DISSERTATION

EARLY DETECTION AND RAPID ASSESSMENT OF INVASIVE ORGANISMS UNDER GLOBAL CLIMATE CHANGE

Submitted by

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY TRACY R. HOLCOMBE ENTITLED EARLY DETECTION AND RAPID ASSESSMENT OF INVASIVE ORGANISMS: GLOBAL CLIMATE CHANGE, ANOTHER PERSPECTIVE BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

EARLY DETECTION AND RAPID ASSESSMENT OF INVASIVE ORGANISMS: GLOBAL CLIMATE CHANGE, ANOTHER PERSPECTIVE

Invasive species alter native species assemblages, effect ecosystem processes, and threaten biodiversity worldwide. Early detection and rapid assessment will help stem the problem, focusing managers attention on newly established invasive species before they spread. This is a big task requiring a coordinated effort and a centralized data sharing effort. One tool that can be used in this effort is Geographic Information Systems (GIS). GIS can be used to create potential distribution maps for all manner of taxa, including plants, animals, and diseases, and may perform well in early detection and rapid assessment of invasive species. As an example application, I created maps of potential spread of the cane toad (*Bufo marinus*) in the southeastern United States at an 8-digit Hydrologic Unit Code (HUC) level using regression and environmental envelope techniques. Equipped with this potential map, resource managers can target field surveys to areas most vulnerable to invasion.

However, there is a general need in invasive species research to quantify the potential habitat of many invasive plant species. I was interested in modeling the shifts in suitable habitat over time, environmental space, and climate change. I used 4-km^2 climate scenarios projected to the years 2020 and 2035 for the continental United States, to examine potential invasive species habitat distributions. I used maximum entropy modeling (Maxent) to create three models for 12 invasive plant species: (1) current potential habitat suitability; (2) potential habitat suitability in 2020; and (3) potential habitat suitability in 2035. These models showed areas where habitat suitability remains stable, increases, or decreases with climate change. Area under the receiver operating characteristic curve (AUC) values for the models ranged from 0.92 for *Pennisetum ciliare* to 0.70 for *Lonicera japonica*, with 10 of the 12 being above 0.83 suggesting strong and predictable species-environment matching. Change in area between the current potential habitat and the year 2035 ranged from a potential habitat loss of about 217,000 km^2 for *Cirsium arvense*, to a potential habitat gain of about 133,000 km^2 for *Microstegium vimineum*. These results have important implications for developing a triage approach to invasive species management under varying rates of climate change.

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Introduction to the Dissertation

Invasive species alter native species assemblages (Stohlgren et al. 2008), effect ecosystem processes (Loreau et al. 2001), and threaten biodiversity worldwide (Wilcove et al. 1998). Invasive plants threaten native species, habitats, and ecological systems. Their ability to compete and displace native species alters hydrologic and nutrient cycles, and changes fire and other disturbance regimes. They crowd out native species and can be very dominant in systems where they are adventive.

As trade and travel increase, so do the opportunities for new invasions (Hodkinson and Thompson 1997, Mack and Lonsdale 2001). Early detection of invasive species is important to keep these invasions to a minimum (Moody and Mack 1988, Rejmanek and Pitcairn 2002). If we are aware of new invasions, we can quickly set priorities for containment and control (Byers et al. 2002). Awareness plays a vital role in slowing the spread of invasive species. In the United States, land managers do not know what species have invaded in their neighboring management systems (Crosier and Stohlgren 2004). This is a large issue that can only be approached with a centralized planning effort and the capability to share and manage invasive species information.

The issue of invasive species is compounded by climate change. It remains unclear what will happen to the habitat distribution of species as the climate changes worldwide (Marshall et al. 2008). Habitats themselves will be shifting; it follows that the species that live in those climates will move with them. It is expected that some species distributions will spread and increase while others may contract, or not spread at all (Bradley et al. 2009).

With this dissertation I addressed the question of early detection and rapid assessment. With the first chapter on detection and early warning of invasive species, I addressed the need to develop a centralized consensus model for early detection and rapid assessment. Invasive species are a large issue that requires a well executed centralized plan of action. I specifically addressed data collection, data sharing, and centralized databases on the internet.

With chapter two, I discussed how Geographic Information Systems (GIS) can be used to assist with the early detection of invasive species. In the past, a simple display of the data was considered a very useful tool. As computing power increased over the years, our ability to utilize computer models has improved. In addition to an overview of the use of GIS in early detection, I compared two models of *Bufo marinus* (cane toad) habitat in the southwestern United States as a first approximation of how far this species may spread. These models were at a very coarse 8-digit Hydrologic Unit Code scale, but they provided a preliminary map of species habitat in the southwest.

The third chapter of this dissertation addressed habitat suitability on a finer scale, covering the continental United States. I examined 12 invasive plants, determining their current suitable habitat using Climate Envelope Models ((Hijmans and Graham 2006). I used these same models to analyze how the habitat of these species will change with climate change in the near term. This provided an initial model at a management scale, using climate change to examine the leading and trailing edges of the invasion.

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Chapter 1: Detection/Early Warning

Introduction

It is well known that invasive species are a problem of epidemic proportions around the world, causing economic losses of up to $120 billion per year in the USA alone (Pimentel *et al.* 2005). As trade and travel across international boundaries increase, so do invasions (Mack and Lonsdale 2001). Early detection and rapid response are effective strategies to minimize the impacts that invasive species have on economies and on ecosystems that they invade (Rejmanek and Pitcairn 2002). Because the task of invasive species control can sometimes be daunting, managers need to be able to set priorities for prevention and control of these organisms (Byers *et al.* 2002). It is important to obtain accurate assessments of location and abundance of invasive species so that managers can set these priorities and have the information to quickly and effectively combat the invaders. It is also important to identify barriers to invasion and habitats where an invasive species cannot persist or cause much harm.

To be informed in the initial stages of a species on the way to becoming a successful invader, we need early detection. Early detection is a very low probability event that is critically dependent on adequate surveillance. It involves sampling strategies sufficiently rigorous to detect incursions at sufficient frequency and, assuming a response program, to influence the chance of establishment and spread.

In our quest for early detection techniques, it is important to remember that invaders can be any type of organism from microbes to mammals and come in many forms. We need to be aware of plants, animals, insects, pathogens and parasites that can all be invasive or be vectors for invasions. Examples of these include plague (*Yersinia pestis*), West Nile Virus (*Flavivirus sp*), gorse (*Ulex europaeus*), common cord-grass (*Spartina anglica*), nutria (*Myocastor coypus)* and sudden oak death (*Phytophthora ramorum*). There are many well know examples of invasive plants and animals, including feral pigs (*Sus scrofa*), miconia (*Miconia calvescens*), red imported fire ant (*Solenopsis invicta*) and starlings (*Sturnus vulgaris*). Fish examples include western mosquito fish (*Gambusia affinis*), carp (*Cyprinus carpio*), brown trout (*Salmo trutta*), and Nile perch (*Lates niloticus*). The spread of these notorious examples would have been minimized and costs reduced with early detection and rapid assessment.

Fire as a metaphor for invasion

A metaphor that has been applied to invasive species is wildfire (Dewey and Andersen 2004). Wildfires sometimes grow large by sending out sparks that start small spot fires in places where conditions are right for fire to spread. Wildland firefighters know this and try to extinguish spot fires expediently, preventing the fire from growing larger. Even if the fire is already fairly large, wildland firefighters will make spot fires a priority over the large burning mass that may be too large to slow under current conditions. It is always best to detect the fire early and prevent it from spreading. This model of movement also applies well to invasions. Invasive organisms put out progeny, similar to sparks, which may move far from the parent, furthering its invasion potential. If invasive species managers, with limited resources, focus first on these smaller invasions this may do more to slow the spread of an invasive species than trying to tackle large well established invasions (Rejmanek and Pitcairn 2002). The challenges are how to find these small invasions of cryptic species, and to assess the risks and threats of each invader.

Definitions

The terms "early detection" and "rapid response" were defined by Worall (2002) as:

> **Early detection**, as applied to invasive species, is a comprehensive, integrated system of active or passive surveillance to find and verify the identity of new invasive species as early after entry as possible, when eradication and control are still feasible and less costly. It may be targeted at areas where introductions are likely (such as near to pathways of introduction) and in sensitive ecosystems where impacts are likely to be great or invasion is likely to be rapid.
>
> **Rapid response** is a systematic effort to eradicate, contain or control invasive species while the infestation is still localized. It may be implemented in response to new introductions or to isolated infestations of a previously established, nonnative organism. Preliminary assessment and subsequent monitoring may be part of the response. It is based on a system and infrastructure, organized in advance so that the response is rapid and efficient.

While this chapter will focus on rapid assessment more than rapid response to invasive species, there are two important points that are made in this rapid response definition. One is that preliminary assessment must be part of the response. This is a crucial step to take once a species has been detected. If the situation is not quickly inventoried, patches or individuals may be missed and the opportunity of catching the species while the invasion is small may be lost. The second important point in the Worall (2002) definition of rapid response is that of having the infrastructure already in place. Early detection and rapid assessment require frequent monitoring, which does require effort, a strategy, and funding. It may be possible to organize a group of volunteers to conduct monitoring, but in many cases someone needs to be hired to carry out this task. In general this is much less expensive than the alternative of doing nothing and letting the species spread. The mimosa tree (*Mimosa pigra)* in Australia illustrates this well (Cook *et al.* 1996). A small stand of mimosa trees were found in Kakadu National Park (KNP) in 1983. The staff at KNP immediately sent out a team to find any mimosa trees in the park and intervene. There are now occasional reports of a tree found in the park that are quickly eliminated, but no large stands. The program costs the park about $2 per hectare per year. In a nearby floodplain called Oenpelli a stand of about 200 ha was found at about the same time. The response was not as swift and by the year 1990 the infestation covered about 8,200 ha of the floodplain. A control effort was finally undertaken and a very large aerial spray operation was carried out. The spray program cost $220 per ha per year for 5 years to get the tree under control. Now they, like KNP, spend about $2 per ha per year for maintenance. This is a clear example of the costs associated with neglecting rapid response.

There are two distinct types of invasion that should be recognized when discussing early detection (Figure 1). The first type of invasion is one in which a native species moves within its own native country, state or habitat. If it moves to an area where it did not previously exist it can be considered as invading that area. For example, many game fish species in the western USA are non-native transplants. These fish disturb the native ecology of the western lakes, yet they have remained in their country of origin.

The second type of invasion crosses international borders and oceans, often moving between similar ecological zones. Tamarisk (*Tamarix sp.*), which comes from very arid regions of the Middle East and Asia, exemplifies this. It has invaded the southwestern United States in a climate similar to its native range (Di Tomaso 1998). It is possible for invasions such as this one to be intercepted at the borders of the country (Lodge *et al.* 2006).

Land managers could benefit from accurate maps showing current distributions and local and sub-regional models of potential habitats of invaders to address both of these types of invasion. Knowing current species distribution would help land managers concentrate on the frontier of invasion and control small invasions in new areas separate from larger invasions. Identifying these small, isolated areas would be beneficial because the most effective time for control is when an invasion is small (Rejmanek and Pitcairn 2002). Determining the potential distribution of invasions would help managers focus on the areas at a high risk of being invaded, aiding in early detection/rapid response of new areas being invaded (Stohlgren and Schnase 2006).

Early Detection and Rapid Assessment

Basic components of an Early Detection and Rapid Response (EDRR) program include:

1. access to current and reliable scientific and management information
2. ability to identify species quickly
3. a functional risk assessment plan
4. mechanisms in place to coordinate a control effort
5. providing adequate technical assistance (e.g. quarantine, monitoring, information sharing, research and development, and technology transfer) and rapid access to stable funding for accelerated research of invasive species biology, survey methods, and eradication options. The system's success will depend in part on public participation in efforts to report and respond to invasions.

Each of these elements, particularly 1 and 2, are important to an early detection and rapid response program. One tool that can aid in those specific processes is 'watch lists'. Watch lists are list of species that are either nearby, or known to invade similar habitats to the area of the list. For example, caulerpa seaweed (*Caulerpa taxifolia*), an aggressive invader introduced to the Mediterranean around 1984, was placed on the US Federal Noxious Weed list in 1999 by the Southern California Caulerpa Action Team, a watch group for early detection of this detrimental organism (Anderson 2005). When it was found offshore of California, US in June 2000 there was already infrastructure in place and action was taken to eradicate the plant within 17 days of its discovery. This was probably due to a well prepared action and assessment team and the fact that the plant was on a watch list before it even entered the country. It is important to know about the biology of an invader before it arrives so that when it appears you can be prepared with strategies and have already determined potential habitat and effects. Ideally, countries would share information about their invaders with each other, but unfortunately official reporting (e.g., to the United Nations Convention on Biodiversity) is very limited, and the global-scale invasive species information exchange systems that collect and share this information do not receive sufficient financial support.

Westbrooks (2003) defines the essential attributes of an early detection/rapid assessment program similarly as; including aids for species identification, authentication/verification of new field observations, reporting records, maintaining a database of species occurrences and locations, alerting appropriate officials and rapid response teams, and monitoring management actions. Simple EDRA programs have been developed for selected taxa in some local areas using these principles. For example, the US state of Wisconsin has an early detection program for purple loosestrife (*Lythrum salicaria*) whereby public service announcements prompt television viewers to call in purple loosestrife locations to a hotline with awaiting weed coordinators. This system incorporates adding new information to a database as soon as a specimen is found with alerting the appropriate officials so that a response team can be notified.

Additional aspects of EDRA components have recently been added for: user ID and validation, reporting, expert verification, occurrence database, and rapid assessment (Simpson *et al.* 2006). This paper highlights the importance of a centralized data sharing system. The authors also mention the importance of species profiles on the web for quick identification of new invaders, biological and ecological information, global distribution with details about instances of invasion, and information about management options, including case studies of early detection and rapid response.

Guiding Principles for Early Detection and Rapid Assessment

Suggested Guiding Principles are as follows:

1. An early detection program must be fully integrated into a comprehensive, science-based research and management program that coordinates aspects of prevention, early detection and rapid assessment, research, surveys and monitoring, and outreach and reporting.
2. The database of observations must remain in the public domain with free and open access to unclassified, peer-reviewed data.
3. Because many aspects of an EDRA program require extensive research and development (e.g. integrating millions of field observations with remotely sensed information and new forecasting tools; greatly improved information technologies; and high-performance computing), basic research and a scientific method must underpin the design, testing, and phased implementation of the program and these programs must be developed prior to new invasions.
4. The long-term success of any national or international EDRA program is dependent on a long-term commitment of funding, personnel, and equipment of all key components in the system, plus the continued cooperation of many

government and non-government organizations, engaged volunteers, and public acceptance.

5. It would be impossible to create a comprehensive EDRA program for the thousands of species on Earth. For any country (or region within a country) it might be more realistic to focus preliminary efforts on those top priority species that are identified as serious potential invaders. Once the system is more fully tested, it could be expanded to cover more species.

Data and Information Management

Data and information management represent the single greatest challenge of an effective EDRA program. Information is needed on probable and current species distribution and abundance, habitat suitability, and containment strategies and techniques. High resolution maps, and models of current and potential spread of harmful species and their effects, which are being used in developed countries to assess and manage invasive species problems, can be used to provide insights into invasion ecology and to develop guidelines for response options for those facing similar problems in other parts of the world. Based on US surveys of resource managers and the public, there is an unprecedented need for a "comprehensive, integrated system" for early detection, and "a systematic effort to scope the severity of the issue" for rapid assessment (Stohlgren and Schnase 2006).

Global and Regional Invasive Species Databases

Biological invasion is a global problem so it is clear that global-scale clearinghouses that share data from all over the world are a crucial component of any effective response. Existing global-scale systems include the Global Invasive Species Database (GISD; *www.issg.org/database*), which has comprehensive information on more than 500 of the world's worst invasive species; the Global Register of Invasive Species (GRIS), which provides the names and full taxonomy of all known invasive species, along with geographic records of introduction and invasion: and the Global Invasive Species Information System (GISIN), which is developing a system for the exchange of invasive species data and information between local, national, regional and international databases over the internet. The Global Organism Detection and Monitoring system (GODM) of the US National Institute of Invasive Species Science (NIISS; *www.niiss.org*), and the International Nonindigenous Species Database Network (NISbase; *www.nisbase.org*) include global information and CAB International (*www.cabi.org*) will launch the first phase of their Invasive Species Compendium in 2008. Regional information systems include Delivering Alien Invasive Species Inventories for Europe (DAISIE; www.europe-aliens.org) and I3N, the invasive species thematic network of the Inter-American Biodiversity Information Network (IABIN; *http://i3n.iabin.net/*).

All of these databases provide data free to the public, but have limited access to those contributing to the system to ensure data quality. Websites such as these are a great benefit to early detection and rapid assessment. They have the potential to form a global network of information on all harmful invasive plants, animals, and pathogens (especially if geographic information gaps are addressed and if they become providers of data to the Global Invasive Species Information System (GISIN)). Here we specifically outline the components and potential uses of the GODM system to illustrate how databases can be used in early detection and rapid assessment. All of these components may not be available in each system but they all represent great future potential.

1. **User ID/Tracking:** This first step involves users that may contribute data registering with the website and entering contact information that includes their name, email address, location, and level of expertise (specifically regarding the information about to be entered). This is important so that the information entered can be tracked to its source and checked for reliability.
2. **Verify Records and "First Alert"**: Only a limited number of well trained users and coordinators may enter data into the system. The user may wish to exclude suspect data in analyses, mapping, and modeling by selecting data that are confidently identified. Location data are matched with other known reported locations and modeled distributions – this step allows for detection of novel, urgent species establishments in new habitats, ecosystems, counties, or states. After taxonomic identifications are verified, novel/urgent observations of occurrences can be sent to officials or agencies responsible for sending specific alerts.
3. **Taking in New Information:** New records are systematically added. Metadata need to accompany all data. Ancillary data (e.g. soil texture, land use characteristics, etc.) should be available for any data points collected in the field. All data are screened for quality (measures within acceptable

ranges), stamped with a "certainty-level," and then served on the web for public consumption or download.

4. **Rapid Assessment, Data Synergy, Invasive Species Forecasting System:** This point illustrates the real power of having multiple databases on the internet. Datasets from one database can be linked with datasets from other inventory and monitoring programs to map the current distribution and abundance of a target species or multiple species. Simple, "first approximation maps" derived from a choice of several commonly used species distribution models (e.g. multiple logistic regression, classification trees) using multiple datasets can be created. For some very common, less-harmful species (e.g. dandelion (*Taraxacum sp.*), lady bug beetle (*Coccinella sp.*)), distribution maps may be all the "modeling" that is needed. For newly detected species, species on "noxious" or "invasive" lists, or watch-list species, more advanced modeling could be performed. Potential distributions can be modeled from occurrence and abundance data, ancillary data, and remotely sensed data to produce maps of probable/potential distribution and abundance, habitat vulnerability analysis, and uncertainty analysis (Stohlgren and Schnase 2006). Modeled information and species attribute data can be used to create "second approximation models" of potential rates of spread, and corridors and barriers to invasion. The current distribution and abundance data can be overlaid on the model outputs and habitat maps to identify priority survey, control, and restoration sites. All data and model outputs can be served on the web, and all data and metadata associated with selected models can be archived.

5. **Rapid Response and Monitoring Effectiveness:** Based on new reports and modeled outputs of distribution and abundance, habitat vulnerability, potential spread rate, and risks, alerts can be targeted to authorities and to groups of concerned citizens where appropriate. Typically, "exotic invasive management teams" can be provided with a location and a method of extermination. We suggest a more sophisticated use of rapid response teams where far more information is provided to the team to maximize efficiency (Table 1).

A first critical step here is to serve, store, and share monitoring data to use in an adaptive management framework when combating invasive species. Initial control efforts may not be successful, and vulnerable habitats may be quickly re-invaded from seeds, other propagules, or source populations nearby. Thus, rapid assessment is an iterative process improved by careful monitoring and information sharing (Stohlgren and Schnase 2006).

A second critical step is to use predictive spatial models to revise maps of current and potential species distributions and abundance to select the next highest priority control sites in a strategic manner. This step may include isolating source populations from vulnerable habitats by concentrating on corridors of invasion or two-pronged attacks on both well-established source populations and newly invading sub-populations (Figure 2). Each habitat must be prioritized and acted upon according to the priority it is assigned. A key feature here is documenting all management actions to better understand the invasion process and to be able to extrapolate successful actions to additional species and habitats.

This will improve costs of future control and restoration efforts, while tracking performance measures and overall cost effectiveness.

Researchers and modelers must also track the accuracy and utility of modeling capabilities for early detection and rapid assessment and document the economic and environmental savings by using modeling products. Likewise, we must document customer satisfaction in the use of modeling products to improve decision support.

Determining the spatial extent and severity of invasions is of utmost importance (Simberloff *et al.* 2005). Unfortunately, ground surveys of each invasive species require large amounts of time and funding, and most managers do not have the resources required to complete the task. Statistical techniques linked to targeted field surveys may achieve fairly accurate measurements of potential distributions in large areas. These models produce maps of habitat suitability or barriers to invasion. The information contained in remotely sensed images can be used in these spatial models of habitat suitability (Reich *et al.* (1998, 2004), Crosier (2004a), Barnett *et al.* (2007). These models provide information on the potential habitat of an organism with minimal field data on newly invading species. These methods could prove invaluable for targeted early detection surveys.

Species Reporting Requirements

While most would agree that reporting new locations of harmful invasive species is important, there are a few published recommended data requirements for early detection.

Extreme minimum requirements include 'who, what, when, and where' data (Table 2, required fields), sometimes referred to as the Dublin Core (See *http://www.gisinetwork.org/Documents/GISINProc2004HTML/GISINProc20041.html* and *http://dublincore.org/*). This general advice could be greatly improved by an understanding of the potential to model species distribution and abundance data in space and time. For example, ancillary data on abundance, dominant native species present, other non-native species present, environmental data (e.g. soils or disturbance information for plants, water depth for fish, nest tree species for birds, etc.) and noticeably absent native and non-native species can be extremely important information in predictive modeling (Table 2; Morisette *et al.* (2006).

Conclusions

Early detection and rapid assessment linked with response could be the most effective tools that land managers have to stop an invasion before it becomes an ecological and economic nightmare. A relatively modest investment in existing global-scale information exchange systems will provide the world with access to information about all known invaders. "Watch lists' should be created, maintained and updated for local areas. When information is obtained about a particular invasive species in a local area, it should be shared on global websites and with local land managers so that others can benefit from this knowledge. It is important to look at the habitat that surrounds an area and determine what species are possible invaders and survey for them. Probable distribution models and habitat suitability maps should be used, and surveys conducted along corridors and entry points for invasion. Early detection and rapid assessment is a very effective tool when used efficiently.

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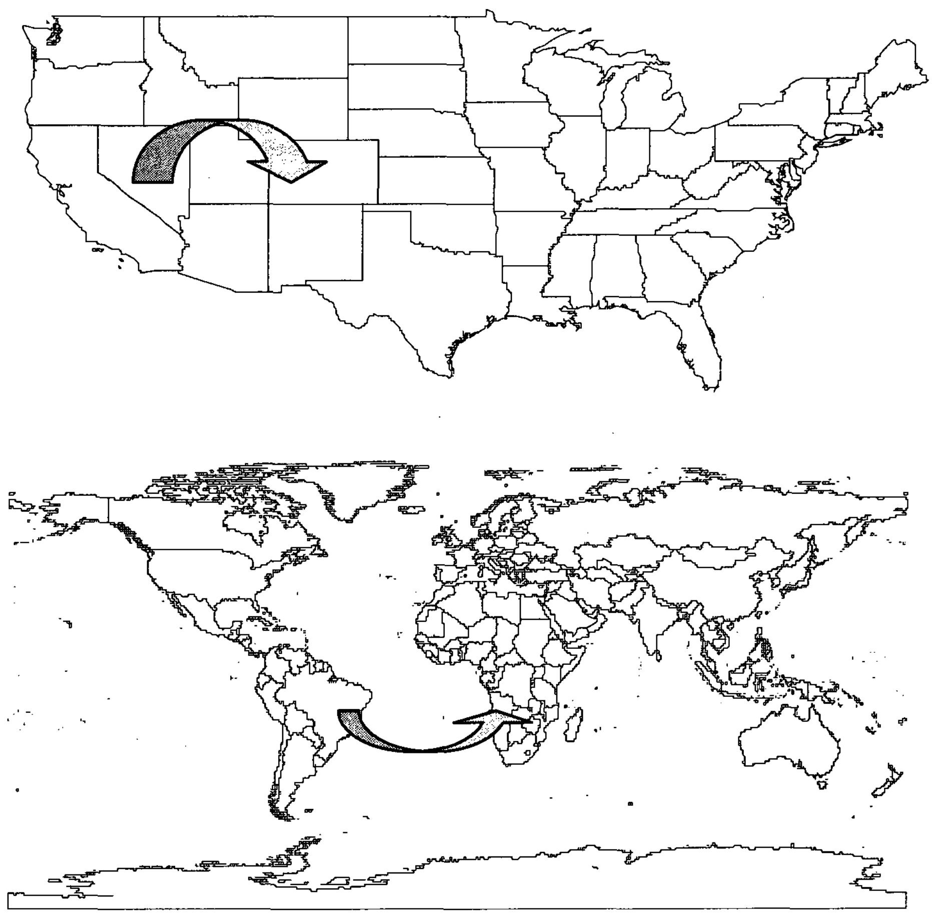
Table 1. Suggested information to provide to rapid assessment teams

Information Provided	Reasoning
Species identification aids	To effectively target cryptic invasive species rather than look-alikes.
Accurate location data of known occurrences and predictive models of target species, information on other highly invasive species in the local area, and high probability sites nearby and along the route to the primary site.	Improves cost-effectiveness of rapid assessment efforts, while reducing propagule pressure and source populations nearby.
Comparable (standardized) monitoring protocols.	To help quantify "what works, where," share success stories, and document performance goals.
Instructions to upload data into a distributed database to share information on what techniques work best in different habitats under a variety of conditions.	Improve accountability and data sharing for better predictive modeling, early detection, and restoration.

Table 2. Generic species reporting requirements, *=required field.

Data Field	Example	Comments
Recorder Name*	Chuck Darwin	Observer
Date*	July 17, 2005	
Time*	17:35	24 hour clock
Y coordinate*	4405547	Exact UTM Northing or Longitude
X coordinate*	106442	Exact UTM Easting or Latitude
Species*	Spotted knapweed	Genus, species, or common name
Abundance	10	Count or % foliar cover
Location certainty	±10	m (Specify meters or feet)
Area surveyed around point	40	m^2 (Specify units as m^2, ft^2, ac, or ha)
Dominant native species present	Pinus ponderosa	Genus, species, or common name
Other non-native species present	Bromus tectorum	Genus, species, or common name
Other non-native species noticeably absent	Yellow sweet clover	Genus, species, or common name
Comments	Old field	Any helpful ancillary information

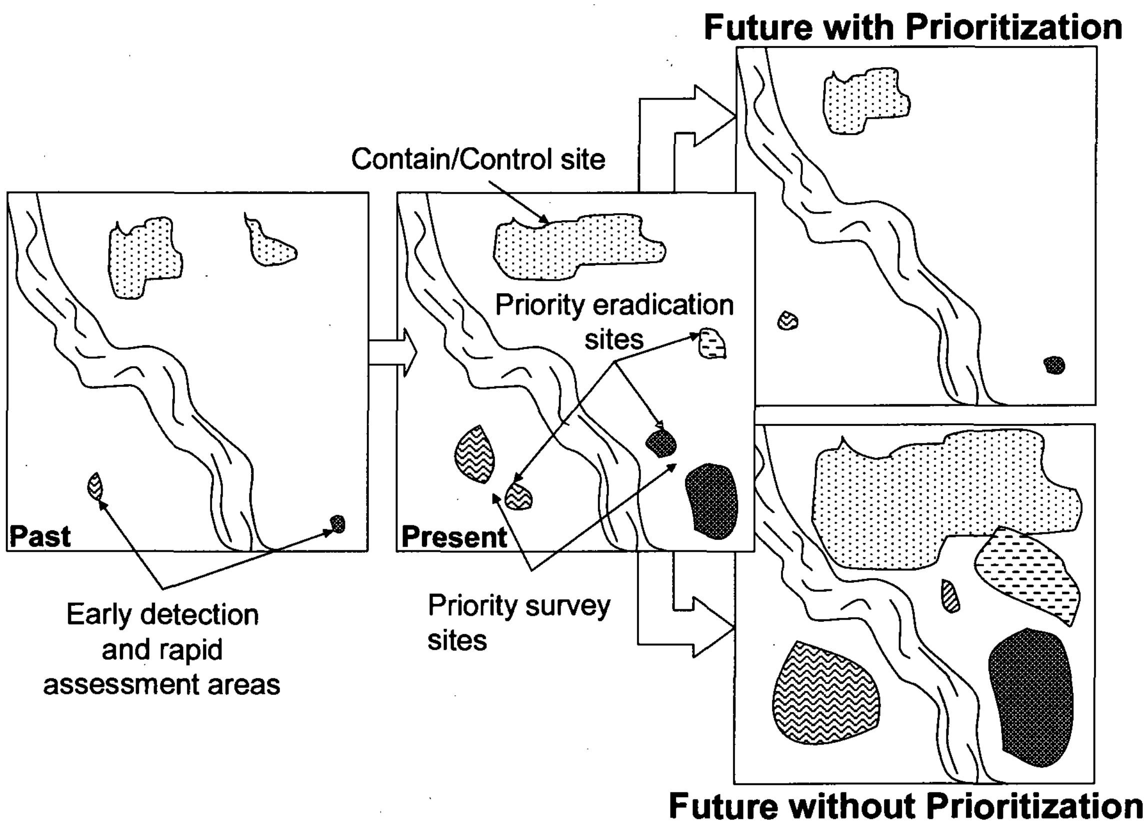
Figure 1. A. Local invasions involve a harmful species moving within a single country, state, or county to a new area within that country, state or county. B. Global or intercontinental scale invasions pertain to a harmful species moving between countries, often over an ocean.



A.

B.

Figure 2. In this conceptual model of invasion the past shows where a species may have been introduced. The present shows where the species is when it is first found. Priority survey sites are areas between two close invasions, contain/control sites are large patches, and priority eradication sites are areas of small populations. If these sites are prioritized expediently the damage can be minimized and money saved. Without prioritization species will continue to spread and cause more ecological and financial burden. The concept of this figure applies equally well to plants, animals and diseases.



Chapter 2: GIS Applications in invasive species management and research

Abstract: Geographical Information Systems (GIS) are powerful tools in the field of invasive species management. They can be used to create potential distribution maps for all manner of taxa, including plants, animals, and diseases. GIS may perform well in early detection and rapid assessment of invasive species. I used GIS applications to investigate species richness and patterns of invasion in fish in the United States at the 6-digit Hydrologic Unit Code (HUC) level. As an example application, I also created maps of potential spread of the cane toad (*Bufo marinus*) in the southeastern United States at an 8-digit Hydrologic Unit Code (HUC) level using its current range and regression and environmental envelope techniques. Equipped with this potential map, resource managers can target their field surveys to the areas most vulnerable to invasion. With advances in GIS technology, maps, data, and many of these techniques can be found on websites such as the National Institute of Invasive Species Science (www.NIISS.org). Such websites provide a forum for data sharing and analysis that is an invaluable service to the invasive species community.

Introduction

The primary purposes of Geographic Information Systems (GIS) and Global Positioning Systems (GPS) are to provide a mechanism to digitally pinpoint a location on Earth, view that location on a map, and use that location and data in spatial analyses. Using a network of satellites, satellite receivers, and mapping software, we are able to quickly and easily produce maps and conduct spatial analyses that would otherwise be difficult or impossible to produce. GIS serves as a data storage and analysis device for spatial data, making data easy to view and manipulate.

Health care, agriculture, environmental industries and ecology are a few of many industries that have been positively altered by the advent of GIS. The large spatial databases that GIS can help create allow companies to track their hard goods and can allow farmers to determine which areas of their fields need more fertilizer, eliminating the need to add fertilizer to the entire field. Ecological data often contain a spatial component. Where an animal spends its time and the patterns of its movements can be important clues to its biology. This type of information provides insight to expanding distributions and provides watch lists of spreading invasive species to managers for early detection and rapid response.

GIS can be a useful tool in the field of invasive vertebrates, especially in the areas of early detection and rapid assessment. Species distributions are largely determined by the environment. A growing number of statistical models, called Species Environmental Matching (SEM) models are being used to determine the current and potential distributions and abundances of invasive species (Stohlgren and Schnase 2006). These models relate observed species distributions to environmental (climatic, topographic, edaphic) envelopes and then, assuming the same stable relationships, project their spatial shifts (local, enrichment, or extinction) in response to envelope changes under current conditions. These environmental envelopes, arranged along a gradient from proximal to distal predictors, have direct or indirect effects on species establishment and survival (Austin 2002). These types of models are either created in GIS or can be displayed in GIS once created, giving a visual representation of the environmental envelope of potential habitat or abundance.

An important consideration for invasive species is that recent invaders may not have filled all suitable habitats, while species naturalized long ago may have filled a larger proportion of suitable habitat. Defining where a species may survive depends heavily on being able to determine its habitat. Technological advances in GIS make this more readily accessible to the general public. Data such as elevation, vegetation type, and climate information are now available for free on the internet, often paired with websites that allow you to view and utilize the information.

How GIS can be used

View data

One very basic and effective way to use GIS is to view data with it. Many datasets are very large and difficult to visualize as a table of numbers. When viewed spatially these data often makes more sense. Stohlgren et al. (2006a) combined native and non-indigenous fish datasets from NatureServe.org and the USGS Florida Integrated Science Center's Non-Indigenous Aquatic Species database and used them to examine numbers of native and non-indigenous species in each 6-digit HUC area (Figure 3). Without performing any analyses on the data, they found that a large majority of the native fish in the United States are centered throughout the Midwest and South Central areas of the country. The non-indigenous fish have higher numbers in the Western and Eastern parts of the US. These patterns were ascertained without conducting any analysis, proving that even simple display of the data in a spatial format can be a useful endeavor.

Data summary

GIS can also be helpful in summarizing large datasets to be used to model habitat quality and distribution. Very often data layers such as digital elevation models (DEM) are used in modeling because they provide a large amount of environmental information. These layers are available for free via the internet, often at either 10- or 30-m^2 resolutions. While these resolutions provide a lot of information on a fine scale, this fine scale is not always necessary, especially if the model to be created is at a coarser scale, like a watershed, county, or state. In these situations, GIS can be used to summarize data, simplifying them into a useful form for the resolution of interest. The Spatial Analyst module of ArcGIS 9 (ESRI 2004) has a function called zonal statistics that will calculate summary statistics from a raster layer like elevation for a large polygonal area like a county, extracting the average, minimum or maximum, and range for each polygon (county). Additionally, GIS can be used to retrieve the value for a specific point in the DEM so that the entire surface does not have to be stored. These functions make the retrieval of dependant data for models readily accessible.

Field data - points, lines, and polygons

Spatial field data can be displayed and managed in a GIS. The data are stored in one of three formats: points, lines, or polygons. Plots or locations of any individual organism are examples of points. These are discrete one-dimensional places in space where there is an item of interest. Lines include rivers, transects, or roads - basically any linear representation of interest. Polygons represent an area of interest, like a stand of trees, an area of habitat, or a lake. These data types are an excellent medium for recording presence and absence of a species because they are discreet. Additional attribute data may be added to a location, including presence or absence.

Lines give similar amounts of information, again lending themselves well to presence, absence, and a few additional attributes. Polygons are unique because they cover an area, which can contain additional information such as abundance or percent cover. These data can be collected in the field using either paper maps to establish location or with a GPS device to collect the data and download it to a computer.

Simple GIS models

GIS can be used to create simple analyses such as buffers and thiessen polygons. A buffer can be created around points, lines, or polygons. It is a new polygon of a specified distance from the original feature (circle around a point, or polygon around a line or polygon) that encompasses the original feature. Any GIS program can create this buffer around points, lines, or polygons to be used for various reasons such as surrogates for habitat for a poorly studied species. Buffers could also define potential habitat for species that have a very specific distance they can be from a given feature such as water. Buffers are a commonly used transformation of original spatial data.

Another analysis performed by GIS is the creation of thiessen polygons, sometimes known as voronoi polygons. Theissen polygons are shapes created around a group of points, one polygon for each point. These polygons are created around each point in such a way that every place lies within the polygon of the point to which it is nearest. The easiest way to think about this is with fast food delivery areas. A fast food pizza chain would divide a city into thiessen polygons, only delivering to customers that were closer to them than they were to the next restaurant. For a wildlife example, if there were twelve nests in an area, polygons would be formed around those twelve nests so that every place on the landscape falls into the polygon associated with the closest nest. This tool has obvious application to studying territorial animals. Data collected on nest locations, could be used to generate thiessen polygons surrounding each nest, and this area would estimate territory range. Buffers and thiessen polygons are a couple of the many possible examples of simple operations that can be done using a GIS. Now we will examine some models that are more complex.

Statistical models

I review potential habitat models in this section. These statistical models use data for a species current distribution to try to predict potential habitat. Conceptually, the Species Environmental Matching (SEM) models assume the fitted observational relationships to be an adequate representation of the realized niche of the species under a stable equilibrium or quasi-equilibrium constraint. As such, the SEM result is only a first approximation of future distributions of individual species (Pearson and Dawson 2003), which are determined also by other processes such as dispersal, adaptation, competition, succession, fire and grazing pressure (Austin 2002). Still, an innovative integrated model may contribute considerably to a robust early warning system for decision makers to design more effective management and control strategies for invasive species. In short, we will be better able to manage and assess risks associated with invasive species, because risk assessments require accurate modeling of current and potential species distributions (Stohlgren and Schnase 2006).

There exist numerous challenges in the traditional SEM or niche-based modeling of current and future species distributions (see reviews by Pearson and Dawson 2003, Soberon and Peterson 2005, Elith et al. 2006, Guisan et al. 2006, Heikkinen et al. 2006, Hijmans and Graham 2006, Pearson et al. 2006, Beaumont et al. 2007). These challenges have not prevented scientists and resource managers from refining, testing, and using SEMs in their work. No two models are identical, and each has advantages and disadvantages (Table 3).

Regression models

Logistic regression is a type of Generalized Linear Model appropriate for data with a binary distribution such as species presence or absence (McCullagh and Nelder 1989). The output from logistic regression models can be taken from the statistical package and used in GIS to create a visual representation of the model created. I have done this with data obtained from the USGS Florida Integrated Science Center's Non-Indigenous Aquatic Species database on the invasive cane toad (*Bufo marinus*). The cane toad has become established in the United States and has invaded several watersheds in Florida. I employed logistic regression with Systat 11.0 (SSI 2004) using minimum temperature, minimum radiation, mean temperature, maximum temperature, maximum humidity, and maximum growing degree days as a predictor variables to determine how much potential habitat there is for the cane toad in the Southeastern US. I conducted a step-wise generalized linear model, and only minimum temperature was selected as a significant variable. The results of the regression had a high predictive power with a McFadden's Rho Squared value of 0.92. When the equation from the GLM results were implemented in the GIS, the map showed that the cane toad had realized most of its suitable habitat in the Florida area, with only a few un-invaded areas left in high and medium habitat suitability (Figure 4). This result is a first approximation model; more data and ecological information on the cane toad will produce better results in the future. This same generation of a map by implementing a model's result in equation form can be done with many different types of equations.

The Envelope Model

The Environmental Envelope model (Holcombe et al. 2007) was developed as a rapid assessment technique to estimate the potential distribution of a species given its present locations and their associated environmental attributes. It is supported by ArcGIS 9x (ESRI 2004) and will be available on the National Institute of Invasive Species Science website (www.NIISS.org). Envelope uses environmental variables, chosen by the modeler to be relevant to the species of interest or to species growth in general, to determine other locations within the environmental envelope (e.g., locations where the species of interest may be able to become established). For all of the locations that the species is present, the minimum and maximum of each independent variable are noted by the program. These minimum and maximum values together become the "envelope" in which the species can survive. For instance, if a species exists in only three counties and the temperature in county A is 45 degrees Fahrenheit, in county B is 40 degrees, and in county C is 43 degrees, then the temperature envelope is 40 to 45 degrees. We would then compare the temperature for other counties to see if they fell within the range for potential habitats. The model can include several different environmental layers to determine suitable habitats, according to current information. The output of the model informs how many of the input variables lie within the environmental envelope of the species.

I conducted this analysis on the cane toad to see what a different model may predict for the same species (Figure 5). I used environmental data retrieved from the Daymet website (http://www.daymet.org/) that was originally at a 1-km^2 resolution for the dependant variables. I used zonal statistics in ArcGIS's Spatial Analyst (ESRI 2004) to summarize the data for the 8-digit HUCs. Variables used included minimum radiation, minimum temperature, mean temperature, maximum temperature, maximum humidity, and growing degree days. I used the same cane toad data used in the regression model. The resulting map showed that as distance grows from the peninsula of Florida there are less and less environmental variables that fall within the cane toad's environmental envelope. This trend supports the regression model that showed the cane toad did not have much more suitable habitat than what it is already occupying.

GIS on the web

Common issues confronting GIS users today include availability and user friendliness. GIS software is often expensive, making it difficult for many people to obtain. Another subset of would-be GIS users have access to the software, but do not have the time required to learn the software. With the advances in GIS technology these issues are changing. Many of the functions that are found in proprietary software can also be found on the internet, where the user interface is often less complex. Much of the species distribution data used in the examples in this paper were found and downloaded from the internet. Many websites, such as The National Institute of Invasive Species Science (www.niiss.org) are encouraging an environment of data sharing. The NIISS website includes an interface to upload data and a GIS interface to view data graphically, create models, and print and save final map products. The technology is very sophisticated and is open to the general user. This is the direction that GIS software is heading, reducing dependence on desktop GIS software in the future.

Conclusions

With the advances that have been made in GIS technology, it has become a useful tool for land managers and academics alike. It is widely used as both a tool to perform basic functions such as displaying data, and more complex functions like creating and displaying Species Environment Matching models. As we look at our computers today, and continue to look to the future of GIS technologies, this is a tool that should, and could be used by many scientists and managers.

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Figure 3. Patterns of (A.) native and (B.) non-indigenous fish by six digit HUC drainage (Stohlgren et al. 2006; used with permission). Numbers in the legend represent number of species.

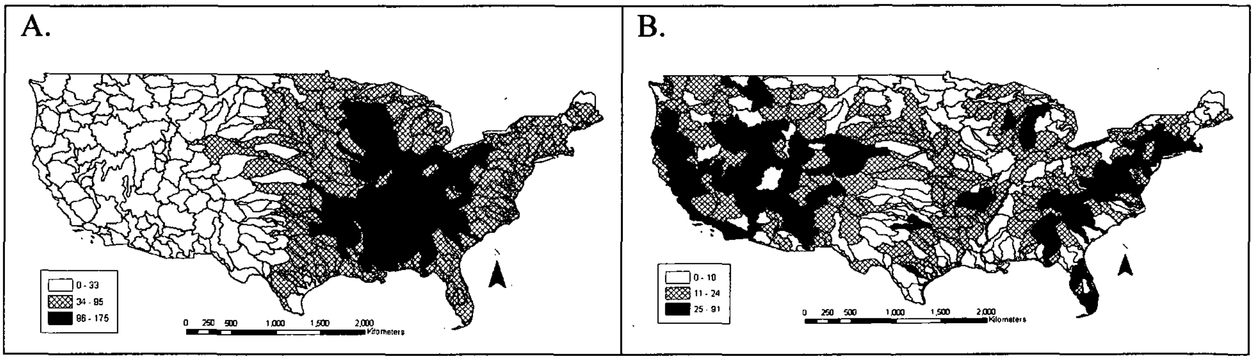


Figure 4. Regression model of *Bufo marinus* showing low, medium, and high likelihood of suitable habitat in each eight digit HUC.

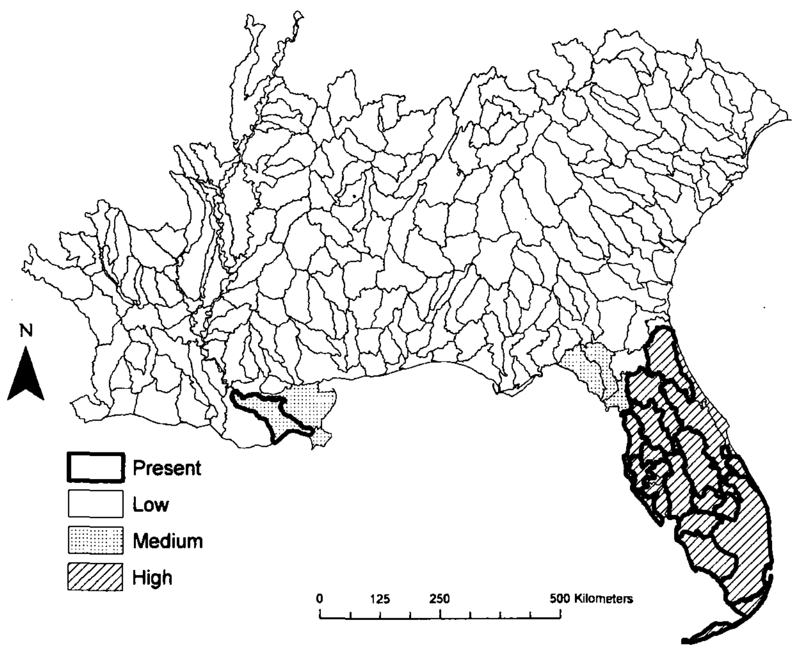


Figure 5. Envelope model of *Bufo marinus* showing the number of parameters in each eight digit HUC that could contain the species.

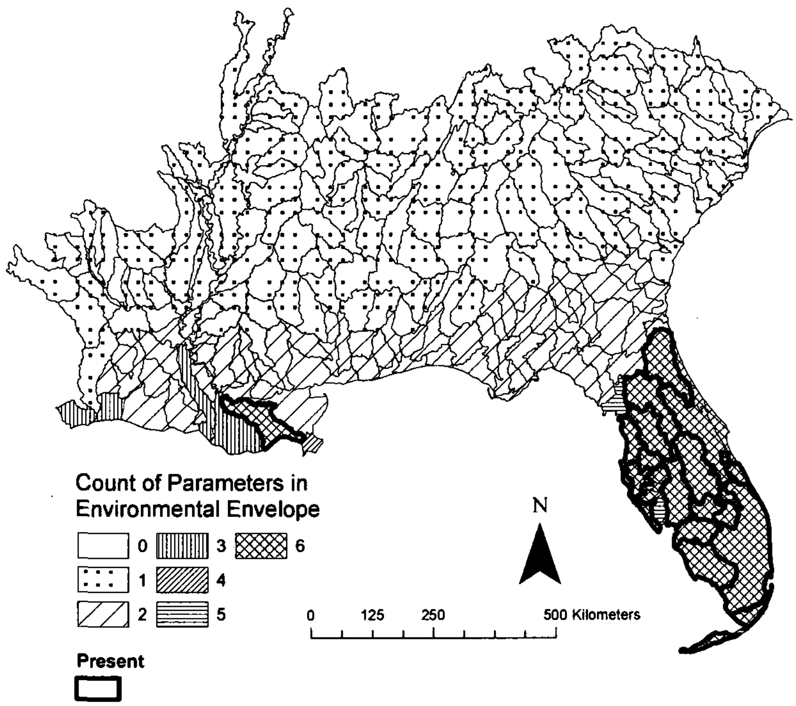


Table 3. Commonly used species environmental matching models for predicting species distributions.

Model	Citation	Advantages	Disadvantages
Maxent	(Phillips et al. 2006)	Presence only, nonlinear, nonparametric, not sensitive to multicollinearity, provides variables' relative importance (jackknifing), easy to run and takes less time, becoming popular	Presence only (no consideration of absence data)
Classification and Regression Tree (CART)	(Breiman et al. 1984)	Non-parametric, Presence/absence, easy to run and interpret	Absence data needed
Boosted Regression Tree	(Friedman 2001, De'ath 2007)	Non-parametric, Presence/absence, limitations with spatial data	Absence data needed, more statistical details
Logistic Regression	(McCullagh and Nelder 1989)	Widely used, presence/absence	Absence data needed, sensitive to multicollinearity
Least square regression	Most statistics software	Widely used, continuous response variable (e.g. species richness)	Needs continuous response variable, sensitive to multicollinearity, decision about significance level (*P* value?)
BIOCLIM	(Busby 1991)	Presence only, simple	Presence only, does not use absences, less accurate than other niche models
DOMAIN	(Carpenter et al. 1993)	Presence only, simple	Presence only, does not use absences, less accurate than other niche models
ENFA (Env. Niche Factor Analysis)	(Hirzel et al. 2002)	Presence only	Presence only, does not use absences
Envelope	(Jarnevich et al. 2009)	Presence only or Absence only models can be run.	All environmental factors are given equal weighting.

Chapter 3: From Points to Forecasts: Predicting Invasive Species Habitat Suitability in the Near Term

Abstract

There is a general need in invasive species research to quantify the potential habitat of invasive plant species, especially in the face of rapid climate change. I used 4-km^2 climate scenarios projected to the years 2020 and 2035 for the continental United States, to model 12 invasive plant species in the conterminous United States. I used maximum entropy modeling (Maxent) to create three models for each species: (1) current potential habitat suitability; (2) potential habitat suitability in 2020; and (3) potential habitat suitability in 2035. Area under the receiver operating characteristic curve (AUC) values for the models ranged from 0.92 for *Pennisetum ciliare* to 0.70 for *Lonicera japonica*, with 10 of the 12 being above 0.83 suggesting strong and predictable species-environment matching. Change in area between the current potential habitat and the year 2035 ranged from a potential habitat loss of about 217,000 km^2 for *Cirsium arvense*, to a potential habitat gain of about 133,000 km^2 for *Microstegium vimineum*. These results have important implications for invasive species management under varying rates of climate change.

Introduction

Invasive species are a major threat to ecosystems worldwide. They play a major role in displacing native species (Noonburg and Byers 2005, Snyder and Evans 2006, Anderson 2007) and cause deterioration of many ecosystem functions (Wilcove et al. 1998, Crowl et al. 2008). The spread of invasive species is the second leading threat to biodiversity following habitat destruction (Wilcove et al. 1998), and costs the United States alone up to $120 billion per year (Pimentel et al. 2005). Resource managers today face the challenge of determining where an invasive species outbreak may occur, and where an invasive species will move next.

Early detection of invasive plants is of the utmost importance, especially discovering and mitigating invasions when they are small (Moody and Mack 1988, Leung et al. 2002, Rejmanek and Pitcairn 2002). This issue becomes particularly relevant in the face of climate change (Vitousek et al. 1996, Thuiller et al. 2008). There is a potential for the area of habitat that is suitable for any given species to shift with rapid climate change. Those populations that are on the edges of the invasion will have the potential to move with the climate change. Some areas will go from being unsuitable habitat to suitable habitat; these areas will be the leading edge of the suitable habitat. Other areas will remain stable as suitable habitat, and a final area will cease to be suitable habitat (Bradley et al. 2009). This third category of habitat does not imply that species will cease to exist in these areas where it is already established, these species may persist from the seed bank for many years in suitable micro-habitats within unsuitable areas for many years (Hampe and Petit 2005, Stohlgren et al. 2008, Thuiller et al. 2008). There is also the potential for an adaptable species such as a habitat generalist to continue to adapt to new climates and not shift at all, populations of species have the opportunity to migrate, adapt, or be extirpated.

Climate Envelope Modeling (CEM) is a method to calculate potential suitable habitat. This method uses various algorithms to examine the habitat of a species and match that environmental space to areas where the species does not currently exist, locating areas of potential suitable habitat beyond the original data points. Hijmans and Graham (2006) offer an evaluation of several CEM methods. Until fairly recently this type of modeling was computing intense, and model creation could take days to weeks to complete. Increases in computing power and subsequent improvement in methods have helped develop the field of CEM from theory to practice. A review of the early methods of species distribution modeling can be found in Guisan and Zimmerman (2000). Since the turn of the century there has been an explosion in the methodology and abilities of species distribution modeling, and in the number of publications on the topic. A Web of Science search on "species distribution model*" from 1960 to 2000 produced 5,155 entries while one third of that time, 2000-2009, produced double the results, 10,296 (accessed April 23, 2009).

Climate envelope models start from a distribution of presence points on a landscape. These data do have drawbacks; they do not provide any information on abundance or absence of the species of interest. There also may be many gaps in the data that are used. Less than 1% of any landscape can be affordably measured (Stohlgren 2007), and we must use what data we have available. These models are a starting point in an iterative process, informing managers of where potential distributions may lie and giving an idea of where to add surveys, and where to sample in the future (Stohlgren and Schnase 2006). Distribution models form the basis of an excellent first approximation map that is especially applicable for early detection programs (Pearson and Dawson 2003).

Many techniques of climate environment matching models for invasive species do not require absence data (Guisan and Thuiller 2005). This is useful for invasive species models because there is no guarantee that a point that is collected as an absence point is truly unsuitable habitat; it may be suitable, but the species has not yet germinated in or migrated to that location. Maximum entropy modeling (Maxent; Phillips et al. 2006) uses presence data and background data in lieu of true absence data. These models are well suited to generate maps of potential distribution and habitat suitability from current point distributions given the caveats above.

Broad scale distribution models are rapidly gaining acceptance. Morisette et al. (2006) used climate envelope modeling to model current tamarisk potential habitat at a 1 km^2 resolution for the continental United States using logistic regression with an Area Under the receiver operating characteristic Curve (AUC) of 0.95, but this model did not address climate change. A worldwide bullfrog model was created at a 10-minute resolution for current conditions (Ficetola et al. 2007). This model had a very wide distribution, but a coarse resolution. Bradley et al. (2009) created models at a 4-km^2 resolution using Mahalanobis distance for five invasive plants in the United States for the year 2100, a management level geographic scale, but a very coarse time scale. I integrated aspects of these studies, by examining a management level resolution, a country level distribution, and a near term time scale.

I recognized that these maps of potential habitat suitability do not address propagule pressure, predation by natural enemies, or other biotic interactions (Ficetola et al. 2007). The next step was to examine how a species might spread and where. I used the current potential suitable habitat model as a mask and developed a distance from seed source surface as a proxy for propagule pressure, a rudimentary invasibility index to address this issue.

My objectives were to: (1) provide a strategic methodology to forecast scenarios of potential spread based on point distributions; (2) create potential distributions of invasive species with Maxent and examine the relationship of these species to their environment; and (3) consider data gaps, distance from seed source and suitable habitat (a surrogate for propagule pressure) to assess risks to invasion.

Methods

Data

I gathered point data for twelve invasive plant species in the continental United States (Table 4). These data were not exhaustive of all locations for each of these species, but were the available data from accurate sources (e.g., the Biota of North America Program, www.BONAP.org) that I gathered for these species. There were gaps in the data; some areas were more completely sampled than other areas. That said, points are our first and best descriptors of distributions (Stohlgren and Schnase 2006). From points, I created a systematic methodology for assessing point distributions relative to environmental predictors and created models of potential suitability.

I chose species with a broad range of current distributions, narrow to wide (Appendix A); recently introduced to well established; and with more than 250 known locations (Table 4). I considered two species as habitat specialists; *Lythrum salicaria* as it is generally confined to wetlands (Galatowitsch et al. 1999); and *Pennisetum ciliare* being confined to sandy soils, that do not freeze for extended periods, with precipitation from 200 to 1200 mm per year (Ibarraf et al. 1995). I harvested most of the species location data from on-line sources, especially the National Institute of Invasive Species Science (NIISS 2008). NIISS is a data clearinghouse on the internet that has quality control measures on the data that it ingests (Graham et al. 2007). Each data source is listed in Appendix A.

The independent variables used for this study were 19 bioclimatic layers created using combinations of minimum and maximum temperatures and precipitation (Nix 1986). These bioclimatic layers were created as variables to capture climatic seasonality important for organisms. The climate variables for current conditions were from the DAYMET dataset for the years 1980-1997 (DAYMET 2006). The modeling resolution for current conditions was approximately 1-km^2 pixels, the finest resolution I could find for each of the data layers over such a broad extent. The climate projection data were derived from Parameter-elevation Regressions on Independent Slopes Method (PRISM) data at a 4-m^2 resolution (PRISM data available at http://www.prism.oregonstate.edu/,PRISM Group , Daly et al. 2002). I used predictions for 2020 and 2035 created by Jarnevich and Stohlgren (2009) by extrapolating climate conditions from the PRISM data for 1895 to 2006. I chose years in the near future to be of imminent use to land managers.

Modeling techniques

Once the data were compiled I used maximum entropy modeling (Maxent 3.2.9; Phillips et al. 2006) to create three predictions for each species: (1) current potential habitat suitability; (2) potential habitat suitability in 2020; and (3) potential habitat suitability in 2035. Maximum entropy modeling is a machine learning method that requires only presence data. This algorithm estimated potential habitat distribution by finding the distribution of maximum entropy, or furthest from random (Phillips et al. 2006). Maxent used background data, or the environmental layers as model inputs (Hijmans and Graham 2006). The program removed duplicate records within a 1-km^2 pixel.

I tested each species for correlations between the variables using Systat v 12 (SSI 2007). I removed variables with correlations of $r \leq -0.8$ or $r \geq +0.8$. The remaining variables were clipped to the counties containing data for the species, constraining the model to counties of known realized habitat (Phillips et al. 2009). These variables were used to train each model, creating a potential habitat suitability surface at approximately 1-km^2 resolution for the current climate. I ran each model 25 times, withholding a different 30% of the presence locations from each model run as a test dataset for model evaluation, and averaged the results of the runs.

Then, I applied the model to the entire United States for the current climate and the climate scenarios for 2020 and 2035. For overall performance, the models were assessed using the Area Under the Receiver Operating Characteristic Curve, or AUC. This is a threshold independent indication of model performance (Phillips et al. 2006). To distinguish the threshold between suitable and unsuitable habitat for further analyses, I used the 10 percentile training presence logistic threshold as determined by Maxent (Table 4). This created an average potential suitability surface and a clamping surface for each species. The clamping surface shows the areas of the map where the model is extended beyond the climatic conditions that it was trained on, and can show areas that the model may be less reliable. I chose to mask out these locations from my analyses. Next, I used raster calculator in ArcMap (ESRI 2008) to calculate areas of potential habitat stability, potential habitat increase, and potential habitat decrease by comparing the current suitability map with the future suitability maps. Stable areas were defined as those with suitable habitat across all three time steps, habitat increase was defined as areas that went from unsuitable habitat in current conditions to suitable habitat in 2020 or 2035, and habitat decrease was defined as areas that went from suitable habitat in current conditions to unsuitable habitat in 2020 or 2035.

Finally, I was interested in finding a surrogate for dispersal of the species. I did not have detailed data available for dispersal mechanisms of each species, so I used distance from known seed source, or nearest data point. For this part of the analysis, I used the clamping and unsuitable habitat surfaces for each species as a mask, effectively excluding these areas from the analysis. I used the straight line distance function in Spatial Analyst of ArcMap (ESRI 2008) to create a surface of the distance from the nearest known presence point. This is a simple first order approximation of invasibility as defined by both suitable habitat and available propagules.

Results

I had a range of available sample sizes from 282 to 9517 (Table 4), all of which represent quite a small proportion of the land in the conterminous United States. Ten of twelve species modeled exhibited excellent performance with AUC values from 0.84 to 0.93 (Swets 1988; Table 4). Both *Lonicera japonica* (Japaneese honeysuckle) and *Microstegium vimineum* (Japanese stiltgrass) had AUC values at or below 0.70 indicating only acceptable model performance. There was little variation between training data AUC and test data AUC, suggesting repeatable and robust models (test data included 30% of the full suite of data). Each model run used a different 30% of the available data as test data, yet produced a similar result to the majority of the points modeled. The exception here, again, was *M. vimineum* which had a test AUC value 0.1 less than its training AUC value, possibly due to the relatively small number of data points available for the species.

The change in potentially suitable habitat area varied dramatically among species (Table 4). The largest increase in potentially suitable habitat was about 133,000 km^2 for *Microstegium vimineum*, a species that has been introduced to the United States after 1900. The largest decrease in potential suitable habitat was about 217,000 km^2 for *Cirsium arvense* a habitat generalist.

Example

Space prohibits me from providing color maps of each of the 12 species modeled individually (but see Appendix B), so I will focus on one example, *Lepidium latifolium* (perennial pepperweed). The main concentration of the 1015 data points that I was able to gather on *L. latifolium* were in the intermountain west of the United States, with some additional data points in California, and a smattering of points in the Northeast. The current potential suitable habitat was well distributed throughout the US with large areas of potential habitat in the west, throughout the plains states, and a large amount of potential habitat in the southeastern United States in an area that was sparse of data. The scenario model, showing potential habitat suitability change between current and 2035, suggests that there are modest areas of change throughout the United States with potential habitat in the west becoming more dispersed and increasing and the habitat in the southeast remaining stable for the most part.

In particular, the models show an overall increase in potential suitable habitat of about 95,000 km^2 in the US between now and 2035 (Table 4). The areas in red on the scenario model have a high potential to be the leading edge of an invasion by this species, just as the areas in blue that go from being suitable to unsuitable have the potential to be the trailing edge of the invasion (Bradley et al. 2009; Table 4). This scenario map shows that areas of increased potential suitable habitat of the species are not confined to any particular part of the country.

For each variable included in the models, Maxent provides a response curve allowing for interpretation of environmental relationships to the distribution of the species' suitable habitat (Figure 7). For *L. latifolium*, the major contributing factors associated with distribution include mean diurnal temperature range (24%), precipitation of the warmest quarter (16%), minimum temperature of the coldest month (12%), and mean temperature of the wettest quarter (10%; Table 5. Top predictors by percent contributed to the model). The response curves associated with these factors show that there may be environmental thresholds for the ideal growth of *L. latifolium* (Figure 7). For example, for mean diurnal range, habitat suitability was low until the range begins to increase around 15 degrees C and steadily increases to around 21 degrees C showing *L. latifolium* to have a stronger relationship to a larger diurnal temperature range. *L. latifolium* also has higher habitat suitability with low or high precipitation in the warmest quarter, with high minimum temperature of the coldest month, and with higher mean temperature of the wettest quarter. Almost all factors in Table 5 are related to temperature. Using these relationships between variables, we can learn about the environmental drivers of the systems that we are modeling.

Invasibility Index Map

The invasibility map of *L. latifolium* shows this species to have less distance between seed sources in the west where most of the presence points were located. The midwest contains potential suitable habitat but very few data points, so potentially minimal propagule pressure, and is therefore less invasible due to distance from nearest propagule pressure according to this model. There are a few data points at the Virginia-Kentucky border that are creating a hot spot. There are also potential hot spots in the northeast. From my data, it appears that the bulk of the propagule pressure is in the western United States. Across all 12 species, the invasibility index ranges from species with a concentrated distribution such as *Pennisetum ciliare* (Buffelgrass) to a wider distribution such as Japanese stiltgrass (*M. vimineum*).

Discussion

I achieved excellent model performance based on AUC with the data and computing power that are currently available, with the understanding that I did not capture every location of each species modeled and that the available data were not collected with probabilistic sampling. And for the locations for which I had data, this was still a resolution that may miss patchily distributed resources at the microscale, focusing mostly on large-scale climate patterns of the invaders (Scott et al. 2002). These models were reliant not only on the quality and number of species data points available, but also on predictor layers used and the extent and resolution of the models being considered (Lobo et al. 2008). Future climate scenario models also contain their own uncertainty, especially concerning frequency of climate station data and interpolation techniques used to create a continuous surface between stations (Scott et al. 2002). I presented first iteration models that can point managers and field crews to gaps in information and guide resource managers to suitable areas to collect more information.

This analysis defines the leading and trailing edge of invasion for these 12 species. Thuiller et al. (2008) suggested looking at these leading and trailing edges, and incorporating migration into the modeling of the leading edge and persistence into the modeling on the trailing edge. Finding a way to incorporate these variables into such a large-scale model is a challenging and worthwhile task for future analysis.

The invasibility index is a simple distance function that does not include human accelerated dispersal such as commerce and trade, trucks, landscaping and disturbance facilitated invasion (Hodkinson and Thompson 1997, Mack and Lonsdale 2001, Reichard and White 2001). These are all important factors in the spread of invasive plants and excellent future projects. The models were also limited by the patchy nature of the presence data I was able to compile. Populations may exist in areas where there were data gaps, and these locations will be under-valued in the index.

Current species-environmental matching models performed well for this group of species with 10 of 12 models having AUC's indicating excellent model performance. The two species that did not perform as well may need additional predictor layers such as canopy cover, soils, or elevation. I also recognize that I had access to large amounts of data, and the models may not perform as well with a smaller sample size (the smallest sample size was 282). However, Maxent models have been used to model rare and threatened species using even fewer than 30 data points (Pearson et al. 2007). Additionally, due to my lack of absence data, I was only able to calculate AUC as a performance metric using a semi-independent data set. Ideally, I would calculate multiple metrics and examine model performance across them all (Lobo et al. 2008), while using an independent data set that may not suffer from the same biases as the dataset used to train the model.

However, given these caveats, this systematic approach has many advantages to resource managers and policy makers. The models are easily updated as information becomes available. Providing predictions of current habitat suitability, highlighting data gaps, and showing maps of clamping may entice resource managers to collect more data and amend the information that currently exists, allowing for the creation of even better models.

Climate scenarios

Forecasts are a tricky business. This does not stop the land managers and policy makers from asking scientists and experts to set priorities or give guidelines for setting priorities for rapid response and containment of invasive species. Forecasts are simply a tool to assess potential spread of a species. These forecasts are particularly important for invasive species early in the invasion process that might not have filled all of their niches. For example, the model predicts that *Microstegium vimineum* will have 133,000 additional km^2 of potential suitable habitat by the year 2035. If land managers are able to keep a watch on these areas before the species spreads it may be possible to contain the invasion (Moody and Mack 1988). The fundamentals of early detection have not changed, but the habitat that is potentially suitable for species may be shifting with the changing climate.

Most of the species modeled in this study were considered habitat generalists. Lobo et al. (2008) have claimed that Maxent models do not perform well on habitat generalists, yet these models did perform well. For the two species that had models that did not perform as well, I may need to add additional predictive layers to the model, use a different resolution, or even a different modeling technique. Not every species will respond to the same modeling format, and there are many techniques to choose from (Guisan and Zimmermann 2000, Elith et al. 2006, Evangelista et al. 2008).

Invasibility Index

While I was not able to address biotic interaction or competition in these models, they could be incorporated by using predictor variables of the competition (Leathwick and Austin 2001, Anderson et al. 2002). However, I did make an initial attempt at addressing propagule pressure, by devising the invasion index and looking at distance from known seed source within potential suitable habitat as a proxy for propagule pressure. I recognize that I do not have data for every location of the species, yet these data give a first order approximation of invasibility.

In addition to looking at the invasibility index, it is important to keep in mind the method of invasion for each species. Some invasive plant species spread primarily by runners and do not move very far with each season, while others spread primarily by seeds on the wind giving them farther reaching potential for spread. Plant dispersal is another worthy task of future analysis.

Utility of this approach

This approach provides a methodology to conduct a triage of invasive species. It has been established that it is cost effective and efficient to control small invasions early in the process (Moody and Mack 1988), and this method gives resource managers the ability to assess where an invasion may move in 10 to 25 years time to determine what may happen in the short term (Jarnevich and Stohlgren 2009), instead of looking at the year 2100. These models help to identify the leading edge of the invasion, the areas of new potential suitable habitat (Anderson et al. 2009). The leading edge is extremely important for watch lists, natural areas, ranches and farmers.

This method can be useful for targeted surveys (Morisette et al. 2006) and monitoring to better track actual spread of species. These models also identify areas where suitable habitat is receding, changing to less suitable habitat, although there is little evidence that, once established, plants ever leave a county-sized area (Stohlgren et al. 2008). Pearson and Dawson (2003) discuss that bioclimatic envelope modeling has its limitations, but it works well as a first approximation, especially applicable for an early detection and rapid assessment program.

Conclusions

My strategy was to assess plant invasion at a broad spatial scale. These same techniques are applicable to natural areas, counties, and state scales. I recognized that this is an iterative process of invasive species mapping and modeling. Models improve with more data, finer resolution prediction variables, and refined climate models. Different modeling techniques such as ensemble models (Araujo and New 2007) may also improve modeling efforts. I relied on Maxent, but other models may have done as good or better job of modeling these species (Elith et al. 2006). I have provided a first approximation model of continental US potential habitat distribution maps for 12 species at a fine temporal scale. I hope it will be useful.

Table 4. Species modeled. The sample size is the number of points used, after duplicates were removed. The training Area Under the Curve (AUC) measures model performance of 70% of the data. The Test AUC measures model performance on the remaining 30% of the data. The Threshold value uses the 10 percentile logistic threshold to distinguish between potentially suitable or unsuitable habitat. The area on the leading edge of the invasion is the area of potential habitat that has shifted from potentially unsuitable to potentially suitable between the current model and the 2035 model. The area on the trailing edge of the invasion is the area of habitat that has shifted from potentially suitable habitat to potentially unsuitable habitat between the current model and the 2035 model.

Scientific name	Common name	Sample size	Training AUC	Test AUC	Threshold value	Area on Leading Edge of invasion ($\sim km^2$)	Area on Trailing Edge of invasion ($\sim km^2$)	Change in Area ($\sim km^2$)	Habitat specialist ?	Introduced after 1900?
Bromus tectorum	Cheat grass	9517	0.84	0.83	0.43	131,000	131,000	0	No	No
Carduus nutans	Muskthistle	4670	0.88	0.88	0.39	372,000	383,000	-11,000	No	No
Celastrus orbiculatus	Oriental bittersweet	282	0.84	0.79	0.24	103,000	156,000	-53,000	No	No
Centaurea stoebe	Spotted knapweed	5899	0.91	0.90	0.46	195,000	245,000	-50,000	No	No
Cirsium arvense	Canada thistle	7960	0.86	0.86	0.45	206,000	423,000	-217,000	No	No
Cynoglossum officinale	Houndstounge	1884	0.89	0.88	0.34	228,000	219,000	9,000	No	No
Lepidium latifolium	Perrennial pepperweed	1015	0.93	0.91	0.36	546,000	451,000	95,000	No	Yes
Linaria dalmatica	Dalmation toadflax	1372	0.92	0.91	0.39	239,000	284,000	-45,000	No	No
Lonicera japonica	Japaneese honeysuckle	2771	0.70	0.68	0.40	170,000	144,000	26,000	No	No
Lythrum salicaria	Purple loosestrife	4921	0.85	0.84	0.37	376,000	293,000	83,000	Yes	No
Microstegium vimineum	Japanese stiltgrass	321	0.78	0.68	0.34	243,000	110,000	133,000	No	Yes
Pennisetum ciliare	Buffelgrass	1876	0.92	0.91	0.37	20,000	20,000	0	Yes	Yes

Table 5. Top predictors by percent contributed to the model

Variable	Percent Contribution
Mean Diurnal Range	24
Precipitation of Warmest Quarter	16
Min Temperature of Coldest Month	12
Mean Temperature of Driest Quarter	10
Mean Temperature of Wettest Quarter	10
Mean Temperature of Warmest Quarter	8
Precipitation of Wettest Month	7
Precipitation Seasonality	4
Precipitation of Driest Month	4
Isothermality	4

Figure 6. Potential habitat suitability modeling process for *Lepedium latifolium.* A. Distribution of data points. B1. Current potential habitat suitability, 2. Potential habitat suitability in 2020, 3. Potential habitat suitability in 2035. C. Scenario model showing stable potential suitable habitat in yellow, decreasing potential habitat suitability in blue, and increasing potential habitat suitability in red. D. Invasion index with colors on the red end of the spectrum closer to potential seed source and colors on the blue end of the spectrum farther away. In the entire figure grey represents unsuitable habitat and black represents clamping, or areas the model was extended beyond the environmental space it was trained on.

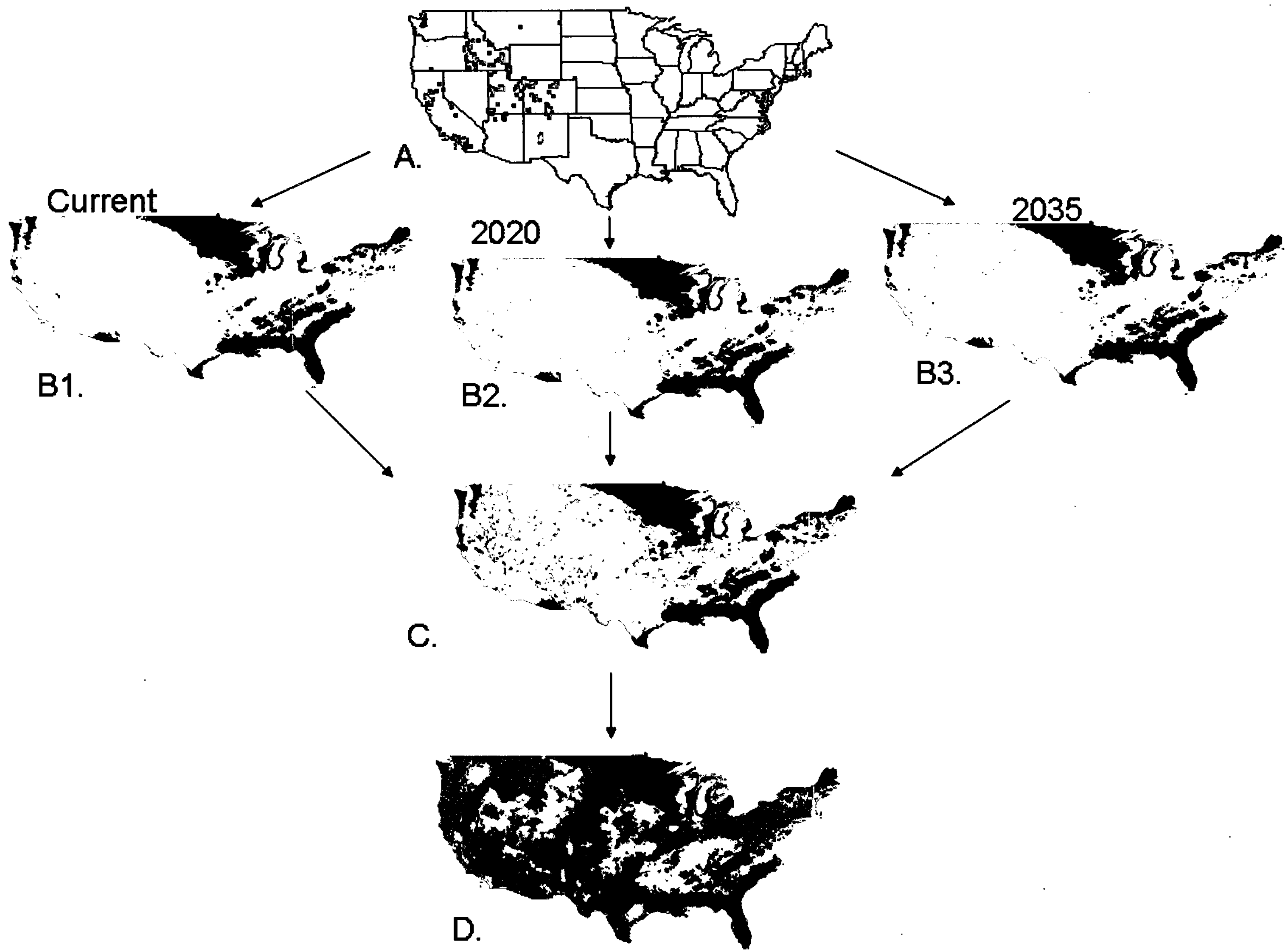

A.
Current
B1.
2020
B2.
2035
B3.
C.
D.

Figure 7. Response curves of the most influential predictors. A) Mean Diurnal Range, B) Precipitation of warmest quarter, C) Minimum temperature of coldest month, D) Mean temperature of wettest quarter.

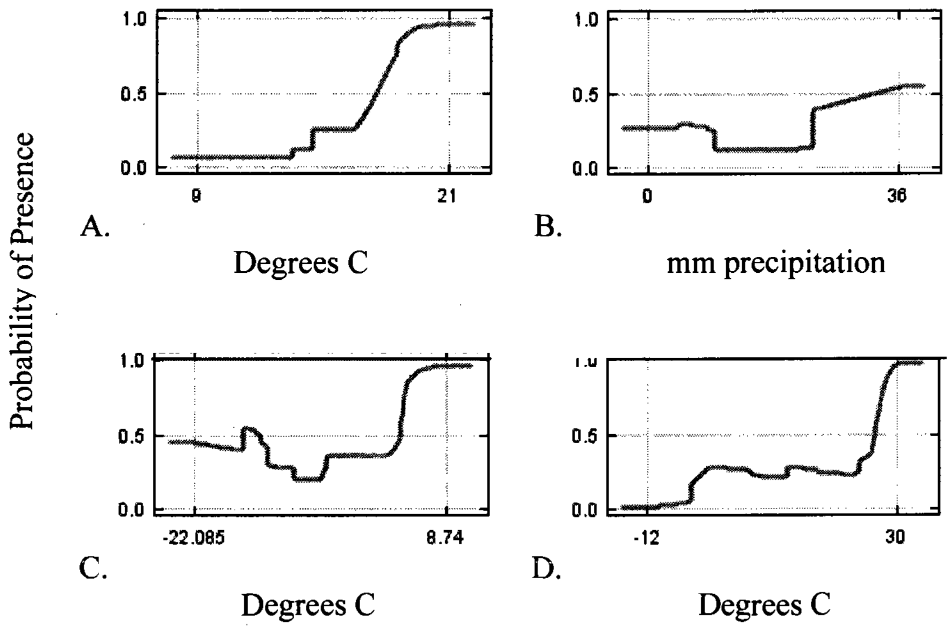
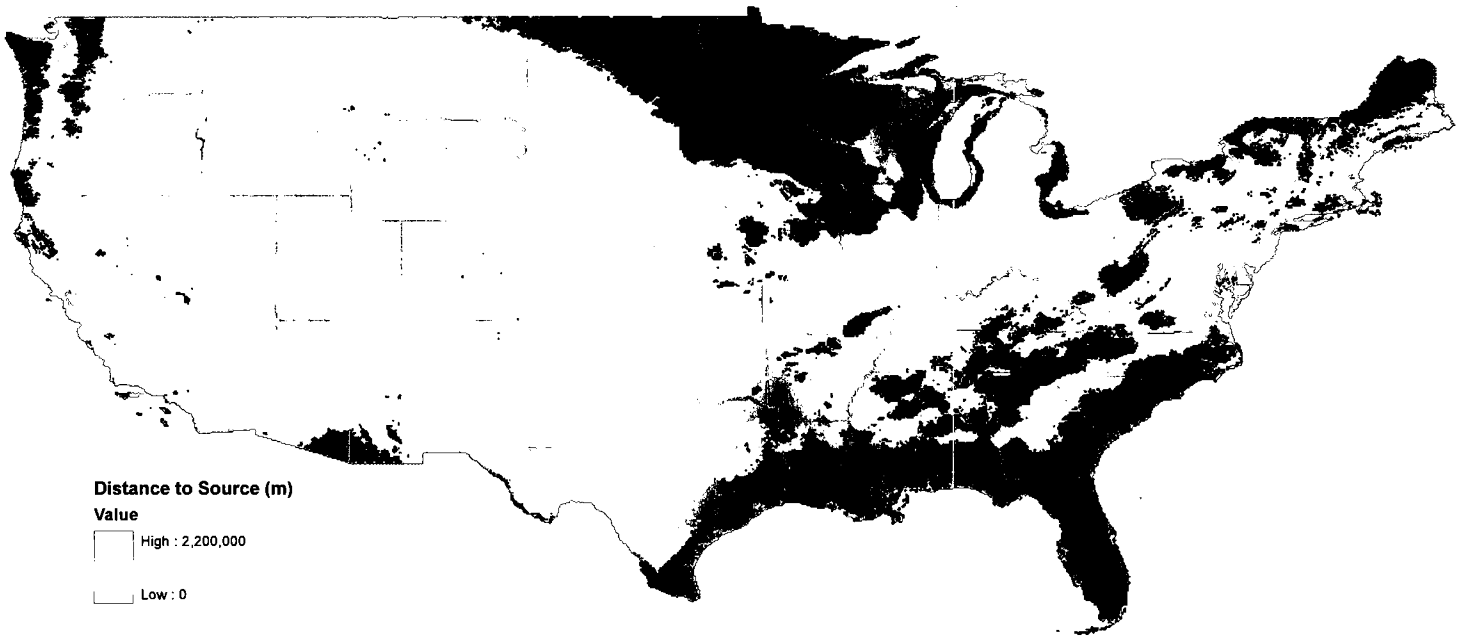


Figure 8. Invasibility Index. Colors on the red end of the spectrum are closer to known seed sources, colors on the blue end of the spectrum are farther away. Grey represents unsuitable habitat, black represents areas of clamping, or where the model was extended beyond the environmental space it was trained on.



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Conclusions to the Dissertation

Early detection of invasive species is such an important task on our national agenda that we need a central methodology and database to manage the problem. This is not just a problem for land mangers, we also need policy makers to address the issue (Lodge et al. 2006). I have outlined a system in the first chapter of this paper to deal with this problem that is costing the US almost $120 billion dollars each year (Pimentel et al. 2005). By using a centralized data collection system and defining the data that are needed, we can develop species watch lists and have more information on what invasive plants are nearest to our management units. These data, and establishing this policy, would help managers to set priorities for containment and control.

With these data, we will be able to use Geographic Information Systems to conduct analysis from simple displays of data to climate envelope modeling. Computing power has come so far in recent years that we are able to carry out complex analysis using desktop computers. I examined the difference between a regression model and an environmental envelope model for *Bufo marinus* finding that the two models produced similar results on the fairly broad scale of a 8-digit HUC for the southwestern United States.

Finally, I examined 12 invasive plants at a much finer scale of 4-m^2 resolution over the conterminous United States at three time scales accounting for climate change in the near term. With these models, I found that Maxent performed robustly for 10 out of the 12 species, with AUC values of 0.84 or higher. After accounting for clamping, areas on the leading edge of the invasion ranged from small increases of approximately 20,000 km^2 to larger increases of approximately 546,000 km^2; on the trailing edge potential suitable habitat shrank anywhere from about 20,000 km^2 to 451,000 km^2. This led the potential habitat of this suite of species to have changes in area of potential suitable habitat from a growth of 133,000 km^2 for *Microstegium vimineum* to a loss of potential suitable habitat of 217,000 km^2 for *Cirsium arvense*. I also looked at invasibility and, according to the currently available data, I found some areas to be far from propagule pressure, making these areas more difficult to invade. Again, these are first iteration models that have room for improvement, and they also give land managers a place to focus their efforts, whether it be filling data gaps or knowing where to look for potential invasions.

I have examined early detection and rapid assessment of invasive species at multiple spatial scales and addressed both policy and management methods in an effort to increase awareness of invasive species. To encourage this awareness we need to share data for species in centralized locations, establish watch lists, and follow through on early detection and rapid assessment programs. There are many data gaps to fill and potential invasions to catch early if we work together, increase awareness, and coordinate local and national scales of information, and data collection potentials. The policies, techniques, and technologies developed in this dissertation can be broadly applied to plants, animals, and pathogens worldwide.

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Appendix A: List of data sources

Data sources used to model the twelve invasive species in Chapter 3.

Data source	Citation
Crosier PhD - Department of Transportation	(Crosier 2004b)
Crosier PhD - Larimer County	(Crosier 2004b)
Crosier PhD - San Luis Valley	(Crosier 2004b)
Crosier PhD - The Nature Conservancy	(Crosier 2004b)
Crosier PhD - Jackson County	(Crosier 2004b)
Crosier PhD - Larimer County	(Crosier 2004b)
Crosier PhD - Otero	(Crosier 2004b)
Crosier PhD - Royal Gorge	(Crosier 2004b)
Crosier PhD - San Luis Valley	(Crosier 2004b)
Crosier PhD - Colorado State Parks	(Crosier 2004b)
Crosier PhD - CNHP	(Crosier 2004b)
Florida Natural Areas Inventory	http://fnai.org/invasivespecies.cfm
Florida Natural Areas Inventory	http://fnai.org/invasivespecies.cfm
The Great Lakes Indian Fish & Wildlife Commission	http://www.glifwc.org/
Idaho State Department of Agriculture	Invasive Species Coordinator
Invasive Plant Atlas of the MidSouth	http://www.gri.msstate.edu/ipams/
Invasive Plant Atlas of New England	http://nbii-nin.ciesin.columbia.edu/ipane/
Montana Fish, Wildlife, and Parks	http://fwp.mt.gov/insidefwp/gis/shapefiles/fasweeds.zip
Modified Whittaker Plot Information	(Stohlgren et al. 2006b)
National Institute of Invasive Species Science project - Air Force Academy Weed Mapping	www.NIISS.org
National Institute of Invasive Species Science project - Bohemian Foundation	www.NIISS.org
National Institute of Invasive Species Science project - Colorado	www.NIISS.org
National Institute of Invasive Species Science project - ELK	www.NIISS.org
National Institute of Invasive Species Science project - Grand Staircase Escalante National Monument	www.NIISS.org
National Institute of Invasive Species Science project - Grazing effects	www.NIISS.org
National Institute of Invasive Species Science project - GVM Weed Test	www.NIISS.org
National Institute of Invasive Species Science project - Hart Mountain National Antelope	www.NIISS.org
National Institute of Invasive Species Science project - Highway 24 Weed Mapping	www.NIISS.org
National Institute of Invasive Species Science project - Invasive Carduus Thistles	www.NIISS.org
National Institute of Invasive Species Science project - National Elk Refuge	www.NIISS.org
National Institute of Invasive Species Science project - National Wildlife Refuge - USGS	www.NIISS.org
National Institute of Invasive Species Science project - Nevada Cheatgrass	www.NIISS.org

National Institute of Invasive Species Science project - New Invaders Watch List	www.NIISS.org
National Institute of Invasive Species Science project - Peterson Air Force Base Weed Mapping	www.NIISS.org
National Institute of Invasive Species Science project - Plains Riparian study	www.NIISS.org
National Institute of Invasive Species Science project - Plants of Concern	www.NIISS.org
National Institute of Invasive Species Science project - Pondicherry National Wildlife	www.NIISS.org
National Institute of Invasive Species Science project - Rocky Mountain NP LANDGAP	www.NIISS.org
National Institute of Invasive Species Science project - SAIN Invasive Plants	www.NIISS.org
National Institute of Invasive Species Science project - SE-EPPC EDDMaps	www.NIISS.org
National Institute of Invasive Species Science project - September 2007 Training at the ELC	www.NIISS.org
National Institute of Invasive Species Science project - Wisconsin Invasive Plants of the Future	www.NIISS.org
National Institute of Invasive Species Science project - Colorado Department of Transportation	www.NIISS.org
National Institute of Invasive Species Science project - Hart Mountain National Antelope	www.NIISS.org
National Institute of Invasive Species Science project - National Bison Range	www.NIISS.org
Personal Collection of Robert K. Peet	The University of North Carolina at Chapel Hill
Personal Collection of James F. Quinn	University of California, Davis
Southwest Exotic Mapping Program	http://sbsc.wr.usgs.gov/research/projects/swepic/swemp/swempA.asp
Bureau of Land Management, Utah State Office	Salt Lake City, UT
TexasInvasives.org	http://www.texasinvasives.org/

Appendix B: Data distribution, spread model, and invasibility for the 12 species in Chapter 3

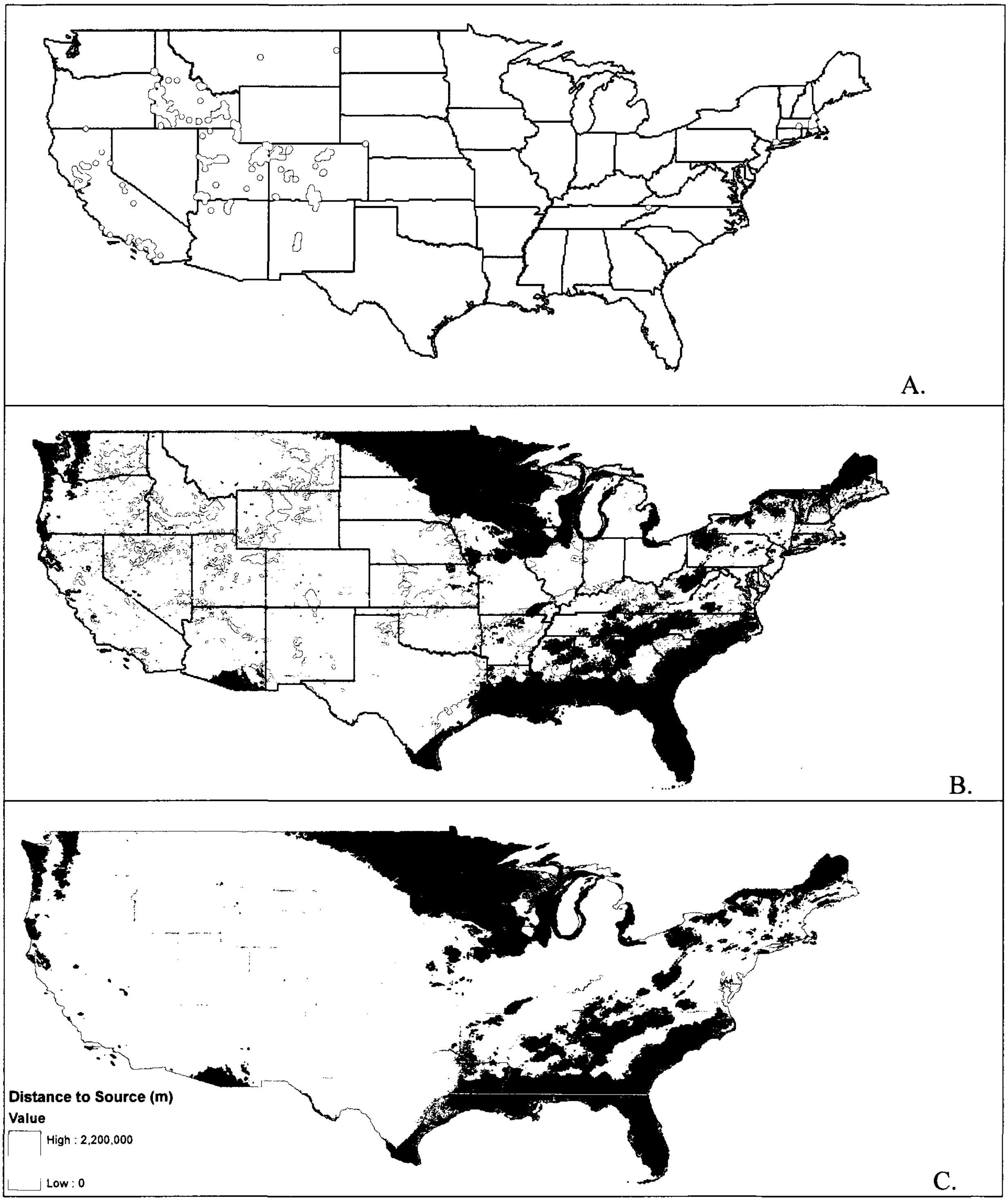

Figure 9. *Lepidium latifolium* models. A. Point distribution, B. Scenario model showing stable potential suitable habitat in yellow, decreasing potential habitat suitability in blue, and increasing potential habitat suitability in red, C. Invasion index with colors on the red end of the spectrum closer to potential seed source and colors on the blue end of the spectrum farther away. In the entire figure grey represents unsuitable habitat and black represents clamping, or areas the model was extended beyond the environmental space it was trained on.

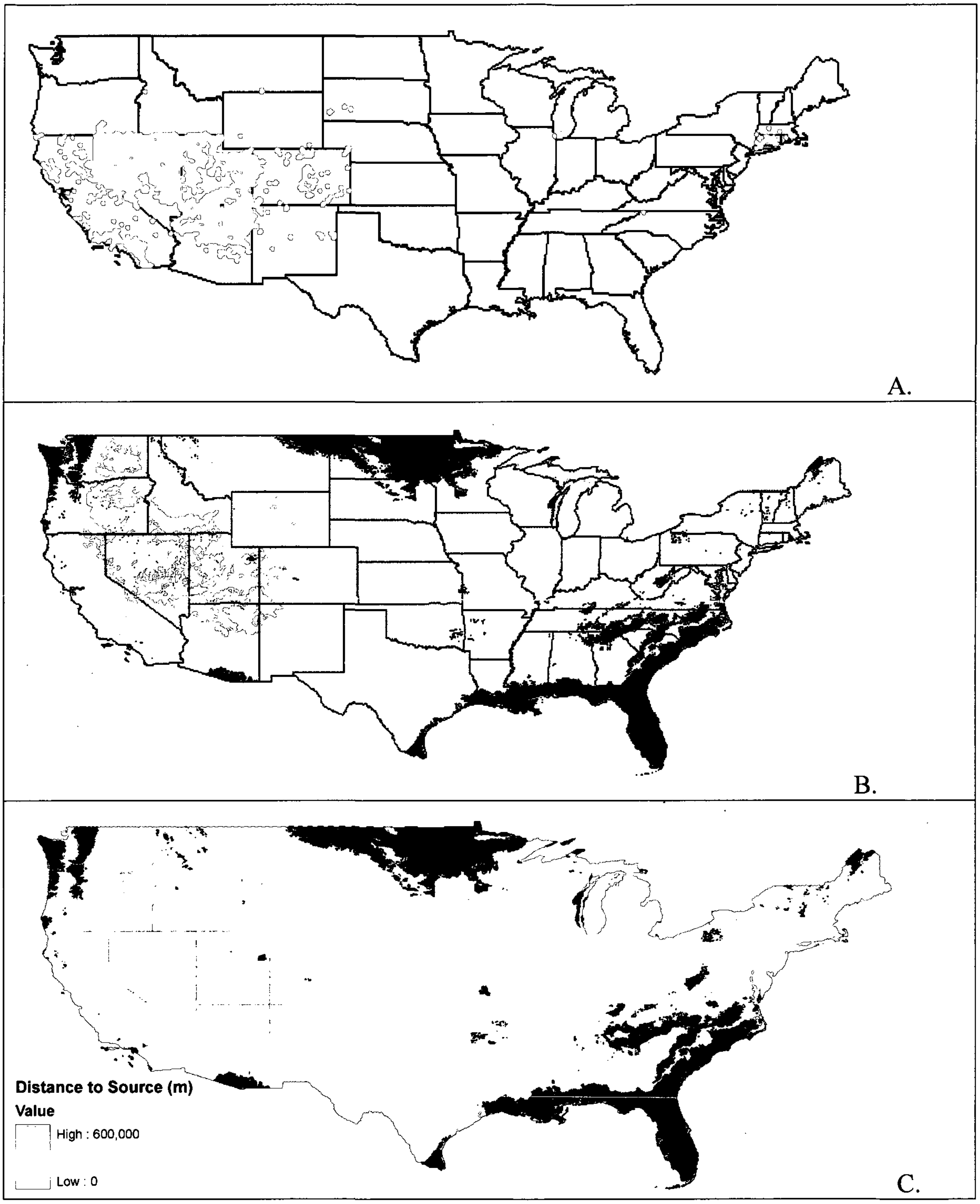

Figure 10 *Bromus tectorum* models. A. Point distribution, B. Scenario model showing stable potential suitable habitat in yellow, decreasing potential habitat suitability in blue, and increasing potential habitat suitability in red, C. Invasion index with colors on the red end of the spectrum closer to potential seed source and colors on the blue end of the spectrum farther away. In the entire figure grey represents unsuitable habitat and black represents clamping, or areas the model was extended beyond the environmental space it was trained on.

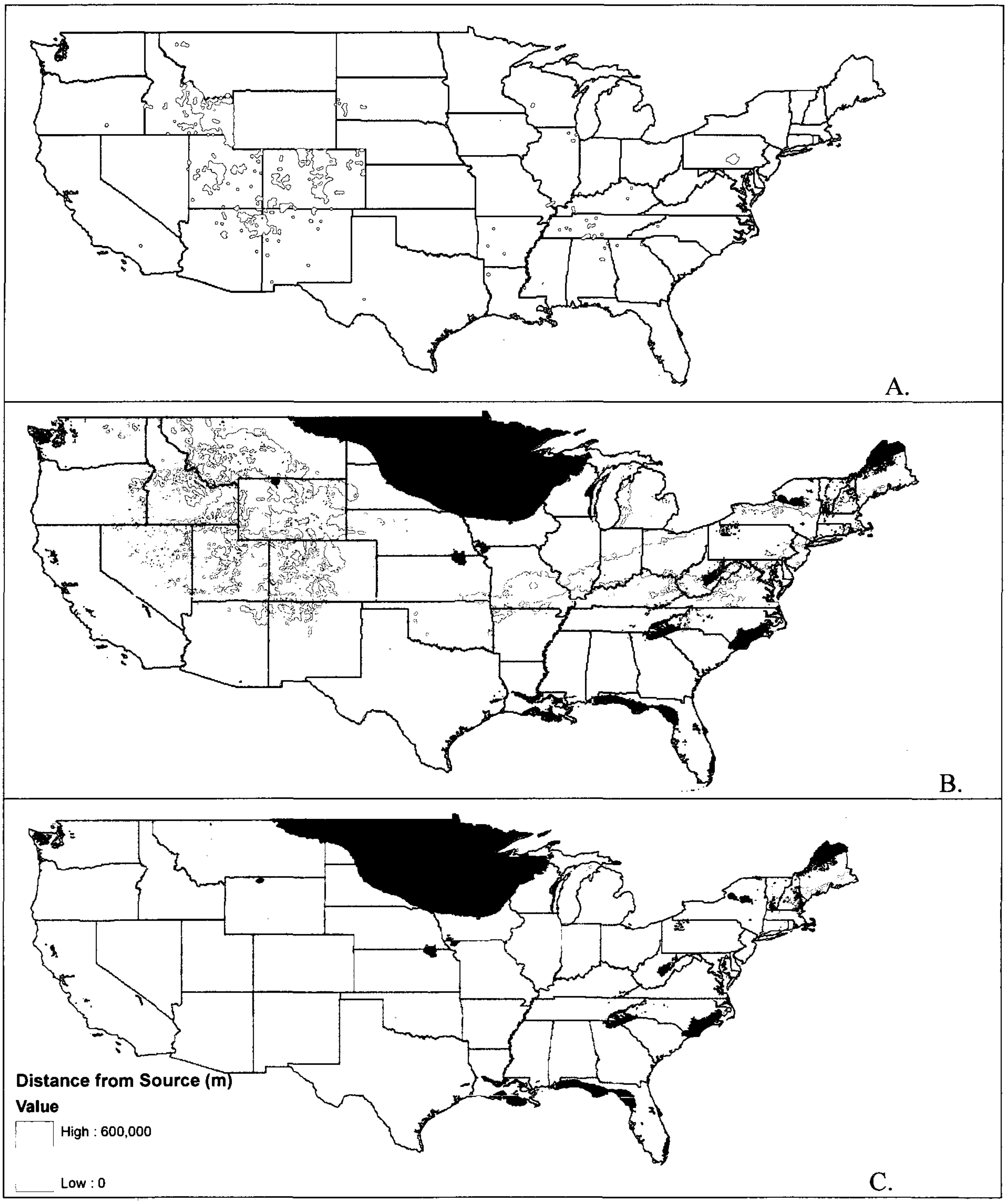

Figure 11. *Carduus nutans* models. A. Point distribution, B. Scenario model showing stable potential suitable habitat in yellow, decreasing potential habitat suitability in blue, and increasing potential habitat suitability in red, C. Invasion index with colors on the red end of the spectrum closer to potential seed source and colors on the blue end of the spectrum farther away. In the entire figure grey represents unsuitable habitat and black represents clamping, or areas the model was extended beyond the environmental space it was trained on.

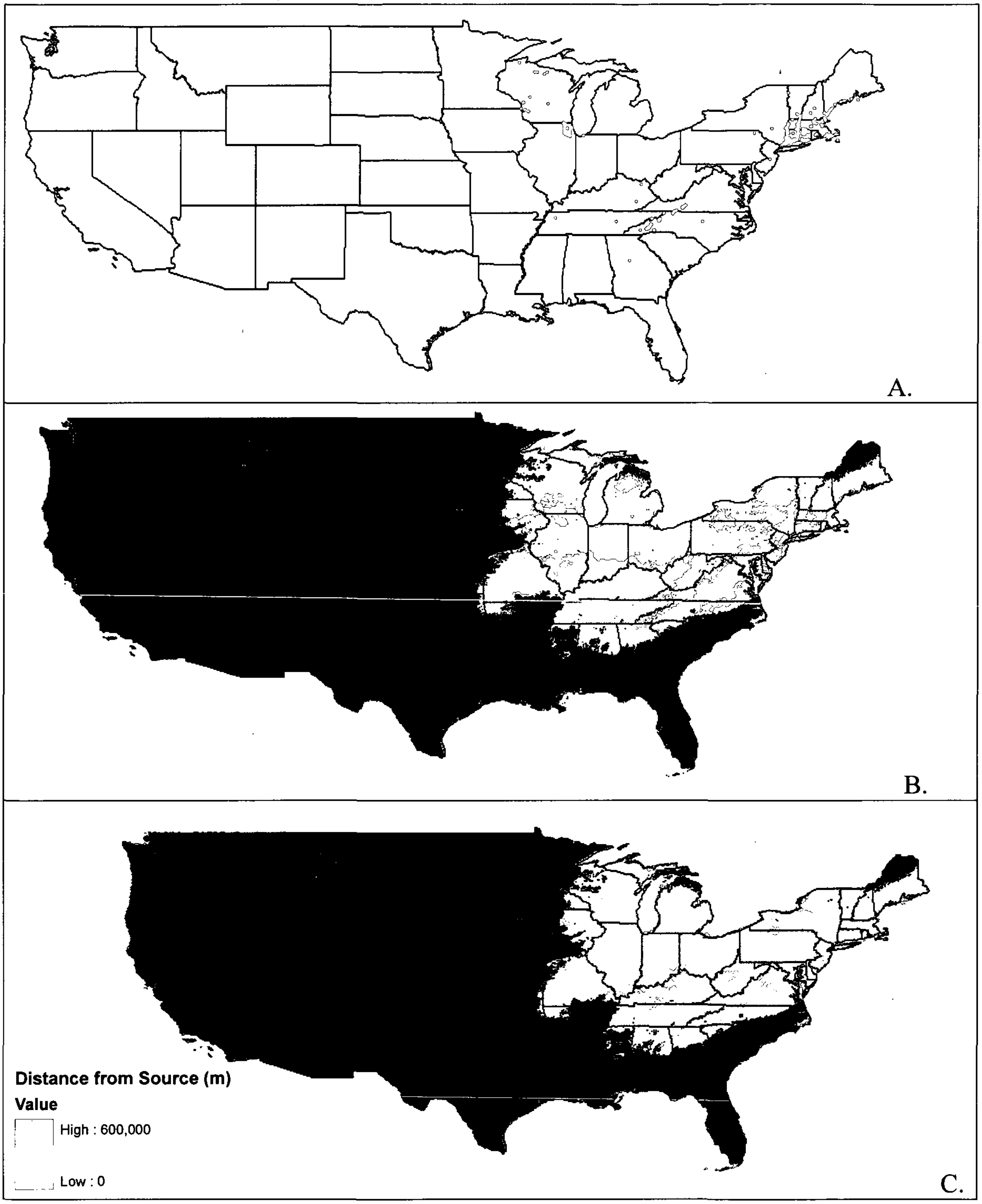

Figure 12 *Celastrus orbiculatus* models. A. Point distribution, B. Scenario model showing stable potential suitable habitat in yellow, decreasing potential habitat suitability in blue, and increasing potential habitat suitability in red, C. Invasion index with colors on the red end of the spectrum closer to potential seed source and colors on the blue end of the spectrum farther away. In the entire figure grey represents unsuitable habitat and black represents clamping, or areas the model was extended beyond the environmental space it was trained on.

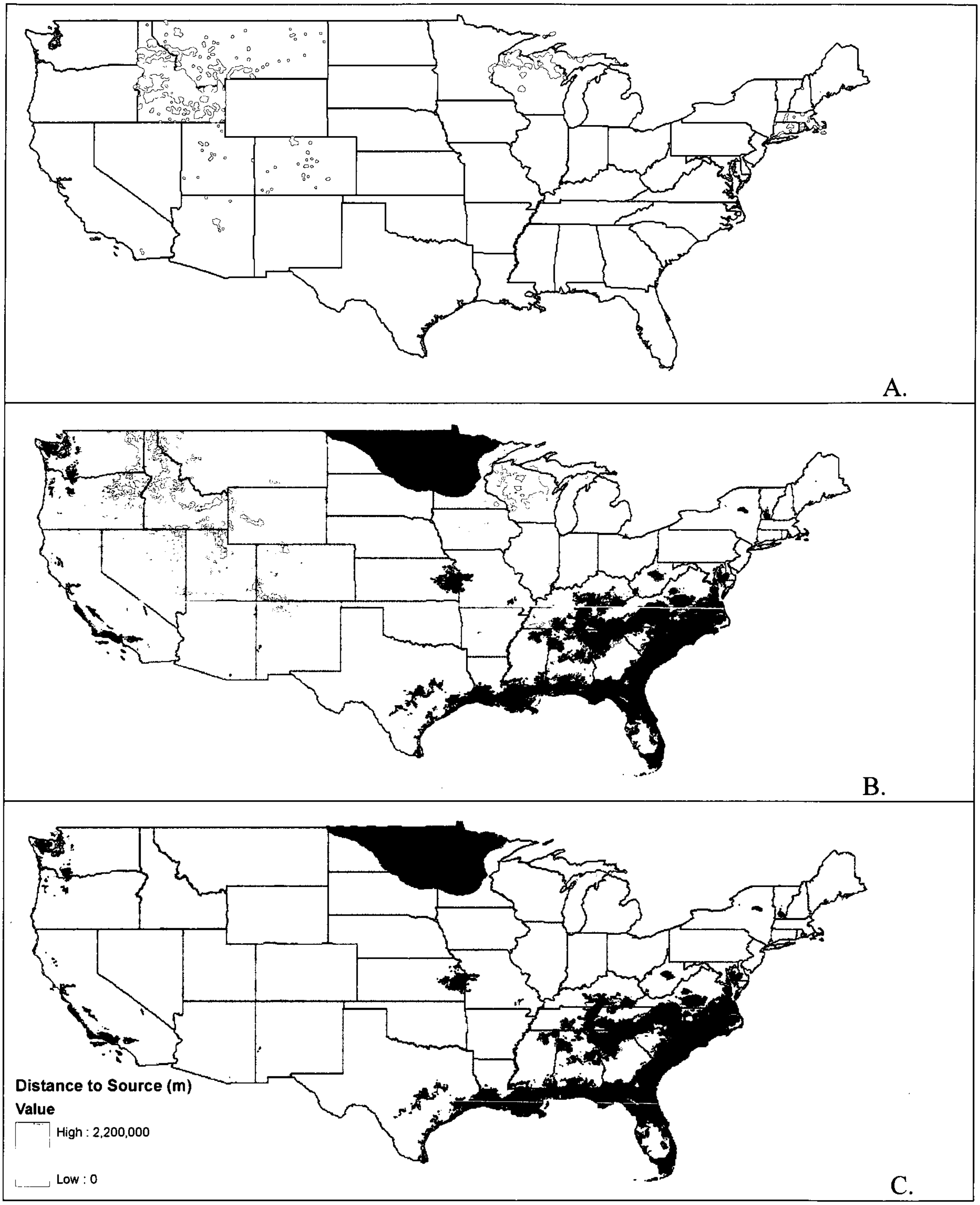

Figure 13. *Centaurea stoebe* models. A. Point distribution, B. Scenario model showing stable potential suitable habitat in yellow, decreasing potential habitat suitability in blue, and increasing potential habitat suitability in red, C. Invasion index with colors on the red end of the spectrum closer to potential seed source and colors on the blue end of the spectrum farther away. In the entire figure grey represents unsuitable habitat and black represents clamping, or areas the model was extended beyond the environmental space it was trained on.

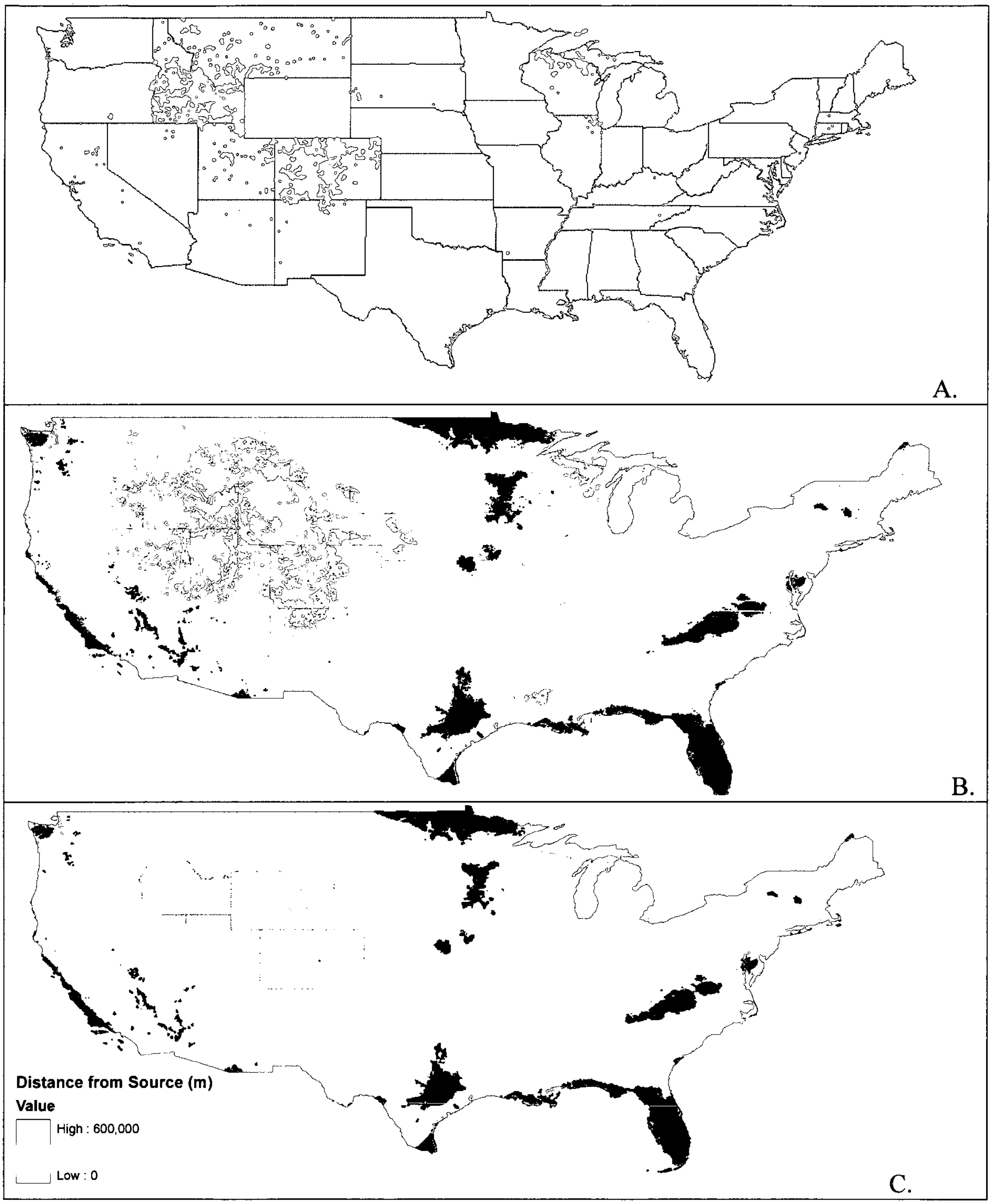

Figure 14. *Cirsium arvense* models. A. Point distribution, B. Scenario model showing stable potential suitable habitat in yellow, decreasing potential habitat suitability in blue, and increasing potential habitat suitability in red, C Invasion index with colors on the red end of the spectrum closer to potential seed source and colors on the blue end of the spectrum farther away. In the entire figure grey represents unsuitable habitat and black represents clamping, or areas the model was extended beyond the environmental space it was trained on.

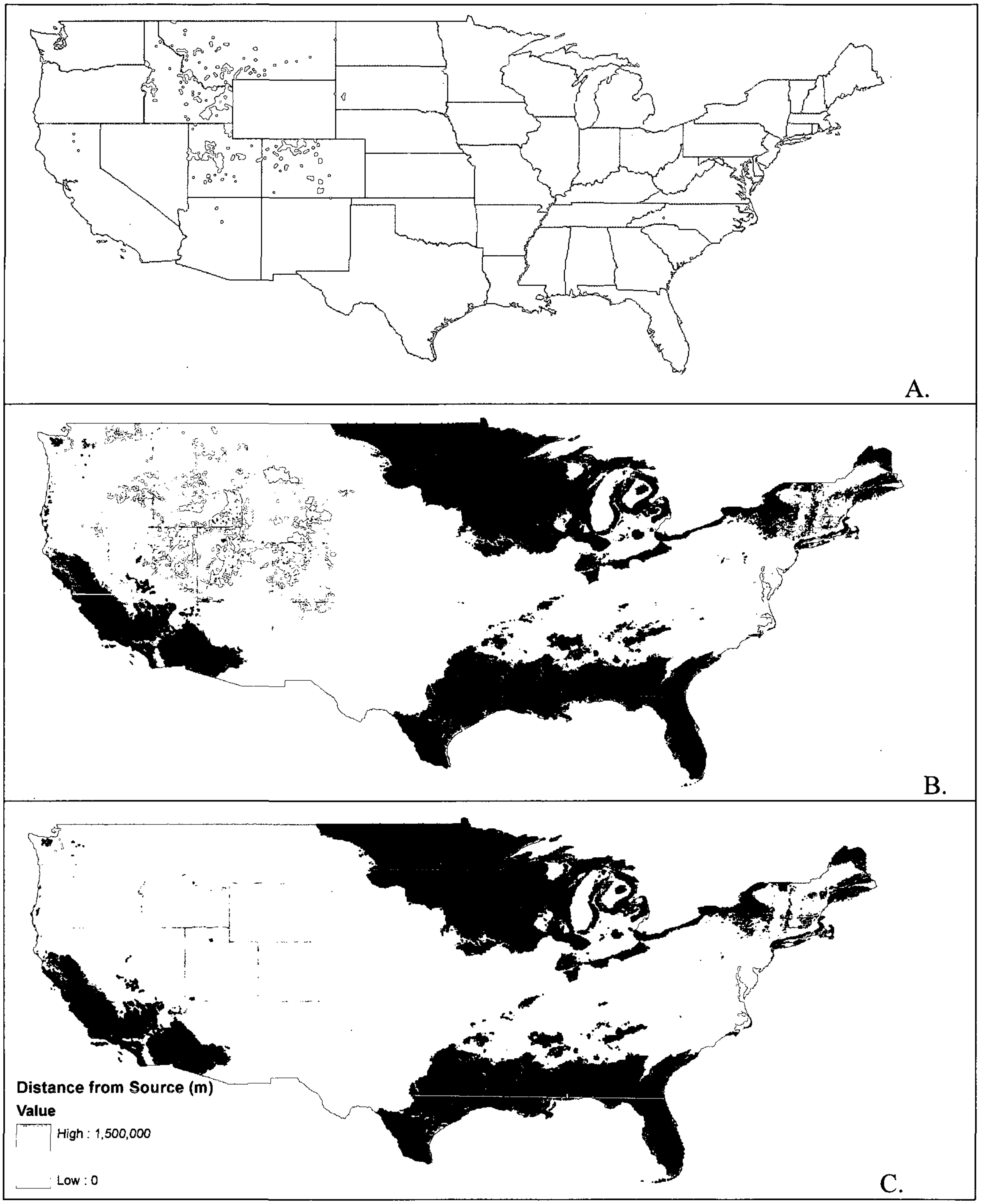

Figure 15. *Cynoglossum officinale* models. A. Point distribution, B. Scenario model showing stable potential suitable habitat in yellow, decreasing potential habitat suitability in blue, and increasing potential habitat suitability in red, C. Invasion index with colors on the red end of the spectrum closer to potential seed source and colors on the blue end of the spectrum farther away. In the entire figure grey represents unsuitable habitat and black represents clamping, or areas the model was extended beyond the environmental space it was trained on.

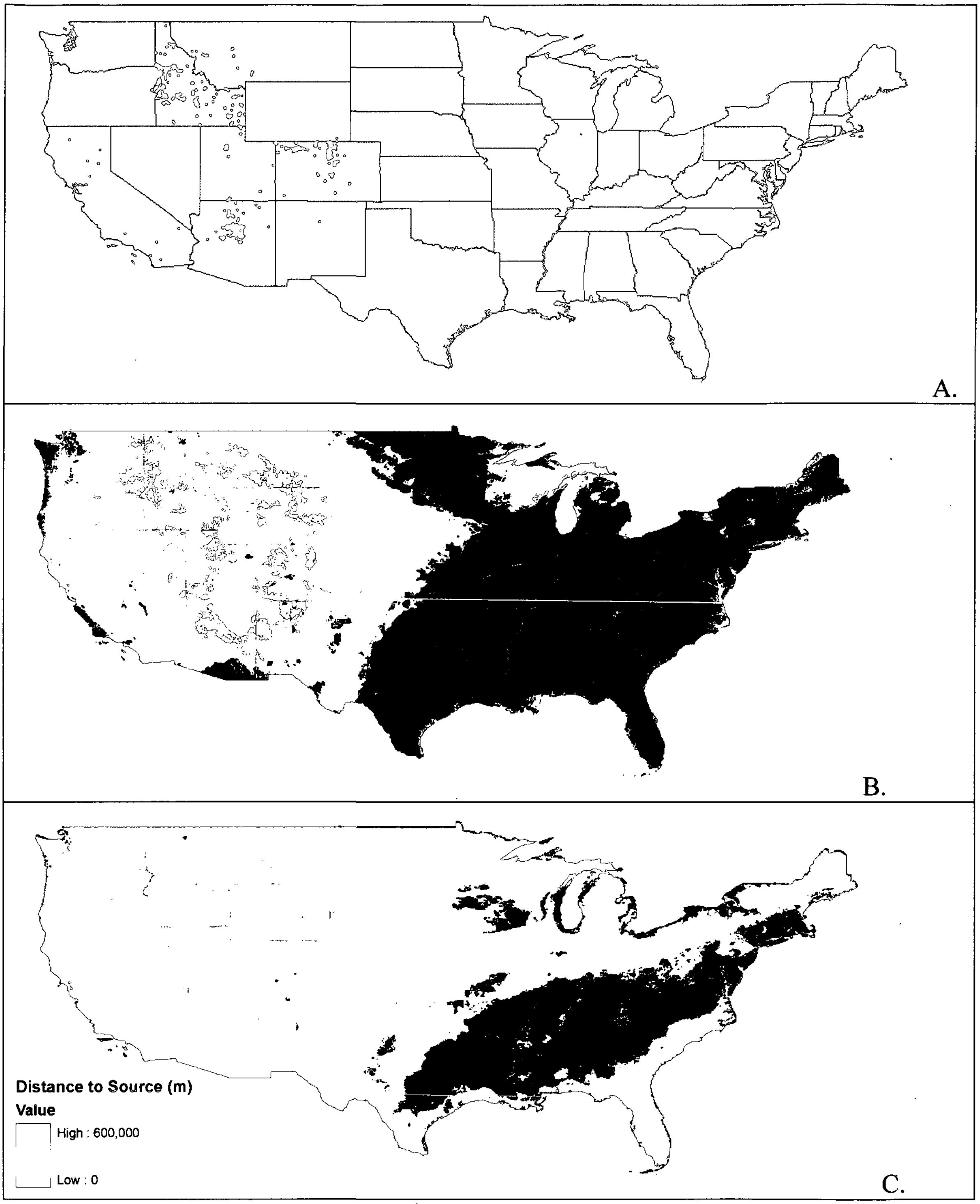

Figure 16. *Linaria dalmatica* models. A. Point distribution, B. Scenario model showing stable potential suitable habitat in yellow, decreasing potential habitat suitability in blue, and increasing potential habitat suitability in red, C. Invasion index with colors on the red end of the spectrum closer to potential seed source and colors on the blue end of the spectrum farther away. In the entire figure grey represents unsuitable habitat and black represents clamping, or areas the model was extended beyond the environmental space it was trained on.

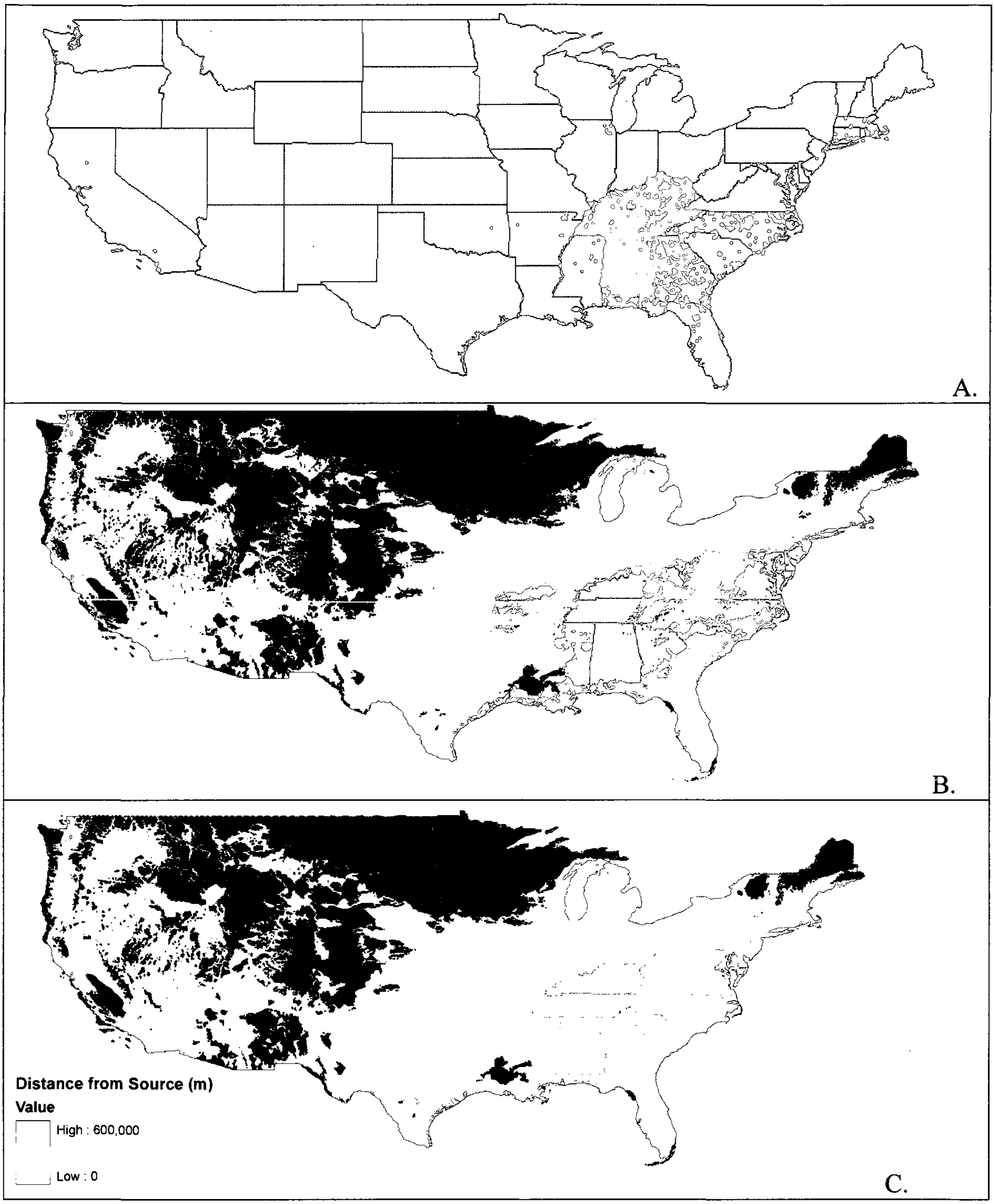

Figure 17. *Lonicera japonica* models. A. Point distribution, B. Scenario model showing stable potential suitable habitat in yellow, decreasing potential habitat suitability in blue, and increasing potential habitat suitability in red, C. Invasion index with colors on the red end of the spectrum closer to potential seed source and colors on the blue end of the spectrum farther away. In the entire figure grey represents unsuitable habitat and black represents clamping, or areas the model was extended beyond the environmental space it was trained on.

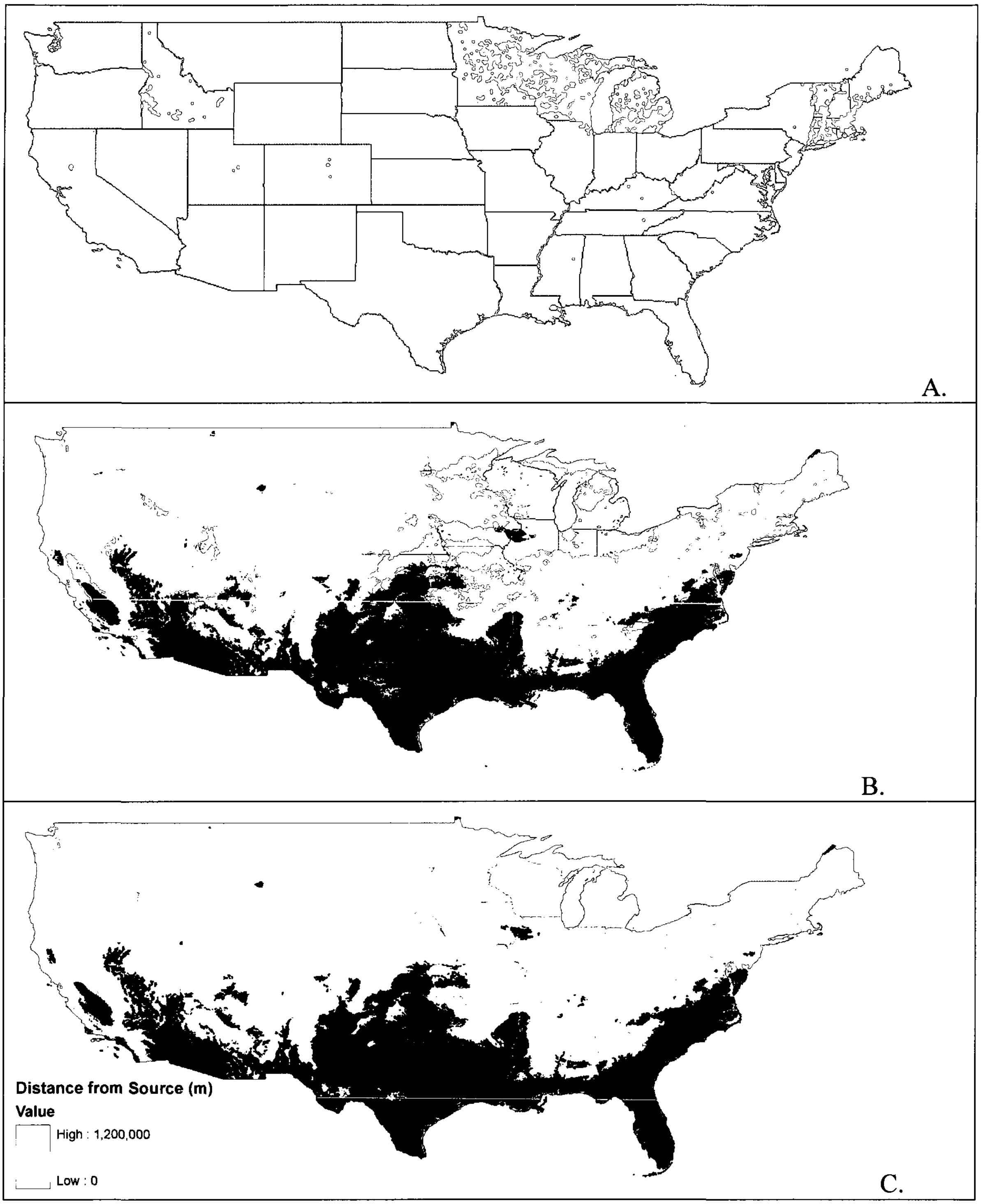

Figure 18. *Lythrum salicaria* models. A. Point distribution, B. Scenario model showing stable potential suitable habitat in yellow, decreasing potential habitat suitability in blue, and increasing potential habitat suitability in red, C. Invasion index with colors on the red end of the spectrum closer to potential seed source and colors on the blue end of the spectrum farther away. In the entire figure grey represents unsuitable habitat and black represents clamping, or areas the model was extended beyond the environmental space it was trained on.

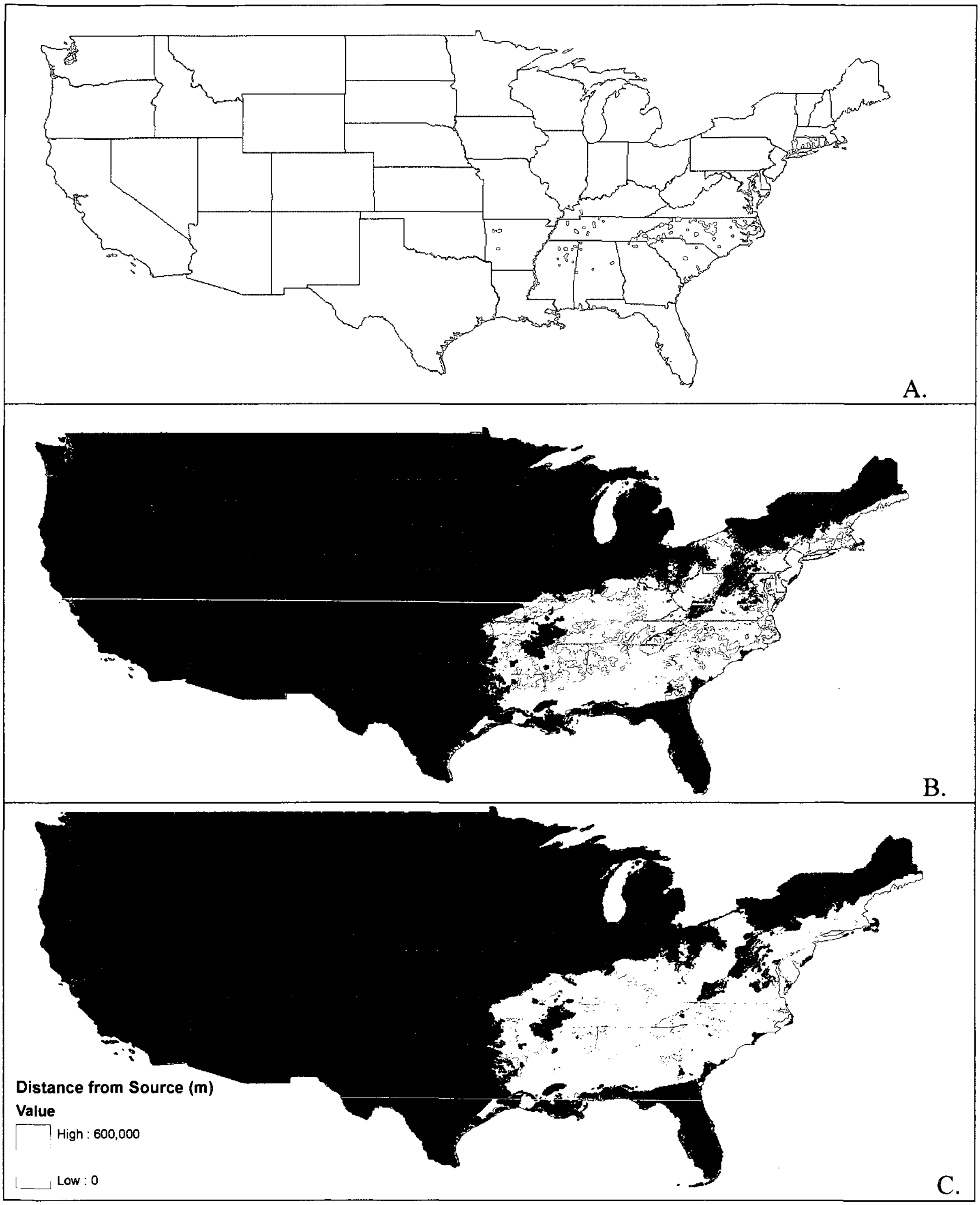

Figure 19. *Microstegium vimineum* models. A. Point distribution, B. Scenario model showing stable potential suitable habitat in yellow, decreasing potential habitat suitability in blue, and increasing potential habitat suitability in red, C. Invasion index with colors on the red end of the spectrum closer to potential seed source and colors on the blue end of the spectrum farther away. In the entire figure grey represents unsuitable habitat and black represents clamping, or areas the model was extended beyond the environmental space it was trained on.

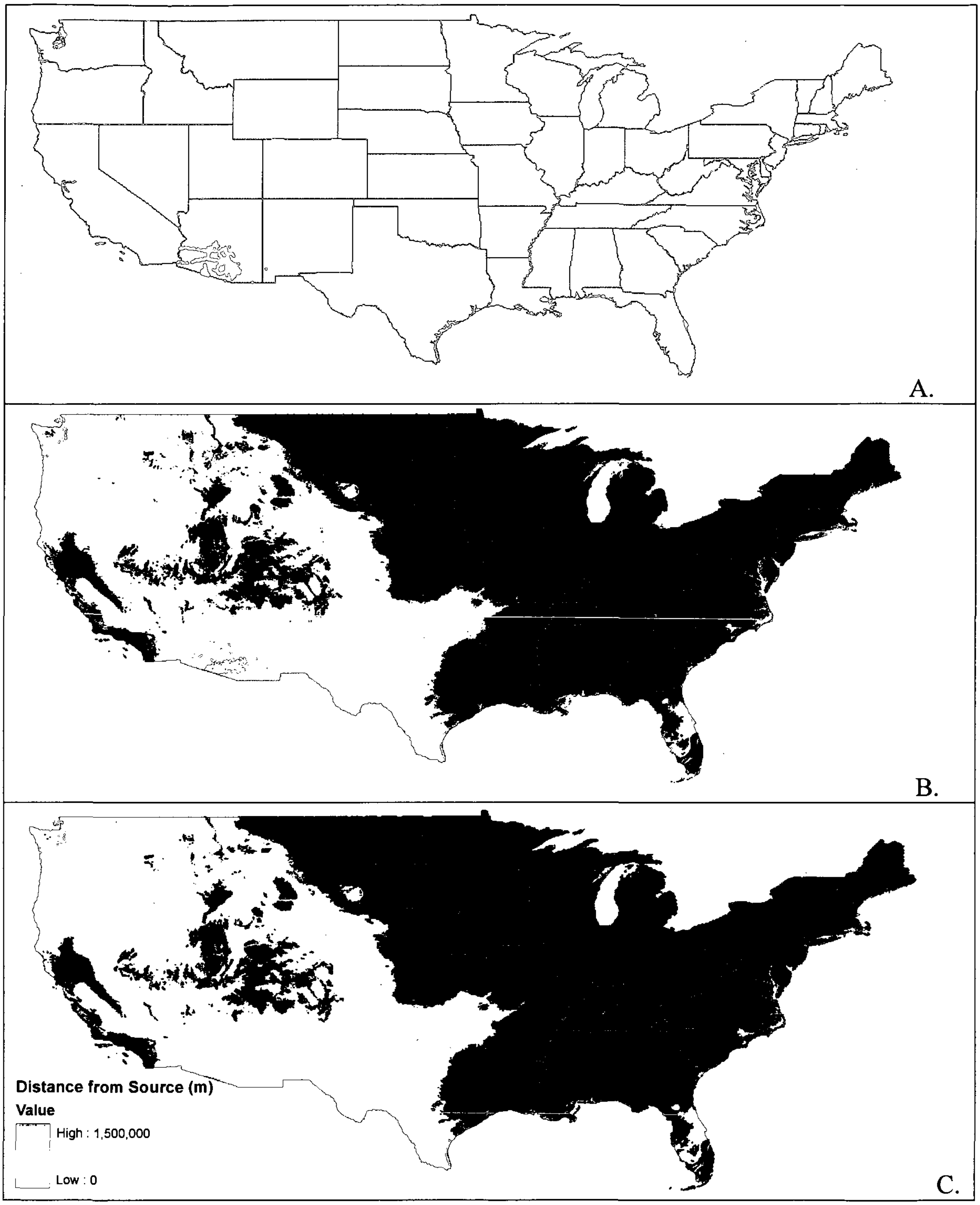

Figure 20. *Pennisetum ciliare* models. A. Point distribution, B. Scenario model showing stable potential suitable habitat in yellow, decreasing potential habitat suitability in blue, and increasing potential habitat suitability in red, C. Invasion index with colors on the red end of the spectrum closer to potential seed source and colors on the blue end of the spectrum farther away. In the entire figure grey represents unsuitable habitat and black represents clamping, or areas the model was extended beyond the environmental space it was trained on.