

# A SUSTAINABLE APPROACH TOWARD INVASIVE SPECIES — COMMUNITY MEMBERSHIP OF *PHRAGMITES AUSTRALIS* OVER TIME

*A St Mary's Project Presented to the Faculty of the Biology Department of St Mary's  
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## **Abstract**

This is an application to the Agricultural and Food Research Initiative Competitive Grants Program, in the Foundational Program Area of Bioenergy, Natural Resources, and the Environment. We propose to research the community membership over time of the invasive wetland reed, *Phragmites australis*, specifically in the Chesapeake Bay area. This is primarily an ecological field study where we will examine the species diversity in populations of *P. australis* that differ based on the length of time occupying a geographical range, as well as populations of the native subspecies *P. australis americanus*. We hypothesize that community membership, the interspecific interactions measured by species diversity, will increase as populations' length of habitation increases. The objective of this project is to provide an empirical basis for a paradigm shift in invasion biology research and invasive species management. This shift will take the form of a sustainability perspective, which forsakes the traditional Eltonian basis of invasion biology that has given rise to many of the extra-ecological and largely fruitless practices of contemporary invasive species management in favor of promoting equilibrium of ecosystems, rather than protecting individual aspects of them. This objective builds its conceptual basis on the existing anti-Elton movement within the field of invasion biology that has emerged within the last decade, which seeks to reimagine how invasive species are scientifically understood.

## **Project Narrative** (Scope: 2-year time frame)

### **Introduction**

Concerns of anthropogenic harm to ecosystems at all scales have become deafening in recent decades. The idea of extant 'wilderness', natural systems un-impacted by human activity,

is being called into question globally as nature conservation areas, from local parks to world heritage areas, are faced with direct and indirect anthropogenic threats. One such threat is that of invasive species: organisms that, for a variety of reasons, establish and spread outside of their native ranges and, in some cases, cause significant ecological change in their newfound ecosystems (Vitousek et al., 1996).

In response to biological invasion, one of the central questions has become: how do we protect these ‘invaded’ ecosystems from the impact of invasive species? In order to most effectively manage ecosystems, as existing invasive species foster change and new biological invasions arise, it is necessary to explore and understand the conceptual underpinnings of invasiveness and how these concepts change over time.

To arrive at a more comprehensive understanding of invasive species, we propose a sustainability model to approach invasive species research and management. We argue that, in keeping with the foundation of sustainability, research and management of invasive species should function to ensure stability and equilibrium of ecosystems with a focus not only on the present, but also far into the future. To bring about this change in ethos, we build on the momentum of recent shifts in perspective within the field of invasion biology towards non-traditional conceptualizations of invasive species, research, management, conservation, and restoration (Davis, 2009). In this proposal, we situate invasive species within holistic ecosystem, long timespan, and large spatial scale contexts by outlining a two-year field research project examining how the community membership of the invasive wetland plant *Phragmites australis* changes over time.

## **Defining Invasive Species**

Invasion biology is a relatively young field and, as a discipline, is characterized by a lack of standardization of terminology. Because of this, the concept of invasive species varies by the purpose of its use (Davis, 2009; Parker et al., 1999; Simberloff et al., 2012). In this section we will develop a comprehensive definition of invasive species (used synonymously with biological invasion). Most definitions of invasive species overlap in some ways and are distinct in others, which creates a confusing and ambiguous foundation onto which invasion biology research builds. Thus, it is necessary to survey different meanings and types of definitions to better understand this complex issue. To clarify the concept, we sort definitions of biological invasion into three general categories: origin, mechanism, and impact. We hold that a complete definition of biological invasion necessitates all three.

An origin-based definition's criterion is that invasive species are not members of the native contingent of species present in an ecosystem, or, alternatively, that they were brought to a region by human activity (Preston et al., 2004; Mooney et al., 2005; Jose et al., 2013). Native species are generally demarcated as those species that 'belong' in their ecological community due to both their ability to survive extant physical conditions and an evolutionary history that has led to their coexistence with other species in that community (Cain et al., 2011). In contrast to this definition, invasive species are described synonymously as non-native, exotic, or introduced, where all three terms mean that the species is not 'of that ecosystem'. A majority of invasive species are, in fact, perceived to be non-native (Simberloff et al., 2012). However, native and non-native are relative terms and difficult to quantify. Willis and Birks (2006) and Preston et al. (2004) raise the question of how long a species must be present in a region in order to be classified as native versus invasive. For instance, of 157 plant species that humans introduced to

Britain between 4000 and 500 years ago, between 31 and 85 are classified as native in published work (Preston et al., 2004). Davis (2009) utilizes a categorization of species based on the duration of their residence in a given ecosystem as an effective way to study invasive species. Taking this categorization to its logical extent, this means that invasive species could, with time, be redefined as native.

Invasive species are introduced to new ecosystems primarily through human activity (Mooney et al., 2005; Davis, 2009; Cain et al., 2011). Many human activities can be understood as ‘vectors of dispersal’ for species, meaning that they provide transportation to new regions outside of their natural dispersal limits (Davis, 2009; Cain et al., 2011). Cain et al. (2011) illustrate this concept with the example of *Dreissena polymorpha*, the zebra mussel. *D. polymorpha* was introduced to the Great Lakes from Europe in the 1980s through the uptake and discharge of ballast water on cargo ships (NOAA, 2008; Cain et al., 2011). As a non-native species, *D. polymorpha* has significant effects on the ecology of the Great Lakes, including increasing the incidence of algal blooms, disrupting the food web (leading to the decline of fish populations), and competing with native bivalves (NOAA, 2008; Cain et al., 2011). While many invasive species are unambiguously non-native (as in this example), there are situations where non-native categorization is less clear, if not entirely false. Therefore, more work needs to be done to fully encapsulate the concept of ‘invasive species’.

Davis (2009) suggests two primary ways of defining invasion through mechanisms: stage-based and cyclic iteration. The (more commonly used) stage-based approach separates the process into well-defined stages of invasion: introduction, establishment, naturalization, dispersal, population distribution, and invasive spread (Davis, 2009; Henderson et al., 2006). The

cane toad, *Bufo marinus*, is a species in Australia whose well-known invasion is understood as a moving front of progressive stages (Phillips et al., 2007; Urban et al., 2007). After being intentionally introduced in northern Queensland in the 1935 to control another pest species, *B. marinus* spread across Australia (Phillips et al., 2007). Phillips et al. (2007) document a spatiotemporal front of invasion across Australia's Northern Territory quantitatively in kilometers per annum while Urban et al. (2007) categorize *B. marinus*' changing mode of invasion by adding the stage of adaptive genetic variation to stages of arrival, establishment, and spread.

Though not incorrect, Davis (2009) argues that this conceptualization leads to the misunderstanding of biological invasion as a discrete temporal and spatial progression; a moving front with no interplay between stages. These stages are not, in fact, discrete; if an invasive species has reached the invasive spread stage, it may also exhibit each of the other stages as well (Henderson et al., 2006). Alternatively, the cyclic iteration approach holds that invasion occurs through the repeated process of individual organisms dispersing and establishing in new areas, where successful invasions have undergone enough iterations of the process to form populations that persist and spread (Davis, 2009). A good example of the cyclic invasion mechanism is *Caulerpa taxifolia*, an invasive seaweed from the Caribbean that was introduced into the Mediterranean Sea by the Oceanographic Museum of Monaco while cleaning aquarium tanks in the 1980s (Cain et al., 2011). Once established, the seaweed was dispersed throughout the Mediterranean by fishing boats, establishing again to form new populations all over the region. This resulted in the formation of a meta-population in the Mediterranean and eventually other parts of the world (Cain et al., 2011). Unlike the top-down approach of the stage-based

mechanism, which examines populations for signs of progression through the stages, the cyclic iteration approach more closely parallels the actual process of invasion: individuals, not populations, disperse across geographic areas. Groups of successful individuals establish populations, while unsuccessful individuals fail to do so.

Definitions of biological invasion must also take into account the impact of species. Impact is concerned with whether or not a species causes harm to the ecosystem that it invades, and is often quantified by degradation or losses to natural resources reserves used by humans (Mooney et al., 2005; Simberloff et al., 2012). The primary shortcoming of defining biological invasion through impact alone is that native species can also harm their home ecosystems; some research even suggests that native and non-native species cause harm in the same proportion (Mooney et al., 2005; Simberloff et al., 2012). For example, Davis (2009) describes native North American shrubs, *Larrea tridentata* and *Prosopis* species, that rapidly spread through their ecosystem following the disruption of fire regimes. Despite this complication, harm is still a common defining feature of invasive species, especially in the absence of decisive information regarding a species' origin (Lodge et al., 2006). Precisely because invasive species impact human resources and health, impact based definitions are often used in policy (Burgiel et al., 2006; Lodge et al., 2006), which, in turn, influences the wider public perception of invasive species.

Harm caused by invasive species ranges from ecologically extreme to relatively tame. For instance, 'invasional meltdown' occurs when the presence of one invasive species facilitates the introduction and spread of further invasive species, causing a shift in the ecosystem (Simberloff, 2006). The introduction of the yellow crazy ant, *Anoplolepis gracilipes*, onto a

tropical island in the Indian Ocean resulted in invasional meltdown, shifting forest from open understory and canopy tree-dominated to dense understory, thick litter layer, and decreased canopy (O'Dowd et al., 2003). Examples of relatively tame invasive species, with less impact than a full invasional meltdown, are discussed throughout this work. In order to categorize the impact of invasive species many states have developed ranking systems, such as the New York Non-Native Plant Species Invasiveness Assessment (Jordan et al., 2012). In this ranking, which borrows methodology from several others, species are ranked in categories such as “ecological impact”, “biological characteristic and dispersal ability”, “ecological amplitude and distribution”, and “difficulty of control” based on a series of point-valued questions (Jordan et al., 2012).

All three components of the definition of biological invasion are suited to different uses and combinations of uses. For instance, when studying the natural history of a region it would be effective to define invasive species based on origin. However, a mechanism definition may be useful, as Davis (2009) demonstrated, in scientific and conservation work in order to study the species and capture the complexity of invasion in an ecosystem. Alternatively, policy efforts may be best served by using a definition that focuses on the impact, in order to try to economically quantify the benefits of managing invasive species or the harm that they perpetrate. In this project, we do not use any one definition of biological invasion. As stated before, a complete conceptualization of invasive species requires all of the components (origin, mechanism, and impact); these comprehensively encompass what we know as invasive species.

## **Causes of Invasion**

Invasive species are primarily introduced and spread through various types of anthropogenic disturbance. Anthropogenic disturbance, that is, impact on natural systems that



originates from human activity, is the primary driver of invasion (Vitousek et al., 1996; Mooney et al., 2005; Occhipinti-Ambrogi, 2007; Davis, 2009). Records of wayward species outside of their range date far into the past, but, since the 19<sup>th</sup> century there has been a growing understanding of how human activity and movement facilitates the introduction of non-native species and how these introductions affect their host ecosystems (Davis, 2009). Starting with simple trade routes, the movement of humans has facilitated the dispersal of species over distances impossible for them to achieve otherwise; recent globalization has only increased the magnitude of this spread (Mooney et al., 2005; Davis, 2009).

Direct introductions, the release of species into regions where they are non-native, can be intentional or accidental, but either mode has equal potential to make an impact on the host ecosystem (Mooney et al., 2005). Intentional introductions are most often due to ignorance about the effects of the introduction: a valuable crop plant's invasive capacity is underestimated or an outlandish animal is kept as a pet before being released into the wild. For example, purple loosestrife, *Lythrum salicaria*, is a European plant that was brought to North America for both ornamental and medicinal purposes (as well as being accidentally introduced through the release of ships' ballast water) and subsequently became invasive (Malecki et al., 1993; Pimentel et al., 2005). It currently continues to spread through the continent's wetlands, reducing plant and animal biodiversity and native plant biomass (Malecki et al., 1993; Pimentel et al., 2005).

Additionally, species may be introduced intentionally in the name of conservation, specifically in order to control the spread of other invasive species. However, the effects of these introductions are not readily predictable. For instance, in the 19<sup>th</sup> Century the Indian mongoose, *Herpestes auropunctatus*, was introduced in Jamaica, and later in other tropical regions, to

control growing rat populations that were affecting agricultural production (Pimentel, 1955; Pimentel et al., 2005). However, while *H. auroguttatus* did fulfill its purpose by preying on rats, it also preyed on native animals, causing extinctions of reptiles and amphibians (Henderson, 1992), and increased the spread of rabies and leptospirosis bacterial infections, affecting humans and animals alike (Pimentel, 1955; Pimentel et al., 2005).

Many introductions, however, are accidental. Carlton and Geller's (1993) study provides a telling estimation of the number of accidental invasions that result from the release of ballast water: 45 species introduced worldwide in the 20 years preceding the study became invasive, including the aforementioned zebra mussel. While zebra mussels provide a significant exception, most vertebrate and plant introductions are intentional, while most invertebrate and microbial introductions are primarily accidental (Pimentel et al., 2005). A well-known and disastrous example of an accidental microbial introduction is the fungus *Cryphonectria parasitica*, the pathogen responsible for the American chestnut blight (Milgroom et al., 1996). Native to East Asia, *C. parasitica* is thought to have been introduced in the United States in the early 20<sup>th</sup> century through the import of other chestnut species (Milgroom et al., 1996). Within 50 years, it had largely wiped out the American chestnut, *Castanea dentata*, across its entire North American range despite attempts, such as the use of chemical sprays, to control the spread of this invader (Anagnostakis, 1987).

However, anthropogenic introduction is not the sole cause of invasion. Invasion can also be caused indirectly, where human activities cause changes in the environment that result in changes in the role that species play in an ecosystem (Dukes and Mooney, 1999; Minchinton and Bertness, 2003; Mooney et al., 2005; Cain et al., 2011). For instance, there is evidence that

temperature shifts deviating from previous seasonal averages, a result of global anthropogenic climate change, can affect competitive interactions between species (Stachowicz et al., 2002; Occhipinti-Ambrogi, 2007). Stachowicz et al. (2002) found that, compared to native species, an introduced species of the class Ascidiacea (a filter-feeding, marine invertebrate in the New England region) began recruitment earlier in the year after warmer winters and exhibited increased relative growth at maximum summer temperatures. Early recruitment, a temporal advantage, increased the dominance of the introduced species relative to the native, a phenomenon that implicates climate change as an indirect driver of species invasion (Stachowicz et al., 2002; Occhipinti-Ambrogi, 2007; Cain et al., 2011).

Another example of biological invasion due to indirect causes is the facilitation of species invasion by disturbance (Dukes and Mooney, 1999; Bertness et al., 2002; Minchinton and Bertness, 2003). For instance, urban development along shorelines affects competitive interactions and, thereby the relative dominance, of many wetland species, including native saltmarsh cordgrass, *Spartina alterniflora* (Bertness et al., 2002; Minchinton and Bertness, 2003). Wetland zonation patterns are determined by abiotic conditions and interspecific competition, and, therefore, disturbance of normal abiotic conditions, such as nutrient availability, can release species from competition by removing physiological barriers to spread (Bertness et al., 2002; Minchinton and Bertness, 2003). Agricultural and urban development increases nitrogen in wetlands, resulting in the competitive release and spread of *S. alterniflora* to higher inland elevations and therefore the growth of zones in which it is dominant (Bertness et al., 2002; Minchinton and Bertness, 2003).

Dispersal through human activity is often part of the definition for biological invasion (Preston et al., 2004; Mooney et al., 2005), but it is important to consider the possibility of non-anthropogenic invasion. Cases that make this claim are primarily concerned with increased, sometimes invasive, impact of native species. Simberloff et al. (2012) investigated the claim that, overall, there is no significant difference in the number of impactful species between native and invasive designations. Their results do not support this claim, with non-native species considered invasive about six times more often than natives, based on their description in the literature (Simberloff et al., 2012). Furthermore, most systems with native species that are considered invasive due to their impact involved some sort of anthropogenic change (Simberloff et al., 2012), such as the above example of *Spartina alterniflora* (Bertness et al., 2002). This reaffirms that human actions are the root of biological invasion, but leaves the question of whether human actions are needed to resolve biological invasion unanswered.

### **Success of Invasion**

The success of certain species' invasion into new ecosystems is often oversimplified, or even entirely misunderstood. While it is popularly misconstrued that invasive species are drastically more successful in their invasive range, some invasive species perform no better compared to their native range (Parker et al., 2013). What makes species particularly successful, or not, is a complex interaction of species-specific characteristics and intra-species relationships (Mooney et al., 2005). Jose et al. (2013) outline five major characteristics that facilitate invasion: efficient resource uptake and use, rapid growth and reproduction, environmental modification, genetic variability, and enemy resistance. Further, recent evidence shows that, on a global scale,

a species' evolutionary history can be a significant predictor of invasion success (Fridley and Sax, 2014).

In order to successfully compete, invasive species need to take advantage of resources not already used by native species; this is accomplished by filling empty niches or by exploiting changes in resource flow (Jose et al., 2013). An example of this is the invasive ascidian species mentioned above, which undergoes recruitment earlier in the spring than the native species. By starting its sessile growth before other species, it exploits an empty temporal niche to compete with native species for resources (Stachowicz et al., 2002). Likewise, *Spartina alterniflora* takes advantage of increasing nitrogen inputs into wetlands to outcompete higher elevation species and dominate the ecosystem (Bertness et al., 2002).

Invasive plants are often able to undergo rapid growth and reproduction when establishing in new areas; this occurs through adaptations such as monocultural growth, large size, and seed quantity and hardiness, or through system specific context, such as a lack of predators or herbivores (Jose et al., 2013). Purple loosestrife (*Lythrum salicaria*), the wetland plant discussed above, was introduced for medicinal and decorative purposes and exhibits several of these traits. The species grows in dense monoculture stands and dominates the canopy with its height (2m), while mature individuals produce more than 2.5 million robust seeds per year (Malecki et al., 1993; Jose et al., 2013). Additionally, there are no herbivores in its invasive range to limit its reproduction and growth (Malecki et al., 1993).

Invasive species can decrease competition by physically altering their host ecosystem. By using biochemical 'weapons', such as allelopathy, or modifying fire regimes, they can facilitate their own spread, as well as the spread of other invasive species (Callaway and Aschehoug,

2000; Callaway et al., 2008; Jose et al., 2013). For instance, the European forb garlic mustard (*Alliaria petiolata*) produces a phytotoxin that is lethal to mutualistic mycorrhizal fungi in North America but to which European fungi have adapted (Callaway et al., 2008). By killing mycorrhizal fungi, *A. petiolata* reduces the competitive ability of plants in its invasive range that have positive mutualistic mycorrhizal associations (Callaway et al., 2008).

An invasive species' success also depends on the amount of genetic variability in invasive populations. Genetic variability affects a species' ability to adapt to its new environment through phenotypic plasticity, hybridization, and the evolution of resistance to management measures (Jose et al., 2013). While very low genetic variability, resulting in a genetic bottleneck, is usually considered counterproductive to the establishment of a population, the Argentine ant, *Linepithema humile*, represents an interesting illustration of the effect of genetic variability on invasion (Tsutsui et al., 2000; Giraud et al., 2002). In its native range, *L. humile* individuals defend their colonies against conspecifics (members of the same species but not the same colony), while in its invasive range they do not, leading to the formation of supercolonies, where individuals move freely between colonies (Tsutsui et al., 2000; Giraud et al., 2002). There is evidence that there is a reduced energy cost associated with the lack of territorial behavior, which results in higher population densities and colony sizes, contributing to *L. humile*'s dominance in its invasive range (Holway et al., 1998; Tsutsui et al., 2000; Giraud et al., 2002). This state of dominance, however, is evolutionarily unstable due to this species' particular brand of sociality and therefore could not exist in the species' native range.

When species invade new ranges, they leave their specialized native predators and pathogens behind, and, with them, some of the limitations that keep them from outcompeting

other species in an ecosystem. In their new range, their lack of vulnerability to these specialist threats is called enemy resistance, or enemy release (Keane and Crawley, 2002; Joshi and Vrieling, 2005; Jose et al., 2013). Evidence of this phenomenon is the invasive tansy ragwort (*Senecio jacobaea*); in its invasive range, the magnitude of *S. jacobaea*'s chemical defense production increases against generalist herbivores and decreases against specialist herbivores, which are present only in its native range (Joshi and Vrieling, 2005). Joshi and Vrieling (2005) hypothesize that if defenses against generalists are 'cheaper' (less energetically costly) than defenses against specialists, then the resource savings would result in increased growth and reproduction. They found higher biomass and reproductive biomass in invasive *S. jacobaea* compared to the native (Joshi and Vrieling, 2005).

Recent evidence suggests that geographical evolutionary history might also contribute to a species' invasion success. That is, some species are more competitive by virtue of having evolved in geographical areas with high phylogenetic diversity (more ecological niches filled) (Fridley and Sax, 2014). The great amount of diversity is both origin and result of strong competition; it forces species to fill niches that might not be filled in less competitive environments. This means that geographic areas with high phylogenetic diversity are likely to be the sources of invasive species, while areas with low phylogenetic diversity are more likely to be invaded (Fridley and Sax, 2014).

Whether or not a species is a successful invader is a complex interaction of many factors. The abilities to access unused resource niches, to grow larger or faster, to reproduce more often, and to modify host environments represent the spectrum of possible physical advantages that contribute to an invasive species' success. The genetic variability, lack of specialist predators,

and, on a global scale, the phylogenetic diversity of its native geographical range foster situations that breed a species' invasion success.

## **Effects of Invasion**

The effects of a species becoming invasive in an ecosystem span a wide range of severity and have both ecological and economic impacts (Parker et al., 1999; Pimentel et al., 2005).

Parker et al. (1999) published a landmark review analyzing the existing methods of measuring impact of invasion. Impact is the result of interactions between three factors: range (area occupied), abundance, and effect (impact per individual); effect is the most complex factor, and therefore is the focus in determining ecological impact (Parker et al., 1999). 'Effect' is subdivided into forms of increasing ecological expansiveness to capture the complex impact of invasive species: effect on individuals, genetic effects, population dynamic effects, community effects, and effects on ecosystem processes (Parker et al., 1999). These different categorizations are not mutually exclusive; that is, invasive species will have impacts spanning multiple, if not all, the categories.

We have already examined several species whose characteristics affect other species on an individual level. A familiar example is purple loosestrife (*Lythrum salicaria*), the invasive wetland plant whose tall, monocultural growth inhibits the ability of native wetland plants to grow (Malecki et al., 1993; Jose et al., 2013). Genetic effects have also been implicated as a form of impact on native species. Genetic effects alter selection patterns and gene flow, causing introgression (movement of genetic information between species) and hybridization (interbreeding between species) (Huxel, 1999; Parker et al., 1999). For instance, one facet of the controversy over genetically modified crops raises the question of introgression as a threat to



ecosystems adjacent to crop fields. Ellstrand (2001) reviews evidence that, historically, ‘crop to wild’ gene flow has led to the transformation of multiple plant species into hard to control weeds and that hybridization between crop and wild species has led to extinction of other species in the ecosystem. Transgenic crops are predicted result in the same kinds of consequences (Ellstrand, 2001).

The most well-studied impact of invasive species is their effect on population dynamics (Parker et al., 1999). Population dynamics refers to factors such as the age distribution or abundance of individuals in populations; as such, extinction and near-extinction events, like the American chestnut blight, are the most extreme examples of invasion’s effect on population (Anagnostakis, 1987; Parker et al., 1999). Also widely recognized are loss of biodiversity and changes in trophic structure that result from invasion, representing effects at the community level (Vitousek et al., 1996; Parker et al., 1999; Tripathi, 2013). A conspicuous example of a species introduction resulting in biodiversity loss that we have already discussed is the Indian Mongoose, which is implicated in the extinction of at least 7 to 12 reptile and amphibian extinctions in Puerto Rico (Henderson, 1992; Pimentel et al., 2005).

Effects on ecosystem processes typically include changes in cycles (such as nutrient or hydrologic cycles), primary productivity and resource acquisition, or disturbance regimes (Vitousek et al., 1996; Parker et al., 1999). For example, the European forb garlic mustard (*Alliaria petiolata*), discussed earlier, has a lethal effect on mycorrhizal fungi; not only does this inhibit other plants’ competitive abilities to take up nutrients, but also affects a host of other major ecosystem processes including nutrient cycles, primary production, and carbon sequestration (Callaway et al., 2008; Pringle et al., 2009).

The economic impact of biological invasion has been recently estimated to be over \$120 billion annually in the United States (Pimentel et al., 2005). However, the exceeding difficulty of expressing ecological damage and restoration as a monetary value encompassing all the effects of invasion has led to criticism against such estimates (Davis, 2009). Furthermore, ecosystem services, the benefits that humanity receives as a result of the processes and cycles of ecosystems and their individual components, are difficult to quantify, and therefore economic estimates relate disproportionately to already-developed systems, such as agriculture (Vitousek et al., 1996; Pimentel et al., 2005; Davis, 2009).

While nationwide or global estimates are an imprecise starting point for estimating the economic cost of invasion, more useful estimates narrow their scope to improve their accuracy. Cook et al. (2007) provide an analysis of the costs over time of a potential invasion of a bee parasite, *Varroa destructor*, in Australia. Because *V. destructor*'s host is the honeybee *Apis mellifera*, a major provider of pollination services in Australia, the ecosystem service costs are more directly measurable (Cook et al., 2007). Pollination is an ecosystem service that is indispensable to agricultural production; therefore, the effect that *V. destructor* has on pollination is going to be proportional to the profits lost due to decreased agricultural output. Similarly, Barbier et al. (2013) provide an easily generalizable model of the environmental costs and corporate profits involved with the nursery sale of purple loosestrife, *Lythrum salicaria*, in the US and Canada.

There is a diversity of ecological effects that are brought about by invasive species, from the individual level to large-scale effects on ecosystem processes. While this discussion is limited strictly to ecological effects, many social and cultural effects exist as well. Due to

society's current systems of valuation, there is an extent to which it is necessary to quantify these effects economically. However, it is important to note, as shown above, the limitations to this endeavor.

## **Management of Invasive Species**

The variety of effects associated with invasive species necessitates a similarly wide range of management strategies to address these effects. We group these management strategies into two categories: preventative strategies and mitigation strategies. Preventative strategies inhibit new invasive species from dispersing and establishing, while mitigation strategies attempt to manage the effects of already established invasive species (Wittenberg and Cock, 2005; Davis, 2009). Because the focus of this project is on species that are already invasive, we will focus primarily on mitigation strategies rather than preventative strategies.

As stated above, the primary cause of biological invasion is species introduction due to the geographic movement of humans, which is increasing with globalization (Wittenberg and Cock, 2005; Davis, 2009). Prevention of these introductions is the most desirable invasive species management strategy because of its cost effectiveness and preemptive prevention of damage to ecosystems (Wittenberg and Cock, 2005; Burgiel et al., 2006; Lodge et al., 2006; Davis, 2009). To prevent biological invasion, Lodge et al. (2006) recommend a dual strategy focused on policy and education to limit unintentional dispersal through well-known invasion pathways (such as transportation or trade involving non-native species), as well as imposing pre-introduction screening and risk analysis of all potentially imported plants and animals. In practice, these measures are grouped into pre-border, at-border, and post-entry measures (Burgiel et al., 2006).

Post-invasion, optimizing mitigation strategies relies on the early detection of invasions, eradication of invasive species (if possible), control of spread, and restoration of ecosystems affected by invasive species (Wittenberg and Cock, 2005; Lodge et al., 2006; Davis, 2009). Early detection of an invasive species will minimize the cost of management, but requires ongoing surveillance for recurrence of the invasive species, which can be costly in itself (Lodge et al., 2006; Davis, 2009). However, this long-term monitoring is becoming more effective. Contemporary efforts combine traditional surveillance measures, such as physical and photographic sampling, and emerging technology, such as genetic diagnostic methods and remote sensing techniques, with collaborative information sharing networks, such as invasive species databases (Lodge et al., 2006; Davis, 2009). As new technology increases the efficacy of such monitoring measures and large-scale collaboration occurs, early detection will become a more viable method of mitigation.

Early detection is only useful to mitigate the effect of invasive species if there is protocol and funding in place for a rapid response should one be detected (Wittenberg and Cock, 2005; Davis, 2009). Anderson (2005) and Cain et al. (2011) describe a successful example of this kind of mobilization of resources. When *Caulerpa taxifolia*, the invasive seaweed described earlier, spread to California, it was detected early by accident; scientists and government groups collaborated quickly to develop an eradication plan, make funds available, and eradicate the seaweed within six years of detection (Anderson, 2005; Cain et al., 2011; Larson et al., 2011). Eradications, such as that of *C. taxifolia* in California, represent the ideal outcome of invasive species management, though only likely to succeed with early detection or when invasive

populations are small and limited in range (Wittenberg and Cock, 2005; Lodge et al., 2006; Davis, 2009).

Eradications have been historically carried out through mechanical, chemical, and biotic means (Wittenberg and Cock, 2005; Lodge et al., 2006; Davis, 2009). Mechanical control can take the form of weeding, trapping, or hunting; these methods target invasive species directly and are thus more labor intensive than more generalized management methods (Wittenberg and Cock, 2005). For instance, while hand-weeding was found to be effective in removing the invasive *Microstegium vimineum*, Japanese stiltgrass, chemical herbicide was deemed to be more efficient due to hand-weeding's labor intensity (Flory and Clay, 2009). Chemical control, such as pesticides or the herbicides used on *M. vimineum*, are broad-spectrum; that is, they are less labor intensive than more targeted methods, but are also likely to target more than one species (Wittenberg and Cock, 2005). Biological control includes introduction of natural enemies of invasive species, disruption of reproductive capacities of the invasive species, and inducing resistance in species affected by the invasive (Wittenberg and Cock, 2005; Davis, 2009). Biological control can be risky due to the inherent complexity of an ecosystem; the case of the Indian mongoose, *Herpestes auropunctatus*, described above, illustrates the potential of a natural enemy introduction to result in further biological invasion (Pimentel, 1955).

There are other drawbacks to methods for eradicating invasive species. Zavaleta et al. (2001) outline several ways in which the eradication of invasive species can cause further harm, otherwise known as non-target effects (Larson et al., 2011). Eradication efforts (such as poisoning) can affect the food chain through bioaccumulation, the magnified accumulation of substances as they travel up the food chain, posing harm to the community at large (Zavaleta et

al., 2001). Further, native species may not be able to recolonize a habitat transformed by the invasive species, such as one with altered fire regimes, as discussed above with the invasive shrubs, *Larrea tridentata* and *Prosopis* species (Zavaleta et al., 2001; Davis, 2009).

Alternatively, eradication can augment impact from invasive species. Eradication may lead to further invasions or greater impact of other invasive species or may reduce available habitat or resources for native species (Zavaleta et al., 2001). To avoid these secondary impacts, eradication strategies should be embedded in a holistic assessment of ecosystems (Zavaleta et al., 2001; Flory and Clay, 2009).

When invasive species are too well established for successful eradication, control is focused on containing invasive species, attempting to prevent or slow further spread, and reducing the species' impact on the host ecosystem (Wittenberg and Cock, 2005; Lodge et al., 2006; Davis, 2009). There are several control strategies beyond the mechanical, chemical, and biotic measures described above; alternative methods include technological innovation, managing the environment, and directed evolution (Davis, 2009). Invasive species management technology is a source of ongoing innovation; one example is the development of technologies that inhibit movement of species through ships' ballast water, such as biocide treatments (Davis, 2009). Managing the environment means manipulating an ecosystem to be less susceptible to invasive species. Methods can include surface level management such as controlled burns, grazing, and hunting, or more integrated methods, such as constructing artificial habitat and managing trophic interactions (Zavaleta et al., 2001; Wittenberg and Cock, 2005; Davis, 2009).

The ideal goal of management efforts based on directed evolution is the coexistence of native and invasive species rather than eradication or containment of the invasive species

(Schlaepfer et al., 2005; Davis, 2009). It is well known that biological invasion affects the evolutionary processes in an ecosystem (Carroll et al., 2005; Schlaepfer et al., 2005; Whitney and Gabler, 2008; Davis, 2009). Management by directed evolution facilitates coexistence between native and invasive species by inducing adaptation of the native species to the effects of the invasive or reducing the invasive species' ability to affect the native (Schlaepfer et al., 2005; Davis, 2009).

Schlaepfer et al. (2005) outlines two strategies for guiding management through directed evolution. First, changing interaction dynamics at the population level, such as providing novel habitat for avoiding predation, can shift selection pressures that provoke evolution of adaptive behaviors (Schlaepfer et al., 2005; Davis, 2009). Second, we can manipulate the genetic composition of native or invasive populations. For example, if individuals of the invasive species, missing certain traits that facilitate these their (interspecific rather than intraspecific) success, are introduced into a population, the absence of these traits could spread through the population, making it 'less invasive' and facilitating coexistence (Schlaepfer et al., 2005; Davis, 2009).

It is clear that preventative and early detection strategies are the most successful and cost-effective means of managing invasive species. However, management of invasive species that slip past these measures remains a moving target: eradication is practically impossible, if not harmful in itself, and traditional control methods are often inadequate. The question remains: how do we manage already established invasive species effectively? Emerging strategies, such as managing the environment or management by directed evolution, are a step in a new direction, ripe for further scientific exploration.

## **Shifting Management Perspective**

We have already described the high ecological and economic cost of invasive species (Parker et al., 1999; Pimentel et al., 2005; Cook et al., 2007; Barbier et al., 2013). A significant portion of actual economic costs are involved in ongoing efforts to contain and control well-established invasive species (Pimentel et al., 2005). In many cases of well-established invasive species, trying to restore a system to a pre-invasion state, based on similarly structured or nearby systems, combines high cost and difficulty with a low chance of success and historical accuracy (Wittenberg and Cock, 2005; Hobbs et al., 2006; Miller and Hobbs, 2007). Beyond unenthusiastic social and political support and holes in scientific knowledge, natural resource managers and researchers are underfunded, leading to relatively small-scale, short-term, ecologically isolated, and reactionary management solutions that belie the ongoing efforts that must be made in order to control these species in the future (Miller and Schelhas, 2008; Davis, 2009; Larson et al., 2011). This kind of management is not effective, let alone sustainable.

We suggest a shift in the management of well-established invasive species to a sustainability perspective. This shift entails ensuring the continuity of invasion management, thereby limiting environmental degradation, without exhausting the resources available to do so, namely funding and sociopolitical support (Larson et al., 2011). To accomplish this objective, a sustainable approach to biological invasion takes into account environmental, economic, and social factors to safeguard the health of ecosystems into the future, whether useful for humanity or not (Larson et al., 2011). This project is focused on the environmental sustainability of invasive species research and management, which we ground in two primary methodologies: holistic evaluation of ecosystems and processes, and the study of these processes through time



and space (Zavaleta et al., 2001; Hobbs et al., 2006; Hulme, 2006; Larson et al., 2011).

Additionally, sustainable management requires a distillation of the goals of invasive species management in order to set measurable, achievable goals for success (Miller and Hobbs, 2007; Miller and Schelhas, 2008; Larson et al., 2011). That is, we need to ask what it is that conservation and restoration efforts realistically hope to achieve, and then determine how best to achieve it.

Holistic evaluation of ecosystems requires full engagement with their complex and dynamic nature as well as the external factors affecting them. Invasive species are not isolated agents acting on the system; their proliferation is both the result and origin of ecosystem change. For instance, *Spartina alterniflora*, discussed above, is invasive in higher elevation wetland zones due to increased nitrogen input from agricultural and urban development (Bertness et al., 2002; Minchinton and Bertness, 2003). However, simply removing *S. alterniflora* from elevations where it is invasive would be a perpetual and useless effort. Rather, management of *S. alterniflora* needs to account for other environmental drivers (Hulme, 2006). As long as high levels of nitrogen runoff continue to facilitate *S. alterniflora*'s greater competitive ability in those zones, targeted control measures will be ineffective.

To accomplish this holistic evaluation of ecosystems, research must be conducted in an ecosystem context. While studies conducted in isolation do further knowledge about a species, they reveal nothing about a species' potential responses to the other factors in its host system (Dukes, 2007). Dukes (2007) recommends a multifactor approach, promoting a broad understanding of invasive species' response to their new communities and vice-versa, and a demographic approach, examining these responses throughout the lifecycle. Rodriguez (2006)

illustrates the advantage of an ecosystem approach: she provides evidence of significant changes wrought in ecosystem dynamics by the facilitation of native species by invasive species, a reciprocal impact and response system that has been ignored historically, and has important implications for understanding invasive species (Rodriguez, 2006; Dukes, 2007).

Historically, the spatial and temporal scales over which invasive species have been assessed have been limited, or not considered at all (Mack, 2005; Willis and Birks, 2006; Larson et al., 2011; Kettenring et al., 2012). Consideration of longer time spans is necessary to fit biological invasion into a larger picture of ecosystem change and to predict species' long-term effects. Willis and Birks (2006) employ a paleoecological approach to elucidate the role of specific invasive species as either drivers or passengers of environmental change. For example, because primary growth forests in North America were established in different climate conditions than currently exist, the forests' vulnerability to species invasion may be a result of climate change rather than an isolated source of ecosystem degradation (Willis and Birks, 2006). Studying species over longer time spans also provides an understanding of what happens to invasive species as they progress with time. Because the field of invasion biology is in its youth, scientists have a relatively short window of available evidence and research from which to draw conclusions. Expanding the time-scale of research, and finding innovative ways to do so, will serve to help us make more informed predictions about the future of invasive species. For example, We have previously discussed the difficulty of distinguishing native from invasive species that have existed in a region for thousands of years (Preston et al., 2004). It is possible that the impact of invasive species diminishes over time; long-term examination would allow for the detection of potentially paradigm-changing trends such as this.

Likewise, studying invasive species over large spatial scales will promote an understanding of their present and future effects that can help guide management efforts. Callaway and Aschehoug (2000) and Tsutsui et al. (2000) illustrate the value of studying invasive species in both their native and invasive range to determine the source of their success in new ecosystems. In a particular case, enemy release in its invasive range allows the Eurasian forb *Centaurea diffusa* to modify habitat through allelopathy (Callaway and Aschehoug, 2000). Comparison of species across different contexts reveals patterns that contribute to a greater understanding of the species' ecology. Kettenring et al. (2012) also praise the value of studying invasive species over large spatial scales in order to investigate generalizable patterns of invasion that could ultimately guide management efforts.

Finally, there needs to be a pragmatic understanding of the goals of sustainable management to guide and measure successful efforts. There are varying understandings of the goals of conservation and restoration; the spectrum ranges from restoring some semblance of 'wild', pristine ecosystems with little to no evidence of invasive species presence, to a focus on retaining only the ecosystem services necessary for human survival, even if invasive species play a part in them (Miller and Schelhas, 2008). Particularly for well-established species, restoration to a historical ideal seems to be an unfeasible goal. We do not know exactly what our historical ideal would be; there are few, if any, ecosystems remaining that are free of anthropogenic effects that could serve as models for this kind of restoration (Vitousek et al., 1996; Hobbs et al., 2006). Additionally, management and restoration efforts themselves can change the character of the system, meaning that efforts towards such a goal would be unsuccessful from the beginning

(Pyšek and Richardson, 2010). Alternatively, the human-ecosystem relationship is far too complex to try to jettison everything not directly related to human survival.

In the conventional sense, sustainable management efforts strike a balance between ecological, economic, and social concerns (Larson et al., 2011). This project is concerned primarily with ecological change associated with invasive species and, therefore, we focus on the ecological goals of sustainable management, conservation, or restoration. As we saw from Miller and Schelhas (2008) above, these goals are almost necessarily vague and subjective. This is further illustrated by Miller and Hobbs' (2007) review, entitled “Habitat Restoration—do we know what we’re doing?”, in which they conclude that a contextual approach to management success is the most realistic: successful management is going to look different in different places. We introduce the idea of *equilibrium* as a way of understanding success in sustainable management. Equilibrium forsakes the idea of wild or pristine ecosystems as realistically untenable, but simultaneously implies a lack of ecological harm and a minimized human impact, a system resilient and ready to follow an updated course of coevolution.

## **Project**

We want to create a shift in the invasive species research and management perspective towards sustainability, grounding these changes in quantifiable, empirical research. We will determine whether there is empirical support for a sustainable management approach to invasive species by studying the invasive wetland reed *Phragmites australis*. Applying our definition of sustainable management, we will scientifically evaluate *P. australis* in a holistic ecosystem perspective and situate scientific knowledge and research of *P. australis* in a historical and landscape context. We predict that expanding the ecological, temporal, and spatial frame in

which we view invasive species will allow for new understandings of invasiveness to become evident, which can ultimately be used to ensure the sustainability of invasive species management. By grounding the shift of research and management perspective in a specific, tractable model, we will provide the practical foundation for scientists to examine this approach centrally for this system and then move towards similar examination of other systems.

Though it is a well-established invasive species in many regions of North America, *P. australis* management efforts remain focused on aggressive eradication practices and short term solutions (Ailstock et al., 2001; Bart et al., 2006; Personal Observation, 2014). Through this project, we hope to build the foundation for exploring the viability of other types of management, including directed evolution and ecosystem management, which may promote equilibrium in wetlands where *P. australis* is currently invasive. Through this research we also hope to predict future behavior of *P. australis* in wetlands, for both small (community) and large (meta-population) scale settings, which will further contribute to effective sustainable management.

We have already designed and carried out a pilot experiment (described in detail later in this work) as an example of the kinds of research questions that will lead towards sustainable management of invasive species. This project addressed the need to for a holistic, long-term, and large-scale perspective by studying the interspecific interactions of *P. australis* at a community level; we compared the plant species diversity of communities that had been invaded by *P. australis* at different points of time post-invasion. Using this experiment as a model for studying *P. australis* through a lens of sustainability, we recommend a future research agenda, utilizing

both well-established (as in our pilot) and emerging methods, which will provide the empirical basis to best manage *P. australis*.

## **Rationale and Significance**

### **Management Shortcomings**

We have previously introduced the question of whether the management of invasive species is sustainable. In this section, we summarize the concrete, recognized shortcomings of current invasion management methods that substantiate the need for a shift in perspective towards sustainability. Though we have indicated above several ways in which contemporary methods fail, particularly for well-established invasive species, Davis (2009) provides a comprehensive and updated understanding. We split these failures into two major groups: 1) problems due to framing invasive species in isolation and 2) problems due to gaps in knowledge or understanding.

Invasive species management problems due to isolated framing are created by viewing the addition of an invasive species as the singular facet of a problem, such that the species' subtraction would immediately and fully solve the problem. Failures in this respect include unintended consequences of management, a conflation of impact and mechanism, and failures of eradication as a strategy (Davis, 2009). Unintended consequences, such as the removal of an invasive plant that provides habitat for an endangered species, have been outlined above in connection with eradication methods, but effects on the ecosystem that outweigh the impact of the original invasive species are not limited to targeted removal efforts. Due to the complex interaction of species within an ecosystem, management methods can have far-reaching and

unpredictable effects on trophic connections and habitat (Zavaleta et al., 2001; Wittenberg and Cock, 2005; Davis, 2009). A conflation of impact and mechanism results in management efforts addressing (highly studied) impacts of invasive species, rather than the less well-understood underlying causes of their presence (White et al., 2006; Davis, 2009). For example, management of *Spartina alterniflora*, described earlier, addresses the species' increasing dominance at higher elevations, but not the underlying problem of altered nutrient input (Bertness et al., 2002). Additionally, the management problems associated with eradication still persist; well-established species are practically impossible to eradicate altogether without an unlimited pool of resources and labor, and, due to the issues outlined above, eradications do not necessarily eliminate impacts on an ecosystem. For instance, native herbivorous tortoises, and, when those were driven to extinction, introduced goats kept vegetation at bay on the Mascarene Islands; when the goats were eradicated as part of a management initiative, several introduced plant species became invasive, reducing the prevalence of native plant species (Zavaleta et al., 2001).

Gaps in knowledge and understanding of biological invasion, primarily involving ecosystem dynamics, taxonomic uncertainty, biological control, and the perception of invasive species impact, also lead to failures of contemporary management efforts. The dynamic nature of ecosystems and their habitats and species compositions are difficult for scientists and natural resource managers alike to keep up with, a phenomenon that Davis (2009) colloquially refers to by saying “the playing field and the players keep changing”. This is illustrated by recent research into novel ecosystems; that is, ecosystems that are home to new and historically unique combinations of species that entail significant changes in ecosystem function, likely due to changes brought about by human activity (Hobbs et al., 2006). We have already reviewed issues

related to taxonomic uncertainty (the occasional ambiguity of whether a species is native or non-native). Whether management should prioritize efforts based on the impact (Byers et al., 2002) or focus efforts on non-native species (Simberloff et al., 2012), is not necessarily the correct question. The problem remains that the difference between native and non-native species is not always well-defined (Preston et al., 2004; Willis and Birks, 2006; Davis, 2009). Biological control methods present similar problems for management to eradication efforts; there is significant uncertainty in the effect of introducing biological control methods, clearly demonstrated by the above examples of the Indian mongoose or the cane toad, which were originally introduced to control other pest species (Pimentel, 1955; Phillips et al., 2007; Davis, 2009). Finally, the perception of the impact made by invasive species can obstruct effective management, leading to overblown or weak responses (Davis, 2009). Ludwig et al. (2003) provide a particularly relevant analysis of the perceptual framing of our model, *Phragmites australis*, and its effects on management efforts, concluding that, due to its notoriety as an incredibly invasive species (whether deserved or not), its management is strongly affected by many, often contradicting, assessments of the species' value. More simply, where *P. australis* is widely held to be a threat, management efforts will look much different than where the species is seen as more neutral, or even as having a positive impact (Kettenring et al., 2012).

The diversity of public perspectives bridges both isolated framing and gaps in knowledge regarding invasive species. Public perception of invasive species is likely to vary by locale, based on the history, impact, and the availability of education about particular species (McNeely, 2005; Davis, 2009). Furthermore, policy makers and the public rarely consider management of invasive species outside of a purely anthropocentric, often economic, lens (Mooney et al., 2005;



Burgiel et al., 2006; Lodge et al., 2006; Davis, 2009). This results in a lamentably short-term view of invasive species management: an anthropocentric view not only isolates invasive species to the space and time of a human life (which, as we have detailed above, is problematic for several reasons) but, because funding for research and management depends on public support, also leads to gaps in knowledge that further impede truly effective management strategies.

Miller and Schelhas (2008), among others who have proposed a shift in invasive species management approach, highlight the apparent lack of organization and effort to address the issue of invasive species. Faced with the shortcomings described above, we must try to address ineffectual management in a way that is sustainable and based in sound scientific research.

### **A Sustainability Approach: Solving Management Problems**

These problems, at the root of which are isolated framing of invasive species and gaps of scientific knowledge, can be traced to the historically predominant understanding of invasion biology, the Eltonian perspective (originating with Charles Elton, a biologist from the mid-20<sup>th</sup> Century) (Davis, 2009). Elton's work, which characterized invasive species as 'extra-ecological' and 'militaristic entities', was influential in shaping the public and scientific views of invasive species, leading to invasion biology's separation from ecology as a discipline and providing a foundation for the way that we approach research of invasive species (Davis, 2009). This tendency to view invasive plants through a thick normative lens is commonplace; Ludwig et al. (2003) noted that research into and management of our own model, *Phragmites australis*, is not purely a matter of natural science but is heavily tinged by perception. The development of invasion biology based on the Eltonian perspective has contributed to the isolated approach and lack of understanding detailed in the previous section.

Shifting to a sustainable perspective will work to solve these issues. Davis (2009) notes an increasing rejection of the Eltonian perspective in the last decade; the separation of invasion biology and ecology research is being eroded, management is being reimagined (Miller and Schelhas, 2008; Larson et al., 2011), and traditional conceptions of “invasiveness” are being questioned (Rosenzweig, 2001; Gurevitch and Padilla, 2004; Hobbs et al., 2006; Davis, 2009). By working towards holistic understandings of invasive species in ecosystems over large spatial and temporal scales, a sustainability perspective and approach builds on these foundations to further mature our understanding of invasive species. This understanding will likewise provide a framework for the sustainable use of resources in managing the current and long-term health of ecosystems, whether they provide direct benefit to humanity or not; by taking into account the environmental, economic, and social factors, we argue that a sustainable perspective will ensure the best possible outcome of invasive species management.

There are specific ways, many of which we have already discussed, in which the commitments of a sustainability perspective may manifest themselves in contemporary research and management. Willis and Birks (2006) advocate the use of paleoecology to broaden our historical understanding of ecosystems. Hobbs et al. (2006) see benefit in incorporating research of invaded ecosystems as simply systems with novel combinations of species. Kettenring et al. (2012) have found valuable insights in collecting knowledge of invasive species over an entire continent to try to draw out important ecological principles. Emerging technology and disciplines, such as genetic analysis, can help answer questions about species’ history (Saltonstall, 2002), and reimagining antiquated methods, such as species diversity indices, can serve to provide more detailed knowledge of ecosystem change (Parker et al., 1999). On the management

side, technological advances could also play a role in promoting equilibrium (Davis, 2009). Alternatively, a laissez-faire approach may be, at times, more expedient (Wittenberg and Cock, 2005). A middle ground, such as management by directed evolution, also fits well into a sustainable management approach (Davis, 2009). All of these strategies promote the idea of equilibrium, which we posit to be the goal of a sustainable perspective. It is the persistence of functioning ecosystems, rather than individual components, that must be the ultimate object of preservation; it is important to remember that it is precisely the change of individual components, the disruption of ‘natural’ balance itself, which leads to evolutionary change (Ludwig et al., 2003).

## **Approach**

We are studying the changing community membership over time of the wetland reed *Phragmites australis*, considered invasive in North America. In order to be considered a member of a community, a species must first be able to disperse to a community, survive the existing abiotic conditions, and develop interspecific interactions with the other organisms (Cain et al., 2011). In its invasive range, *P. australis* obviously fulfills the first two conditions: it has, through human agency, already succeeded in dispersing outside of its native range, and, by continuing to do so, exhibits its compatibility with existing abiotic conditions in this new range. Therefore, as a model for a sustainability approach in invasive species research and management, we focus on the interspecific interactions of *P. australis* within wetland communities over time in order to gain a holistic understanding of the ecosystem and to situate ecosystem changes in a historical context.

There is evidence that, while invasive plants can evolve to enhance their ability to spread, the surrounding community can likewise evolve to respond and adapt to the new selective pressures imposed by invasive species, as we briefly described above (Callaway and Aschehoug, 2000; Schlaepfer et al., 2005; Davis, 2009). Specifically, plant communities, and the interactions between species in these communities, are a product of coevolution, having reached a kind of equilibrium within their system (Callaway and Aschehoug, 2000). Our approach is to determine whether *Phragmites australis* is in the process of such a coevolution, and possibly its own future equilibrium. Through this model, we are trying to develop the empirical support for understanding *P. australis* in this way, as well as outline further investigation into larger questions of invasion biology similarly influenced by our sustainability approach.

### ***Phragmites australis***

*Phragmites australis* is a vegetative perennial wetland grass, commonly held to be invasive in North America (Saltonstall, 2002). There are currently three distinct *Phragmites* lineages recognized in its North American range: an introduced Eurasian lineage, a Gulf Coast lineage, and the native lineage endemic to, at least, the mid-Atlantic and northeast coasts (Saltonstall et al., 2004; Kettenring et al., 2012). We focus on the introduced Eurasian lineage and the native lineage. Historically, *P. australis* has been present as a minor native wetland plant throughout North America, with evidence of the species dating back 4000 years (Chambers et al., 2008). However, within the past 200 years, its status within tidal wetland communities has changed significantly (Chambers *et al.*, 1999). Saltonstall (2002) provided genetic evidence that an introduction of *P. australis* from Europe had occurred. The original time of introduction of *P. australis* is estimated to be in the mid-19<sup>th</sup> Century in the New England region of the United

States, though specifics about the source, location, and time period are not well-known (Saltonstall, 2002; Chambers et al., 2008; Mozdzer et al., 2013). It is now invasive throughout North America, from Canada to Central America (Saltonstall et al., 2004; Chambers et al., 2008).

Evidence suggests that *P. australis* invasion is generally facilitated by wetland disturbance, land development, and nutrient enrichment (Chambers et al., 2008). Human expansion along the northeastern coast of the US and the Chesapeake area over the last century has led to large increases in these environmental pressures, which has resulted in the species' proliferation in these regions and spread throughout the continent (Chambers et al., 2008; Kettenring et al., 2012). In Maryland specifically, there is evidence that *P. australis* has expanded considerably in wetland marshes since the early 20<sup>th</sup> century (Rice et al., 2000).

There are two primary explanations for the swift expansion of *P. australis*. The ecological explanation centers on recent shifts in habitat suitability due to anthropogenic disturbance: rapid development has led to destruction of wetland habitat and changes in nutrient and hydrological regimes that ease the invasion of introduced *P. australis* (Chambers et al., 1999). The genetic explanation is based on evidence of dominant 'aggressive' genotypes within certain populations (Rice et al., 2000; Chambers et al., 2008). The significant genetic and ecological diversity within the *P. australis* species itself results in the opportunistic character of its invasion across North America, allowing it to establish itself in ecosystems with exceedingly variable conditions (Kettenring et al., 2012).

Saltonstall et al. (2004) have distinguished morphologically and genetically distinct characters differentiating a native *P. australis* (subspecies *americanus*) from the Eurasian lineage. Genetic evidence indicates insignificant hybridization between the two lineages, since

indicative alleles of one lineage were seldom found in the other (Saltonstall et al., 2004). The ecology of the native lineage also differs from the introduced lineage. In contrast to the introduced lineage, the native does not grow in dense monocultural stands (Saltonstall et al., 2004). Additionally, while the clonal nature of *P. australis* reproduction is often cited as a reason for its success, the native actually grows larger clone sizes, which is implicated in its continued competitive resistance of the introduced lineage (Duhovnikoff and Hazelton, 2014).

The invasive Eurasian lineage of *P. australis* is widely associated with significant ecosystem impacts at the individual, community, and ecosystem level, as described above. The species grows in dense, high biomass monoculture, and has been associated with direct and indirect effects on ecosystems in which it is invasive (Windham and Lathrop, 1999). There is evidence that *P. australis* may reduce biodiversity in highly diverse tidal marshes, especially in the number and abundance of plant species (Windham and Meyerson, 2003; Bart et al., 2006; Chambers et al., 2008). Its competitive ability with other plant species is due to several factors: *P. australis* spreads through rhizomes, leading to the growth of dense stands that leave little space for other species, and grows tall, blocking light from reaching other species (Rice et al., 2000; Chambers et al., 2008).

Animal diversity is affected through habitat loss of benthic invertebrates, wetland birds, and fish (Bart et al., 2006; Mozdzer et al., 2013). Monocultural and vegetative growth changes soil hydrology (Windham and Lathrop, 1999), filling in areas previously accessible to fish and other aquatic animals (for which wetlands are a valuable nursery and feeding grounds) thereby also physically and functionally excluding wading wetland birds (Ailstock et al., 2001; Chambers et al., 2008).

*P. australis* also affects larger ecosystem processes such as nutrient cycles and biogeochemical traits (Bart et al., 2006; Mozdzer et al., 2013). Windham and Meyerson (2003) show that the presence of *P. australis* has significant effects on nitrogen cycling, though the manifestation of those effects depends more on how *P. australis* interacts with the system in which it is invasive than on the qualities of *P. australis* itself. However, there is evidence that the rhizomatous nature of *P. australis* makes it a better competitor for changing availability of nitrogen: the matrix of rhizomes characteristic of *P. australis* stands creates a more oxic environment, changing belowground organic nitrogen into a usable form more quickly (Windham and Lathrop, 1999).

The ability of *P. australis* to colonize disturbed substrates and persist under adverse conditions has had some positive effects. It is often the first species to recolonize land cleared or affected by construction or coastal development, and can even make soil conditions more amenable to life (Bart et al., 2006; Chambers et al., 2008). There is evidence that *P. australis*-dominated wetlands improve the quality of water that flows through them, though differences in water quality compared to uninvaded wetlands have not been studied (Chambers et al., 2008); these invaded wetlands also trap and stabilize sediments, combatting subsidence due to sea-level rise or erosion (Ailstock et al., 2001; Chambers et al., 2008; Mozdzer et al., 2013).

Management of *P. australis* has centered around three policies: eradication, control, and tolerance under certain context (Ailstock et al., 2001). Conventional control methods primarily include chemical and mechanical control (Ailstock et al., 2001). Chemical control, such as herbicide application, has seen some short-term success in controlling *P. australis* in specific sites, but, several years after the study was conducted, regrowth of *P. australis* rivaled

pre-application density (Cross and Fleming, 1989; Ailstock et al., 2001). Mechanical control, such as mowing, bulldozing, and ‘discing’ (using specialized machinery to break up belowground biomass), and similar methods seem to have limited effectiveness (Cross and Fleming, 1989). Another form of mechanical control, flooding *P. australis* colonies, has been successful in controlling spread, but high water levels must be maintained and therefore are not very feasible as a large-scale strategy (Cross and Fleming, 1989; Hellings and Gallagher, 1992). Burning *P. australis*, a third form of mechanical control, has had variable success and, like flooding, poses a large disturbance to the ecosystem (Cross and Fleming, 1989; Ailstock et al., 2001). The overall effectiveness of these control methods is contentious; the ecological costs and benefits are largely unknown and the effectiveness of the methods themselves are highly variable (Bart et al., 2006). Yet, these measures persist in management and scientific research through the time of writing (Personal Observation, 2014).

### **Pilot Experiment**

The aim of this pilot was to determine whether community membership of *Phragmites australis* changes over time. A recent study of wetlands around the Chesapeake Bay by Rice *et al.* (2000) provides unique evidence and motivation for our study. In a survey of recently and historically invaded freshwater and brackish marshes, this study found trends indicating a lower intrinsic rate of increase in *Phragmites australis* where it had been established for a longer period of time (Rice *et al.*, 2000). These data hint at the theoretical basis of this proposal: the significant slowing of *P. australis* expansion over time could be caused by the changing status of *P. australis* within the community. If this is the case, then further evidence may be found in



studying the diversity of these assemblages, through the interspecific interaction of *P. australis* and other plants within the ecosystem.

We tested differences in the number of plant-plant interactions between saltmarshes that have been historically and recently invaded by *P. australis* by sampling the plant species diversity (species richness and evenness) in patches of *P. australis*. The rationale is that the extent of interspecific interaction, measured by species diversity, is a good proxy for community membership of a species. To sample species diversity, we identified and defined three conditions of *P. australis* that would allow us to take a ‘snapshot’ of its community membership at different points in time since invading a certain area: 1) historically invaded, defined as being present at a site in 1970, 2) recently invaded, defined as being absent at a site in 1970, and 3) native, defined as a site having current evidence of the native subspecies *P. australis* subspecies *americanus*. We chose 1970 to differentiate the two due to the availability of information about *P. australis* presence at that time; the Maryland Department of Natural Resources completed aerial surveys of wetlands in the Chesapeake Bay area in 1970 (Ailstock et al., 2001; Personal Communication, 2014). We chose sites based on recommendations from researchers at the University of Maryland and indications in the literature (Rice et al., 2000; Tulbure et al., 2012) that certain areas contained patches of *Phragmites australis* that adhered to the characteristics required by our experimental design (Table 1).

We used a transect-quadrat method to survey species diversity in patches of *Phragmites australis*. Once we identified a suitably large patch of *P. australis* on-site, we measured a 25-meter line transect through the patch, oriented the transect to remain within the patch, and placed five 1m<sup>2</sup> quadrats along its length. We then counted and recorded the number of

individuals of each plant species present in the quadrat. In the lab, we identified and recorded the plant species sampled from the field using multiple field guides (Tiner, 1993; Silberhorn, 1999) and made herbarium specimens for later verification. We quantified the plant species diversity using Simpson Diversity Index (Table 2) (Simpson, 1949; Ailstock et al., 2001).

**Table 1. Categorization of the different site locations used, as well as sources of evidence for their inclusion in our study.**

Category	Location	Salinity	GPS Coordinates	Evidence
Historical	Jug Bay Wetland Sanctuary	0.1	N38° 46.889' W076° 42.300'	Rice <i>et al.</i> , 2000
Historical	American Chestnut Land Trust (ACLT)	0.5	N38° 31.913' W076° 32.532'	Personal Communication (Whigham, 2014)
Recent	Elms Environmental Center	11.45	N38° 12.006' W076° 22.238'	Personal Communication (Rochow, 2014)
Recent	Flag Ponds Nature Park (FPNP)	1.3	N38° 27.100' W076° 27.366'	Personal Communication (Whigham, 2014)
Native	Kings Creek Preserve (KC)	2.95	N38° 46.402' W075° 58.529'	Tulbure <i>et al.</i> , 2012

**Table 2. Abundance of 29 species found at our study sites. Simpson's diversity index was used to determine species diversity.**

	Jug Bay	ACLT	KC	FPNP	Elms
<b>Simpson's Index</b>	<b>1.19</b>	<b>2.85</b>	<b>1.49</b>	<b>1</b>	<b>1.33</b>
<i>Boehmeria cylindrica</i>	16	-	-	-	-
<i>Carex crinita/stricta</i>	18	3	-	-	-
<i>Hibiscus moscheutos</i>	3	32	30	-	-
<i>Murdannia keisak</i>	10	-	-	-	-
<i>Panicum virgatum</i>	-	1	-	-	-
<i>Peltandra virginica</i>	-	37	-	-	-
<i>Periscaria glabra</i>	-	-	2	-	-

<i>Phragmites australis</i>	802	110	-	596	1851
<i>Phragmites australis</i> spp. <i>Americanus</i>	-	-	85	-	-
<i>Polygonum artifolium</i>	17	-	18	-	-
<i>Sambucus canadensis</i>	-	2	-	-	-
<i>Schoenoplectus americanus</i>	-	-	44	-	-
<i>Spartina patens</i>	-	-	-	-	297
<i>Teucrium canadense</i>	-	-	1	-	-
<i>Typha angustifolia</i>	-	-	5	-	-
<i>Typha latifolia</i>	2	-	-	-	-
Unknown 1	-	-	17	-	-
Unknown 2	-	3	-	-	-
Unknown 3	-	-	-	-	7
Unknown 4	-	6	-	-	-
Unknown 5	7	-	-	-	-
Unknown 6	-	-	3	-	-
Unknown 7	-	-	1750	-	-
Unknown 8	-	-	197	-	-
Unknown 9	-	5	-	-	-
Unknown 10	-	2	-	-	-
Unknown 11	-	1	-	-	-
Unknown 12	-	2	-	-	-
Unknown 13	-	-	-	-	8

## Project Aims

Mirroring our pilot experiment, future research will focus on studying *Phragmites australis* in a way that expands the spatiotemporal scale on which its invasion is examined, and situating *P. australis* in holistic ecosystem context, seeking to establish how ecosystems invaded by *P. australis* could achieve a kind of equilibrium. We outline the specific aims of the project, as well as metrics of measurement, expected outcomes, approaches to interpretation, and shortcomings, below.

### Specific Aim #1: Augment Ecosystem Context

We will open this line of research by expanding and improving upon the pilot experiment described above. The ways in which the pilot study situates *P. australis* in a holistic ecosystem

context should be augmented in tandem with investigation of its community membership. Beyond plant species diversity, research should include examination of animal diversity; patterns of animal presence (such as macroinvertebrates or birds) in *P. australis* dominated wetlands are not well known (Ailstock et al., 2001; Chambers et al., 2008). Study of interactions between *P. australis* and the rest of the ecosystem should be thorough. For example, there is little to no previous literature on a fungus that affects the native subspecies of *P. australis*, but not the invasive (Swearingen and Saltonstall, 2010). We expect trends in community membership to correlate; that is, patterns of animal diversity will parallel those of plant diversity. Results will be interpreted to explain trends in community membership of *P. australis*.

### **Specific Aim #2: Increase Time Scale**

While the pilot experiment looks at change over time, the time span examined will be longer and more differentiated. For instance, the “historical” and “recent” invasions in the pilot were defined as before and after 1970, respectively, leaving the age difference between a historical and recent populations to potentially span only a few years. Unfortunately, there seems to be no reliable data on *P. australis* presence available from before 1970 (Personal Communication, 2014). Ideally, studying populations that are more separated in age (for instance, before 1970 and after 2000 puts nearly half a century between the potential ages of the populations) would provide a much clearer idea of whether community membership conditions had changed over time. Alternatively, population age could be grouped based on the existing aerial surveys conducted by scientists and government departments in the Chesapeake Bay area periodically since 1970 (Ailstock et al., 2001; Personal Communication, 2014). With the time and resources allotted by this grant, we could survey approximately 20-30 sites 2-3 times per

growing season, depending on the identification of this number of available sites that match the experimental design parameters. Additionally, in second sense of expanding time-scales, a multi-year study would be useful to replicate the experiment and add empirical weight to the study. We expect that, as the time of invasion of different populations diverges, community membership differences will increase. Results will be interpreted to explain whether patterns suggest that community membership is increasing, decreasing, or unchanged.

### **Specific Aim #3: Increase Spatial Scale**

Following Kettenring et al. (2012), increasing the spatial-scale of the experiment serves to provide more generalizable conclusions about the invasion of *P. australis* and the behavior of its populations over time. While the pilot experiment only sampled from five sites, an expanded operation could sample many populations across diverse geography in the Chesapeake Bay watershed region, and categorize populations by important characteristics that differentiate types of wetlands, such as salinity. With 20-30 sites spread across multiple states bordering the Chesapeake Bay, we could obtain far more representative data. As necessary to find sites matching our experimental parameters, we would expand the spatial scale to sites throughout the watershed. Additionally, more complete descriptions of the ecosystems under study would help control for confounding variables, for instance, the fact that freshwater marshes typically have differing levels of species diversity than more saline wetlands. For long-term research goals, conducting the same kind of research across regions in North America for comparative purposes would achieve this end to an even greater extent (Kettenring et al., 2012). We expect that community membership trends will be similar in similar landscapes. By grouping populations by similar landscape characteristics, species diversity measurements can be effectively compared,

specifically by utilizing community similarity indices, such as Sorenson's Coefficient. By doing so, conclusions about the community membership over time could take landscape difference into account while still being widely applicable.

## **Shortcomings**

Possible shortcomings of this study include problems with using *Phragmites australis* as a model organism and using species diversity as a proxy for community membership. *P. australis* is largely a clonal organism, meaning that its vegetative, asexual form of reproduction gives rise to genetically identical progeny (Douhovnikoff and Hazelton, 2014). This may pose a problem for our research in the long run; if genetic information in *P. australis* does not spread through populations in the same way as most plants, then research and recommendations for management may not be generalizable or relatable to other invasive organisms. Additionally, if species diversity does not provide a good proxy for community membership, then the design of the experiment must be adaptable to other, possibly better, metrics of community membership, such as quantifying the number of interactions themselves.

However, at this time, the benefits of using *P. australis* as a model outweigh the costs. For instance, because *P. australis* has a native subspecies, as described above, there is a strong dimension of comparison between native and invasive that does not commonly exist elsewhere. Additionally, there is also a large amount of historical data and large body of research available for *P. australis*, especially in the Chesapeake Bay area, which situates the empirical basis for a sustainability perspective in strong context. This wealth of information is partly due to a strong public perception of the invasiveness of *P. australis*, another benefit to using this species as a

model: research regarding *P. australis* is more likely to gain public and political support, increasing the potential of continued funding.

## **Future Research**

There are several further steps and directions to pursue with this research after termination of the two-year time frame allotted by this grant funding. Beyond the threshold of this grant, research into *Phragmites australis* incorporating a sustainability perspective can be further advanced beyond ecological field studies. Saltonstall (2002) and Saltonstall et al. (2004) pioneered the use of genetic techniques to do landmark research into the species history and current state of *P. australis* in North America. There is significant potential for using emerging genetic techniques for studying *P. australis*. The patterns of genetic relatedness and change over time could lay the foundation for an important step towards finding management strategies that promote equilibrium in *P. australis* invaded ecosystems; for instance, directed evolution, the manipulation of genetic material of *P. australis* to promote coexistence, may be a viable sustainable management strategy to discuss pursuing.

## **Applications**

The applications of this research are two-fold. First, the ultimate application of a sustainable perspective on invasive species is to guide management. Therefore, we hope that this research provides the empirical impetus to break the status quo of *Phragmites australis* management, to try to work towards equilibrium rather than an endlessly costly program of eradication techniques to beat back the perceived tide of *P. australis*' spread. Secondly, we hope that this research will aid education and outreach efforts in consolidating public perspective

relating to *P. australis* and invasive plants generally. The toxicity of public perspective on *P. australis* is such that the word *Phragmites* alone sparks knowing smiles and shaking heads. Successfully and practically implementing a sustainability perspective for invasive species should provide a new framework for thinking and learning about invasive species. Rather than sensationalized, all-or-nothing, militaristic metaphor (Davis, 2009), popular opinion should regard invasive species in a more solution-based light, embracing preventative measures and systematic management. This will hopefully breed public, and political, support for research into and sustainable management of invasive species, a step in the right direction in solving the shortcomings described above.

## **Hazards**

The hazards associated with fieldwork pertaining to *P. australis* are straightforward. Fieldwork involves necessary risk; the location of fieldwork can be remote and the dangers of outdoor work very real. *Phragmites australis* is found in wetlands, which, even when adjacent to populated areas, can still be remote and difficult or dangerous to access. Working in groups is required to ensure safety of researchers, both in providing and obtaining emergency assistance should it become necessary. The difficulty of access provides another hazard. Access to many wetland areas may be restricted to foot or watercraft access only. This requires that researchers have a level of physical fitness and the proper training compatible with carrying or boating survey equipment relatively long distances to study sites. Protective clothing should be standard to avoid the inevitable abrasions and lacerations associated with working in wetlands.

## **Timeline and Evaluation Plan**



**Table 3. Timeline and evaluation plan summary.**

	<b>Objectives</b>	<b>Timeline</b>	<b>Measurable Outcome</b>
<b>First Year (2015-2016)</b>	Aim 1: Establish spatial limits of study	Aug-Oct	Establish distribution of <i>P. australis</i> populations in region of interest; ensure permission for access to land
	Aim 2: Track sources of historical data	Oct-Dec	Survey government and academic databases, maps, and literature to determine age and categorize populations and wetland types
	Aim 3: Methods, materials, and logistics	Dec-Mar	Develop protocol for sampling, procure materials, and plan logistics for field trips
<b>Second Year (2016-2017)</b>	Aim 4: Carry out field research	Mar-Aug	Conduct field research
	Aim 1: Analyze results and adjust course	Sep-Dec	Compile data and analyze results to establish trends; adjust course and details of the study accordingly
	Aim 2: Methods, materials, and logistics	Dec-Mar	Adjust protocol, procure any additional materials, and plan logistics for field trips
	Aim 3: Carry out field research	Mar-Aug	Conduct field research

After field research concludes in August, we will compile and analyze the results of our second season of sampling. Upon completion, as well as during the project if the opportunity arises, we plan to compile the findings of this study into one or more scientific papers. These will be submitted to the relevant journals for peer-review and publishing.

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