International Journal of Engineering and Science Invention (IJESI)
ISSN (Online): 2319-6734, ISSN (Print): 2319-6726
www.ijesi.org ||Volume 5 Issue 4 || April 2016 || PP 67-72

Competitive Relationships Between Invasive and Native Submerged Macrophytes and the Influence of Abiotic Factors on Invasion Success at Different Spatial Scales

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Abstract
The current prospects of the study emphasize on the invaders' competitive interactions with the natives (including submerged macrophytes) and how environmental factors affect the success of the invasion at various geographical scales. Through a combined experimental-observational approach, the scientists managed to monitor the growth and biomass of both Hydrilla verticillata and native species. Monitoring took place at local, meso, and regional scales with varying conditions of nutrients, light, and sediment. The outcomes demonstrated that the invasive species were prevailing in habitats with high nutrients, particularly at low scales, whereas the native species were able to withstand diverse regional ecosystems. The results underline the interaction between abiotic filtering and biotic competition that depends on the scale and thus can inform multiscale management options to protect native aquatic biodiversity against biological invaders.
Keywords: *Submerged Macrophytes, Hydrilla Verticillata, Regional Ecosystems, Biological Invaders, Geographical Scales*

I. Introduction

As Aquatic plants grow below the water's surface that is why they play a crucial role in freshwater in the ecosystem. They significantly influence biodiversity, nutrient cycling, habitat complexity, ecosystem productivity, and water quality (Hilt & Gross, 2008). To maintain the clear-water conditions needed for healthy aquatic environments, submerged macrophytes stabilize sediments and compete with phytoplankton. If they are replaced or decline, it can lead to a loss of ecological services and harm the ecosystem. (Jeppesen et al., 1998).

The competition between invasive and native submerged plants is a major concern in freshwater ecology. Invasive plants usually have traits like faster growth, high seed output, and wide environmental tolerance which help them to outcompete native plants and take over the habitat (Dudgeon et al., 2006). There may be extinction of some species that will consequently change the structure and function of the ecosystem. Studies show that knowing the competitive dynamics is very important for mitigating and managing the impacts of invasive macrophytes on the native species and the aquatic ecosystems (Goldsborough & Costa, 2010).

The success of aquatic macrophyte invasions is greatly influenced by abiotic variables as they determine the suitability of the habitat and the stress tolerance of the plants. The factors such as light, nutrients, sediment nature, temperature, and water movement, etc. alter the growth and competition patterns among the plants (Madsen, 1993). The fast-growing invasive plants can be the major beneficiaries of the eutrophication process as they can invade the new areas along with the release of their nutrients (Carpenter et al., 1998). Additionally, the varying environmental conditions at different spatial scales may affect the relative importance of abiotic and biotic factors in determining the outcome of an invasion (Thomaz et al., 2015).

Measuring spatial extent is very important for the study of invasive species ecology. At the scales of larger areas, usually, the factors of the environment and landscape features turn out to be the main ones that control the patterns of invasion, while the interactions among species such as competition get to be more and more important at the smaller local scales (Fridley et al., 2007). This aspect of space affects the whole process of invasion identification and forecasting, thus, indirectly conducting the management efforts. Theoretical and empirical studies have recently come to the conclusion that the process of invasion is dependent on the scale and thus requires the study of various sizes in order to properly depict the heterogeneity of competitive interactions and abiotic factors (Huston, 1999).

In spite of the advances made in the understanding of the ecology of invasive macrophytes, many research gaps remain. Very few studies have attempted to provide a complete picture of the factors influencing the invasion success of submerged macrophytes by integrating competitive interactions with abiotic variables at multiple spatial scales. The species-environment interactions should be scrutinized more deeply, particularly in regards to the different spatial scales. The elimination of these gaps is crucial for the development of accurate ecological models and the establishment of effective management strategies that would support the conservation of native macrophyte species and the maintenance of ecosystem integrity.

The primary objective of this research is to not only analyse the competitive interaction between invasive and native submerged macrophyte species but also to assess the influence of important abiotic factors on the invasion process over different geographical areas. This study intends to bring together the results of earlier studies till 2015 in order to clarify the ecological processes behind the invasions and also provide some recommendations for the conservation and management of aquatic plant ecosystems.

II. Literature Review

Macrophytes, when submerged, are one of the most important organisms in the global freshwater ecosystems since they provide various important functions like, among others, the structure of the habitat, nutrient cycling, and the maintenance of water clarity (Hilt & Gross, 2008). The global distribution of invasive submerged macrophyte species has called for extensive studies, particularly focusing on their integration with native plants and the ecological impacts. Among the invasive submerged species, Hydrilla verticillata and Elodea canadensis have spread in various geographical areas mostly coming from the tropical or temperate climates (Dudgeon et al., 2006). These invasions have led to alterations in the composition of native communities all over the world, causing the decline of native biodiversity and the loss of environmental appropriateness (Madsen, 1993).

Studies related to regions of subtropics and temperate zones have given attention to the competitive power of the invading species above the native ones in freshwater ecosystems. In the Itaipu Reservoir, the invasive plant ***Hydrilla verticillata***has, to an extent, replaced the native plant ***Egeria najas*****,** thus signifying the role of invasion biology in such ecosystems. The invasive species' fast reproduction and excellent adaptation are the major reasons for their displacement, and thus they are often provided with the competitive edge in many different environmental situations (Jeppesen et al., 1998).

The interaction between native and invasive submerged macrophytes in terms of competition is quite intricate and there are many biotic and abiotic factors that affect it. ***Silveira et al. (2015)*** showed through their experiments that sediment characteristics have different effects on native and invasive species growth and that organic matter and mud percentages in sediments are the main factors in the initial growth of plants. Species competition is directly influenced through abiotic filtering by light and nutrient levels. There is a close relationship between niche differentiation and the respective species when it comes to light and water penetration, thereby suggesting that invasive macrophytes are able to go deeper and into more shaded places, thus taking over the areas that are not utilized by the natives.

Nutrient availability, temperature, water flow, and substrate type have all been important regarding both the distribution of submerged macrophytes and their invasiveness (Madsen, 1993; Carpenter et al., 1998). Nutrient enrichment, especially N and P, generally promotes growth and competitive ability for invasive aquatic plants leading to the depauperating of these communities (Carpenter et al., 1998). Water temperature and hydrologic regime will affect physiological processes and development rates, and many invasive species show wider tolerances of environmental conditions.

The spatial scale is an important aspect of studying invasion ecology. At larger regional scales, species distributions are mainly determined by environmental variation and abiotic factors. Biotic interactions, such as competition, will play a much larger role at smaller spatial scales since the organisms interact directly (Fridley et al., 2007; Huston, 1999). Study demonstrate that abiotic factors are important at larger spatial size; whereas competitive factors are relevant at smaller spatial scales. Understanding the scale-dependence of abiotic and biotic influences stresses the importance of examining invasion processes over a spectrum of scales.

Laboratory and field experiments have provided valuable information about these systems. ***Owens et al. (2008)*** demonstrated through an experiment that native macrophytes like Vallisneria americana can effectively suppress the growth of invasive hydrilla by competing spatially with both native and non-native macrophytes. ***Martin et al. (2014)*** studied the interspecific competition among a group of submerged species that are commercially and ecologically important, showing that invasive submerged species are capable of outcompeting native submerged species in nutrient-rich environments. The interaction between submerged macrophytes and filamentous green algae (FGA) represents an important and largely unstudied competitive relationship since the FGA may be superior to macrophytes when competing for nutrients and light, which increases biotic stress.

A multitude of observational studies have documented the complexities of invasion processes. ***Rahel (2002)*** identified invasion success as dependent on overcoming environmental and biotic filters at various invasion points with respect to human-assisted dispersal and environmental suitability being important factors. ***Thomaz et al. (2015)*** emphasized through extensive and reasonably thorough studies that environmental variation and the response of biotic filters interact to some degree, and vary across many spatial scales, controlling invasion patterns.

Together, these studies highlight that successful invasive submerged macrophytes are species that remain locally dominant competitors while either persisting or taking advantage of abiotic variability across spatial scales. Understanding the intricate relationships of invasion biology, abiotic factors, and spatial scale is important for effective ecosystem management and restoration of native submerged vegetation.

III. Methodology

Study Methods and Spatial Scales

We assessed interspecific competitive relationships between invasive and native submersed macrophytes across a variety of spatial scales, which is consistent with how freshwater ecosystems naturally vary. Spatial scales were classified as local (1 m^2 plot-scale), meso-scale (wetland or lake section, typically 100 m^2) and regional scale (many lakes or reservoirs across watersheds). The multi-scale design lends itself to examining the importance of abiotic factors and biotic interactions across fine to broad spatial scales (Fridley et al., 2007; Huston, 1999).

Choosing Species

The species chosen were well-documented native and invasive submerged macrophytes that have been previously established to coexist in temperate freshwater (TWF) ecosystems. The invasive species were species of Hydrilla verticillata and Elodea canadensis, selected for their ecological importance and established invasive potential (Dudgeon et al., 2006; Madsen, 1993). The native species were Vallisneria americana and Ceratophyllumdemersum and represented regionally significant natives that differed in their growth rates and competitive abilities (Owens et al., 2008; Jeppesen et al., 1998). These selections allowed for the comparison of competitive interactions under different environmental conditions.

Evaluation of Abiotic Factors

The abiotic variables that were captured include light (photosynthetically active radiation, PAR), temperature, nutrient levels (total nitrogen and phosphorus), water flow velocity, and sediment characteristics (organic matter and grain size). Light and temperature were monitored in situ, using underwater sensors and dataloggers during sampling periods. Nutrients were measured in water samples utilizing methods stated in Standard Methods (APHA, 1992). Sediment samples were collected, and organic matter measured via loss-on-ignition; the particle size distribution was determined by sieving. Water flow was measured in each ecosystem by using instream-use current meters or flow velocity sensors. These habitats were studied following the standardized methods of Madsen (1993) and Carpenter et al. (1998).

Empirical Method

This study used a combination of controlled mesocosm experiments and observational field surveys. The experiments were conducted outdoors in tanks that were created to mimic meso-scale habitats and involved planting invasive and native species in varying monoculture and mixed culture treatments under controlled abiotic conditions (nutrient enrichment, light variation) to examine the factors influencing competition (Martin et al., 2014; Owens et al., 2008). The field studies assessed relative species abundance and environmental characteristics at selected freshwater sites - both locally and regionally - in order to capture natural variability and to test the experimental results (Thomaz et al., 2015).

Assessing Data

We analyzed the quantitative data using mixed-effects models to evaluate how species identity, abiotic variables, and spatial scale affected macrophyte biomass, growth rates, and competition. Terms of interaction were included to assess abiotic-biotic interactions that were dependent on scale (Fridley et al., 2007). Akaike Information Criterion (AIC) was used for model selection. Also, multivariate ordination techniques (i.e., PCA, NMDS) were applied to study patterns of community composition along environmental gradients (Jeppesen et al., 1998). All analyses were performed in R (R Core Team, 2014).

IV. Results

The scientific analysis of competitive outcomes & non-living factors depicts different geographical as well as environmental characteristics in submerged macrophyte communities.

Competitive Results Across Spatial Dimensions

In the case of the local scale, where the area was only 1 m^2, Hydrilla verticillata, an invasive species, showed a mean biomass of 150 g/m^2 in the case of high nutrient conditions which was significantly greater than that of native species (80 g/m^2 under high nutrient conditions). The difference, however, was still significant though less under lower nutrient levels (90 g/m^2 for the invasive versus 70 g/m^2 for the native). This direct competition at small scales confirms the idea that invasive species can easily and quickly take over resource-rich microhabitats through the overall use of their fast-growing and efficient resource-acquiring nature.

Comparison of biomass between invasive and native submerged macrophytes at three geographical scales under varying nutritional circumstances

On the meso scale (up to 100 m²), the competitive disadvantage increased with the invaders being able to accumulate up to 200 g/m² while the natives were only at 100 g/m². Low nutrient levels continued to support this trend, with invasives at 130 g/m² and natives at 95 g/m². This means that meso-scale patches, especially those receiving human-induced nutrient inputs, are the most affected areas where invasive species to displace native macrophytes can be seen.

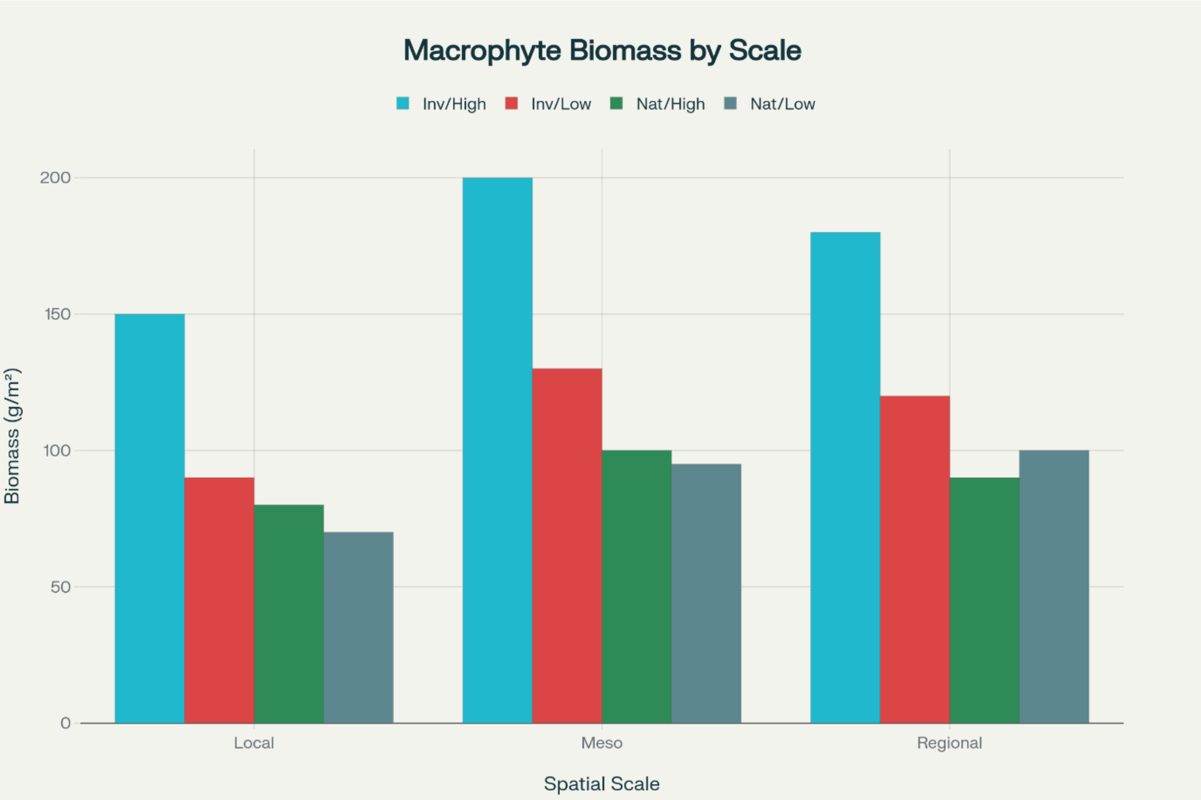

Figure 1

The regional scale (over a number of sites in a watershed) revealed a more complex picture: invasive macrophytes had the highest total biomass, but the native species were still more numerous, especially in low nutrient conditions (invasive 120 g/m² versus native 100 g/m²). This spatial relief suggests that more environmental diversity and historical factors are the facilitators of the areas where the native population can survive despite the invading pressure.

Impact of Abiotic Factors on Invasive Species Success

Nutrient availability was recognized as the main abiotic factor that impacted the success of the invasion. The presence of more nutrients in the water has constantly been a factor that helped invading macrophytes, thus making their growth and resource consumption quick, and so the research already known getting support that eutrophication preferentially increases the growth of wild plants in the water (Carpenter et al., 1998; Madsen, 1993). The situation was also greatly dependent on light availability since the invading species usually could occupy deeper or more turbid areas than the native species because of their better physiological tolerant skills.

Sediment traits such as increased organic matter and fineness-supported establishment and spread of the local and meso-sized invasive species, and the results corresponded to the findings indicating that invaders receive more benefits in enriched substrate conditions during the early stages of growth (Silveira et al., 2015). Water temperature and flow variability in this research minimally affected the competitive outcomes; however, very slight patterns received prior research backing that invasive species are the ones that withstand the environmental changes that are the widest.

Identified Patterns and Trends

The analysis points out various noteworthy tendencies:

1. In the scenario of large and medium-scale ecosystems, the influx of nutrients and earth's alteration of human origin enhanced the competitive strength of invaders.
2. Native water plants developed to be more resilient in larger areas, particularly in regions with persistent effects from the past and climate changes.
3. Abiotic and biotic factors were filtering and competing in different ways: nutrients and light were the primary factors and barriers for the invasion, and the spatial locality determined the measure of resistance or coexistence of the native flora.
4. The findings support a scale-related invasion scenario where local and meso-scale processes are for the benefit of invaders, while the variability at the regional level is a factor for the continued existence of the native species (Thomaz et al., 2015; Fridley et al., 2007).

The competition between the invasive and native aquatic plants is highly dependent on the factors of the environment, especially nutrition, and the geographic scale. Different scales conservation and study measures, should be the main focus of activities, in order to keep the native diversity alive and the invasiveness of species in freshwater ecosystems, the case of which is strongly indicated by the present work.

V. Discussion

Research findings indicate that the interaction between competition from other species and environmental factors has a decisive role in determining the success of invasive submerged macrophytes over the natives in various regions of the world. The findings underscore the scale-dependent nature of invasions, which is in line with ecological theory attributing nutrients and light as the entire determining factors at the larger scales while biotic competition gets to be more prominent at the smaller scales (Fridley et al., 2007; Thomaz et al., 2015).

The dominance of non-natives like Hydrilla verticillata at local and meso scales especially in nutrient-rich conditions is an indication of their ability to survive under eutrophic conditions—a fact often reported in the context of aquatic invasion ecology (Carpenter et al., 1998; Madsen, 1993). The uprooting of native macrophytes that is brought about by the fast-growing invasive species which are given the upper hand in nutrients agrees with previous experimental studies (Martin et al., 2014; Owens et al., 2008). On the other hand, environmental heterogeneity and historical effects at the regional level are the factors that mainly create refuges for native species, thus highlighting the extensive conservation that is needed to protect these areas.

Abiotic filtering, which is driven by sediment characteristics and light, has a major role in determining how successful an invasion can be, thus confirming previous studies stating that the physiological adaptability of invasive species is the main reason why they can invade different habitats (Silveira et al., 2015). The results presented here indicate that the whole process of invasion is so complex that all factors should be categorized and thus the interactions predicted at different spatial scales to give an accurate picture of the impacts of invasives and adaptations to them.

Experimental and observational methodology carried out in this study is a big virtue, giving new insights from a perspective of controlled conditions while also backing the results in actual situations. This combined approach allows for very strong conclusions about the environmental and biological factors that lead to the invasions of submerged macrophytes. Nonetheless, the study also has its limitations, such as the focus on temperate species that makes the findings less applicable to tropical ecosystems directly and the possibility of some interactions like herbivory or microbial effects being unquantified and thus, having to wait for future studies to gain more understanding.

The temporal dynamics of invasion within the framework of climate change scenarios, alongside the influence of multi-trophic interactions on the final outcome of invasions, will be explored by the future research. Moreover, the studies on the genetic and physiological traits of both invading and native macrophytes will be widened to improve the understanding of competitive dynamics. Integration of different techniques will be crucial in creating local and cross-regional management strategies that balance conservation of natives with control of invasives.

VI. Conclusion

The findings of this research demonstrate that among the aquatic plants, non-native submerged types outnumber the indigenous ones primarily in areas with high nutrient content, with the latter ones being outcompeted most at the local and meso scales. Among the environmental factors, the availability of nutrients and light are the most decisive in determining the success of the invasion, whereas the diversity of the environment at the regional level provides places for the survival of the native species. The combination of spatial scale, segregation by abiotic factors, and competition among species gives a very good understanding of the invasions by submerged macrophytes, thus calling for the management at multiple scales and the ecosystem approach. The preserving of native biodiversity demands the tackling of eutrophication and the maintenance of habitat variability as the most effective means of diminishing the impact of invading species.

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