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A habitat assessment to locate tree of heaven [Ailanthus altissima, (Mill.) Swingle] in Mammoth Cave National Park

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To the Graduate Council:

I am submitting herewith a dissertation written by Belinda D. Esham entitled "A habitat assessment to locate tree of heaven [Ailanthus altissima, (Mill.) Swingle] in Mammoth Cave National Park." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Natural Resources.

Scott E. Schlarbaum, Major Professor

We have read this dissertation and recommend its acceptance:

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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and recommend its acceptance:

Frank Van Manen

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David Ostermeier

David Ostermeier

Bruce Tonn

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Accepted for the Council:

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A HABITAT ASSESSMENT TO LOCATE TREE OF HEAVEN [*Ailanthus altissima*, (Mill.) Swingle] IN MAMMOTH CAVE NATIONAL PARK

A Dissertation

Submitted for the

Doctor of Philosophy Degree

University of Tennessee, Knoxville

Belinda D. Esham
May 2009

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ABSTRACT

Invasive, nonnative plants pose a significant threat to national parks. Effective and efficient tools are needed to help managers detect, prioritize and target nonnative plants for control. I used spatial modeling techniques to predict the occurrence of tree of heaven (*Ailanthus altissima*, (Mill.) Swingle) in Mammoth Cave National Park (MACA), Kentucky. Tree of heaven is known to be a problematic invasive, nonnative plant species and was identified as a priority for control at MACA. I developed a multivariate habitat model to determine optimal habitat for tree of heaven within MACA. Habitat characteristics of 135 known tree of heaven locations were used in combination with seven environmental variables to calculate the predicted probability of occurrence of tree of heaven in MACA using logistic regression analysis. Variables for predicting habitat were created from public records, MACA databases, and a geographic information system (GIS). Twenty-seven *a priori* models were developed based on the biological requirements of the species and observations of invasion pattern in MACA and the most parsimonious model was selected using Akaike's Information Criteria. The seven variables included in the optimal model were derived from soil, site classification, geology, topography, and canopy coverage. I tested the predictive power of the model with independently collected presence and absence data. Ninety seven percent of test locations for tree of heaven were associated with predicted probabilities in the 0–0.30 range. The model improved the probability of finding tree of heaven compared with random searches by approximately 10%. It had poor discrimination (false positive = 0.31, false negative = 0.38, overall reliability = 0.41) and was not well calibrated. Based on its low predictive power, this habitat model could not be recommended for use in managing tree of heaven populations at MACA. Model failure could be attributed to a number of factors and/or combinations of factors including insufficient data, inappropriate scale and the generalist nature of the species. However, results from this study elucidate areas for future research into the applicability of habitat modeling to invasive, nonnative species at local scales.

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CHAPTER I

INTRODUCTION

Nonnative (i.e., nonindigenous, nonnative, alien, exotic) organisms are species that have been transported outside their original biogeographic range. Humans have moved nonnative species throughout the world accidentally and intentionally throughout history. In modern times, however, efficient transportation systems have dramatically increased the rate of nonnative species introduction (Loope 2004, Mooney and Hobbs 2000). The adverse effects of invasive, nonnative species on native populations, communities, and ecosystems have been well documented (Drake et al. 1989, Elton 1958, Mooney and Drake 1986, Vitousek et al. 1997).

The threat posed by nonnative species has been recognized in the U.S. In 1977, President Jimmy Carter signed the Nonnative Organisms Executive Order 11987, which mandated federal agencies to restrict the introduction of nonnative species on federal lands and encourage state and local governments to do the same. It also restricted the importation of nonnative species that have an adverse effect on native ecosystems. The next major federal milestone was an Office of Technology Assessment (OTA) Report on Harmful Non-indigenous Species (1993), which pointed out the estimated economic losses caused by nonnative species and lack of effectiveness in both national and international policy to address the problem. In 1999, Executive Order 11987 was revoked to be replaced by the more specific Executive Order 13112, which was signed by President William Clinton. It expounded on the Executive Order 11987, and directed responsible federal agencies to: 1) prevent the introduction of invasive species; 2) detect and respond rapidly to control populations; 3) monitor invasive species populations; 4) provide for restoration of native species and habitat conditions in ecosystems that have been invaded; 5) conduct research on invasive species; and 6) develop technologies to prevent introduction and control invasive species.

Federal landowners are required to translate national policy into organizational policy. The National Park Service (NPS) is mandated with preservation of natural heritage, including native plant resources, in the enabling legislation that created the agency. As part of this mandate, the NPS must find ways to cope with the impacts of nonnative species (NPS Organic Act 1916). Problems caused by nonnative forest insects and pathogens are typically addressed on a case-by-case basis within each national park but some are not addressed at all. A more coordinated approach exists regarding nonnative plants. Seventeen Nonnative Plant Management Teams (EPMTs) have been formed and are deployed regionally to control nonnative plants in national parks. The teams are a relatively new approach and were modeled after the rapid response approach used in wildland fire fighting. Each EPMT has a regional scope (e.g., the EPMT for the southeastern U.S. is responsible for 15 NPS units). Because the time a team can spend in an individual park is limited, EPMTs rely on directed survey methods and information from NPS staff to locate and prioritize areas to control nonnative plants.

STUDY JUSTIFICATION

Controlling nonnative plants before they become established is a key focus of invasive species programs (Rejmánek and Pitcairn 2002, Timmins and Braithwaite 2002). Once established, nonnative plant populations can become major infestations, displacing native vegetation and altering disturbance regimes (Simberloff 1996). Identifying sites of initial infestation is of primary importance because once an invasive, nonnative plant becomes easy to detect, it is often too late to effectively control it. Eradication is the best option, but is often unsuccessful if the invasive species is not detected early (Simberloff 1996).

Nonnative species are a threat to biodiversity in the terrestrial ecosystems at Mammoth Cave National Park (MACA) (National Park Service 1996a). Major infestations of Japanese stilt grass [*Microstegium vimineum* (Trin.) Camus] and garlic mustard [*Alliaria petiolata* (Bieb) Cavara and Grande] have already overtaken large areas within the national park, and eradication is not a management option anymore (M. DePoy, NPS, personal communication). The MACA Science and Resources Management division has articulated concern with protecting and conserving unique plant communities in the park and would like to prioritize management of nonnative species based on that criterion (M. DePoy, NPS, personal communication).

Currently MACA responds to nonnative plant infestations on a case-by-case basis. Park staff direct EPMTs and volunteer groups to areas where infestations are highly visible (e.g., roadside infestations) or where nonnative plants have been observed while conducting other fieldwork. Often, infestations in the forest occur and spread before they are discovered. No coordinated effort has been undertaken to rank the severity of different nonnative plant infestations in the park and no decision tools exist to assist staff in setting priorities for eradication and control efforts (M. DePoy, NPS, personal communication).

Resource managers at MACA are interested in using science tools to evaluate, map, and manage invasive, nonnative plants within the national park. Habitat models have been used to predict the occurrence of plants across relatively large areas (Boetsch et al. 2003, Thompson et al. 2006) and have been used successfully to map habitats of native plants impacted by nonnative pests (van Manen et al. 2002). Applying modeling techniques to nonnative plants is challenging because they tend to be habitat generalists and are often highly adaptable to varying environmental conditions, which is attributable to their success as invaders. A few studies have used habitat modeling for invasive, nonnative plant species (Higgins et al. 1999, Zalba et al. 2000, Welk et al. 2002, Peterson et al. 2003, and Morisette et al. 2006) and Thompson et al. (2006) successfully created a habitat model for a native tree being impacted by a nonnative pathogen at MACA. However, to date no one has tested habitat modeling as a method of delineating priority areas for control of nonnative, invasive plants at local scales.

The overall goal of this study was to determine whether habitat models could be developed to predict the occurrence of invasive, nonnative plants at MACA and if so, how models could be best utilized to make management decisions. My research objectives were (1) to identify and rank nonnative, invasive plant species in the forests of MACA, (2) to determine the applicability of habitat modeling as a tool for predicting the occurrence of invasive, nonnative plants based on a case study, and (3) to describe how habitat modeling can be used to make management decisions regarding nonnative plants in MACA. Tree of heaven [*Ailanthus altissima*, (Mill.) Swingle] was selected for the case-study.

CHAPTER II

BACKGROUND

Environmental Impacts of Nonnative, Invasive Species

Nonnative species are considered a major component of biotic homogenization, second only to habitat destruction for endangering species, and are inextricably linked to biodiversity loss (DiCastri 1989, Wilson 1992, Wilcove et al. 1998, Vitousek et al. 1997, Mooney and Cleland 2001 and Clavero and Garcia-Berthou 2005). Simberloff (2002) described how invasive species can negatively affect native species through habitat change, competition, predation, herbivory, disease, and hybridization.

Changing modes of transportation combined with expanding world trade has increased the rate of introduction of nonnative species, resulting in profound ecosystem impacts (Ewel et al. 1999). Cox (2004) estimates the worldwide total of species introduced to new geographical regions by humans to be around half a million (Pimentel et al. 2001).

Cox (2004) detailed how nonnative species can even affect evolutionary processes through hybridization, when closely related native and nonnative species are brought together, and evolutionary adaptation to the physical and biotic conditions in their new environment. Often, nonnative species change explosively from innocuous to highly invasive. Cox (2004) attributed this in part to adaptive breakthroughs. The responses of newly established alien species to their environment are largely dependent on their genetic variability. The number of individuals, their geographic origins, frequency of dispersal events, and reproductive strategy all impact an alien species' evolutionary potential. Cox (2004) noted that most invasive alien plants show high levels of genetic variability, usually as a result of multiple introductions and often from different regions of their native range. If an invader finds favorable conditions for population growth (physical habitat, available resources, mutualists) and has escaped from biotic limitations (e.g., predators, parasites, diseases, competitors) this results in altered pressures of natural selection. For many species, the consequence is often rapid evolutionary adaptation to the new conditions, which leads to species invasiveness (Cox 2004). In addition to the negative impacts of individual nonnative species through their interactions with native species, Simberloff and Von Holle (1999) documented that facilitative interactions among multiple nonnative species are at least as common, potentially resulting in more severe environmental impacts to native ecosystems.

The potential negative impacts of nonnative species was noted in the U.S. as early as the mid-1800s by Marsh (1864), who wrote: "the ravages of imported insects injurious to cultivated crops, not being checked by the counteracting influences which nature had provided to limit their devastations in the Old World, are much more destructive here than in Europe." By the late 1800s, the problem was so evident that a conference to discuss nonnative pest problems was held by the U.S. Department of Agriculture (Howard 1898). By the mid-1900s, the destruction of natural ecosystems prompted Charles Elton (1958) to state "We must make no mistake: we are seeing one of the great historical convulsions in the world's fauna and flora."

Anticipating invasions of nonnative species and developing early detection and rapid response protocols are important to control efforts but predicting which nonnative species will become invasive and harmful is complicated (Simberloff 2002). The biological characteristics of invasive species (Rejmanek and Richardson 1996, Williamson and Fitter 1996, Sakai et al. 2001, and Grotkopp et al. 2002) and characteristics of the recipient ecosystem, such as species richness, biodiversity, and disturbance history (Elton 1958, Levine and D'Antonio 1999, Stohlgren et al. 1999), are important determinants of the probability of establishment of nonnative species. Also, some nonnative pests are innocuous in the environment for years until they suddenly become problematic; this phenomena has been termed a “lag phase” by ecologists (Mack et al. 2000, Simberloff 2002). To date, the only dependable criteria for assessing the invasiveness potential of a species is whether that species has been invasive elsewhere, in similar ecosystems (Lockwood et al. 2001).

Economic Impacts

Nearly every region of the U.S. is negatively affected by nonnative species, with some of the worst problems occurring in eastern states (Windle 1997). Recent studies indicate that economic losses in the U.S. due to nonnative species are approximately $120 billion/year (Pimentel et al. 2005). This estimate includes the cost of control measures, losses to agricultural and forestry crops, and the costs of public health impacts. That estimate however does not include ecological costs because so little is known about interactions among native and nonnative species (Pimentel et al. 2005). Moreover, an economic estimate of the cost of environmental changes due to invasive, nonnative plants is difficult to determine.

International and National Policy

Introductions of nonnative species into the U.S. will likely increase in the future. Global trade has greatly expanded during the past century, but legal protections intended to reduce the introduction of nonnative species into the U.S. have decreased (Campbell and Schlarbaum 2002). Part of the accords establishing the World Trade Organization (WTO) include the Sanitary and Phytosanitary (SPS) Agreement, which assumes that a nonnative species will cause no harm unless it can be demonstrated via risk assessment and risk is only assessed when previous information indicates that one exists (Campbell and Schlarbaum 2002, Simberloff 2005). In most instances there is insufficient knowledge to predict whether or not a species may become invasive and what impacts may result. Simberloff (2005) points out that nonagricultural environments receive little attention from the risk assessment process. There are several federal laws in the U.S. that apply to invasive species, mostly focused on impacts to the agriculture industry, whereas potential impacts on natural resources receive little attention (Environmental Law Institute 2002).

National Park Service

In addition to state, federal, and local laws, the NPS is guided by three internal documents regarding nonnative species: (1) USDI NPS Management Policies (2001), (2) Natural Resources Management Guidelines (NPS-77; National Park Service 1991), and (3) an individual national park’s management plan. Additionally, the NPS developed a strategic plan for managing nonnative plants on national park lands in 1996 (Andrascik et al. 1996). The NPS Management Policies (2001) give high priority to managing harmful or potentially harmful nonnative species and to prevent nonnative species from displacing native species. NPS-77 stresses the importance of cooperation among agency resource managers and adherence to Integrated Pest Management (IPM) principles when dealing with nonnative species. IPM includes cultural, physical-mechanical, chemical, and biological control methods to maximize the effectiveness of control measures while minimizing ecological impacts.

The NPS recognizes nonnative species as one of the most important challenges to the management of national park lands. An entire issue of Park Science was dedicated to invasive species in 2004 (volume 22, issue 2) and a 2005 report issued by the National Parks and Conservation Association (NPCA) listed nonnative species as the 7th most important reason to reinvest in national parks (NPCA 2005). The NPS Biological Resources Management Division develops ecosystem management and restoration strategies for parks, including control of nonnative and invasive animal and plant species. This division also funds and oversees EPMTs and provides technical assistance to address animal health, IPM, and management of federally threatened and endangered species (National Park Service 2002). Additionally, the NPS Inventory and Monitoring Program is developing national protocols for early detection of and rapid response to nonnative plant invasions.

Despite increasing attention and available resources, problems with nonnative species on public land remain substantial. The NPS estimates that 234 parks have invasive animal problems and approximately 2,832,799 hectares (7 million acres) (out of a total 33,588,904 ha) of parklands are infested with nonnative plants (Fraley 2004). That is likely an underestimate because most national park units have not been surveyed extensively for nonnative species (Benjamin and Hiebert 2004). EPMTs have been formed and are deployed regionally to control nonnative plants on national parks. This program is understaffed for the amount of responsibility assigned. For example, the southeast EPMT, established in July 2003, is responsible for 15 national parks in 7 southeastern states (excluding Florida) and over 115,335 hectares, but has only two full-time employees, one temporary seasonal employee, and six Student Conservation Association summer interns (N. Fraley, NPS, personal communication).

TREE OF HEAVEN IN THE U.S.

History and Biology

Tree of heaven, a tree in the family Simaroubaceae and native to central China, is considered to be an invasive, nonnative weed tree in the U.S. It was noted for its invasive potential as early as the late 1800s by Harvey (1883). More recently, numerous studies have addressed the invasiveness of tree of heaven and nearly every state nonnative pest plant council has it listed as a problem plant. It is a fast-growing tree and prolific seed producer that can sprout from the stump or roots. It can be an aggressive competitor with surrounding vegetation, in part because of its allelopathic properties (Lawrence 1991). Mergen (1959) found that an aqueous extract from tree of heaven leaves was toxic to 35 conifers and 10 broadleaf hardwoods species. Heisey (1996) recommended tree of heaven for the development of natural herbicides.

Tree of heaven has been introduced into the U.S. multiple times since 1784, when it was first brought into Philadelphia by the horticulturalist William Hamilton (Newton 1986). It was likely introduced into the U.S. a second time by Chinese immigrants during the western railroad expansion (Feret 1985). Tree of heaven has become widely distributed in the Americas and occurs from Massachusetts to Oregon and from Canada to Argentina (Hu 1979).

Because of its attractive foliage, fecundity, and ability to withstand diverse environmental conditions, tree of heaven was once considered an attractive ornamental tree and was widely planted throughout cities in Europe and the Americas. Three *A.*

altissima varieties native to China are recognized by Chen (1997), var. *altissima* (Miller) Swingle, var. *tanakai* (Miller) Swingle and var. *sutchuensis* (Dode) Rehder. Under cultivation, tree of heaven has been developed into numerous horticultural varieties including but not limited to: *Ailanthus altissima* var. *erythrocarpa* (Carrière) Rehder, *Ailanthus altissima* var. *leucoxyla* B.C.Ding and T.B.Chao, *Ailanthus altissima* var. *microphylla* B.C.Ding and T.B.Chao, *Ailanthus altissima* var. *myriocephala* B.C.Ding and T.B.Chao, and *Ailanthus altissima* var. *tanakae* (Hayata) Kanehira & Sasaki.

Tree of heaven was also planted for afforestation purposes. Sargent (1888), founder of the Arnold Arboretum, stated in the first issue of Garden and Forest, "…for hardiness and rapidity of growth, for the power to adapt to the dirt and smoke, the dust and drought of cities, for the ability to thrive in the poorest soil, for beauty and for usefulness, this tree is one of the most useful which can be grown in this climate…". He also described the virtues of tree of heaven for firewood and furniture.

Tree of heaven is mostly dioecious. It reproduces both sexually (seed) and asexually (vegetative sprouting from stumps or roots) (Hu 1979). An individual tree can produce 325,000 seeds per year, which are easily dispersed by wind (Hoshovsky 1988). Seedlings produce a well-formed tap root in less than 3 months and can form extensive lateral roots in compacted soil (Hoshovsky 1988). Tree of heaven has a short juvenile period, producing seed as early as 10 years of age (Howard 2004). Most seed are viable regardless of whether they are dispersed or remain on the mother tree (Howard 2004). Seed can travel great distances. Matlack (1987) reported that tree of heaven seed traveled a significantly greater distance than 37 other wind-dispersed species. Seeds generally retain dormancy for less than 1 year and so do not build up long-term seed banks.

However, seed banks can be established from off-site sources (Howard 2004). For example, in Tennessee, Dobberpuhl (1980) found viable seed in the soil seed bank where no trees were present in the overstory.

Tree of heaven grows quickly in full sun and has been recorded to grow an average of 1 m per year for the first four years (Hoshovsky 1988). Howard (2004) suggested that it may be the fastest growing tree in North America. Tree of heaven has been documented to grow over 80 feet tall (Rhoads and Block 2002). The life span of tree of heaven is generally considered to be short (30 – 50 years), but some trees over 90 years of age have been documented in MACA (A. Datillo, NPS, personal communication).

Tree of heaven typically grows in clumps and, once established, can increase its density by root sprouting (Howard 2004). One ramet can occupy over a 0.4 ha (1 acre) (Howard 2004). One study found 42% of 1-year-old, excavated tree of heaven stems were seedlings and 58% were root sprouts (Pan and Bassuk 1985). Root sprouting is a rare strategy for a hardwood species but an effective one (Howard 2004). Roots can store more nutrients and photosynthate than rhizomes. By that mechanism, the plants are more protected from disturbances aboveground (e.g., fire) and can sprout vigorously after a disturbance (Howard 2004). Tree of heaven root sprouts have been recorded 15–27 m (49 - 90 ft) from the parent stem (Illick and Brouse 1926, Howard 2004).

Habitat

Because of its low-shade tolerance (Grime 1965), tree of heaven has been considered a pest plant primarily in disturbed areas (natural or human caused), urban settings, and along roadsides (Santamour 1983), but it can invade and establish in forests as well. Strausbaugh and Core (1977) described the invasion pattern as starting with a few stems along forest edges or roads and then encroaching into the hardwood forests, eventually moving into the canopy. Meloche and Murphy (2006) similarly described tree of heaven as invading forest gaps along forest edges, followed by infiltration into interior forests. Hutchinson et al. (2004) found that tree of heaven invaded sites disturbed by forest management activities (e.g., thinning, burning, and thinning with burning) and Rebbeck et al. (2005) demonstrated that the distribution of tree of heaven prior to treatments (thinning, burning, and thinning with burning) was the primary determinant of its post-treatment distribution pattern. Knapp and Canham (2000) documented the successful invasion of tree of heaven into an old-growth hemlock-hardwood forest in New York and suggested that it was a gap obligate species (Orwig and Abrams 1994). Gap obligate species are able to take their place in the forest canopy by rapid height growth when released by large light gaps. Thus, shade-intolerant species may become established in a forest through gap dynamics.

Once tree of heaven becomes established in the forest, it is capable of persisting and reproducing even after the canopy has closed, due in large part to its overall adaptability. Kowarik (1995) investigated a case where a stand of tree of heaven had developed in a dense, closed forest in West Virginia. Seeds and seedlings were not able to survive but a strong bank of ramets had developed under shady conditions, which the author hypothesized may indicate a strategy for ensuring tree of heaven's persistence in the forest. He noted the morphological plasticity of the species, as tree of heaven clones exhibited slow growth rates, which are normally associated with shade-tolerant species.

Hamerlynck (2001) speculated that tree of heaven may be unique in that it demonstrates shade-plant like characteristics in terms of high photosynthetic efficiency and high photosynthetic capacity in high radiation, while stomatal attributes that optimize water use efficiency are maintained in the shade. He found that tree of heaven can efficiently photosynthesize at low light levels. Espenschied-Reilly and Runkle (2008) note that because understory clonal sprouts of tree of heaven remain photosynthetically active in shady conditions and may receive resources reallocated from the parent tree, they can persist for years, growing slowly, and awaiting a canopy disturbance. Sprouts may not be the only contributing factor to tree of heaven's successful gap obligate strategy. Although tree of heaven's seed viability is documented as low, Kota et al. (2007) found that its seed bank remained viable for at least one year in a closed-canopy forest.

Beyond its adaptability to differing light conditions, tree of heaven can adjust to varying levels of soil moisture and nutrients as well (Meloche and Murphey 2006). Feret (1985) noted that it is able to grow on a variety of sites, from sterile soils to rich alluvial bottoms. This has been documented elsewhere in the literature as Newton (1986) observed that tree of heaven was highly competitive on dry, urban sites because its root system is capable of reaching water even in dry soils but Kiviat (2004) noted it occurring extensively along a tidal shoreline in Jug Bay Wetlands Sanctuary in Maryland.

Plasticity in biomass allocation (roots vs. shoots, depending on conditions) may be the primary contributing factor to tree of heaven's adaptability to different soil characteristics (Kowarik 1995). Kostel-Hughes et al. (2005) noted that tree of heaven seed was capable of germinating under a variety of leaf-litter depths and that the species exhibited root:shoot ratios based on litter depth. Correspondingly, Pan and Bassuk

(1985) found that tree of heaven altered its root growth habit in response to soil compaction.

Not only is tree of heaven capable of colonizing a variety of sites, it alters site conditions upon arrival. Vilå et al. (2006) noted that the impact of tree of heaven on several Mediterranean islands varied by site. However, they found that the presence of tree of heaven increased soil pH overall. Using mixed plantings in greenhouse experiments, Call and Nilsen (2005) found that tree of heaven was a more successful competitor than the black locust tree (*Robinia pseudoacacia* L.), another pioneer species native to the U.S. They noted that the two species exhibit similar characteristics but perform different ecosystem functions after a disturbance. Tree of heaven inhibited succession by creating a toxic soil environment (Lawrence 1991), whereas black locust fixed nitrogen, enriching the soil and promoting succession.

Feret (1985) reported high genetic variability for North American populations of tree of heaven, probably because of multiple introductions of genetically different individuals from China. Miller (2008) stipulates that tree of heaven has likely become differentiated into genetically different subpopulations based on seed traits, citing a study of 11 seed sources from California and the eastern states, which found that seed width and weight were correlated with latitude (Feret 1974). It is unclear whether or not the genetic diversity within the species is associated with its adaptive ability.

CHAPTER III

STUDY AREA

The study site was the 21,380 hectare (52,830 acre) Mammoth Cave National Park, located in south central Kentucky, approximately 56 km northeast of Bowling Green (Figure 1). MACA was authorized as a national park in 1941 and is one of the 15 U.S. national parks designated as an International Biosphere Reserve (United Nations Educational Scientific and Cultural Organization 2002). Biosphere reserves are intended to reconcile the conservation of biodiversity with sustainable use, where sustainable use and management principles can be tested (United Nations Educational Scientific and Cultural Organization 2005). The United Nations Educational Scientific and Cultural Organization (UNESCO) also recognize MACA as a World Heritage Site for its unique cave system, overall biodiversity, threatened and endangered species, and outstanding universal value. MACA was primarily established to protect the most extensive recorded cave system in the world, where over 579 kilometers (360 miles) have been explored and mapped to date. It is a prototype long-term ecological monitoring (LTEM) park for the NPS cave and karst biome category. Prototype parks provide guidance on the design, development, and testing of monitoring protocols (National Park Service 2002).

MACA divides the functioning ecosystems in the park into three broad categories: the cave (subdivided into aquatic and terrestrial components), the riverine (subdivided into sinking streams and base-level rivers), and the forest system (composed of several

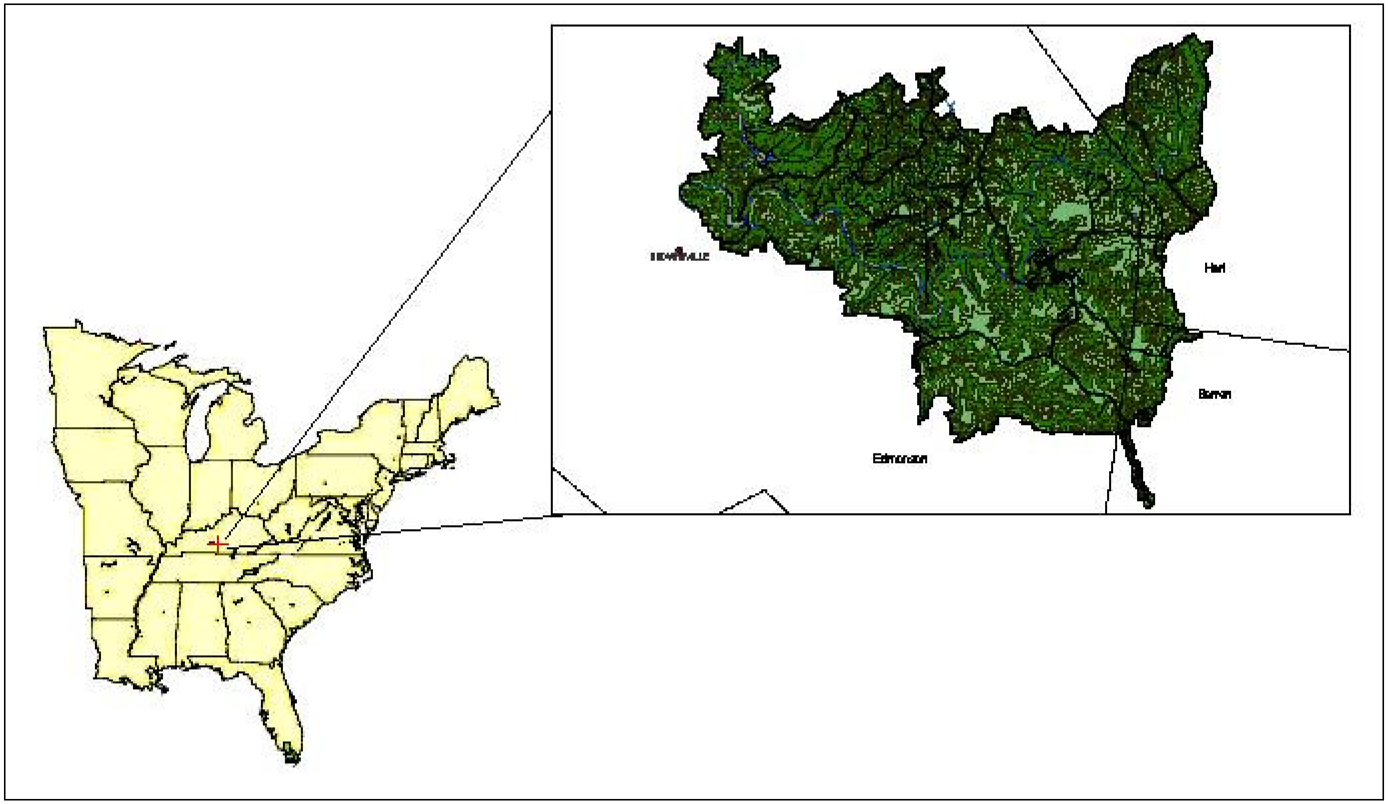

Figure 1. Geographic location of Mammoth Cave National Park.

natural communities) (National Park Service 1996). The Green River runs east to west through the national park and is joined by the Nolin River on the western boundary. The rivers support 82 species of fish and 250 species of invertebrate fauna, of which 50 are freshwater mussels. The cave contains both aquatic and terrestrial species and is among the most diverse cave systems in the world. It contains over 130 species, including many endemics. The terrestrial forest system has 82 species of trees and over 1,100 species of plants have been identified to date.

The Forests at Mammoth Cave

My research was focused on the terrestrial forest ecosystem within MACA. Forests are by far the most common vegetation cover type, totaling approximately 21,125 ha (52,200 ac) of the park's area. Forest ecosystems are mostly in middle stages of succession, although some mature forests remain, including the 121-ha (300-ac) Big Woods. Prairie and savanna maintained by fire were common before settlement, but have largely been converted to agriculture over the past two centuries. A few small remnants of prairie and barrens still remain, but none are greater than 16 ha (40 ac) (Olson and Noble 2005). Most forested areas in the national park are secondary, having re-vegetated from farmland. Olson et al. (2000) identified seven vegetation types in MACA (Table 1, Figure 2).

Table 1. Vegetation types of Mammoth Cave National Park, Kentucky, as identified by Olson et al. (2000).

Vegetation	**Typical Species**
Subxeric deciduous forest-savannah	Chestnut oak (*Quercus prinus* L.)
	Post oak (*Quercus stellata* Wangenh.)
	Chinquapin oak (*Quercus muhlenbergii* Engelm.)
	Blackjack oak (*Quercus marilandica* Münchh.)
Mesic upland deciduous	White oak (*Quercus alba* L.)
	Pignut hickory (*Carya glabra* (Mill.) Sweet)
	Black oak (*Quercus velutina* Lam.)
	Tulip poplar (*Liriodendron tulipifera* L.)
Mesic hollow/floodplain deciduous	Sugar maple (*Acer saccharum* Marsh.)
	American beech (*Fagus grandifoli* Ehrh.)
	Box elder (*Acer negundo* L.)
	American sycamore (*Platanus occidentalis* L.)
Mixed deciduous/coniferous	Red maple (*Acer rubrum* L.)
Mixed coniferous/deciduous	Tulip poplar (*Liriodendron tulipifera*)
	Dogwood (*Cornus florida* L.)
	Sweetgum (*Liquidambar styraciflua* L.)
Coniferous	Virginia pine (*Pinus virginiana* Mill.)
	Eastern red cedar (*Juniperus virginiana* L.)
Prairie/open areas	Native grasses and forbes
	Mown grass

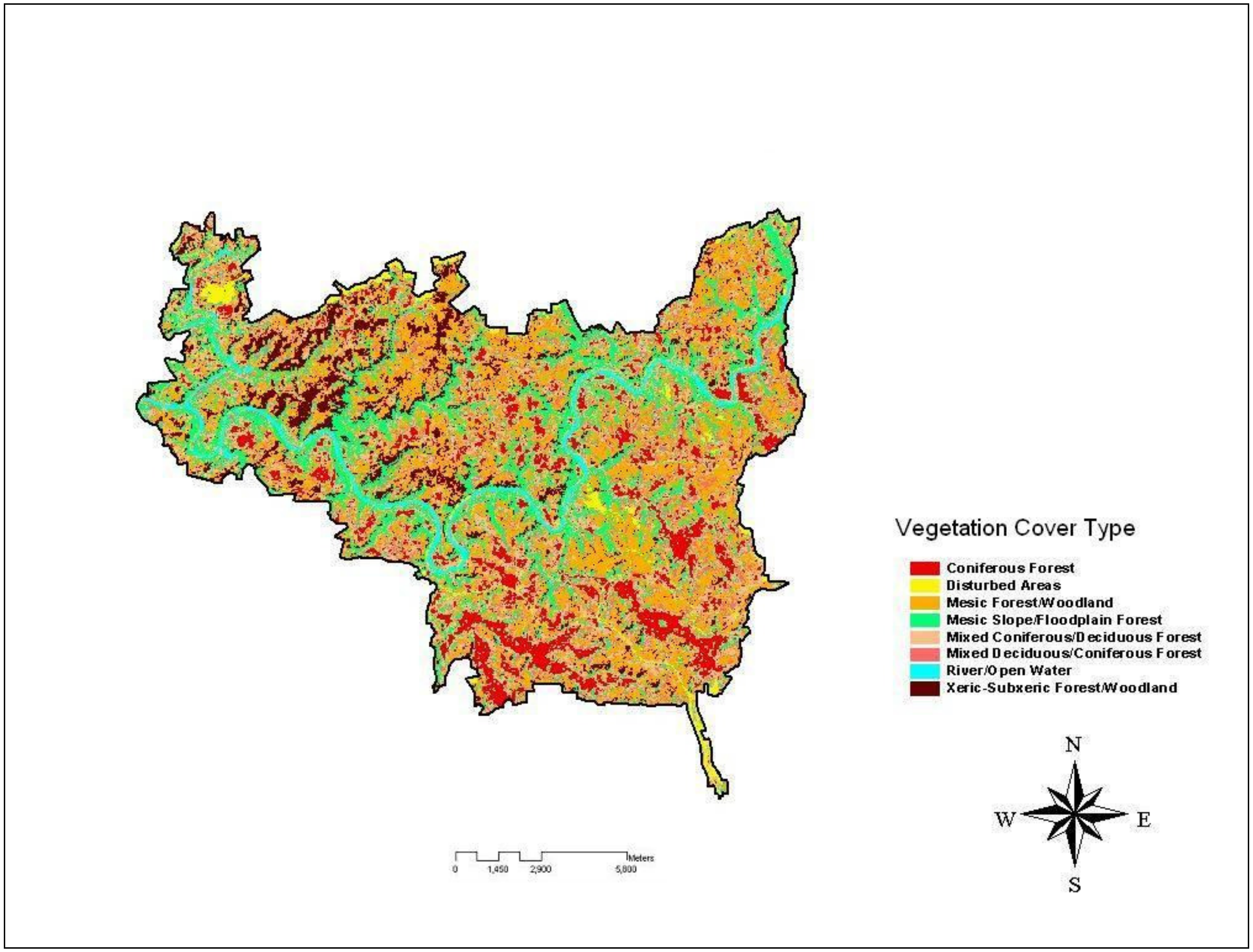

Figure 2. Vegetation types of Mammoth Cave National Park, Kentucky (based on Olson et al. 2000).

Land use prior to designation as a national park included small, 4–61 ha (10–150 ac) farms with fields of corn, hay, and tobacco on the level land along floodplains, in valleys, and in uplands. The slopes were primarily used as pasture for pigs and cattle and were selectively cut for timber. Geology and soil were an important determinant to historic land-use at MACA. South of the Green River, limestone valleys and broad flat ridges provided better farming than areas north of the river, which were dominated by sandstone (Woodman and Thomas 2003). The diversity of the forests at MACA can be attributed in large part to variations in aspect, slope, elevation, and soil moisture combined with parent material. The combination of limestone ridges capped with sandstone and layered with shale and sandstone create a variety of microsite conditions.

The national park area was classified by Braun (1950) as part of the Western Mesophytic Forest, which includes Mixed Mesophytic Forest on moist slopes and Oak-Hickory Forest on ravine flats. Important species on moist slopes include *Fagus grandifolia* (American beech), *Liriodendron tulipifera* (tulip poplar), *Acer sacharrum* (sugar maple) and 15 additional canopy species. Upland flat ridges and xeric habitats are dominated by oaks (*Quercus spp.* L.). Tree associations correspond with geology and soil. Natural glades occur in areas with few trees and shallow soils (Woodman and Thomas 2003).

The floodplain forest has changed over time. Ellsworth (1936) described it as a river birch-sycamore forest association, with some sycamores reaching over 30 m (~100 ft) tall with 2 m diameters (~6 ft). Badger (1997) characterized the floodplain forest as a tulip-poplar-mixed maple association. He made note of tree of heaven growing along the Nolin and Green Rivers and two other nonnative plant species, *Alliaria officinalis* (garlic mustard) and *Glecoma hederaceae* L. (gill-over-the-ground), which are common in river floodplains (Woodman and Thomas 2003).

In a small area of the northwestern part of MACA, a hemlock-tulip poplar-beech forest exists. There are pure stands of *Tsuga canadensis* (L.) Carrière, but common associates include *Betula spp.* L.*,* *Ilex spp.* L., *Magnolia tripetala* (L.) L., and, in the understory, *Kalmia latifolia* L. and *Vaccinium spp.* L. are present (Woodman and Thomas 2003). This association is considered a rare and disjunct community in Kentucky because it occurs so far west in the state. Faller and Jackson (1975) and Badger (1997) both considered tree of heaven to be a threat to the hemlock forests.

Nonnative Plants in Mammoth Cave National Park

MACA is one of 14 units of the National Park System included in the Cumberland-Piedmont Network (CUPN) under the NPS Inventory and Monitoring (I&M) program (2002). In 2000, the Appalachian Highlands and Cumberland-Piedmont regions released their proposal for an EPMT to address invasive, nonnative plant problems for national park units within the two regions. The southeastern EPMT was established in July 2003 (National Park Service 2004). The EPMT proposal included an assessment of four large parks in the two regions: Big South Fork National River and Recreation Area (BISO), Blue Ridge Parkway (BLRI), Cumberland Gap National Historical Park (CUGA), and MACA. The author of the proposal identified farming, timber harvest and rural development prior to park establishment as the primary means by which plants invaded MACA but also cited utility corridors, roads and trails, developed areas within the park, and rivers as internal vectors (Ulrey and Fry 2000). The proposal determined that 154 nonnative plants occurred in MACA, of which they listed

14 as serious threats (Ulrey and Fry 2000; Table 2) according to the Tennessee Nonnative Pest Plant Council (TN-EPPC) guidelines (1996). The TN-EPPC criteria for a severe threat refer to an nonnative plant possessing characteristics that allow the species to spread, easily invading and displacing native plant communities, (Tennessee Nonnative Pest Plant Council 2004). Prior to this study, no research had been conducted to determine whether or not the TN-EPPC guidelines were applicable to the forests of MACA.

Tools to address nonnative plant invasions in MACA prior to this study were limited to a vegetation map, developed using satellite remote sensing data (Olson et al. 2000), a vegetation classification (Olson and Franz 1998) and an incomplete nonnative plant survey (Figure 3). The survey largely covered developed areas and roads. No random surveys had been conducted in the forest to determine the extent of invasion by nonnative plants and no methodology for surveying/monitoring nonnative plants in the forest had been developed.

Table 2. Nonnative plants listed as a severe threat to Mammoth Cave National Park by Nonnative Pest Management Teams in 2000.

Latin name	**Common name**
Ailanthus altissima (Mill.) Swingle	Tree of heaven
Alliaria petiolata (Bieb.) Cavara & Grande	Garlic mustard
Carduus nuitans L.	Musk thistle
Euonymus fotunei (Turcs.) Hand.-Mazz.	Climbing euonymous
Lespedeza cuneata (Dum.-Cours) G. Don	Sericea lespedeza
Ligustrum sinense Lour.-*vulgare* L.	Chinese-European privet
Lonicera joponica Thunb.	Japanese honeysuckle
Microstegium vimineum (Trin.) A. Camus	Japanese grass
Paulownia tomentosa (Thunb.) Sieb. & Zucc. ex Steud.	Princess tree
Pueraria Montana (Lour.) Merr.	Kudzu
Rosa multiflora Thunb. ex Murr.	Multiflora rose
Sorghum halepense (L.) Pers.	Johnson grass
Spirea japonica L. f.	Japanese spirea
Albizzia julibrissin Durazz.	Mimosa

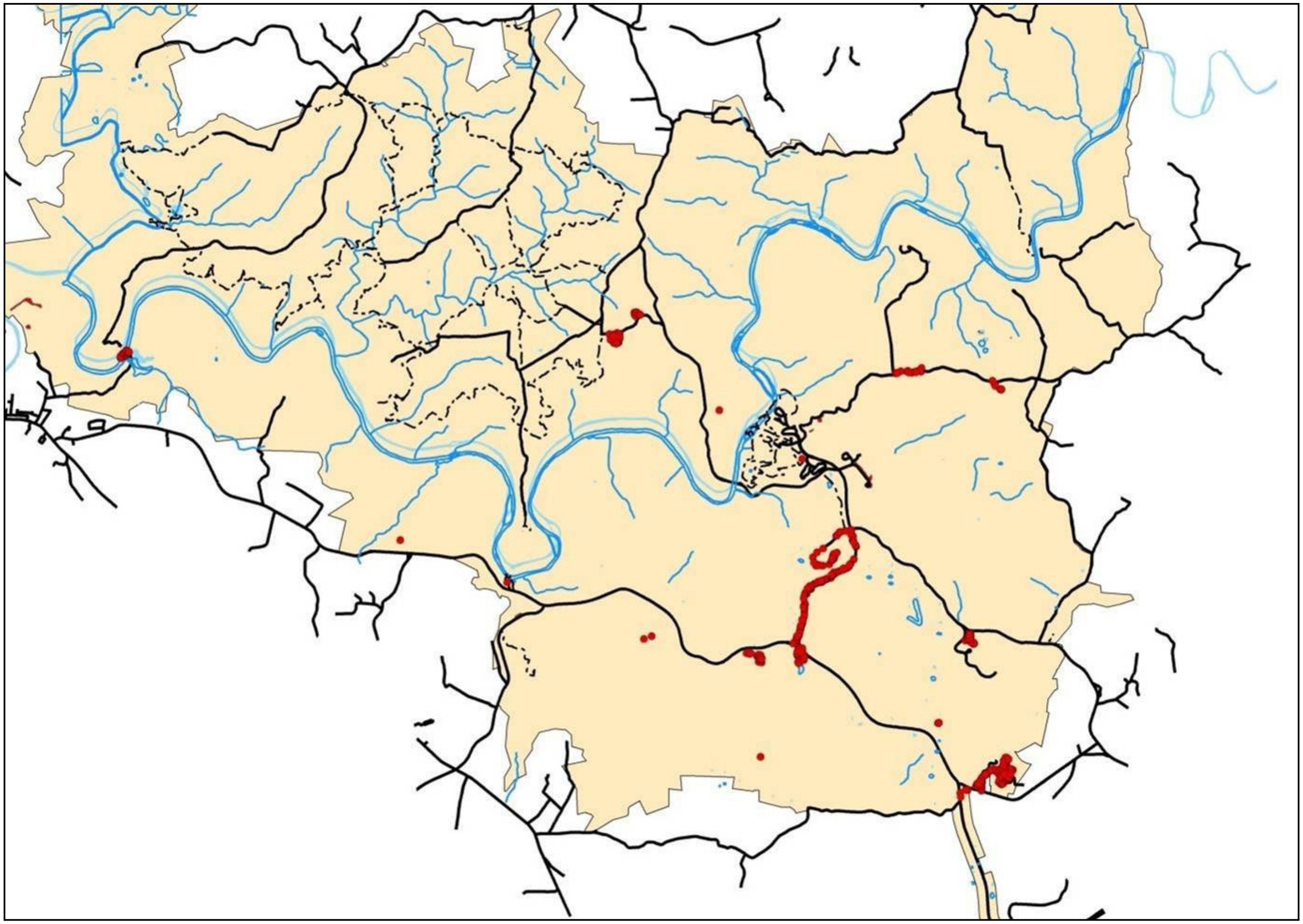

Figure 3. Nonnative plant locations provided by Mammoth Cave National Park and Nonnative Plant Management Teams.

CHAPTER IV

METHODS

Nonnative Plant Surveys

I conducted surveys along random transects in forested areas of MACA to determine the magnitude of invasion by nonnative plants, identify the most prolific species, determine whether the list of 14 severe threats developed by the EPMTs (Table 2) had applicability to the park, and select the focal species for the habitat model case-study.

I performed surveys in July and October 2005 and in May and July 2006. Starting locations were randomly generated along travel vectors (i.e., roads, trails, waterways, and the national park boundary). I used Hawth's Analysis Tools for GIS (Beyer 2004) in combination with ArcView® GIS (version 3.1; ESRI, Redlands, California, USA) and ArcGis® (version 9; ESRI, Redlands, California, USA) to generate locations. I established a 500-m transect from starting locations, perpendicular to the vector. If a pair of transects overlapped, I generated a new starting location for one of the transects. I followed transect routes using a map and compass and used a GPS receiver (Garmin GPS 12 XL, Olathe, Kansas, USA) to acquire universal transverse mercator (UTM) location coordinates at 30-m intervals. At each 30-m interval, I recorded the presence or absence of any nonnative plants within my field of vision and noted the species.

After the first field season (2005), I was able to determine which species were regularly noted in the forest and select tree of heaven as the focus of the habitat modeling case-study. During the 2006 surveys I only recorded locations for tree of heaven. If tree of heaven was present, I also recorded the number of stems per clonal cluster. I augmented the number of presences in the database by adding locations provided by MACA staff and EPMTs (Figure 3).

Horizontal positional accuracy was recorded for all presence locations collected along random transects and averaged 7.0 m (range = 5.0–14.0 m). Accuracy was not recorded for locations provided by MACA staff. However, all locations were recorded with a GPS and I assumed that those locations accurately represented the corresponding GIS pixel. I corrected all data for duplicate records and other errors. Additionally, I excluded duplicate presence locations for the same GIS pixel.

Tree of Heaven Habitat Model

In habitat modeling, data are collected on numerous variables within the environment, the variables with the strongest relationship to species occurrence are selected and models that describe species location are developed (Heglund 2002). The underlying assumption behind habitat modeling is that predictable relationships exist between a species occurrence and certain environmental features (Heglund 2002). This is the concept of niche as first defined by Grinnell (1917), who considered it to be an elemental distributional unit of species. Elton (1930) described niche as the “role” or “profession” of a species in its community, a behavior-based concept. Hutchinson (1957) proposed the first quantitative concept of niche which combined the behavioral and distributional concepts of Elton and Grinnell. The term ‘niche’ has been used confusingly in the ecological literature to describe both the environmental requirements needed for a species to exist and interspecies relationships, which cannot be studied with the same tools (Hirzel and Le Lay 2008). Kearney (2006) suggests that statistical models describing species' distributions should be termed 'habitat models' because they depict the links between species' distributions and numbers across a landscape and physical or biotic features. He suggests that models that capture interactions between organisms and their environments, and their fitness consequences, are best described as 'niche models'. In this study, I follow his definitions.

Habitat models developed using a Geographic Information System (GIS) relate habitat suitability to raster-based layers such as land use-land cover, elevation, topographic position, and human disturbance (e.g., distance from roads, road density, etc.). Integration of multivariate statistical techniques with GIS data provides a powerful approach as predictions can be made for large spatial extents (Clark et al. 1993, Dettmers et al. 2002) and at different spatial scales (Morrison 2002). The application of predictive habitat models to nonnative species has been limited to a few studies, but shows promise (e.g., Beerlin et al. 1995, Hill et al. 1998, Zalba et al. 2000).

A variety of habitat modeling techniques are available and range from literature-based, expert-assisted models to empirical, statistical models. Selection of a modeling technique depends on the set of criteria for a given situation of interest. If presence-absence data are available for the species in the study area, then empirical models can be created by relating that data to habitat variables. Statistical techniques such as generalized linear or generalized additive models (e.g., logistic or Poisson regression), artificial neural networks, classification and regression trees (CART), and genetic algorithms can be used to create a map depicting the probability of occurrence of a species at any pixel in the landscape (Majka et al. 2007).

Logistic regression is a commonly used statistical technique to develop habitat models (Franklin 1995). Zalba et al. (2003) used logistic regression to evaluate the risk of invasion of an Australian halophytic shrub, the old man saltbush, *Atriplex nummularia* Lindl., for a small nature reserve. Morisette et al. (2006) used logistic regression to develop and test a national-scale habitat suitability model for tamarisk (*Tamarix spp*. L., salt cedar), a high priority invasive species in the western U.S.

I used logistic regression to develop a predictive model to identify habitat for tree of heaven in MACA to assist park staff in locating and eradicating or controlling this invasive, nonnative tree. Model creation involved 5 steps: (1) collecting and compiling a dataset of tree of heaven locations from the current population at MACA; (2) developing a set of GIS variables to describe tree of heaven occurrence; (3) selecting a suite of variables to characterize occurrence of tree of heaven using Akaike's Information Criterion (AIC); (4) predicting the probability of occurrence of tree of heaven for MACA based on the chosen logistic regression model; and (5) testing the habitat model with independent field data.

I selected tree of heaven for the case study because it was identified as a priority species for control by MACA and because it showed promise for habitat modeling. Although it is documented to be a highly adaptable species, capable of establishing and proliferating under a variety of different environmental conditions, its strategy as a gap obligate in the forest is somewhat predictable. Geology, soil and site conditions at MACA are largely related to past land use and correspondingly, to vegetation types and forest gap dynamics. South of the Green River, I observed tree of heaven most often in the cedar/pine forests that have established from farm fields historically used to grow row crops (McInteer 1944, Olson 2007). Soils in these areas have been subject to erosion and site quality is generally poor. The overstory trees are nearing the end of their life span, and tree falls that create large canopy gaps are common. Gaps are typically colonized by tulip poplar and tree of heaven. In the deciduous forests north of the Green River, tree of heaven was regularly found on rocky outcroppings and along cliffs, where gaps in the canopy occurred and native species are not competitive. Data representing geology, soil and site characteristics as well as canopy coverage were available, leading me to believe that the range of resources most important for the occurrence of tree of heaven in MACA could be captured in a habitat model.

Habitat Variables

Guisan and Zimmerman (2000) reviewed the factors influencing plant distributions and divided them into three gradients: resource, direct, and indirect. Resource gradients are directly used by individual plants, such as water or soil nutrients. Direct gradients influence resource gradients such as soil type, sunlight, water availability, and temperature. Indirect gradients represent relatively large-scale factors such as geology, topography, and climate, and govern the configuration of direct and, ultimately, resource gradients (Guisan and Zimmerman 2000). Because of limitations in data availability and mapping technology, only direct and indirect gradients are typically measured over large areas with GIS data. Occasionally surrogates for resource gradient levels can be derived from coarser scales. For example, existing digital terrain models can be used to estimate solar radiation (van Manen et al. 2005).

The variables I chose represented direct and indirect gradient. Corsi et al. (2000) considered data availability and quality the principal limiting factors of GIS-based modeling. GIS data (30 x 30-m) for MACA, however, were extensive, partially because of previous studies (Thompson et al. 2006). I assumed that resolution was appropriate for the detection of tree of heaven.

To identify landscape conditions in the study area that were similar to the locations where tree of heaven occurred, I created a database of GIS variables (Table 3). Topographic variables were created from elevation data obtained from a digital elevation model (National Elevation Dataset; U.S. Geological Survey, Reston, Virginia, USA). All topographic variables were generated in ArcInfo® GRID (ESRI, Redlands, California, USA). I used the Normalized Difference Vegetation Index (NDVI) to measure vegetation gap characteristics. The NDVI equation produces values ranging from -1.0 to 1.0, where increasing positive values represent increasing green vegetation and negative values signify nonvegetated areas (Myneni et al. 1995).

I used 4 categorical variables: vegetation type, geology, soil and site class, to create binary design variables (dummy variables). The dummy variables sg1 and sg2 represented the soil and geology types that had more than 5 tree of heaven presences/type. The soil categories for this variable included WbF (Wellston silt loam, 6–12% slope), LyC2 (Lily loam, 6–12% slope), WeC2 (Wallen Bledsoe Donahue Complex, 35–50% slope), CoC (Clark range, 6–12% slope) and the geology classes included Big Clifty Member, Haney Member, Hardinsburg Sandstone, Glen Dean, Tradewater, and Caseyville Formation. The dummy variables sc1 and sc3 represented site classes most frequently associated with tree of heaven (sc1 = calcareous sub-xeric, sc3 = acid mesic). Site classes were developed by MACA as a vegetation habitat

Table 3. Variables considered for inlcusion in logistic regression models to predict the occurrence of tree of heaven in Mammoth Cave National Park, Kentucky.

Variable[a]	**Description**	**Classes or value range**	**Data source**
Topographic relative moisture index (TRMI)	Index of moisture considering the effects of slope position, aspect, and elevation	0.0–60.0	Calculated based on Parker (1982)
Solar insolation (solar)	Average solar insolation. Measures the relative amount of sunlight striking the surface throughout the year.	1.0–227	Calculated from elevation with the HILLSHADE command (ArcInfo GRID).
Relative slope position (RSP)	Indicates where on a slope a pixel is located	0.0–100.0	Calculated from elevation based on Wilds (1997)
Terrain shape index (TSI)	Measure of local topographic variability indicating convex (<0.05) or concave (>0.05) landforms	-72.0–73.0	Calculated based on McNab (1989)
Beers transformation of aspect (Beers)	Transformation of aspect to a continuous scaled variable, set to maximum for NE slopes (coolest slope)	0–2.0	Calculated from aspect based on Beers et al. (1966)
Normalized difference vegetation index (NDVI)	Provides a crude estimate of vegetation health and a means of monitoring changes in vegetation over time.	-1.0–1.0	Thompson et al. (2003)
Slope_Veg1 (sv1) Slope_Veg2 (sv2)	Derived from slope and vegetation to assess historic land use.		

Table 3, contd.

Variable[a]	Description	Classes or value range	Data source
Elevation	Elevation (m)	13–2,038	U.S. Geological Survey 30- Digital Elevation Model (DEM)
Soil_Geo1 (sg1) Soil_Geo2 (sg2)	Derived from soil and geology		
SiteClass1 (sc1) SiteClass2 (sc3)	Derived from site class		
Organic matter (orgmatter)	The estimated content of organic matter expressed as a percentage, by weight, of the soil material that is less than 2 millimeters in diameter.		Natural Resources Conservation Service (NRCS)
pH (phwater)	Measure of soil acidity or alkalinity.		Natural Resources Conservation Service (NRCS)
Percent clay (clay)	Composed of mineral soil particles less than 0.002 mm in diameter. Clay affects the productiveness and physical state of the soil and the ability of the soil to retain moisture.		Natural Resources Conservation Service (NRCS)
Depth to restrictive layer (dep2reslyr)	A restrictive layer is a virtually unbroken layer that significantly impedes water and air movement through the soil and that impedes roots.		Natural Resources Conservation Service (NRCS)

Table 3, contd.

Variable[a]	**Description**	**Classes or value range**	**Data source**
Depth to water table (dep2wattbl)	The depth to a water table in the soil during a specified period of time. Water table refers to a saturated region in the soil.		Natural Resources Conservation Service (NRCS)
Available water capacity (AWC)	The quantity of water that the soil is capable of storing for use by plants. AWC is not an estimate of the quantity of water actually available to plants at any given time.		Natural Resources Conservation Service (NRCS)

[a] Terms in parenthesis indicate the acronym used to symbolize the variable during analysis.

classification based on soil and geology. It was used to develop the vegetation classification.

To determine whether past agricultural practices were related to tree of heaven presence, I created a variable as a surrogate for land use history (slope_veg), by considering areas with slopes less than 9% and coniferous, coniferous-deciduous, or deciduous-coniferous vegetation. These areas largely correspond to the re-vegetated old fields south of the Green River (Olson 2007). To determine whether there was a relationship with certain soil and geology classifications and the presence of tree of heaven, I created soil_geo variables following the same process I used to represent land-use history. I created a suite of variables that addressed specific soil properties using Soil

Data Viewer 5.2 (NRCS 2007). The extent of all spatial data layers was the boundary of MACA. Sampling unit was the 30- x 30-m square sample plot, representing a GIS pixel. All spatial data were set at a 30- x 30-m resolution.

Habitat Analysis

Logistic Regression

I used logistic regression (PROC LOGISTIC; SAS Institute, Inc. 2006) to determine relative habitat use probability for tree of heaven. The predicted probability can only be interpreted as a true probability of occurrence if data are collected according to a randomized design (Keating and Cherry 2004). Logistic regression requires relatively large sample sizes for presence and absence locations. Because initial surveys did not result in sufficient sample sizes for adequate statistical power, I added locations collected by MACA staff to the dataset. These locations were acquired by staff while carrying out other duties in the park. Because these locations were not collected according to a random sampling protocol, strict interpretation of the results as a probability of use is inappropriate unless bias can be estimated or probability of use is small for all habitats (Keating and Cherry 2004). I evaluated bias during calibration testing to ensure that the addition of nonrandom points did not compromise the design of the study or interpretation of results as a probability of use. I used the coefficients of the selected logistic regression model to calculate and map the predicted probability of occurrence of tree of heaven with Map Calculator in ArcView® 3.3 and used ArcMap® 9.1 to develop the habitat map.

I chose a presence-absence modeling approach as opposed to presence-only modeling (e.g., Mahalanobis Distance, Ecological Niche Factor Analysis) because all available information is used (presences and absences) and presence-absence models can be more intuitive and powerful than presence-only models, especially when species occupy available habitats in proportion to their suitability, making absence data dependable (Brotons et al. 2004). Given its size and distinctive characteristics, misclassification of tree of heaven is unlikely, making presence and absence easy to determine. Absence can reflect lack of dispersal. I assumed that tree of heaven was not expanding its range because it was introduced into the eastern U.S. in the 1700s, sufficient time to colonize all available habitats. There is no record of when it was introduced into the MACA area but park staff recently dated one tree at over 90 years of age. It is possible that a seedbank was present and undetectable but, given that seed viability for tree of heaven is usually no longer than one year, this was unlikely (Hunter 2000).

Logistic regression is a technique for analyzing problems in which there are one or more independent variables that determine an outcome. The dependent variable is binary, generally representing the presence ($y = 1$) or absence ($y = 0$) of a species in ecological studies. Independent variables describe habitat characteristics. Logistic regression is an appropriate choice for habitat analysis when the independent variables are categorical or a mix of continuous and categorical (Hosmer and Lemeshow 2000). No distributional assumptions are required for the independent variables and the primary assumption is that the dependent variable be discrete (Tabachnick and Fidell 1996). The goal of this type of analysis is to predict the category of outcome (i.e., presence or absence) for individual cases using the simplest suite of descriptive independent variables (i.e., habitat model). Logistic regression is based on the assumption that occurrence of a species relates to environmental gradients in a logistic rather than a linear fashion. Species may exhibit tolerance over part of a gradient, decreasing tolerance once a threshold has been reached, and then intolerance over the remainder, which produces a sigmoid-type curve (Osborne and Tigar 1992).

Logistic regression is based on a logit transformation of the probability of presence:

$$g(x) = \beta_0 + \beta_1 * x_1 + \beta_2 * x_2 \ldots\ldots \beta_i * x_i, \quad (1)$$

where β_i represents the parameter estimates, x_i are the data values, and $g(x)$ is the logit of the odds of a presence observation relative to absence (Quinn and Keough 2003). The logit is a common transformation for linearizing sigmoid distributions of proportions (Armitage and Berry 1994).

The probability output of a logistic model can be used as raw probabilities or indexes (Real et al. 2006) where greater values characterize increasingly better habitat (Albert and Thuiller 2008). The raw probability outputs are calibrated so they depend on the frequency (ratio between the number of presences and the total number of records in the dataset) of the dataset. The mean fitted value across all sites is equal to the frequency in the dataset (Albert and Thuiller 2008). This is why logistic regression can be affected by an uneven proportion of presences and absences. The logit is used to calculate the probability of presence (P) in the following transformation:

$$P = \frac{e^{(g(x))}}{1 + e^{(g(x))}}. \qquad (2)$$

Model Selection

I used an information-theoretic approach to select the combination of variables that best fit the data. I first developed a global model and then derived a set of *a priori* models representing scientific hypotheses about tree of heaven's habitat requirements and pattern of invasion in MACA (Burnham and Anderson 2002).

I used Akaike's information criterion (AIC; Akaike 1973) as the criterion to select the best-fitting model (Burnham and Anderson 2002). AIC is based on the principle of parsimony, balancing goodness of fit with model complexity (Burnham and Anderson 2002). Lower AIC values indicate more parsimonious models. AIC is defined by the following equation:

$$AIC=-2LogL(\beta)+2(k+1), \qquad (3)$$

where $-2LogL(\beta)$ is a measure of the lack-of-fit of the model and $2(k+1)$ is a term that penalizes for increased model complexity (Mutua 1994). One important assumption is that the true model be among those tested (Burnham and Anderson 2002). True models probably do not exist but the selection procedure still performs well if a global model, including all influential variables, is tested, along with the *a priori* models (Burnham and Anderson 2002). I calculated AIC for 27 *a priori* models (Table 4) and chose the one with the lowest AIC value. Variable combinations that captured canopy closure, geology, soil and site characteristics, and amount of solar radiation were the focus of hypothesis testing.

Assessing Model Fit

I assessed model fit using the the Hosmer-Lemeshow goodness-of-fit statistic ($\hat{C}$) by creating 10 ordered groups of subjects and then comparing the observed number of

Table 4. Models representing *a priori* hypotheses to explain the occurrence of tree of heaven at Mammoth Cave National Park, Kentucky, tested using AIC selection criterion in logistic regression analysis.

Model Number	**Model variables**
1 (Global)	sg1 sg2 sv1 sv2 sc1 sc3 RSP Beers elevation solar TSI TRMI NDVI orgmatter phwater AWC clay dep2reslyr dep2wattbl[a]
2	solar TRMI NDVI
3	sg1 sg2 sc1 sc3
4	sg2 sc3 solar TRMI NDVI
5	solar TRMI NDVI Beers elevation
6	sg2 sc3 NDVI solar Beers elevation
7	sg2 sc3 TRMI TSI
8	sg1 sc3 Beers RSP NDVI
9	sg2 sc3 NDVI solar
10	sg1 Beers elevation solar TRMI NDVI
11	sg1 sc3 Beers elevation solar NDVI
12	sg2 Beers solar NDVI
13	sg2 sc3 Beers solar NDVI
14	sg1 sg2 sc3 Beers solar NDVI
15	sg1 Beers elevation solar NDVI
16	sg1 Beers orgmatter phwater AWC clay dep2reslyr dep2wattbl
17	orgmatter phwater AWC clay dep2reslyr dep2wattbl

Table 4, contd.

Model Number	Model variables
18	sg1 Beers phwater AWC clay dep2reslyr
19	sg1 Beers orgmatter phwater AWC clay dep2reslyr
20	sg1 Beers orgmatter clay dep2wattbl
21	sg1 sc3 Beers elevation solar NDVI phwater clay d2wattbl
22	sg1 sc3 Beers elevation solar NDVI phwater
23	sg1 sc3 Beers elevation solar NDVI clay
24	sg1 sc3 Beers elevation solar NDVI dep2wattbl
25	sg1 sc3 Beers elevation solar NDVI phwater dep2wattbl
26	sg1 sc3 Beers elevation solar NDVI clay dep2wattbl
27	sg1 sc3 Beers elevation solar NDVI phwater clay

[a] See Table 3 for acronym definition

tree of heaven presences in each group with the predicted number of presences based on the logistic regression model. The 10 ordered groups are created based on their estimated probability (Lemeshow and Le Gall 1994). Groups are typically formed in probability increments of 0.1. A significant difference between observed and predicted frequencies among the 10 groups indicates a lack of model fit.

I evaluated overall model performance using percent concordance, which analyzes the association of predicted probabilities and observed responses. Percent concordance reflects the accuracy of the classification of responses. A pair of observations with different observed responses is said to be concordant if the observation with the lower ordered response value (x = 0) has a lower predicted mean score than the observation with the higher ordered response value (x = 1) (Kleinbaum 1994). Hence, the higher the predicted event probability of the larger response variable, the greater percent concordance will be.

Model Testing

Data Collection

I tested the tree of heaven habitat model with independent field data, which is the best method for evaluating predictive performance (Pearce and Ferrier 2000). Because the area of habitat designated as favorable by the model was relatively low, I stratified the number of random test locations according to model predictions (Thompson et al. 2006). I created 38 sampling locations in each of 4 classes of predicted probability values (n=152), with each successive class doubling in area according to the following geometric formula:

$$n + 2n + 4n + 8n = 100 \text{ (percent total pixels in favorable habitat)}, \quad (4)$$

where n represents the number of pixels in the stratification with the highest predicted probabilities. According to this sampling scheme, areas in the first stratification were sampled with twice the intensity as those in the second stratification, which, in turn, were sampled twice as intensively as areas in the third stratification, and so on.

All test plots were located within MACA. No overlap occurred with presence or absence locations used to build the model. I sampled plots during May 2007 (n=117). I used a GPS receiver to navigate to the center of the test plot and I surveyed a 30- x 30-m area for the presence of tree of heaven. I also surveyed areas representing the eight neighboring GIS pixels to account for any error associated with the GPS or GIS data. Thus, I searched an area equivalent to nine 30- x 30-m pixels (90- x 90-m test plot area).

If tree of heaven was present, I recorded the number of stems per colony, differentiated from seedlings, which were recorded as separate presence locations. Seedlings were distinguished from sprouts by excavating around the root system. The number of stems was of interest because habitat characteristics could be associated with species abundance in addition to presence. I recorded the presence of any tree of heaven encountered en route to sample plots as an incidental location. Test plots where tree of heaven was not observed were counted as absences.

Statistical Power

To determine whether the habitat model was affected by sample size, I combined all presences (*n*=190) and absences (*n*=1079) collected for tree of heaven during field surveys, in test plots, and locations provided by MACA and repeated the model selection procedures using AIC. Different results would indicate that sample size was insufficient. I additionally assessed statistical power using PROC POWER in the LOGISTIC procedure (SAS 9.2), ($\alpha = 0.05$; power = 0.90).

Model Performance

I tested for correlation among variables in the selected model using PROC CORR in SAS 9.1 (SAS Institute, Inc. 2006). I assessed how well the model performed versus random searches by comparing the proportion of presences to total observations collected in the survey with the proportion of presences to total observations from test plots. An increase in this proportion would indicate that the model was successfully predicting suitable habitat. I used the LOGISTIC procedure in SAS to test whether the predicted probability of occurrence was statistically related to presence in test plots. If the model was sufficiently powerful, a statistical relationship between the probability values and the occurrence of the species would be expected. Finally, I used linear regression (PROC REG; SAS Institute, Inc. 2006) to determine whether the number of stems per test plot was associated with the predicted probability of occurrence based on the habitat model.

Discrimination and Calibration

Pearce and Ferrier (2000) recommend testing discrimination and calibration to assess the performance of habitat models generated with logistic regression. Discrimination refers to the ability of a model to discern between occupied and unoccupied sites whereas calibration refers to the concurrence between predicted probabilities and observed proportions of species presences (Pearce and Ferrier 2000). I tested discrimination by classifying predicted and observed presences and absences in the test plots in a 2 x 2 frequency table (Pearce and Ferrier 2000).

Discrimination testing requires the selection of a probability threshold, which I defined as the value that separates suitable and unsuitable habitat. Model accuracy will vary according to which threshold value is selected so I chose a probability threshold value that represented the best balance between sensitivity (the proportion of actual positives which are correctly identified) and specificity (the proportion of negatives which are correctly identified) (Dettmers et al. 2002). To further assess the discrimination capacity of the model, I developed a relative operating characteristic (ROC) curve, which relates relative proportions of correctly and incorrectly classified predictions over a continuous range of threshold levels (Pearce and Ferrier 2000). I used sensitivity and specificity values based on the survey data to develop the ROC curve (PROC LOGISTIC; SAS Institute, Inc. 2006). I was not able to develop an ROC curve using the test data because there were not enough data to generate sufficient statistical power for testing. The area under the resulting ROC curve (AUC) reflects how well the model discriminates between occupied and unoccupied sites (Pearce and Ferrier 2000). An AUC value of 1.0 indicates a perfect model (i.e., 100% sensitive and 100% specific) whereas a value of 0.5 indicates no discrimination. This is graphically represented by a straight, diagonal line extending from the lower left corner to the upper right (Fan et al. 2006).

Model calibration was also tested according to methods described by Pearce and Ferrier (2000). Calibration has three components: bias, spread, and unexplained error (Pearce and Ferrier 2000). Very little can be done to address unexplained error, but bias (a consistent under- or overestimation of presence) and spread (a systematic departure from the regression line that is fitted to the predicted and observed occurrence) can be analyzed graphically (Pearce and Ferrier 2000). If the model is perfectly calibrated, observations should lie along a 45° regression line (Pearce and Ferrier 2000). Bias is represented by an upward or downward shift of the observations compared with the 45° regression line, whereas spread error is a consistent departure from the regression line. No spread error exists if the observations are parallel to the 45° regression line (Pierce and Ferrier 2000). Because the predicted probabilities ranged from 0 to 0.54, I rescaled the predicted probabilities to a 0–1.0 for calibration analysis.

Post-Hoc Analyses

Variable Bias

I evaluate the effect of the dummy variables sg1 and sc3 on model performance. Because those variables were created based on the combinations of soil type, geology, and site class with the most initial presences, they could be inherently biased. Therefore, I evaluated discrimination and calibration without these 2 variables using methods previously described.

Testing for Resolution Effects

To examine whether statistical relationships were affected by scaling, I calculated mean predicted probability values for areas surrounding the pixels of the test plots using the AGGREGATE function in ArcGIS® 9.2, Spatial Analyst (Figure 4). I calculated this mean value based on square "windows" of 90 meters on a side. I used logistic regression to determine the relationship between tree of heaven occurrence and the averaged pixel values corresponding to test plots.

Mahalanobis Distance Analysis

Because I had a large number of absences relative to the number of presences and logistic regression can be sensitive to unequal sample size (Jones et al. 2006), I evaluated a presence-only modeling technique. I used Mahalanobis distance (Clark et al. 1993) to create a predictive multivariate model for tree of heaven occurrence in MACA based on the same data and habitat variables used in logistic regression analysis. I conducted this analysis using presence locations collected in surveys and provided by MACA (n = 135).

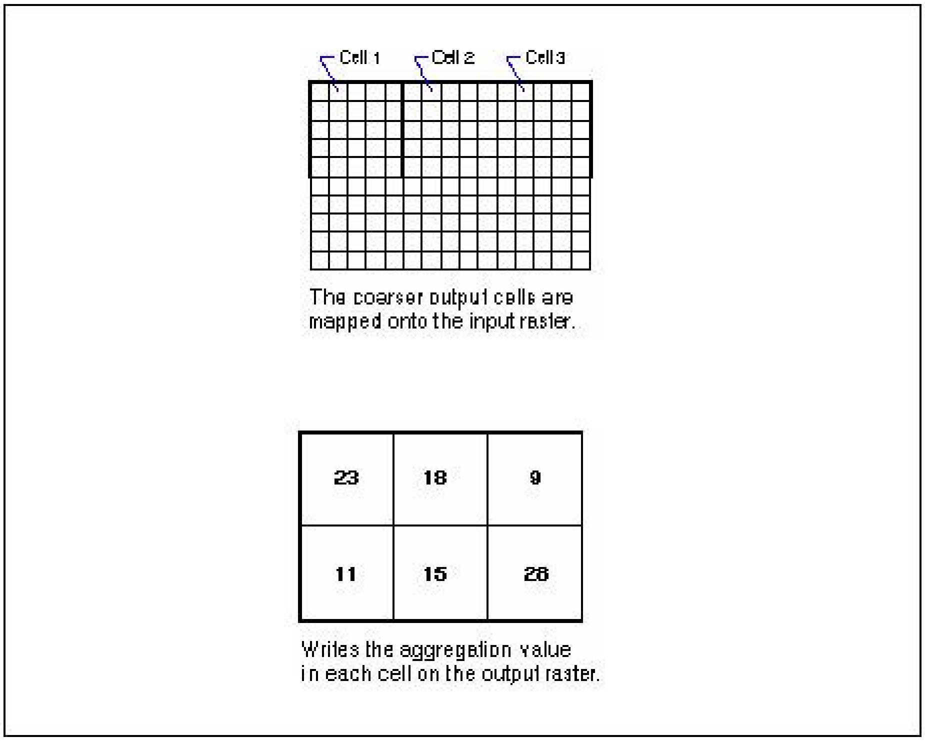

Figure 4. Illustration of how the Aggregate function in Spatial Analyst generalizes a raster grid to a lower spatial resolution (modified from ArcGIS 9.2® Desktop Help).

The Mahalanobis distance statistic (D^2) is a measure of dissimilarity between pixel values associated with presence locations representing “ideal” habitat characteristics and the remaining pixel values in a landscape. Low D^2 values indicate landscape conditions similar to those where tree of heaven was found (Knick and Rotenberry 1998) and is calculated as follows:

$$D^2 = (\underline{\bar{x}} - \underline{\hat{u}})' \Sigma^{-1} (\underline{\bar{x}} - \underline{\hat{u}}), \quad (5)$$

where $\underline{\bar{x}}$ is the vector of habitat measures associated with each pixel in a grid layer, $\underline{\hat{u}}$ is the mean vector of habitat measures estimated from tree of heaven locations, and Σ^{-1} is the inverse covariance matrix, also estimated from the tree of heaven locations. Assumptions of this technique are that the species has reached and colonized the best available habitats in the study area (Knick and Rotenberry 1998). Mahalanobis distance offers several advantages over other commonly used modeling techniques, such as logistic regression. It does not require absence data, and thus avoids potential biases because of false negatives (Clark et al. 1993). In addition, the distance values are uncorrelated standardized scores, correlated variables are adjusted by the variance-covariance matix, and distributional assumptions do not have to be met (Clark et al. 1993). I chose logistic regression to determine the relationship between tree of heaven occurrence and the D^2 values of the pixels corresponding to the test plots.

CHAPTER V

RESULTS

Nonnative Plant Surveys

During 2005 field surveys, I collected 342 locations, of which 16 represented tree of heaven, 40 were Japanese honeysuckle; 11 were multiflora rose; and 109 were Japanese stilt grass (Figure 5). Other less prolific species noted included garlic mustard (*n*=1), sericea lespedeza (*n*=5), and gill over the ground *Glechoma hederacea* L. (*n*=2). In 2006, I collected an additional 781 locations, of which 38 were tree of heaven presences and 647 were absences. In 2005 and 2006 I completed 80 transects (Figure 6), which resulted in 54 total presence locations for tree of heaven and 972 total absences. Ninety two presence locations were provided by MACA staff, resulting in a total of 146 presences. After correction for duplicate observations within the same pixel, there were 135 presences (Figure 7) and 972 absences resulting in 1,107 locations represented in the final dataset.

Logistic Regression

Based on AIC values, I identified models 21, 24, 25, and 26 (Table 5) as the most parsimonious. Of those, I selected model 24 because it contained the fewest number of parameters. Model 24 consisted of seven variables: sg1, sc3, Beers, elevation, solar, NDVI, and depth to water table. I detected no correlation among variables. Parameter estimates were significant and negative for variables sg1, NDVI, and depth to water table

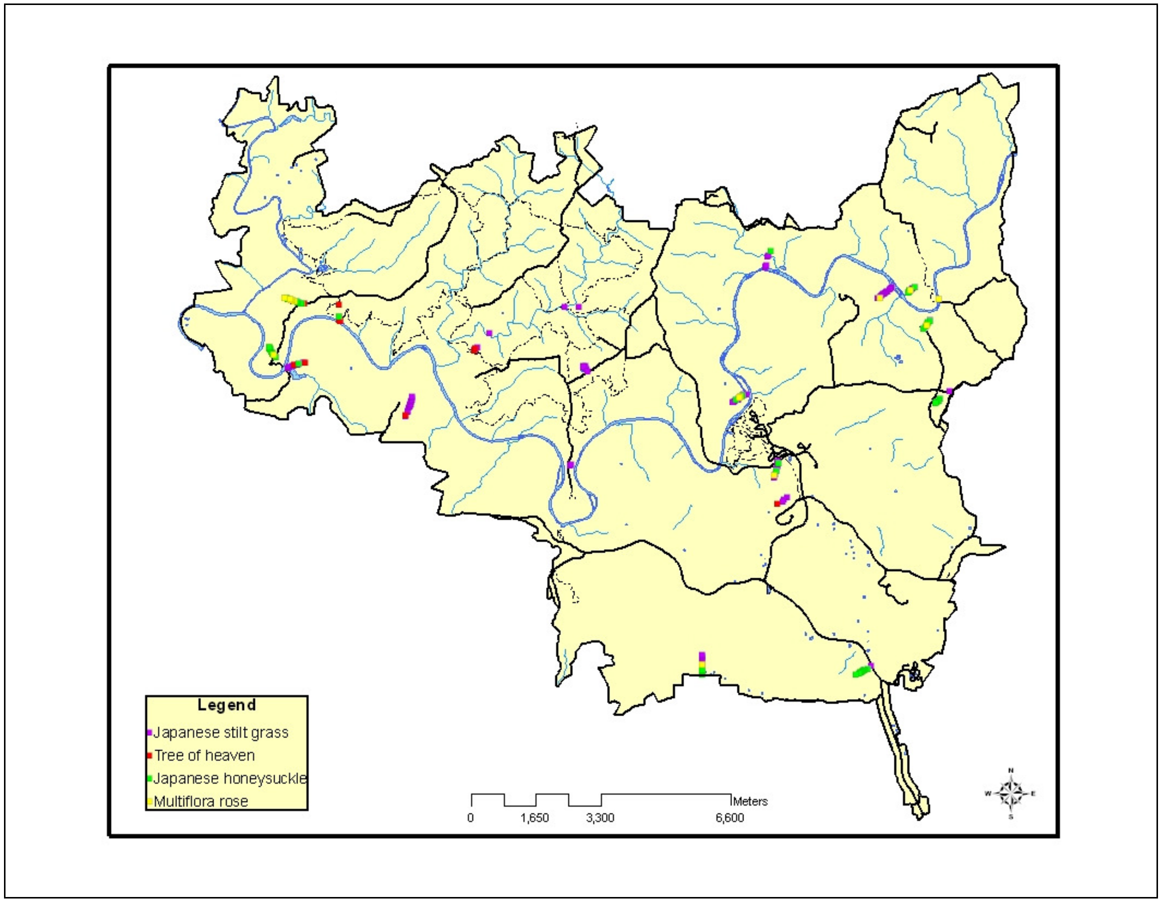

Figure 5. Nonnative plant locations collected during initial transect surveys at Mammoth Cave National Park, Kentucky, 2005.

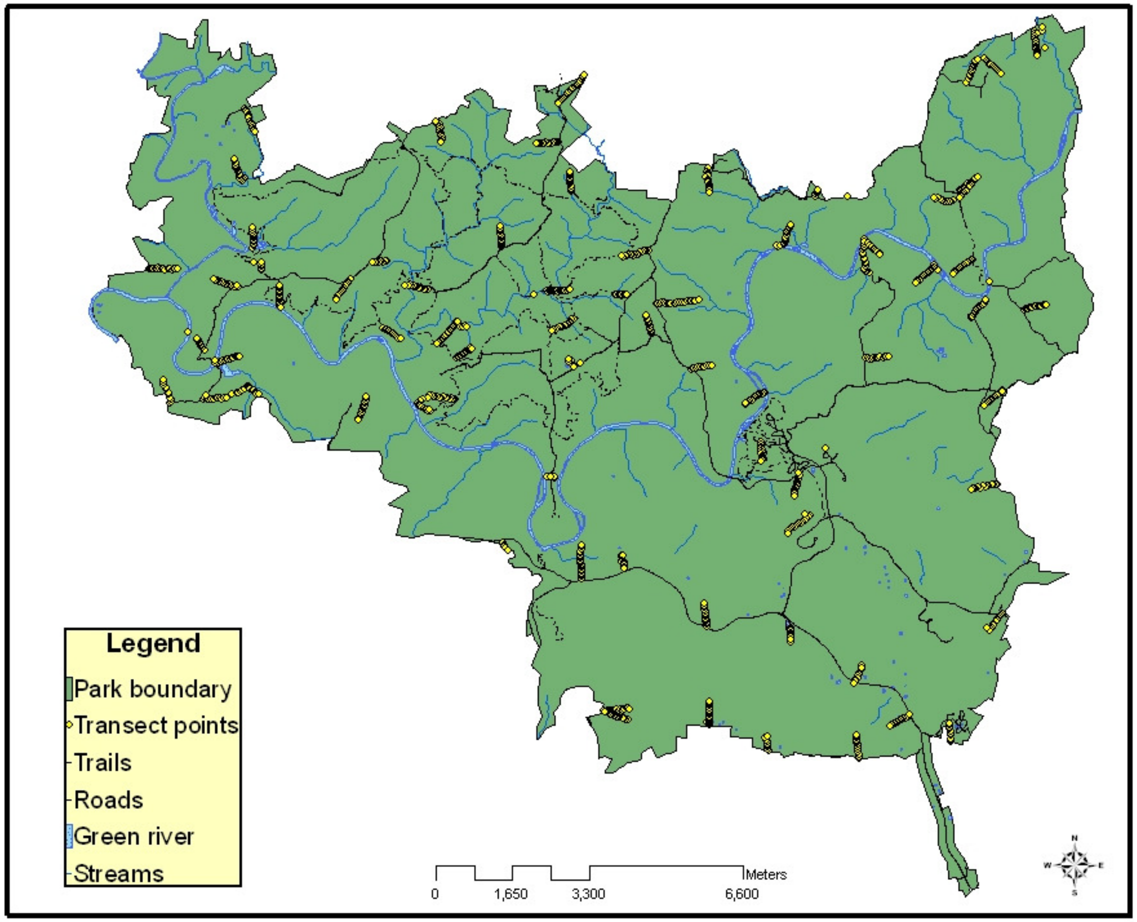

Figure 6. Comprehensive map of random transects surveys conducted in Mammoth Cave National Park, Kentucky, 2005–2006.

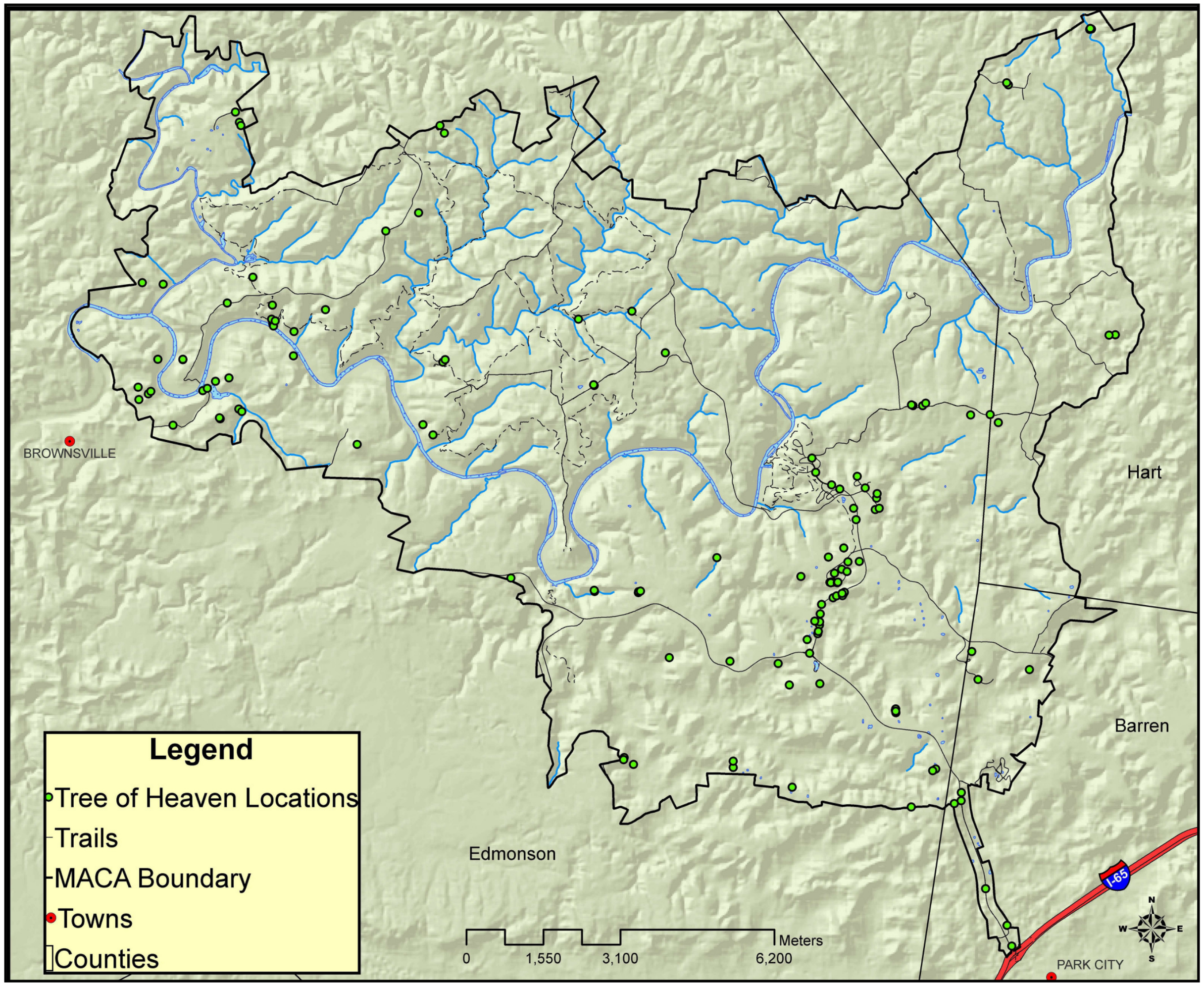

Figure 7. Presence locations of tree of heaven in Mammoth Cave National Park, Kentucky, collected during field surveys conducted in 2005–2006 and compiled from other sources (MACA and EPMTs).

Table 5. AIC values generated from logistic regression analysis of models representing habitat for tree of heaven in Mammoth Cave National Park, Kentucky, 2005–2006. Lower AIC values indicate more model parsimony. A difference in AIC values <3 among models indicate no difference.

Model Number	**Model Structure**	**AIC Value**
1 (Global)	sg1 sg2 sv1 sv2 sc1 sc3 RSP Beers elevation solar TSI TRMI NDVI orgmatter phwater AWC clay dep2reslyr dep2wattblb	759.415
21	sg1 sc3 Beers elevation solar NDVI phwater clay d2wattbl	753.574
24	sg1 sc3 Beers elevation solar NDVI dep2wattbla	753.857
25	sg1 sc3 Beers elevation solar NDVI phwater dep2wattbl	754.703
26	sg1 sc3 Beers elevation solar NDVI clay dep2wattbl	755.293
27	sg1 sc3 Beers elevation solar NDVI phwater clay	768.238
23	sg1 sc3 Beers elevation solar NDVI clay	771.564
11	sg1 sc3 Beers elevation solar NDVI	772.437
22	sg1 sc3 Beers elevation solar NDVI phwater	773.044
15	sg1 Beers elevation solar NDVI	775.782
10	sg1 Beers elevation solar TRMI NDVI	777.741
16	sg1 Beers orgmatter phwater AWC clay dep2reslyr dep2wattbl	783.853
20	sg1 Beers orgmatter clay dep2wattbl	785.432
14	sg1 sg2 sc3 Beers solar NDVI	789.958
6	sg2 sc3 NDVI solar Beers elevation	790.647
13	sg2 sc3 Beers solar NDVI	794.979
12	sg2 Beers solar NDVI	796.089

Table 5, contd.

Model Number	Model Structure	AIC Value
17	orgmatter phwater AWC clay dep2reslyr dep2wattbl	798.627
5	solar TRMI NDVI Beers elevation	799.939
9	sg2 sc3 NDVI solar	801.1
4	sg2 sc3 solar TRMI NDVI	802.977
18	sg1 Beers phwater AWC clay dep2reslyr	804.874
19	sg1 Beers orgmatter phwater AWC clay dep2reslyr	806.873
2	solar TRMI NDVI	810.313
3	sg1 sg2 sc1 sc3	810.642
8	sg1 sc3 Beers RSP NDVI	815.046
7	sg2 sc3 TRMI TSI	820.875

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[a] Model 24 was selected as the best model for predicting tree of heaven.

[b] Refer to Table 3 for acronym values.

and significant and positive for variables Beers and solar. The variables elevation and sc3 were marginally significant (Table 6). The model fit the data (Hosmer and Lemeshow goodness-of-fit statistic = 8.27, 8 df, $P = 0.41$). Predicted probabilities ranged from 0.0 to 0.54 (Figure 8).

The logistic regression diagnostics indicated 72.7% concordance and 26.7% discordance. Based on a predicted probability threshold of 0.120, the sensitivity and specificity of the model were 67.4% and 66.6% respectively, with an overall 66.7% correct classification. The false positive and false negative fractions were 78.1% and 6.4%, respectively. Regardless of the threshold chosen, false positive rates were never below 50.0. ROC analysis produced an AUC of 0.73 (Figure 9). When I removed locations provided by MACA and repeated analysis, model 24 again emerged as most parsimonious. Model parameters were not as strong reflecting the loss of statistical power, but the direction of the relationship did not change (Table 7).

Table 6. Estimated parameters (coefficients) of a logistic regression model to predict tree of heaven occurrence in Mammoth Cave National Park, Kentucky, 2005–2006.[a]

Parameter	**Estimate**	**Standard error**	**Wald Chi-square**	**P-value**
Intercept	-4.343	1.768	6.037	0.014
Sg1	-1.078	0.213	25.612	<0.001
Sc3	0.421	0.226	3.475	0.062
Beers transformation of aspect	0.534	0.177	9.107	0.003
Elevation	0.006	0.003	3.422	0.064
Solar insolation	0.027	0.007	13.253	<0.001
Normalized Difference Vegetation Index (NDVI)	-3.723	1.259	8.750	0.003
Depth to water table	-0.008	0.002	19.956	<0.001

[a] Model statistics: Hosmer-Lemeshow goodness-of-fit statistic = 8.3, 8 df, $P = 0.41$.

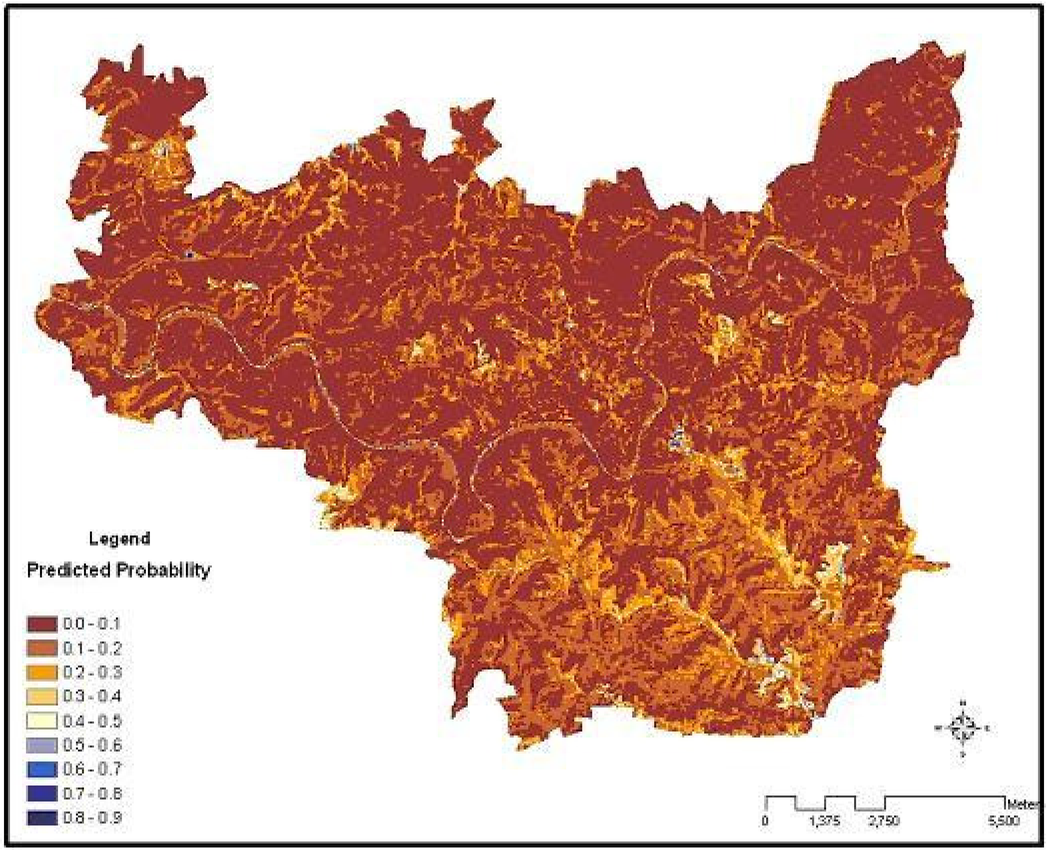

Figure 8. Predicted probability of the occurrence of tree of heaven in Mammoth Cave National Park, Kentucky, 2005–2006. Higher predicted probability values indicate more favorable habitat.

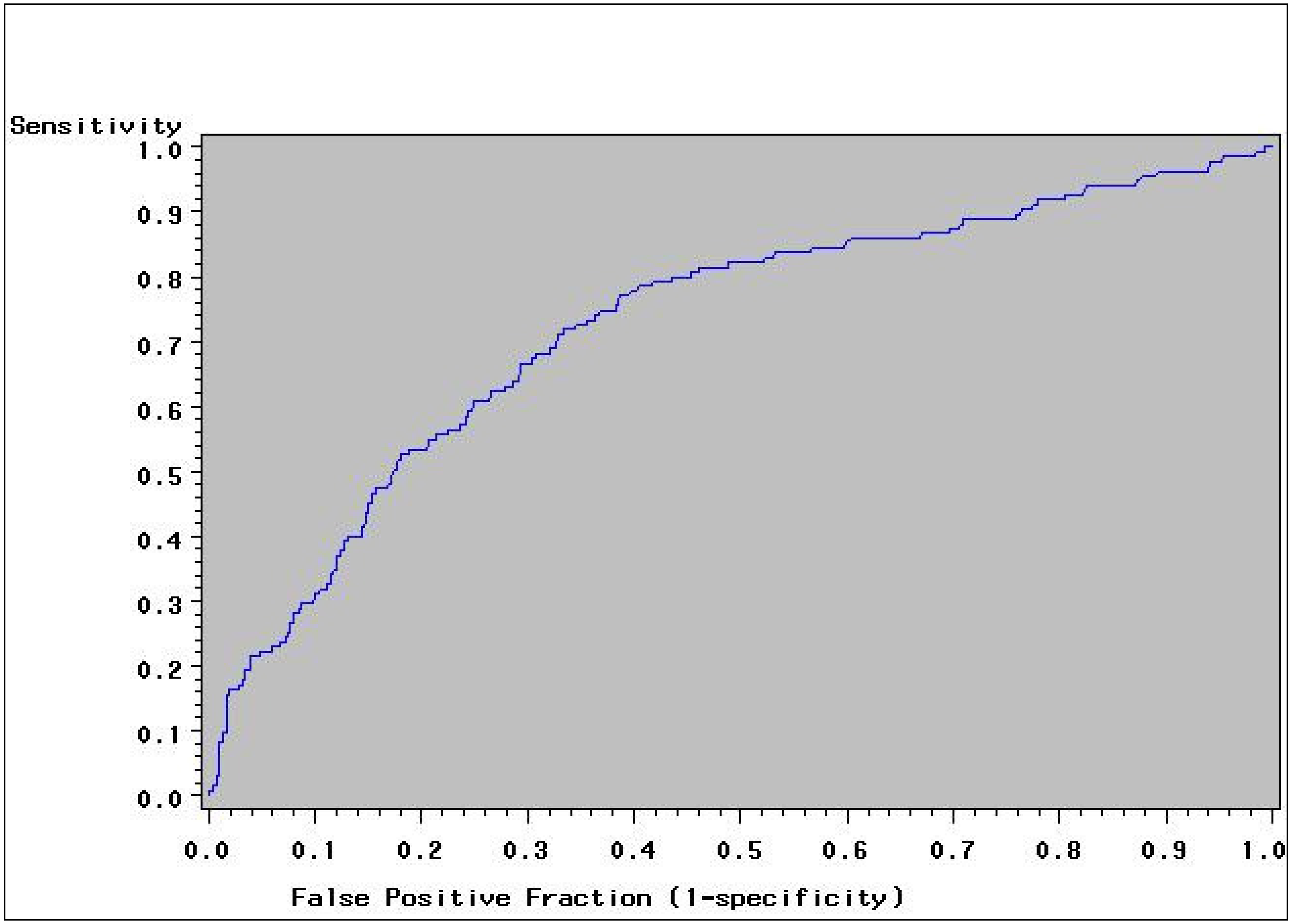

Figure 9. ROC Curve of data collected during field surveys in 2005–2006 in Mammoth Cave National Park, Kentucky. The Area Under the Curve (AUC) = 0.73.

Table 7. Estimated parameters (coefficients) of a logistic regression model to predict tree of heaven occurrence in Mammoth Cave National Park, Kentucky, developed from data collected during random field surveys to test for bias, 2005–2006.[a]

Parameter	**Estimate**	**Standard error**	**Wald Chi-square**	**P-value**
Intercept	-4.412	1.949	5.125	0.024
Sg1	-1.094	0.237	21.275	<0.001
Sc3	0.381	0.252	2.283	0.131
Beers transformation of aspect	0.325	0.198	2.708	0.100
Elevation	0.007	0.004	3.851	0.050
Solar insolation	0.023	0.001	7.540	0.006
Normalized Difference Vegetation Index (NDVI)	-3.424	1.326	6.666	0.010
Depth to water table	-0.006	0.002	8.434	0.004

[a] Model statistics: Hosmer-Lemeshow goodness-of-fit statistic = 15.9, 8 df, *P* = 0.044.

Model Testing

Test plots generated 16 presence locations and 107 absences. I recorded 39 incidental locations resulting in a total of 55 presence locations used to test the model. Ninety seven percent of presence locations were associated with predicted probabilities in the 0–0.30 range (Table 8). Average predicted probability values corresponding to presences and absences collected in test plots were 0.16 and 0.18, respectively. Five percent of total locations from surveys were presences compared with 15% from test plots indicating that the model improved the probability of finding tree of heaven compared with random searches by approximately 10%.

When I combined all presences and absences (*n* = 1,270; 190 presences, 1,080 absences) and re-ran the AIC selection procedure, model 24 was identified as most parsimonious. Power analysis ($\alpha = 0.05$, response probability = 0.10) indicated that sample size was sufficient for variables sg1, Beers, NDVI and solar and insufficient for sc3 (Table 9). Power analysis was inconclusive for elevation and depth to water table because both had odds ratios of ~ 1. Power calculations are not very useful in such instances (A. Saxton, University of Tennessee, personal communication).

Table 8. Number of tree of heaven test locations per predicted probability range. Probabilities were generated in a logistic regression model to predict tree of heaven occurrence in Mammoth Cave National Park, Kentucky, 2007.[a]

Predicted probability	**Number of presences**	**Percentage of total presences**
0.51–0.60	1	>1
0.41–0.50	1	>1
0.31–0.40	0	0
0.21–0.30	11	20
0.11–0.20	23	42
0.0–0.10	19	35
Total	55	100

[a] No presences for tree of heaven were recorded in predicted probability levels higher than 0.60.

Table 9. Results of a power analysis using logistic regression for the variables included in a habitat model to predict the occurrence of tree of heaven in Mammoth Cave National Park, Kentucky, 2007.

Variable Name	**n totala**	**Power**
sg1	350	0.90
sc3	500	0.36
Beers	100	0.98
NDVI	500	0.83
solar	50	>0.99

[a] This column refers to the minimum number of samples required to achieve the percentage of statistical power reported in the third column.

Logistic regression analysis using 3 different test data sets indicated no statistical relationship with predicted probability values: (1) locations collected in test plots (16 presences and 107 absences; *P* = 0.540), (2) locations collected in test plots minus duplicates (13 presences and 107 absences; *P* = 0.180), and (3) incidental locations included (55 presences and 107 absences; *P* = 0.131). The number of stems per test plot was not associated with predicted probability (*P* = 0.502).

Discrimination testing yielded a false positive fraction of 0.31 and a false negative fraction of 0.38. Overall reliability of the model was 0.41 (Table 10). Calibration testing revealed positive bias when presences from the test plots and incidental locations were combined (*n*=55; Figure 10) and did not change significantly when incidental locations were removed (*n*=16; Figure 11).

Table 10. Discrimination testing of a logistic regression model to predict the occurrence of tree of heaven in Mammoth Cave National Park, Kentucky, 2007.

	Recorded presence	**Recorded absence**	**Total**
Predicted presence	34	74	108
Predicted absence	21	33	54
Total	55	107	

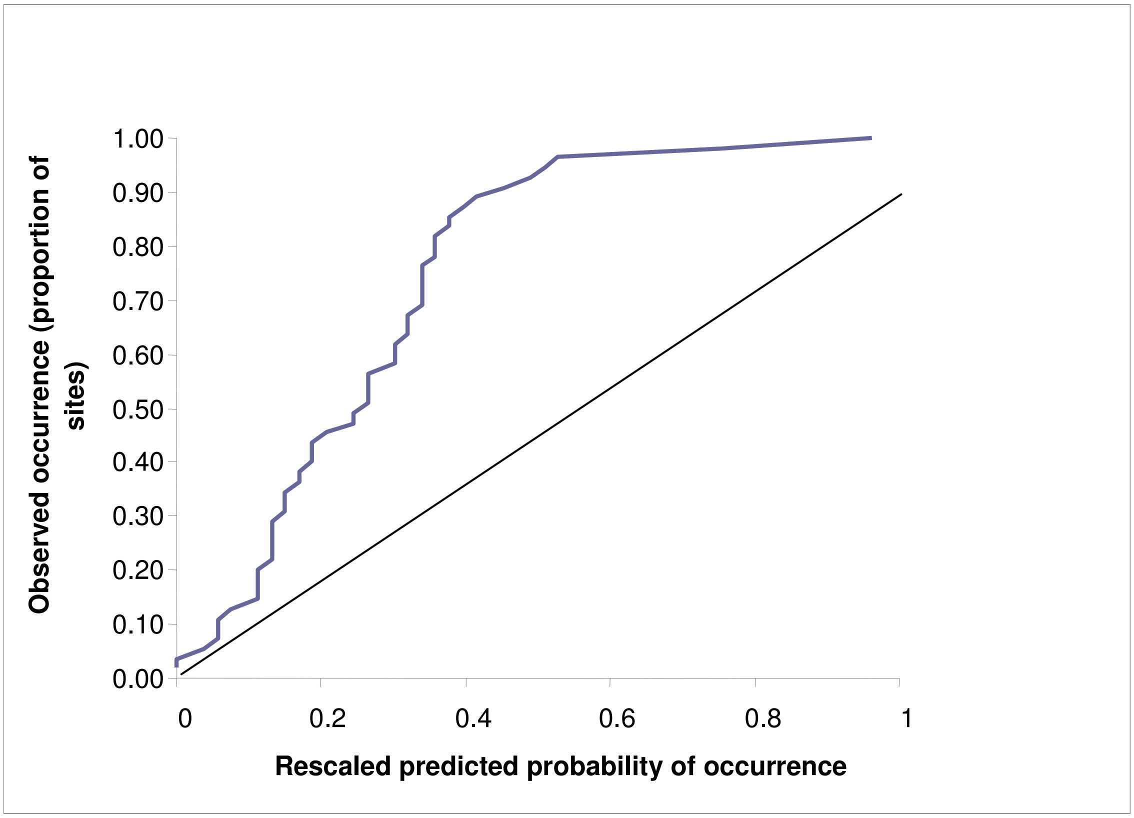

Figure 10. Calibration testing of a tree of heaven habitat model, developed with data collected in random test plots, including incidental locations in Mammoth Cave National Park, Kentucky, 2007. The departure from the 45^{o} regression line indicates positive bias in the model.

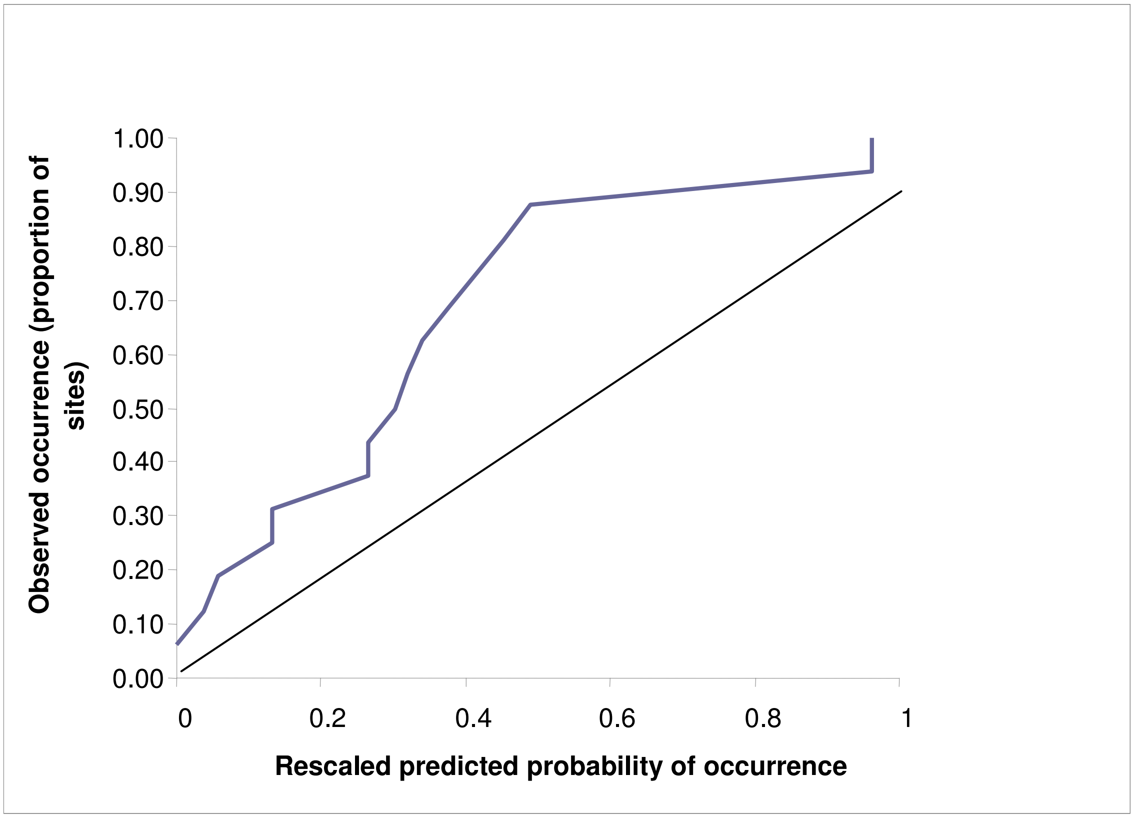

Figure 11. Calibration of a tree of heaven habitat model, developed with data collected in test plots only in Mammoth Cave National Park, Kentucky, 2007. The departure from the 45° regression line indicates positive bias in the model.

Post-Hoc Analyses

Removing the single variable sg1 or removing sc3 and sg1 in combination resulted in significantly better calibration (Figure 12). Thus, sg1 contributed bias to the model. Discrimination of the model remained low when these variables were removed.

There was no relationship between test locations and averaged predicted probability values ($P = 0.86$), indicating that lower spatial resolution did not improve the model.

The habitat map generated using Mahalanobis distance identified different habitat as suitable (Figure 13) but logistic regression analysis did not indicate a statistical relationship between the presence of tree of heaven and D^2 values ($P = 0.18$).

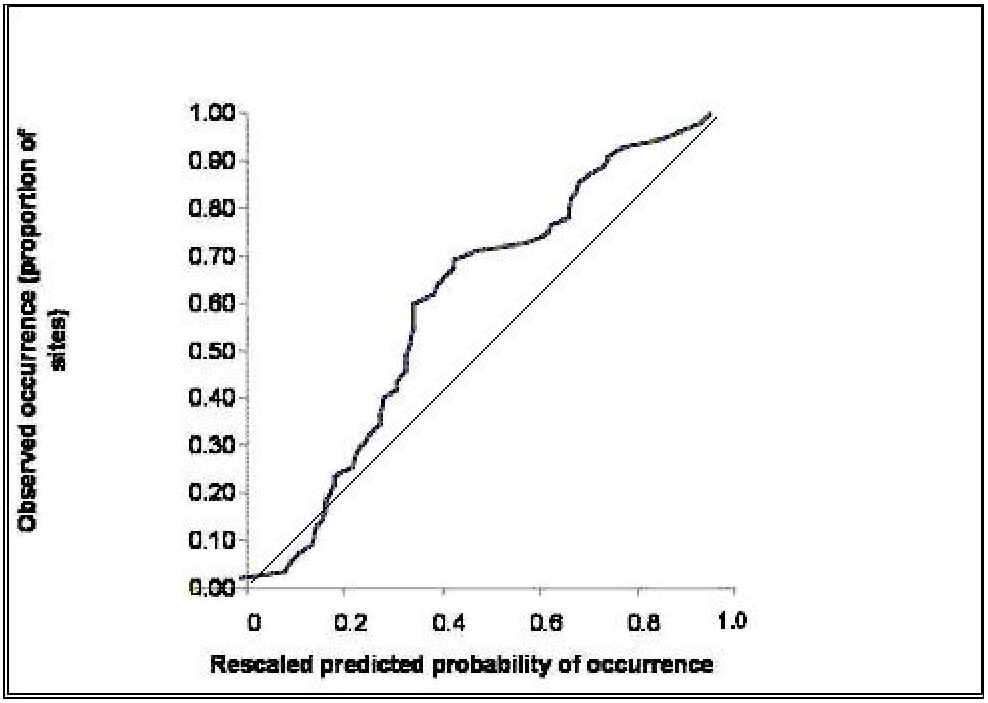

Figure 12. Calibration testing of tree of heaven model, without the variable sg1. Mammoth Cave National Park, Kentucky.

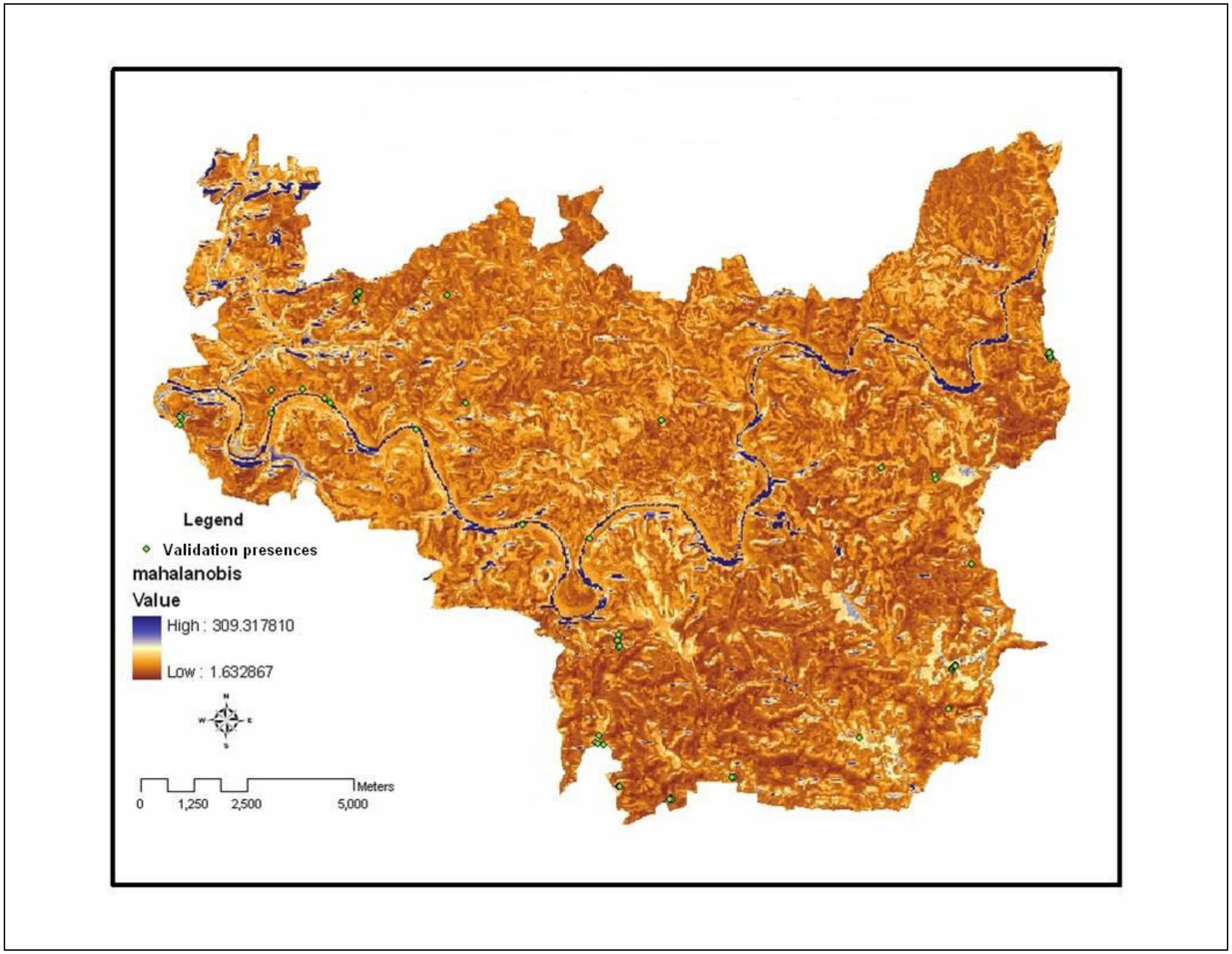

Figure 13. Habitat model for tree of heaven generated using Mahalonobis distance, using 135 presence locations used to build the logistic regression model, Mammoth Cave National Park, Kentucky.

CHAPTER VI

DISCUSSION

Invasive Plants in MACA

The list of severe threats developed by the southeastern EPMT largely was not applicable to MACA. Of the species on that list, only Japanese stilt grass, Japanese honeysuckle, multiflora rose, and tree of heaven were noted with any regularity. One nonnative species was not listed (gill over the ground) but could become invasive in floodplain areas. I did not select Japanese stilt grass the focal species for the habitat model because it was so prolific across all park habitats that modeling would not be useful. I rejected Japanese honeysuckle and multiflora rose as candidates for habitat modeling because individuals did not seem to noticeably impact forest regeneration or be in serious competition with native vegetation. Tree of heaven was a good candidate because its invasion strategy as a gap obligate appeared to have a predictable pattern of occurrence, as noted during field surveys.

Tree of Heaven Habitat Model

Although classification accuracy of the tree of heaven model was low, model fit was good. Hosmer and Lemeshow (2000) found that $\hat{C}$ may be biased with sparse data, so it is possible that model fit was not as good as the analysis indicated. Additionally, Fielding (2002) noted that the classification accuracy of logistic regression models is largely independent of goodness-of-fit. The model showed poor refinement, possibly because it did not generate predictions that span the entire zero-to-one probability (Pearce and Ferrier 2000, Pearce et al. 2002), and had poor discrimination. The model was not well calibrated, showing positive bias. The predicted probabilities from the habitat model were lower than what the observed proportions of occurrences in the test data indicated, particularly at higher predicted probability levels. Thus, predictions from this model cannot be used to estimate the probability of occurrence of tree of heaven in MACA.

Modeling species occurrence is always subject to uncertainty. It is difficult to determine sources of error, how they may have been conveyed throughout the modeling process, and what effect they may have had on the final product (Gonzalez-Rebeles et al. 2002). Error can come from failure to include critical habitat variables and other factors (e.g., predation, competition) into the modeling process, incorrect spatial resolution of habitat variables (Pearce et al. 2002), modeling technique, insufficient sample size, and measurement errors in the survey data. Below I discuss how different sources of error could have affected my study.

It is possible that important variables were missing from this model. Franklin (1995) noted the importance of interpolated climatic variables related to physiological tolerances in addition to topographic variables in vegetation modeling. I incorporated topographic variables into my analysis but did not include climatic variables because I assumed they were not applicable due to the small geographic extent of the study. In retrospect, variables that influence seed dispersal, such as prevailing winds, may have been informative had they been available. Tree of heaven likely invaded MACA by wind blown seed produced by populations established along interstate 65, southeast of the park. Propagule pressure from this seed may have been greater in some areas of MACA than in others due to wind patterns. This information in combination with data that better captured canopy gap dynamics would likely have added predictive power to the model because it would have captured the areas in MACA where the most seed was being disseminated and where canopy gaps were most frequently occurring, providing conditions for tree of heaven establishment. If variables at appropriate scales can be developed that capture prevailing winds and gap dynamics, incorporating them into models might improve performance.

Incorrect temporal and spatial resolution of habitat variables likely was an important factor contributing to the weakness of the model. The variable NDVI was used to delineate canopy gaps, which appeared to be extremely important to the occurrence of tree of heaven at MACA (personal observation). NDVI is typically used as surrogate measure of vegetation coverage and has been commonly used to capture canopy gaps. However, NDVI may introduce errors into models applied to landscapes with high spatial heterogeneity (Buyantuyev et al. 2007). Although MACA is not particularly spatially diverse, the karst topography created a variety of microsite conditions, which could have been problematic for this variable. NDVI has shown poor correlation to field observations when used to measure canopy gaps in some areas (Asner et al. 2002). Also, NDVI was only available for 2006 and before so it is highly likely that recent temporal dynamics of forest canopy gaps at MACA were not captured. Exploring other measures that capture vegetation characteristics may improve accuracy (Asner et al. 2002, Koukoulas and Blackburn 2004) but forest gap dynamics can occur quickly and may not be adequately measured using GIS data periodically collected by satellites. At MACA, capturing canopy gaps is a critical component of predicting tree of heaven occurrence. It is unlikely that strong predictive models can be developed without gap measurements on short temporal scales.

Microtopographic variation is a common cause of pattern in the local distribution of plant species (Kashimura 1985) and may have played an important role in tree of heaven distribution (Guisan and Thuiller 2005). The importance of soil and site characteristics to tree of heaven presence is evidenced by the fact that models were stronger (lower AIC values and more significant parameter estimates) with the addition of variables derived from the NRCS soil data. The four models with the lowest, equivalent AIC scores all contained variables sg1, sc3, Beers, elevation, solar, NDVI, and the NRCS variable measuring depth to water table (models 21, 24, 25, and 26). However, the soil variables may not have been fine-scaled enough to capture microsite characteristics associated with species occurrence. Also, subsequent analysis revealed that the variables derived from soil and geology and site class (sg1 and sc3) were problematic, strengthening the assumption that more specific data describing local site characteristics are needed.

The importance of land-use history and the severity of associated soil disturbance to nonnative plant presence and abundance are well documented in ecological literature (Dupouey et al. 2002, Neill et al. 2007, Rhemtulla and Mladenoff 2007, and Von Holle and Motzkin 2007) and probably play an important role in the distribution of tree of heaven at MACA. The variable I used (derived from slope and vegetation layers) did not show a statistical relationship with tree of heaven presence, most likely due to imprecision in the vegetation variable. Although most intensive row crop farming would have occurred in flat areas (derived based on slope) and those areas have largely re-vegetated into conifer forests dominated by eastern red cedar and Virginia pine (derived based on vegetation type), the variable slope_veg remained broadly defined. The vegetation variable characterized forests dominated by cedar and forests dominated by pine collectively as "coniferous", although the associated species and vegetation structure differ as do their susceptibility to invasion by tree of heaven (personal observation). Tree of heaven was almost never found in the pine dominated forests along Great Onyx Cave Road but was common in the cedar forests on Joppa Ridge and Mammoth Cave Ridge. The reason for this is unknown. The sites have similar slope, soil types, and past land-use history, with the exception that pines along Great Onyx Cave Road were largely planted. This could have contributed to a difference in gap dynamics (cedar dominated forests may be more prone to windthrow). The difference in susceptibility to invasion could also be due to wind patterns and associated propagule pressure, but examining those questions is beyond the scope of this study. Regardless, the broad classification of these two forest types into one vegetation type likely failed to identify factors that were important to the occurrence of tree of heaven. Correspondingly, the derived variable slope_veg probably failed to adequately capture past land use. Data collected at a finer spatial scale likely would improve performance of the model by better capturing past land use and delineating vegetation types. However, collecting these data would require a significant investment of time and resources, which may or may not be efficient for park managers.

Choosing the appropriate reality against which predictions should be judged is critical to achieving strong and useful habitat models (Fielding 2002). Incorrect choices of scale and spatial resolution can introduce error into a model, as was likely the case with some of the habitat variables used in this study. To determine whether any error introduced by the improper scale of some habitat variables could be remedied by lowering resolution, I expanded it from 30-m to 90-m, which did not improve predictive power.

Although expanding resolution did not remedy errors due to scale in this study, predictive models have been successfully developed for invasive, nonnative plants on much larger scales, indicating that there is promise for the applicability of modeling techniques. However, application of such models would be based on different model objectives. For example, one approach is to focus on predicting potential distributions in a new environment using variables that capture the species' entire native range, such as temperature and elevation. On larger scales (e.g., global, national, regional) this approach has been applied successfully for several different nonnative plant species to predict their invasion potential (Higgins et al. 1999, Welk et al. 2002, Peterson et al. 2003, Morisette et al. 2007). These models are more accurate because less specificity is required and large sample sizes are available. Although sample size was not an issue in this study according to my power analysis, it could be that nonnative species require much larger samples because of their generalist nature. It may be that habitat models for nonnative species are simply not applicable for local-scale predictions based on current distributions and that overall modeling goals should be focused on risk assessment, not on site management.

The modeling approach I chose also could have been a factor contributing to the lack of predictive power. Logistic regression can be sensitive to the prevalence of the species being modeled (Jones et al. 2006). The high number of absence locations compared with the presence locations may have biased results. To investigate this possibility, I developed a Mahalanobis distance model, which was based only on presence locations. The results did not show significant improvement in predictive ability. If finer scale habitat variables are developed, future research into the differences among techniques such as logistic regression and Mahalanobis distance to test the applicability of habitat modeling for nonnative species at local scales would be interesting.

Beyond potential errors associated with the modeling process, the development of a successful predictive model for tree of heaven may have been impacted by species characteristics, including genetic factors (Albright et al. 2006). Invasions of nonnative species can result in genetically different populations over space and time as species adapt to their new environments (Lee 2002). For this reason, models that treat invasive species as homogeneous entities will often fail (Lee 2002). There have been established cases where invasion success was affected by source population genetics, and natural selection on the genetic architecture has led to rapid adaptations (Lee 2002). Even small numbers of genes can have profound effects on the success of invasions. Genetic diversity within MACA populations may have influenced the effectiveness of habitat models to predict occurrence because different genotypes could be responding differently to environmental variables. Although no genetic studies on tree of heaven at MACA have been conducted, there is some indication of diversity from other studies. For example, Dallas et al. (2005) developed microsatellite markers for tree of heaven on Mediterranean islands and found indications of high diversity, although it was unclear whether this was due to adaptation from natural selection or to multiple introductions.

Greer and Aldrich (2005) speculated that U.S. populations of tree of heaven may have developed ecotypes that vary in toxicity and invasiveness due to adaptations to local environments. Determining whether or not genetic adaptation of tree of heaven at MACA is a real factor is beyond the scope of this study, but it is worthwhile to note that possibility.

Traits of Successful Invasions

The impact of an invasive species depends on the species characteristics and the recipient ecosystem (Simberloff 2003). There are no widely accepted criteria about which characteristics contribute to the invasion success of certain species or which ecosystems are more susceptible to invasion but some generalizations can be made, specifically when discussing plants. Rejmánek and Richardson (1996) successfully connected the level of invasiveness of pines (genus *Pinus* L.) based on a few biological characteristics. By comparing different species of pines, they found that a short juvenile period and short intervals between large seed crops led to rapid population growth (Rejmánek and Richardson 1996). Additionally, they found that small seed mass could be important as it is generally associated with larger numbers of seed produced, better dispersal, high germination rates, shorter chilling period to overcome dormancy, and higher relative growth rate in seedlings (Rejmánek and Richardson 1996). Grotkopp et al. (2002) found that seedling relative growth rate (RGR) and measures of invasiveness were positively associated across species within the genus *Pinus*. Their results have implications for other woody species of seed plants.

These studies point to characteristics commonly associated with *r*-selected species. Invasive, nonnative plants often can be considered *r*-selected, particularly in their introduced environments but often in their native environments as well. In their theory of island biogeography, MacArthur and Wilson (1967) define *r* strategists as opportunistic or pioneer species. They have high reproductive capacity, short juvenile periods, broad ecological tolerances and well-developed dispersal mechanisms. These are the adaptations that allow them to invade disturbed areas. MacArthur and Wilson (1967) suggest that *r*-selected species are replaced by *K*-selected species or "equilibrium" species, which have less-well-developed dispersal mechanisms, and are less adapted to open tracts but are better competitors over time. Native to northern China, tree of heaven has a long association with human habitation and disturbance (Whitney and Adams 1980), indicating that it exhibits traits associated with *r*-selected species in both native and introduced environments.

Johnston (1993) suggested that *K* strategists base their survival and success on local resources, making them relatively easy to model using a GIS if local resources can be captured in available data layers. Conversely, *r* strategists can be problematic in GIS modeling because their success is determined more by the rate of population increase and therefore on spatial interactions among organisms, which are difficult to capture (Goodchild 2002). Because *K*-selected species are adapted to produce a small number of highly developed offspring, they generally compete well in a specific set of habitats (Boone and Krohn 2002). It is this habitat specificity that allows modelers to more successfully predict their occurrence. Because *r*-selected species produce numerous, fast growing offspring, populations can be irruptive. Consequently, optimal habitat may not contain the species in a particular time period, whereas it may even be detected in relatively unsuitable habitats at other times (Boone and Krohn 2002), which could confound modeling efforts. As a probable *r* strategist, tree of heaven's irruptive population growth may be one reason for the commission error in this model.

Implications for Modeling Nonnative Plants

As the results of my study suggest, modeling invasive, nonnative species at local scales can be confounded by several factors. In this study, I followed Kearney's (2006) suggestion that statistical models describing species' distributions are 'habitat models' because they depict the link between species' occurrences across a landscape and physical or biotic features associated with those occurrences. Models that additionally capture interactions among organisms and include fitness or population response measures are best described as 'niche models' (Kearney 2006). Variables that capture species interactions and population responses may be critical to develop successful models for nonnative species at local scales, particularly considering that they commonly exhibit *r*-strategist characteristics. Indeed, there is increasing evidence that positive biotic interactions, such as mutualism and facilitation, may be as important as negative interactions, such as competition and predation, for species survival (Araújo and Guisan 2006). Simberloff and Von Holle (1999) describe what they term 'invasional meltdown', where introduced species frequently interact with one another and facilitative interactions are at least as common as detrimental ones. They found that habitat modification and mutualism were common among invasive, nonnative species and facilitated further invasion, potentially enhancing the level of negative impact to ecosystems.

As this study suggests, and because of the evidence that nonnative plant occurrence is strongly related to historical land-use and past disturbance, a sampling regime that captures the localized effects of historic events will lead to better models for invasive, nonnative species. Rhemtulla and Mladenoff (2007) stressed the importance of history in landscape ecology, whether it is information derived from pollen and tree rings, old land survey records, or oral interviews. The importance of history in shaping the structure and function of ecosystems has become more apparent in the ecological literature (Dupouey et al. 2002, Rhemtulla and Mladenoff 2007). Dupouey et al. (2002) showed that past land use can have irreversible effects on soil composition and chemistry, vegetative diversity, and species richness. Von Holle and Motzkin (2007) and Neill et al. (2007) connected land use and disturbance history to native and nonnative plant distributions in New England and determined that nonnative plant cover was influenced by abiotic conditions, particularly soil characteristics associated with past disturbance. Their findings suggest that GIS-based predictions of nonnative plant habitat at local scales may require site-specific soil information.

Finally, because nonnative, invasive species often exhibit characteristics associated with *r* strategists, they can be complicated to model. Most GIS-derived variables are not constructed on short temporal scales, thereby making it difficult to predict the irruptive population growth typical of *r*-selected species. For example, the inability to capture forest gap dynamics at MACA with the NDVI variable likely was a large component of model failure in this study.

CHAPTER VII

CONCLUSION

The research objectives of this study were not entirely met. I was able to rank nonnative, invasive plant species in MACA based on my field research and inform MACA staff of nonnative plant infestations in the national park. Furthermore, I was able to determine that the list they were currently using to prioritize nonnative plants by threat was not entirely applicable. I used tree of heaven as a case study for habitat modeling but was unable to prioritize areas for detection and control, because of the model's limited predictive power.

The habitat model I developed for tree of heaven could have failed because of problems associated with both the modeling process itself (e.g., lack of appropriate, sufficient variables, inappropriate spatial and temporal scale for variables, inappropriate resolution, insufficient sample size, modeling technique) and the species' characteristics (e.g., short juvenile period, short intervals between large seed crops, small, wind dispersed seed, high seed germination rate, prolific root sprouting, rapid growth). I speculate that the most important overall shortcoming was that the temporal and spatial scale of this data could not capture tree of heaven's occurrence because of its generalist nature. The NDVI variable likely could not capture the short temporal scale and small spatial scale associated with canopy gap dynamics, which contribute to the irruptive population growth patterns of tree of heaven.

Regardless of model failure, my findings provided important insights into predicting nonnative species occurrences at local spatial scales. Based on this study, modeling efforts for invasive, nonnative species may be more effective if variables that capture biologically relevant species interactions, site-based disturbance history and soil characteristics, and shorter temporal scales can be developed. If invasive, nonnative species are an important management concern, development of local-scale habitat models could be a good investment over time. At broader scales, developing predictive habitat models for invasive, nonnative species with variables derived from existing GIS data shows promise (Higgins et al. 1999, Welk et al. 2002, Peterson et al. 2003, Morisette et al. 2007.

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