Spatial Modeling of a Realized Niche: Investigating the Invasion of Sweet Fennel (*Foeniculum vulgare* Mill.) into Coastal Habitats of Virginia's Eastern Shore

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ABSTRACT

Establishment is an important phase in the invasion process during which an exotic species escapes cultivation and successfully survives and reproduces in its new habitat, ultimately becoming naturalized and potentially invasive in its new range. One of the earliest cultivated plants, Sweet Fennel (*Foeniculum vulgare* Mill.) has gained a global distribution due to anthropogenically mediated dispersal; it alters vegetative structure and function by forming dense stands and threatens invasion into coastal shrub and grassland habitats worldwide. Like many Mediterranean species adapted to disturbed habitats, fennel produces numerous small seeds that are capable of forming a persistent seedbank. The interaction of dispersal, anthropogenic disturbance and competition for suitable micro-habitat sites in a species that is on the verge of regional invasion make Virginia's Eastern Shore an interesting system for studying the invasion process. By modeling the distribution of fennel vegetation and seedbank at the Eastern Shore of Virginia National Wildlife Refuge, I am investigating the anthropogenic activities, abiotic conditions and biotic interactions that are contributing to fennel's success. I conducted field surveys of fennel stem and seed densities with a stratified sampling design with variation for distance to anthropogenic features and refuge management sites. Using spatially applied statistical models for zero-inflated count data and an information theory approach to model selection, I estimate the relative influence of multiple environmental and site variables to explain fennel occurrence. Results indicate that like most invasions, there is a combination of factors related to habitat and disturbance regimes that shape the distribution of sweet fennel and which could have implications for future management decisions.

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INTRODUCTION

Background/Significance of Study

The study of biotic invasion has become increasingly important for effective and cost-efficient biological conservation of indigenous species and habitats. Invasive species are those species which once transported, not only survive and reproduce in a previously uninhabited location, but proliferate to the detriment of endemic species. As such, biotic invasion has been identified as a proximal force driving the global decline of biodiversity (Walker and Steffen 1997). In the United States, competition with or predation by invaders is implicated as a primary factor in the decline of 42% of listed threatened and endangered species (Wilcove et al. 1998). While the negative effect on biodiversity is cause for concern, there are also negative economic impacts to consider. One study found that introduced weeds cost the U.S. agriculture industry roughly $27 billion annually in crop damage and cost of removal (Pimental 2005); this cost is passed on to the consumer in rising prices for food and fiber products (Mack et al. 2000). Invaders can negatively impact the structure and function of entire ecosystems by altering fire regimes, nutrient cycling, or hydrology (Mack et al. 2000). One study has linked biotic invasion to declining pollinator populations (Montero-Castano & Vila 2012). The loss of ecosystem services like these are much more difficult to quantify and often become externalities, or costs not reflected in the price of global market goods (Perrings et al. 2005). Although biotic invasion is a global and far-reaching problem, theories of invasion have yet to provide generalizations for effective management and control that can be broadly applied across taxa and continents (Blackburn et al. 2011). Released from geographical or biotic constraints, some invasive species occupy a different realized niche than may be expected from observations of their home range (Beaumont et al. 2009, Broennimann et al. 2007). This lack of theory and predictability makes planning for control or eradication of invasive populations difficult and underlies the significance of this study. Knowledge of the invasive herb sweet fennel, Foeniculum vulgare (Mill.), and the realized niche it occupies on the Eastern Shore of Virginia is needed to inform state-agency management decisions.

Theoretical Framework of Invasion Ecology

Charles Darwin and other early naturalists made observations on interactions between exotic and endemic species, but they could not have foreseen the immense impact exotic species would have on an increasingly globalized world. It was not until Charles Elton wrote The Ecology of Invasions by Animals and Plants in 1958 that the systematic study of invasion was launched. His work remains the most cited source in the field with 1500 citations; a number still increasing by more than 100 a year (Richardson & Pysek 2008) – evidence of how much research has been and still is being devoted to understanding the mechanisms of biotic invasion. As a young but important field of ecology, invasion science faces some criticism that it has failed to provide reliable conclusions regarding the underlying mechanisms of invasion (Davis 2001, Williamson 1999). In one review, 29 different hypotheses regarding drivers for invasion were identified (Catford et al. 2009). This multitude of invasion hypotheses is ascribed to vast differences among taxa and environments being studied (Blackburn et al. 2011) or to the "dissociation" of invasion ecology from other related fields (Davis 2001). Only recently have unified frameworks emerged that seek to reconcile the interactions of biotic, abiotic and anthropogenic influences on the chronological process of biotic invasion (Williamson 1996, Richardson et al. 2000, Catford et al. 2009, Blackburn et al. 2011, Mack et al. 2011).

Most invasion theory recognizes that biotic invasion can be divided into a series of stages. At each stage there are 'barriers' that need to be overcome by the invading organism in order to progress to the next (Blackburn et al. 2011). The first stage is transportation of a species outside of its home range to a new environment, thus overcoming the barrier of geography. The second stage is introduction, in which the organism must escape from cultivation or captivity. The third stage is establishment, during which the challenges of survival and reproduction must be met in order to establish a naturalized population capable of reaching the final stage. In the final stage, the organism overcomes dispersal and environmental barriers in a sequence of establishment events as it spreads across an ever widening range of environmental conditions (Blackburn et al. 2011). It is only in this final stage that an organism should be truly classified as invasive (see the end of this section for a discussion of invasion terminology). It should be noted that, theoretically, species can move back and forth between stages in this framework, and that failure is possible at any stage. There is research to suggest that only a small percentage of the many species transported actually become established, and then only a few of the established species go on to become invasive (Williamson 1996). The observation of what has become known as the ‘tens rule’ has prompted studies, like this one, which attempt to identify the factors driving invasion success.

Since it is unlikely that any single transported individual organism is going to escape cultivation and survive to establish a robust population in a new environment, it is understood that the number of individuals and the temporal frequency of introductions has the potential to drive the success or failure of an invasion. The measure of this introduction effort is called propagule pressure, and it is a composite measure of the number of individuals in any one escape event and the number of discreet escape events (Lockwood et al. 2005). In the context of plant invasions, propagule pressure can be understood as the number and frequency with which seeds or other viable plant materials are introduced into a new environment. As the extent and frequency of human travel and trade intensify, so do incidents of human-mediated transportation of species outside their native range (Catford et al. 2009). The constant background of human mediated transport means propagule pressure can be a continuous process contributing new individuals and genetic material to the newly introduced population. Genetic variation and sufficient number of individuals increase the probability that an introduced population will survive environmental or demographic stochasticity (Lockwood et al. 2005) to become a successfully established species.

Once individuals are introduced to a new home range, their successful establishment is determined by their biotic suitability to the abiotic conditions of the new habitat. This is especially true for sessile organisms, like plants, whose success is greatly reliant upon the chance that they land in suitable habitat. Large scale abiotic conditions such as climate and seasonality can be equally important as micro-site conditions like sunlight and soil moisture for such organisms. Studies of the abiotic conditions that explain invasion success have found that changes in resource availability, such as disturbance, are also important abiotic factors (Catford et al. 2009). Human activities often facilitate disturbance or change natural disturbance patterns in such a way as to make invasion more likely.

Abiotic factors of the environment act in concert with biotic or evolutionary interactions to influence the success of an invasion. Certain biotic conditions of the new habitat have been identified as factors influencing invasion, including open or under-utilized niches and measures of biodiversity (Mack et al. 2000). Biotic interactions between the invader and native species such as competition, grazing, pollination and predation can enhance or limit an invasion. Declining endemic populations, biodiversity loss and climate change are all human mediated conditions that may put the native species assemblage at a disadvantage in biotic interactions. Contrast this disadvantage with the notion that there is likely a set of biotic traits that successful invaders possess that allow them to take full advantage of available resources and outcompete native species. No conclusive set of biotic traits has been found that can reliably predict the success of invasions across all taxa, although some success has been made within groups of species (Mack et al. 2000).

To summarize the theory of invasion and its relevance to this study, it should be noted that establishment is a key phase of the invasion process in which continual propagule pressure can combine with the suitability of the new habitat to increase the probability of successful survival and reproduction. It is also the phase in which the suitability of the potential invader to its new habitat can be observed, and in which biotic interactions between the invader and surrounding species assemblage start to become apparent. Due to the intricacies of policies and regulatory agencies in the United States, an invasive species is usually identified only after it has become successfully established and its negative impact identified (Simberloff 2005). The further along in the invasion process a potential invader proceeds, the more cost of removal increases and the likelihood of successful eradication decreases (Mack et al. 2011). Once an exotic species becomes established, further dispersal may eventually lead to an extensive distribution sometimes with a lag time before the disruptive ‘bust and boom’ cycle of invasion begins (Williamson 1996).

Life History and Ecology of Sweet Fennel

In plant invasions the biotic traits of invaders often overlap with the characteristics of the ‘ideal weed’ as defined by Baker (1974). The geographic definition of invasive as a species outside its presumed home range should not be confused with the biological definition of a weed as a species specialized to establish transient populations in unstable disturbed habitats before dispersing to the next (Williamson 1996). Intrinsic rate of growth, high fecundity, genetic plasticity, abundance and range in native habitat, degree of genetic isolation, and classification as a weed elsewhere are all considered biotic predictors of plant invasion success (Williamson 1996). Sweet fennel belongs to a family of plants called Apiaceae, previously known as Umbelliferae and well known to possess weedy traits (Baker 1974).

The monotypic genus Foeniculum Mill. contains the species F. vulgare Mill. called sweet fennel or common fennel as its specific epithet implies. It is an erect perennial herb, standing in excess of 1-2 m tall with finely dissected leaves and a strong anise scent. Numerous (10-20) stems emerge from a deep taproot each with an array of primary and secondary compound umbels showing small yellow flowers through a long and often variable flowering period (Falzari et al. 2005). The dissected leaves and deep taproot suggest an adaptation to drought and the ability to survive mowing by using stored root resources (Colvin 2002). New stems emerge in the early spring, only palatable to grazers while young and quickly becoming fibrous and strongly anise scented as they mature (Beatty 1991). Allelopathic properties have been supported in experimental studies using vegetative and seed extracts of sweet fennel to slow the germination of other plant species in vitro (Jalali 2013). Once established sweet fennel tends to grow into dense stands (Bell 2008), often displacing endemic grasses and forbs. The phenology of sweet fennel in California is reported as April through June (Beatty 1991, Ogden 2005, Bell 2008), while in northeast Spain it flowers from July through October (Retana 2004), which is a closer approximation to personal observations from Virginia in 2013.

Reproductive capability is density dependent as the height and number of stalks and the number of umbels per stalk varies with plant density; more robust individuals often grow at lower densities (Falzari et al. 2005). The nectarless, protandrous flowers require cross-pollination (Sagar 1981) which is facilitated by a complicated pattern of flower opening (Raven et al. 2005). A dry pollen attracts generalist pollinators to showy displays of tall yellow umbels. The most frequently observed pollinators of sweet fennel in Old World agricultural settings are honeybees and syrphid flies (Chaudhary 2006). While one study has described the the plant as a host for lepidopteran larvae in California (Graves 2003), no other entomological study of sweet fennel in the New World is known at this time. However the exposed style of the sweet fennel flower assures that almost any flower visitor could potentially become a flower pollinator, and thus pollen limitation is unlikely to be a factor limiting wild populations (Bell 1971).

The plant reproduces primarily through prolific production of achene -like fruit that dry while on the stem where they remain into the late fall. The fruits, commonly referred to simply as seeds, are 3-6 mm long and flattened dorsally with acute ribs. They have no morphologies suggesting anemochory (dispersal by wind) or exozoochory (dispersal by external attachment to animals). Local dispersal is on the magnitude of 1-5 meters and occurs when the seed falls from the infructescence (Jongejans & Telenius 2001). The height of the stem, speed of the wind, density of surrounding vegetation and subsequent transfer by birds, rodents and ants are also factors influencing local dispersal (Pulliam 1971, Lacey 1983, Jongejans & Telenius 2001, Lengyel et al. 2010). In Australia sweet fennel has been observed growing along riparian corridors, leading to the hypothesis that its seeds are dispersed by water (Parsons 1973). Coastal plants, mainly halophytes, are thought to disperse seeds by water (Koutstaal et al. 1987) but no direct observation of sweet fennel seeds transported by this mechanism has been published. Seeds of other exotic and weedy species achieve dispersal by roads, getting caught up in roadside mud and attaching to passing vehicles (Von der Lippe 2012), again a phenomena which has not been explicitly demonstrated with sweet fennel.

Like many weedy plants, sweet fennel disperses not only through space but also through time by contributing a portion of seed production to a persistent seed bank. Morpho-physiological dormancy (MPD) of seeds acts to delay germination, broken by a two-step process of embryo development induced by the right environmental conditions (Baskin 1998). Although one study predicts the persistence of sweet fennel seeds in the underground seedbank at less than 5 years (Thompson 1993), other estimates claim 20 years and most likely longer (Torres 1989, 1990). A persistent seedbank allows a plant to overcome environmental stochasticity, minimize seedling death due to less than adequate conditions, and to buffer genetic changes to the population over time (Fenner 1985). In particular, the possibility of a widespread persistent sweet fennel seedbank raises concerns over the potential for new populations to establish in locations where adult growth is not presently observed. A species with high rates of growth like sweet fennel is generally considered a good candidate for successful invasion; however, unless propagules arrive at unoccupied locations with suitable habitat, the population may never reach the invasive stage (Bass et al. 2006).

Previous Studies

Thus far very few ecological studies of sweet fennel have been undertaken, and none have been conducted in North American Atlantic coast maritime communities. Previous studies fall into three categories: those that are not in English (numerous studies originate from India, Egypt, Israel and other countries where sweet fennel is an important industrial crop); those that seek to address increased oil yield, seed priming, pollinator profiles and weed removal in agricultural fields where sweet fennel is the crop plant; and finally there is a small set of ecological studies many of which were conducted on Santa Cruz Island off the coast of California. The agricultural literature has been useful in identifying edaphic conditions that suit sweet fennel (Mangal 1986, Graifenberg 1996, Abou El-Magd 2008). Empirical laboratory experiments to test seed longevity (Torres 1989, 1990) and allelopathic effects (Jalali 2013) provided useful background information on the characteristics of sweet fennel seeds and the nature of important competitive interactions.

On Santa Cruz Island, sweet fennel occurred for over a century before reaching the invasion stage after grazing pressure was lifted following the cessation of sheep ranching and the eradication of feral animals (Beatty 1991, Beatty & Licari 1992). Brenton and Klinger (1994) used state-transition models to reach the conclusion that release from grazing pressure coinciding with a pattern of increased rainfall is the most likely explanation for the sudden expansion of the sweet fennel population on the island. Release from grazing pressure is an alteration to the disturbance regime - one which almost always causes a change in dominance among a community of plants (Crawley 1989). Removal of vertebrate herbivores has been observed to trigger a population explosion in other exotic herbaceous species like Asparagus declinatus L. (Bass et al. 2006). This shift in dominance is predicted to occur more frequently in plant populations which are considered seed-limited (Crawley 1990).

Other studies from Santa Cruz Island investigate biotic interactions between sweet fennel and native species (Crooks 1994, Gibson 2000, Thompson 1988 and 1993); the impact on native plant species recovery (Colvin & Gliessman 2002, Ogden & Rejmanek 2005); and the efficacy of management methods (Bell 2008). Controlled burns resulted in reduced sweet fennel abundance but only to be replaced by other exotic species (Colvin & Gliessman 2002). Studies of restoration sites show success in eradicating adult sweet fennel plants with herbicides and manual root removal, but seedbank presence and an affinity for disturbance require sowing seeds of competitors after removal to improve the effectiveness of those control methods (Ogden 2005, Bell 2008). Many land managers are still using Parson's 1973 observations of sweet fennel invading Australia to guide management decisions, which may or may not be accurate when applied to the North American continent. An exploratory landscape level study of sweet fennel in maritime communities of the Mid-Atlantic coast seems timely and warranted.

Invasive Species Modeling

Multivariate statistical models can be powerful tools for testing the relationship of observed species occurrence to a set of multiple hypotheses for explaining its occurrence and persistence in the landscape. Generalized linear models (GLM's) are a class of multivariate models commonly used by ecologists to model presence-absence and count data. For example, Buckley et al. (2003) were able use a series of GLM's) to draw conclusions about which intrinsic traits and environmental factors influence the invasion of Hypericum perforatum L. in Australia.

Hyperspectral remote sensing and LiDAR imagery has made spatially explicit models possible by providing input surface data for landscape-level environmental variables. Spatially explicit models are especially useful for evaluating space use and species – habitat relationships for sessile organisms in terrestrial environments where focal predictors summarizing the nearby landscape usually account for most resource use (Elith & Leathwick 2009). Bradley & Mustard (2006) used remote sensing data and land use variables to predict the distribution of invasive cheatgrass (Bromus tectorum L.). Mortensen et al. (2009) used a combination of field observations and environmental data from remote sensing imagery to evaluate habitat suitability and the possibility that roads through forests constitute corridors that facilitate dispersal of exotic plants. Similar applications of remote sensing data to model distributions of rare or invasive species are used in numerous other studies, only a few examples of which are mentioned here (Neilson et al. 2011, Porches et al. 2012, Isdell et al. 2015).

It should be noted that there is a distinction between studies which use field observations of the target species to estimate the current distribution and those which use remote sensing imagery to do the same. In the former case, data from relatively few field sampling sites are combined with environmental surface data to extrapolate a model to the entire study area and to either predict occurrence on un-sampled sites or predict habitat suitability on those sites. In the latter case, field observations are not necessary because a more complete estimate of the species distribution can be achieved through the visual detection of the species from imagery or by the systematic classification of pixels matching the spectral signature of an area that has been verified on the ground as the target species. Once the distribution has been defined in this way, conclusions can be drawn by using relevant environmental and land cover datasets in the same way as with models built around field observations. The difference is in the accuracy and precision of the response variable; presumably using the latter method would involve less extrapolation and hence provide better input data for the model. Previous work has shown that it is possible to locate flowering stands of sweet fennel using remote sensing instruments (Dahlin et al. 2008); however use of this approach is predicated on the availability of high resolution hyperspectral imagery flown during the peak flowering period. While aerial imagery and LiDAR data of the study area were available for use in this experiment, this data was gathered during the leaf-off season and hence could not be used to locate sweet fennel populations.

Objectives

The first aim of this study was to examine the distribution of an established plant with the potential to become invasive in upland coastal communities of Virginia's eastern shore peninsula in relation to its occurrence in the underground seedbank. Maritime communities of the Atlantic coast have historically been used for timber and agricultural production; but following a modern shift in land use practices, many coastal areas have a large proportion of early successional patches (Naumann & Young 2007). Land managers of Mid-Atlantic coastal habitats are often concerned with the progress of succession as they attempt to restore land previously under heavy agricultural disturbance regimes back into natural maritime communities. Underground seedbanks are a major source for species recruitment following heavy disturbance (Picket and McDonnel 1989); and there is concern that sweet fennel may dominate the new community and alter succession to desirable climax forest and shrub assemblies. In order to understand the true extent of sweet fennel's distribution and its potential to impact succession following disturbance, the spatial overlap of adult plant growth with underground seeds needed to be better understood.

Hypothesis 1a: The sweet fennel invasion is dispersal limited, such that the colonization of sites currently unoccupied by adult plants depends on the population's ability to disperse to that new location.

If this hypothesis is supported, I predict sweet fennel seeds occur in the underground seedbank at sites where sweet fennel vegetation is also present above-ground. This prediction is based on prior observations that dispersal limitation is more common in early successional species (Turnbull et al. 2000).

Hypothesis 1b: The sweet fennel population is habitat limited, such that the colonization of sites currently unoccupied by adult plants depends on the already present seed's ability to germinate and become established.

If this hypothesis is supported, I predict sweet fennel seeds occur in the underground seedbank at sites regardless of the presence of adult plants above-ground. This prediction is based on weed ecology theory of persistent seedbanks acting as a buffer for local extinctions caused by environmental stochasticity.

In addition, this study aims to narrow down and find the relative importance of anthropogenic, abiotic, and biotic features of the landscape that could be driving the successful invasion of sweet fennel. Oftentimes historical observations of when and where an exotic species first became established can shed light onto dispersal corridors and drivers of population growth when the original extent of the population is compared to the current extent. However, a detailed history of fennel on the eastern shore of Virginia is not well known to current land managers. Herbarium records indicate that sweet fennel was occurring on the western shore of the Chesapeake Bay by 1969; its original introduction was most likely centuries earlier since European colonists found it useful and records indicate that they often brought it along with them to the New World. Lacking temporal information to recreate the spread of the population from original loci, I approached this study by looking for spatial patterns in the current distribution that may be associated with potential drivers of invasion. In order to do this I assume that the current sweet fennel population is a result of the expansion of one or more original population loci into surrounding areas with favorable habitat conditions, the right balance of biotic interactions, and according to the location of potential dispersal corridors.

Hypothesis 2a: The sweet fennel invasion is driven by anthropogenic features, such that occurrence and population density depend on dispersal or habitat disturbance related to human land use and management practices.

Hypothesis 2b: The sweet fennel invasion is driven by abiotic features of the habitat, such that occurrence and population density depend on the suitability of environmental conditions at the sampling site.

Hypothesis 2c: The sweet fennel invasion is driven by biotic interactions, such that occurrence and population density depend on a favorable balance of diversity and competition from the surrounding plant community.

These hypothesis are not mutually exclusive, and the acceptance of any one of them will be based on the spatial correlation of the local sweet fennel population to a spatial variable representing these potential drivers. Factors were chosen for the model based on previous observations of sweet fennel seed dispersal and studies of human mediated propagule transport. Each factor for invasion can affect the response in different ways and at different scales. These different linear, non-linear and scaled relationships of each factor serve as nested hypothesis within each category and serve to further characterize the nature of the relationship between the predictor and response variable, if any. Variable selection of the modeling process is itself a form of hypothesis testing, and so the presence of a variable in the final model will indicate that it serves as a viable hypothesis and plays a role in the current species distribution. I predict that the final model will include variables from each category, as it has been well established that invasions usually result from the additive effects of human activities, habitat suitability and biotic interactions (Richardson et al. 2000, Catford et al. 2009, Blackburn et al. 2011, Mack et al. 2011).The main approaches to the study are field surveys and hypothesis testing with a multivariate statistical analysis to find which combination of explanatory factors best explains the success of sweet fennel invasion. Invasion success was measured by how aggressively the plant was established on a site via field surveys of sweet fennel stem count. Soil samples were also collected from the field and sifted to identify the presence of sweet fennel in the underground seedbank. As a supplement to field surveys to address the probability of detecting seeds in the soil, I conducted two small experimental studies on seed detection in the field and during the soil sifting process. Explanatory variables were developed using GIS software from observations made in the field and spatial data sets. Stem count was modelled as the response to a set of explanatory variables in an effort to test hypotheses about biotic, abiotic and human mediated factors driving its distribution.

Limitations

Because sampling was limited to one summer season, the assumption that the sweet fennel population was in equilibrium is implied in the modeling process but is not likely to be true of invasive populations (Hulme 2003). In the statistical modeling process, a connection between response and predictor at this level of inquiry does not imply a causative effect, rather it points in the right direction to look for causative effects. Sampling was also limited in geographic extent by land access restrictions. Therefore, the extension of results outside of the maritime communities of the Mid-Atlantic coastal region needs to be interpreted with caution.

Delimitations

Detection probability is often a confounding element of species that occur infrequently across a landscape. This study assumes 100% detection probability of adult plant growth, not an unreasonable assumption based upon the conspicuousness stature of sweet fennel in the landscape. Counting stems is a process where some observer error was expected to occur but on a small scale not likely to influence the results of the study. Seed detection is a whole different process confounded by the labor intensive nature of soil seedbank sampling and the tediousness of sifting sandy loam soil to find seeds 3 mm in length. Attempts have been made to find the sampling effort needed to achieve a reasonable assessment of seed presence. Seeds were counted after sifting but I chose not to interpret these results as a reliable measure of seed abundance. Rather, based on results of seed detection testing, seed count greater than 0 was simply considered a measure of seed presence.

There is always a trade-off between how much information can be gathered from any single sampling site, and the total number of sampling sites that can be observed based on time and resources. For this study there was not time to do an extensive survey of biotic interactions at all the sites necessary to achieve a viable minimum sample size, so in the context of this study biotic interactions refers to plant-on-plant competition but does not extend to herbivory, pollination or other potentially important interactions with invertebrate or vertebrate species. These were not observed as part of the sampling process and this study makes no assumptions or conclusions about the relative importance of such interactions to the success of sweet fennel invasion.

Terminology

There are numerous systems of vocabulary for discussion of biotic invasions. For simplicity I will follow the system which correlates to the description of the invasion process given earlier in the chapter (Blackburn et al. 2011). An invasive species is one which is located outside its purported geographical range and is perceived as harmful in their new environment. That definition can easily be confused with those for alien/exotic species, introduced species, established species, and weed species. An alien or exotic species is any species that has overcome the barrier of long distance transport and is located outside its home range. Once an exotic species has escaped captivity/cultivation it can be defined as casual or introduced. The term established implies that an introduced species has managed to survive and reproduce well enough to sustain a wild population outside its home range. The term invasion process refers to the entire set of stages outlined by Blackburn et al.; an alien, introduced, or established species that otherwise would not be referred to as invasive can still be undergoing the invasion process.

The definition of a weedy species exists outside the framework of invasion ecology, and simply refers to any species whose life history strategy is adapted to rapidly colonize open soil resulting from disturbance. Some definitions differentiate between natural and human disturbance, and restrict truly weedy species to those who are reliant on (and as such may have an evolutionary relationship with) anthropogenic activities such as agriculture.

METHODOLOGY

The general purpose of this study was to investigate factors driving the invasion of sweet fennel into coastal habitats of the Eastern Shore of Virginia. The application of this purpose took place in two parts. Because this species has been identified as a weedy species capable of appearing absent above-ground but retaining a potential presence through the persistence of an underground seedbank, the first step in understanding its distribution was comparing the occurrence of adult plants and seeds. Once the true detection probability for the species was established, plots where sweet fennel was recorded absent could be interpreted in terms of habitat or dispersal limitation. Then zero-inflated negative binomial models were applied to identify significant abiotic, biotic and anthropogenic factors driving the success of sweet fennel in the invasion process.

Study Area

The Eastern Shore of Virginia National Wildlife Refuge (ESVNWR) is located on the southernmost portion of Northampton County, Virginia. Situated geographically as the southern tip of the Delmarva Peninsula, forming the eastern border of the Chesapeake Bay, this area is a high priority for conservation of avian migratory habitat. The landscape is characterized by a mosaic of low density urban development, agricultural land use, upland maritime forest and shrub communities, sandy beach along the Chesapeake shoreline and salt marsh forming the Atlantic shoreline. Although human land use has remained primarily agricultural in nature since English colonists first settled the area in the 1600's, there has been a recent increase in subdivision and development of formerly large agricultural parcels in response to increased traffic and tourism enabled by the opening of the Chesapeake Bay Bridge Tunnel in 1969 (ESVNWR Land Protection Plan, 2004).

Biological conservation efforts by ESVNWR are focused on increasing the cover of maritime forest, coastal shrub, grassland, salt marsh and beach habitats that serve as critical stopover habitat for large concentrations of raptors, songbirds, shorebirds and waterfowl. The southern tip area is considered critical to the conservation of both temperate and Neotropical migratory birds by the American Bird Conservancy / National Audubon Society (ESVNWR Land Protection Plan, 2004). There is evidence to suggest that the southern tip is already falling short of providing the food and cover needed to support such large concentrations of migrants (Southern Tip Habitat Meeting Notes, 2013). Conservation goals include acquisition of land for restoration to forest or shrub cover and protecting the structure and function of existing habitat. Changes to the structure and function of ecosystems by invasive plants is of serious concern to land managers in this context, and gives rise to the practical need for this study. The visible presence of fennel along roadways, interspersed in ruderal thickets and occasionally occurring as dense mono-cultural stands suggests it has the potential to displace native vegetation highly valued as stopover habitat.

Field Data Collection

I collected fennel stem counts at each of 155 sites surveyed between May 10th and August 6th 2014. Survey sites were randomly assigned within the study area using ArcMap 10.1 (ESRI 2011), stratified across a gradient of distance to roads and a minimum of 100 m distance from one another. The choice to stratify sampling locations was made to ensure heterogeneity of sampling locations within patches (i.e. to avoid too many samples in edge habitat).

Sites were located in the field using a handheld Garmin CSX 60 GPS unit accurate to ±3 meters. Each sampling point served as the center of a 10 m x 10 m square plot, laid out with corners pointing to the NE, SE, SW and NW with the aid of a compass and forestry tape. Each site was surveyed for plant species composition, species cover and vertical community structure. Species composition includes a list of all woody and herbaceous plant species observed within the plot boundaries; where appropriate, collections of unidentified species were made and kept organized for further identification efforts. Ocular estimates of species cover were recorded in nine cover classes (trace, <1%, 1-2%, 2-5%, 5-10%, 10-25%, 25-50%, 50-75%, 75-100%). When transferring species cover into the data matrix used for modeling, a single value representing the midpoint of these cover classes was input as a cover estimate for each species at each plot. Ocular estimates of vertical community structure were made in much the same way, using six classified height categories. Since vertical structure data were not used as predictors in the modeling process, it was not necessary to create midpoint values for these classes.

In addition, I counted the number of fennel stems present within the plot. Stems were counted instead of individual plants for two reasons: 1) it is difficult to discern individuals within dense patches of stems, 2) stem count is more directly related to whether or not a site is covered by a problematically dense stand than is individual number of plants. Stems are defined as new green growth exceeding 10 cm in height, a distinction made to exclude late germinating seedlings which represent juvenile individuals rather than parts of a reproductive adult plant. I noted the presence of dry mature stems from previous year's growth. This was possible because mature fennel stems often remain standing long after seeds have been released, and are readily distinguishable from new growth. Presence of adult plants within 20 m of the plot's edge in any direction was also recorded. Detection probability of adult stems was assumed to be 1 based on the easily distinguished features of the plant and its prominent stature.

I collected soil samples from 12 systematically randomized locations within each plot. Excessive litter was brushed away from the surface, then a metal soil core tube of 1 cm diameter was pushed 10 cm into the ground, twisted, and carefully removed to retain the soil inside. The subsamples for each plot were mixed and stored in soil collection bags, which were then kept in a cooler (temperature <10° C) until they were returned to the lab and processed. Once in the lab a 15 mL subsample of soil was separated for salinity and pH testing while the remaining ~362 mL were spread on trays until dry enough for sifting. Soil was sifted through a metal screen attached to a wooden frame. A 2 mm mesh size was chosen after testing multiple sizes to find one that would retain all fennel seeds (American Society for Testing and Materials size #10). The seeds and whatever other particles remained in the sifting box after vigorous shaking were then emptied into trays and examined closely for the presence of seeds. The oblong shape, ribs along the long axis of the seed coat, and anise scent of seeds were used to make a positive identification of sweet fennel seeds; very few seeds of other species were collected through this process and those that were observed could be distinguished from sweet fennel by size and shape.

Soil salinity and pH testing took place in the laboratory. Soil subsamples were removed from cool storage (8° C) and mixed with 75mL of distilled water. A drop of this solution applied to the lens of a handheld refractometer was used to assess salinity and a digital handheld pH tester was submerged in the remaining solution for 1 minute to assess acidity.

Seed Detection

Tests for determining detection probability of seeds were conducted in two parts, one to assess the necessary sampling effort required for collection of soil in the field, and another to determine the detection probability of the soil sifting process. Since the top 10cm of soil over the entire plot could not be sampled and sifted due to time and labor constraints, it was necessary to find out how many subsamples were needed to reasonably assess seed occurrence at the site. The location for the field collection test was chosen in a place where false negatives would be unlikely in the extreme, within a managed grassland unit where a moderately dense but quite extensive stand of fennel was growing. Three plots were laid out in the same shape and orientation as described in the prior section. A total of 20 soil core subsamples were collected in sets of four, each set consisting of four 15mL core from along four imagined axes extending outwards from the center of the plot. Each 60 mL set of soil cores was dried, sifted and fennel seeds were counted. The counts were treated cumulatively within each test plot so that the ability to detect seed occurrence within each at 4, 8, 12, 16 and 20 subsamples was afforded (Figure 1). Subsample size was set to the lowest size which detected seeds on all four test plots, including Plot 4 which had a minimal number of adult stems.

In a separate detection experiment, 3 replicates of 4 different seed treatments were prepared by adding fennel seeds to the same volume of sandy loam soil as collected by 12 subsamples. These treatments were sifted and surveyed for fennel seeds as described in the prior section by an observer blind to the treatment number.

Geospatial Data Collection

Explanatory variables were collected from a combination of field observations and available GIS datasets. Biotic factors were observed at the plot level, by field estimation of canopy cover, species cover, invasive plant cover (Appendix A), and soil type. Other plot level biotic factors, like species richness and invasive species richness, were calculated from the species composition list for each plot. Abiotic and anthropogenic variables for the model were gathered from available GIS data sets. Precise elevation data was extracted from a Bare Earth LiDAR digital surface map (CWM-CGA 2013). The coastline and linear water features were identified and hand corrected from public hydrology maps (USGS 2014) then combined with hand-digitized reservoirs and ponds observed from aerial imagery to complete a set of hydrological explanatory variables. A roads layer was locally hand-corrected and buffered to 5m on each side, then converted to binary raster grid format (TIGER 2012). Roads were classified into categories as follows: primary roads (highways), secondary roads (county roads), mostly unpaved rural driveways, and walking trails. Since these road categories experience different levels of vehicular and pedestrian traffic along with different roadside maintenance routines, a different binary raster was made for each so that if the response differs by type of road, it could be detected. Urban development and agricultural fields within the study area were delineated by hand from 2011 aerial imagery and these features were also converted into binary raster files. Moving window analyses of increasing radius from 50m to 1km were performed on all hydrologic, road, developed and agricultural layers in order to create new raster datasets representing the proportion of each variable. Multiple window sizes were used because the scale at which these factors may be acting upon the response could not be determined a priori. The value of each explanatory variable at each of the 155 sample sites was extracted from these raster datasets and used along with field data to build the data matrix for the modeling process. All geospatial data was edited and analyzed in ArcMap 10.1 (ERSI 2012).

Model Fitting

Although generalized linear regression approach with a Poisson distribution is commonly used in analyses of count data, I found the stem count data to be zero-inflated and over-dispersed. A zero-inflated model is built to account for extra zeros in the distribution of the response; specified with a negative binomial distribution it can also accommodate over-dispersion (Zuur 2009). Vuong's test, which provides a likelihood-ratio based statistic to test whether competing models are equally close to the truth (Vuong 1989), was used to determine which distribution was the best fit to the data.

Based on the results of the Vuong's test, I selected a zero-inflated negative binomial model (ZINB). A ZINB is a two-part model which assumes the data can be separated into two groups, the false zeros and the count data which may include zeros (true zeros) and values larger than zero (Zuur 2009). We assumed a binomial distribution for the binary part of the data (false zeros versus all other types of data) and define the probability of measuring a zero so that π_i is the probability that an absence at site i is a false zero (Equation 1). The count data was defined as a function of the mean (μ_i) and a set of explanatory variables – all of which are conditional upon the zero process (Equation 2). The probability functions for the two parts of a ZINB model, as defined by Zuur (2009) are as follows:

$$f(y_i = 0) = \pi_i + (1 - \pi_i) \times \left(\frac{k}{\mu_i + k}\right)^k \qquad \textit{(Equation 1)}$$

$$f(y_i | y_i > 0) = (1 - \pi_i) \times \left(\frac{\Gamma(y_i + k)}{\Gamma(k) \times \Gamma(\pi_i + 1)}\right) \times \left(\frac{k}{\mu_i + k}\right)^k \times \left(1 - \frac{k}{\mu_i + k}\right)^{y_i} \qquad \textit{(Equation 2)}$$

The two part structure of this model provides a framework for testing the hypothesis that presence and absence of adult plants are distinct processes and possibly influenced differently by the same set of explanatory variables (Zuur 2009). Just as in a Poisson GLM, the mean of the count data is modeled in terms of covariates (X) as follows:

$$\mu_i = e^{\alpha+\beta_1 X_1+\cdots+\beta_q X_q} \qquad \textit{(Equation 3)}$$

Like a standard logistic regression with an intercept, the probability of measuring a false zero (π_i) is modeled in terms of a unique set of covariates (Z) as follows:

$$\pi_i = \frac{e^{\upsilon+\gamma_1 Z_1+\cdots+\gamma_q Z_q}}{1+e^{\upsilon+\gamma_1 Z_1+\cdots+\gamma_q Z_q}} \qquad \textit{(Equation 4)}$$

Variable Selection

This section describes how multiple rounds of variable selection defined the unique set of variables for each part of the model. Variable selection for this study was guided by the nested hypotheses underlying the selection of variables in the first place and the additional hypothesis implied by the zero-inflated model structure. The variable selection process necessarily was undertaken in two parts since there was no a priori reason to believe the same set of variables should be used for both the zero and count processes. An Information Theoretic (I-T) approach selected models based on the best combination of fit and complexity; a method suited to testing multiple working hypothesis at one time (Burnham 2011). In each round the univariate or multivariate model with lowest Information Criterion value was retained and carried forward into the next round. Akaike's Information Criteria corrected for small sample sizes (AICc) was used in favor of standard Akaike's Information Criteria (AIC) based on recommendations for small samples sizes.

Categories for explanatory variables (Abiotic, Biotic, Hydrologic, Road, Agriculture or Development) were based on corresponding alternative hypotheses regarding invasion drivers that could be important in describing either the zero or count process. Within each category the amount of space surrounding a sampled site which was covered by the particular variable was tested using a moving window analysis at different circular neighborhood size (50m, 100m, 200m, 500m, 1km) and as either a linear or quadratic relationship. Each of these serve as nested hypotheses about how and at what neighborhood extent these factors may be influencing species occurrence and/or stem count. The purpose of selecting the best univariate model in each category first was to determine which nested variable (i.e. nested hypothesis) best describes the relationship of the response to each category (i.e. primary hypothesis).

Since the count process is conditional upon the zero process, I first set out to identify the best set of explanatory variables for the zero process. I used a standard binary GLM with a logit link function (R package 'stats' version 3.0.1) to narrow down variables within each category to just one per category on the basis that these nested hypotheses are simply different ways that any one factor may be related to the response. It should be noted that variables whose AICc values indicated they failed to explain more variation than the null model were not considered, even if that meant an entire category (factor) would not be represented in the final model. Then I compared all possible multivariate combinations of the best univariate models to find the best combination of covariates for the zero process (R package '*MuMIn*' version 1.12.1).

The best set of variables for explaining the probability of false zeros was then carried forward into the second part of variable selection: selecting covariates to best estimate the count data. I used a ZINB model with logit link function specified for the zero process and a negative binomial distribution and corresponding log link function for the count process (R package "*pscl*" version 1.4.8). The zero process covariates were held constant while variable selection for the count part of the model was undertaken. Again, univariate models were narrowed down to the best one in each category. Then all possible multivariate combinations of the best univariate models from each category were compared and the best combination of covariates for the count process selected.

Pearson correlation coefficients for all covariates were analyzed and certain agriculture and development covariates were found to be correlated (>0.69) with each other and with the covariate for latitude. Based on the linearity of the study area along a north-south axis, there was a priori reason to believe that latitude was an important covariate in the logistic portion of the model. The best combination of agriculture and development variables were chosen which both 1) had an AICc value lower than the null model and 2) were free of correlation to latitude. There was less reason to believe latitude important for the count process, so latitude was left out in the second case in favor of a pair of independent agriculture and development variables with lower AICc values.

Model Averaging

The best combination of zero process covariates and count process covariates were combined into one final ZIMB model. Using the dredge function one more time, all possible combinations of the best set of candidate models were compared by AICc and Akaike weights (w_i). Akaike weights (w_i) quantify the plausibility of each candidate model as being the best model (Symonds and Moussalli 2010). Model averaged coefficients were used in final model equation to spatially apply the results and are interpreted as partial regression coefficients (β values) for the optimized ZINB model.

FINDINGS

Field Observations

Within the study area, sweet fennel was observed growing predominantly on previously disturbed sites where weedy species are common and canopy cover is minimal. It appears to be patchily distributed in some areas more than others, occurring in clustered stands of variable density that reoccur on the same sites from year to year. Adult plants (i.e. stems) were observed at 34% of sites surveyed (n=155). Stem counts range from 3 to 950 and average 166.21 stems per plot (SD = 184.26). A map showing the location of sample sites with graduated symbols representing the stem count illustrates these findings (Figure 2). Of the 52 plots occupied by stems, almost all of them (92.5%) were adjacent to areas with more adult growth and many (87%) showed evidence of previous years' growth.

Seeds were observed at 19% of the sites, all of which were also occupied by adult plants (Table 1). The average stem density on plots where seeds were detected (19.42 ± 4.21 stems/m^2) is less than the average stem density on plots where no seeds were found (42.89 ± 16.42 stems/m^2) therefore seed detection does not appear to be dependent on the density of adult stems.

The detection probability of the seed sifting process was equal to 1 based on the results of the sifting test (n= 12) which revealed that only a negligible number of seeds were missed (2.69%), and seed presence was correctly identified in all samples (Figure 3). Since I can be reasonably sure that if an underground seedbank was present that it would be detected, and because none of the plots contained only seeds (Table 1), these results support the hypothesis that the sweet fennel population is dispersal limited.

Zero-inflated Modeling

Soil type did not vary much among sites, with the majority of sites (80.6%) on sandy loam soil with a few exceptions where less well drained wetland soils were encountered. Soil salinity was observed to be low at all sites surveyed (0-5 ppT) and soil pH ranged from 5.5 to 7, which does not exceed the range within which sweet fennel has been observed to occur (Simon, as cited in Colvin 2002). Although edaphic factors probably contribute to the distribution of sweet fennel, it was concluded that not enough variation exists within the study site to evaluate that relationship and these variables were not used in the modeling process.

The Vuong's test suggested the zero-inflated negative binomial model (ZINB) is an improvement over a standard negative binomial GLM ($Z = 2.90$) and over models with Poisson distributions whether zero-inflated ($Z = 4.45$) or standard ($Z = 9.13$). Based on the statistical evidence and supporting ecological theory to explain the zero process implied by the model structure, I chose to move forward with a zero-inflated negative binomial mixture model (ZINB) as the best fit for the data. The results of the model averaging procedure produced one top model carrying more than half of the 'evidence' for being the best model, but in most cases there is information in the second, third, fourth, etc. models that is missed by the single best model (Burnham et al. 2011). In order to capture that information I took the 6 candidate models included in the 95% confidence set (Burnham & Anderson 2012) to create model averaged estimates of the partial regression coefficients describing each variable (Table 2).

Variable selection narrowed down 45 potential explanatory variables (Appendix B) into two unique sets of explanatory variables for the zero and count portions of the final ZINB model. Model averaged estimates accompanied by adjusted standard errors and 90% confidence intervals are reported for each variable included in the optimal ZINB model (Table 3). The final set of variables describing the zero process did not include development or hydrologic variables, therefore these factors are not considered important for explaining the probability of false zeros. Of the 4 variables identified as having a positive effect on the probability of measuring a false zero, distance to agriculture was the strongest ($\beta = 4.72$) followed by latitude ($\beta = 1.95$), canopy cover ($\beta = 1.60$), and the distance to busy roads ($\beta = -1.50$) – an effect which decays as distance increases. In contrast, the final set of variables describing the count process did not include roads, agriculture or hydrologic variables so these factors are not considered important for explaining stem count. Among the 3 variables that were included, distance to developed areas had the strongest effect on stem count ($\beta = 1.86$). Distance to the coast was also a positive relationship ($\beta = 0.79$). The percentage of Morella shrub cover shows a slight negative relationship ($\beta = -.302$) with stem count however a complete spatial dataset for Morella shrub cover was not available and so this variable could not be included in the spatial application of the model. The following is the final equation used to spatially apply the statistical results:

Mean Stem Count = (1 / (1 + Exp(1.56 + 4.72 * "agdist" + 1.6081 * "cancov" + 1.9596 * "latitude" + (- 1.5016 * Exp("busyrds" / -10))))) * (Exp(4.9249 + 0.1416 + .7900 * "coast" + 1.8656 * "devdist"))

(*Equation 5)*

DISCUSSION

This study is the first to address the invasion ecology of sweet fennel in the Mid-Atlantic coastal plain. The spatial extent of sweet fennel in the study area is most likely limited by seed dispersal, rather than habitat suitability. Long-distance dispersal is the final barrier to invasion that separates established species from invasive species, and so it was necessary to investigate the possibility that propagule pressure in this study area was high and that seeds may be distributed in a pattern that reveals their origin or mode of transportation (i.e. along roadsides). However, field observations indicate that sweet fennel seeds are not widespread or frequent in the seedbank except at sites where adult growth was also present, implying the seeds did not travel far from the parent plant. Seeds occur only in plots that also have adult growth, a pattern matching predictions of the dispersal limitation hypothesis described in the introduction. This also consistent with the lack of morphological seed adaptations for long-distance dispersal (Bell 1971), seed rain distributions in other umbelliferous species (Lacey 1980), and sweet fennel population expansion on Santa Cruz Island (Beatty & Licari 1992). A review of seed-sowing experiments found dispersal limitation occurs more frequently among early successional species and in early successional habitats (Turnbull et al. 2000).

This is good news for land managers; it means that areas being newly restored to natural habitats are not likely to already have sweet fennel present. If the plant is indeed a slow spreading clustered population currently being blocked from reaching its full distribution potential by its predominantly short-distance seed dispersal system - then management action aimed at preventing long distance dispersal events from turning into established stands should confine the invader to its current extent. These findings reaffirm the efficacy of management actions aimed at addressing potentially invasive species before they become established (Pimentel 2005, Blackburn et al. 2011).

Sweet fennel was observed growing predominantly on open canopy sites alongside other early successional, weedy and colonizing species. The ZINB models demonstrate how the mean predicted stem count decreases with increasing canopy cover. Observations from California of sweet fennel's inability to invade closed canopy shrub communities (Beatty & Licari 1992) and reaffirmed by this study, which observed relatively few adult plants growing in even partial shade and none growing under forest canopy. However, once fennel is established stand density is inversely related to the cover of endemic bayberry shrubs (Morella spp). Sweet fennel and Morella shrubs compete for the same space in open woodlands and fields with well-drained sandy soil, but it remains unclear which one has the competitive advantage and causation should not be assumed without further information. Either way, the invasive perennial herb is occupying space that endemic shrubs are now excluded from and hence has the potential to threaten regeneration of climax coastal shrub communities. These bayberry shrub communities are the primary goal of local land managers who value Morella species for their benefit as songbird habitat and nitrogen fixers. Future studies to elucidate what effect, if any, that sweet fennel is having on these important successional habitats for songbirds.

The potential for further spread and the suitability of unoccupied habitat is addressed directly by the second set of hypotheses presented by this study. As predicted, model results indicate that the sweet fennel invasion is being driven by a complex combination of anthropogenic, abiotic and biotic interactions. All three of the most prominent anthropogenic features on the landscape were included as significant factors in the final model – agriculture, roads and development. Freshwater hydrologic variables did not perform well in the modeling process and were not included in the final model set, even though observations of sweet fennel growing along riparian corridors in

Australia suggest dispersal by water (Parsons 1973). It may be that water is simply a more valuable resource for determining habitat suitability in more arid climates like Australia and California, but that the low elevation and higher rates of precipitation in the Mid-Atlantic make water less of a limiting factor.

As the distance to agriculture increases so does the probability that an unoccupied site is potentially good habitat. At first glance this could be interpreted as an indication that agriculture has an overall negative effect on sweet fennel, which may be contrary to the usual association of cropland with fragmentation that encourages invaders (Stohlgren et al. 2006). At the regional scale, fragmentation of natural habitats into a complex landscape matrix may encourage invasion (Brothers & Spingarn 1992, Zimmerman et al. 1993) but on the local scale the effect may be due to the environment within and around the edge of the field. One recent study found that cropland actually impedes the invasion of honeysuckle (Lonicera japonica Thunb.) possibly by providing a barrier to seed dispersal or by providing a land cover that is unlikely to be traversed by animals carrying seeds (Gorchov 2014). Herbicide application and the tree canopy often left standing adjacent to fields could create poor habitat conditions for sweet fennel.

Like agricultural fields, urban development is often associated with the general effects of fragmentation that lead to an increase in invasive species. Again, on a smaller scale that trend seems to be reversed. The model results show that as the distance to developed land cover increases the predicted stem count also increases. Intermediate forms of disturbance like mowing, weeding and herbicide treatments may also be responsible for this relationship.

Sweet fennel is well known for occupying waste places and roadsides, along which weedy species are often prevalent (Greenberg et al. 1997, Christen and Matlock

2006). The relationship of sweet fennel to roads is described by a negative decay function which predicts the probability of suitable habitat declines sharply outside of 10 m from the road. Dispersal by vehicles traveling along roads has been suggested as an explanation for this common pattern (Schmidt 1989, Gelbard & Belnap 2003), and supported in some cases where seeds were physically collected (Von der Lippe 2012). If dispersal was the explanation for the significance of roads then I would expect fennel to be more strongly correlated to higher traffic roads like Highway 13 than the low traffic county roads represented by the variable included the final model. The stronger relationship with lower traffic roads could be related to the level of roadside management along those roads; infrequent mowing of narrow berms (1-2 m) is an intermediate disturbance compared to the regularly trimmed berms more than twice as wide (5-10 m) found along high traffic secondary roads like Highway 13. I conclude that the inclusion of this roads variable indicates the importance of disturbance associated with the road for creating suitable habitat rather than the potential for facilitating dispersal. Harrison et al. (2002) reached the same conclusion while tracking herbaceous invasive populations on a peninsular refuge in California.

Spatial patterns show sweet fennel is most dense on the southernmost tip of the peninsula and modeling results indicate that as latitude and distance to the coast increase so does the potential for good habitat that is yet unoccupied. Although elevation was not an important abiotic variable in the ZINB model, distance to the coast was included and may have an indirect interaction with elevation because the topography of the landscape changes. As the peninsula narrows and topography flattens towards the southernmost tip there is increased maritime influence and the habitat is characterized by exposure to more wind, salt spray and storm inundation (Sorrie & Weakley 2001). On the other hand, as the peninsula rises from sea level into a flattened central ridge that widens northward the land is protected from heavy maritime influence.

Commonly included in spatial models, latitude can be an indirect measure of conditions that may affect habitat suitability for plant populations over large extents (Guisan 2000, Austin 2002). Disjunct South-Atlantic plant species do occur on the extreme southern tip of the Delmarva (Stalter & Lamont 2000), an indication the area is somewhat distinct from the northern peninsula, but sweet fennel has been observed as far north as Canada and is certainly not constrained to the southern Atlantic region (USDA Plants Map). The relatively small size of the study area and the wide range of climactic conditions under which sweet fennel can survive makes climactic variation an unlikely explanation here. An alternate explanation is reached by considering latitude as an anthropogenic factor indirectly representing differences in historical land use between the wildlife refuge and areas to the north. Heavy disturbance associated with former military land use could have been keeping the sweet fennel population in check on what is now the wildlife refuge in the same way that heavy grazing pressure may have been suppressing sweet fennel on Santa Cruz Island (Beatty & Licari 1992). The heavy disturbance regime on the former military land is not consistent with the traditional agricultural land use of surrounding areas and may explain latitude as an indirect representation of human disturbance patterns.

While this model does not address the cause behind the correlation of the response with predictors, it does indicate that the central upland flats of this peninsula are more suitable habitat for sweet fennel than the wooded wetlands, maritime forest and salt marsh directly along the coast. The southernmost tip and central upland ridge are also the areas of heaviest anthropogenic activity on the peninsula, which may be an indirect explanation for the increasing probability of measuring a false zero as the distance to the coast and latitude increase. As the map of habitat suitability (Figure 2) suggests, this sweet fennel population will likely spread north along that upland ridge where suitable environmental conditions and the right amount of anthropogenic disturbance could provide the perfect opportunity to colonize new sites.

This study is only the first step in understanding the invasion of sweet fennel into coastal habitats of Virginia's eastern shore. Observations of the sweet fennel population and its seed limitation seem to indicate the population has not yet come into equilibrium in its new range and is most likely still spreading. Further spread and development into a full blown invasion is currently limited by the plant's ability to disperse and the location of suitable habitat most likely associated with the right combination of human disturbance. Both maps seem to be indicating an area just north of the refuge that is at risk for future invasion. I recommend land managers monitor this area and the roadways leading from the current invasion loci towards this location for new sweet fennel growth. Expedient removal of the pest species before a robust stand develops is most likely the best way to protect new acquisitions.

Table 1: Comparison of stem and seed occurrence. The percentage of total plots sampled for each possible combination of the two factors is given, with totals, in the table below.

		Stems		
		Present	*Absent*	Totals:
Seeds	*Present*	19.36%	0.00%	19.36%
	Absent	14.84%	65.80%	80.64%
	Totals:	34.20%	65.80%	

Table 2: The 95% confidence set of candidate models used for model averaging of partial regression coefficients for final interpretation.

MODEL	r^2	*K*	***logLik***	***AICc***	***ΔAICc***	w_i
baycov + coast + dev_dist | ag_dist + busy_d_10m + cancov + UTM_Y	0.44	10	-361.8830	745.4715	0.0000	0.67
coast + dev_dist | ag_dist + busy_d_10m + cancov + UTM_Y	0.42	9	-364.0538	747.4923	2.0208	0.24
baycov + dev_dist | ag_dist + busy_d_10m + cancov + UTM_Y	0.40	9	-366.4081	752.2008	6.7292	0.02
baycov + coast + dev_dist | busy_d_10m + cancov + UTM_Y	0.40	9	-366.4203	752.2252	6.7537	0.02
dev_dist | ag_dist + busy_d_10m + cancov + UTM_Y	0.39	8	-367.7309	752.5609	7.0894	0.02
coast | ag_dist + busy_d_10m + cancov + UTM_Y	0.39	8	-367.7966	752.6924	7.2209	0.02

Table 3: Model averaged regression coefficients, standard errors and confidence intervals for all variables included in both parts of the final ZINB model. Variables were centered and scaled to make β estimates directly comparable. The first column contains corresponding common names for each variable (Appendix B).

Model Averaged Coefficients				*90% CI's*		
	Covariate	**β**	**SE**	**Lower**	**Upper**	**Wt_{VAR}**
Intercept (Count)	count_Intercept	4.9249	0.24	4.53	5.32	1.00
Bayberry Shrub Cover	count_baycov	-0.3026	0.14	-0.73	-0.11	0.72
Distance to Coast	count_coast	0.7900	0.25	0.39	1.26	0.96
Distance to Urban	count_dev_dist	1.8656	0.61	0.87	2.93	0.98
Intercept (Zero)	zero_Intercept	1.5581	0.66	0.45	2.67	1.00
Distance to Agriculture	zero_ag_dist	4.7235	1.80	1.80	7.87	1.00
Decay Distance to Roads	zero_busy_d_10m	-1.5016	0.48	-2.30	-0.70	1.00
Canopy Cover	zero_cancov	1.6081	0.44	0.93	2.29	1.00
Latitude	zero_UTM_Y	1.9596	0.56	1.09	2.83	1.00

Figure 1: A graph of the results of tests for seed detection in the field for all 4 test plots. It is only with 12 or more subsamples that false absences were avoided in all test plots, which is how soil sampling effort for field surveys was chosen.

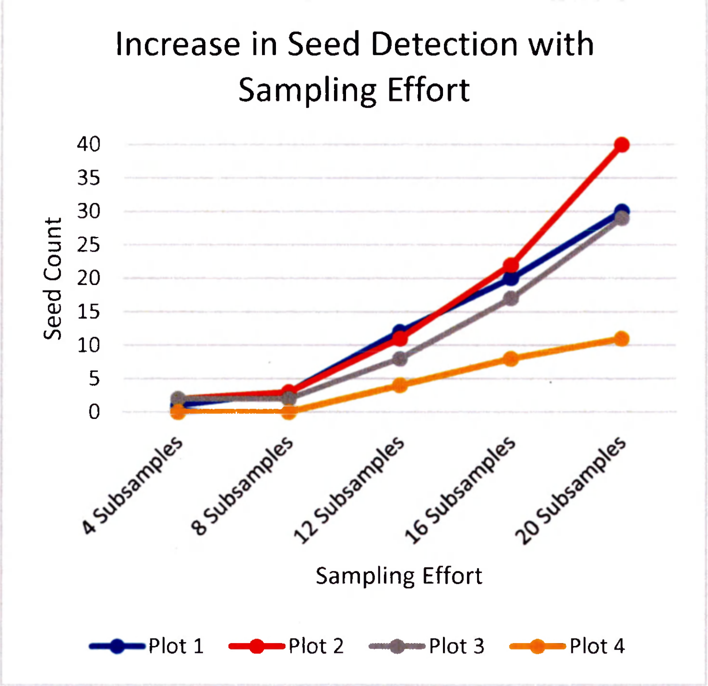


Figure 2: A map of the central portion of the peninsula, showing sampling sites for 2014 (n = 141). The legend shows graduated symbols representing increasing count values. Count values are defined as the number of sweet fennel stems within a 10 m x 10 m plot (stems / 100 m^2). Green areas are forest cover, grey is urban development and the lines cover agricultural fields.

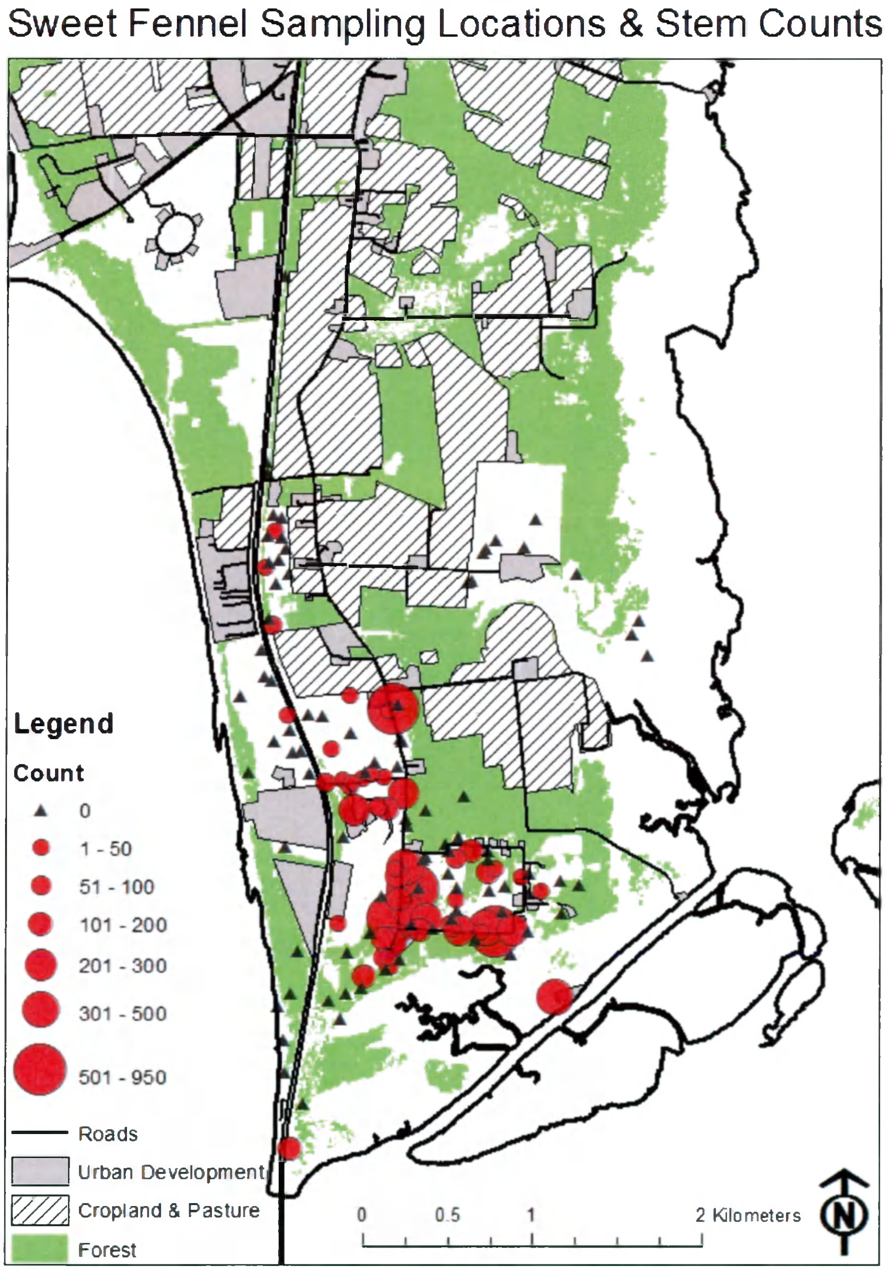


Figure 3: A graph of the results from tests for seed detection during the soil sifting process. Seeds were added to soil in 4 amounts (treatments) and compared to the number of seeds found. Less than 3% of seeds went unnoticed, indicating detection probability for the soil sifting process was high and unlikely to generate false negatives.

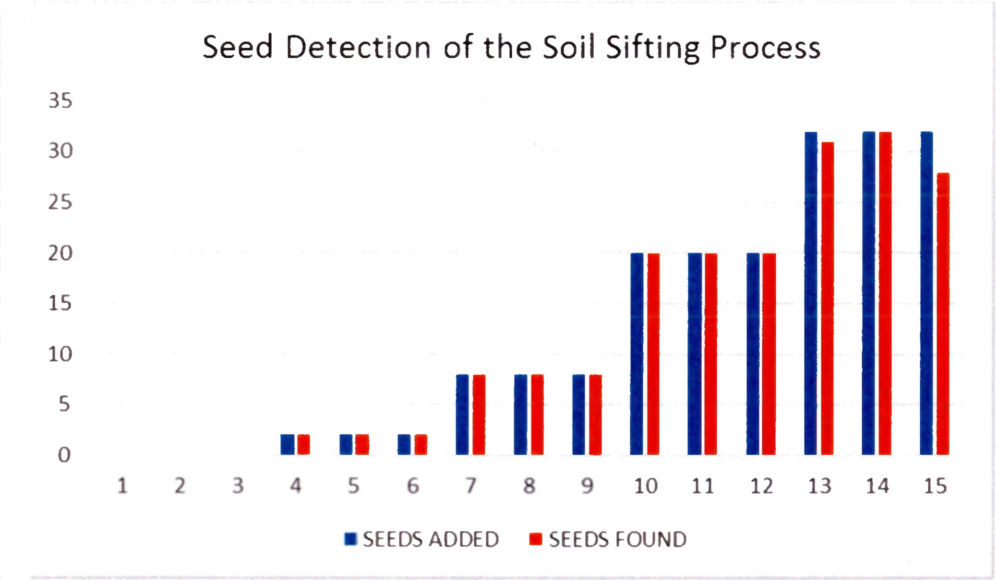


Figure 4: This map is the spatial application of the zero process to the central portion of the study area. Increasing probability of good habitat as the color fades from green to red. Urban and agricultural features are also shown.

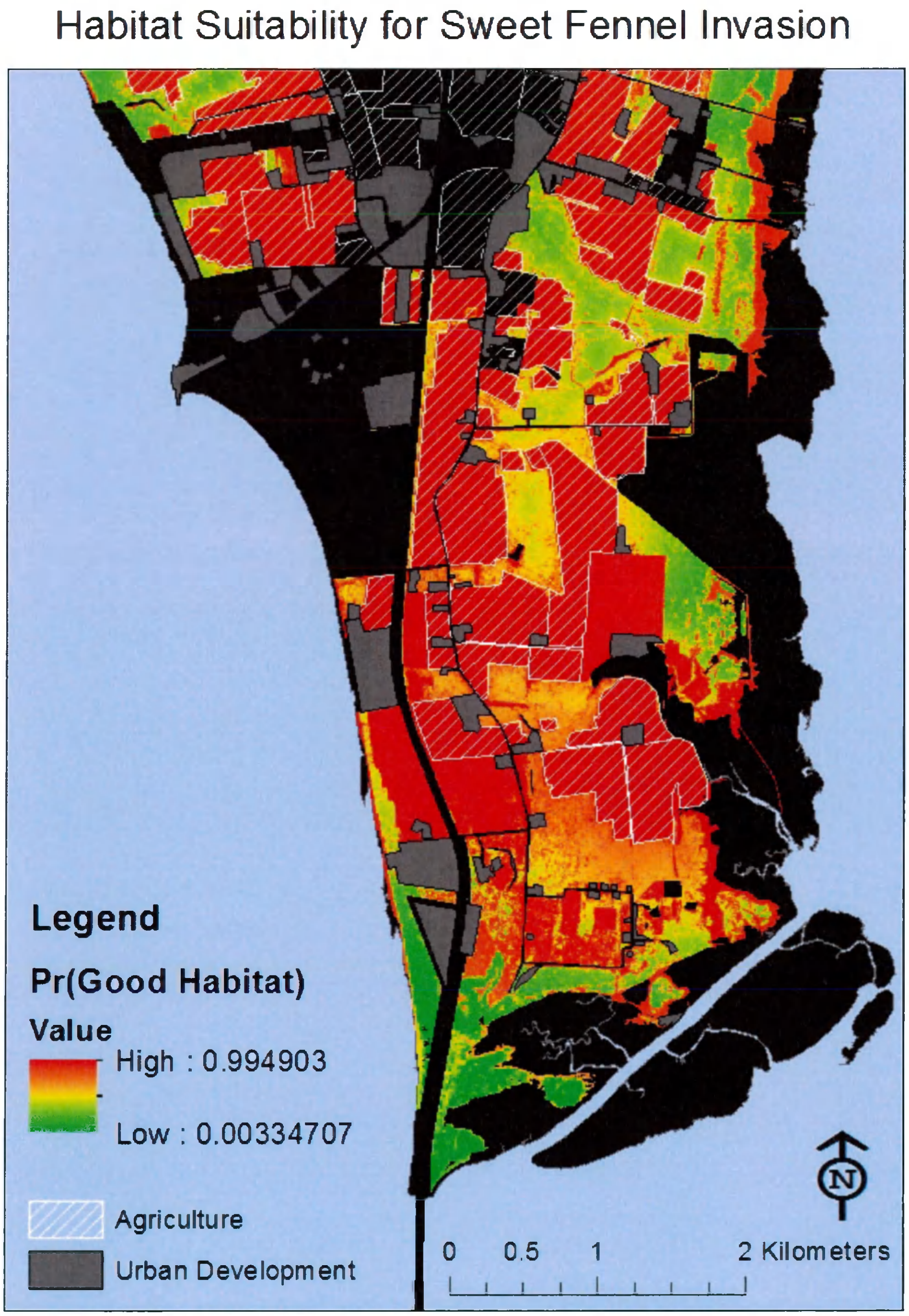
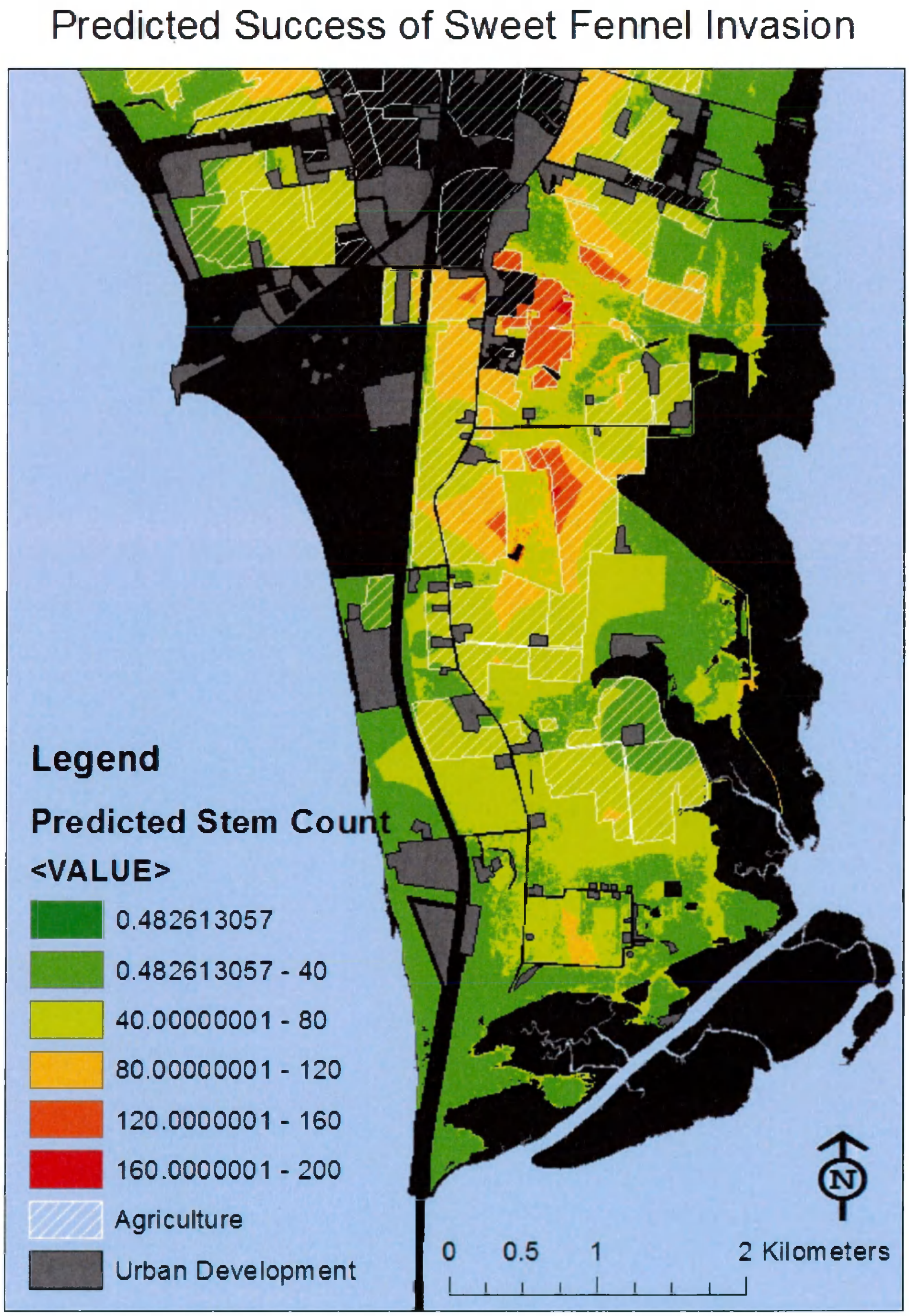


Figure 5: This map is a spatial application of the count process to the central portion of the study area. Increasing predicted mean stem count as the color fades from green to red. Urban and agricultural features are also shown.



Appendix A: Priority list of invasive species provided by ESVNWR staff and used to classify species found in field surveys as invasive or otherwise.

Common Name	Scientific Name
Chinese tree-of-heaven	Ailanthus altissima (Mill.)
thistle	Cirsium vulgare (Savi)
Russian olive	Elaeagnus angustifolia (L.)
Autumn olive	Elaeagnus umbellata (Thunb.)
weeping lovegrass	Erogrostis curvala (Shrad.)
privet	Ligustrum spp (L.)
Japanese honeysuckle	Lonicera japonica (Thunb.)
common reed	Phragmites australis (Cav.)
kudzu	Pueraria montana (Lour.) var. lobata (Willd.)
Callery pear	Pyrus calleryana (Decne.)
multiflora rose	Rosa multiflora (Thunb.)
wisteria	Wisteria sinensis (Sims)

Appendix B: List of all 45 explanatory variables hypothesized to affect either the zero or count process.
A value of "na" indicates that the model did not converge.

Category	Variable	Description	Units	AICc_Zero	AICc_Count
Roads	busy_d_10m	Decay distance to busy roads at 10m scale	meters	***162.87***	***829.32***
	busy_d_5m	Decay distance to busy roads at 5m scale	meters	***163.50***	***830.32***
	busy	Euclidean distance to busy roads	meters	***168.59***	***825.09***
	rds_25m	Proportion of road cover within 25m radius of plot	count	***172.97***	***830.41***
	allrds_d_10m	Decay distance to all roads and walkways at 10m scale	meters	***174.27***	***830.43***
	hwy13	Euclidean distance to primary hwy	meters	***174.79***	na
	walk	Euclidean distance to walking paths	meters	***179.42***	830.19
	allrds_EucDist	Euclidean distance to all roads and walkways	meters	***179.46***	***825.64***
	allrds_d_5m	Decay distance to all roads and walkways at 5m scale	meters	***180.54***	***830.80***
	hwy13_d_10m	Decay distance to primary hwy at 10m scale	meters	***185.07***	830.98
	hwy13_d_5m	Decay distance to primary hwy at 5m scale	meters	***185.68***	830.98
	rds_50m	Proportion of road cover within 50m radius of plot	count	***186.26***	830.97
	walk_d_5m	Decay distance to walking paths at 5m scale	meters	***187.09***	830.98
	walk_d_10m	Decay distance to walking paths at 10m scale	meters	***187.26***	830.98
	rds_200m	Proportion of road cover within 200m radius of plot	count	***188.37***	***828.27***
	rds_500m	Proportion of road cover within 500m radius of plot	count	***188.87***	***828.12***
	rds_100m	Proportion of road cover within 100m radius of plot	count	188.90	***830.29***
Agriculture	agr_500m	Proportion of agricultural cover within 500m radius of plot	count	***178.19***	***826.76***
	agr_1km	Proportion of agricultural cover within 1km radius of plot	count	***179.98***	827.31
	agr_200m	Proportion of agricultural cover within 200m radius of plot	count	***182.82***	***825.60***
	ag_d_10m	Decay distance to agricultural fields at 10m scale	meters	***185.11***	***830.46***
	ag_dist	Euclidean distance to agricultural fields	meters	***185.47***	na
	agr_100m	Proportion of agricultural cover within 100m radius of plot	count	***185.71***	826.96
	ag_d_5m	Decay distance to agricultural fields at 5m scale	meters	***186.65***	***830.58***
Development	dev_d_5m	Decay distance to developed areas at 5m scale	meters	***184.44***	na
	dev_d_10m	Decay distance to developed areas at 10m scale	meters	***184.64***	***825.08***
	dev_dist	Euclidean distance to developed areas	meters	***186.39***	***828.10***
	dev_1km	Proportion of development cover within 1km radius of plot	count	***186.86***	830.97
	dev_100m	Proportion of development cover within 100m radius of plot	count	***188.12***	***830.46***
	dev_sq	Quadratic relationship to development		***188.71***	***830.39***
	dev_200m	Proportion of development cover within 200m radius of plot	count	***188.78***	830.98
	dev_500m	Proportion of development cover within 500m radius of plot	count	***188.81***	***829.98***
Hydrology	coast	Euclidean distance to coastline	meters	***178.14***	825.32
	coast_sq	Quadratic relationship to coastline	meters	***181.36***	***826.51***
	wtr_100m	Proportion of water within 100m radius of plot	count	***182.32***	830.91
	coast_d_10m	Decay distance to coastline at 10m scale	meters	***184.64***	na
	wtr_200m	Proportion of water cover within 200m radius of plot	count	***185.18***	830.92
	coast_d_5m	Decay distance to coastline at 5m scale	meters	***185.38***	na
	allwtr_d_10m	Decay distance to all water at 10m scale	meters	***186.37***	na
	allwtr_d_5m	Decay distance to all water at 5m scale	meters	***187.36***	***828.89***
	strm_d_10m	Decay distance to streams at 10m scale	meters	***188.57***	***829.93***
	all_wtr	Euclidean distance to coastline, stream or inland waterbody	meters	***188.75***	830.98
	strm_d_5m	Decay distance to streams at 5m scale	meters	***188.83***	830.21
	streams	Euclidean distance to streams	meters	***188.89***	830.95
	wtr_500m	Proportion of water cover within 500m radius of plot	count	188.90	***830.59***
Biotic	cancov	Canopy Cover observed (>5m)	%	***168.33***	na
	sprich	Species Richness	count	***186.95***	830.97
	invcov	Cover of invasive plants (See Appendix)	%	***187.71***	830.75
	invrich	Invasive Species Richness	count	***188.04***	830.96
	baycov	Cover of *M. pensylvanica* and *M. cerifera* observed	%	***188.52***	***830.84***
	herbcov	Cover of Herbaceous Plants	%	***188.55***	na
	shrubcov	Total shrub cover observed	%	***188.76***	***830.37***
Abiotic	UTM_Y	Latitude	meters	***179.77***	***822.25***
	elev	Elevation	meters	***188.68***	***830.49***
	UTM_X	Longitude	meters	***188.85***	830.98

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VITA

It appears the species is in the establishment stage of invasion, a prime target for management control before the invasion proceeds too far. I will use a combination of field studies and spatial modelling techniques to investigate the potential dispersal pathways and habitat characteristics associated with fennel establishment. I hope that my high resolution spatial analysis will provide insight into the establishment phase of the invasion process, characterize the invasion of this species and aid in the future management of coastal habitats.