12-15-2012

Mechanisms and Patterns of Invasion in Macrophyte Communities

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Recommended Citation

Fleming, Jonathan Paul, "Mechanisms and Patterns of Invasion in Macrophyte Communities" (2012). *Theses and Dissertations*. 3052.
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Mechanisms and patterns of invasion in macrophyte communities

By

Jonathan P. Fleming

A Dissertation
Submitted to the Faculty of
Mississippi State University
in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy
in Forest Resources
in the Department of Wildlife, Fisheries and Aquaculture

Mississippi State, Mississippi

December 2012

Mechanisms and patterns of invasion in macrophyte communities

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Pages in Study: 117

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Aquatic plants (macrophytes) are important components of freshwater ecosystems and serve numerous purposes, physical and biological, that help to structure aquatic communities. Although macrophytes represent an essential component of stable aquatic communities, invasive macrophytes may negatively alter ecosystem properties. Non-native, invasive species have been identified as a major cause of biodiversity loss and the increasing prevalence of invasive species has prompted studies to help understand their impacts and to conserve biodiversity. Studying mechanisms of invasion also gives insight into how communities are structured and assembled. This study examined mechanisms that contribute to macrophyte invasion. First, I reviewed literature concerning mechanisms of macrophyte invasion. Mechanisms identified with this review were then placed within the context of the invasion process and potential taxonomic biases were discussed. Second, a set of classic invasion hypotheses were tested, including biotic resistance, disturbance, and stress, using mixed-effects models on survey data collected from twenty-nine lakes across the United States. Finally, using the same survey data, I performed an observational test of Darwin's Naturalization Hypothesis at a small (point) and large (lake) scale for two highly invasive macrophytes, *Potamogeton crispus* and *Myriophyllum spicatum*. Results of the first study indicated that many invasion mechanisms have been tested with fully aquatic macrophytes with varied levels of support. In addition, there is likely a taxonomic bias depending on geographic location of the invaded area. The second study indicated that biotic interaction, disturbance, and stress interact, often in non-linear ways to influence probability of an invasive species occurring at a location. However, models containing these variables explained a relatively low percentage of variation in probabilities. Finally, there was no support for Darwin’s naturalization hypothesis at either a point or lake scale. Future research should continue the search for mechanisms that allow introduced species to establish. It is likely that general principles do not exist, at least among comparisons across ecosystem types. However, ecologists should continue to search for general patterns within definable ecosystem units to increase understanding about factors contributing to invasibility.

DEDICATION

For my family…

ACKNOWLEDGEMENTS

To sufficiently thank everyone that has helped me get to this point I would have to include another chapter and it still probably would not be enough. Many thanks are owed to the Department of Wildlife, Fisheries, and Aquaculture, the Forest and Wildlife Research Center, and the Geosystems Research Institute at Mississippi State University for the use of facilities and resources. Ryan Wersal assisted with questions about the data used in this research. Dr. Greg Gaston at the University of North Alabama never failed me with his encouragement, wisdom, and guidance. I am indebted to him for his inspiration. I would like to thank Dr. Bruce Leopold for giving me opportunities and responsibilities that have made my graduate education unique and fulfilling. Dr. Jerry Belant provided new perspectives as a committee member and always challenged me beyond my comfort zone. Dr. Gary Ervin has greatly impacted my graduate education through things he taught me and his constructive feedback as a committee member. I certainly cannot thank Dr. John Madsen enough for initially providing me with the opportunity to attend MSU. In addition, he is responsible for providing me with the data used in this research and for that I am grateful. I won the professor lottery when Dr. Eric Dibble became my adviser. He has taught me much more than he will ever know about being a good scientist and student mentor. My parents, Gary Don and Cindy Fleming, are my foundation. My love of nature and the outdoors results from the experiences they provided to me from the time I could wear a life jacket. They have supported me through

all my adventures and were always there to help, always supportive, and never complacent.

To every one of these people and the ones that I undoubtedly left out I give my greatest thanks.

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CHAPTER I

INTRODUCTION

Introduction

Aquatic plants (macrophytes) are important components of aquatic ecosystems. They inhabit numerous environments including fresh and salt-water as well as lentic and lotic systems. Macrophytes serve numerous purposes, physical and biological, that help to structure the aquatic community (Carpenter and Lodge 1986). Macrophytes help to stabilize sediments and reduce erosion and impacts from wind (and wave) action (Barko and James 1998, Sand-Jensen 1998, Madsen et al. 2001). In addition, they can affect the physicochemistry of their surrounding water column by altering carbon-oxygen dynamics, contributing carbon to the detrital food-web, and fueling microbial trophic dynamics (Sand-Jensen et al. 1982, Honnell et al. 1993, Barko and James 1998). They may also reduce turbidity which can serve as positive feedback mechanism for macrophyte persistence and may also alter the foraging ability of phytophylic visual predators, thus impacting the trophic dynamics of the aquatic food web (Scheffer 1998, Scheffer 1999).

In addition to the physicochemical impacts of macrophytes, they also serve numerous biological roles. Macrophytes serve as a basal resource in the aquatic food web, facilitating other primary producers (e.g., epiphytes and periphytes; Campeau et al. 1994, Kornijow et al. 1995, de Szalay and Resh 2000) which may be the most important contributor to the productivity of a system (Cattaneo and Kalff 1980, Cattaneo et al. 1998). They contribute structure and complexity to the littoral zone of aquatic ecosystems which provides refuge for juvenile fishes as well as other prey items such as invertebrates and zooplankton (Lodge et al. 1998, Burks et al. 2002, Taniguchi et al. 2003, Dibble et al. 2006). The complexity provided by macrophytes has been repeatedly demonstrated as contributing to the biodiversity of aquatic communities (Crowder and Cooper 1982, Killgore et al. 1989, Diehl 1992, Cheruvelil et al. 2002, Cottenie and De Meester 2004, Thomaz et al. 2008). Greater complexity also may provide greater ecosystem resilience especially from disturbances (Dodds 2009) such as cultural eutrophication that might otherwise have significant negative impacts (Barko and James 1998, Sondergaard et al. 2007).

Although macrophytes represent an essential component of stable aquatic communities, invasive macrophytes may negatively alter ecosystem properties. Non-native, invasive species have been identified as a major cause of biodiversity loss (Clavero and Garcia-Berthou 2005). The increasing prevalence of invasive species has prompted studies cross multiple ecosystem and community types in an effort to understand their impacts and help to conserve biodiversity.

Invasive macrophytes impact the aquatic community in numerous ways. These species may form dense monotypic stands which have been demonstrated to negatively impact fish foraging (Theel and Dibble 2008) and invertebrate diversity (Cheruvelil et al. 2002). Heterogeneity is potentially a mechanism to explain patterns of species diversity, and the homogenization of aquatic plant assemblages leads to a decrease in littoral heterogeneity. Invasive macrophytes may also alter physical properties of systems by changing hydrologic regimes through flow alterations, and the associated costs to human society (Madsen et al. 2001, Pimentel et al. 2005).

Studying macrophyte invasions provides an opportunity to learn more about how communities are structured and assembled (Herben et al. 2004). In addition, a major goal of invasion ecology is the explanation of why some species are invasive and/or if some communities are more likely to be invaded than others (Shea and Chesson 2002). To study mechanistic hypotheses related to these invasions, patterns of invasions must be identified and then hypotheses developed and tested to explain the invasions (Daehler 2001). This is particularly interesting because mechanisms could be properties of a species, community, environment, or interactions among and between them which makes testing mechanistic hypotheses even more difficult without established patterns. This highlights the importance of pattern identification before addressing questions related to the processes that cause them.

Invasions are often viewed as a process as opposed to a discrete event. The invasion process may be described and assessed by a series of stages including transport, introduction, establishment, spread, and finally impact (Lockwood et al. 2007). At each phase there is opportunity for a given species to succeed (filter through to the next phase) or fail (die or fail to reproduce). The establishment phase may be of most interest to community ecologists because this is the phase where properties of the species, community the species is introduced into, or the environment determine if the species is successful (Shea and Chesson 2002). This is also the stage where the most insight into community assembly can be assessed because it is governed by biotic interactions that may facilitate or deter a species from establishing, regardless of the characteristics of the species or abiotic environment.

There are numerous competing hypotheses that attempt to explain patterns of invasion (invader success) at the community level. Mitchell et al. (2006) identified several hypotheses that specifically invoke biotic interaction. These authors argued that success is a function of enemies, mutualists, competitors, and abiotic conditions, as well as interactions among them. A long standing debate is if native diversity stabilizes a community and provides resistance to invasions (Levine and D'Antonio 1999, Herben et al. 2004). Many studies have assessed the native-exotic richness relationship (NERR) to address this debate. On one end of the argument, biotic resistance is suggested (negative NERR; e.g., Kennedy et al. 2002) whereas the "rich get richer" hypothesis, which explains patterns of invasion based on resource availability (positive NERR; e.g., Stohlgren et al. 2003) lies on the other end. Biotic resistance is based on the premise that ecological communities are constrained by numerous micro-habitats and/or finite resource availability, and that these habitats can become saturated under conditions of increased diversity, thus leading to intense competition (Levine et al. 2004, Smith and Shurin 2006). These seemingly conflicting results known as "invasion paradox" (sensu Fridley et al. 2007) are unresolved because empirical studies across different systems and scales have conflicting results. These hypotheses are supported by a body of theoretical and empirical models, but universalities that cross ecosystem boundaries and multiple scales have not been supported.

The importance of scale in understanding ecological pattern and process has been increasingly recognized in development of community ecology theory (Levin 1992). As identified in the invasion paradox, hypotheses regarding the native-exotic richness relationship are not immune to the potential impacts of scale. For example, in empirical studies, NERR patterns have been found to be intensively scale dependent. In small scale studies (e.g., 1 - 10m^2), negative NERR patterns have been identified, but when the scale of observation increases the relationship shifts to positive (Byers and Noonburg 2003, Fridley et al. 2007). This may be explained by increased environmental heterogeneity (and therefore microhabitats) at larger scales which allow greater opportunity for a variety of species to co-exist (Davies et al. 2005).

Within aquatic communities, specifically submersed macrophyte assemblages, patterns do not show a clear trend, and these hypotheses have not been extensively evaluated (but see Capers et al. 2007, and Thomaz and Michelan 2011). Aquatic systems provide a unique opportunity because ecosystem boundaries are more easily defined, there are physical parameters that can be used to divide the system into numerous zones that have related but expressively different properties (e.g., littoral and pelagic zones), and hypotheses can often be tested at multiple scales.

Competing but not mutually exclusive hypotheses to explain co-occurrence of native and invasive species have also been developed. In addition to questions of species establishment, richness relationships, and biodiversity (common community descriptors), there are also hypotheses that can be tested concerning patterns of phylogenetic diversity in communities. Although the writings and ideas of Charles Darwin have provided a fundamental base for ecological insight, some of his hypotheses have rarely been tested empirically, especially in macrophyte assemblages with fully aquatic invasives (but see meta-analysis by Ricciardi and Atkinson 2004, and Thomaz and Michelan 2011 for example using the invasive macrophyte *Urochloa subquadripara* – tropical signalgrass). Darwin's naturalization hypothesis (DNH) predicts that an introduced species is unlikely to succeed in its introduced environment if a congeneric native is already present (i.e., closely related species are less likely to coexist; Darwin 1859). This can be attributed to intense competition between an invader and a congeneric species already adapted to the current environment. If explanations for patterns of species diversity are central to the science of ecology, evaluations of DNH may have large practical implications, especially in the context of invasion ecology and biological conservation.

Few studies have empirically tested DNH or its extensions and analyses of additional groups are needed to test its generality (Daehler 2001). There are numerous observational studies which cross numerous ecosystems which have used predictions of DNH (e.g., Proches et al. 2008). However, few experimental studies have been conducted, and those occurred in a limited number of systems (Jiang et al. 2010). More importantly, there is little known about how scale actually affects congeneric co-occurrence in different systems. Few studies have addressed DNH in aquatic communities and none that I am aware of have addressed this hypothesis specifically with fully aquatic macrophytes. Finally, there is little information available concerning the interactions between NERR, DNH, and scale. This provides an opportunity to study these hypotheses independently, but also as they relate to one another to gain insights into community and invasion ecology.

Knowing the large importance and impacts of macrophytes on aquatic ecosystems and in particular, fish, a more thorough understanding of mechanisms that contribute to invasion or resistance can contribute to overall improvement in aquatic resource management and biodiversity conservation. Whereas several studies have attempted to review the current state of knowledge regarding macrophyte impacts on aquatic fauna (e.g., Dibble et al. 1996, Schultz and Dibble 2012), none that I am aware of have specifically reviewed mechanisms contributing to macrophyte invasion. This presents a potentially large disconnect between invasion mechanisms as a whole, and those that specifically contribute to macrophyte invasion. A review of invasion mechanisms with a specific focus on fully aquatic macrophytes will begin to help identify gaps or trends in this current state of knowledge. This assessment is essential because current recommendations may be based on generalities that have no support in the literature and may simply represent conjectures and extrapolations.

Objectives

Based on the previously mentioned studies and the current lack of knowledge in how these patterns compare in macrophyte communities I propose the following objectives to address in this dissertation. First, I will review the literature to identify ecological mechanisms that have been studied in aquatic plant invasions, identify trends in the taxonomic groups studied, and put these into a framework of the invasion process. The goal of this research is to provide a summary that will assist in management decisions and to highlight areas that need further study. Second, I will investigate patterns of native-richness/exotic-presence relationships in aquatic macrophyte assemblages at a small (point) scale. Specifically I will test for patterns indicative of biotic resistance, disturbance, and stress. Finally, I will investigate patterns of congeneric co-occurrence for two highly invasive macrophytes, *Potamogeton crispus* and

Myriophyllum spacutum, at two scales. Specifically, for this objective I will perform an observational test of Darwin's naturalization hypothesis (using congeneric species).

Study Area Description and Data Collection

The study area for the second and third objectives spanned the conterminous United States, where lakes and reservoirs (hereafter collectively referred to as lakes; n = 29) were surveyed once at various times from 1997 to 2011 (Figure 1.1, Appendix A). Lakes represented a variety of areas ranging from 7-36,000 ha and 9 freshwater ecoregions (Appalachian Piedmont 1, Chesapeake Bay 2, Colorado 1, Columbia Glaciated 3, Laurentian Great Lakes 8, Lower Mississippi 7, St. Lawrence 1, Upper Mississippi 3, Upper Missouri 3). Each lake was originally surveyed for a specific project goal to obtain a baseline of invasive and native species occurrence and distribution using the point-intercept method (Madsen 1999). For each lake, a grid of points was generated in a GIS and integrated with field GPS to navigate to each point by boat. Point spacing varied by lake area to ensure representative sampling in each lake. At each sample point, a rake was tossed and retrieved to collect plants occurring at that location. Rake tosses generally collect plants directly under the boat and are dragged 1-2 m along the bottom. This method allowed a large number of samples to be collected and insured that all plants occurring in an area were accounted for. Each plant collected in a given lake was identified to species and recorded as present (1) or absent (0) at the location. The resulting data were used to fit models based on probability of occurrence of invasive species using a variety of environmental and community based metrics.

Scope and Importance

Several studies have examined relationships between native species richness and invasions. However, few studies have been performed in aquatic systems and even fewer with submersed macrophytes. In addition, no studies have used a multi-regional dataset. This study will contribute to our currently limited knowledge regarding native-richness/exotic-presence relationships and how relatedness impacts community invasiveness in macrophyte assemblages. Results of this study will contribute to our understanding of community assembly, especially in the context of ecological invasions, and may help predict potential extinctions and loss of native biodiversity. This also will help to prioritize management goals based on characteristics of communities and newly introduced species. For example, a community invaded by a novel genus or distantly related species may be a higher management or eradication priority than one invaded by a closely related species, at least in the short term. However, the opposite may be the case if insights into species specific requirements are discovered which can indicate greater importance of abiotic conditions as opposed to biotic interactions. In addition, a literature review of mechanisms of invasion with a specific focus on fully aquatic macrophytes will highlight future research needs and allow for more accurate management recommendation.

Figure 1.1 Location of 29 lakes surveyed in the conterminous United States for aquatic invasive plants from 1997-2011.

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CHAPTER II

ECOLOGICAL MECHANISMS OF INVASION SUCCESS IN AQUATIC MACROPHYTES

Introduction

Invasive species are a leading force of global change. They can displace native species, act as ecosystem engineers, and cause local extinctions (Vitousek et al. 1997, Mooney and Cleland 2001). For this reason, scientists have spent considerable effort trying to predict which species will become invasive or which environments are most likely to be invaded. However, species traits and environmental characteristics have been identified as factors regulating invasion potential. (Kolar and Lodge 2001, Levine 2000, Chadwell and Engelhardt 2008, Jacobs and MacIsaac 2009).

Many studies have found that single factor hypotheses alone cannot explain invasion success, but interactions, indirect, and additive effects of these factors can. Additionally, these mechanistic hypotheses have been derived through studying a wide variety of ecosystems, and the mechanisms identified in one ecosystem type may not be directly applicable to other types (e.g., terrestrial vs. aquatic systems). It follows that scientists interested in species invasions in their respective systems and taxa should identify relevant mechanisms (of the major ones proposed) that can be applied to those systems to improve the predictive understanding of factors governing invasions.

Understanding how mechanistic factors differ between ecosystem types also contributes more broadly to the study of invasion ecology as a whole.

Aquatic plant communities have received only limited study regarding mechanism of invasions. Aquatic plants are recognized widely as important components of freshwater ecosystems, and invasive species may significantly degrade aquatic systems and displace native species. Some plants exhibit prolific growth when introduced into a new area or if the environment changes in a way that alters normal growth regulation (Madsen 2004). For example, an increased nutrient load into a small pond may cause a benign species to become problematic due to an increase in plant growth. Canopy forming or floating macrophytes can significantly increase shading in the water column which prevents photosynthesis and oxygen release from phytoplankton, resulting in reduced dissolved oxygen concentrations. In addition, high plant densities can prevent water column mixing which reduces atmospheric oxygen diffusing into surface waters from reaching lower into the water column. With high plant densities also comes increased organic material and decomposition in the benthos which consumes oxygen that may be available. The net result is habitat displacement of fish and other fauna that depend on dissolved oxygen for survival (Madsen et al. 1991, Madsen 2005). An increase in plant density can reduce the foraging ability of several fish species (Theel and Dibble 2008) which may indirectly lead to growth restrictions (Olsen et al. 1995) and stunted populations. Prolific growth also may be aesthetically unpleasing, sometimes leading to improper control measures and ultimately harm to the aquatic environment. Pimentel et al. (2005) reported that the costs of nuisance aquatic plants totaled over $100 million in the U.S. annually. Therefore, the economic impact of these species also is an important consideration.

My objectives are to review the literature to identify ecological mechanisms studied in aquatic plant invasions, and put these into a framework of the invasion process. The goal of this research is to provide a summary that will assist in management decisions and to highlight areas that need further study. I restricted my review to fully aquatic freshwater species (with a few exceptions), to partition studies of wetland, estuarine, and marine from fully aquatic freshwater environments. Furthermore, to avoid overlap with recent reviews (e.g., Schultz and Dibble 2012), I have not included studies on the impact of invasive aquatic species unless the impact facilitated subsequent invasion by conspecifics or other species (as in “invasional meltdown” sensu Simberloff and Von Holle 1999). Although mechanisms are rarely mutually exclusive, I have grouped mechanisms based on context of authors (usually based on which papers authors cited). Resulting groups are 1) Influences of interspecific interactions in the recipient environment, 2) Influences of species traits on invasion success, 3) Influences of abiotic factors on invasion success, and 4) Other mechanisms of invasion success.

Influences of interspecific interactions in the recipient environment

Competition

Competition is widely regarded as one of the most important mechanisms of species invasions and has been shown to be an active force in macrophyte communities (Moen and Cohen 1989, McCreary 1991). Competitive ability (resource acquisition) of a species is regarded as an invasive trait. Additionally, biotic resistance is also based on competitive interaction theory and suggests increasing diversity increases interspecific resource competition and thus can limit establishment potential of an introduced species.

Madsen (1998) found that water column total phosphorus was one of the best predictors of *M. spicatum* dominance. This may indicate a superior resource acquisition ability which gives it a competitive advantage over native species. This may also indicate a window of opportunity (see below) in which *M. spicatum* can become dominant depending on ambient nutrient fluxes. Titus and Adams (1979) found that *Vallisneria americana* could co-exist with *M. spicatum* during mid-summer conditions because of its physiological adaptability to lower light conditions. However, during other seasons, *M. spicatum* had a competitive advantage, possibly due to increased carbon uptake abilities at lower water temperatures. In experiments evaluating competition between *M. spicatum* and *M. sibiricum*, Valley and Newman (1998) found that native *M. sibiricum* was a superior competitor, but this was at least partially due to pre-emptive growth. However, they conceded that this was not typical of field observations where *M. spicatum* displaces the native species. They suggest factors other than competition influence the invasibility of *M. spicatum*, possibly through resource pulses or phenological differences. In Lake Nassar, Egypt, *M. spicatum* was found to alter habitat conditions which further promoted its spread and allowed it to displace native species (Ali and Soltan 2006).

In an interesting study testing competitive abilities of *Hydrilla verticillata*, Spencer and Rejmanek (1989) found that type of vegetative propagule from which plants established, potentially influenced competitive abilities. They found that *H. verticillata* plants growing from turions were weaker competitors than plants growing from tubers.

However, they found that even those growing from turions could establish in existing beds of *P. pectinatus* and *P. gramineus*. They argue that once established (whether from turions or tubers), subsequent production of tubers can occur, resulting in stronger competitors better able to out-compete existing native species. Researchers also found that *H. verticillata* out-competed *V. americana* under conditions of high sediment nutrient availability (Van et al. 1999). However, under lower nutrient conditions its competitive effects were diminished, indicating that particular environmental conditions facilitated competitive displacement.

Herb and Stefan (2006) experimentally tested competition between several macrophytes and based on their results they predicted that invasive species can suppress growth of native species over a wide range of environmental conditions. Roberts et al. (1999) did not specifically test the mechanism by which *E. densa* displaces *V. americana* but suggested that that competition for light (*E. densa*'s canopy cover) was conceivable. Light is often noted as one of the most limiting resources for macrophyte growth and thus canopy forming invasive species may out-compete natives.

In neotropical rivers and lakes, Thomaz et al. (2009) tested if diversity affected occurrence of invasive *Urochloa subquadripara* or *H. verticillata*. They found a positive relationship with *U. subquadripara* but a negative relationship with *H. verticillata*. They noted that microhabitat partitioning (colonization depth) was different with *H. verticillata* which may explain its lower occurrence with native species (as opposed to competitive exclusion by natives). Michelan et al. (2010) found that *U. subquadripara* could out-compete most native macrophytes for light. However, because of its growth habit, it also facilitated colonization of floating species, although this did not offset a net loss in native species diversity.

Scientists concerned with climate change have studied its potential influences on competitive interactions of aquatic plant invasions. Murmul et al. (2012) observed that although temperature did not seem to have an effect, water "brownification" (increased organic carbon concentrations, resulting in browner water) owing to changing climatic conditions resulted in increased growth of invasive *E. canadensis* and decreased growth of native species. They suggest that this brownification gives *E. canadensis* a competitive advantage, facilitating increasing future spread. Sousa et al. (2009) found that environmental conditions influenced the ability *of H. verticillata* to compete with native *Egeria najas*. They found that in riverine conditions, *H. verticillata* could accumulate biomass more quickly which allowed it to suppress and out-compete native *E. najas*. In another competition experiment, Stiers et al. (2011) found that *Lagarosiphon major* could out-compete the cosmopolitan *Ceratophyllum demersum* because of plastic responses to stressful conditions (low free CO_2 and high pH). They observed, however, that some niche partitioning occurred which facilitated co-existence as opposed to full competitive exclusion. Floating plants make potentially good invaders because of their propensity to restrict light penetration into the water column. In competition growth experiments, Netton et al. (2010) found that under simulated warming conditions and nutrient loading (predicted as part of future climate change), introduced floating *Salvinia natans* could effectively out-compete the introduced (but naturalized) *E. nuttallii*. In another interesting paper, Urban et al. (2006) found that invasive *Utricularia inflata* formed dense canopies that affected nutrient cycling processes (redox and pH) provided by *Equestium aquaticum* which could result in changes that impact native species, providing an example of an indirect effect of competition on native community structure.

All of these examples highlight the potential for competition to influence successful invasion. Ultimately, competition may be the most important mechanism because it is generally associated with the success of one organism over another. Other mechanism may promote or facilitate competition (as noted below), and therefore competition may only be the outcome of a much more complex interaction chain during the invasion process.

Enemy Release and EICA

The enemy release hypothesis predicts that invasions are successful because natural enemies (predators, parasites, or pathogens) of the invasive species are absent in the introduced environment (Colautti et al. 2004, Torchin and Mitchell 2004). In aquatic macrophytes, this concept has important ramifications because of the need to develop effective management options, namely biological control (Cuda et al. 2008). Evidence supporting enemy release has been mixed and many studies have found that biotic resistance from enemies in the receiving community is stronger than effects of natural enemies in its native environment. Parker and Hay (2005) found that introduced (exotic) macrophytes were preferentially eaten by native herbivores over native macrophytes in the receiving community. Their results indicate that enemies do impact invasion success but that biotic resistance from native herbivores was indeed stronger than any potential advantage gained through enemy release. This has been supported in other studies where generalist herbivores preferentially consumed non-indigenous plants and suggests that past invasion successes could be the result of native generalist herbivore removal from the recipient community which would weaken potential biotic resistance (Morrison and Hay 2011). On the other hand, studies of a generalist herbivorous snail found that it consumed native plant species preferentially over exotic species (Xiong et al. 2008). Although this is not directly linked to enemy release, it does indicate that it receives less pressure from enemies in the recipient environment than native species which could give the invader a competitive advantage.

In studies of *Elodea canadensis* and *E. nuttallii*, two introduced species in Europe, researchers found that herbivores exhibited seasonal differences in consumption of these two species (Boiche et al. 2010). They hypothesized that these differences could be attributable to temporal variation in the arrival of these species (*E. canadensis* was introduced first and is less acceptable to native herbivores in summer).

In some cases, hybrid vigor (heterosis) is used to explain the success of aquatic plant species. In an experiment to test if enemy release was due to heterosis, Roley and Newman (2006) tested preferential colonization and consumption of invasive *Myriophyllum spicatum*, native *M. sibiricum*, and their hybrid by a native milfoil weevil. They found, however, that the species preferentially occurred on *M. spicatum* and did not exclude the hybrid milfoil, lending no support for enemy release hypothesis in either case.

Although enemy release hypothesis was not invoked, Cuda et al. (2002) found that a natural enemy of *Hydrilla verticillata* could potentially limit its growth in the introduced range. However, the natural enemy does not occur in all introduced populations (and may not be able to survive in all introduced climates) and this may at least partially explain *H. verticillata*'s invasion success in portions of its introduced range. Doyle et al. (2007) found that an herbivore from *H. verticillata*'s native range was able to limit its growth when additive effects of competition were also included.

Franceschini et al. (2010) tested strength of herbivory on *E. crassipes* in its native range. They found that although consumption was high, it did not significantly impact the plant population. This would indicate that success of this highly invasive species in introduced areas is likely unaffected by release from enemies. In China, where *Alternanthera philoxeroides* is a prolific invader, impact of herbivory from a natural and newly associated enemy was tested to see if enemy release could explain its success (Lu and Ding 2012). Results indicated that prior exposure to any type of herbivory allowed the plants to partially compensate for subsequent herbivory by accumulating greater root mass. Lu and Ding (2012) suggest that enemy release may only be temporary with generalist herbivores forming new associations in the introduced environment, and should be a consideration in developing biocontrol strategies. In the north-eastern United States where the introduced water-chestnut, *Trapa natans*, is a problematic invader, researchers assessed if a native herbivorous beetle could limit its spread (Ding and Blossey 2005). They found that the native beetle did consume *T. natans*, but did not appear to limit its spread. These researchers hypothesized that although natural enemies may be lost in an introduced range, if the intensity of herbivory was not strong in the invaders native range then enemy release isn't likely to impact the ability of a species to spread in the introduced range.

Although not a fully aquatic species, *Lythrum salicaria* is a highly invasive wetland invader in the U.S. Studies have shown that it has evolved the ability to grow larger in its introduced range at the expense of defensive abilities. In experiments in its native range, plants from the introduced range grew taller than those from the native range but were consumed more by herbivores, although their survival was not impacted (Blossey and Notzgold 1995).

These examples highlight the potential for enemy release to influence invasion success. However, this mechanism has not been consistent across taxa. As a result, it is likely that enemy release only applied under a limited set of circumstances and ultimately influences outcome of competition between invaders and native species in a recipient community.

Mutualisms and Invasional Meltdown

Although competition has often been regarded as the most important interaction shaping communities and impacting species invasions, there is some evidence that mutualistic relationships can also play a central role (Richardson et al. 2000a). In addition, some researchers have proposed that invasions may be characterized as an "invasional meltdown" where introduced species may facilitate the successful establishment of other introduced species by creating suitable environmental conditions (Simberloff and von Holle 1999). Ricciardi (2001) reviewed the potential for mutualisms and invasional meltdown in the Great Lakes and found that facilitative relationships were common among invasives. The Great Lakes have been a focus of invasive species study in freshwater systems, particularly due to the highly invasive bivalve *Dreissena polymorpha*. Skubinna et al. (1995) and MacIsaac (1996) found that *D. polymorpha* induced turbidity reductions were linked to the spread of macrophytes, although not only restricted to invasives. Likewise, Zhu et al. (2006) found an increase in several macrophytes including the highly invasive *Potamogeton crispus*, following invasion by *D. polymorpha*.

In a potential example of invasional meltdown, Maezo et al. (2010) studied interactions between invasive *M. spicatum* and invasive crayfish *Orconectes rusticus*. They found positive and negative interactions between the species but noted that microhabitat partitioning would likely result in very little realized interaction. In a regional scale study, Santos et al. (2011) found that invasion by *M. spicatum* could have facilitated the spread of *Egeria densa* in the California delta. However, *E. densa* currently limits growth of *M. spicatum* which indicates interactions are dynamic, rather than static between invasive species, and points out the importance of assembly order.

Although invasional meltdown has been identified in some systems, its overall influence on invasion success in fully aquatic macrophytes appears to be limited. This is possibly due to limited understanding of the mechanisms that contribute to patterns exposed by invasional meltdown (i.e., mutualisms). As a result, it is currently limited in ability to contribute to accurate prediction of invasion success.

Influences of species traits on invasion success

Novel weapons and allelopathy

Some mechanistic hypotheses explaining invasion success are attributable to specific characteristics of an invader. In some cases this is a generalized factor affecting all species equally and in some cases impacts are only detected with a particular species or subset of species within a community. The novel weapons hypothesis predicts that some species have a larger negative impact on species in a recipient community than on species in their native range which facilitates their success (Callaway and Aschehoug

2000). For plants, weapons are often manifested through allelopathic chemicals (Ervin and Wetzel 2003). Morris et al. (2009) noted that dilution is a major hurdle for allelopathy in aquatic systems indicating that its effects may be less than those in terrestrial systems. Allelopathy has, however, been implicated in aquatic macrophytes (Gopal and Goel 1993) such as *C. demersum* (Wium-Anderson et al. 1983), and Gross (2003) noted that allelopathy does occur in all aquatic habitats and is especially common in fully aquatic species. This would result in increased competitive ability which could promote invasion and change succession trajectories in aquatic communities. Doyle et al. (2003) suggested that (although unmeasured) allelopathy potentially contributed to the ability of *Hygrophila polysperma* to outcompete native *Ludwigia repens*. For other *Ludwigia* spp., Dandelot et al. (2008) experimentally tested if water that *Ludwigia* grew in affected germination, mortality, culture yield percentages, seedling growth and health of 15 day old seedlings of native species. Their results suggest that allelopathic compounds released from *Ludwigia* could potentially negatively impact native seedlings and contribute to its invasion success.

Many studies of allelopathy in aquatic macrophytes have indicated that it has major impacts on phytoplankton communities. van Donk and van de Bund (2002) reviewed studies where allelopathy had been tested in submersed plants, including invasive species (i.e., *M. spicatum*). Their findings indicated that negative impacts were mainly detected on cyanobacteria and not other macrophytes per se. Nakai et al. (1999) found that *M. spicatum* and *Cabomba caroliniana* had negative impacts on blue-green algae growth. They also illustrated that allelopathic influence varied by species.

Furthermore, Nakai et al. (2000) identified four polyphenolic compounds released by *M. spicatum* that synergistically inhibited growth of the blue-green algae *M. aeruginosa*.

Use of allelopathy to influence invasion through phytoplankton growth inhibition also has implications for alternative stable states in shallow lakes (indicating indirect effects). Hilt and Gross (2008) described the framework for which allelopathy from submersed macrophytes could potentially influence a switch to a clear water state. They indicated that this is possible, but note that allelopathy seems to inhibit phytoplankton (mainly cyanobacteria) rather than epiphytic algae even though the latter grows more closely to the chemical release sites.

It is evident that allelopathic interactions among macrophytes are not clearly understood. Glomski et al. (2002) studied exudates from two highly invasive macrophytes, *M. spicatum* and *H. verticillata*. They found that toxic secondary metabolites found in these species were not detectable in the water column and therefore may contribute nothing to increased competitive ability. Likewise, Erhard and Gross (2006) identified allelopathic compounds in invasive *E. canadensis* and *E. nuttallii* but were unable to attribute these compounds to invasiveness, although they did note that allelopathy had the potential to impact phytoplankton and cyanobacteria in epiphytic biofilm, which could indirectly lead to a competitive advantage. In one of the few examples of a study which explicitly related allelopathy to invasiveness, Marko et al. (2008) found that invasive *M. spicatum* had higher concentrations of carbon, polyphenols, and lignin than the native *M. sibiricum*. They suggest that higher concentration of polyphenols and lignin in *M. spicatum* relative to *M. sibiricum* may provide advantages that facilitate invasion and displacement of natives.

Phenotypic plasticity

Some researchers have attributed invasion success to the ability of a species to adjust to either stressful environmental conditions or enhance competitive abilities in favorable environments (Richards et al. 2006). Although di Nino et al. (2007) did not specifically test if phenotypic plasticity contributed to invasion potential of *E. nuttallii*, they did find that the species had high plasticity not due to genetically different ecotypes. This indicates that highly plastic clonal species might have a competitive advantage over natives. Riis et al. (2012) found that *E. canadensis* had highly plastic responses to temperature which allowed it to be an early colonizer and generalist, thus promoting its invasibility. Similarly, Geng et al. (2007) found that invasive *A. philoxeroides* was highly plastic and readily colonized different habitat types. They speculate that this may give the species an advantage by allowing it to colonize any aquatic habitat. Geng et al. (2006) also noted that high phenotypic plasticity of *A. philoxeroides* could not be explained by genetic variability although plasticity of a native congener was. Pan et al. (2006) found that plasticity in *A. philoxeroides* gave it an advantage, especially in resource rich microhabitats which facilitated its invasion into riparian zones.

Carter and Sytsma (2001) analyzed the genetics of invasive populations of *E. densa* in Oregon, U.S.A., and Chile. Interestingly, they found little genetic variability between populations, indicating similar bottleneck events or low genetic diversity in the source population. This indicates that even with low genetic variation, plastic species may be better suited to invade a variety of environments. In China, researchers found that there were at least three clones in all the *E. crassipes* populations they sampled suggesting that clonal growth is the predominant mode of regeneration. Interestingly, they found that a single clone dominated each population indicating initially introduced clones or clones with greatest phenotypic plasticity are able to reproduce in various habitats (Ren and Zhang 2007). Similarly, Zhang et al. (2010) found that most invasive populations of *E. crassipes* were clonal, pointing to an introduction bottleneck. This may indicate that genetic variation in source populations has allowed highly invasive genotypes to become widespread. Phenotypic plasticity may be a species trait that promotes invasion potential, however, it should be noted that ultimately this trait only promotes increased competitive ability and therefore is only a component of invasion success.

Naturalization of related species

Darwin's naturalization hypothesis predicts that invasive species are less likely to colonize areas where native congenerics are present (Darwin 1859, Daehler 2001). This hypothesis is based on the conjecture that more closely related species have similar resource requirements, and native species are better adapted to their native environments than introduced species. This hypothesis has received almost no attention regarding aquatic macrophyte invasions. However, Thomaz and Michelan (2011) did explicitly test associations between invasive *U. subquadripara* and native confamilial genera. They found that co-occurrence of confamilial genera did not explain associations between the native and invasive species at small or large scales. Nonetheless, this hypothesis should be tested with additional macrophyte species and finer phylogenetic resolutions.

Influences of abiotic factors on invasion success

Empty niche

The empty niche hypothesis is one of the oldest in invasion ecology (Elton 1958). It basically states that unused resources (the resource dimension of niche space) in a community make the community susceptible to invasion from a species that can exploit those resources. Although not an explicit test of empty niche hypothesis, Khanna et al. (2012) found that *E. crassipes* and submersed aquatic macrophyte dynamics were opposite which indicated it was colonizing available "empty" space. They noted that even when submersed vegetation growth was pronounced, *E. crassipes* only colonized new sites, but in general did not show much growth when submersed vegetation was topped out. Owens et al. (2008) found that *H. verticillata* was able to establish in containers not already containing native *V. americana*. They considered empty containers "empty" niches and thus supported this hypothesis. However, Chadwell and Engelhardt (2008) observed reduction in growth of *H. verticillata* due to *V. americana* presence, but that this only occurred in greenhouse experiments and not in the field. They also found that even artificial (plastic) plants could potentially trap propagules of *H. verticillata* and facilitate invasion which is directly opposite of predictions of empty niche hypothesis. In New Zealand, where few native macrophytes exist, McCullough (1997) suggests that because of low native species richness, there is prime real-estate for invaders to colonize. This appears to be the case in particular for members of the aquatic Hydrocharitaceae family. James et al. (1999) noted that *Lagarosiphon major* was able to raise pH faster and photosynthesize at a greater rate, thus creating environmental conditions that may give it a competitive advantage, although they noted that a wider range of factors are probably involved in actual competition. Empty niche is an environmental characteristic, but opportunity it provides actually promotes species interaction in a recipient community, allowing competition to dictate success of the invader.

Fluctuating resources and opportunity windows

In some cases, invasion has been attributable to dynamic environmental conditions which gave rise to the fluctuating resource hypothesis (Davis et al. 2000). This hypothesis is closely tied to Johnstone's (1986) opportunity window hypothesis which states that under a particular set of temporary conditions a species may invade an area. In an explicit example of this hypothesis tested with macrophytes, Thiebaut (2005) found that *E. nuttallii* was able to successfully invade because of fluctuations in phosphate in space and/or time. The result was induced competition between this invasive species and natives. He also found that factors could act synergistically such as the creation of dense stands of *E. nuttallii* that slowed water movement which allowed diffusion of soluble reactive phosphorus into leaf tissues and degraded habitat of native species. Barrat-Segretain and Cellot (2007) found that *E. nuttallii* was highly resilient to drawdowns which contributed to its success as an invader and has potentially allowed it to displace an earlier invader *E. canadensis*. In an example of resource fluctuations acting synergistically with phenotypic plasticity, Garbey et al. (2004) found that morphological characteristics of *Ranunculus peltatus* varied by chemical factors of the environment. In nutrient rich areas this species took on a competitive strategy, in nutrient poor environments a stress tolerant strategy, and in disturbed sites a ruderal strategy (sensu Grime 1977). They found that especially in nutrient rich environments, *R. peltatus* can spread and invade, potentially outcompeting natives.

In an experimental study testing nutrient uptake ability and relative growth rates of *M. spicatum* and *E. nuttallii* based on varied sediment nutrient levels, Angelstein et al. (2009) found that these species were highly competitive in their acquisition abilities. These species declined at low nutrient levels, but *E. nuttallii* maintained high nutrient uptake efficiency which potentially allowed it to grow taller and outshade *M. spicatum*, thus giving it a competitive advantage under certain resource conditions. In another example of resource fluctuations improving invasion success, Xie et al. (2010) found that in nutrient rich sites, invasive *E. nuttallii*, *M. aquaticum*, and *M. propinquum* performed better than natives. They further found that rooting efficiency and root growth were greater in these sites. They noted that the invasive species also had superior traits in nutrient poor sediment, but to a lesser degree than nutrient rich sediment. They concluded that under conditions of high sediment nutrient availability, asexual propagation is more effective from these invaders. Xie and Yu (2011) went further to find that there was a positive relationship between auto-fragment size of *M. spicatum* and nutrient rich sediments. This indicates that in resource rich environments, *M. spicatum* has the potential to spread more rapidly through auto-fragment production and thus may facilitate its spread.

In another resource competition experiment, Zhang and Liu (2011) found that *H. verticillata* was able to accumulate a greater quantity of phosphorus when grown in a mixed culture with *V. americana*. They concluded that *H. verticillata* has a potential competitive advantage over *V. americana* when interspecific interactions are realized. In a multi-scale study, Quinn et al. (2011) assessed factors that influenced aquatic macrophyte invasion. They found that invasive species responded more positively to disturbed landscapes than natives (which had no significant response), but that native and alien abundance was not correlated. They suggest that invasion success is due to disturbed areas that receive nutrient pollutants from urban and agricultural areas. Spierenburg et al. (2009) conducted an experiment to test if a rise in CO_2 could potentially facilitate invasion. They found that the elodeid species studied probably couldn't invade isoetid dominated softwater lakes at low CO_2 concentrations. However, if sediments contained enough nutrients, a rise in CO_2 could allow invasion and cause displacement and local extinctions of slow growing isoetids.

Resource availability due to temporal variation in native species phenology may also facilitate invasion opportunities. Hofstra et al. (1999) found that in experimental tanks, *H. verticillata* failed to outperform other species unless given a head-start on growth. They note that in New Zealand, invasive macrophytes are already prolific, but their results demonstrate that *H. verticillata* can compete with already invasive species which may create additional problems for management. Hussner (2010) noted that in Germany, invasions are correlated with human population density and cultural eutrophication. Thus if eutrophication continues, there are additional opportunities for subsequent invasions to occur.

Fluctuating resources and opportunity windows are important components of the invasion process during the establishment phase. This is particularly true in disturbed communities, and communities with species that have particular phenological traits that only exploit resources at particular times. As with other mechanisms listed, competition as a result of establishment or as a result of increased resources availability (with a species better able to exploit excess resources) may ultimately serve as the mechanism of invasion success, even when resource fluctuations are present.

Other mechanisms of invasion success

Propagule pressure

Propagule pressure is likely the most promising factor for predicting species invasions (Reaser et al. 2008). It is generally most important in the pre-establishment phase, where species have crossed a geographic boundary and reached an introduction site. Lockwood et al. (2009) noted that propagule size and number (components of propagule pressure) contribute to invasion success. However, propagule pressure is difficult to quantify. Few, if any, studies have quantified propagule pressure in aquatic macrophytes and attributed it to successful invaders. However, numerous researchers have studied transport vectors to better understand potential propagule pressure. Johnson et al. (2001) studied overland dispersal of *D. polymorpha* and found that they were frequently transported on macrophytes entangled in boat trailers. Although their focus was not on macrophytes per se, their results do indicate overland transport of macrophytes is an important factor in dispersal. Ricciardi and Kepp (2008) note that the risk of an aquatic species becoming invasive is enhanced by transport vectors (and thus propagule pressure). Some researchers have noted that predicting establishment success and spread of an invasive species can be enhanced by combining gravity models and environmental niche modeling approaches. Jacobs and MacIsaac (2009) found this to be the case in predicting the spread of *C. caroliniana*. In addition, Cohen et al. (2007) found that thousands of non-indigenous propagules reach the St. Lawrence River each year from the aquarium trade, a widely known but largely unregulated transport vector. They found that this was particularly true for *E. densa* and *C. caroliniana*, two of the most frequently purchased plants in the Montreal aquarium plant trade, and highly invasive in that area. Finally, Boedeltje et al. (2008) noted a negative correlation between generative (sexual) and vegetative (asexual) propagules in aquatic plants. If taken in the context of species invasions, if most invasive species spread through vegetative reproduction and clonal genotypes contribute to the species' invasiveness, this could help to explain why some aquatic plant invaders are so successful.

Roles of establishment mechanisms in the invasion process

Species invasions have often been described in terms of a linear process. Propagules must cross geographic boundaries, reach suitable environmental conditions, find a suitable niche role in the introduced location, successfully reproduce, and spread (Williamson 1996, Richardson et al. 2000b). Although aquatic macrophytes have to deal with different conditions than their terrestrial counterparts, the invasion process is much the same. The mechanisms described above are mostly part of the establishment phase of the invasion process. However, this phase can become increasingly complex as mechanisms interact or have indirect impacts on other factors dictating successful establishment (Figure 2.1).

Aquatic plants have crossed geographic barriers through ballast water of ships, boat trailers, waterfowl, and the ornamental and aquarium plant trade (Cronk and Fennessy 2001). Many of these species have been accidentally introduced, whereas some were intentionally introduced (e.g., *E. crassipes* as an ornamental pond plant). Regardless of the difficulty, geographic barriers are not preclusive for aquatic plants, but are likely impacted by propagule pressure. When species have reached a target location, they must find environmental conditions (i.e., abiotic factors) conducive to colonization. Mechanisms invoked at this stage include empty niche, fluctuating resources, and opportunity windows which may all be influenced by natural or anthropogenic disturbances.

Interaction with other species must simultaneously be conducive to growth and reproduction (i.e., biotic factors). This step in the invasion process is likely the most complex because other species may influence abiotic conditions (see above), leading to indirect effects (Figure 2.1). For example, as noted previously, some species provide mutualistic services that promote colonization by an introduced species. However, competition at this stage is also a factor in establishment success. Competition is particularly important during stages of reproduction and spread. For example, even if a species finds available colonization space, their reproductive propagules (whether sexual or asexual) must be able to spread and colonize new areas. This may be prevented if interspecific competition is high and resources are limited. As a result, invasion success may ultimately be determined by the outcome of competition between the introduced species and species in the introduced range. In addition, there must be a sufficient lack of enemies that either allows the species to reproduce and spread more efficiently than natives in the introduced range, or there must be sufficient time for the evolution of competitive strategies that give the species an advantage over natives. Provided a species can cross a threshold at each of these stages, it will potentially become a naturalized and possibly problematic invader.

Conclusion and Future Research:

Although there have been numerous mechanisms proposed to explain invasion success or “invasibility”, most have not been fully tested in aquatic macrophyte communities, and therefore, successful prediction of aquatic plant invasion may be limited. In many cases, consequences (i.e., impacts) are studied more than causes (i.e., mechanisms of invasion success) in aquatic plant communities because scientists and the public are often only interested in invasive species after they become problematic. This is evident for aquatic plants because much of what is known about aquatic plant invasions is found in the management literature. However, by understanding the mechanisms contributing to invasion, management strategies can be more easily designed to either help prevent invasions, rapidly eradicate invasive species, or control their growth and dispersal.

One of the most promising areas of research for invasibility and impact is the naturalization concept as it applies to related species. Simply using characteristics of a species (which is commonly done) does not explain risk because successful invasion depends on the receiving environment (Lockwood et al. 2007). Likewise, characteristics of communities or areas alone cannot be used for risk assessment because their component functional parts may not be susceptible at all. However, considering species relatedness (i.e., Darwin’s naturalization hypothesis) implicitly considers traits of species and receiving environments (biotic and abiotic factors). A more detailed and promising approach within this realm of research would be to focus on phylogenetic diversity, and the correlation of phylogenetic diversity to functional diversity and functional redundancy. For example, redundancy could potentially be present with high phylogenetic diversity, but not with high species diversity (e.g., if there are many related species in an area). If functional diversity, redundancy, phylogenetic diversity, and species diversity are all high, the area could be highly stable (or ‘mature’). Because this area of research has received very little study, it is not known what patterns these relationships reveal. The expectation is that if species diversity is high but functional diversity is low, phylogenetic diversity would be high which may ultimately influence invasibility of that community.

Table 2.1 Mechanisms of invasion success studied by species and family in aquatic macrophytes.

Mechanism(s)	Species
Novel Weapons/Allelopathy	*Hygrophila polysperma*
Enemy Release/EICA, Phenotypic Plasticity	*Alternanthera philoxeriodes*
Novel Weapons/Allelopathy, Propagule Pressure	*Cabomba caroliniana*
Fluctuating Resources/Opp Window	*Myriophyllum aquaticum*
Fluctuating Resources/Opp Window	*Myriophyllum propinquum*
Enemy Release/EICA, Mutualism/Invasional Meltdown, Competition, Novel Weapons/Allelopathy, Fluctuating Resources/Opp Window	*Myriophyllum spicatum*
Mutualism/Invasional Meltdown, competition, Phenotypic Plasticity, Propagule Pressure	*Egeria densa*
Enemy Release/EICA, Competition, Novel Weapons/Allelopathy, Phenotypic Plasticity	*Elodea canadensis*
Enemy Release/EICA, Novel Weapons/Allelopathy, Phenotypic Plasticity, Fluctuating Resources/Opp Window	*Elodea nuttallii*
Enemy Release/EICA, Competition, Novel Weapons/Allelopathy, Empty Niche, Fluctuating Resources/Opp Window	*Hydrilla verticillata*
Competition, Empty Niche	*Lagarosiphon major*
Competition	*Utricularia inflata*
Enemy Release/EICA	*Lythrum salicaria*
Enemy Release/EICA	*Trapa natans*
Novel Weapons/Allelopathy	*Ludwigia repens*
Competition, Naturalization	*Urichloa subquadripara*
Enemy Release/EICA, Phenotypic Plasticity, Empty Niche	*Eichornia crassipes*
Mutualism/Invasional Meltdown	*Potamogeton nodosus*
Fluctuating Resources/Opp Window	*Ranunculus peltatus*
Competition	*Salvinia natans*

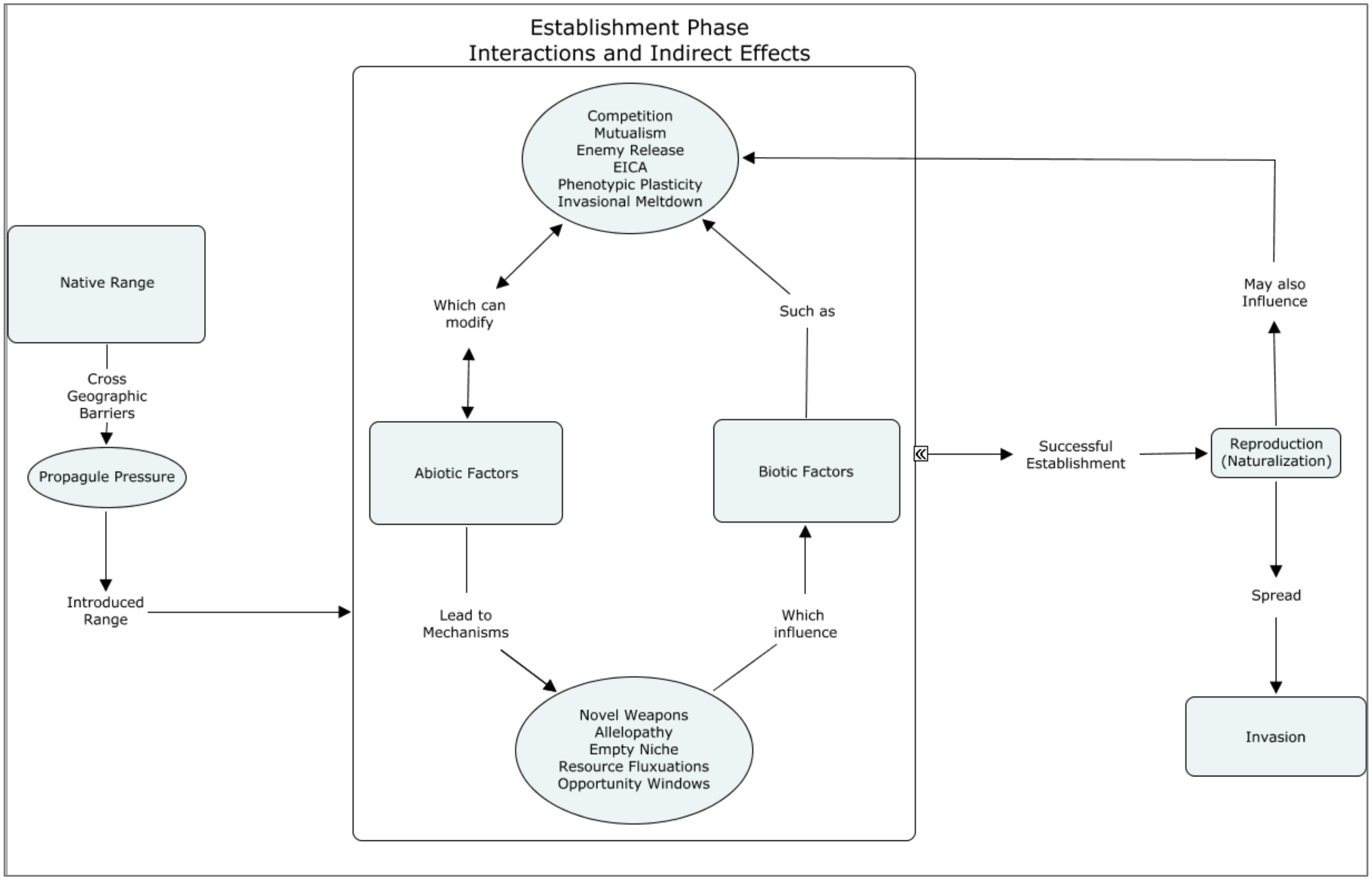

Figure 2.1 Conceptual diagram of the invasion process for aquatic macrophytes. Invasion barriers are in boxes and mechanisms that govern successful crossing at each barrier are in circles.

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CHAPTER III

ECOLOGICAL FACTORS AFFECTING THE OCCURRENCE OF INVASIVE MACROPHYTES

Introduction:

Invading plants have become pervasive in a vast number of ecosystems and their negative impacts on ecosystem process have been described (Parker et al. 1999, Mack et al. 2000, Ricciardi et al. 2000, Simberloff 2003, Simberloff et al. 2005, Hershner and Havens 2008). Invasive species may alter ecosystem functioning, in some cases disrupting ecosystem services, food web interactions, and native species diversity (Shea and Chesson 2002). For this reason, identifying the mechanisms governing invasions has become an urgent need (Shea and Chesson 2002, Dietz and Edwards 2006). Biological invasions are one of the least reversible forms of human caused degradation and not only impact local ecosystems, but also local economies (Pimentel et al. 2000, Pimentel et al. 2005, Lockwood et al. 2007, Rahel 2007, Rahel and Olden 2008). For example, Pimentel et al. (2005) estimated the annual cost of invasive species management in the United States to exceed \$120 billion, \$34 billion for plants alone. This sobering statistic highlights the importance of understanding species invasions and ways to prevent invasion for ecosystem and economic conservation. Unfortunately, ecological theory has struggled to find general principles that predict these invasions (Dietz and Edwards 2006).

Major hypotheses have been presented to identify potential mechanisms that lead to ecological invasion. Of these hypotheses, two major themes have emerged. First, the probability of invasion may be a property of a species (e.g., high reproductive output, competitive superiority, dispersal ability; Cadotte and Lovett-Deurst 2001, Kolar and Lodge 2001, Cadotte et al. 2006), or may be a property of the community or environment (Levine 2000, Chadwell and Engelhardt 2008, Jacobs and MacIsaac 2009). This second theme, environmental determinants of invasibility, is likely the most intuitive for synecologists because it explicitly considers interactions among and between organisms and their environment in a given location. Despite the impacts of species invasions, very little predictive understanding of how some species succeed in invading new areas has been achieved (Colautti et al. 2004, Hierro et al. 2005, Mitchell et al. 2006)

A major interest in environmental and community characteristics as determinates of invasibility was brought to the forefront of ecological study by the seminal work of Charles Elton with the publication of *The Ecology of Invasions by Plants and Animals* (Elton 1958). Since then, Elton's conjecture that greater diversity may mitigate potential harm from invaders has received a great deal of attention, perhaps because it fits synergistically with efforts of biodiversity conservation (Mitchell et al. 2006). For example, if species rich areas are demonstrably more resistant to invasion, policy-makers may lend greater support for biodiversity preservation.

Although diversity of a community may be an important determinate of invasion success, results of experimental and observational studies have been inconclusive and have differed across spatial scales (e.g., Kennedy et al. 2002, Stohlgren et al. 2003). Fridley et al. (2007) reviewed evidence for native-exotic richness relationships and found that, in general, small scale studies reported a negative relationship whereas large scale studies reported the opposite. These conflicting results, known as "invasion paradox" (*sensu* Fridley et al. 2007), open new doors for inquiry into the causes of these seemingly scale-dependent patterns. Additionally, there is a need to address or clarify the differences between invasibility (by any given species) and the likelihood of subsequent invasion (invasional meltdown *sensu* Simberloff and Von Holle 1999). Furthermore, although the conceptual basis for Elton's hypothesis is firmly rooted in niche theory, the mechanism for this biotic resistance is poorly understood, but is often attributed to competition at the microhabitat scale (Levine and D'Antonio 1999, Levine et al. 2004). This mechanism, however, has less support at larger spatial scales where native species richness appears to correlate positively with invasive species occurrence (Levine and D'Antonio 1999, Lonsdale 1999).

All species occupy a portion of environmental space, often referred to as the species' niche (Hutchinson 1959). The space for any given species depends on numerous environmental factors that are generally related to resource availability (nutrients, light, food, etc.), disturbance regime, stress, or biological inhibition by competitors or predators. Most of these factors can be measured at a particular point in space and can therefore theoretically be used to assess if probability of an invasion is greater or lesser at that given location. Disturbance may influence invasibility because of its ability to open niche spaces or free resources that allow pre-adapted species to succeed (Davis et al. 2000, Havel et al. 2005, Facon et al. 2006). However, it is increasingly difficult to elucidate patterns of cause and consequence at a given place in space and time because of the complexity of ecological systems (McMahon and Cadotte 2002).

Given the seemingly conflicting results of previous studies, it may be that a general theory of invasibility does not exist (Colautti et al. 2004, Hierro et al. 2005, Mitchell et al. 2006). However, this may be true only for comparisons among ecosystem types where communities are structured through different mechanisms due to environmental heterogeneity, as opposed to comparisons within the same ecosystem type. It follows that there is a great need to collect data, not only at multiple scales, but also at multiple locations of a given ecosystem type (e.g., forests, grasslands, lakes). This is especially important in aquatic environments which are particularly prone to invasion but have received less study than some other systems (e.g., grasslands; Shea and Chesson 2002, Havel et al. 2005, Capers et al. 2007).

Species invasions are highly non-random in freshwater ecosystems (Strayer 2010). Ecologists who specialize in aquatic systems, and particularly aquatic plants, will note the relative paucity of studies regarding the development and testing of invasion hypotheses (e.g., biotic resistance) in invasive aquatic plant assemblages (Capers et al. 2007, Thomaz and Michelan 2011). Perhaps this is because of the difficulty in collecting the necessary data due to time or lack of equipment (e.g., boats). However, aquatic plant assemblages are valuable for ecological study because they typically have fewer species than many terrestrial systems (Capers et al. 2007) and exist mostly within definable ecosystem boundaries (i.e., margin of a water body).

Aquatic plants are important components of the freshwater environment and provide the basal resource for the aquatic food web (Carpenter and Lodge 1986). In general, aquatic plants have strong engineering effects in aquatic ecosystems (Strayer 2010). They provide substrate for periphytic organisms, refuge for invertebrates and juvenile fishes, and foraging areas for many recreational sportfish (Dibble et al. 1996, Diehl and Kornijow 1998). They also serve an important function for the abiotic environment by stabilizing substrate, and regulating oxygen, pH, and suspended sediment dynamics in the water column (Madsen et al. 2001, Rooth et al. 2003, Huang et al. 2007).

Although native macrophytes are beneficial in aquatic ecosystems, invasive aquatic plants can cause significant ecological and economic harm. High densities of macrophytes such as invasive *Myrophyllum spicatum* and *Hydrilla verticillata* interfere with foraging and spawning of some fish species (Valley and Bremigan 2002, Theel and Dibble 2008). Canopy forming plants reduce light transmittance and oxygen diffusion into the water column which can lead to anoxic zones unsuitable for other aquatic organisms (Thomas and Room 1986, Caraco and Cole 2002). Because of differences in the physiology of introduced plants, nutrient cycles may be altered in some systems (Templer et al. 1998, Angeloni et al. 2006). They may also interfere with recreational opportunities and navigation, and can block water intakes. In addition, invasive aquatic plants may hybridize with native species, threatening native diversity (Boylen et al. 1999, Ailstock et al. 2001, Houlahan and Fridley 2004, Moody and Les 2007). Reservoirs and impoundments may facilitate invasion (Havel et al. 2005, Johnson et al. 2008), and therefore, understanding the factors that lead to increased probability of invasion is of high importance to ecologists and aquatic resource managers.

There are numerous factors that influence the distribution of aquatic plants and may also contribute to species invasion. Abiotic factors such as water depth and clarity cause differing levels of stress on aquatic plants along with disturbances caused by fetch (Koch 2001). Because disturbances are thought to contribute to invasions, stressed and disturbed ecosystems (such as those found in lakes and reservoirs) may be especially susceptible to aquatic plant invasion. It has been suggested that competition may play a lesser role in structuring submersed macrophyte assemblages because of environmental influences such as those caused by increased stress or disturbance (McCreary 1991, Wilson and Keddy 1991). However, existence or interaction of biotic factors along with abiotic stressors may make it easier or harder for introduced species to invade and establish themselves (Strayer 2010).

In addition to the importance of understanding how these factors impact aquatic plant assemblages, in the broader context of invasion ecology it is also important to highlight the fundamental differences between the aquatic environment and terrestrial systems (e.g., grassland systems). Much of the previous work regarding native-invasive plant relationships has been done in systems that are relatively stable compared to the aquatic environment (Lonsdale 1999, Naeem et al. 2000, Von Holle et al. 2003). For example, aquatic plants must deal with carbon limitation, reduced light availability, fluctuating water levels, and nutrient sequestration (Cronk and Fennessey 2001). This increased amount of stress and disturbance may alter or become synergistic with factors such as native species richness in determining invasion success (Thomaz et al. 2003, Capers et al. 2007, Strayer 2010).

The goal of this research is to investigate the hypothesis that the probability of invasion by an exotic aquatic plant is a function of biotic interaction, degree of stress, degree of disturbance, or a combination of these biotic and abiotic factors at a small (site) scale. These three factors are all components of major hypotheses that attempt to explain invasion success (Mitchell et al. 2006) and also potentially influence the distribution of aquatic plants within aquatic systems. Based on previous studies of biotic interaction, a negative association is expected between probability of an invasive species occurring at a small scale and number of native species occurring at that site. In addition, probability of invasion is expected to increase with disturbance and stress, but may be non-linear based on intermediate disturbance hypothesis (assuming interspecific biotic interaction also occurs). To investigate these hypotheses, I addressed the following questions using a combination of field data, geographic information systems, and statistics modeling: 1) Do native species richness, water depth (stress), fetch (disturbance), and/or interactions between abiotic factors (depth and fetch) contribute to the probability of invasive species occurrence at a small (point) scale in aquatic systems?, 2) Are relationships positive, negative, or non-linear?, 3) to what degree do each of these factors contribute to invasive species occurrence?, and 4) What is the relative importance of each of these factors in contributing to the probability of invasive species occurrence?

Methods

Study Areas and Design

The study area spanned the conterminous United States, where lakes and reservoirs (hereafter lakes; *n* = 29) were surveyed once at various times from 1997 to 2011 (Figure 3.1, Appendix A). Lakes represented a variety of areas ranging from 7-36,000 ha and 9 freshwater ecoregions (Appalachian Piedmont 1, Chesapeake Bay 2, Colorado 1, Columbia Glaciated 3, Laurentian Great Lakes 8, Lower Mississippi 7, St. Lawrence 1, Upper Mississippi 3, Upper Missouri 3). Each lake was originally surveyed for a specific project goal to obtain a baseline of invasive and native species occurrence and distribution using the point-intercept method (Madsen 1999). For each lake, a grid of points was generated in a GIS and integrated with field GPS to navigate to each point by boat. Point spacing varied by lake area to ensure representative sampling in each lake. At each sample point, a rake was tossed and retrieved to collect plants occurring at that location. Rake tosses generally collect plants directly under the boat and are dragged 1-2 m along the bottom. This method allowed a large number of samples to be collected and insured that all plants occurring in an area are accounted for. Each plant collected was identified to species and recorded as present (1) at the location.

Water depth at each point was collected using depth sonar or sounding rod to the nearest 0.1 ft and converted to meters. To calculate fetch, angle of wind direction was collected for each day in the given year of the lake survey (if available) at the nearest weather station (NOAA weather stations accessed through weatherunderground.com). If wind direction data were not available for the survey year, I used the closest year available. Angular measurements were rounded to the nearest 30 degree angle and the mode calculated to estimate prevailing wind direction. Wind directions were used to calculate fetch distance with 10-meter resolution following Finlayson (2005). Using this method, radials ($n = 9$) spaced every three degrees on each side of the input degree of wind direction is weighted by the cosine of angle deviation. Effective fetch for each pixel was calculated using:

$$L_f = \Sigma x_i * \cos\gamma_i / \Sigma\cos\gamma \tag{3.1}$$

where L_f is the effective fetch, x_i is the distance to land for a given angle, and γ_i is the deviation angle. The resulting grid contains fetch distances for each location and accounts for potential variation and uncertainty in prevailing wind direction. ArcGIS

(ESRI 2012; Redlands, CA) was used to extract fetch values to each survey point for use in analysis.

Modeling

To estimate probability of an invasive aquatic macrophyte occupying a given sampling location, generalized linear mixed models with environmental and native species richness data were used and their performances were compared to select models that included the most appropriate variables and to infer the relative importance of biotic interaction, stress, and disturbance. Models were developed using the lmer package in R (R Development Core Team 2012), and all models were fit using the binomial family and a logit link function (presence/absence of invasive species was coded as a binary response) with lake as a random effect.

Model terms specific to the original hypotheses (biotic interaction, stress, and disturbance as determinants of the probability of occurrence of an invasive species) were selected. For presence of an invasive species, NSPP (native species richness), $NSPP^2$, DEPTH (water depth), $DEPTH^2$, FETCH (effective fetch distance), $FETCH^2$, and the interaction term DEPTH × FETCH were used. Quadratic terms for native species richness, depth, and fetch were included to test for potential non-linear effects on probability of occurrence of invasive species. The interaction between depth and fetch were also included because of potential modification of effects by one term on the other. For the set of models, the global model was included which contained all terms relevant to the hypotheses, and the null (intercept only) model. All relevant combinations of these model terms were fit to separate models because I made no *a priori* assumptions that a particular subset of these model terms would provide more explanatory power than another.

Native species richness, depth, and fetch values were centered and standardized by 2 standard deviations (Mean = 0, Stand. Dev. = 0.5) to improve model convergence and parameter interpretation, and to avoid large differences in scale due to the ranges of values. Only sites with depth > 0 and where a plant occurred (whether native or invasive) were included in the analysis. Because all growth forms of aquatic plants encountered in the survey were included, using only sites where depth > 0 insured that submersed species could potentially co-occur there, even if an emergent plant was present (for example, if an emergent plant was recorded on the shoreline at depth = 0 it was excluded from analysis). Likewise, sampled sites where no plants occurred were excluded because it is likely that no plants can occur at those locations due to environmental limitations.

Seventeen models were created (including a null model). All models converged after variables were standardized. Performance of each model was evaluated by calculating Pseudo-R^2 values and model comparisons were made using Akaike Information Criterion (AIC). Akaike weights (w) were calculated to measure model support and model selection uncertainty. Using ranked AIC scores and Akaike weights, a 95% confidence set of models was selected and the relative importance of each variable was estimated. Model averaging was used for models contained within the 95% confidence set to estimate model parameters, decrease model selection uncertainty, and evaluate the relative strength of each predictor (Burnham and Anderson 2002).

Results:

Surveys were performed in 29 lakes containing invasive macrophytes between 1997-2011 (Figure 3.1). Ninety-one species were identified including 11 species considered invasive (Table 3.1). A total of 10,547 sites were surveyed. Of these, 4,113 (39%) contained at least one plant and had a depth greater than zero. Invasive plants occurred at 1,846 sites. Total number of sites surveyed averaged 363.7 (SD = 421.0) per lake ranging from 55 to 1,623. Total number of sites used in the analysis (N = 4,113) averaged 141.8 (SD = 120.7) per lake ranging from 24 to 636. Sites where plants occurred had a mean depth of 2.26m and a mean fetch of 761.2m. Sites where an invasive species occurred had 2.2 native species on average with mean depth 2.1m and mean fetch 657.1m.

Seven models were included in the 95% confidence set which included the global model (Rank = 2; Table 3.2). Native species richness, quadratic native species richness, depth, fetch, quadratic fetch, and the interaction between depth and fetch were included in the highest ranked model (Rank = 1) which was also the most parsimonious model (Rank = 1, ΔAIC < 2 and contained the least number of model parameters). However, model performance was relatively low (Pseudo-$R^2 = 0.03$). In each of the top two models (ΔAIC < 2), all terms were significant at $P < 0.1$ except for depth and quadratic depth in the global model. Although depth and quadratic depth were included in the 95% confidence set, depth was not significant in 4 of the 6 models that included it and quadratic depth was not significant in any of the 4 models that included it ($P > 0.1$).

Based on averaged parameter estimates and relative importance calculated from AIC weights for the 95% confidence set, native species richness and quadratic native species richness were the most important variables included in the model (Table 3.3). Fetch and quadratic fetch were the next most important followed by depth. Although quadratic depth was included in the model averaged estimates, it had the least importance.

Based on model results, biotic interaction (i.e., influence of native species richness) had a significant impact on the probability of an invasive species co-occurring at a site but its influence changed at a threshold of native species richness (Figure 3.2). There was a slight decline in probability of occurrence of an invasive species with increasing native species richness but this relationship changed to a positive association as native species richness increased beyond the mean value. Stress also appeared to be a significant factor and as stress (depth) increased, probability of occurrence of an invasive species decreased (Figure 3.3). Fetch and quadratic fetch were highly significant, indicating that as fetch increased, probability of occurrence of an invasive species decreased. However, beyond two standard deviations (1 SD = 1200m), probability of occurrence increased with increasing fetch (Figure 3.4). Furthermore, the interaction between depth and fetch was significant supporting the hypothesis that fetch distance becomes less important as depth increases. These results suggest that stressful or disturbed conditions along with competition from native species may act synergistically but in a non-linear way to effect colonization by an invasive macrophyte.

Discussion:

General mechanisms governing invasion success have eluded ecologists. Perhaps this is because heterogeneity among ecosystems influences success of invaders and therefore, general mechanisms can only be identified within a specific ecosystem context.

One of the most widely hypothesized mechanisms of invasion success (or lack of success) is biotic resistance. This hypothesis, based in niche theory, predicts that as more species accumulate in an area, available environmental space (micro-habitat) decreases and therefore increased interspecific interference (i.e., competition) is more able to exclude invaders.

There is a great need to test hypotheses regarding invasibility in a wider variety of ecosystem and community types. There is a paucity of information available regarding invasion mechanisms within aquatic plant communities (Capers et al. 2007). The reasons for this are unclear but are probably due to logistic and financial constraints as well as the overall complexity of all ecological systems. Nonetheless, aquatic plants represent an important component of aquatic ecosystems and studying invasibility of these systems is imperative for future aquatic resource management.

Results of this study suggest there is little or no support that biotic interaction, stress, or disturbance influence the probability of invasive species occurrence in littoral areas of lakes and reservoirs throughout the U.S. Model performances were relatively poor (Pseudo-R^2 0.02-0.03), indicating a large amount of unexplained variation in predicting probability of occurrence. Disturbance is widely regarded as a mechanism influencing invasions and it has been suggested that fetch, acting as disturbance, can indeed limit species diversity in some reservoirs (Thomaz et al. 2003). Although I did not assess the relationship between disturbance and overall species diversity, I did find a weak relationship between invasion probability and degree of disturbance (fetch distance). However, the relationship was non-linear and only negatively impacted invasion probability at relatively shorter distances. This result merits further study because intermediate disturbance hypothesis predicts greater species diversity at intermediate levels of disturbance. Taken in an ecosystem context, if disturbance facilitates invasion, and biotic resistance increases with diversity as has been hypothesized, a positive relationship between invasion probability and disturbance might be expected at lower and higher degrees of disturbance (Connell 1978). In addition, disturbances may open environmental space which can be exploited by species pre-adapted to those spaces or with inherent physiological traits that allow them to establish without interspecific interaction from natives (e.g., phenological differences; Davis et al. 2000).

I found no strong support that biotic interaction via native species richness tended to decrease probability of occurrence of an invasive species, and it is likely the relationship is non-linear (does not hold true for locations with high native species richness). This should receive further investigation because most studies thus far in native/exotic richness relationships have simply identified a positive or negative relationship and have led to the popular notion of an "invasion paradox" (Fridley 2007). However, results of this study indicate that even at small scales the relationship may not in fact be linear (or exist at all). Because this study used occurrence of invasive species at a point scale and all lakes in this study had at least one invasive species, multi-scale analysis was not possible. However, it is expected that species richness increases with area (Gleason 1925). Therefore, at larger scales and greater species richness, these results suggest there would indeed be a positive relationship between invasive species occurrence and native species richness. Thus, the invasion paradox may be an artifact of a situation where area simply increases, species accumulation occurs at an expected rate, and non-random patterns indicate a particular phase of the relationship between invasion and native species richness.

There are several reasons these patterns could occur, even at the small scale. First, with a limited number of native species, specialists (in a relative sense) may be more suitably adapted to exploit limited resources in areas where they occur. However, as resources become plentiful and less limiting, or as environmental heterogeneity increases number of microhabitat types, invasive species may be able to co-exist with high numbers of native species. With increasing species richness, likelihood of facilitation also occurs. For example, as number of species increases, the physical complexity of the environment may also increase as species seek to exploit different volumes of space in the water column (Capers et al. 2007). This may result in increased likelihood that propagules of invasive species encounter reduced mobility through normal dispersal processes, become trapped, and have enough time to establish. Alternatively, as species richness increases, the likelihood of indirect effects such as apparent facilitation or competition may also increase and result in successful colonization of an invader.

These results also lead to new questions with respect to which resources may be important in understanding invasion success. Although this study simply classified species as invasive or native, it may also be prudent to look at species specific attributes of native and invasive communities to identify species and characteristics that influence invasion success in a more precise context (e.g., functional diversity or physical structure). In addition, density of plants may be a more important factor than richness per se. Capers et al. (2007) found this in five of the six invasive aquatic plants they studied in Connecticut lakes.

Ecological effects of invasive species may either increase or decrease through time (Strayer et al. 2006, Gherardi 2007, Hawkes 2007). In addition, the invader or invaded community may evolve as species composition shifts toward species insensitive to the invaders, masking the real influence of native richness on invasiveness. There is currently little predictive knowledge regarding what factors lead to species invasions (Colautti et al. 2004, Hierro et al. 2005). Future research should continue the search for mechanisms that allow introduced species to establish. It is likely that universal principles do not exist, at least among comparisons across ecosystem types. However, ecologists should continue to search for general patterns within definable ecosystem units that increase understanding about factors contributing to invasibility.

Table 3.1 List of 29 lakes surveyed across the United States and the plants identified in the surveys from 1997-2011.

	Bass	BigCrooked	BigSeven	Blue	CabinetGorge	Camp	Clear	Ennis	Gaston	Havasu	Hebgen	Holcombe	Hortonia	Jackson	Lamoka	LittleEagle	Lobdell	Middle	Mossy	Noxon	Onondaga	PendOreille	Pinchback	RossBarnett	Swan	Toston	Townsend	Waneta	Wolverine
Alternanthera philoxeroides (Mart.) Griseb.				•										•		•			•				•	•			•		
Bidens beckii Torr. ex Spreng.												•																	
Bidens laevis (L.) Britton, Sterns & Poggenb.														•		•													
Brasenia schreberi J.F. Gmel.	•	•					•																						
Butomus umbellatus L.																				•		•							
Cabomba caroliniana A. Gray																								•					
Callitriche sp.																						•							
Carex sp.												•						•							•				
Carex rostrotta Stokes																									•				
Ceratophyllum demersum L.	•	•	•	•	•	•	•	•	•		•	•	•	•	•	•	•	•	•	•	•	•		•	•			•	•
Chara sp.	•	•	•		•		•	•	•	•	•	•	•		•		•	•		•		•			•			•	•
Colocasia esculenta (L.) Schott																								•					
Egeria densa Planch.									•																				
Eichhornia crassipes (Mart.) Solms																								•					
Elatine sp.											•																		
Eleocharis sp.	•											•	•									•							
Elodea canadensis Michx.	•	•	•		•	•		•			•	•	•		•		•			•	•	•			•	•		•	•
Heteranthera dubia (Jacq.) MacMill.	•	•	•		•	•						•	•		•			•		•	•				•			•	•
Hippurus vulgaris L.									•													•							
Hydrilla verticillata (L.f.) Royle																								•					

Table 3.1 (continued)

Hydrocotyle ranunculoides L.f.																								•					
Hydrocotyle Umbullata L.				•										•		•			•				•				•		
Juncas Pelocarpus E. Mey.					•																	•							
Lemna minor L.				•		•	•					•	•	•		•		•	•			•	•	•	•	•	•		
Lemna trisulca L.						•									•										•				
Ludwigia leptocarpa (Nutt.) H. Hara														•					•										
Ludwigia peploides (Kunth) P.H. Raven				•																				•					
Lymnobium spongia (Bosc) Rich. Ex Steud.				•												•			•					•					
Lythrum salicaria L.																						•							•
Myriophyllum aquaticum (Vell.) Verdc.																								•					
Myriophyllum hippuroides Nutt. Ex Torr. & A. Gray																						•							
Myriophyllum quitense Kunth																										•			
Myriophyllum sibiricum Kom.	•		•		•		•	•			•		•							•		•				•			
Myriophyllum spicatum L.	•		•		•	•	•		•	•		•	•		•		•	•		•	•	•			•	•		•	•
Myriophyllum verticillatum L.												•																	
Najas flexilis (Willd.) Rostk. & Schmidt	•		•				•					•			•		•					•			•			•	
Najas guadalupensis (Spreng.) Magnus	•	•					•		•	•					•						•							•	•
Najas marina L.										•											•								
Najas minor All.									•															•					
Nitella sp.					•			•		•	•	•		•								•							
Nuphar advena (Aiton) Kartesz & Gandhi	•	•	•			•	•		•			•	•		•		•								•			•	•
Nuphar lutea (L.) Sm.									•							•							•	•					
Nymphaea odorata Aiton	•	•	•			•	•								•		•							•	•			•	•
Nymphaea odorata spp. *tuberosa* (Paine) Wiersma & Hellquist		•				•						•																	
Phalaris arundinacea L.	•	•	•				•						•									•							•
Phragmites communis Trin.	•	•	•			•																			•				
Polygonum sp.														•															
Polygonum amphibium L.																						•				•			

Table 3.1 (continued)

Potamogeton sp.		•	•				•																						
Potamogeton amplifolius Tuck.									•			•	•		•		•											•	
Potamogeton cripsus L.	•	•	•		•		•	•		•	•	•	•		•					•	•	•				•			
Potamogeton diversifolius Raf.			•									•																•	
Potamogeton epihydrus Raf												•																	
Potamogeton foliosus Raf.	•				•		•	•		•	•							•		•	•	•			•				•
Potamogeton gramineus L.	•				•		•				•		•									•							
Potamogeton illinoensis Morong		•			•		•				•		•				•			•		•							
Potamogeton natans L.	•	•	•									•	•				•					•							
Potamogeton nodosus Poir.			•							•		•					•	•				•		•	•				
Potamogeton praelongus Wulfen	•	•				•							•		•							•						•	
Potamogeton pusillus L.			•				•		•			•	•									•						•	
Potamogeton richardsonii (Benn.) Rydb.		•			•	•					•	•					•	•		•		•			•				
Potamogeton robbinsii Oakes		•					•					•	•		•							•						•	
Potamogeton spirillus Tuck.	•					•						•																	•
Potamogeton zosteriformis Fernald	•	•	•		•		•				•	•	•		•		•	•				•			•			•	
Ranunculus sp.	•						•						•		•		•												
Ranunculus aquatilis L.					•			•			•									•		•							
Ruppia sp.		•								•																			
Sagittaria americana																		•							•				
Sagittaria cuneata Sheldon								•														•							
Sagittaria graminea Michx.							•															•							
Sagittaria latifolia Willd.												•												•					
Sagittaria rigida Pursh												•																	
Scirpus sp.		•				•			•								•	•											
Scirpus americanus Pers.																		•							•				
Scirpus validus Vahl																									•				
Sium suave Walter							•					•																	
Sparganium sp.												•													•				
Spirodela polyrhiza (L.) Schleid.							•					•		•		•	•										•		

Table 3.1 (continued)

Stuckenia filiformis (Pers.) Börner										•																			
Stuckenia pectinata (L.) Börner	•	•	•		•	•		•		•	•		•				•	•		•	•	•			•	•			•
Typha sp.																													
Typha angustifolia L.										•		•			•			•							•				
Typha latifolia L.		•							•	•	•			•								•	•	•		•			•
Utricularia gibba L.													•																
Utricularia minor L.							•					•																	•
Utricularia vulgaris L. p.p.	•	•	•				•		•		•	•	•		•		•	•	•			•		•	•				•
Vallisneria americana Michx.	•	•				•	•					•	•		•		•			•					•			•	•
Wolffia sp.				•										•															
Zannichellia palustris L.															•							•							
Zizania aquatica L.												•																	
Zizaniopsis miliacea (Michx.) Döll & Asch.														•									•	•					

Table 3.2 Model results for factors influencing probability of occurrence of an invasive macrophyte from 29 lakes surveyed across the United States, 1997-2011.

Model[a]	***K*** [b]	**AIC**[c]	**ΔAIC**[d]	w_i [e]	***Pseudo-* R²**	**Rank**
NSPP + DEPTH + FETCH + $NSPP^2$ + $FETCH^2$ + DEPTH × FETCH	6	3875.301	0.000	0.478	0.03	1
NSPP + DEPTH + FETCH + $NSPP^2$ + $DEPTH^2$ + $FETCH^2$ + DEPTH × FETCH	7	3877.051	1.750	0.199	0.03	2
NSPP + FETCH + $NSPP^2$ + $FETCH^2$	4	3878.432	3.131	0.100	0.02	3
NSPP + DEPTH + FETCH + $NSPP^2$ + $DEPTH^2$ + $FETCH^2$	6	3879.138	3.837	0.070	0.03	4
NSPP + DEPTH + $NSPP^2$	3	3879.331	4.030	0.064	0.02	5
NSPP + DEPTH + FETCH + $NSPP^2$ + $DEPTH^2$ + DEPTH × FETCH	6	3880.467	5.166	0.036	0.03	6
NSPP + DEPTH + $NSPP^2$ + $DEPTH^2$	4	3881.331	6.030	0.023	0.02	7

[a] Model terms are native species richness (NSPP), water depth (DEPTH), and fetch distance (FETCH). Input variables were all standardized to 2 SD.

[b] K = no. of parameters in model.

[c] Akaike's Information Criterion Score

[d] ΔAIC = the difference between the AIC value of the best supported model and successive models.

All models in the 95% confidence model set are included

[e] w_i = Akaike model weight.

Table 3.3 Model averaged parameter estimates of invasive species occurrence, from 29 lakes surveyed across the United States, 1997-2011.

			95% Confidence Limit		
Model Term[a]	**Parameter Estimate**	**Standard Error**	**Upper**	**Lower**	**Relative Importance**
NSPP^2	0.837	-0.123	0.597	1.078	0.970
NSPP	0.032	0.128	0.282	-0.218	0.970
FETCH^2	0.208	-0.088	0.035	0.380	0.883
FETCH	-0.353	-0.194	-0.733	0.027	0.883
DEPTH^2	-0.030	-0.076	-0.179	0.120	0.329
DEPTH × FETCH	-0.399	-0.203	-0.797	0.000	0.713
DEPTH	-0.207	-0.149	-0.499	0.084	0.870

[a] Model terms are native species richness (NSPP), water depth (DEPTH), and fetch distance (FETCH). Input variables were all standardized to 2 SD.

Figure 3.1 Location of 29 lakes surveyed in the conterminous United States for aquatic invasive plants from 1997-2011.

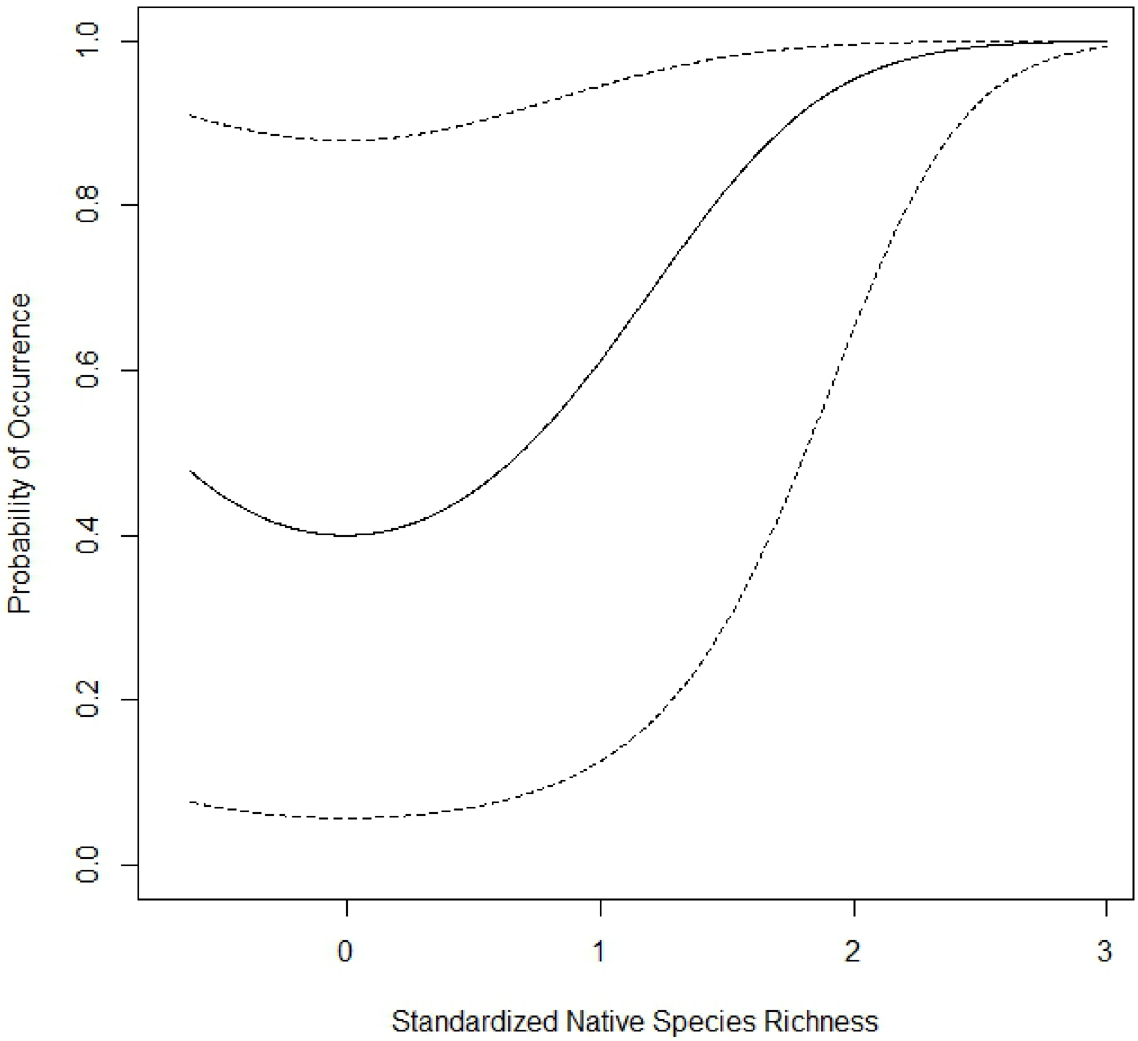

Figure 3.2 Probability of occurrence of an invasive species as a function of quadratic standardized native species richness based on the best model fit (Rank = 1) with 95% confidence intervals (dashed lines). Native species richness values were standardized to 2 standard deviations (For original values of native species richness, 1 SD = 1.79)

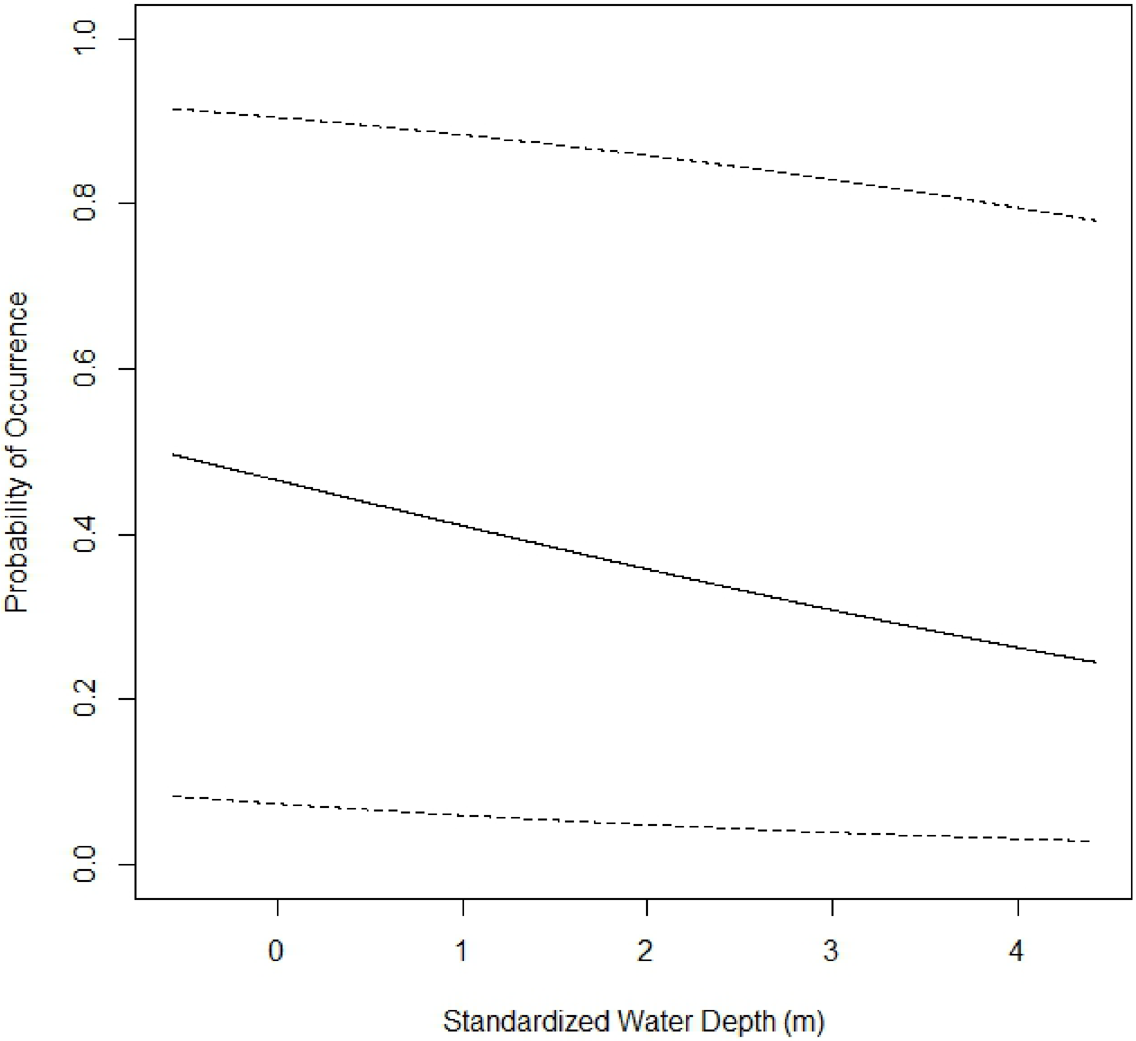

Figure 3.3 Probability of occurrence of an invasive species as a function of water depth based on the best model fit (Rank = 1) with 95% confidence intervals. Water depth values were standardized to 2 standard deviations (For original values of water depth, 1 SD = 1.95m)

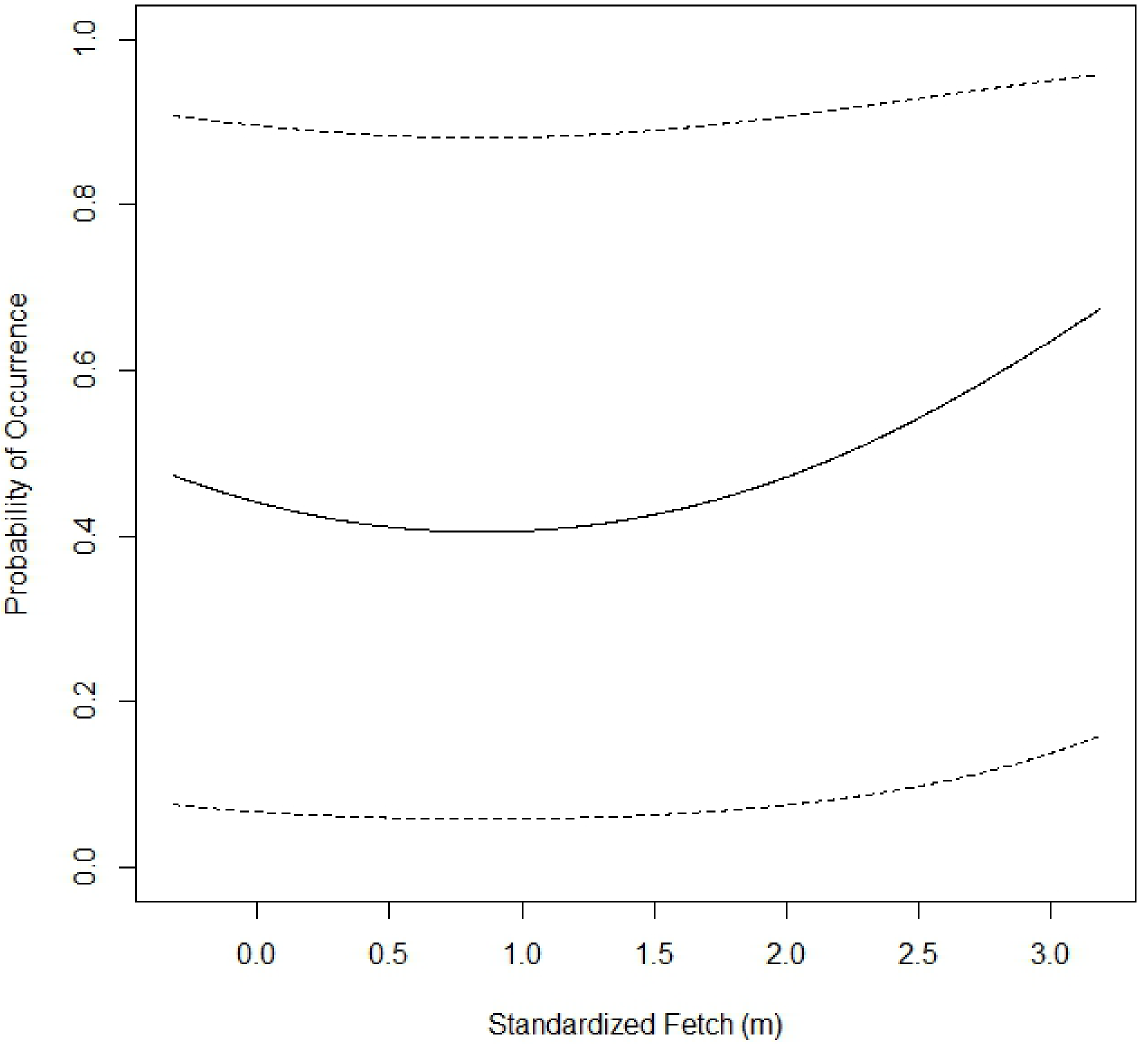

Figure 3.4 Probability of occurrence of an invasive species as a function of quadratic fetch based on the best model fit (Rank = 1) with 95% confidence intervals. Fetch distance values were standardized to 2 standard deviations (For original values of fetch distance, 1 SD = 1200m).

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CHAPTER IV

OBSERVATIONAL EXAMINATION OF DARWIN'S NATURALIZATION HYPOTHESIS AT TWO SCALES

Introduction:

Invasive species are acknowledged as one of the most severe problems facing today's ecosystems (Vitousek et al. 1997). They cause numerous problems ranging from displacement of native species to extinctions (Mooney and Cleland 2001). They also cause numerous problems for the human population including high costs related to their control and disruption of essential ecosystem services (Pimentel et al. 2005). Due to the magnitude of impacts, understanding the mechanisms that lead to species invasion is of primary importance for ecologists and conservationists.

Species invasions are highly non-random in freshwater ecosystems (Strayer 2010), and although native macrophytes are beneficial in aquatic ecosystems, invasive aquatic plants can cause significant ecological and economic harm. High densities of macrophytes such as invasive *Myriophyllum spicatum* and *Hydrilla verticillata* interfere with foraging and spawning of some fish species (Valley and Bremigan 2002, Theel and Dibble 2008). Canopy forming plants reduce light transmittance and oxygen diffusion into the water column which can lead to anoxic zones unsuitable for other aquatic organisms (Thomas and Room 1986, Caraco and Cole 2002). Because of physiological differences of introduced plants, nutrient cycles may be altered in some systems (Templer et al. 1998, Angeloni et al. 2006). They may also interfere with recreational opportunities and navigation, and can block water intakes (Madsen et al. 1991a). In addition, invasive aquatic plants may hybridize with native species, threatening native diversity (Boylan et al. 1999, Ailstock et al. 2001, Houlahan and Findley 2004, Moody and Les 2007). Reservoirs and impoundments may facilitate invasion (Havel et al. 2005, Johnson et al. 2008); therefore, understanding the factors that lead to increased probability of invasion is of high importance to ecologists and aquatic resource managers.

Although the problems associated with invasive species are widely acknowledged and studied, there has been little predictive understanding of the mechanisms that lead to species invasion (Cadotte et al. 2006). There have been numerous studies attributing invasiveness to the characteristics of a species, whereas other studies link invasion to characteristics of the invaded community (including biotic and abiotic characteristics; Levine 2000, Kolar and Lodge 2001, Chadwell and Engelhardt 2008, Jacobs and MacIsaac 2009). Although there is theoretical support for these divergent claims, empirical evidence has not reconciled the differences, and it has been suggested that studying the match between invader and invaded community is key to understanding invasiveness (Ricciardi and Atkinson 2004).

It has been proposed that invasions can be understood through the framework of community ecology theory (Shea and Chesson 2002, Fargione et al. 2003). This may be an interesting approach but defining the framework requires an assumption of how communities are assembled. There are two general theories of community assembly that may be applied to the study of species invasions (Gravel et al. 2007). Niche theory of community development predicts that the community evolves as species interact and natural selection occurs (MacArthur and Levins 1967, Levine 2000). Competitive exclusion therefore would limit the ability of species with related traits to co-exist. The alternative is a neutral theory in which species are equivalent, co-occurrence patterns are simply treated as random, and competition between related species plays only a small role in the structure of the community (Hubbell 2001).

The usefulness of neutral theory of biodiversity may be simply to provide a null model to test patterns of species co-occurrence (i.e., to test if assembly rules exist; Dodds 2009). In the context of species invasions, if niche theory and species interaction are responsible for species co-occurrence patterns, we would see interaction patterns among closely related species when niche conservatism is high within a group, and biogeographically disjunct populations are a result of vicariant or random dispersal events (i.e., evolutionary histories of species are were not sympatric; Cavender-Bares et al. 2009).

The origin of these ideas goes back to the classical development of ecological theory. Charles Darwin hypothesized that introduced species would be less likely to naturalize (although his original hypothesis was opposite) in areas containing closely related species (Darwin's Naturalization Hypothesis (DNH); Darwin 1859, Daehler 2001). The underlying assumption of this idea is based in niche theory and suggests that competition between closely related species could limit the naturalization potential from an introduced species (Fargione et al. 2003, MacDougall et al. 2009). Several studies have argued that phenotypic similarity between native communities and invaders reduces the success of invading species. This means that potential biotic resistance can be identified for a particular subset of species when gauging invasion risk, if assumptions are made that phenotypic similarity correlates with phylogenetic relatedness (Strauss et al. 2006, Proches et al. 2008). In addition to competition, closely related species may also share similar enemies which may provide another mechanism of community resistance to invasion (Strauss et al. 2006). Phylogenetic relatedness is implicitly expected to correlate with net ecological similarity (Strauss et al. 2006). The alternative interpretation of this potential mechanism is that more closely related species also may have similar resource requirements (and traits), which would facilitate co-existence. However, this would be expected where resources are not limiting (Shea and Chesson 2002).

Although community attributes may be an important determinant of invasion success, results of experimental and observational studies have been inconclusive and have differed across spatial scales (e.g., Kennedy et al. 2002, Stohlgren et al. 2003, Thomaz and Michelan 2011). Fridley et al. (2007) reviewed evidence for native-exotic richness relationships and found that, in general, small scale studies reported a negative relationship whereas large scale studies reported the opposite. This "invasion paradox" (*sensu* Fridley et al. 2007) opens new doors for inquiry into the causes of these seemingly scale dependent patterns and also provides opportunity to include community descriptors other than species diversity (e.g., congeneric richness) to predict invasion success.

Testing DNH may prove useful for studies of species invasion because it relates characteristics of a species to the characteristics of an invaded community (implied ecological similarity due to congeneric relatedness; Ricciardi and Atkinson 2004). In addition, species invasions provide an interesting opportunity to test hypotheses of community assembly by examining phylogenetic attraction vs. phylogenetic repulsion

(Cavender-Bares et al. 2004). The expectation would be that if phylogenetic repulsion is present, competition may indeed limit the absolute number of niches able to occupy a given area (e.g., niche saturation potential).

Two macrophyte species of special concern are Eurasian watermilfoil (*Myriophyllum spicatum*) and curlyleaf pondweed (*Potamogeton crispus*). *Myriophyllum spicatum* is an invasive vascular plant that has invaded freshwater lakes across the United States. The introduction of this species has likely resulted in the alteration of the complex interactions occurring in littoral habitats (Madsen 1997). *Myriophyllum spicatum* has been associated with declines in native plant species richness and diversity (Madsen et al. 1991b, Madsen et al. 2008), reductions in habitat complexity resulting in reduced macroinvertebrate abundance or diversity (Keast 1984, Cheruvelil et al. 2001), and reductions in fish growth (Lillie and Budd 1992). *Myriophyllum spicatum* poses nuisance problems to humans by impeding navigation, limiting recreation opportunities, and increasing flood frequency and intensity (Madsen et al. 1991a). It is primarily spread by fragmentation and can be easily transported between water bodies by many vectors making it difficult to control after establishment. *Potamogeton crispus* also causes significant nuisance problems where it has become established (Catling and Dobson 1985, Bolduan et al. 1994, Woolf and Madsen 2003). It, like *M. spicatum*, is an influential invader that can accelerate internal nutrient loading and eutrophication (James et al. 2002). Management of this species is often more difficult due to its life history strategy (turion production) and the limited availability of effective management options.

The goal of this research was to test Darwin's Naturalization Hypothesis using two species of highly invasive aquatic plants, *M. spicatum* and *P. crispus*, and assess whether results were consistent at small and large scales. Based on DNH, probability of occurrence of an invasive species should be less as number of congeneric species increases at a location (i.e., have a negative relationship). I also tested the alternative hypothesis that native species richness and/or distance to nearest known occurrence of these species were related to the probability of occurrence at the point scale and that native species richness and/or area were related to the probability of occurrence at the lake scale. To address these hypotheses I asked the following questions at a small (point) and large (lake) scale: 1) Is presence of invasive species related to number of congeneric species occurring at a sampling location?, 2) Is presence of invasive species related to native species richness occurring at a sampling location?, 3) At a point scale, is presence of invasive species related to distance to nearest known location of the species (indicating dispersal rather than community attributes might be responsible for probability of occurrence)?, and 4) At the lake scale, is presence of invasive species related to lake area (indicating absolute areal scale vs. ecosystem level scale as contributing factors)? In addition, if significant relationships existed, I noted whether they were positive, negative, or non-linear and evaluated which hypothesis was best supported by the data.

Methods:

Study Areas and Design

The study area spanned the conterminous United States, where lakes and reservoirs (hereafter lakes; *n* = 29) were surveyed once at various times from 1997 to 2011 (Figure 4.1, Appendix A). Lakes represented a variety of areas ranging from 7-36,000 ha and 9 freshwater ecoregions (Appalachain Piedmont 1, Chesapeake Bay 2, Colorado 1, Columbia Glaciated 3, Laurentian Great Lakes 8, Lower Mississippi 7, St.

Lawrence 1, Upper Mississippi 3, Upper Missouri 3). Each lake was originally surveyed for a specific project goal to obtain a baseline of invasive and native species occurrence and distribution using the point-intercept method (Madsen 1999). For each lake, a grid of points was generated in a GIS and integrated with field GPS to navigate to each point by boat. Point spacing varied by lake area to ensure representative sampling in each lake. At each sample point, a rake was tossed and retrieved to collect plants occurring at that location. Rake tosses generally collect plants directly under the boat and are dragged 1-2 m along the bottom. This method allowed a large number of samples to be collected and insured that all plants occurring in an area were accounted for. Each plant collected was identified to species and recorded as present (1) or absent (0) at the location.

Additionally, distance (DIST) of each point to the nearest reported location of *P. crispus* and *M. spicatum* was calculated. Using data obtained from the USGS Nonindigenous Aquatic Species (NAS) database, points where each species was recorded was plotted in ArcGIS. Euclidian distances were then calculated for each point intercept survey location to the nearest recorded USGS NAS database location. Because random or auto-correlated dispersal may be responsible for presence of invasion and not specific characteristics of the community per se, this allowed me to test the alternative hypothesis that processes not related to a species' niche (i.e., neutral or random processes) may be more supported than niche based hypotheses.

All input variables (NC, NSPP, and DIST) were centered and standardized to 2 standard deviations (Mean = 0, SD = 0.5) to improve model convergence because of differences in parameter value scales. This also allows more direct interpretation of the relative strength of parameter estimates for a given dataset.

I tallied numbers of native *Potamogeton* and *Myriophyllum* species for each survey location (native congenerics; NC). This allowed modeling presence of *P. crispus* and *M. spicatum* as a function of number of respective congenerics at a particular location. To test DNH at a larger scale, species and congeneric richness were aggregated, and total area was calculated for each lake.

Modeling and Analysis:

To estimate probability of invasive *P. crispus* or *M. spicatum* occupying a given sampling location, generalized linear mixed models with congeneric and native species richness data along with distances to nearest recorded location were used, and their performances were compared to select the best supported hypothesis. Models were developed using the lmer package in R (R Development Core Team 2012) and fit using the binomial family and logit link function with lake as a random effect.

For point scale analyses, model terms specific to the original hypotheses were selected. For presence of an invasive species, NC (native congenerics), NC^2 (quadratic native congenerics), DIST (distance to nearest recorded location), NSPP (native species richness), and $NSPP^2$ (quadratic native species richness) were used. Quadratic terms for congeneric and native species richness were included to test for potential non-linear effects on probability of occurrence of invasive species. Congeneric and native species richness were collinear for *Potamogeton* (Spearman correlation coefficient > 0.4), and were not included in the same model in any model set including those for *Myriophyllum* (for consistency). I also included global (excluding either NSPP or NC as noted above) and null models. All relevant combinations (i.e., avoiding collinearity) of these model terms were fit to separate models because I made no *a priori* assumptions that a particular subset of these model terms would provide more explanatory power than another.

For a test of DNH at the lake scale, the aggregated totals for NC, NC^2, NSPP, $NSPP^2$ and AREA (lake area) were used. These terms were centered and standardized to 2 standard deviations (Mean = 0, S.D. = 0.5). To estimate probability of invasive *P. crispus* or *M. spicatum* occupying a given lake, I fit a generalized linear model for binary data using the lake scale variables. The modeling approach was identical to the one used at the point scale; however, I did not include random effects because each lake represented the experimental unit of interest.

Ten models were created (including a null model) for each species (*P. crispus* and *M. spicatum*) at point and lake scales (i.e., four separate sets of 10 models). Performance of each model within a set (i.e., DNH and each alternative hypothesis) was evaluated using Akaike Information Criterion (AIC). At the point scale, sample sizes were sufficiently large relative to number of explanatory variables and therefore no adjustments were made to AIC scores. However, at the lake scale I used AIC corrected for small sample size (Burnham and Anderson 2002). Determination coefficients (pseudo-R^2 values) were also calculated to estimate amount of variation actually explained by each model.

Results:

Twenty-nine lakes containing invasive macrophytes were surveyed between 1997-2011. Ninety-one species were identified including 11 species considered invasive. A total of 10,547 points were surveyed. Of these, 4,113 (39%) contained at least one plant and had a depth greater than zero. Total number of points surveyed averaged 363.7

(SD = 421.0) per lake, ranging from 55 to 1,623. Total number of points used in analyses (N = 4,113) averaged 141.8 (SD = 120.7) per lake ranging from 24 to 636. Invasive *P. crispus* occurred at 307 points and in 15 lakes and *M. spicatum* occurred at 1130 points and 19 lakes. In total, there were 15 native species belonging in the *Potamogeton* genus and 4 in *Myriophyllum*.

For models testing competing hypotheses for *P. crispus* at the point scale, all models (n = 10) converged. Interestingly, native congeneric species richness (NC) and NC^2 were significant model terms when modeled separately from NSPP (Table 4.1). However, contrary to the predictions of DNH, the relationship between congeneric richness and presence of *P. crispus* was positive and non-linear. This evidence does not support DNH (the expectation of a negative relationship), except at extremely high values of native congeneric richness. Native species richness (NSPP) and $NSPP^2$ showed a positive, non-linear relationship with *P. crispus* occurrence. However, when comparing performances of NSPP and NC models, NSPP models performed better (i.e., had a lower AIC score and greater determination coefficient; Table 4.1). Also interestingly, NSPP and NC have non-linear effects. Although the relationship is initially positive, at large values of native species or congeneric richness, the influence changes to negative. Distance to nearest recorded location (DIST) was not a significant variable in any *P. crispus* model where it was included as a term.

Models testing DNH for *P. crispus* at the lake scale indicated a significant positive relationship between probability of occurrence and NC, providing no evidence to support DNH at this scale (Table 4.2). Other competing hypotheses did not indicate significant support although NSPP was significant when it was included by itself in the model. The model containing only NC performed best in the set.

For models testing DNH for *M. spicatum*, only eight of the ten models converged. Models containing NC^2 (for *Myriophyllum*) did not converge. Although there were 4 native *Myriophyllum* species located in the study, there was never more than one native *Myriophyllum* at a sample point. This is likely responsible for model convergence failure because this causes the terms NC and NC^2 to be perfectly collinear. Unlike models for *P. crispus*, native *Myriophyllum* species richness (NC) was not a significant model terms when modeled separately from NSPP, providing no evidence to support DNH (Table 4.3). However, NSPP, $NSPP^2$, and DIST were all significant, and the model containing all three terms outperformed all other models. Unlike the patterns for *P. crispus*, patterns of native species richness for *M. spicatum* were negative and non-linear providing some evidence to support biotic interaction with native species other than congenerics. DIST was significantly negatively correlated with *M. spicatum* presence, and models containing NSPP, $NSPP^2$, and DIST performed better than the models containing only the individual terms, indicating that dispersal events also play an important role in determining which areas may be invaded by this species. However, the relatively low determination coefficient indicated very little variation is actually explained by the model.

Models testing DNH for *M. spicatum* at the lake scale indicated a significant positive relationship between probability of occurrence and native species richness (Table 4.4). However, the relationship between occurrence and NC was not significant, providing no evidence to support DNH at this scale. Only native species richness was significant in the whole set of models and the model containing only native species richness performed best (lowest AIC and greatest determination coefficient).

Discussion:

Studying invasions in the context of community ecology theory has been suggested as a way to rectify some problems encountered by invasion ecologists who have struggled to identify consistent theories of species invasion (Shea and Chesson 2002). One way to investigate patterns of species invasions accounting for characteristics of a species and the invaded community is by testing Darwin's Naturalization Hypothesis (MacDougall et al. 2009, Thomaz and Michelan 2011). This hypothesis is also useful for testing niche based theories that form the foundation of community assembly rules by assuming that related (congeneric) species share similar traits, and by extension resource requirements, making them less likely to co-exist in the event that one species is introduced into a community that already contains a congeneric species (Fargione et al. 2003, Cavender-Bares et al. 2009). DNH has been tested rarely (Ricciardi and Atkinson 2004) but has made a recent resurgence in the ecological literature (e.g., Daehler 2001, Lambdon and Hulme 2006, Jiang et al. 2010). However, there are still limited data from only a few ecosystem types, a deficiency which necessitates further inquiry.

I found no evidence to support DNH, and where congeneric richness provided a significant contribution to prediction (which only occurred with *P. crispus*), the relationship was positive (the opposite of DNH predictions). Similar results have been reported on studies of plants inhabiting Mediterranean islands (Lambdon and Hulme 2006). At the point scale, native species richness outperformed congeneric richness indicating species relatedness may be less important than number of native species occupying an area. Models for *P. crispus* showed the relationship was positive and non-linear for total native species and congenerics indicating that resources only become limiting when richness is high, or that *P. crispus* has a competitive advantage over a small subset of the species pool which only disappears with greater species richness. Theoretically this is plausible because as species richness increases, accumulation of niches occurs which potentially increases interspecific interaction (Proches et al. 2008). This could also indicate that in many sampling locations community assembly has not reached equilibrium (i.e., is not yet mature), assuming assembly is based on niche theory (Shea and Chesson 2002, Wilson 2007). At the lake scale, DNH was similarly unsupported but there was a significant positive relationship between probability of occurrence and native congeneric richness for *P. crispus*. Probability of occurrence of *P. crispus* also had a marginally significant positive relationship with native species richness, but at the lake scale, congeneric richness performed best. The latter of these results supports previous work that has found a positive relationship between invasive species and native species richness at large scales (Fridley et al. 2007). The former may be an indication that mechanisms contributing the "invasion paradox" may also act on congeneric species at large scales (i.e., positive relationships manifested at large scales due to increases environmental heterogeneity). However, it may also provide evidence that an introduced species closely related to species in a native community can naturalize more easily because of shared resource requirements and/or traits. If this is the case, interspecific interaction would be weak between introduced species and those in the native community, and it is likely that resource competition would not provide a biotic resistance to invasion. Careful consideration should be made when inferring from these patterns because studying these organisms at scales irrelevant to the mechanisms being tested is meaningless (Proches et al. 2008).

Although these results did not support DNH, there is still a great need to investigate how community level factors influence species invasions. This could be useful in reconciling patterns revealed by the “invasion paradox” which notes species diversity is negatively related to invasion at small scales but positively related at larger scales (Fridley et al. 2007). This is generally explained by strong interspecific interaction at small scales and greater environmental heterogeneity at large scales (Fridley et al. 2007). One of the major issues contributing to this paradox may be a limitation of using species diversity as a community descriptor. Using species diversity as a contributing factor to species invasions assumes that more resources are sequestered (used by a particular dimension of niche space) with increasing numbers of species. This, however, does not account for any functional diversity or evolutionary history of the community other than how many species currently occupy an area, and does not reveal any patterns of community assembly (Proches et al. 2008); the diversity observed in a community could still be based on random dispersal events, not the accumulation of niches resulting in a decrease in available space within particular niche dimensions. Phylogenetic diversity (based on relatedness), however, may be better at elucidating patterns of community assembly because it explicitly considers evolutionary history and assumes that related species share similar functional traits (as assumption that is lost altogether with species diversity calculations; Cavender-Bares et al. 2009). Phylogenetic relatedness is also expected to be more important at a small scale where interspecific interaction potential is greatest.

Unfortunately, phylogenetic information isn't always available or easy to interpret (Cavender-Bares et al. 2009). This may be why species diversity has so far been more widely applied as a community descriptor. However, if the assumption is made that congeneric species are more related, and that they share similar functional traits, DNH may provide a way to gain insight into how invasions are related to community assembly processes in other ecosystems and allow better risk assessments for potential invaders.

Figure 4.1 Location of 29 lakes surveyed in the conterminous United States for aquatic invasive plants from 1997-2011.

Table 4.1 Model results for *P. crispus* at the point scale. Where parameters estimates have been omitted in the table, those parameters were not fit in the model. Models are listed in order of performance (best to worst). Data were collected from 29 lakes in the United States from 1997-2011.

Model Terms[a]																		
Potamogeton NC	L	U	*Potamogeton* NC^2	L	U	NSPP	L	U	NSPP^2	L	U	DIST	L	U	AIC[b]	ΔAIC[c]	w_i[d]	*psuedo* - R^2
						1.72 (0.22)	1.29	2.15	**-0.28 (0.15)**	-0.57	0.01				**1471.54**	**0.00**	**0.522**	0.06
						1.41 (0.15)	1.12	1.70							**1473.43**	**1.89**	**0.203**	0.06
						1.72 (0.22)	1.29	2.15	**-0.28 (0.15)**	-0.57	0.01	-0.26 (1.04)	-2.30	1.78	**1473.48**	**1.94**	**0.198**	0.06
						1.41 (0.15)	1.12	1.70				-0.25 (1.03)	-2.27	1.77	1475.37	3.83	0.077	0.06
1.20 (0.22)	0.77	1.63	**-0.34 (0.16)**	-0.65	-0.03										1524.76	53.23	0.000	0.02
1.20 (0.23)	0.75	1.65	**-0.34 (0.16)**	-0.65	-0.03							-0.41 (0.98)	-2.33	1.51	1526.59	55.05	0.000	0.02
0.85 (0.14)	0.58	1.12													1527.54	56.00	0.000	0.02
0.84 (0.14)	0.57	1.11										-0.41 (0.98)	-2.33	1.51	1529.37	57.83	0.000	0.02
															1558.64	87.10	0.000	Null
												-0.54 (0.99)	-2.48	1.40	1560.33	88.80	0.000	0

[a] Model terms are native congenerics (NC), native species richness (NSPP), and distance to nearest recorded location (DIST). Non-binary input variables were all standardized to 2 SD.

[b] Akaike's Information Criterion Score

[c] ΔAIC = the difference between the AIC value of the best supported model and successive models.

[d] w_i = Akaike model weight.

***Bold** parameter estimates are significant at $p < 0.1$

Table 4.2 Model results for *P. crispus* at the lake scale. Where parameters estimates have been omitted in the table, those parameters were not fit in the model. Models are listed in order of performance (best to worst). Data were collected from 29 lakes in the United States from 1997-2011.

									Model Terms[a]										
Potamogeton NC	L	U	*Potamogeton* NC^2	L	U	NSPP	L	U	NSPP^2	L	U	AREA	L	U	AIC$_c$[b]	ΔAIC[c]	w_i[d]	*psuedo* - R^2
2.48 (1.03)	**0.46**	**4.50**													36.88	0.00	0.432	0.19
2.48 (1.1)	**0.32**	**4.64**	1.24 (2.82)	-4.29	6.77										39.16	2.28	0.139	0.2
						2.04 (0.99)	**0.10**	**3.98**							39.19	2.30	0.137	0.14
2.46 (1.05)	**0.40**	**4.52**										0.28 (1.48)	-2.62	3.18	39.34	2.46	0.126	0.19
						2.02 (1.01)	**0.04**	**4.00**	0.21 (1.83)	-3.38	3.80				41.67	4.79	0.039	0.14
						2.02 (1.02)	**0.04**	**4.04**				0.01 (1.21)	-2.36	2.38	41.68	4.79	0.039	0.14
2.49 (1.12)	**0.29**	**4.69**	1.3 (3.01)	-4.60	7.20							0.32 (1.80)	-3.21	3.85	41.83	4.95	0.036	0.2
															42.32	5.43	0.029	Null
												0.65 (0.95)	-1.21	2.51	44.05	7.17	0.012	0.1
						2.01 (1.03)	**-0.01**	**4.03**	0.19 (1.87)	-3.48	3.86	0.08 (1.25)	-2.37	2.53	44.38	7.49	0.010	0.14

[a] Model terms are native congenerics (NC), native species richness (NSPP), and lake area (AREA). Non-binary input variables were all standardized to 2 SD.

[b] Corrected Akaike's Information Criterion Score

[c] ΔAIC = the difference between the AIC value of the best supported model and successive models.

[d] w_i = Akaike model weight.

***Bold** parameter estimates are significant at $p < 0.1$

Table 4.3 Model results for *M. spicatum* at the point scale. Where parameters estimates have been omitted in the table, those parameters were not fit in the model. Models are listed in order of performance (best to worst). Data were collected from 29 lakes in the United States from 1997-2011.

							Model Terms[a]									
Myriophyllum NC	L	U	*Myriophyllum* NC^2	NSPP	L	U	NSPP^2	L	U	DIST	L	U	AIC[b]	ΔAIC[c]	w_i[d]	*psuedo* - R^2
				-0.24 (0.14)	**-0.51**	**0.03**	**0.73 (0.13)**	**-0.98**	**-0.48**	**-6.82 (1.73)**	**-10.21**	**-3.43**	**2761.40**	**0.00**	**1.000**	0.03
				0.31 (0.11)	**0.09**	**0.53**				**-6.87 (1.72)**	**-10.24**	**-3.50**	2794.85	33.45	**0.000**	0.02
				-0.25 (0.14)	**-0.52**	**0.02**	**0.75 (0.13)**	**-1.00**	**-0.50**				2796.36	34.95	0.000	0.02
										-6.84 (1.71)	**-10.19**	**-3.49**	2801.05	39.65	0.000	0.01
0.14 (0.19)	-0.23	0.51								**-6.83 (1.70)**	**-10.16**	**-3.50**	2802.50	41.10	0.000	0.01
				0.31 (0.11)	**0.09**	**0.53**							2830.92	69.52	0.000	0
													2837.12	75.72	0.000	Null
0.15 (0.19)	-0.22	0.52											2838.53	77.13	0.000	0
NA			NA							NA			NA	NA		NA
NA			NA										NA	NA		NA

[a] Model terms are native congenerics (NC), native species richness (NSPP), and distance to nearest recorded location (DIST). Non-binary input variables were all standardized to 2 SD.

[b] Akaike's Information Criterion Score

[c] ΔAIC = the difference between the AIC value of the best supported model and successive models.

[d] w_i = Akaike model weight.

***Bold** parameter estimates are significant at $p < 0.1$

Table 4.4 Model results for *M. spicatum* at the lake scale. Where parameters estimates have been omitted in the table, those parameters were not fit in the model. Models are listed in order of performance (best to worst). Data were collected from 29 lakes in the United States from 1997-2011.

Model Terms[a]																		
Myriophyllum NC	L	U	*Myriophyllum* NC^2	L	U	NSPP	L	U	NSPP^2	L	U	AREA	L	U	AIC$_c$[b]	ΔAIC[c]	w_i[d]	*psuedo* - R^2
						3.28 (1.38)	**0.58**	**5.98**							32.77	0.00	0.475	0.24
						3.30 (1.25)	**0.85**	**5.75**	-2.41(1.93)	-6.19	1.37				33.98	1.21	0.259	0.28
						3.34 (1.41)	**0.58**	**6.10**				-0.41 (1.57)	-3.49	2.67	35.21	2.44	0.140	0.24
						3.33 (1.30)	**0.78**	**5.88**	-2.37 (1.97)	-6.23	1.49	-0.12 (1.20)	-2.47	2.23	36.68	3.91	0.067	0.28
1.56 (1.05)	-0.50	3.62													39.05	6.28	0.021	0.07
															39.51	6.74	0.016	Null
0.30 (182.8)	-357.99	358.59	12.2 (2232.4)	-4363.30	4387.70										41.23	8.45	0.007	0.08
												0.55 (1.06)	-1.53	2.63	41.48	8.71	0.006	0
1.54 (1.08)	-0.58	3.66										0.17 (1.38)	-2.53	2.87	41.53	8.76	0.006	0.07
0.27 (181.9)	-356.25	356.79	12.4 (2221.7)	-4342.13	4366.93							-0.21 (1.87)	-3.74	3.32	43.92	11.15	0.002	0.08

[a] Model terms are native congenerics (NC), native species richness (NSPP), and lake area (AREA). Non-binary input variables were all standardized to 2 SD.

[b] Corrected Akaike's Information Criterion Score

[c] ΔAIC = the difference between the AIC value of the best supported model and successive models.

[d] w_i = Akaike model weight.

***Bold** parameter estimates are significant at $p < 0.1$

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CHAPTER V

CONCLUSION AND SYNTHESIS

Invasive species are a leading cause of global change. There is still a great need to identify causes and consequences of species invasions to promote conservation of Earth's biota. Although there have been numerous mechanisms proposed to explain invasion success or "invasibility", most haven't been fully tested in aquatic macrophyte communities and therefore successful prediction of aquatic plant invasion may be limited. Nonetheless, aquatic plants represent an important component of aquatic ecosystems and studying invasibility of these systems is imperative for future aquatic resource management. In many cases, consequences (i.e., impacts) are studied more than causes (i.e., mechanisms of invasion success) in aquatic plant communities because scientists and the public are often only interested in invasive species after they start causing problems. This is evident for aquatic plants because much of what is known about aquatic plant invasions is found in the management literature. However, by understanding the mechanisms contributing to invasion, management strategies can be more easily designed to either help to prevent invasions, rapidly eradicate invasive species, or control their growth and dispersal.

Although I found numerous mechanistic hypotheses in the literature applied to aquatic plants (Chapter 2), it is evident that there is still a great need to study the mechanistic factors that allow macrophyte invasions to occur. In addition, more representative taxa should be included to form a more complete picture of the current state of knowledge regarding active invasion mechanisms in aquatic systems. In addition, ecologists should continue to develop new hypotheses and to integrate multiple hypotheses together with the goal of identifying general patterns of invasion.

One of the most widely hypothesized mechanisms of invasion success (or lack of success) is biotic resistance. This hypothesis, based in niche theory, predicts that as more species accumulate in an area, available environmental space (micro-habitat) decreases and therefore increased interspecific interference (i.e., competition) is more able to exclude invaders. The results of my study as related to the biotic resistance hypothesis (Chapter 3) suggest that biotic interaction, stress, and disturbance co-vary to influence the probability of invasive species occurrence in littoral areas of lakes and reservoirs throughout the United States. Although biotic interaction via native species richness tended to decrease the probability of occurrence of an invasive species, the relationship was non-linear and did not hold true for locations with high native species richness. In fact, probability of invasive species occurrence increased when native species richness approached numbers greater than two. This represents an interesting finding because most studies thus far in native/exotic richness relationships have simply identified a positive or negative relationship and have led to the popular notion of an "invasion paradox" (Fridley et al. 2007).

Disturbance is widely regarded as a mechanism influencing invasions and I found a significant relationship between invasion probability and degree of disturbance (fetch distance). However, the relationship was non-linear and only negatively impacted invasion probability at relatively lower degrees of disturbance. This result represents an interesting finding because intermediate disturbance hypothesis predicts greater species diversity at intermediate levels of disturbance. Taken in an ecosystem context, if disturbance facilitates invasion, and biotic resistance increases with diversity as has been hypothesized, a positive relationship between invasion probability and disturbance might be expected at lower and higher degrees of disturbance (Connell 1978). In addition, disturbances may open environmental space which can be exploited by species pre-adapted to those spaces or with inherent physiological traits that allow them to establish without interspecific interaction from natives (e.g., phenological differences; Davis et al. 2000).

Because this study used occurrence of invasive species at a point scale and all lakes in this study had at least one invasive species, lake-scale analysis was not possible. However, it is expected that species richness increases with area (Gleason 1925). Therefore, at larger scales and greater species richness, my results suggest there would indeed be a positive relationship between invasive species occurrence and native species richness. Thus, the invasion paradox may be an artifact of a situation where area simply increases, species accumulation occurs at an expected rate, and non-random patterns indicate a particular phase of the relationship between invasion and native species richness. In addition, models had relatively low explanatory power in terms of the amount of variation they explained. This indicates that more factors need to be identified that contribute to invasion by these species.

Although this study simply classified species as invasive or native, it may also be prudent to look at species specific attributes of native and invasive communities to identify species and characteristics that influence invasion success in a more precise context (e.g., functional diversity or physical structure). In addition, density of plants may be a more important factor than richness per se. Capers et al. (2007) found this in five of the six invasive aquatic plants they studied in Connecticut lakes.

Studying invasions in the context of community ecology theory has been suggested as a way to rectify some problems encountered by invasion ecologists who have struggled to identify consistent theories of species invasion (Shea and Chesson 2002). One of the most interesting areas of research for invasibility and impact is the naturalization concept, as it applies to related species. Simply using characteristics of a species (which is commonly done) does not explain risk because successful invasion depends on the receiving environment (Lockwood 2007). Likewise, characteristics of communities or areas alone cannot be used for risk assessment because their component functional parts may not be susceptible at all. However, considering species relatedness (i.e., Darwin’s naturalization hypothesis; DNH) implicitly considers traits of species and receiving environments (biotic and abiotic factors). Although supported theoretically, my analysis (Chapter 4) did not indicate that number of congeneric species had any negative impact on probability of invasion for *Potamogeton crispus* or *Myriophyllum spicatum* at small or large scales. This could be an artifact of community assembly process, or indicate equilibrium has not been reached (i.e., is not yet mature), assuming assembly is based on niche theory (Wilson 2007, Shea and Chesson 2002).

Although these results did not support DNH, there is still a great need to investigate how community level factors influence species invasions. This could be useful in reconciling patterns revealed by the “invasion paradox” which notes species diversity is negatively related to invasion at small scales but positively related at larger scales (Fridley et al. 2007). One of the major issues contributing to this paradox may be due to limitations of using species diversity as a community descriptor. Using species diversity as a contributing factor to species invasions assumes that more resources are sequestered (used by a particular dimension of niche space) with increasing numbers of species. This, however, does not take into account any functional diversity or evolutionary history of the community other than how many species currently occupy an area, and does not reveal any patterns of community assembly (Proches et al. 2008); the diversity observed in a community could still be based on random dispersal events, not accumulation of niches resulting in a decrease in available space within particular niche dimensions.

A more detailed and promising approach within this realm of research would be to focus on phylogenetic diversity and the correlation of phylogenetic diversity to functional diversity and functional redundancy. For example, redundancy may be present with high phylogenetic diversity but not with high species diversity (e.g., if there are many related species in an area). If functional diversity, redundancy, phylogenetic diversity, and species diversity are all high, the area could be highly stable (or ‘mature’). Because this area of research has received very little study, it is not known what patterns these relationships reveal. The expectation is that if species diversity is high but functional diversity is low, phylogenetic diversity would be high which may ultimately influence invasibility of that community. Careful consideration should be made when inferring from these patterns because studying these organisms at scales irrelevant to the mechanisms being tested is meaningless (Proches et al. 2008).

Ecological effects of invasive species may either increase or decrease through time (Strayer et al. 2006, Gherardi 2007, Hawkes 2007). In addition, the invader or invaded community may evolve as species composition shifts toward species insensitive to the invaders, masking the real influence of native richness on invasiveness. Future research should continue the search for mechanisms that allow introduced species to establish. It is likely that general principles do not exist, at least among comparisons across ecosystem types. However, ecologists should continue to search for general patterns within definable ecosystem units that increase understanding about factors contributing to invasability.

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APPENDIX A

PUBLISHED REPORTS OF AQUATIC PLANT SURVEYS

Table A.1 Published reports of aquatic plant surveys conducted from 1997-2011 in lakes and reservoirs across the conterminous United States.

Lake Name	Year	Citation
Bass	1997	Unpublished Data
Big Crooked	1997	Unpublished Data
Big Seven	1997	Unpublished Data
Blue	2008	Wersal, R.M. and J.D. Madsen. 2008. Pre-Treatment Aquatic Plant Community Assessment in Six Mississippi Delta Lakes, June 2008. Mississippi State University: GeoResources Institute.
Cabinet Gorge	2008	Madsen, J.D. and J. Cheshier. 2009. Eurasian Watermilfoil Survey of Three Reservoirs in the Lower Clarks Fork River, Montana: I. Results of the Field Vegetation Survey. GRI Report #5033. Mississippi State University: Geosystems Research Institute.
Camp	1997	Unpublished Data
Clear	1997	Unpublished Data
Ennis	2011	Wersal, R.M., J.P. Fleming, C. Duncan, and J.D. Madsen. 2011. Aquatic Invasive Plant Survey of the Missouri River Headwaters Area, Montana. GRI Report #5050. Mississippi State University: Geosystems Research Institute.
Gaston	1999	Madsen, J.D., R.M. Stewart, A. Way, and C. Owens. 2000. Quantitative Assessment of Aquatic Vegetation of Lake Gaston, North Carolina and Virginia. Letter Report, US Army Engineer Research and Development Center, Vicksburg, MS.
Havasu	2011	Madsen, J.D., R.M. Wersal, A. Fernandez, and G. Turnage. 2012. Lake Havasu Aquatic Plant Monitoring 2011 Interim Report. GRI Report #4008. Mississippi State University: Geosystems Research Institute.
Hebgen	2011	Wersal, R.M., J.P. Fleming, C. Duncan, and J.D. Madsen. 2011. Aquatic Invasive Plant Survey of the Missouri River Headwaters Area, Montana. GRI Report #5050. Mississippi State University: Geosystems Research Institute.
Holcomb	1996	Madsen, J.D. and J.W. Barko. 1999. Holcombe Lake Aquatic Vegetation Report. Letter Report, US Army Engineer Waterways Experiment Station, Vicksburg, MS.
Hortonia	1999	Unpublished Data
Jackson	2008	Wersal, R.M. and J.D. Madsen. 2008. Pre-Treatment Aquatic Plant Community Assessment in Six Mississippi Delta Lakes, June 2008. Mississippi State University: GeoResources Institute.
Lamoka	2007	Madsen, J.D., R.M. Steward, K.D. Getsinger, R.L. Johnson, and R.M. Wersal. 2008. Aquatic plant communities in Waneta Lake and Lamoka Lake, New York. Northeastern Naturalist. 15: 97-110.

Table A.1 (continued)

Little Eagle	2008	Wersal, R.M. and J.D. Madsen. 2008. Pre-Treatment Aquatic Plant Community Assessment in Six Mississippi Delta Lakes, June 2008. Mississippi State University: GeoResources Institute.
Lobdell	1997	Unpublished Data
Middle	2001	Madsen, J.D., R.M. Wersal, and M. Tyler. 2004. Diversity and Distribution of Aquatic Macrophytes in Swan and Middle Lakes, Nicollet County, Minnesota: Letter report to the Minnesota Waterfowl Association. Mississippi State University: GeoResources Institute.
Mossy	2008	Wersal, R.M. and J.D. Madsen. 2008. Pre-Treatment Aquatic Plant Community Assessment in Six Mississippi Delta Lakes, June 2008. Mississippi State University: GeoResources Institute.
Noxon	2008	Madsen, J.D. and J. Cheshier. 2009. Eurasian Watermilfoil Survey of Three Reservoirs in the Lower Clarks Fork River, Montana: I. Results of the Field Vegetation Survey. GRI Report #5033. Mississippi State University: Geosystems Research Institute.
Onondaga	2006	Unpublished Data
Pend Oreille	2008	Madsen, J.D. and R.M. Wersal. 2009. Aquatic Plant Community and Eurasian Watermilfoil (Myriophyllum Spicatum L.) Management Assessment in Lake Pend Oreille, Idaho for 2008. GRI Report #5032. Mississippi State University: Geosystems Research Institute.
Pinchback	2008	Wersal, R.M. and J.D. Madsen. 2008. Pre-Treatment Aquatic Plant Community Assessment in Six Mississippi Delta Lakes, June 2008. Mississippi State University: GeoResources Institute.
Ross Barnett	2006	Wersal, R.M., J.D. Madsen, and M.L. Tagert. 2007. Aquatic Plant Survey within the Littoral Zone of the Ross Barnett Reservoir for 2006. GeoResources Institute Report #5011. Mississippi State University: GeoResources Institute.
Swan	2001	Madsen, J.D., R.M. Wersal, and M. Tyler. 2004. Diversity and Distribution of Aquatic Macrophytes in Swan and Middle Lakes, Nicollet County, Minnesota: Letter report to the Minnesota Waterfowl Association. Mississippi State University: GeoResources Institute.
Toston	2011	Wersal, R.M., J.P. Fleming, C. Duncan, and J.D. Madsen. 2011. Aquatic Invasive Plant Survey of the Missouri River Headwaters Area, Montana. GRI Report #5050. Mississippi State University: Geosystems Research Institute.
Townsend	2008	Wersal, R.M. and J.D. Madsen. 2008. Pre-Treatment Aquatic Plant Community Assessment in Six Mississippi Delta Lakes, June 2008. Mississippi State University: GeoResources Institute.
Waneta	2007	Madsen, J.D., R.M. Steward, K.D. Getsinger, R.L. Johnson, and R.M. Wersal. 2008. Aquatic plant communities in Waneta Lake and Lamoka Lake, New York. Northeastern Naturalist. 15: 97-110.
Wolverine	1997	Unpublished Data