference and conservation purposes if they are precise. For example, the ranking of sites for species richness would be the same using true or estimated richness if the estimated values are always 20% below the true species richness of the site (i.e. negatively biased but highly precise). In contrast, site rankings may not be preserved and gradients in species richness may not be detected when estimator bias fluctuates greatly across a set of sites, such as the value being negatively biased by 5% at one site, 20% at another site, and 35% at another site (i.e., there is low precision).

The bias, precision, and accuracy of species richness estimators have been assessed primarily using computer-simulated datasets or empirical data from a single site where true species richness is known for a defined area and then sampled at different levels of intensity. The use of simulated and empirical datasets has highlighted that estimator performance can vary with the true richness of the community, sampling intensity, and degree of spatial heterogeneity in species composition (Brose et al. 2003, Walther and Moore 2005, Chiarucci 2012, Xu et al. 2012, Chiu et al. 2014). To our knowledge, only one previous study (Palmer 1990) has assessed the performance of species estimators in relation to known true richness. Palmer (1990) compared species richness as estimated by species observed in plots, four rarefaction estimators, Jack1, Jack2, and Boot to true species richness across 30, 0.1 ha, hardwood forest plots that each contained 40 nested 2-m^2 plots for use in richness estimation. He found that all the estimators were biased, and that Jack1 appeared to be the most precise and least biased of all eight estimators he examined (Palmer 1990). Although Palmer (1990)provided insight on how the estimators performed on average across the 30 plots in a single forest, he did not present results that increased understanding on how using estimated richness in place of true richness could impact evaluation of hypotheses regarding species richness or conservation and management strategies based on species richness. In addition, Palmer's (1990) study was completed more than twenty years prior to ours and several new methods have been developed since that time. We therefore do not understand how estimator performance may impact conservation strategies, management policies, or studies that test ecological hypotheses when more than a single site is of interest. For this reason, there is a need to evaluate estimator performance using field-based studies where true species richness can be measured (Walther and Moore 2005, Gotelli and Colwell 2011).

Here we ask how well 10 species-richness estimators predict the true species richness of woody plants over a large set of forested reservior islands where true species richness is known. We conducted complete inventories of all woody plant species on small forested reservoir islands along the Savannah River between South Carolina and Georgia, USA, and compared the true richness of each island with estimates derived from a series of plots that were measured on each island to study species composition (Chapter 2). We used methods based on those presented in Walther and Moore (2005) to evaluate the bias, precision, and accuracy relative to the true species richness of each island for 9 non-parametric species richness estimators and a sample-based interpolation and extrapolation method that uses the Bernoulli product model (Colwell et al. 2012, Colwell 2013). Additionally, we present how restricting the dataset using a conservative criterion for sample completeness on each island affects the performance of each estimator.

Lastly, we illustrate how use of estimated species richness in place of true species richness may obscure the species-area relationship among our set of islands.

METHODS

Study area

We quantified species richness on forested reservoir islands in Lake J. Strom Thurmond (Lake Thurmond) and Lake Richard B. Russell (Lake Russell) located in the southeastern piedmont physiographic region, along the border between South Carolina and Georgia, USA. Lake Thurmond and Lake Russell were created for flood control and hydroelectric power by impounding large areas along the Savannah River in 1954 and 1984, respectively (Chapter 2). Impoundment created these islands by isolating forested hilltops from what was once contiguous forest. The islands were not logged prior to, or following, impoundment and have never been inundated.

The southeastern piedmont physiographic region is defined as the area from the Brevard Fall Line at the base of the Blue Ridge Mountains to the Sandhills Fall Line, which demarks the Coastal Plain to the east (Fairchilds and Trettin 2006). This region is characterized by poor soils that range from deep clays to exposed bedrock (Chapter 2; Fairchilds and Trettin 2006). Currently, much of the region is dominated by secondary forests of *Quercus* spp. - *Carya* spp. (oak – hickory; Chapter 2). Mean annual rainfall along these reservoirs is 116.8 cm yr^{-1}, and average monthly temperature ranges from 9.4°C to 23.9°C (Chapter 2; SCSCO 2007).

Site selection

We examined aerial photographs and topographic maps and used field observations to identify islands that were continuously isolated from the mainland and other islands since the date of reservoir creation (Chapter 2). Our sampling was limited to islands < 3 ha in size as there were no islands ≥ 3 ha that had been completely isolated since the date of reservoir construction and were not greatly impacted by historic roads or settlement (Chapter 2). Thirteen islands fit these criteria in Lake Thurmond. From the 62 islands that fit these criteria in Lake Russell, 22 were randomly selected for study. The 35 selected islands across both lakes ranged in size from 0.08 to 2.47 ha (Chapter 2).

Quantifying true richness on each island

To quantify true species richness for each island, we performed an exhaustive survey of each island by walking the entire island in concentric circles approximately 5 m wide and recording the presence of all woody plant species that were ≥ 50 cm in height or length, in the case of lianas (Chapter 2; Kadmon and Pulliam 1993). Three people were always used to complete these exhaustive surveys, with two people walking about 2 m from one another and the third recording species occurrences and also verifying that no species were missed (Chapter 2). We are therefore confident that this method produced an accurate measure of true richness for woody plant species on each island (Chapter 2). All vegetation sampling occurred between May and September in 2007, 2008, and 2009. Plant species nomenclature follows Weakley (2006).

Plot-based sampling on each island

We sampled vegetation in plots running from the vegetated edge toward the approximate center of each island (Chapter 2). Using ArcGIS 9.2 (ESRI 2006), we randomly placed the start of two transects per island on the vegetated edge and oriented them toward the center of each island. We censused vegetation within 4 m x 5 m (20-m^2) plots centered along each transect starting 2 m from the edge of where vegetation was present on each island. On the smallest islands, plots were also placed 8 m from the edge as well as in the center for a total of up to 5 plots (100 m^2) per island. Additional plots were placed at 18 m on larger islands so that medium-sized islands had up to 7 plots (140 m^2) per island, and at 18 and 30 m on the largest islands for up to 9 plots (180 m^2) per island. There were four islands that were narrow, and a center plot would not fit without overlapping other plots. In addition, on one small island we were able to sample two plots located at 18 m from the edge, rather than a single center plot, for a total of 6 sample plots. In total, 239 plots were sampled across all 35 islands. In each 20-m^2 plot, individual woody and semi-woody plants (i.e., trees, shrubs, and lianas) ≥ 50 cm in height or length were tallied and identified to species. Detailed explanation of formulas used to compute each estimator can be found in the supporting information for EstimateS v. 9.1.0 and SpadeR v. 0.1.0 (Colwell 2013, Chao et al. 2015).

Assessment of sample-completeness for each island

We recognized that all 35 islands may not have been sampled with enough plots to produce a reliable estimate of species richness, so we used two increasingly conservative criteria of sample completeness to select two sets of islands suitable for our assessment of estimator performance. First, Chao suggests that sample size should be adequate for a reasonable estimate using the Chao1 and ACE non-parametric species richness estimators if the number of singletons (*F1*) is less than half of the total number of individuals (*n*) detected within plots (i.e., F1/n; Colwell 2013). For the Chao2 and ICE non-parametric species richness estimators, Chao suggests that the number of uniques (*Q1*) should be less than half of the total number of species found at least once (*M*) within the plots (i.e., *Q1/M*; Anne Chao, personal communication, Colwell 2013). We call these criteria the "Chao sample completeness index", and we make the assumption that this sample completeness criterion is appropriate for the other non-parametric estimators examined here. For each island, the Chao sample completeness index ranged from 2% to 14% for abundance-based measures, and from 10% to 30% for incidence-based measures. As all 35 islands fell well below the threshold value of 50%, all islands were retained for initial evaluation of estimator performance. The percentage of area sampled per island ranged from 0.7% to 15%.

Second, we used the criterion that ≤ 1 additional species should be expected to be captured if sampling was continued to create a subset of data, hereafter referred to as our reduced dataset. This more conservative measure of sample completeness was conducted by constructing classic sampling curves to determine the number of species expected to be observed had sampling continued on each island. This value ranged from 0.65 to 3.40 species on the complete series of 35 islands, with the majority of islands having values ranging from 1.2 to 2.8 additional species expected. Our reduced dataset contained just six islands out of the possible 35, and the percentage of area sampled on the reduced dataset of six islands ranged from 0.7% to 2.6%.

Estimation of species richness

We calculated 10 species estimators appropriate for replicated abundance or incidence data. Specifically, we used these four for replicated abundance data: sample-based rarefaction and extrapolation based on the Bernoulli product model (S*est*; Colwell et al. 2012), ACE (Chao and Lee 1992, Chazdon et al. 1998), Chao1 (Chao 1984), and iChao1 (Chiu et al. 2014). We used these six for incidence data: ICE (Chao and Lee 1992, Chazdon et al. 1998), Chao2 (Chao 1984), iChao2 (Chiu et al. 2014); Jackknife1 (Jack1; Burnham and Overton 1978, 1979, Heltshe and Forrester 1983, Smith and van Belle 1984); Jackknife2 (Jack2; Burnham and Overton 1978, 1979, Heltshe and Forrester 1983, Smith and van Belle 1984), and Bootstrap (Smith and van Belle 1984). Estimators based on species incidence rather than abundance are preferred when it is difficult to determine whether plants represent distinct genetic individuals (Chiarucci et al. 2003, Gotelli and Colwell 2011, Gotelli and Chao 2013). On the forested islands, some shrubs and lianas are clonal, and therefore we had reason to compare the incidence- and abundance-based estimators.

We calculated all but iChao1 and iChao2 using the freely available software EstimateS (Colwell 2013). For *Sest*, we followed recommendations by Colwell et al. (2012) and extrapolated species richness out to 15 samples, which is three times the smallest number of plots sampled on any island. We were interested in comparing the point estimates with true richness on each island, as opposed to investigating how the estimators performed with respect to one another in a single site, and therefore we randomized plots one time without replacement (Walther and Moore 2005, Chao et al. 2009, Colwell 2013). We used the program SpadeR by Chao et al. (2015) to calculate the iChao1 and iChao2 estimators for each island, which extends the Chao1 and Chao2 estimators by incorporating not only singletons and doubletons, but also tripletons and quadrupletons (Chiu et al. 2014, R Development Core Team 2015). The iChao2 estimator was undefined for 6 of the 35 sites, so for iChao2 we only consider 29 of the 35 islands.

Assessment of estimator bias, precision, and accuracy

To describe how each estimator performed in relation to true richness on each island, we calculated scaled error (SE) and squared scaled error (SSE) for each estimator on each island (Table 4.1). We use SE and SSE because true richness varied widely among the islands, and scaling is required when comparing performance of estimators among sites with different levels of species richness (Walther and Moore 2005). As used here, SE produces a measure of bias indicating the proportion that the estimator either over- or under-estimated true richness on each island (Table 1). By squaring the SE, SSE becomes a directionless measure of accuracy for each estimator on each island (Table 4.1). Precision for each estimator was defined as the coefficient of variation (CV) of mean scaled error for each island dataset (35 islands or 6 islands) for each estimator (Table 4.1). We used t-tests to determine if SE was significantly different from zero (i.e., true richness) for each dataset and estimator. To explore whether sampling intensity was correlated significant predictor of error, we regressed SSE on the percentage of area sampled for each island for each estimator.

Lastly, we determined whether a species-area relationship among the 35 islands was detected with the 10 estimators of species richness to illustrate how estimator performance may affect ecological inference. We used linear regression of $\log_{10}$ area with true richness and each of the 10 species richness estimators. Calculation of CV, t-tests, and regression analyses were performed in the R 3.2.3 base package (R Development Core Team 2015).

RESULTS

Across all 35 islands, we found 125 woody plant species during our exhaustive island surveys. The 239 plots captured 92 (74%) of these species. True species richness ranged from 30 to 62 species on individual islands. Mean true species richness (± 1 SD) across our datasets of 35 and 6 islands was 46.7 (±8.1) and 42.8 (±9.3) species, respectively. Only a single species, *Ulmus alata* Michx. (winged elm), occurred on all 35 islands, although it was missed during plot surveys on two islands (Table 4.S1). This species was also one of the most abundant species in plot surveys, accounting for nearly 11% of the 4448 individuals sampled. Of the 92 species detected within plots, 16 species (17%) were detected only in a single plot, while another 50 species (72%) occurred in fewer than 30 plots. Detectability (i.e., relative abundance pooled across all 35 islands) and presence within plots on an island for each species varied widely, with several species detected in thorough island-wide surveys but then missed within plots on that island (Table 4.S1).

Performance of richness estimators

Nine of the 10 estimators examined here significantly underestimated true species richness (i.e., were negatively biased; Fig. 4.1) and were highly variable in the degree to which they predicted true richness across all 35 islands (were irregularly imprecise and inaccurate; Table 4.2). Scaled error (i.e., bias) was not significantly related to the percentage of area that was sampled on an island (Figs. 4.2 and 4.3). The iChao2 method was the only estimator that did not differ significantly from true richness (Fig. 4.1), but the estimator was very imprecise and therefore was the least accurate of the estimators (Table 4.2). The Bootstrap method was the most negatively biased estimator, but it was the most precise across the 35 sites (Fig. 4.1 and Fig. 4.3; Table 4.2). Using our reduced dataset, average negative bias greatly increased for all estimators examined, but precision of the estimators was improved (Table 4.2). Because of the large increase in bias, there was no improvement in accuracy for any of the estimators (Table 4.2). In addition, the more recently developed estimators did not perform any better than their older counterparts.

Species-area relationship

True richness showed a significant and positive species-area relationship ($R^2 = 0.32$, $p = 0.002$; Fig. 4.4; Chapter 1). However, none of the estimators detected this species-area relationship (Figs. 4.4 and 4.5). Even when assessing our reduced dataset, site rankings based on estimated species richness were not consistent with rankings based on true richness (Table 4.3).

DISCUSSION

All 10 species richness estimators provided highly inaccurate estimates of species richness for woody plants in temperate forest fragments (i.e., reservoir islands) where true species richness could be determined. All 10 of the estimators were negatively biased, as has been found in other studies (Table 4.2; Brose et al. 2003, Chiarucci et al. 2003, Xu et al. 2012). This result is not surprising as negative bias has been recognized repeatedly for several estimators when a small number of plots are surveyed within a site (Gotelli and Colwell 2011, Chao et al. 2015). What was unexpected, however, was the lack of precision (i.e., how widely bias varied across the 35 islands) even for estimators where sample completeness was thought to be sufficient to produce a reliable lower-bound of species richness (Colwell 2013).

Due to the this lack of precision, all the estimators we assessed here obscured the species-area relationship that was detected using true species richness for both the 35-island dataset (Chapter 1). Even when sampling of the islands was thorough enough so that less than a single species would have been expected with an additional sample, site rankings based on estimated richness did not match the ranking based on true species richness. Thus, the species richness estimators examined here appear to be unsatisfactory tools for testing for the presence of the species-area relationship in our system of reservior islands. They may also be inadequate for detecting differences among sites in studies testing other ecological hypotheses.

Of paramount concern is that that use of species richness estimators may lead to spurious conclusions regarding biological and ecological processes. Several studies of species richness in fragmented habitats have demonstrated departures from the expected species-area relationship and have suggested that these departures result from the influence of edge effects or other disturbances (Debinski and Holt 2000, Harper et al. 2005, Laurance 2008, Koh et al. 2010). For instance, it is thought that multiple, and at times interacting, edge effects may cause disproportionate loss of forest interior species, while at the same time creating favorable habitat for the establishment of species not typically common in continuous forest (Laurance et al. 2006). However, problems detecting a species-area relationship in some studies may be due, in part, to the variable performance of the species richness estimator used rather than an underlying biological phenomenon. In our study system, we found a species-area relationship using true species richness, despite the presence of marked edge effects for light levels and stem density on these islands (Chapters 1 and 2). In contrast, had we used any of the species richness estimators examined here we would have concluded, wrongly, that there was not a positive species-area relationship among the 35 reservoir islands.

Exceeding some threshold of percent area sampled may not be a useful guideline for ensuring satisfactory estimator performance over a series of sites (Fig. 4.2 and Fig. 4.3). While increasing sampling intensity has generally been found to decrease error in species richness estimators (Brose et al. 2003, Chiarucci et al. 2003, Hwang and Shen

2010, Xu et al. 2012), we found that increasing the percentage of area sampled had no effect on the performance of the estimators across sites. Similar to our study, Wei et al. (2010) also found that the accuracy of non-parametric methods varied greatly along a sampling intensity gradient of a fully surveyed 20-ha plot in subtropical forest of southern China. In contrast, two studies conducted on computer-simulated sampling of plots in a high-diversity shrubland of southwestern Australia and tropical forests of Panama and Malaysia, found that a minimum of 10% to 15% of the study area needed to be sampled in order to provide reliable estimates of species richness (Chiarucci et al. 2003, Hwang and Shen 2010). However, species richness of those sites is 3.5 to 13 times higher than the isolated temperate forests studied here, and lower species richness of the forested islands in our system should mean that less area needs to be sampled. Our study is similar to many other plant community studies where species richness estimators are employed and less than 1% of the area is sampled (Chiarucci et al. 2003). As such, our results are highly relevant and reflective of the outcome that can be expected when field sampling can only capture a small proportion of the study area.

Most interesting is why the estimators appeared to work well on some, and poorly on other, islands with similar sampling intensites. Although we only had five islands that were sampled in excess of 5% of total island area, these five islands were not part of our reduced dataset for which sampling curves indicated ≤ 1 additional species were predicted to be found had sampling continued. Moreover, estimator bias for these islands still varied quite widely with predicted richness values ranging anywhere from 27% above to 65% below the true species richness for the island. In fact, the percentage of area sampled ranged from 0.65% to 2.63% for the six islands conforming to the most conservative sample completeness criterion where ≤ 1 additional species was expected if sampling had continued, well below the 10% to 15% threshold suggested by Chiarucci et al. (2003) and Hwang and Shen (2010). Unfortunately, there does not appear to be a single sampling completeness reccomendation that would produce precise estimates across a set of sites.

CONCLUSION

Our results highlight that estimators of species richness can be highly inaccurate and we caution their use in theoretical inference, conservation planning, and management. We recommend that the richness estimators examined here only be employed when a single site is of interest, with the caveat that depending on the estimator that is used true richness could be anywhere from 60% lower to 90% higher than the estimated richness value. We recognize that an exhaustive inventory of many study sites may not be possible, but determination of how an estimator performs in relation to true richness should be investigated for at least a subset of sites along the gradient of interest before use. Additional studies comparing true species richness to estimated richness from multiple, thoroughly inventoried areas will be critical for testing and improving species richness estimators.

REFERENCES

Benítez-Malvido, J. and M. Martínez-Ramos. 2003. Impact of forest fragmentation on understory plant species richness in Amazonia. Conservation Biology **17**:389-400.

Brose, U., N. D. Martinez, and R. J. Williams. 2003. Estimating species richness: sensitivity to sample coverage and insensitivity to spatial patterns. Ecology **84**:2364-2377.

Burnham, K. P. and W. S. Overton. 1978. Estimation of the size of a closed population when capture probabilities vary among animals. Biometrika **65**:625-633.

Burnham, K. P. and W. S. Overton. 1979. Robust estimation of population size when capture probabilities vary among animals. Ecology **60**:927-936.

Chao, A. 1984. Non-parametric estimation of the number of classes in a population. Scandanavian Journal of Statistics **11**:265-270.

Chao, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. Biometrics **43**:783-791.

Chao, A., R. K. Colwell, C.-W. Lin, and N. J. Gotelli. 2009. Sufficient sampling for asymptotic minimum species richness estimators. Ecology **90**:1125-1133.

Chao, A., W. H. Hwang, Y. C. Chen, and C. Y. Kuo. 2000. Estimating the number of shared species in two communities. Statistica Sinica **10**:227-246.

Chao, A. and S.-M. Lee. 1992. Estimating the Number of Classes via Sample Coverage. Journal of the American Statistical Association **87**:210-217.

Chao, A., K. H. Ma, and T. C. Hsieh. 2015. Species Prediction and Diversity Estimation with R. R Package.

Chazdon, R. L., R. K. Colwell, J. S. Denslow, and M. R. Guariguata. 1998. Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of northeastern Costa Rica. Pages 285-309 *in* F. Dallmeier and J. A. Comiskey, editors. Forest biodiversity research, monitoring and modeling: conceptual background and Old World case studies. Parthenon Publishing, Paris, France.

Chiarucci, A. 2012. Estimating species richness: still a long way off! Journal of Vegetation Science **23**:1003-1005.

Chiarucci, A., N. J. Enright, G. L. W. Perry, B. P. Miller, and B. B. Lamont. 2003. Performance of nonparametric species richness estimators in a high diversity plant community. Diversity and Distributions **9**:283-295.

Chiu, C.-H., Y.-T. Wang, B. A. Walther, and A. Chao. 2014. An improved nonparametric lower bound of species richness via a modified good–turing frequency formula. Biometrics **70**:671-682.

Colwell, R. K. 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9.0. Users Guide and application published at http:\\purl.oclc.org/estimates.

Colwell, R. K., A. Chao, N. J. Gotelli, S. Y. Lin, C. X. Mao, R. L. Chazdon, and J. T. Longino. 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. Journal of Plant Ecology **5**:3-21.

Colwell, R. K. and J. A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society of London B **345**:101-118.

Debinski, D. M. and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology **14**:342-355.

ESRI. 2006. ArcGIS, Version 9.2. ESRI, Redlands, California.

Fairchilds, L. H. and C. C. Trettin. 2006. History and legacy of fire effects in the South Carolina piedmont and coastal regions. United States Department of Agriculture Forest Service, Southern Research Station, Asheville, North Carolina.

Fleishman, E., R. F. Noss, and B. R. Noon. 2006. Utility and limitations of species richness metrics for conservation planning. Ecological Indicators **6**:543-553.

Gotelli, N. J. and A. Chao. 2013. Measuring and estimating species richness, species diversity, and biotic similarity from sampling data. Pages 195-211 *in* S. A. Levin, editor. Encyclopedia of biodiversity. Academic Press, Waltham, Massachusettes, USA.

Gotelli, N. J. and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters **4**:379-391.

Gotelli, N. J. and R. K. Colwell. 2011. Estimating species richness. Pages 39-54 *in* A. E. Magurran and B. J. McGill, editors. Biological Diversity: Frontiers In Measurement And Assessment. Oxford University Press, Oxford, UK.

Harper, K. A., S. E. MacDonald, P. J. Burton, J. Chen, K. D. Brosofske, S. C. Saunders, E. S. Euskirchen, D. Roberts, M. S. Jaiteh, and P.-A. Esseen. 2005. Edge influence on forest structure and composition in fragmented landscapes. Conservation Biology **19**:768-782.

Heltshe, J. F. and N. E. Forrester. 1983. Estimating species richness using the Jackknife procedure. Biometrics **39**:1-11.

Hwang, W. H. and T. J. Shen. 2010. Small-sample estimation of species richness applied to forest communities. Biometrics **66**:1052-1060.

Kadmon, R. and H. R. Pulliam. 1993. Island biogeography - effect of geographical isolation on species composition. Ecology **74**:977-981.

Koh, L. P., T. M. Lee, N. S. Sodhi, and J. Ghazoul. 2010. An overhaul of the species-area approach for predicting biodiversity loss: incorporating matrix and edge effects. Journal of Applied Ecology **47**:1063-1070.

Laurance, W. F. 2008. Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. Biological Conservation **141**:1731-1744.

Laurance, W. F., H. E. M. Nascimento, S. G. Laurance, A. C. Andrade, P. M. Fearnside, J. E. L. Ribeiro, and R. L. Capretz. 2006. Rain forest fragmentation and the proliferation of successional trees. Ecology **87**:469-482.

Magurran, A. E. 2004. Measuring biological diversity. Blackwell Publishing, Oxford.

Magurran, A. E. and B. J. McGill, editors. 2011. Biological Diversity Frontiers in Measurement and Assessment. Oxford University Press, Oxford, UK.

Mori, A. S., T. A. Spies, K. Sudmeier-Rieux, and A. Andrade. 2013. Reframing ecosystem management in the era of climate change: issues and knowledge from forests. Biological Conservation **165**:115-127.

Paciencia, M. L. B. and J. Prado. 2005. Effects of forest fragmentation on Pteridophyte diversity in a tropical rain forest in Brazil. Plant Ecology **180**:87-104.

Page, N. V., Q. Qureshi, G. S. Rawat, and C. G. Kushalappa. 2010. Plant diversity in sacred forest fragments of Western Ghats: a comparative study of four life forms. Plant Ecology **206**:237-250.

Palmer, M. W. 1990. The estimation of species richness by extrapolation. Ecology **71**:1195-1198.

Poulos, H. M., A. H. Taylor, and R. M. Beaty. 2007. Environmental controls on dominance and diversity of woody plant species in a Madrean, Sky Island Ecosystem, Arizona, USA. Plant Ecology **193**:15-30.

R Development Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available at URL: http://www.R-project.org.

Russo, L., M. Park, J. Gibbs, and B. Danforth. 2015. The challenge of accurately documenting bee species richness in agroecosystems: bee diversity in eastern apple orchards. Ecology and Evolution **5**:3531-3540.

Sánchez-González, A., E. Á. Zúñiga, and J. D. Tejero-Díez. 2010. Richness and distribution patterns of ferns and lycopods in Los Mármoles National Park, Hidalgo, Mexico. The Journal of the Torrey Botanical Society **137**:373-379.

Smith, E. P. and G. van Belle. 1984. Nonparametric estimation of species richness. Biometrics **40**:119-129.

SCSCO. 2007. Historic climate data. South Carolina State Climate Office. http://www.dnr.sc.gov/climate/sco/ClimateData/sc_historical_climate_data.php.

Walther, B. A. and J. L. Moore. 2005. The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. Ecography **28**:815-829.

Walther, B. A. and S. Morand. 1998. Comparative performance of species richness estimation methods. Parasitology **116**:395-405.

Weakley, A. B. 2006. Flora of the Carolinas and Virginia. University of North Carolina, Chapel Hill, North Carolina.

Wei, S.-g., L. Li, B. A. Walther, W.-h. Ye, Z.-l. Huang, H.-l. Cao, J.-Y. Lian, Z.-G. Wang, and Y.-Y. Chen. 2010. Comparative performance of species-richness estimators using data from a subtropical forest tree community. Ecological Research **25**:93-101.

Xu, H., S. Liu, Y. Li, R. Zang, and F. He. 2012. Assessing non-parametric and area-based methods for estimating regional species richness. Journal of Vegetation Science **23**:1006-1012.

TABLES

Table 4.1. Equations and variable definitions for calculations of scaled error (SE; bias), coefficient of variation (CV; precision), and squared scaled error (SSE; accuracy) adapted for use with point estimates of true richness data across a set of 35 and 6 islands per Walther and Moore (2005).

Measure	Equation
Scaled error (bias)	$SE = \frac{(E-T)}{T}$
Coefficient of variation of scaled error (precision)	$CV = \frac{SD}{\lvert \mu \rvert}$
Squared scaled error (accuracy)	$SSE = \left(\frac{(E-T)}{T} \right)^2$

Variable	Definition
E	Estimated richness for the island
T	True richness for the island
CV	Coefficient of variation over all 35 or 6 islands
SD	Standard deviation of mean scaled error (μ) over all 35 or 6 islands

Table 4.2. Mean bias (mean of scaled error), precision (coefficient of variation for mean scaled error), and accuracy (mean of squared scaled error) for abundance-based (*Sest*(15), ACE, Chao1, iChao1) and incidence-based (ICE, Chao2, iChao2, Jack1, Jack2, Bootstrap) species richness estimators over the entire 35 island dataset. The six island dataset resulted from using a conservative measure of sampling completeness that excluded 29 islands where under-sampling could potentially be connected to estimator error.

	Abundance-based estimators				Incidence-based estimators					
Performance indicator	*Sest*(15)	ACE	Chao1	iChao1	ICE	Chao2	iChao2	Jack1	Jack2	Bootstrap
All 35 islands										
Bias	-0.29	-0.30	-0.30	-0.15	-0.20	-0.18	-0.04	-0.28	-0.17	-0.39
Precision	0.58	0.52	0.65	1.99	0.92	1.83	8.59	0.53	1.01	0.33
Accuracy	0.12	0.12	0.13	0.11	0.07	0.13	0.14	0.09	0.06	0.16
6 islands										
Bias	-0.60	-0.49	-0.55	-0.48	-0.49	-0.53	-0.43	-0.49	-0.44	-0.56
Precision	0.19	0.16	0.16	0.19	0.15	0.19	0.34	0.21	0.25	0.18
Accuracy	0.30	0.25	0.31	0.24	0.24	0.29	0.20	0.25	0.21	0.32

Table 4.3. Abundance-based (*Sest*(15), ACE, Chao1, iChao1) and incidence-based (ICE, Chao2, iChao2, Jack1, Jack2, Bootstrap) species richness values for the six islands with 1 or fewer species expected to be observed if sampling continued (No. of species). We also present the number of species observed in plots for each site (S*obs*). Sites are presented in order of greatest to lowest true richness. The estimator iChao2 was undefined for two of the six islands presented here.

			Abundance-based estimators				Incidence-based estimators					
No. of species	True richness	*Sobs*	S*est* (15)	ACE	Chao1	iChao1	ICE	Chao2	iChao2	Jack1	Jack2	Bootstrap
1.00	59	19	23	26	24	28	29	24	27	27	30	23
1.00	47	21	26	23	22	23	26	27	33	27	31	24
0.67	41	14	17	18	17	23	18	16	NA	18	20	16
0.71	40	22	24	25	24	27	25	24	27	27	29	25
0.62	38	13	15	22	15	17	18	16	16	17	18	15
0.80	32	10	12	15	12	15	14	12	NA	13	14	12

FIGURES

Fig. 4.1. Mean (+1 SD) scaled error for observed species richness (*Sobs*), four abundance-based estimators, and six incidence-based species estimators over the entire 35 island dataset. The zero reference line represents true richness.

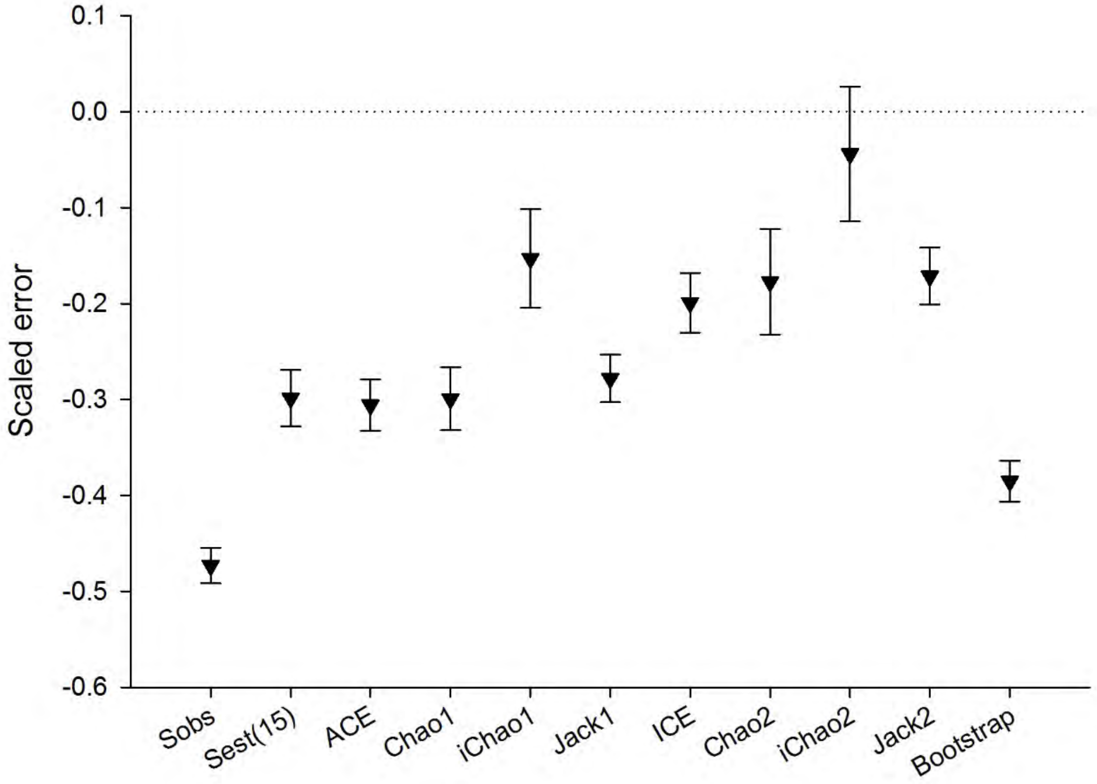


Fig. 4.2. Scaled error for S_{obs} and the abundance-based estimators: *Sest* (15), ACE, Chao1, and iChao1 plotted against the percentage of area sampled for all 35 islands. Islands in Lakes Russell and Thurmond are indicated by black and white circles, respectively. True richness for each site is indicated by the dotted reference line at zero.

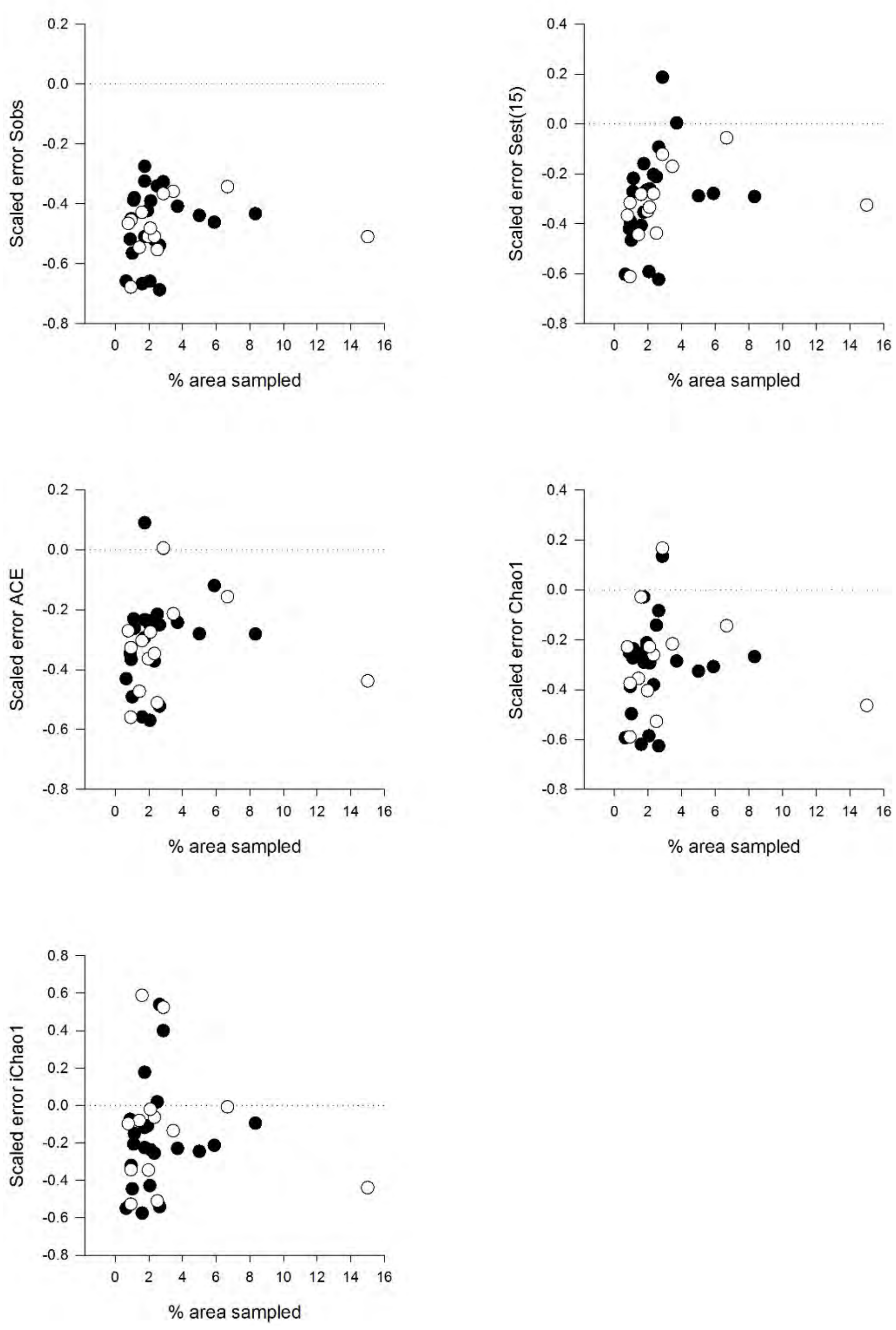


Fig. 4.3. Scaled error for the incidence-based estimators: ICE, Chao2, iChao2, Jack1, Jack2, and Bootstrap plotted against the percentage of area sampled for all 35 islands. Islands in Lakes Russell and Thurmond are indicated by black and white circles, respectively. True richness for each site is indicated by the dotted reference line at zero.

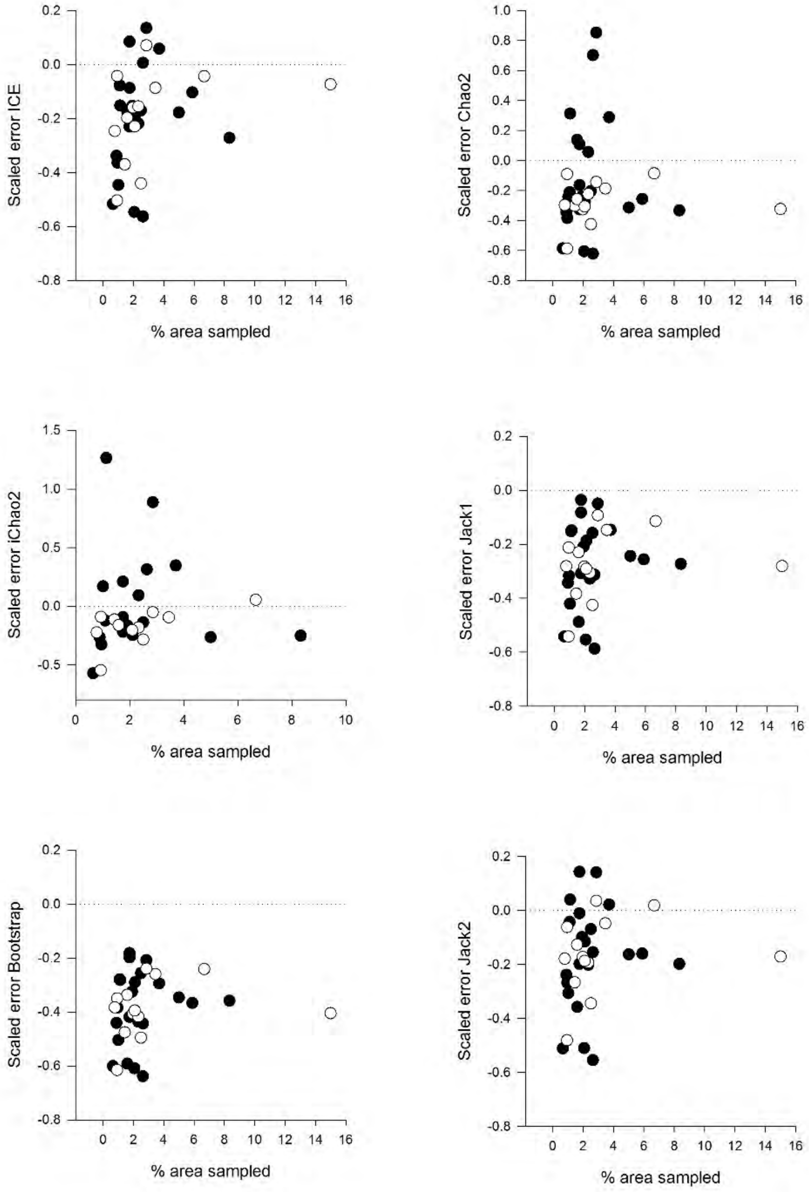


Fig. 4.4. Relationship between island area and true species richness for all 35 islands. We also illustrate the relationship between island area and abundance-based species richness estimators: S_{est} (15), ACE, Chao1, and iChao1. Islands in Lakes Russell and Thurmond are indicated by black and white circles, respectively. Only true species richness increased significantly across island size in both lakes (upper left; $R^2 = 0.27$, $p = 0.002$), exhibiting a positive species-area relationship. The regression lines for true species richness in Lakes Russell and Thurmond are solid and dashed, respectively.

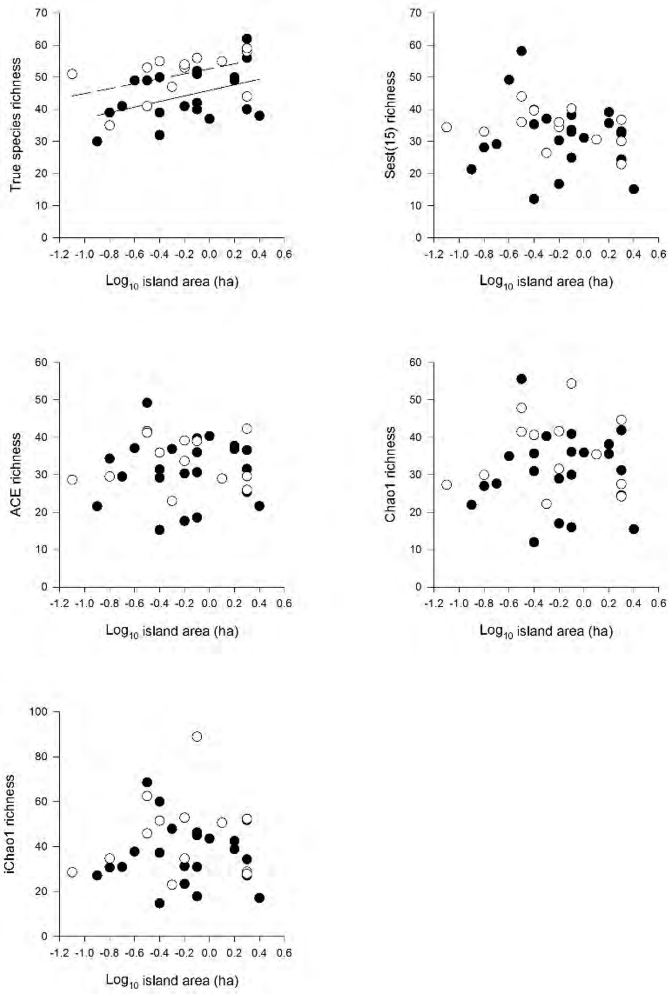
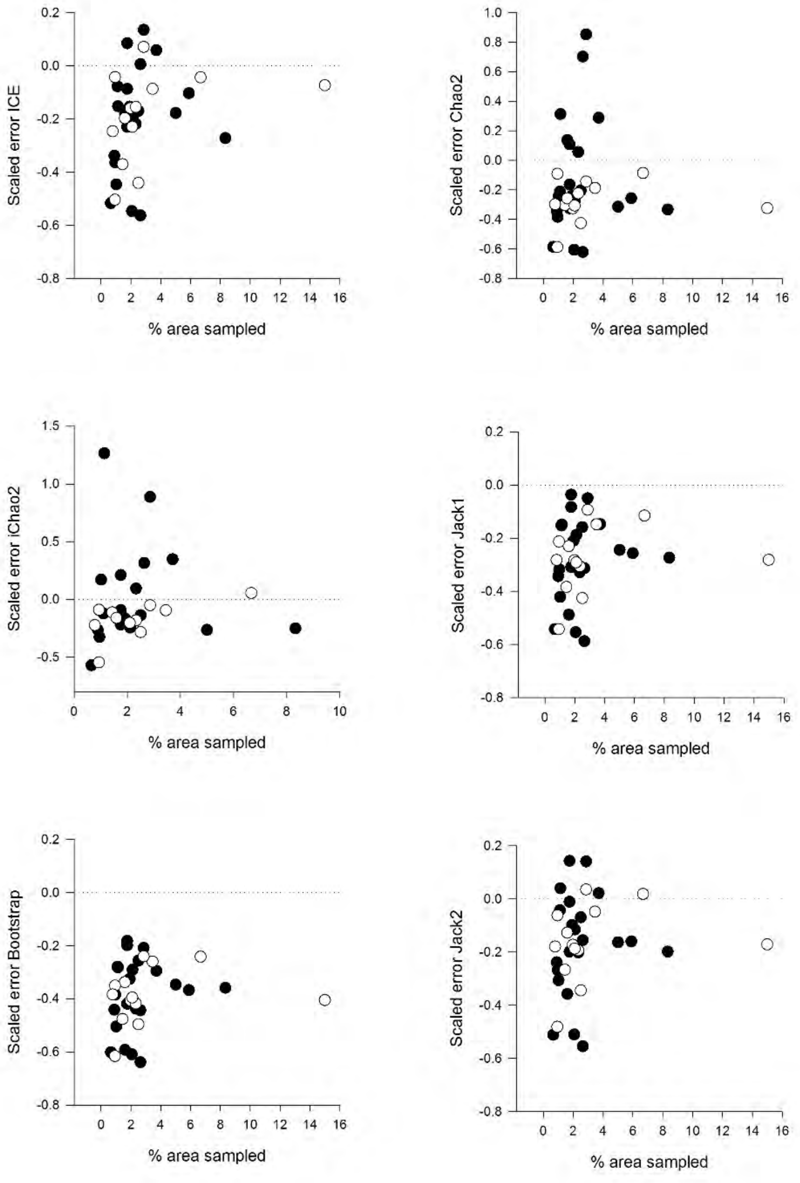


Fig. 4.5. Relationship between island area and and incidence-based species richness estimators: ICE, Chao2, iChao2, Jack1, Jack2, and Bootstrap. Islands in Lakes Russell and Thurmond are indicated by black and white circles, respectively.



SUPPLEMENTAL MATERIAL

Table 4.S1. Species detected during island inventories, the number of individuals sampled across all islands, the number of plots (out of 239) each species was detected, the number of islands (out of 35) on which each species appeared in plot samples or thorough island inventories, and the species detectability. Species are listed in order of increasing abundance.

Species	Individuals sampled	# of plots	# of islands found in plots	# of islands	Species detectability†
Acer negundo	0	0	0	1	0
Asimina parviflora	0	0	0	1	0
Betula lenta	0	0	0	1	0
Celastrus orbiculatus	0	0	0	1	0
Elaeagnus umbellata	0	0	0	1	0
Fraxinus pennsylvanica	0	0	0	1	0
Gonolobus suberosus	0	0	0	1	0
Gordonia lasianthus	0	0	0	1	0
Hedera helix	0	0	0	1	0
Juglans nigra	0	0	0	1	0
Melia azedarach	0	0	0	1	0
Nandina domestica	0	0	0	1	0
Prunus angustifolia	0	0	0	1	0
Pyrus calleryana	0	0	0	1	0
Quercus muhlenbergii	0	0	0	1	0
Rhodedendron canescens	0	0	0	1	0
Triadica sebifera	0	0	0	1	0
Ulmus americana	0	0	0	1	0
Vitis cinerea	0	0	0	1	0
Alnus serrulata	0	0	0	2	0
Amelanchier laevis	0	0	0	2	0
Ilex vomitoria	0	0	0	2	0
Fagus grandifolia	0	0	0	3	0
Sambucus canadensis	0	0	0	3	0
Amorpha fruticosa	0	0	0	4	0
Crataegus sp3	0	0	0	4	0
Matelea carolinensis	0	0	0	4	0
Gleditsia triacanthos	0	0	0	5	0
Ligustrum sinense	0	0	0	5	0
Quercus coccinea	0	0	0	7	0
Platanus occidentalis	0	0	0	8	0
Populus deltoides	0	0	0	8	0
Salix nigra	0	0	0	9	0

Cyrilla racemiflora	1	1	1	1	0.0002
Quercus laurifolia	1	1	1	1	0.0002
Tilia americana	1	1	1	1	0.0002
Celtis laevigata	1	1	1	2	0.0002
Acer floridanum	1	1	1	3	0.0002
Frangula caroliniana	1	1	1	3	0.0002
Quercus sinuata	1	1	1	3	0.0002
Chionanthus virginicus	1	1	1	4	0.0002
Passiflora lutea	1	1	1	4	0.0002
Vitis aestivalis	1	1	1	4	0.0002
Magnolia grandiflora	1	1	1	6	0.0002
Liriodendron tulipifera	1	1	1	10	0.0002
Cephalanthus occidentalis	1	1	1	20	0.0002
Elaeagnus angustifolia	2	1	1	1	0.0004
Ilex cuthbertii	2	1	1	4	0.0004
Clinopodium georgianum	2	1	1	5	0.0004
Betula nigra	2	2	1	5	0.0004
Ulmus rubra	2	2	2	2	0.0004
Mimosa microphylla	2	2	2	9	0.0004
Quercus marilandica	3	1	1	1	0.0007
Smilax walteri	3	3	2	5	0.0007
Robinia pseudo-acacia	4	2	1	2	0.0008
Aesculus sylvatica	5	3	1	3	0.001
Asimina triloba	5	3	1	3	0.001
Passiflora incarnata	5	3	3	8	0.001
Ceanothus americanus	5	5	3	7	0.001
Quercus rubra	5	5	4	6	0.001
Styrax grandifolius	5	5	5	17	0.001
Fraxinus americana	6	6	5	17	0.001
Callicarpa americana	7	7	6	15	0.002
Berchemia scandens	8	4	2	5	0.002
Ilex opaca	8	4	4	11	0.002
Sassafras albidum	8	6	5	20	0.002
Morus rubra	9	5	3	10	0.002
Acer leucoderme	9	7	3	18	0.002
Viburnum rufidulum	9	5	4	5	0.002
Vaccinium stamineum	9	7	4	14	0.002
Rhus glabra	10	8	6	12	0.002
Crataegus sp1	11	9	9	16	0.002
Albizia julibrissin	12	9	3	14	0.003
Bignonia capreolata	12	7	5	11	0.003
Smilax rotundifolia	12	9	6	9	0.003
Cocculus carolinus	12	10	6	16	0.003
Oxydendrum arboreum	13	5	1	8	0.003
Smilax smallii	17	8	5	12	0.004
Amelanchier arborea	18	12	7	20	0.004
Campsis radicans	18	14	8	14	0.004
Parthenocissus quinquefolia	18	11	9	27	0.004

Pinus virginiana	18	12	9	20	0.004
Ilex decidua	19	8	4	9	0.004
Lonicera sempervirens	19	19	10	18	0.004
Baccharis halimifolia	20	10	5	14	0.004
Viburnum prunifolium	20	11	8	19	0.004
Quercus falcata	21	15	8	20	0.005
Rubus argutus	21	21	11	31	0.005
Elaeagnus pungens	22	8	3	4	0.005
Hypericum hypericoides	22	18	12	26	0.005
Quercus phellos	22	19	14	32	0.005
Celtis tenuifolia	25	15	10	20	0.006
Cornus florida	25	16	10	26	0.006
Aralia spinosa	29	10	5	7	0.007
Cercis canadensis	29	10	6	14	0.007
Prunus umbellata	29	18	10	24	0.007
Euonymus americanus	31	16	11	17	0.007
Toxicodendron radicans	33	23	12	28	0.007
Crataegus sp2	38	30	14	23	0.009
Vaccinium pallidum	38	33	17	30	0.009
Quercus alba	41	31	15	27	0.009
Quercus velutina	46	35	16	27	0.01
Rhus copallina	50	31	18	32	0.01
Ostrya virginiana	55	29	15	24	0.01
Pinus echinata	63	46	19	31	0.01
Nyssa sylvatica	65	22	16	28	0.01
Carya glabra	74	45	16	30	0.02
Prunus serotina	78	51	21	28	0.02
Diospyros virginiana	89	51	24	35	0.02
Quercus stellata	90	57	21	30	0.02
Acer rubrum	92	44	18	29	0.02
Myrica cerifera	103	21	6	8	0.02
Vaccinium elliottii	116	46	19	32	0.03
Quercus nigra	122	65	27	34	0.03
Vaccinium arboreum	123	42	16	31	0.03
Carya alba	137	57	20	28	0.03
Smilax bona-nox	138	91	28	34	0.03
Smilax glauca	139	95	27	34	0.03
Lonicera japonica	149	79	25	31	0.03
Vitis rotundifolia	175	97	31	35	0.04
Pinus taeda	224	85	24	33	0.05
Liquidambar styraciflua	226	74	24	33	0.05
Juniperus virginiana	394	126	30	32	0.09
Gelsemium sempervirens	418	135	31	32	0.09
Ulmus alata	468	133	33	35	0.11

†Species detectability is calculated as the relative abundance of each species across the entire set of 35 islands.

CHAPTER 5

CONCLUSIONS

The goals of this research were to understand how forest fragmentation impacts woody plant species richness and composition in southeastern US Piedmont oak-hickory forests; elucidate whether or not woody species commonly observed on forest fragment edges have the ability to invade relatively undisturbed forest interior; and determine whether species richness estimation techniques can be reliably used in place of true richness to examine gradients in species richness. With few exceptions, studies of forest fragmentation have typically focused on single species responses or only aim to quantify vegetation responses to a single fragmentation process (i.e., reduced area, increased isolation, edge effects, or time since fragmentation; Ibáñez et al. 2014). Rarely, have studies attempted to integrate examination of these processes for a more general view of how fragmentation is acting to degrade woody plant communities of forest ecosystems. One notable exception is the Biological Dynamics of Forest Fragments Project (BDFFP), in Amazonian rainforest, where tracts of rainforest were fragmented into various sized fragments (Laurance et al. 2011) over 30 years ago. While I certainly did not have 30 years to examine these processes in southeastern oak-hickory Piedmont forests, I purposefully chose to study the entire woody plant community, incorporated edges and interior forest, and examined two distinct forest fragment habitats (small forested islands and nearby remnant mainland forest with only a single exposed edge). I used 35 forested islands and 10 remnant mainland forest sites in two reservoirs along the South

Carolina/Geogia border that were created 30 years apart, and have been isolated for nearly 40 and 70 years. I took both a community-level and species-specific approach to how oak-hickory forest communities may respond to fragmentation into small, isolated forest fragments. It was through this work that I identified that species richness estimators may not be useful tools for assessing species richness responses, and investigated whether or not any of the species richness estimation tools performed well in my study system.

In order to take a more integrated approach to how fragmentation is impacting forested communities, I addressed several questions related to the various processes proposed to be at work in forest fragments. First, I hypothesized that small forest fragments would have species-area and species-isolation relationships as predicted by the Equilibrium Theory of Island Biogeography (MacArthur and Wilson 1967). I found that forested islands in my study system did conform to the species-area relationship (SAR), although when I considered woody habits separately I found that it was tree species – and not shrubs and lianas – primarily driving this relationship. However, the number of liana and shrub species were markedly greater in Lake Thurmond, which is 30 years older than Lake Russell, and time since isolation may explain why liana and shrub species richness was higher in the older set of fragments.

Forest species composition was significantly impacted by fragmentation such that while typical overstory species associated with oak-hickory forest appear to be surviving, a host of disturbance-tolerant and non-native woody species have become a significant part of woody plant species community on forest reservoir islands. These changes in composition are similar to findings in the BDFFP, where the smallest fragments have significantly diverged in species composition from the largest fragments and intact forest primarily due to proliferation of pioneer tree and liana species (Laurance et al. 2002, Laurance et al. 2011). By integrating examination of the overstory, understory, and seedling layer for sites in one lake, I conclude that species composition will likely continue to degrade, and that nearly 50% of the tree species on some islands are at risk of extinction.

An experimental outplanting of two non-native woody species, *Albizia julibrissin* Durazz. (Fabaceae, mimosa/silk tree) and *Lonicera japonica* Thunb. (Caprifoliaceae, Japanese honeysuckle), to the edges and interiors of forest islands and mainland sites provided unique insight on how species-specific responses can vary in response to fragmentation. While both species appear to have the capability of surviving in conditions typical of forest interior, *L. japonica* showed a much greater tolerance to low light levels. In contrast, *A. julibrissin* had significantly lower survival and growth under interior forest conditions, although a small number of individuals did survive in this habitat over the three-year duration of the study. In addition, herbivory on *A. julibrissin* was markedly higher in forested fragment interiors, and this was the first study to quantify leaf herbivory for this species. It appears that control of propagule flow for *L. japonica* is the only way to curb eventual invasion to forest interior, while maintenance of undisturbed forest interior will limit invasion for *A. julibrissin*.

Examination of 10 species richness estimators for use with abundance or incidence (presence-absence) data for all woody species that occurred on the 35 islands sampled found that estimator performance varied widely, and that use of estimated species richness obscured the species-area relationship I identified using true species richness of the islands. Nine of 10 species richness estimators were significantly negatively biased. All of the estimators were not precise, meaning that estimated richness values in relation to the true richness fluctuated greatly across all 35 islands. This result highlights how estimated species richness is not appropriate to use when comparisons of species richness among sites is the goal, and I recommend that these techniques not be used when more than a single site is of interest.

Future research directions

Forest fragmentation is not a problem limited to the past, but is a process that is continuing across the globe as forests are being fragmented into smaller and more isolated patches (Haddad et al. 2015). Recent meta-analysis of how fragmentation impacts plants and plant communities highlights the importance of taking a broader view of fragmentation processes in order to identify consistent patterns (Ibáñez et al. 2014). My research highlights how an integrated community-level and species-specific approach was able to provide novel insights to forest degradation due to fragmentation in southeastern oak-hickory forests. I found patterns in oak-hickory forest that are similar to those found in the long-term BDFFP project, where overall species richness declined with fragment size but that richness on a per area basis was higher on islands compared to mainland forest and changes in species composition are largely due to the proliferation of disturbance-tolerant tree and liana species (Laurance et al. 2011). Long-term study of forested islands and mainland forests in and around reservoirs would provide additional insight into how immigration and extinction of long-lived woody plant species behaves in this system and may indicate if forest fragments ever truly reach an equilibrium. Experiments that not only test the germination and seedling performance of non-native woody plant species on edges and interior of forest fragments, but also include typical overstory species associated with southeastern oak-hickory forests would prove fruitful to determine whether small forest fragments have any capacity to continue to house these species. A valuable addition to the meta-analysis performed by Ibáñez et al.(2014) would be to expand upon their findings to identify if there is a particular fragment size for which all the community response variables they identified are consistently negatively impacted.

In addition, species richness estimation techniques can only improve if there are robust datasets where true richness of the areas of interest are known (Palmer 1990, Walther and Moore 2005). Future research to correct the issue of estimator inaccuracy are desperately needed. Species richness estimation tools are attractive because they allow the user to truncate the sampling effort needed to gain the true value for species richness and they are widely available in free statistical software packages. However, there is little doubt that patterns in species richness based on estimated richness are flawed, and caution should be used when employing these techniques. It will be imperative in future research efforts regarding richness estimators to determine if there are truly any sample completeness criteria that can be used to ensure that an estimator will perform accurately across a set of sites. It may be that particular estimators work best with particular species abundance patterns, but this has yet to be investigated thoroughly. Most modern estimators have used data from tropical communities to validate their usefulness which may have limited their applicability in other regions of the world. It may be that even slight variations within species abundance patterns for the same community may produce wildly disparate estimates and perhaps general estimators are not appropriate, but must be specialized for the community type of interest.

REFERENCES

Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, W. M. Cook, E. I. Damschen, R. M. Ewers, B. L. Foster, C. N. Jenkins, A. J. King, W. F. Laurance, D. J. Levey, C. R. Margules, B. A. Melbourne, A. O. Nicholls, J. L. Orrock, D.-X. Song, and J. R. Townshend. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances **1**.

Ibáñez, I., D. S. W. Katz, D. Peltier, S. M. Wolf, and B. T. C. Barrie. 2014. Assessing the integrated effects of landscape fragmentation on plants and plant communities: the challenge of multiprocess-multiresponse dynamics. Journal of Ecology **102**:882-895.

Laurance, W. F., J. L. C. Camargo, R. C. C. Luizão, S. G. Laurance, S. L. Pimm, E. M. Bruna, P. C. Stouffer, G. Bruce Williamson, J. Benítez-Malvido, and H. L. Vasconcelos. 2011. The fate of Amazonian forest fragments: A 32-year investigation. Biological Conservation **144**:56-67.

Laurance, W. F., T. E. Lovejoy, H. L. Vasconcelos, E. M. Bruna, R. K. Didham, P. C. Stouffer, C. Gascon, R. O. Bierregaard, S. G. Laurance, and E. Sampaio. 2002. Ecosystem decay of Amazonian forest fragments: A 22-year investigation. Conservation Biology **16**:605-618.

MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

Palmer, M. W. 1990. The estimation of species richness by extrapolation. Ecology **71**:1195-1198.

Walther, B. A. and J. L. Moore. 2005. The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. Ecography **28**:815-829.