2018

Predicting Invasive Carp Habitat Suitability in the Minnesota River, Minnesota

Melissa Oubre
Minnesota State University, Mankato

Recommended Citation

Oubre, M. (2018). Predicting Invasive Carp Habitat Suitability in the Minnesota River, Minnesota [Master's thesis, Minnesota State University, Mankato]. Cornerstone: A Collection of Scholarly and Creative Works for Minnesota State University, Mankato. https://cornerstone.lib.mnsu.edu/etds/820/

Predicting Invasive Carp Habitat Suitability in the Minnesota River, Minnesota

By

Melissa Joy Oubre

A Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of
Master of Science
In
Biology

Minnesota State University, Mankato
Mankato, Minnesota
July 2018

July 10, 2018

Predicting Invasive Carp Habitat Suitability in the Minnesota River, Minnesota

Melissa Oubre

This thesis has been examined and approved by the following members of the student's committee.

____
Dr. Phillip Larson

____
Dr. Luis Escobar

____
Dr. Matthew Kaproth

____
Dr. John Krenz

Acknowledgements

There were many times I worried this project would be the end of my academic career. I am beyond grateful for the multitude of people who played a role in making sure that fear never came to fruition.

First, I must thank my family for guiding me through life. My father, David Oubre, is always available to solve life's problems and give the best pep talks around. My mother, Diane Oubre, taught me to be creative and to never stop fighting for what you believe in. My older brother Chris Oubre, who inspired my dream to become Dr. Oubre before I could read. Finally, my sources of sanity and safety in a chaotic world, my brother, Jacob Oubre, and my sisters, Raeann Boyer and Erica Chadwick.

Academically, I have been blessed with an abundance of brilliant minds to learn from. Amongst these is Dr. Phil Larson, who was my role model to success in my freshman year at Arizona State University when graduate school was still just a dream. As my advisor he has become my mentor, pushing my limits intellectually, mentally, and physically further than I thought possible. Dr. Luis Escobar was my saving grace at one point on this project. He taught me to push out of my comfort zone into the foreign world of ecological niche modeling and to be meticulous, but not get lost in the small details. Drs. John Krenz and Matthew Kaproth pushed me to think critically and not forget the biology side of biogeography. I would like to thank the College of Science, Engineering, and Technology, the Department of Biological Sciences, the Department of Geography,

AGES research lab, and the Water Resource Center for always having my back and supporting my journey in science.

Part of what has made my time at Minnesota State so enjoyable is the friends I have made here. I must thank Nathan Lederman for the hours he invested into editing my work, my writing is better because of him. Also, Jessica Nelson and Andy Brown for answering my millions of computer questions, you both saved me hours on google and I am so grateful. And of course, Scott Matlocka and the super nerds for always reminding me life is fun.

Last, but not least, I need to thank the town of Courtland, Minnesota for solidifying that home isn’t always your birth state, it is where you are surrounded by people you love.

Funding

This project would not be possible without funding from the Lessard-Sams Outdoor Heritage Council (https://www.lsohc.leg.mn/) supported by the Minnesota Department of Natural Resources.

Abstract

Since the 1980's invasive carp have been expanding their range northward up the Mississippi River. Consisting of four species, grass carp (*Ctenophaygodon idella*), silver carp (*Hypophthalmichthys molitrix*), bighead carp (*H. nobilis*), and black carp (*Mylopharyngodon piceus*), these fish have the potential to naturalize and expand into large Mississippi River tributaries like the Minnesota River (MNR). Thus, understanding the likelihood of naturalization in these tributaries is vital in guiding prevention or mitigation efforts. This study evaluates the environmental suitability of the Minnesota River, the largest tributary to the Mississippi in Minnesota, for invasive carp. Environmental suitability for invasive carp is modeled using a two-stage framework. The first stage models the climatic suitability of the river with the NicheA model algorithm. The models were then refined using higher resolution MODIS remotely sensed data in the MaxEnt model algorithm. MaxEnt model results were connected to different floodplain inundation levels on the Minnesota River to forecast at risk backwaters. While variable, models forecast suitable habitat for all four species of invasive carp in the Minnesota River watershed. Combined, these data can be used to inform prevention and mitigation strategies for invasive carp management efforts in the Minnesota River watershed.

Table of Contents

Figures

Chapter 1: Literature Review

Aquatic Invasive Species

Invasive species, as defined by Executive Order 13112 during the Clinton administration (1993-2001), are "non-native to the ecosystem…whose introduction causes or is likely to cause economic or environmental harm or harm to human health". Invasive species typically possess characteristics that make them an immense ecological and monetary concern (*e.g.* high number of offspring, fast growth rate, high dispersal rate) (Lodge 1993; McMahon 2002). Successful invasive species typically have: 1) high abundance in their native range, 2) utilize a broad food source, 3) rapid population turn-over facilitated by quick sexual maturation, 4) the ability for fertilized females to colonize alone, 5) high genetic variability, 6) beneficial use to humans, and 7) are tolerant of a wide variety of habitats (Ehrlich 1984). These traits may be necessary for a species to survive in their native range, or the area a species historically originated from (McMahon 2002). In new environments, invasive species lack many controls to their population (*e.g.* predators, competition for food or space, and diseases) that would otherwise limit their populations (Simberloff 1989). The traits of a successful invasive species are not limited to terrestrial species.

Aquatic invasive species have multiple vectors of introduction which can be grouped into two major categories: natural and anthropogenically assisted (Lovell, Stone, and Fernandez 2006). Natural vectors conduce the movement of invasive species to new areas without anthropogenic forcing (*e.g.* natural dispersal, parasitism on waterfowl, and movement to new waterways during high flood stages) (Rasmussen 2002; Hermann and

Sorensen 2009). Anthropogenically assisted vectors require human assistance through intentional or accidental behavior. Many invasive species are unintentionally released along trade routes or through recreational activities (*e.g.* zebra mussel (*Dreissena polymorpha),* Eurasian water milfoil (*Myriophyllum spicatum*), and hydrilla (*Hydrilla verticillata*)) (Coetzee, Hill, and Schlange 2009; Rasmussen 2002; Horsch and Lewis 2009). Not all human assisted introductions are accidental, some species are brought intentionally through the pet trade (*e.g.* lionfish *(Pterois volitans*)), as ornamental vegetation (*e.g.* purple loose strife (*Lythrum salicaria*)), to enhance recreation or trade (*e.g.* Northern pike (*Esox lucius*) in California), or as a biological controlling agent (*e.g.* black carp (*Mycophatgynodon piceus*) controlling trematode populations) (Blossey, Skinner, and Taylor 2001; Ferber 2001; Lee 2001; Semmens et al 2004).

Human-caused disturbances promote the spread of invasive species by creating new microhabitats, reducing predator or competing populations making it less possible for them to control invading populations, and increasing the area of accessible habitat to invaders (Byers 2002). Anthropogenic alterations (*e.g.* dams, river channelization, river straightening) can alter an ecosystem so that native species are no longer adapted to the modified conditions, leaving an open niche for invasive species to exploit (Aguiar, Ferreira, and Moreira 2001; Byers 2002; Johnson et al. 2008). For example, invasive parrot feather watermilfoil (*Myriophyllum aquaticum*) encroached on the Mondego River's riparian zone after river straightening and bank reinforcement (Aguiar, Ferreira, and Moreira 2001).

Once established, invasive species disrupt ecosystems (Carlton 2001). Invasive species are the second leading cause of reduction in biodiversity, or variety of species, an indicator of a healthy ecosystem (Vitousek et al. 1997). For example, after the introduction of Nile perch (*Lates* spp.), Lake Victoria experienced the extirpation of approximately 200 vertebrate species in less than a decade (Goldschmidt, Witte, and Wanink 1993). In addition to altering the community, invasive species can alter the physical habitat. Common carp (*Cyprinus carpio*), a common invasive species within the United States, can decrease water quality by increasing turbidity, or the amount of sediment within the water, and mobilizing nutrients (*e.g.* phosphorous) that contribute to toxic algal blooms (Weber and Brown 2009). The effects of invasive species are not limited to biological and environmental systems. Environmental effects often manifest as devastating economic costs, with national estimates suggesting upwards of $128 billion spent annually to mitigate the effects of invasive species (Pimentel et al. 2000; Lovell, Stone, and Fernandez 2016).

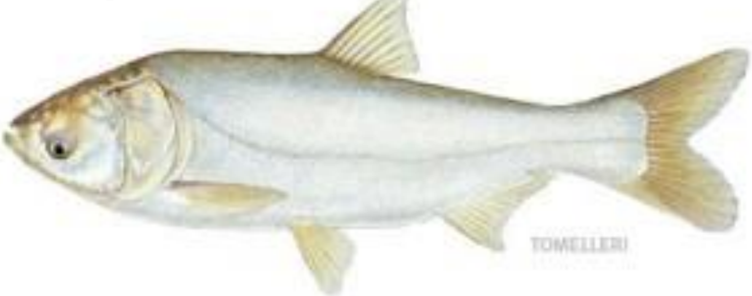
Invasive Carp

Invasive carp are one group of aquatic invasive species that are of major concern throughout the United States (Ferber 2001; Herborg et al. 2006; Kolar et al. 2007; Sass et al. 2014; Zhang et al. 2016). There are four species of invasive carp: grass carp (*Ctenophaygodon idella* ; Valenciennes in Cuvier and Valenciennes 1844),), silver carp (*Hypophthalmichthys molitrix*; Valenciennes in Cuvier and Valenciennes 1844), bighead carp (*Hypophthalmichthys nobilis* ; Richardson 1845), and black carp (*Mylopharyngodon piceus*; Richardson 1846) (Figure 1.1).

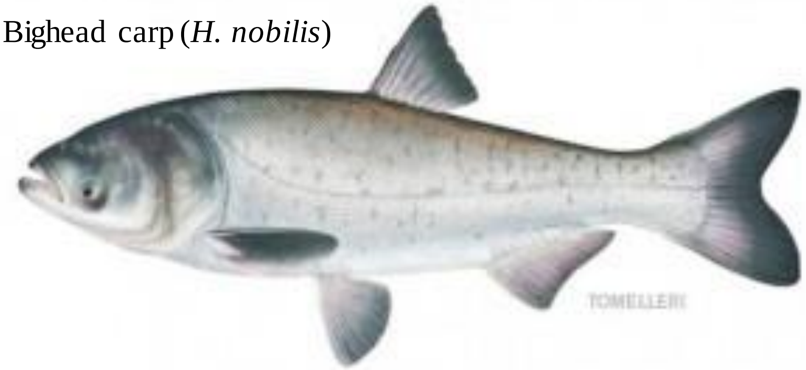
Figure 1.1 Four species of invasive carp © Joseph R. Tomelleri

Grass carp (*C. idella*)

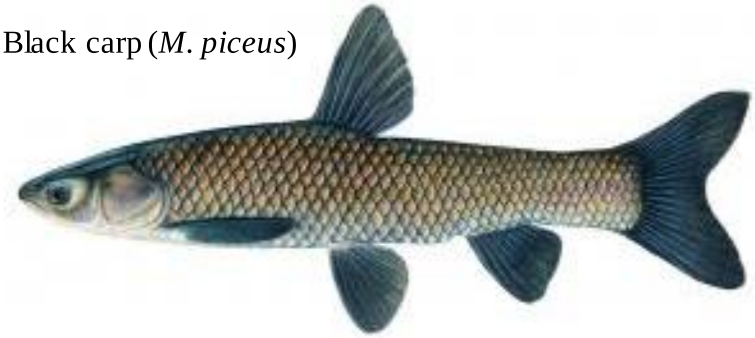
Silver carp (*H. molitrix*)



Bighead carp (*H. nobilis*)

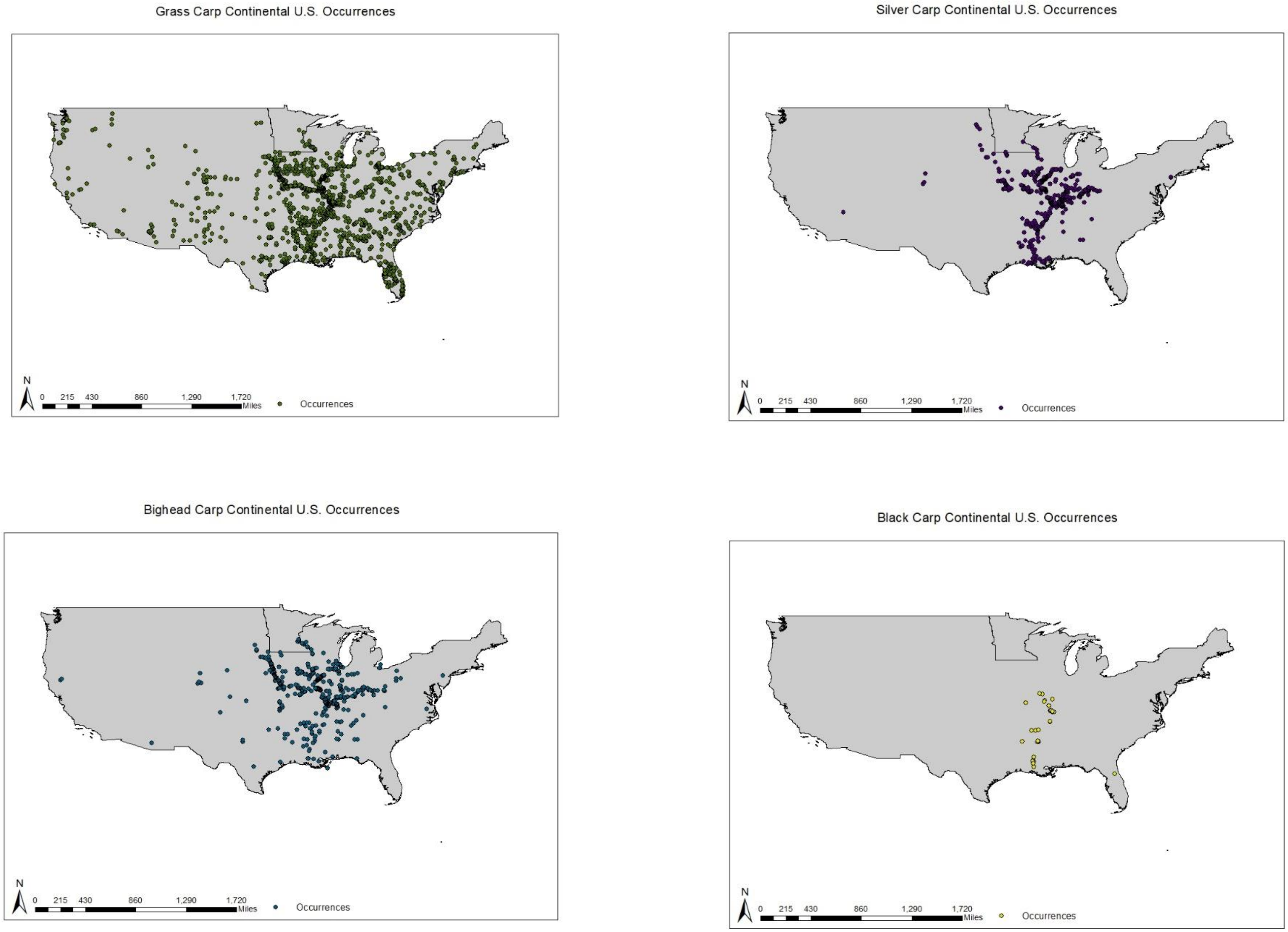


Black carp (*M. piceus*)



Invasive carp share evolutionary roots in the Yangtze River on the Asian continent, but were intentionally brought to the United States for use in aquaculture (Kolar et al. 2007). By the 1990s, invasive carp had escaped captivity and were reproducing in the Mississippi River. Invasive carp have quickly expanded their range upstream and through tributaries of the Mississippi River Basin (Kolar et al. 2007; Figure 1.2).

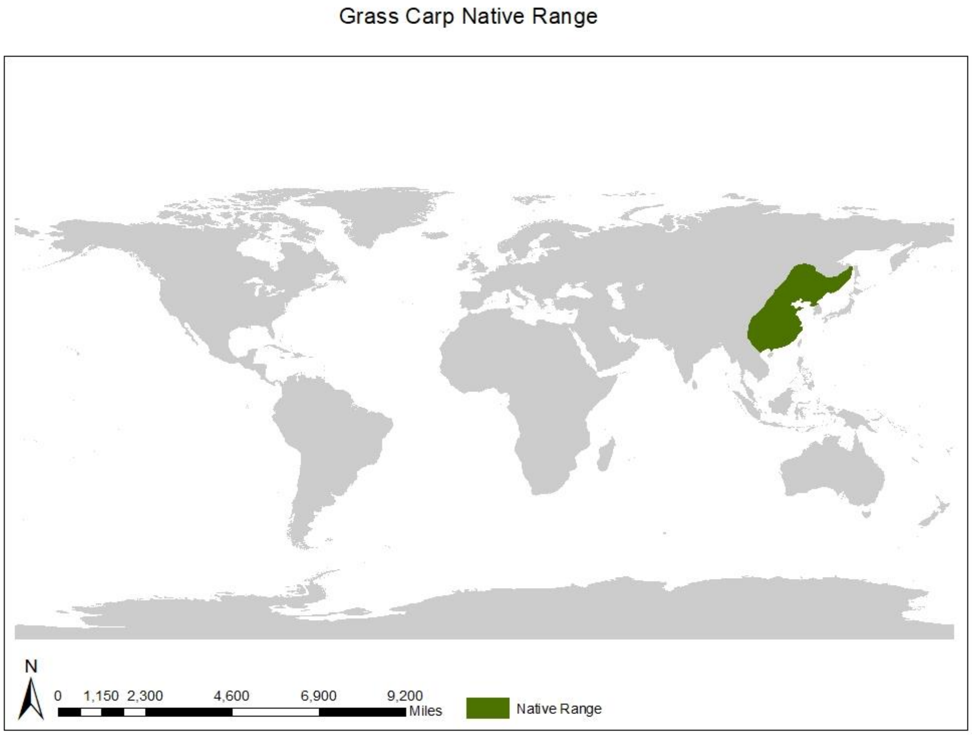
Figure 1.2 Invasive carp United States' distributions



Grass Carp (*C. idella*)

Grass carp are native to waters stretching from southern Russia into northern Vietnam (Cudmore and Mandrak 2004; Figure 1.3). This area experiences average air temperatures between -6° C and 25° C (Cudmore and Mandrak 2004). Commercial fishing records provide the little information available on the abundance of wild grass carp within their native range (Cudmore and Mandrak 2004). Catch rates suggest localized population decline in parts of the native range due to overfishing during the 1950s and 60s (Shireman and Smith 1983). Despite limited population declines, grass carp are populations are on the rise in many locations outside of their native range (Raibley, Blodgett, and Sparks 1995; Pflieger 2011; Chapman et al. 2013). This is in part to grass carp being exposed to a broad range of environmental conditions in its native range.

Figure 1.3 Grass carp's (C. idella) native range, adapted from Cudmore and Mandrak 2004



Grass carp can acclimatize to new conditions well, surviving in a diverse environmental conditions. For example, adult grass carp can survive in water temperatures as high as 35°C, but can overwinter in temperatures as low as 1°C (Opuszynski 1972). Despite the large range, grass carp show preference for water around 25°C (Bettoli et al. 1985). Grass carp are also tolerant to low water quality, with yearlings surviving dissolved oxygen concentrations as low as 0.22 mg/L (Opuszynski 1967). Grass carp fry are more susceptible to low dissolved oxygen levels than older carp (Opuszynski 1967). Additionally, adult grass carp can utilize brackish waters, surviving in salinity concentrations up to 19 parts per trillion (PPT) for brief periods (Shireman and Smith 1983).

Adult grass carp are capable of growing up to one meter in length and weighing 36 kg in their native range (Shireman and Smith 1983; Chilton and Muoneke 1992; Cudmore and Mandrak 2004). Wild grass carp, within their native range, typically live 5-11 years, becoming sexually mature between year 2-10 depending on food availability, temperature, and dissolved oxygen levels (Shireman and Smith 1983; Cudmore and Mandrak 2004). In the United States however, grass carp as old as 33 years have been caught and records indicate sexual maturation between years 4-5 (Chilton and Muoneke 1992; Cudmore and Mandrak 2004). Adult grass carp favor densely vegetated habitat in backwaters, ponds, and lakes and usually remain in the littoral zone (Shireman and Smith 1983; Page and Burr 1991). Adult grass carp utilize rivers, particularly during spawning.

Sexually mature grass carp will migrate to the main river channel, particularly areas with rapids or sand bars, to spawn once triggered by river conditions. Spawning triggers include a rise in water level of at least 122 cm in 12 hours, an optimum water temperature of 20°C to 22°C, and a river velocity between 0.6-1.5 m/sec (Stanley, Miley and Sutton 1978; Shireman and Smith 1983; Chilton and Muoneke 1992). In their native range, grass carp begin migrating to their spawning grounds when water temperatures are around 15-17°C and will begin spawning once water temperatures surpass 18°C. Grass carp spawns peak at different temperatures, between 20°-22°C in Russia and 26°-30°C in China (Cudmore and Mandrak 2004). Areas with temperate climate tend to have spawns that are well defined and short lived. In contrast, spawns can be much more ambiguous in tropical regions (Cudmore and Mandrak 2004). In rare years, if conditions are met often enough, multiple spawnings have been documented (Shireman and Smith 1983). Successful spawns have been known to occur outside of the idealized ranges (Shireman and Smith 1983; Crossman, Nepszy, and Krause 1987; Cudmore and Mandrak 2004). However, if the optimum conditions are not met female carp will reabsorb their eggs (Gorbach 1970).

Even if environmental conditions for a spawn to be successful are met, grass carp eggs must stay afloat within well oxygenated water for 50-180 km (Niklosky 1963; Stanley, Miley and Sutton 1978; Chilton and Muoneke 1992). If the eggs sink and settle on the river bottom during the incubation period, the embryo will suffocate. Research suggests an optimal velocity of 0.8 m/s for incubation, although a velocity as low as 0.23 m/sec has shown to keep grass carp eggs afloat long enough to hatch (Cudmore and Mandrak 2004). For this reason, preferred spawning sites are turbid, turbulent reaches near large river confluences as the water in these areas are typically well oxygenated and provide a large enough area for incubation (Stanley, Miley and Sutton 1978). During the incubation period, the ideal water temperature is between 21-26°C, with marked increased in deformities and death below 20°C (Shireman and Smith 1983). Once hatched, in order to survive, larval grass carp must move into calmer water, which typically occurs in habitat adjacent to the river, such as floodplain lakes.

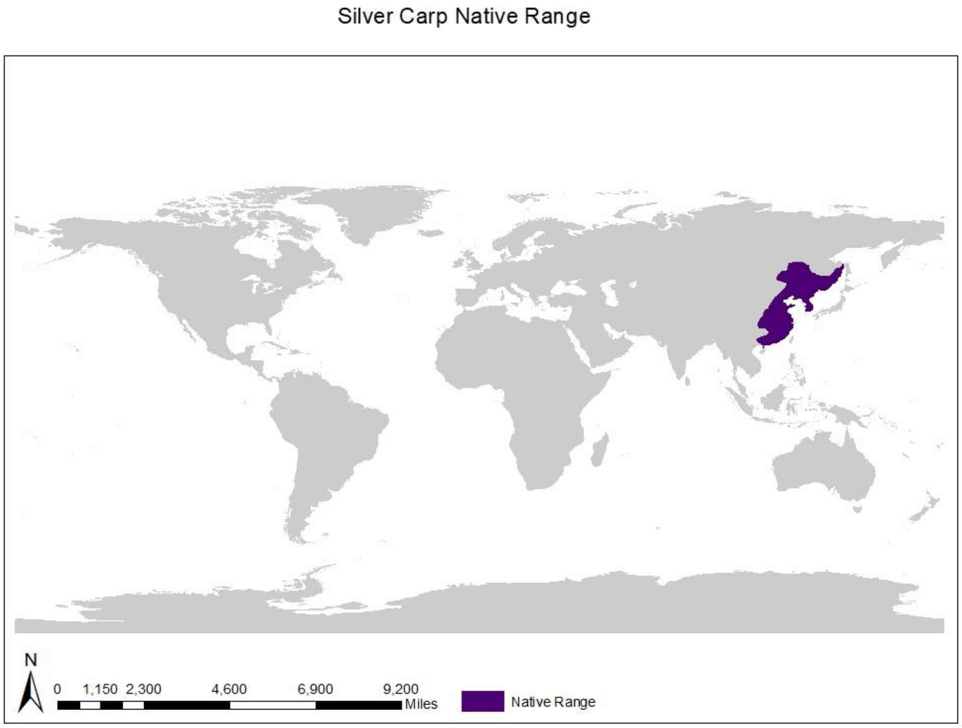
Larval grass carp consume zooplankton and insect larvae until their growth exceeds 30 mm when they become almost exclusively herbivores (Opuszynski and Shireman 1995). As adults, 95% of a grass carp's diet is made up of macrophytes, or aquatic plants (Fedorenko and Fraser 1978). These "selective generalists" are known to eat more than 50 genera of food items, but show a preference for soft-leafed plants over firm-leafed plants or filamentous algae (Van Dyke, Leslie, and Nall 1984; Bain et al. 1990; Opuszynski and Shireman 1995; Dibble and Kovalenko 2009). In areas where there is little to no aquatic vegetation, grass carp have a more variable diet. Although grass carp do show plasticity in diet, when consuming non-preferred items (*e.g.*, crayfish or emergent vegetation) individuals tend to be in poorer condition (*e.g.* lower body weight) (Cudmore and Mandrak 2004). The preference for macrophytes makes grass carp appealing for use in aquaculture.

Grass carp have established self-sustaining populations in 50% of the 115 countries they were introduced in globally despite occurring in low densities in their native range (Cudmore and Mandrak 2004). The large bodied omnivores are used to control aquatic vegetation in aquaculture (Cudmore and Mandrak 2004). Grass carp were imported into the United States for use in aquaculture in 1963 and escaped into open water shortly after. The presence of grass carp has been recorded in 45 states since their introduction. Grass carp are capable removing all the aquatic vegetation from an area which can have drastic impact on an ecosystem (Dibble and Kolvalenko 2009; Van Dyke, Leslie, and Nall 1984; Wiley, Tazik, and Sobaski 1987). After the introduction of grass carp, modifications in plant communities towards invasive plants or non-palatable species has been documented, disrupting the food web and in some cases causing trophic cascade (Van Dyke, Leslie, and Nall 1984; McKnight and Hepp 1995; Dibble and Kolvalenko 2009). A decrease in water quality has also been reported due to sediment resuspension during grass carp feeding and the collapse of nutrient cycling mechanisms responsible for vegetated growth leading to algal blooms (Shireman and Smith 1983; Kirkagac and Demir 2004; Dibble and Kolvalenko 2009). Despite the risk, triploid, or sterile, grass carp are still used in aquaculture, although the efficiency of these genetic modification to prevent spawns are still in question (Wiley, Tazik, and Sobaski 1987; Cudmore and Mandrak 2004; Dibble and Kovalenko 2009).

Silver Carp (*H. molitrix*)

Silver carp are native to Asia between the latitudes of 22°N and 54°N (*e.g.* China, northern Vietnam, and Siberia) (Xie and Chen 2001; Figure 1.4). The historical limits of silver carp's range is not known due to wide introductions in eastern Asia (Kolar et al. 2007). Silver carp was able to be wide introduced because it can survive in variable environmental conditions (Xie and Chen 2001). Larval silver carp are capable of surviving in water temperatures ranging from 0°C to 46°C, although the optimal range is between 26°C and 39°C (Opuszynski et al. 1989; Kolar et al. 2007). Additionally, silver carp can survive in brackish waters. For example, larval and fingerlings have been reported migrating to the Caspian Sea, with 6-12% salinity, to grow until sexual maturity (Abdusamadov 1987). Little information exists on adult silver carp use of brackish water, but there are recorded captures in estuarine areas in Brazil (Garcia et al. 2004). Normally, silver carp are found in slow flowing rivers and backwaters. Favoring open and eutrophic water, silver carp show preference for the upper and middle levels of the water column (Kolar et al. 2007).

Figure 1.4. Silver carp's (H. molitrix) native range, adapted from Cudmore and Mandrak 2004



Adult silver carp are often found in large schools (Kolar et al. 2007). Large adults can reach up to 40 kg and over one meter in length (Kamilov and Salikhov 1996; Kolar et al. 2007). Silver carp grow quickly and live upwards of 20 years, becoming sexually mature between year 3-6 (Berg 1964; Konradt 1965; Abdusamadov 1987; Kolar et al.2007). A highly fecund species, female silver carp produce an average of 171 eggs per gram of body mass, with records showing up to 1.3 million eggs per female (Jhingran and Pullin 1985; Abdusamadov 1987).

Sexually mature silver carp, triggered by environmental conditions, migrate to swift waters, usually near the mouths or confluences of rivers, to spawn (Konradt 1965). Spawning conditions are not universally agreed upon, but research suggests that an increase in water level, a minimum velocity of 0.7 m/s, water temperature of at least 17°C, and flooded backwaters are suitable for spawning events (Verigin et al. 1978; Krykhtin and Gorbach 1981; Schrank et al. 2001; DeGrandchamp et al. 2007; Lohmeyer and Garvey 2009). It is argued the increase in flow may not initiate the spawn, but instead causes an increase in turbidity which triggers the silver carp to start spawning (Stanley et al. 1978). This hypothesis is supported by evidence in the highly turbid Kara Kum Canal, which is controlled for water level, but meets the flow and temperature criteria during part of the year. This canal has had occurrences of silver carp spawning events despite consistent water level, supporting that the spawning criteria may be flexible (Aliyev 1976). Silver carp are known to spawn up to 3 times in a year (Ruebush 2011), but if environmental conditions are not ideal, female carp will reabsorb some or all their eggs, conserving energy (Gorbach 1970). Eggs released in a spawning event will continue downstream until hatched.

Flow velocity is important in maintaining egg buoyance, as the eggs must stay afloat until they are hatched (Niklosky 1963; Murphy and Jackson 2013). It was believed that at least 100 km of river is needed for the eggs to hatch (Krykhtin and Gorbach 1981), but more recent research suggests incubation time is site specific and dependent on water temperature and velocity (Murphy and Jackson 2013). In some cases, the eggs floated as little as 25 km before hatching (Murphy and Jackson 2013). Once hatched, larval silver carp migrate to slower water in flooded backwaters where they consume zooplankton and grow (Krykhtin and Gorbach 1981; Williamson and Garvey 2005). At around 18 days old the primary diet of silver carp switches to phytoplankton, which remains their preferred food choice for the remainder of their life (Sobolev 1970; Cremer and Smitherman 1980; Spataru, Wohlfarth, and Hulata 1983; Williamson and Garvey 2005).

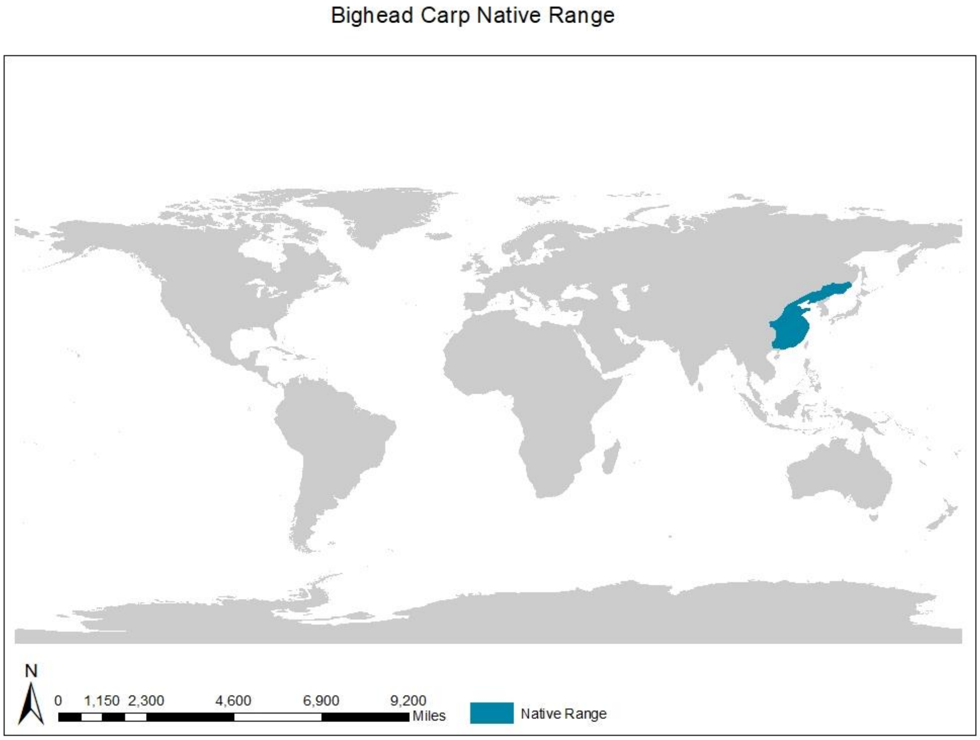
Highly modified gill rakers allow silver carp filter plankton and other particles out of the water (Kolar et al. 2004). The gill rakers are capable of filtering particles as small as 3.2 µm (*Chorella* spp. Algae) (Kolar et al. 2007). Research has found no difference in the proportion of taxa or particle size in the gut of silver carp in comparision to water samples, suggesting they are not selective (Cremer and Smitheran 1980). When phytoplankton densities are low, silver carp will also consume algae, zooplankton, bacteria, and detritus in large quantities (Schroeder 1978; Opuszynski 1981; Spataru and Gophen 1985). The ability of silver carp to filter large quantities of plankton made the fish appealing for biocontrol.

Silver carp have been imported or spread to 88 countries globally (Kolar et al. 2007). Of those, 23 (26%) countries have reproducing populations and 32 (36%) countries are unsure if silver carp are established. There are multiple accounts of silver carp being imported to the United States for aquaculture or biofiltration of sewage ponds (Cremer and Smitheran 1980; Shelton and Smitherman 1984). There is evidence that silver carp initially escaped from Arkansas into tributaries of the Mississippi River (Kolar et al. 2004). As of 2018, silver carp occur in 21 states. Silver carp's ability to indiscriminately filter small particles from the water was useful in biofiltration and aquaculture, but now makes the species a danger to native populations. For example phytoplankton communities experience a species composition shift towards smaller species in the presence of silver carp (Kucklentz 2017). Similar shifts can be seen in zooplankton communities, but this may be due to competition for food, not predation (Fukushima et al. 1999; Radke and Kahl 2002). In addition to altering species communities, silver carp also affect human recreational activities. Adult silver have a physical reaction to noise disturbances in the water. When startled by noise, like a boat motor, the fish jump out of the water (Nikolsky 1963). Jumping may be a defense mechanism in response to a perceived predator (Perea 2002). This reaction does pose a serious danger to boaters, as jumping silver carp capable of breaking bones or causing concussions as they fly through the air and come into contact with people (Kolar et al. 2007).

Bighead Carp (*H. nobilis*)

Bighead carp are native to eastern China, Siberia, and far northern portions of North Korea, between latitudes of 24°N and 47°N (Figure 1.5). Similar to silver carp, bighead carp's natural native range may never be known because of wide introductions throughout eastern Asia (Kolar et al. 2007). Chinese commercial fisheries catch records suggest that bighead carp populations are abundant in their native range. In 1998, silver carp and bighead carp combined made up more than 60% of the 1,294,000 metric ton commercial fishing haul from Chinese reservoirs (Kolar et al. 2007). The native distribution for bighead carp has a large air temperature range of -30°C to 40°C (Kolar et al. 2007).

Figure 1.5 Bighead carp's (H. nobilis) native range, adapted from Cudmore and Mandrak 2004



Bighead carp can tolerate a range of environmental conditions. In a laboratory study, bighead carp preferred water temperatures of 25.0-26.9°C (Bettoli et al. 1985). The same study concluded bighead carp's thermal maximum as 38°C (Bettoli et al. 1985). The lower thermal limit has not been identified, but bighead carp survive in the Manchurian Plain, which remains frozen for 4 to 6 months of the year, so it is assumed they are cold tolerant (Kolar et al. 2007). Similar to the previous species of invasive carp, bighead carp are able to survive in brackish water with low salinity. A study conducted on bighead carp fry in Laguna Lake in the Philippines, which experiences saltwater intrusion, concluded that bighead carp must have some osmoregulation abilities that allowed them to continue to grow after facing exposure to saline water (Garcia et al. 1999). Habitat use by bighead carp is also very similar to silver carp. Most adult bighead carp remain in waters that are slower than 0.3 m/s within the river channel or neighboring backwaters. Staying below 3 meters, bighead carp are not seen at the surface unless spawning or feeding (Kolar et al. 2007). Bighead carp tend to be rather stationary moving less than 15 km daily, except during a spawn (Peters, Pegg, and Reinhardt 2006).

Bighead carp are capable of growing to lengths over 1.5 meters long and 40 kg (Kolar et al. 2007). Not much is known about the longevity of the species in the native range. The oldest bighead carp caught in the United States was 8-10 years old and showed evidence of recent growth (Morrison et al. 2004). Generally, bighead carp become sexually mature during their third to fourth year of life, although environmental factors will influence this (Jennings 1988). Female bighead carp are highly fecund, usually producing 126 eggs per gram of body weight (Jhingran and Pullin 1985).

The bighead carp spawn typically occurs between April and June in Asia, peaking in late May (Kolar et al. 2007). Akin to the other invasive carp species, bighead carp are triggered to migrate upstream to spawning grounds by a rise in water level (Jennings 1988). Characteristic bighead carp spawning grounds are found where the mixing of waters in occurring (*e.g.* confluences, rapids, behind sandbars). Native spawning sites typically have rapidly flowing turbid water with a velocity of 0.6-2.3 m/s and visibility of 10-15 cm (Verigin et al. 1978). Ideal water temperature ranges from 18°C to 30°C (Verigin et al. 1978; Kolar et al. 2007). Evidence of successful spawns have occurred outside these conditions (*e.g.* Kara Kum Canal), suggesting plasticity in spawning requirements (Aliev 1976; Opuszynski and Shireman 1995). Once laid, the drifting eggs must stay afloat in an oxygenated current until mature enough to migrate into nursery habitat (*e.g.* backwaters) where they feed on zooplankton (Kolar et al. 2007; Deters, Chapman, and McElroy 2013)

Bighead carp remain zooplanktivorous throughout their lives (Cremer and Smitherman 1980; Jhingran and Pullin 1985). Bighead carp have two feeding methods, pump feeding and ram suspension feeding (Kolar et al. 2004). When pump feeding, bighead push water through their gill rakers, filtering out particles (Kolar et al. 2007). Ram suspension feeding occurs at the surface, where bighead swim through the water with their mouth open, pushing water through their gill rakers in intermittent gulps (Kolar et al. 2007). Unlike silver carp, bighead carp will selectively feed when food densities are high (Jennings 2988). However, bighead carp are known to be opportunistic when zooplankton densities are low, switching to phytoplankton or detritus.

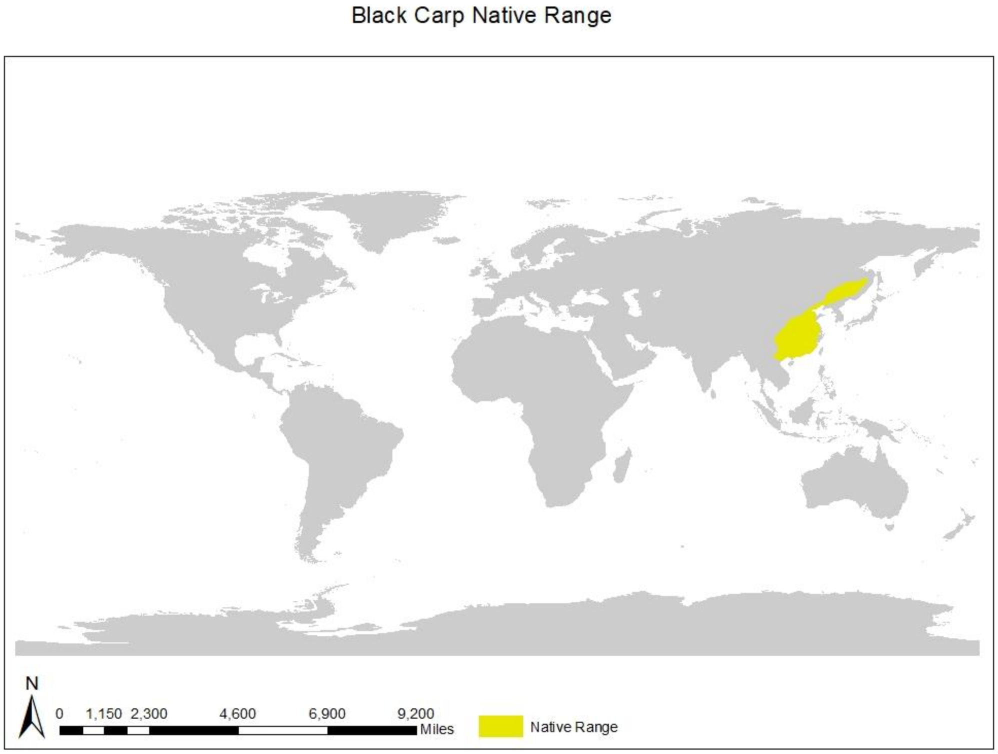
Bighead carp have records in 73 countries and have established populations in at least 19 countries (Kolar et al. 2007). Introduced to the United States in 1972, bighead carp were used in aquaculture farm in Arkansas to improve water quality (Jennings 1988). It is unknown when bighead carp escaped containment, but the first captures in open waters occurred during the early 1980s (Jennings 1988). Once in a system, bighead carp are a great risk to native planktivores that have overlapping diets, like the gizzard shad (*Dorosoma cepedianum*) and bigmouth buffalo (*Ictiobus cyprinellus*) (Irons et al. 2007; Sampson, Chick, and Pegg 2009). Studies done on the Illinois River showed a decline in population and condition of gizzard shad and bigmouth buffalo post silver and bighead carp invasion (Irons et al. 2007).

Black Carp (*M. piceus*)

Black carp have a native range from southern Russia to southern China, but are absent from the Korean peninsula (Nico, Jelks, and Williams 2005; Figure 1.6). This includes most Pacific Ocean draining watershed in east Asia from 22°N and 51°N (Nico, Jelks, and Williams 2005). Unfortunately, due to incomplete records and introductions into non-native waters the true historical range is not known. Similar to grass carp, wild native black carp populations may also be in decline in some areas due to overfishing (Berg 1945; Nico, Jelks, and Williams 2005). Black carp are so rare in Russia, they were listed as a species threatened with extinction in the early 2000s (Nico, Jelks, and

Williams 2005). However, black carp are thriving in other parts of their native range, including the Chang River basin (Berg 1949; Nico, Jelks, and Williams 2005).

Figure 1.6. Black carp's (M. piceus) native range, adapted from Cudmore and Mandrak 2004



Little research exists on black carp outside their use in aquaculture but these benthic fish are hypothesized to have all the same life requirements as the other invasive carp species previously described here (Nico and Jelks 2011). Black carp are native to a variety of climates, ranging from subtropical to cold (Nico, Jelks and Williams 2005). Thermal limits for wild black carp are not known, but research shows the fish do best between 4°C and 30°C (Nico, Jelks and Williams 2005). Their large native range suggests black carp are cold tolerant, as portions of the Amur River are frozen for part of the year (Nico, Jelks and Williams 2005). There is also no data on the salinity limits of black carp, but they have been captured in brackish water before (Gorbach 1961; Nico, Jelks and Williams 2005). Black carp prefer clear water, with dissolved oxygen levels around 5 mg/L, but can survive dissolved oxygen levels as low as 2 mg/L (Nico, Jelks and Williams 2005). Similar to the other invasive carp species, black carp can be found in rivers, backwaters, and lakes depending on their life stage (Nico, Jelks and Williams 2005).

Black carp are large-bodied with records showing growth up to 1.5m in length and over 70kg (Nico, Jelks, and Williams 2005). Growth rates and age of maturity are related to latitude, with carp at lower latitudes becoming to sexual mature at a younger age (Nico, Jelks, and Williams 2005). Male black carp reach maturity anywhere from six to eleven years of age, although there have been instances of sexually mature males as young as three in China (Nico, Jelks, and Williams 2005). Female black carp are highly fecund, producing 82 ova per gram body mass, with research showing occurrence of up to a million eggs (Jhingran and Pullin 1985). Adult black carp inhabit slow moving water within the middle and lower portions except during spawning events where they move to large rivers (Nico and Jelks 2011).

In their native range, black carp spawn in late spring into summer, depending on seasonal flooding (Nico, Jelks, and Williams 2005). Surges in water level, increased velocity, and water temperatures between 26°-30°C are cues for black carp to move to large rivers to spawn (Soklov 2002; Nico, Jelks, and Williams 2005). In aquaculture, black carp spawn later than silver carp or bighead carp despite similar spawning requirements (Atkinson 1977). Multiple black carp spawns have been suggested in the literature, but the occurrence of multiple spawns has never been recorded (Nico, Jelks, and Williams 2005). Similar to other invasive carp, black carp eggs need to remain buoyant until hatched (Nico, Jelks, and Williams 2005). Once hatched, larval black carp migrate to nursery habitat in backwaters and attached lakes to feed (Chang 1966).

Larval black carp consume zooplankton until their pharyngeal teeth grow, at which point they become full time molluscivores, consuming mostly bivalves and snails (Nico, Jelks, and Williams 2005). Pharyngeal teeth are a distinguishing feature of black carp in comparison to other invasive carp species. The structure allows black carp to crack the hard outer shells of their prey (Nico, Jelks, and Williams 2005). Information on wild black carp diet, particularly selectivity of taxa, is lacking. Most information available about black carp diet is from aquaculture, where mollusks are supplemented (Nico, Jelks, and Williams 2005). This lack of data makes interpreting the trophic ecology of black carp difficult. Despite the unknown trophic risk, black carp were widely introduced to control mollusk populations (Nico, Jelks, and Williams 2005).

Black carp have been introduced in 30 countries globally (Nico, Jelks, and Williams 2005). Initially, black carp were imported into the United States as a contaminant fish in grass carp stocks in 1973 (Nico, Jelks, and Williams 2005). Beginning in the 1980s, black carp were used as a biocontrol for parasites hosted in snails and reared for food (Nico, Jelks, and Williams 2005). It was also believed black carp could be used as a biocontrol for zebra mussels, but further research did not support this

(Nico, Jelks, and Williams 2005). In 1994, black carp escaped into open waters, but a wild invasive black carp was not captured in the wild until 2003 (Chick et al. 2003; Nico, Jelks, and Williams 2005). Eleven states are now listed as having black carp occurrences (Nico, Jelks, and Williams 2005). Black carp are rarely detected and typically only captured in hoop nets, indicating low abundances or an aversion to current sampling methods (Nico and Jelks 2011). Listed as injurious in the US in 2007 under the Lacey Act, black carp are still used in Arkansas and Mississippi for aquaculture in their fertile diploid form, but can no longer be imported or transported across state lines (Nico and Jelks 2011). Due to lack of data it is difficult to describe and predict the impact this species will have (Nico, Jelks, and Williams 2005).

Efforts to Control Invasive Carp

The most effective way to manage aquatic invasive species is to prevent their arrival and establishment (Lovell et al. 2006). In systems where invasive carp are established, managers work to control their spread and population size in attempts to prevent them from causing further harm to native ecosystems. Strategies for controlling invasive fish post invasion include mechanical removal (*e.g.* electrofishing or gill netting), piscicides such as Rotenone or other chemicals, or habitat modifications through barriers (Moy et al. 2011). Mechanical removal, particularly electrofishing, allows the selective removal of species, but is more labor intensive. Piscicides are less labor intensive, but can cause more non-target species mortality. Neither mechanical removal nor piscicides is a long-term solution if the waterbody is connected to other infested waters. Many times, they are used in conjunction with environmental modifications (*e.g.* gates, barriers).

Anthropogenically created barriers are one of the most commonly used methods for slowing the spread of invasive fish. Some types of barriers include: strobe lights, acoustic deterrents, bubble curtains, velocity barriers, hypoxic zones, magnetic fields, or electric barriers (Ruebush 2011; Noatch and Suski 2012; Escobar et al. 2018).

An example of barriers to prevent species spread is the Chicago Sanitary Shipping Canal. Completed in 1858, the Chicago Sanitary Shipping Canal was created to manage sewage away from Chicago's water source, Lake Michigan, and to increase trade productivity (Rasmussen 2002; Moy et al. 2011). Reversing the flow hydrologically connected the watershed of the Great Lakes to that of the Mississippi River, allowing for species exchange between the two watersheds, which had previously been disconnected towards the end of the last ice age (Rasmussen 2002; Moy et al. 2011). However historically, the Chicago Sanitary Shipping Canal was so highly polluted that it could not support aquatic life (Rasmussen 2002). Following the enactment of the Clean Water Act in 1972, water quality was improved and the system is now capable of supporting life and facilitating the flow of species between systems (Rasmussen 2002; Moy et al. 2011). For example, zebra mussels and round gobies (*Neogobius melanostomus*) utilized the channel to invade and establish in the Mississippi River basin (Ray and Corkum 1997; Rasmussen 2002). Electric barriers were first installed in 2002 to prevent invasive carp from moving into the Great Lakes (Rasmussen 2002; Moy et al. 2011). Radio-telemetry research on the effectiveness of the electric barrier was conducted using common carp (Sparks et al.

2010). Of the 130 tagged common carp released, only one fish was tracked as having passed through the barrier (Sparks et al. 2010). Further telemetry research conducted by the Illinois Department of Natural Resources (IL DNR) corroborates that the electric barrier is effective, with zero live fish, out of 215, moving upstream of the barrier (IL DNR 2016). However, electric barriers are not entirely effective and have associated issues (*e.g.* maintenance costs, malfunctions, reduced effectiveness for smaller fish, and reduced efficiency during high water stages) (Rasmussen 2002; Sparks et al. 2010; Noatch and Suski 2012). The barriers in the Chicago Sanitary Ship Canal cost approximately $1.5 million to build and continue to cost tax payers over $22,000 annually to maintain (Rasmussen 2002). Regardless, barriers only assist in preventing the spread of invasive carp, they do not control population sizes (Rasmussen 2002; Sparks et al. 2010).

The electric barriers on the Chicago Sanitary Shipping canal are not the only course of action being taken in Illinois to prevent the spread of invasive carp into the Great Lakes. IL DNR is also being proactive about lowering the density of invasive carp in the Illinois River, a tributary of the Mississippi River infested with grass carp, silver carp, and bighead carp (IL DNR 2017). Contracting commercial fisherman to deploy 2,901.6km of gill nets, IL DNR harvested a total of 2,504 tons of invasive carp from the Illinois River between 2010-2016 (IL DNR 2016). This equates to 3,226 grass carp, 474,264 silver carp, and 85,710 bighead carp, a total of 563,200 fish, removed from the system in the last six years (IL DNR 2016). Sampling detected a 62% decrease in invasive carp density between 2015 and 2016 in portions of the Illinois River (IL DNR

2016). Despite efforts in Illinois, the range of invasive carp is still expanding in other previously uninfested areas of the Mississippi River Basin (MN DNR 2017). When practiced preventative strategies can help mitigate the threat posed by invasive carp to remaining uninfested waters (Lovell et al. 2006).

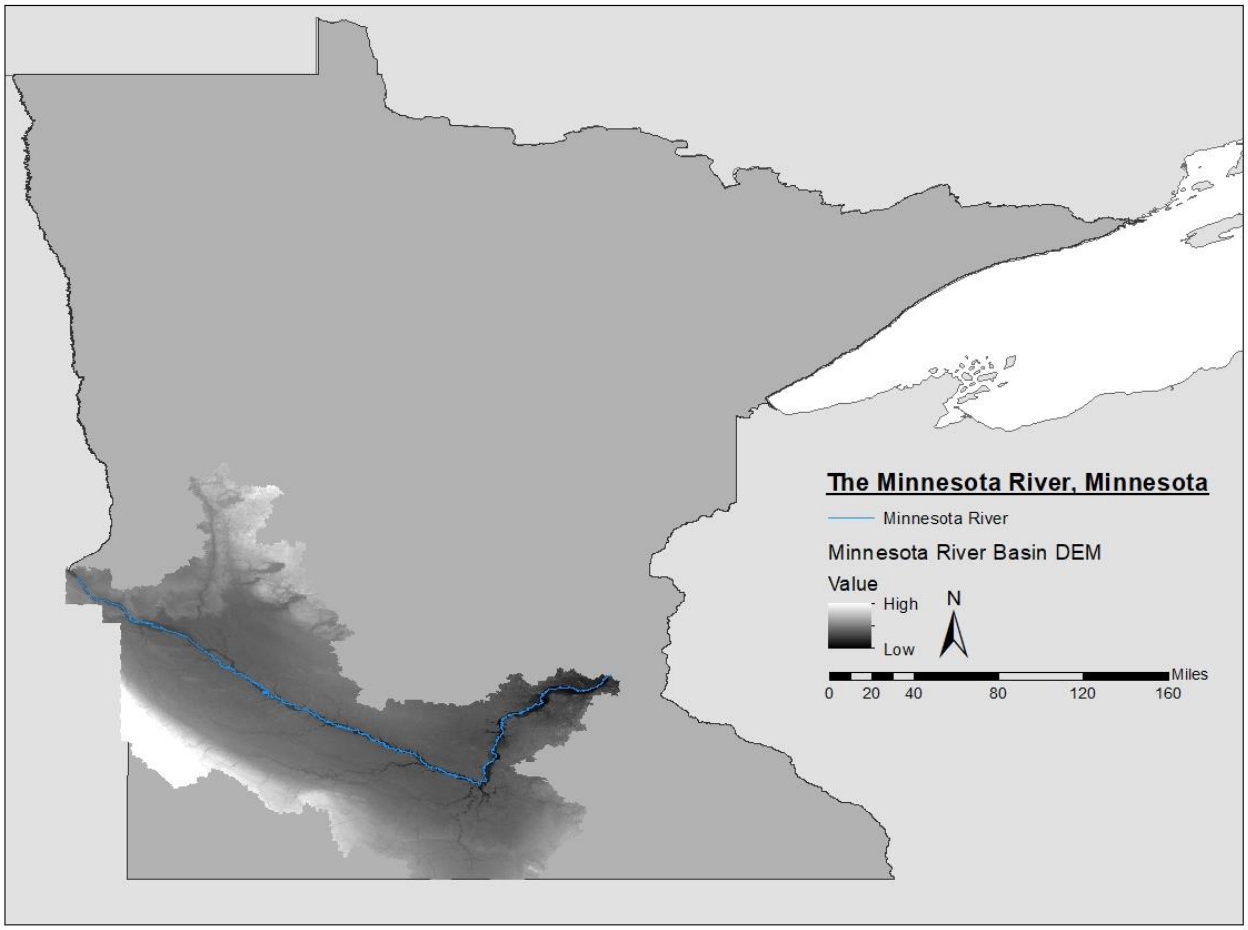
Predicting Invasive Carp Habitat with Ecological Niche Modeling

Ecological niche models are useful and efficient tools to forecast the spatial location of suitable environmental conditions for species (Elith et al. 2006; Chen et al. 2007; Herborg et al. 2007; Kulhanek, Leung, and Ricciardi 2011; Escobar et al. 2017 Romero-Alvarez et al. 2017). An ecological niche model estimates the possible ecological niche, or the environmental conditions that a species requires to have a sustainable population (Peterson et al. 2011). Ecological niche models identify tolerable environmental conditions for a target species based previous occurrences and creates thresholds to compare to other spatial locations to reconstruct a proxy of the species fundamental niche (Peterson et al. 2011). Environmental factors (*e.g.* temperature, precipitation, pH) can limit the distribution of an invasive species. The product of ecological niche models will indicate where a species' distribution may be limited by abiotic factors. Previous ecological niche modelling for some species of invasive carp successfully predicted 93.7% of the known silver carp occurrences and 71.8% of the bighead carp occurrences within the United States (Chen et al. 2007). This study suggests that ecological niche models should be able to predict the potential for invasive carp expansion into a new aquatic systems.

Study Site: Minnesota River Basin, Minnesota, United States

The modern Minnesota River valley, of southern Minnesota, USA, developed following Late Wisconsian glaciation, carved by episodic outburst floods from glacial Lake Agassiz (Matsch and Wright 1967; Fisher 2004; Gran et al. 2013). Preceded by glacial River Warren, the modern day Minnesota River flows from Big Stone Lake on the Minnesota and South Dakota border to the confluence with the Mississippi River in Saint Paul, Minnesota, a total of 515 km (MN DNR 2018d; Figure 1.7). A 7th-8th order stream, the Minnesota River drains an area of 44,030 km^2 across Minnesota, South Dakota, and Iowa (MN DNR 2018d). The Minnesota River is highly altered for agricultural and urban development, including five dams located in the upper reaches. Despite the dams, the Minnesota River still flows freely for 386 km and is inhabited by large migratory fish species such as the paddlefish (*Polyodon spathula*) (MN DNR 2018d). Unfortunately, the Minnesota River is affected by large inputs of sediment and nutrients, lowering water quality (Gran et al. 2009; Belmont et al. 2011; MN DNR 2018d). In spite of undesirable changes in water quality, the Minnesota River ecosystem is diverse with over 80 species of fish utilizing the main channel (MN DNR 2018d). This diverse fish community could be altered by the introduction of invasive carp (Feber 2001; Schrank, Guy and Fairchild 2003; Sampson, Chick, and Pegg 2009; Sass et al. 2014; Zhang et al. 2016).

Figure 1.7. Study site: Minnesota River, Minnesota, U.S.A.



There is growing concern about invasive carp reaching the Minnesota River and sustaining an established, reproducing, population in the system (MN DNR 2018). As of 2017, all four species of invasive carp occurred in the connected Upper Mississippi River watershed. Bighead carp and grass carp, specifically, have been caught in the Minnesota River prompting the Minnesota Department of Natural Resources to list the river as infested by those species (MN DNR 2017). While invasive carp have been caught in the Minnesota River Basin, there is no evidence that breeding, or naturalized, populations exist (MPR News 2017).

If invasive carp were to establish in the Minnesota River, they could put many native species population under increased pressure due to increased food competition, loss of habitat, or predation (Ferber 2001; Schrank, Guy, and Fairchild 2003; Sampson, Chick, and Pegg 2009; Sass et al. 2014; Zhang et al. 2016). External to damaged ecosystems, changes in the aquatic community from these effects could affect the quality of recreational activities (*e.g.* fishing, boating, water sports) having powerful economic impacts. For example, recreational fishing creates 43,000 jobs and $2.8 billion in retail spending in Minnesota annually (MN DNR 2011). The consequences of invasive carp infesting the Minnesota River are not limited to Minnesota, as the river connects to the Red River of the North during high flood stages flowing into North Dakota and Canada (Levine 2017). To prevent this, Minnesota is implementing plans to assist in early detection and quick, calculated, response if invasive carp are found (MN DNR 2014).

Research Question

The Minnesota Invasive Carp Prevention Workplan began in 2014 with the aim to collect geomorphic and hydrologic to inform decisions being made regarding invasive carp prevention and management in the Minnesota River. Both types of data provide crucial information that allows researchers to better understand the factors contributing to a fish species' biologic needs. Fluvial geomorphology, or the physical characteristics of a river and the river's interactions with the landscape, is the template for habitat and controls the physical structure (*e.g.* river type, length, water depth, substrate type), whereas hydrology impacts how species interact with their habitat (Schramm 2017). As the final stage of the project, this study connects geomorphic and hydrologic data on the

Minnesota River to the environmental requirements of invasive carp to better inform managers of habitat suitability within the region.

The goals of this study are:

1) Evaluate the success of using an ecological niche model to predict invasive carp occurrences
2) Employ ecological niche modeling to predict habitat suitability for invasive carp in Minnesota
3) Employ high resolution ecological niche modeling to predict and quantify habitat suitability for invasive carp in the Minnesota River

Chapter 2: Evaluating Ecological Niche Models for Predicting Invasive Carp in Minnesota

Introduction

The U.S. Fish and Wildlife Service listed invasive species as a top contributing factor in endangerment and extinction of freshwater fishes (USFWS 2012). Establishment of invasive carp could be especially detrimental to Minnesota's 162 species of fish (MN DNR 2018a; MN DNR 2018b). For example, silver carp and bighead carp could place direct competition for food resources on imperiled planktivorous native species like the black buffalo (*Ictiobus niger*) and paddlefish (*Polyodon spathula*) (Schrank, Guy and Fairchild 2003; Sampson, Chick, and Pegg 2009; MN DNR 2018e).

When researching the risk aquatic invasive species pose to a system, it is beneficial to forecast areas most vulnerable to invasion (*e.g.* environmentally suitable, accessible to species) (Kulhankek, Leung, and Ricciardi 2011). Using species occurrence data and environmental variables, ecological niche models can predict locations that are environmentally suitable for a target species (Peterson 2003; Peterson and Robins 2003; Peterson and Nakazawa 2008; Pyron, Burbink, and Guiher 2008; Jimenez-Valverde et al. 2011; Kulhankek, Leung, and Ricciardi 2011; Escobar et al. 2017; Romero-Alvarez et al. 2017). The objectives of this chapter are to 1) evaluate the success of ecological niche models in predicting invasive carp occurrences and 2) employ ecological niche models to predict habitat suitability for invasive carp in Minnesota.

Methodology

Algorithm Selection

Many ecological niche modeling algorithms exist, but the most appropriate algorithm for a study is data and system dependent (Qiao, Soberon, and Peterson 2015). Algorithms vary in complexity, data requirement, and necessary computing power. To evaluate abilities of a model to predict previous invasive carp occurrences an algorithm requiring small data quantities with quick computing time was desired and thus the NicheAnalyst (NicheA) algorithm was selected. NicheA is an open source algorithm that allows multiple environmental variables to be incorporated, utilizes presence-only occurrence data, and produces simple results that can be evaluated statistically (Qiao et al. 2016).

Occurrence Data

Scientific name search phrases were used to compile occurrence data from https://nas.er.usgs.gov/, http://www.fishnet2.net/, https://www.gbif.org/, https://bison.usgs.gov/, http://splink.cria.org.br/. The search terms included current names: *Hypophthalmichtys moilitrix, Hypophthalmichtys nobilis, Ctenopharyngodon idella,* and *Mylopharyngodon piceus,* as well as historic names*: Mylopharyngodon aethiops, Myloleuciscus atripinnis,* and *Aristhichtys nobilis*. Current and historic names were both used to increase the likelihood obtaining a dataset with true global distribution of all targeted species.

Occurrence data from each source was compiled into a single database for each species. All data older than 1900 were deemed too old to be relevant climatically and removed. Occurrences were also deleted if they had the terms preserved specimen, aquaculture, fish market, or aquarium associated with them because such reports were considered artificial occurrences. Reports missing coordinate information were georeferenced in Google Earth using details about locality. Occurrence records that could not be georeferenced were deleted. Due to potential duplication in occurrence data, as multiple sources were used, replicated occurrence points were deleted. Occurrence data were plotted in ArcMap (ESRI version 10.5.1) using the display X, Y data tool and compared to a base map to verify the country listed matched the spatial location (Figures 2.1A-D).

Figure 2.1A. Grass carp (C. idella) global occurrence data gathered from 5 database sources

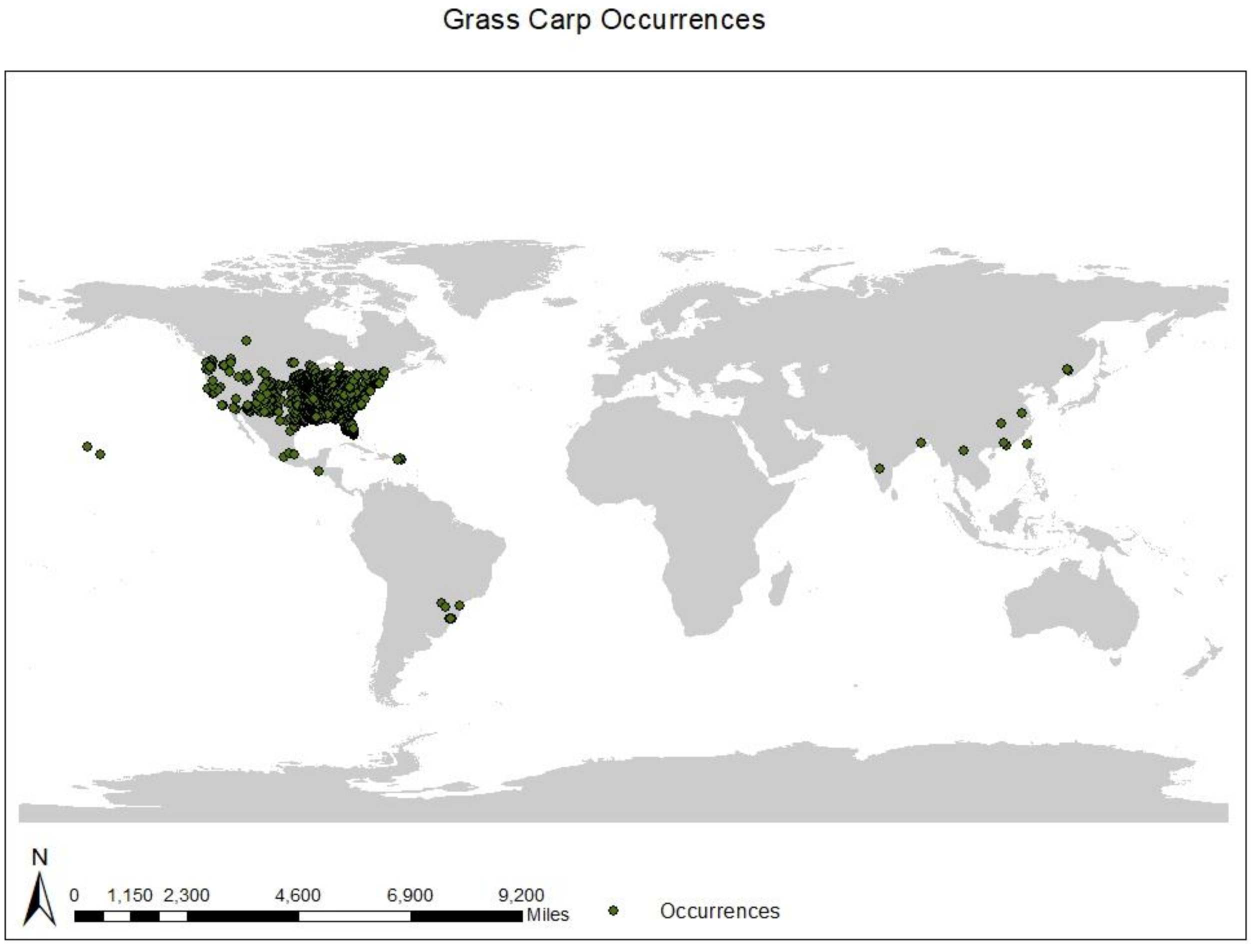


Figure 2.1B. Silver carp (H. molitrix) global occurrence data gathered from 5 database sources

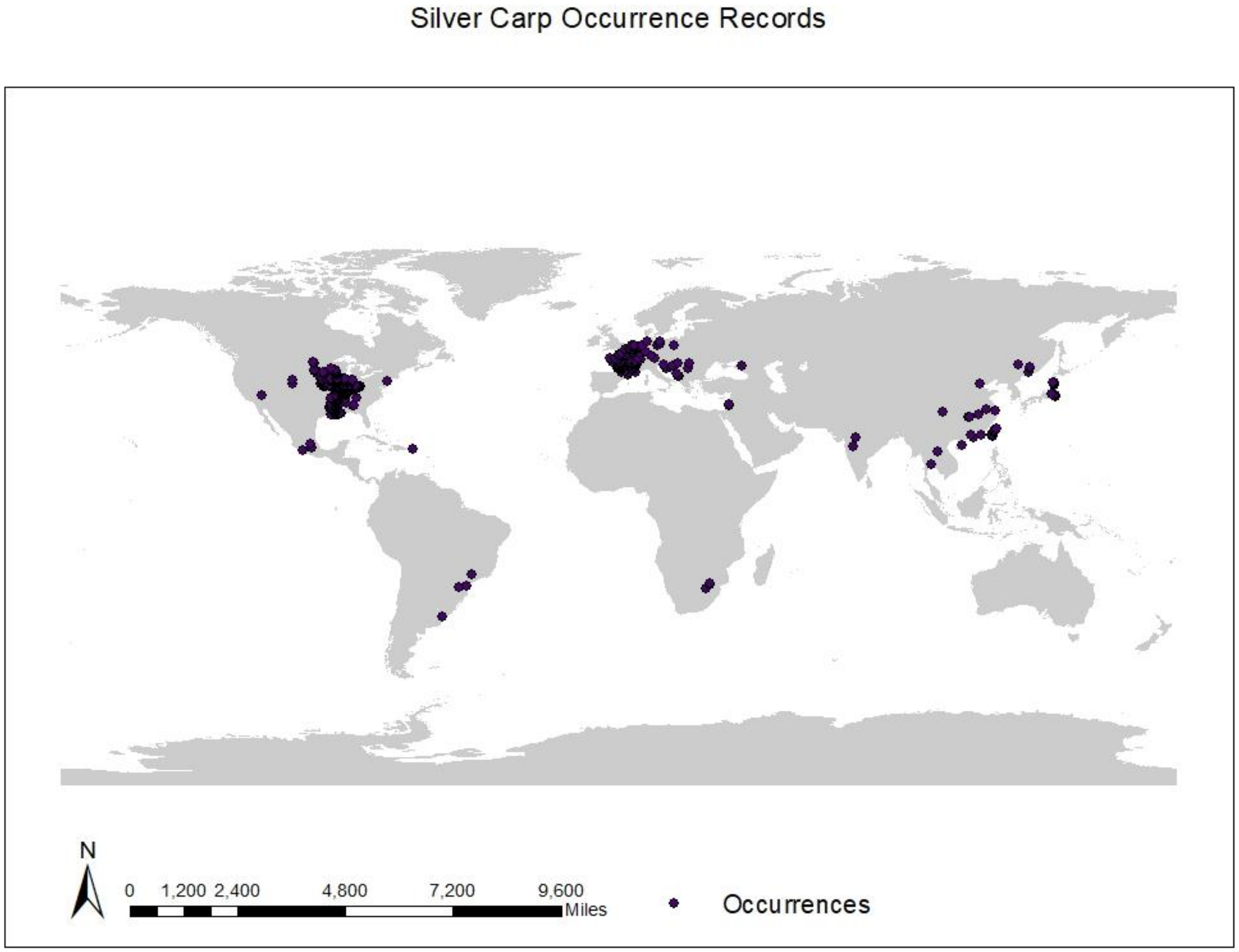


Figure 2.1C. Bighead carp (H. nobilis) global occurrence data gathered from 5 database sources

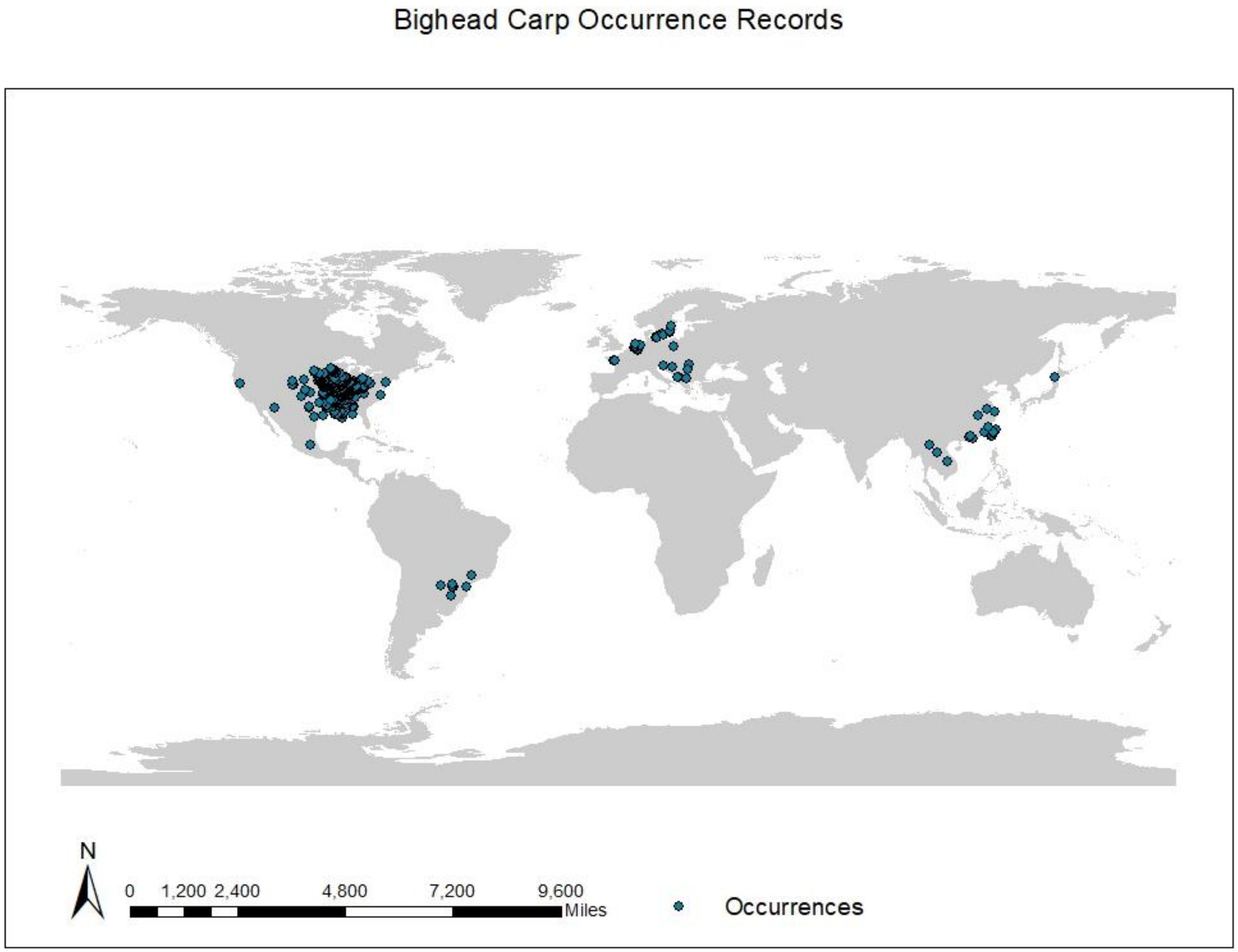
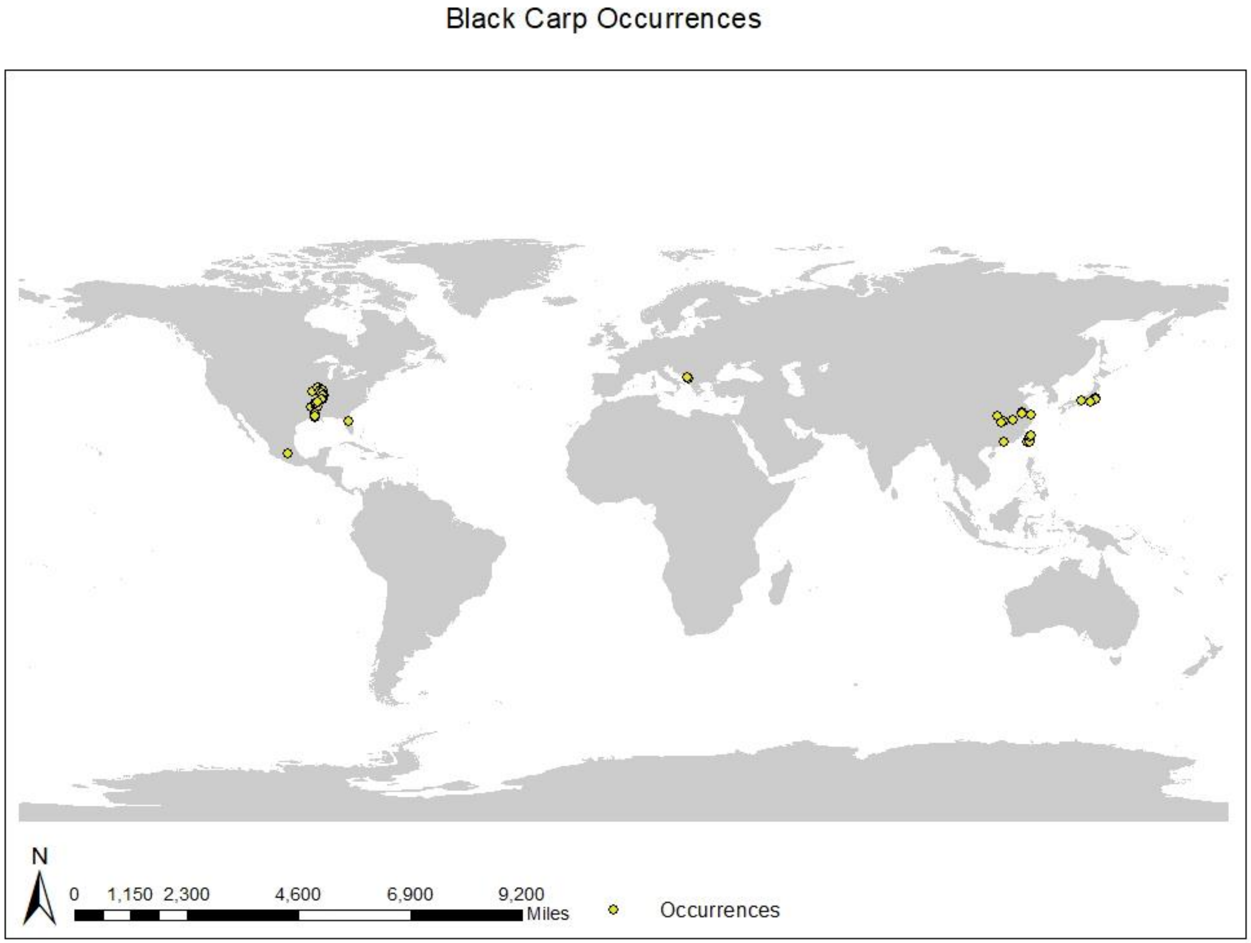


Figure 2.1D. Black carp (M. piceus) global occurrence data gathered from 5 database sources



Environmental Data

In selecting environmental variables, river level variables (*e.g.* water temperature, dissolved oxygen, pH) were not a viable option because they are not globally standardized in collection method or available in all countries. Thus, climate variables were used as an indicator for river data because they are consistent and globally available. Environmental data were downloaded from http://ecoclimate.org/downloads/ (Lima-Ribeiro et al. 2015) by selecting present raster file under the modern category. The downloaded file included 19 variables related to temperature and precipitation at a spatial resolution of 0.5° (Table 2.1). A principal component analysis was run utilizing the spatial analysis toolbox in ArcMap to determine variable correlation between the 19 ecoclimate variables (Peterson et al. 2011; Merow et al. 2013). The top three principal components contained over 80% of the variance and would be used as the environmental input to best capture the benefit of a multivariate approach without the redundancy of highly correlated variables.

Limiting Environmental Variables

When using environmental variables to train ecological niche models it is important to limit the spatial area to only areas that are relevant to the species (Barve et al. 2011). The data in these files should be limited to spatial locations that would be accessible to the species of interest (Barve et al. 2011; Merow et al. 2013). Studies have shown that altering ecological niche modeling calibration extents may cause shifts in the location and amount of suitable habitat (Phillips and Dudik 2008; Anderson and Raza 2010; Barve et al. 2011). In the validation stages of modeling, larger than necessary extents can result in the models being less ecologically relevant than they appear when using evaluation metrics (Lobo, Jimenez-Valverde, and Real 2007; Barve et al. 2011)

In order to restrict the environmental variables to areas reasonably accessible to invasive carp within a region, the average distance between occurrence points within the region of interest was found. The average distance is representative of the average distance travelled by an invasive carp. This provides a good proxy of the species dispersal under accessible areas. The average distance was calculated for each species individually and the zones decided qualitatively by identifying clusters of occurrence points. Silver carp and bighead carp had three zones: the United States, Europe, and the species' native range. Grass carp and black carp had two zones: the United States and the species' native range. Native and European ranges were included in the data to try and capture the entirety of the fundamental niche for each species of invasive carp, not just the US niche. The non-US ranges were also used to increase the number of model trials used to evaluate prediction success.

To calculate the average distance within the US based on hypothesis of dispersal potential of the species, a shapefile was created from the US occurrence data records using the display X, Y data function in ArcMap. Using the new occurrence point shapefile, a polygon was created that contained all the occurrence points using the minimum bounding geometry tool in the data management tool box. A centroid for the polygon was calculated using the feature to point tool in the data management toolbox. Mean average distance between occurrence points and centroid points was then calculated using the point distance tool in the analysis toolbox. This distance is representative of the average movement or mobility of the species in that region. The mean average distance was used to limit the environmental area used to inform the models. To do this, the global occurrence file for the species was then uploaded in ArcMap and the points plotted using the display X, Y data tool. Using that mean average distance, a fixed distance buffer was created around each of the global occurrence points using the buffer tool in the analysis toolbox. The dissolve tool from the data management toolbox was then used to merge the buffers into a single polygon. This polygon represents an estimate of the area that would be accessible to the species, quantified by the average distance from each occurrence point to the centroid in a specified region. The same process was replicated for the Europe-limited environmental files, using European occurrences to calculate average distance.

The procedure used to limit the United States and Europe files was not possible for the native range due to low occurrence records in the region. To take into account the entirety of the native range, a figure of each native range from Mandrak and Cudmore 2004 was digitized and georeferenced in ArcMap to create a shapefile. A centroid was then calculated using the feature to point tool in the data management toolbox. Lines were drawn from the centroid to the most distance parts of the native range and their total length was measured using the add geometry attributes tool in the data management toolbox. The average distance was manually calculated using the values found above. A fixed distance buffer using the calculated average distance was then created and dissolved to create a single polygon representative of the area accessible to a species using the procedures previously described.

The environmental data were then clipped by the resulting polygons by utilizing the extract by mask tool in the spatial analyst toolbox. The process was repeated for each species individually in each zone. In total, ten files were created.

Model Evaluation

In order for a model to be successful in predicting the fundamental niche, it should be able to predict occurrences better than at random. For the model to be better than at random, it must successfully predict an occurrence as suitable correctly for more than 50% of the occurrence. The NicheA modeling algorithm has the capability to produce binary results that classify a cell as suitable or unsuitable allowing for a simple evaluation of correct prediction.

To evaluate the NicheA model results, a species' occurrence data was divided into two groups, calibration (cal) and evaluation (evl), in R (version 3.4.2) (Appendix A). These groups were then used within the NicheA algorithm to predict the fundamental niche. The goal of this process was to see how many of the evl occurrence, or occurrences not used to calibrate the model, were correctly predicted by the cal trial results, and vice versa.

First, the environmentally limited variables for a region were uploaded into the model using the create a background cloud (BC) function. This function plots the environmental data in three dimensional space. The niche for the trial was then created using the Generate N(s) from occurrences function utilizing the cal occurrence group previously created in R as the input. This function creates a convex hull that contains the occurrences points plotted onto of the environmental data and a minimum-volume ellipsoid (MVE) that is representative of the fundamental niche. The Generate N(s) from occurrence function creates a file that contains a raster version of the suitable area within the MVE information and can be used in ArcMap to geographically visualize the predicted niche. This procedure was repeated using the same environmental file, but inputting the evl occurrence instead.

To collect the data for calculating the percentage of success, the present.tif file from the cal trial and the cal and evl occurrence files were uploaded in ArcMap. The occurrence data was plotted using the display X,Y data tool and the symbology changed so they were easily distinguishable. The resulting raster file automatically produces stretched symbology, this is not useful however because there is only one value. To correct this, the file was reclassified using the reclassify tool in the spatial analyst toolbox to create one class. The reclassified raster file was then used as raster input with the evl point data in the extract values to points tool in the spatial analyst toolbox. The resulting attribute table for the evl occurrences lists the value of the reclassified present.tif file as a field and can be more easily counted. The data in this attribute table was used in Excel to calculate the percent chance of an occurrence point being correctly predicted in climatically suitable habitat. To calculate the percent success, the number of points correctly predicted as suitable was divided by the total number of occurrence points. The p-value was also was calculated using a binomial distribution function and the totals calculated above. This process was repeated for every species and limited environmental variable combination and resulted in 20 trials.

Results

NicheA model trials for silver carp had the highest probabilities of an occurrence point being correctly predicted as suitable, with an average percent of 70.12%. Grass carp had the second highest probabilities, with an average of 62.03% of the occurrences being forecasted correctly. All of the bighead carp or black carp model trials had a percent of correctly identifying occurrences under 50%. Bighead carp had an average percent of 29.25%, while black carp was even lower with an average percent of 23.64%. The average percent of correctly predicting occurrences in all of the model trials combined was 46.94%. All of the models had a p-value of < 0.0001 except two black carp models. Only one of the black carp models was not statistically significant, with a p-value of 0.6595 (Table 2.2).

According to the NicheA model, grass carp had the most suitable habitat in Minnesota of the invasive carp, with only a small area in the northern Minnesota being unsuitable (Figure 2.2). Silver carp also had a large amount of suitable habitat, especially in central and southern Minnesota (Figure 2.3). Bighead carp had less suitable habitat than grass and silver carp, all of which is located in southern Minnesota (Figure 2.4). The NicheA models for black carp did not predict any suitable habitat within the State of Minnesota (Figure 2.5).

Figure 2.2. Grass carp (C. idella) NicheA model results when calibrated with coarse climatic data. The green area represents climatically suitable habitat.

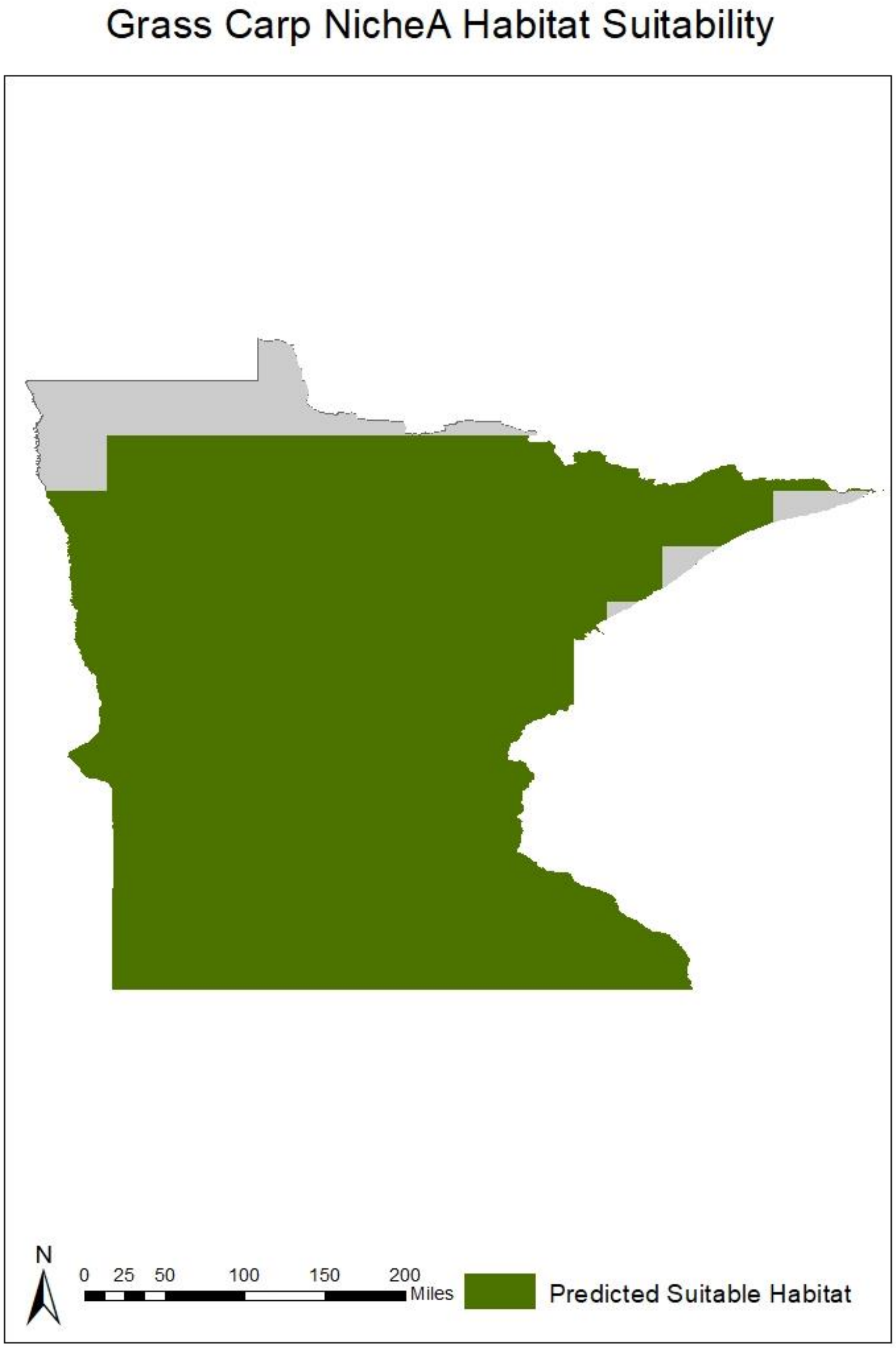


Figure 2.3. Silver carp (H. molitrix) NicheA model results when calibrated with coarse climatic data. The purple area represents climatically suitable habitat.

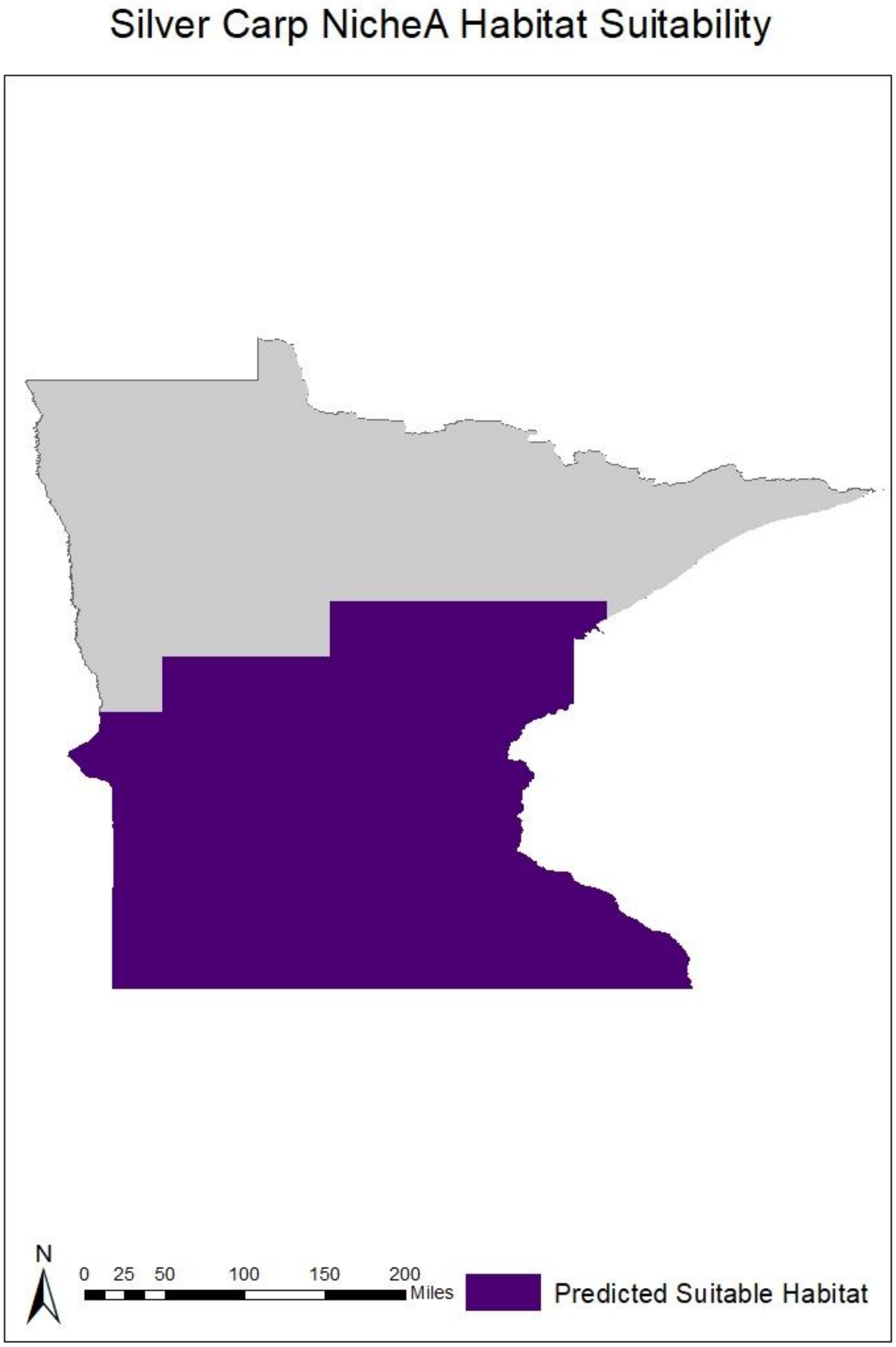


Figure 2.4. Bighead carp (H. nobilis) NicheA model results when calibrated with coarse climatic data. The blue area represents climatically suitable habitat.

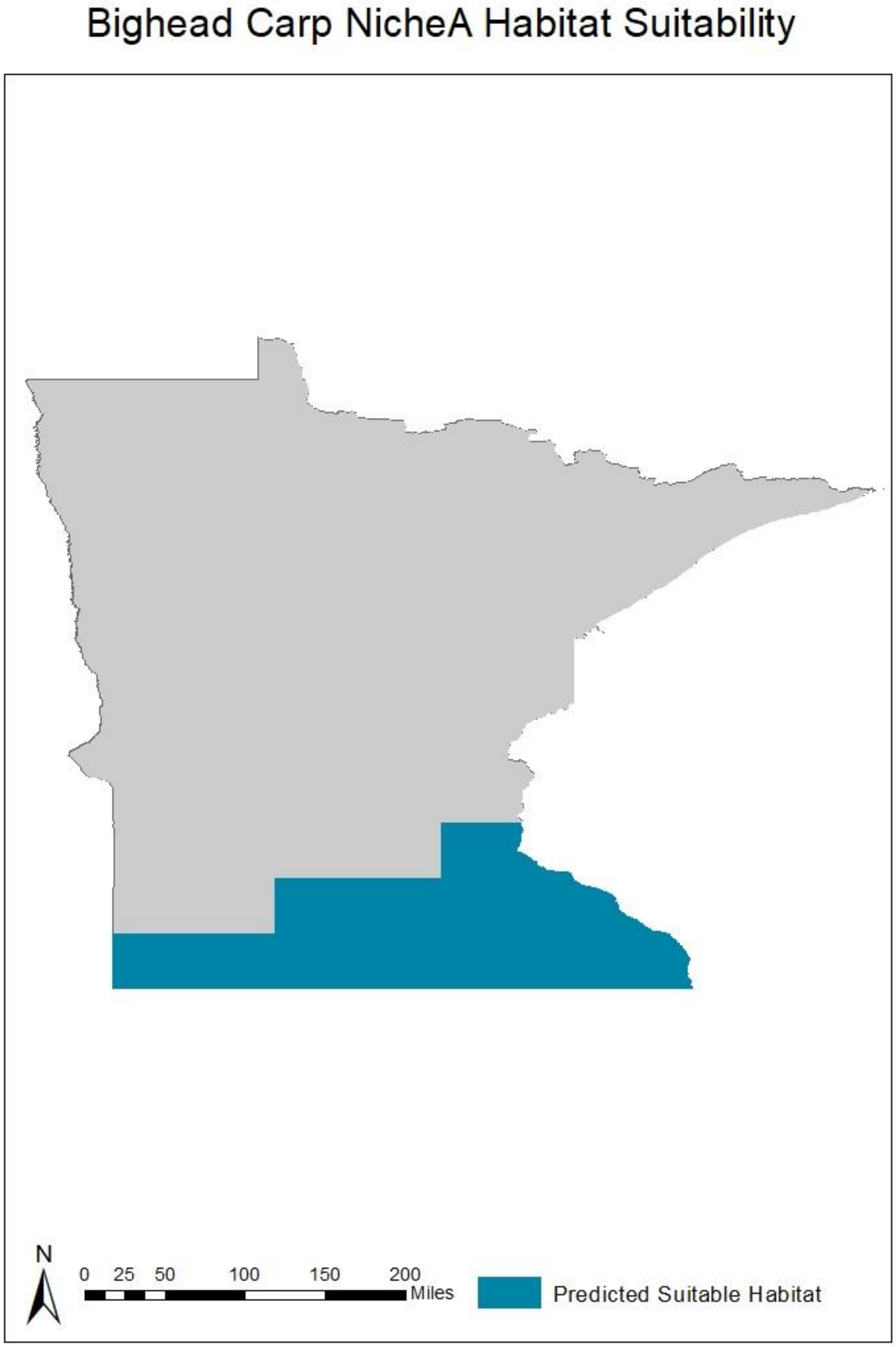
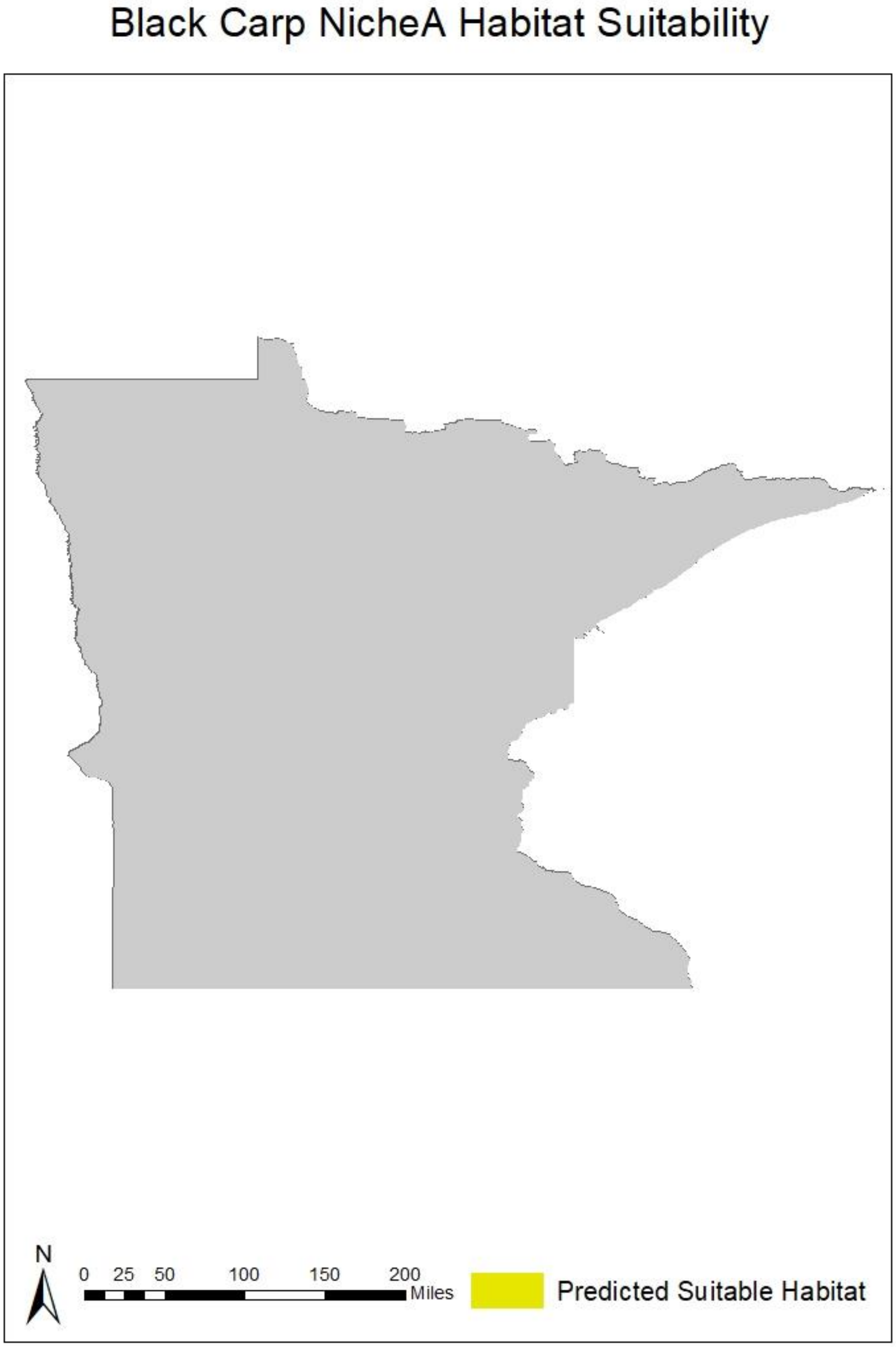


Figure 2.5. Black carp (M. piceus) NicheA model results when calibrated with coarse climatic data. The model predicted no climatically suitable habitat in Minnesota.

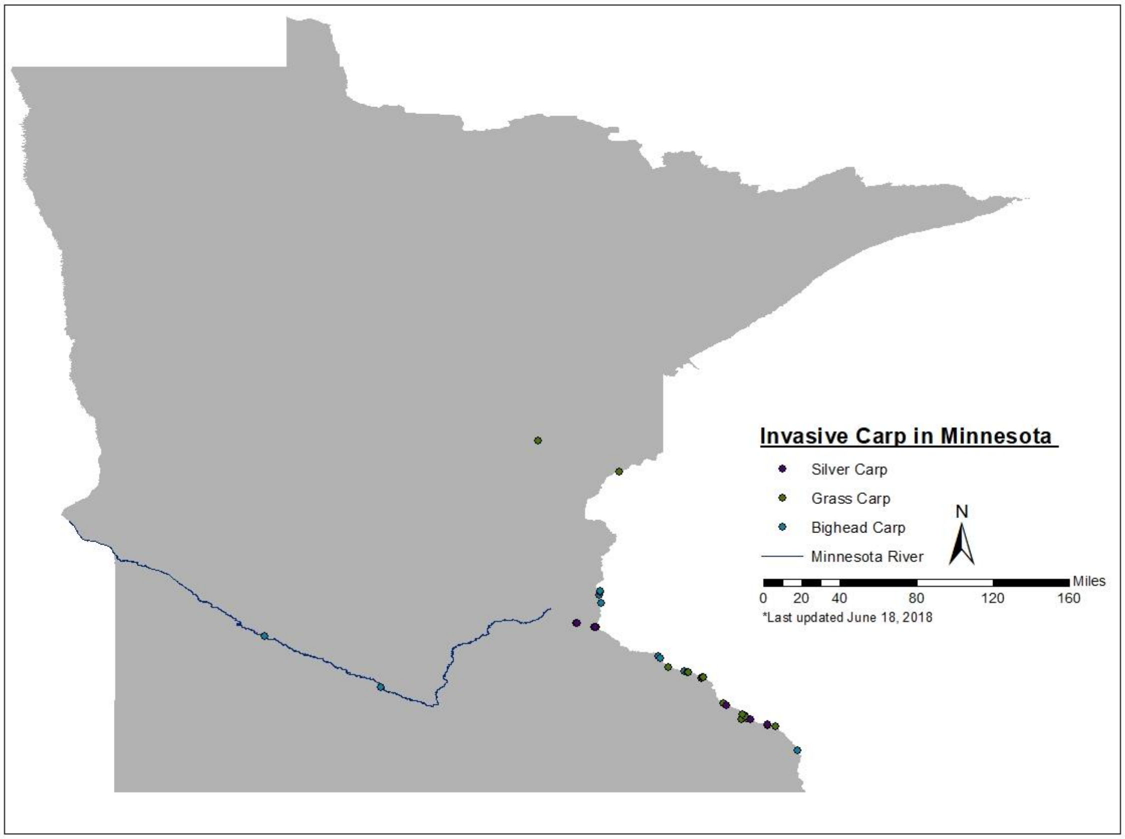


Discussion

The NicheA modeling algorithm, using coarse climatic data, predicted climatically suitable areas within Minnesota for three of the four invasive carp species. While alarming, only 50% of model trials were successful in predicting suitable habitat for invasive carp better than at random. This low success rate could be linked to a variety of sources of error within the modeling process.

Prediction results may have been influenced by the differing amounts of occurrence records for each species. Models trials for silver and grass carp were successfully better than random, but were also informed over 2,400 occurrence records each. Contrastingly, bighead carp model trials were informed by 1,632 occurrences and black carp trials only a meager 72 total records and neither species had a trial better than at random chance. NicheA may overfit the data, or restrict predicted suitability to only areas spatially near an occurrence record. This could be part of the reason black carp did not have any suitable habitat in Minnesota, as it is the only species without an occurrence record in the state (Figure 2.6). To better grasp the risk invasive carp, particularly black carp, pose to Minnesota, a modeling algorithm that is sensitive to low occurrence data quantities may provide better results.

Figure 2.6. Invasive carp occurrences in Minnesota as of June 18, 2018.



The quantity of occurrence points is not the only source of error within the data; sampling bias in the occurrence records may have also effected model results. Highly sampled areas, particularly in the US near the Mississippi River, may have biased the range of climate data being used to calibrate the model. Lack data reporting may also cause range gaps during calibration. This was apparent in the species' native where supplementary methods were needed to limit the environmental variables, but invasive carp are large commercial fisheries and highly sampled for. Regions without occurrences within the native range would not be climatically included in the values predicted as tolerable. Unequal sampling efforts, or data availability, may lead to a region appearing unsuitable even though invasive carp are present. These sources of bias are compounded by using coarse resolution environmental data.

The climatic variables used to inform the NicheA models had a spatial resolution of 0.5° x 0.5°. This equates to a pixel covering around a 3,080 km^2 area. To place this in perspective, the state of Minnesota has an area of 225,180 km^2 and the Minnesota River is 515 km long. At this pixel size, the clumped distribution of the occurrence data is going to result in many of the data points having the same climatic value. A resolution this coarse may not be biologically relevant because it assumes habitat homogeneity, or continuous similar habitat, over such a large area. A small area that would be highly suitable and act as a refuge for the species could be masked by surrounding unsuitable environments, and therefore be classified as unsuitable. In order for model results to be relevant on a finer scale higher resolution data that captures the variability in available environments is needed.

Conclusion

Ecological niche modeling using the NicheA algorithm successfully predicted climactically suitable habitat better than at random in 50% of the trials conducted for four species of invasive carp. Model success rate may have been influenced by limited amounts of occurrences or sampling bias in the occurrence data used in the trials. The coarse resolution of the environmental data used also contributed to results that may have excluded small areas of suitable habitat that could act as refuge. Nonetheless, the NicheA models predicted suitable habitat in Minnesota for three of the four invasive carp species.

Chapter 3: Predicting Invasive Carp Habitat Suitability in the Minnesota River Using Ecological Niche Models

Introduction

Grass carp (*Ctenophaygodon idella*), silver carp (*Hypophthalmichthys molitrix*), bighead carp (*Hypophthalmichthys nobilis*), and black carp (*Mylopharyngodon piceus*) (collectively referred to as invasive carp hereafter) were transported to the United States for their use in aquaculture (Kolar et al. 2007). After escaping into the Mississippi River and spreading to many of its tributaries (*e.g.* Illinois River, Missouri River and Ohio River), the qualities that were beneficial in aquaculture are now detrimental to native ecosystems (Feber 2001; Schrank, Guy and Fairchild 2003; Sampson, Chick, and Pegg 2009; Sass et al. 2014; Zhang et al. 2016). Invasive carp are capable of destroying aquatic habitat and reducing food availability (Schrank, Guy and Fairchild 2003; Dibble and Kovalenko 2009; Sampson, Chick, and Pegg 2009; Sass et al. 2014; Zhang et al. 2016; USFWS 2017). Currently, a lack of high-resolution data on the suitability of habitat within Minnesota for invasive carp exists, making it difficult to manage risks associated with their invasion.

Ecological niche models are commonly used in invasive species research because they forecast habitat suitability in areas without occurrences by utilizing environmental variables and available occurrences from other locations (Peterson 2003; Peterson and Robins 2003; Peterson and Nakazawa 2008; Pyron, Burbink, and Guiher 2008; Jimenez-Valverde et al. 2011; Kulhankek, Leung, and Ricciardi 2011; Escobar et al. 2017; Romero-Alvarez et al. 2017). The ecological niche models completed in chapter two were low resolution. The spatial resolution used, 0.5°, would be unable to show variability in small reaches of the Minnesota River and broadly classified large areas as either suitable or unsuitable. This would make it difficult to identify which portions of the Minnesota River were most at risk. The objective for this chapter was to employ high-resolution ecological niche modeling to predict and quantify habitat suitability for invasive carp in the Minnesota River.

Methodology

Algorithm Selection

The ecological niche models produced in chapter two used the modeling algorithm NicheA. These models produced simple, binary, results that classified an area as suitable or unsuitable, making it impossible to narrow results to reaches of the Minnesota River that were the most vulnerable to invasion. There was also concern that the algorithm may have underestimated suitability for black carp due to low occurrence record quantities. To overcome these issues, the MaxEnt modeling algorithm was selected (Phillips et al. 2005; Phillips et al. 2006). MaxEnt is the “gold standard” in ecological niche modeling and works by contrasting environmental conditions in the area of interest against the conditions where occurrences are located (Merow et al. 2013; Qiao, Soberón and Peterson 2015). In a comparison study, MaxEnt ranked amongst the most effective presence-only ecological niche models (Elith et al. 2006). Research comparing the effect of sample size on ecological niche models showed that MaxEnt had the best extrapolative power across a range of sample sizes, including inputs as low as ten occurrence records (Wisz et al. 2008). This algorithm produces a continuous gradient of suitability, which can be transformed for analysis using geographic information systems

(GIS). The MaxEnt software is open source (https://biodiversityinformatics.amnh.org). The most updated version of MaxEnt, 3.4.1, was used for this study.

Occurrence Data

The occurrence record datasets created in chapter two were used as the species input for the MaxEnt models.

Environmental Data

Many types of variables were considered for the environmental input into the MaxEnt models. River level variables (*e.g.* water temperature, dissolved oxygen, pH) collection methods are not globally standardized nor were they available in all countries so they were not selected. The models created in the previous chapter were informed by coarse climactic data and did not produce results that would be biologically relevant due to the large cell size. To improve upon this work, Moderate Resolution Imaging Spectroradiometer (MODIS) data was used. The MODIS/Terra Vegetation Indices 16-day L3 global 250m product (MOD13Q1) were downloaded for the years 2000, 2008, and 2016. This product measures canopy greenness by utilizing the surface reflectance values of three spectral bands, blue red, and near infrared(NIR), at a spatial resolution of 250m/pixel. The greenness of vegetation is related to environmental conditions such as temperature and precipitation. The MOD13Q1 corresponds to the enhanced vegetation index (EVI) equation and is more sensitive to variation in areas that have dense vegetation.

MOD13Q1 data are available for download from the Land Processes Distributed Active Archive Center (LP DAAC). The data are classified into different tiles based on spatial location. A kml file indicating the extent and name of each tile was downloaded from http://spatial-analyst.net/KML/MODIS_tiles.kmz. This kml file was opened in google earth, as well as all four species occurrence records. Tiles containing occurrence records for the desired years were downloaded using R (Appendix B). Downloaded files were then converted from .hdf to .tif using the MODIS reprojection tool (LP DAAC). Tiles for the same 16-day group (*e.g.* all tiles created on 02/18/2000) were mosaic together in ArcMap using the mosaic tool in the data management toolbox. In order to minimize computing time, the average and standard deviation of each season was found using the cell statistics tool in the spatial analyst toolbox in ArcMap. Seasons were defined by the 2016 solstices and equinoxes: winter December 21- March 18, spring March 19- June 19, summer June 20- September 21, and fall September 22- December 20. The season files were then converted into .asc files using the raster to ASCII tool in the conversion toolbox.

Executing and Evaluating a Model

Each species of invasive carp was modelled individually using MaxEnt's default settings. Once models were completed, the resulting .asc files were converted to rasters using the ASCII to raster tool in the conversion toolbox within ArcMap.

A receiver operating characteristic (ROC) approach was utilized to evaluate if the MaxEnt model predictions were better than at random. The MaxEnt program automatically creates an area under the curve (AUC) plot for each model. AUC summarizes a model's ability to predict an occurrence record using a nonparametric measure (Peterson et al. 2011). AUC can range from 0-1and are plotted twodimensionally with predicted area on the x-axis and sensitivity, or 1- the number of cells that have occurrences within them, but are predicted as not suitable (omission rate). A random prediction is expected to have an average slope, or AUC, of 0.5. A model that is better than random will have an AUC closer to 1.

Limiting results to accessible areas

To better predict the risk of invasive carp establishment, the model results needed to be clipped to areas that would be accessible to the carp. The raw results did not provide any indication of the spatial location where the habitat transitions from aquatic to terrestrial. Instead, previously modeled floodplain inundation for 5 year, 10 year, 25 year, 50 year, and 100 year floods (Smith 2016) limited the model results to only aquatic areas accessible to invasive carp within the Minnesota River. This was completed using the extract by mask tool in the spatial analyst toolbox.

Analysis

The visual representation provided by ecological niche modeling results is useful when looking for general areas of concern, but does not provide quantitative amounts of area that are highly suitable. To provide this kind of data, all of the clipped result data were converted to integer using the raster calculator tool in the spatial analyst toolbox using int([FILE] *1000000) as the equation. Now integers, attribute tables were created for the raster files using the build raster attribute table tool in the data management toolbox. The files were then reprojected to NAD 1983 UTM Zone 15 using the project raster tool in the data management toolbox ensuring the output cell size was set to 250, 250. The files needed to be reprojected to convert cell size units from degrees to meters. Lastly the extract by attribute tool in the spatial analyst toolbox was used to extract cells that fit within a threshold. Threshold to rank suitability have not been evaluated for invasive carp in the literature, so quartiles were used. The following equations were used in the extract by attribute tool:

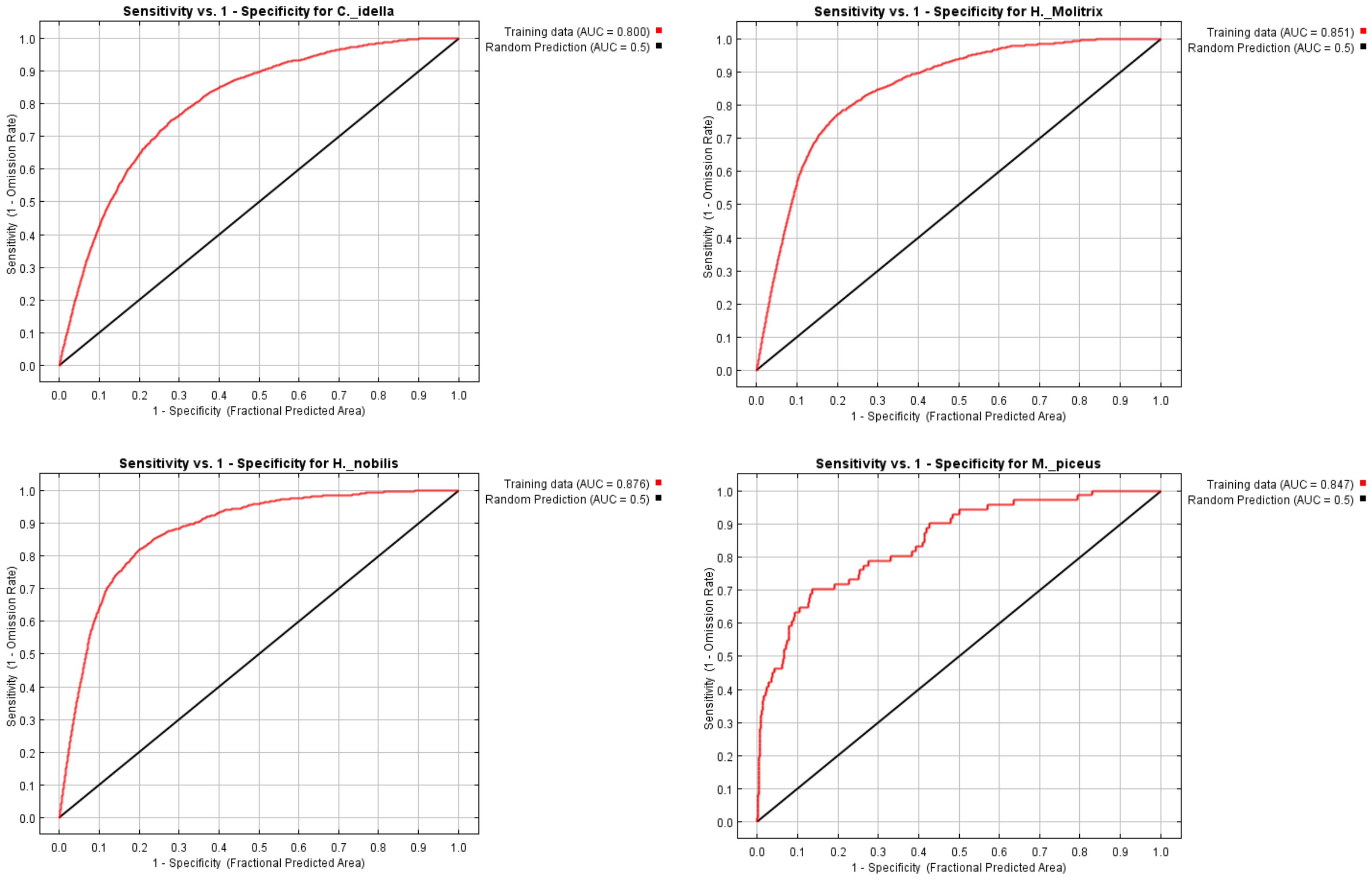
Poor Suitability	"VALUE" < 250000
Low Suitability	"VALUE" ≥ 250000 AND "VALUE" < 500000
Moderate Suitability	"VALUE" ≥ 500000 AND "VALUE" < 750000
High Suitability	"VALUE" ≥ 750000

Area was found to quantify the amount of habitat in each suitability category. Area was calculated by multiplying cell size by cell count (*e.g.* cell count * 250^2). Percent of total area for each suitability class was also calculated to make general comparisons easier. Percent area was found by dividing the suitability class area by total area and then multiplying the subtotal by 100.

Results

The MaxEnt modeling algorithm, when informed by vegetation indices, predicted suitable habitat in the Minnesota River for all species of invasive carp. The amount of each class of suitable habitat was dependent on the species. (Table 3.1A-B). Across all species, most of the highly suitable habitat in the Minnesota River can be found near the headwaters. However, there are localized pockets of highly suitable habitat throughout the river. All four species of invasive carp had AUC values better than at random (Figures 3.1)

Figure 3.1 Maxent model results' AUC. All AUCs were higher than 0.5, suggesting the results are better than random.



Grass Carp (C. idella)

Grass carp had the highest percentage of moderately suitable habitat with an average of 62.3% of the accessible area (Figures 3.2A-E). However, a majority of the remaining habitat, 34.8%, had low suitability. An average of 2.3% of the predicted grass carp habitat was highly suitable. This left only 1.3% of habitat as poorly suited, the lowest predicted average in the study. Grass carp experienced a decline in highly and moderately suitable habitat as flooded area increased while simultaneously experiencing an increase in low suitability. The percent of poorly suited habitat had a small decline, 0.1%. The grass carp model predicted occurrences better than at random with an AUC of 0.800.

Figure 3.2A. Predicted suitable habitat for grass carp (C. idella) in the Minnesota River during a 5 year flood

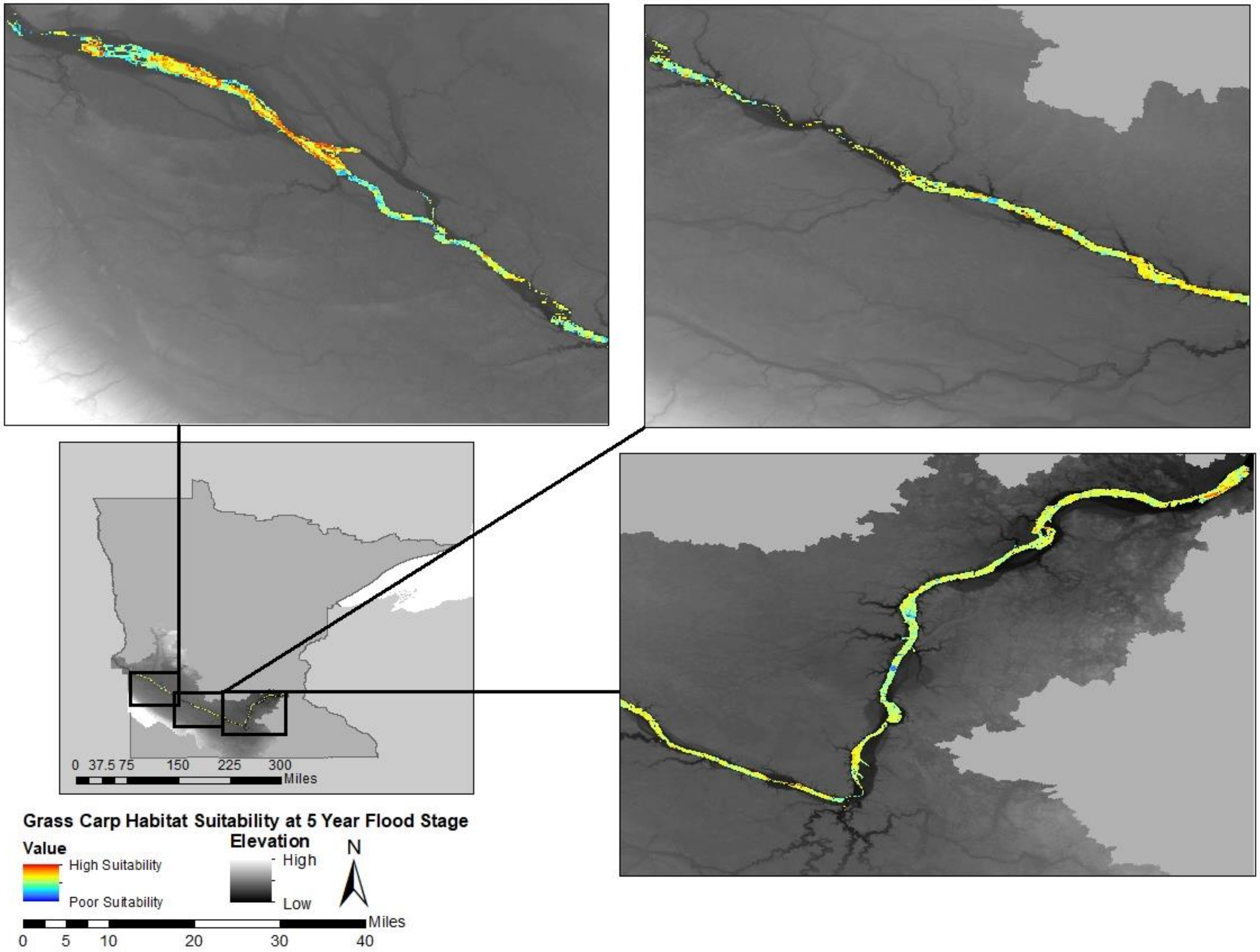


Figure 3.2B. Predicted suitable habitat for grass carp (C. idella) in the Minnesota River during a 10 year flood

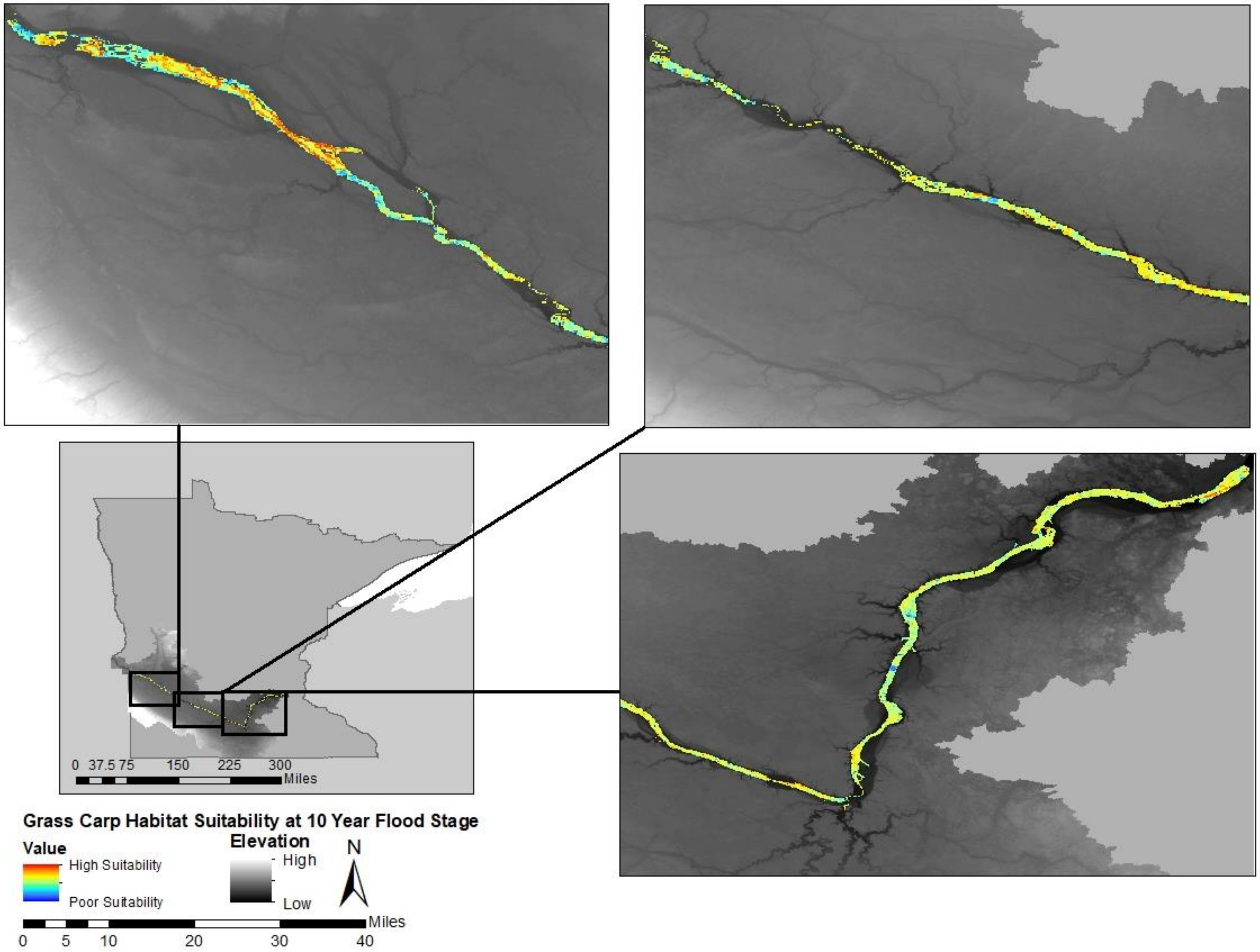


Figure 3.2C. Predicted suitable habitat for grass carp (C. idella) in the Minnesota River during a 25 year flood

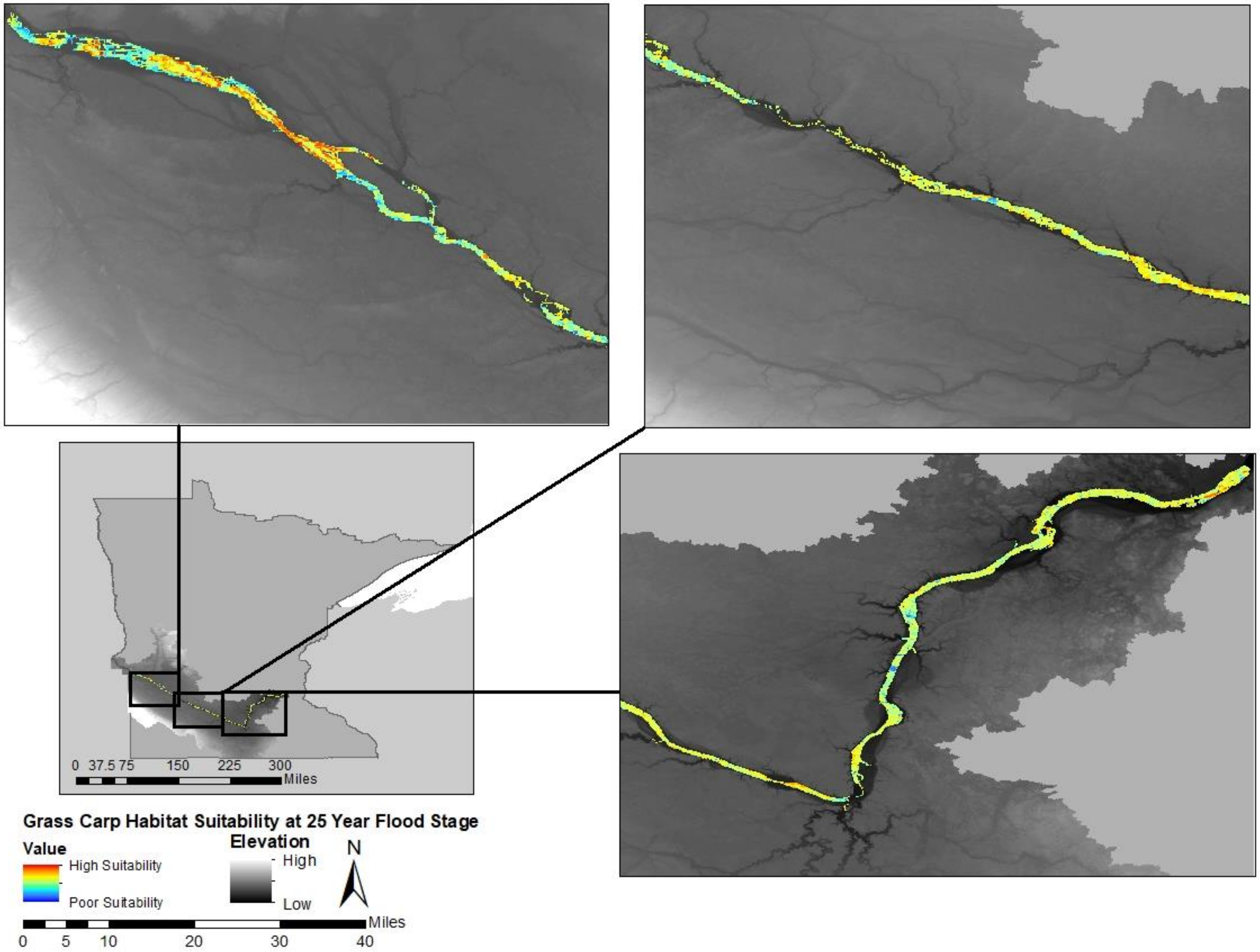


Figure 3.2D. Predicted suitable habitat for grass carp (C. idella) in the Minnesota River during a 50 year flood

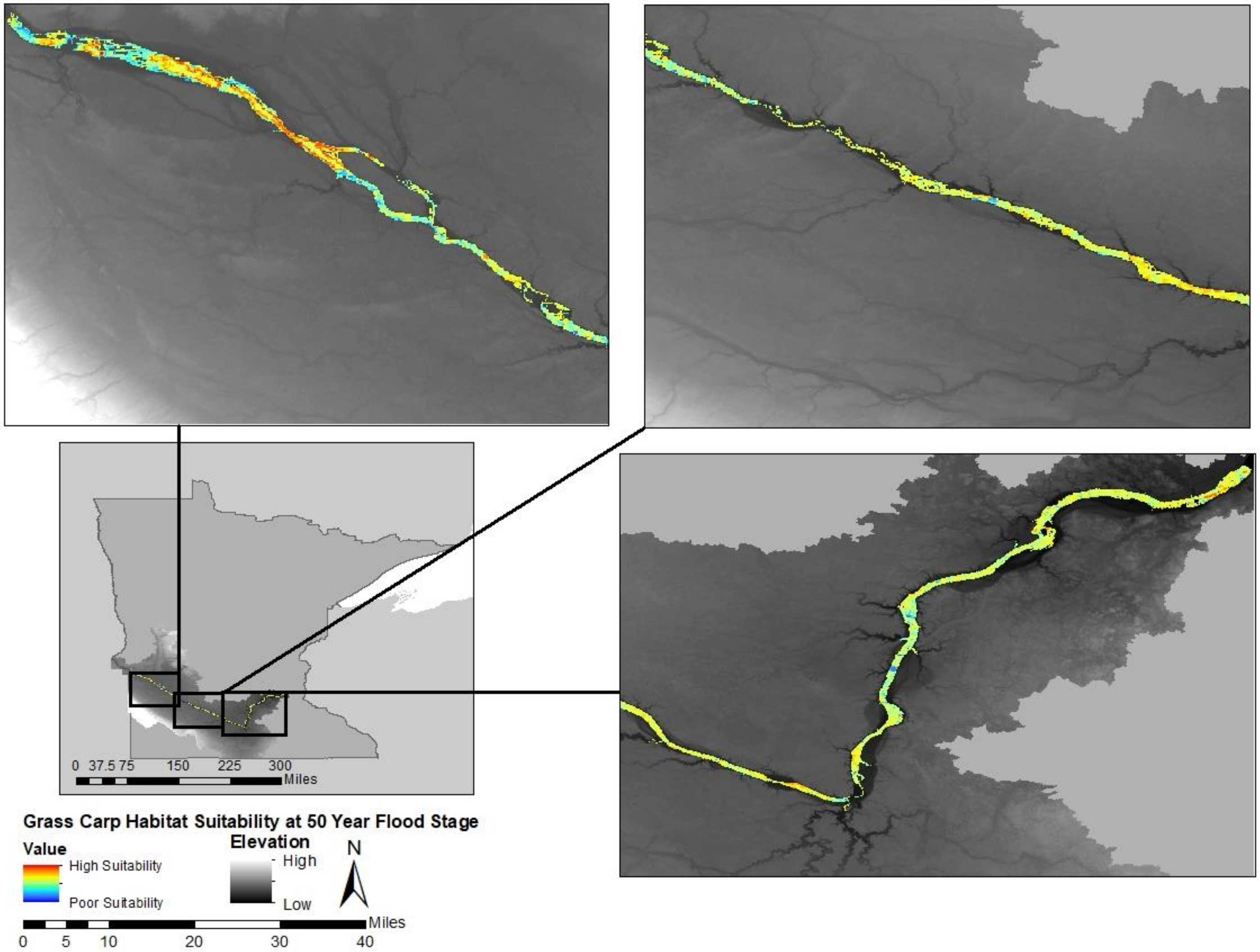
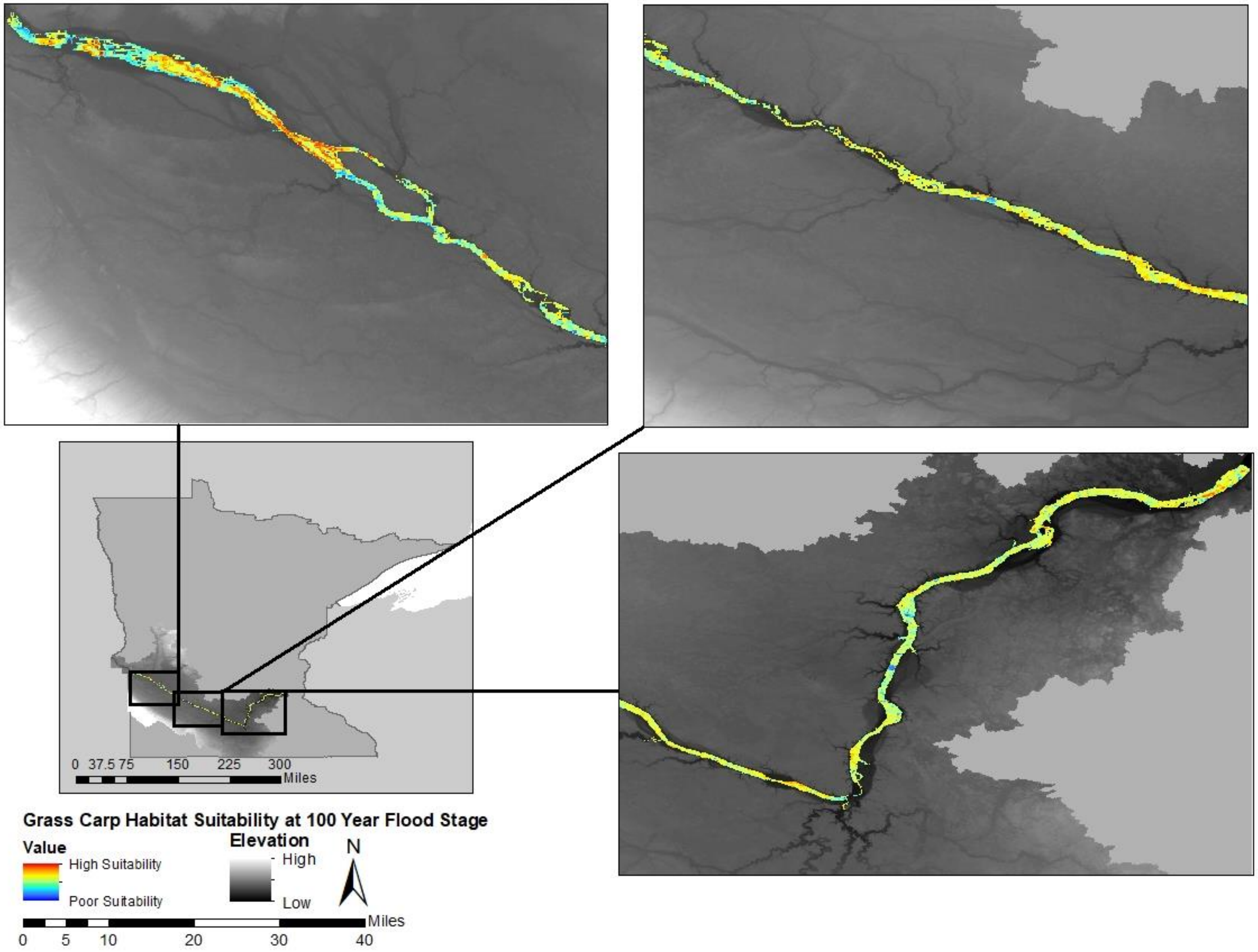


Figure 3.2E. Predicted suitable habitat for grass carp (C. idella) in the Minnesota River during a 100 year flood



Silver Carp (H. molitrix)

A majority of potential habitat for silver carp had moderate or low suitability. On average across flood years, 5.2% of the area had poor suitability, 52.8% had low suitability, 41.3% had moderate suitability, and 1.3% had high suitability (Figures 3.3a-e). There was not a large shift in the percent of each class of habitat suitability between the 5 year flood stage and the 100 year flood stage for silver carp. However, as the inundated area increased, the percent of highly and moderately suitable habitat decreased less than 2%, while low and poor suitability increased by less than 2%. The model for silver carp had an AUC of 0.851.

Figure 3.3A. Predicted suitable habitat for silver carp (H. molitrix) in the Minnesota River during a 5 year flood

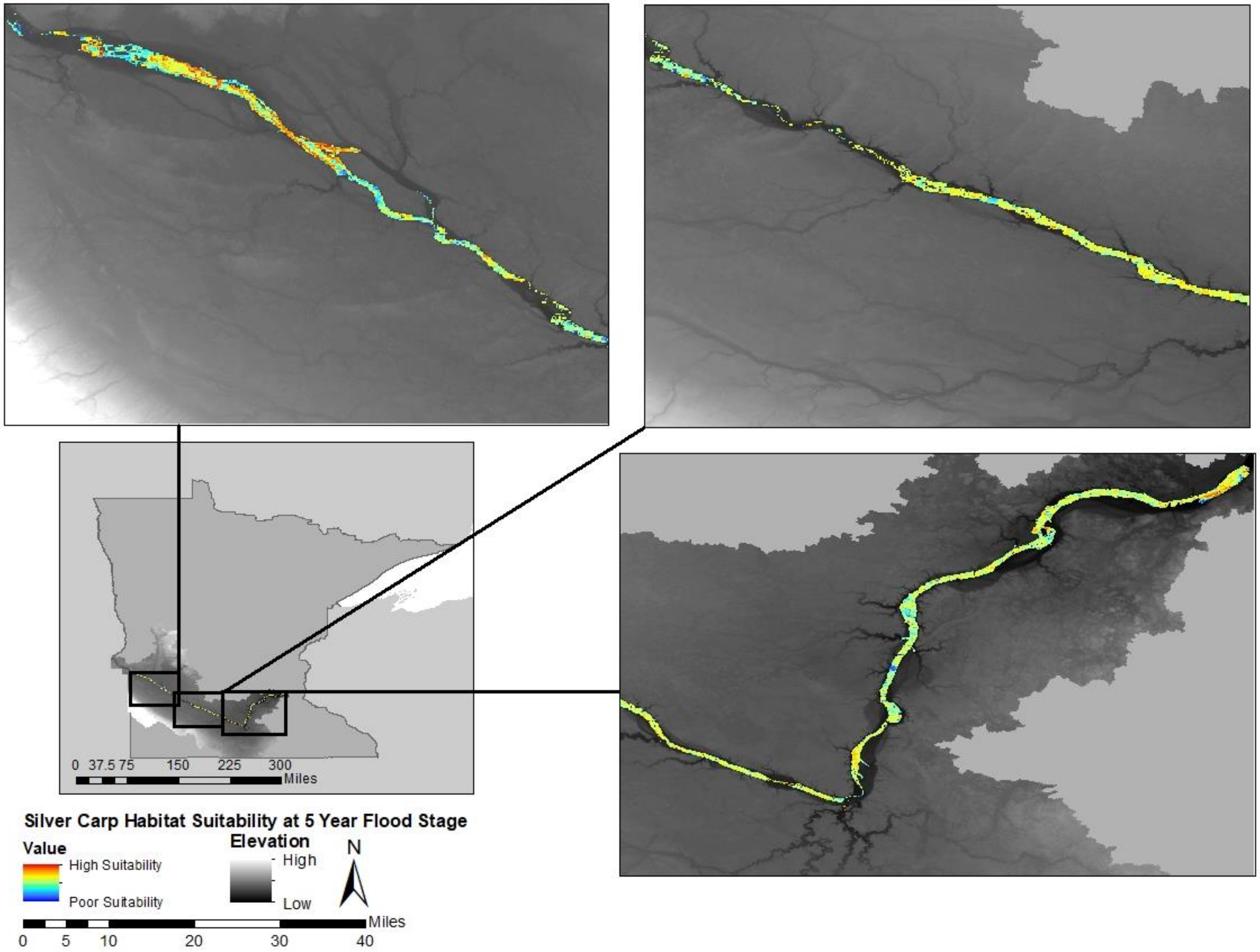


Figure 3.3B. Predicted suitable habitat for silver carp (H. molitrix) in the Minnesota River during a 10 year flood

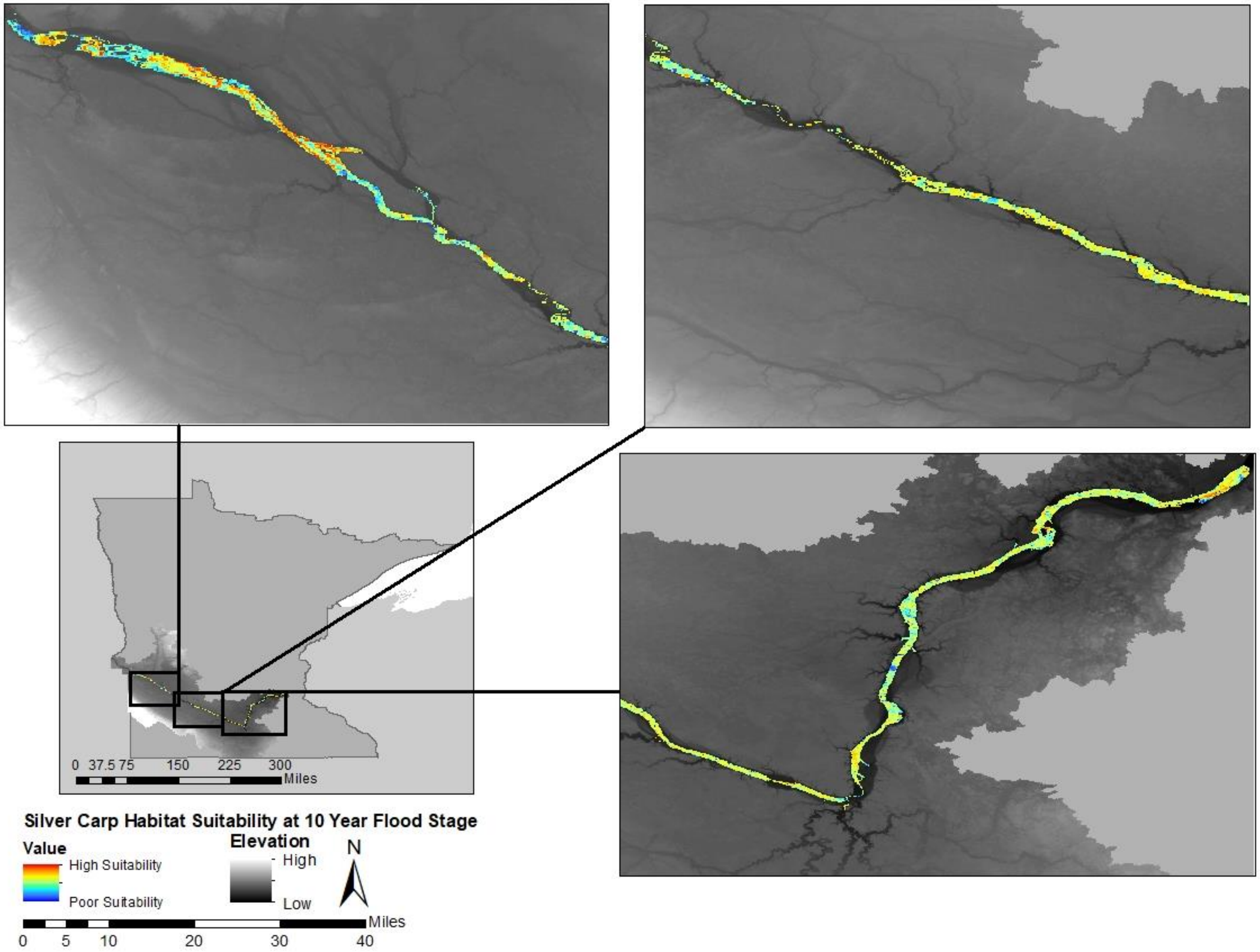


Figure 3.3C. Predicted suitable habitat for silver carp (H. molitrix) in the Minnesota River during a 25 year flood

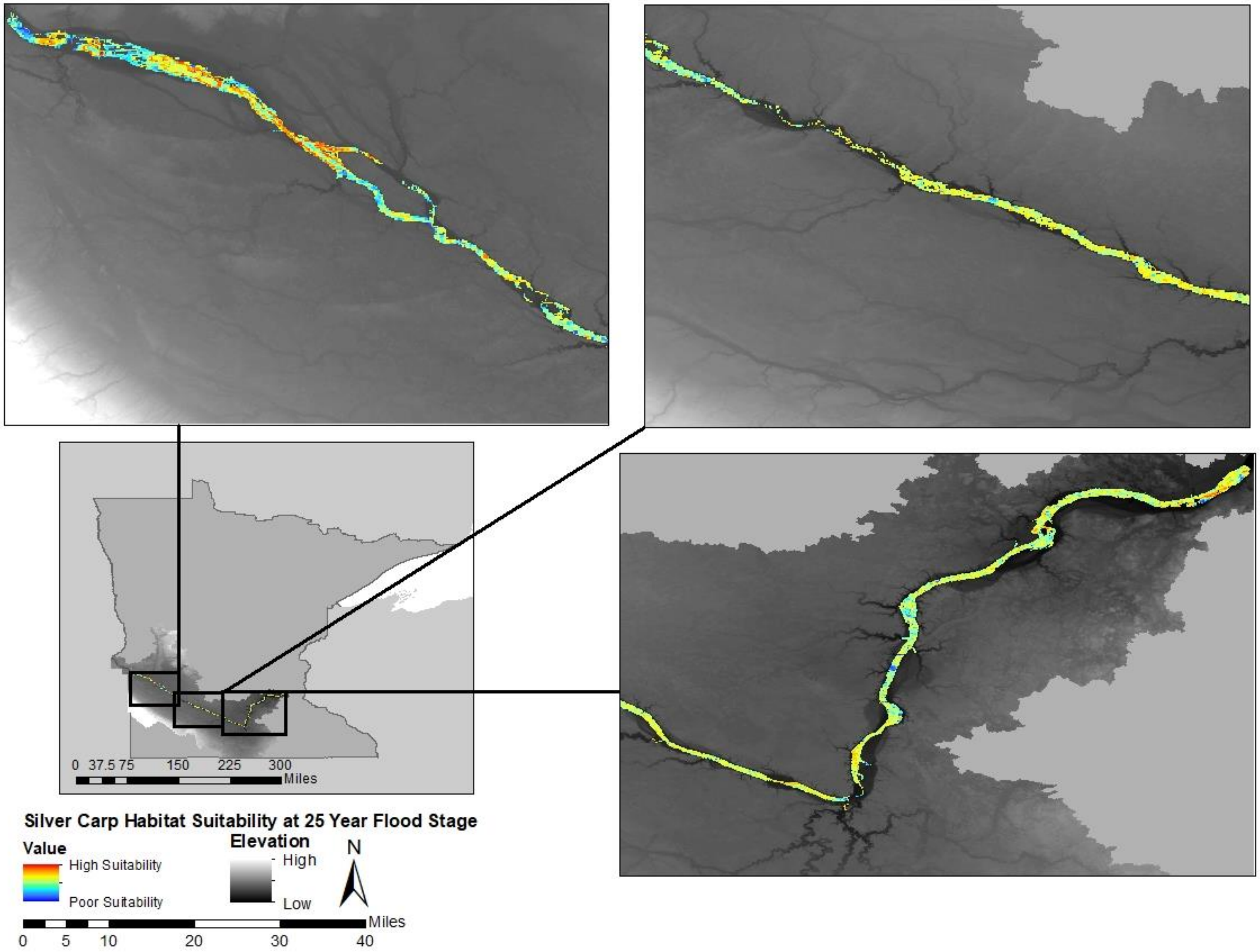


Figure 3.3D. Predicted suitable habitat for silver carp (H. molitrix) in the Minnesota River during a 50 year flood

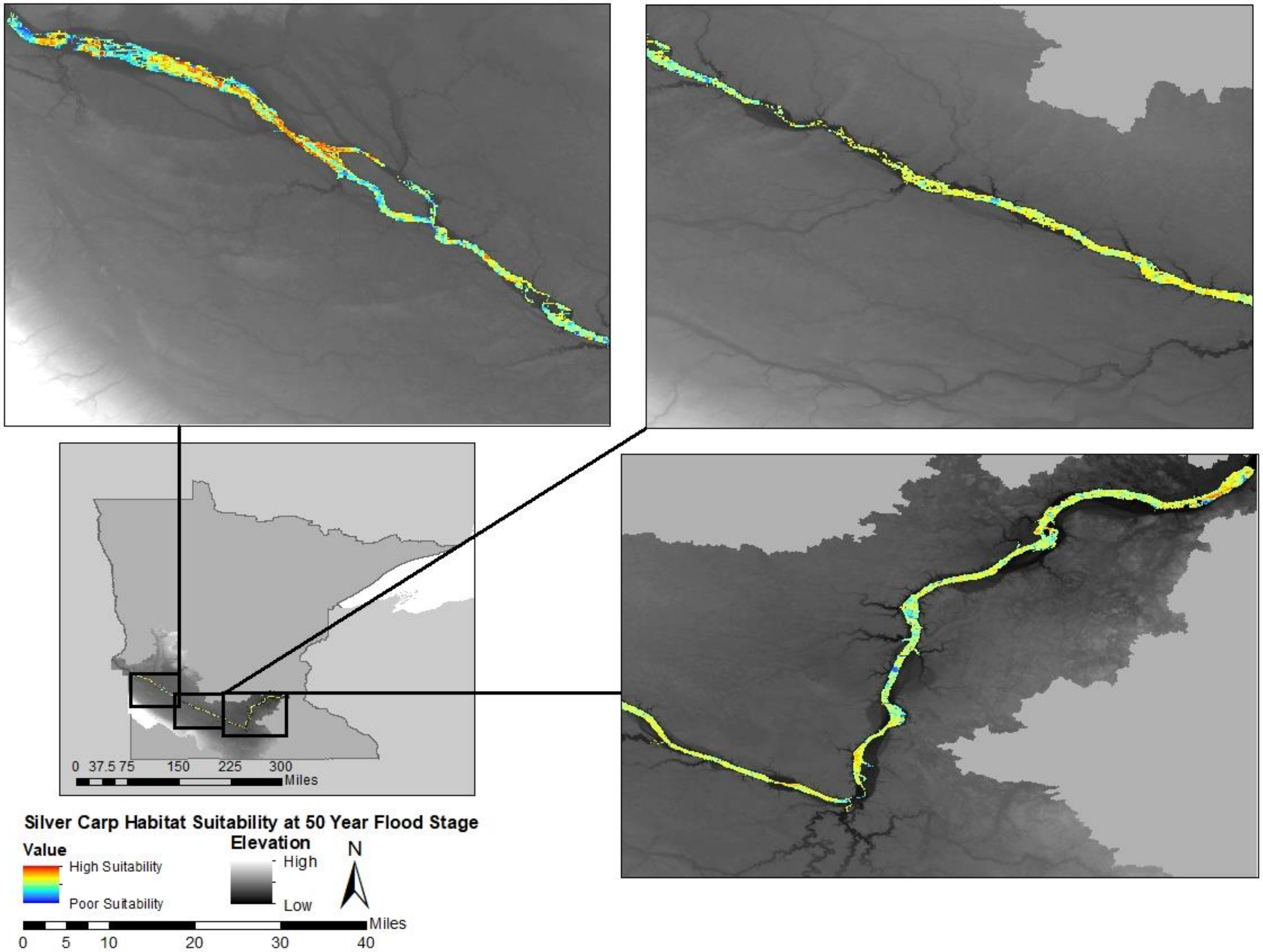
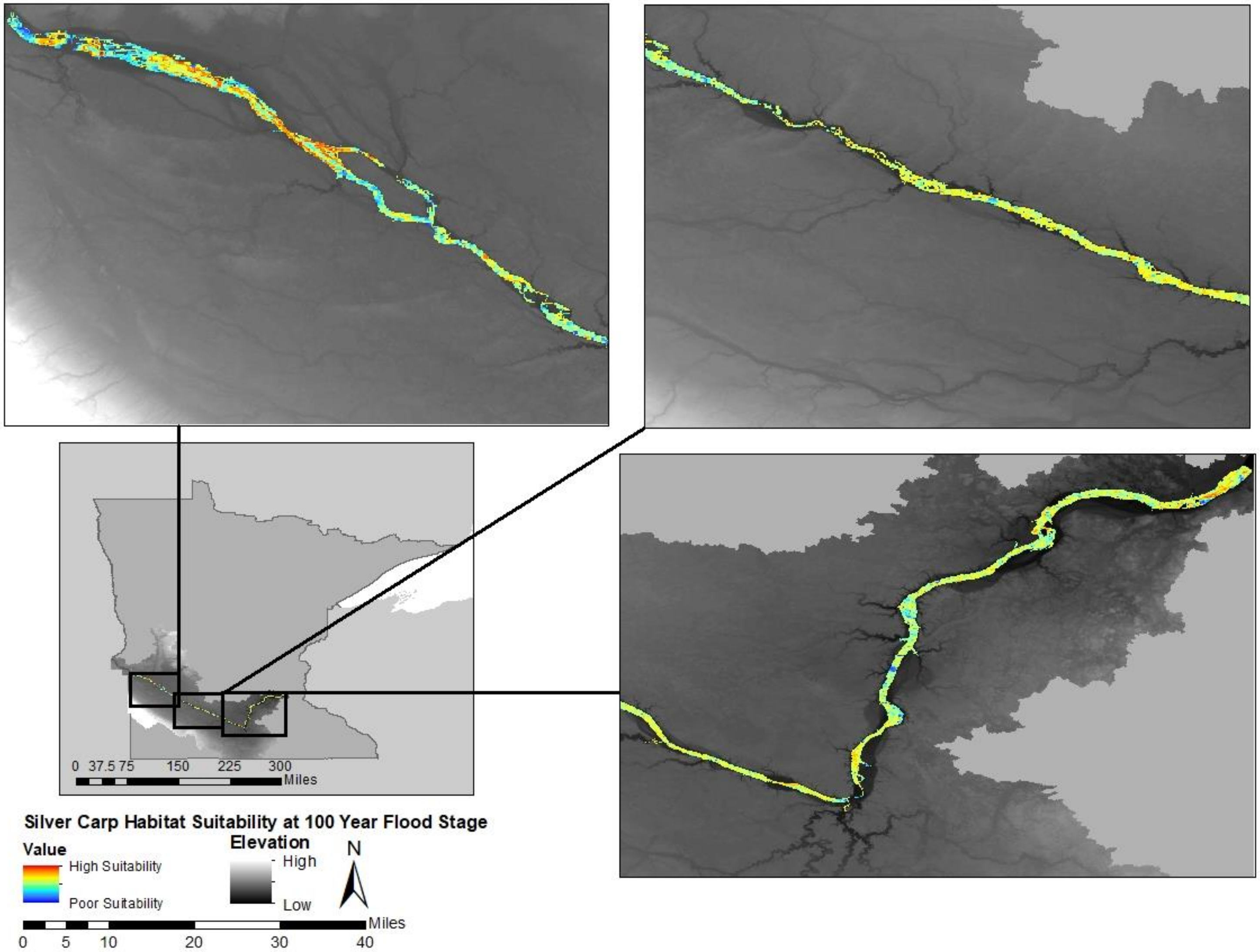


Figure 3.3E. Predicted suitable habitat for silver carp (H. molitrix) in the Minnesota River during a 100 year flood



Bighead Carp (H. nobilis)

Bighead carp had the highest average percentage of highly suitable habitat at 15.9% (Figures 3.4A-E). When averaging the flood years, the majority of area, 53.9%, was moderately suitable. Despite that, there was still a large percentage, 31.0%, of area that was classified as having low suitability or poor suitability. Similar to silver carp, as inundated area increased, the percent of highly suitable habitat decreased. Concurrently, the percentage of habitat with low or poor suitability increased. The bighead carp model had an AUC of 0.876.

Figure 3.4A. Predicted suitable habitat for bighead carp (H. nobilis) in the Minnesota River during a 5 year flood

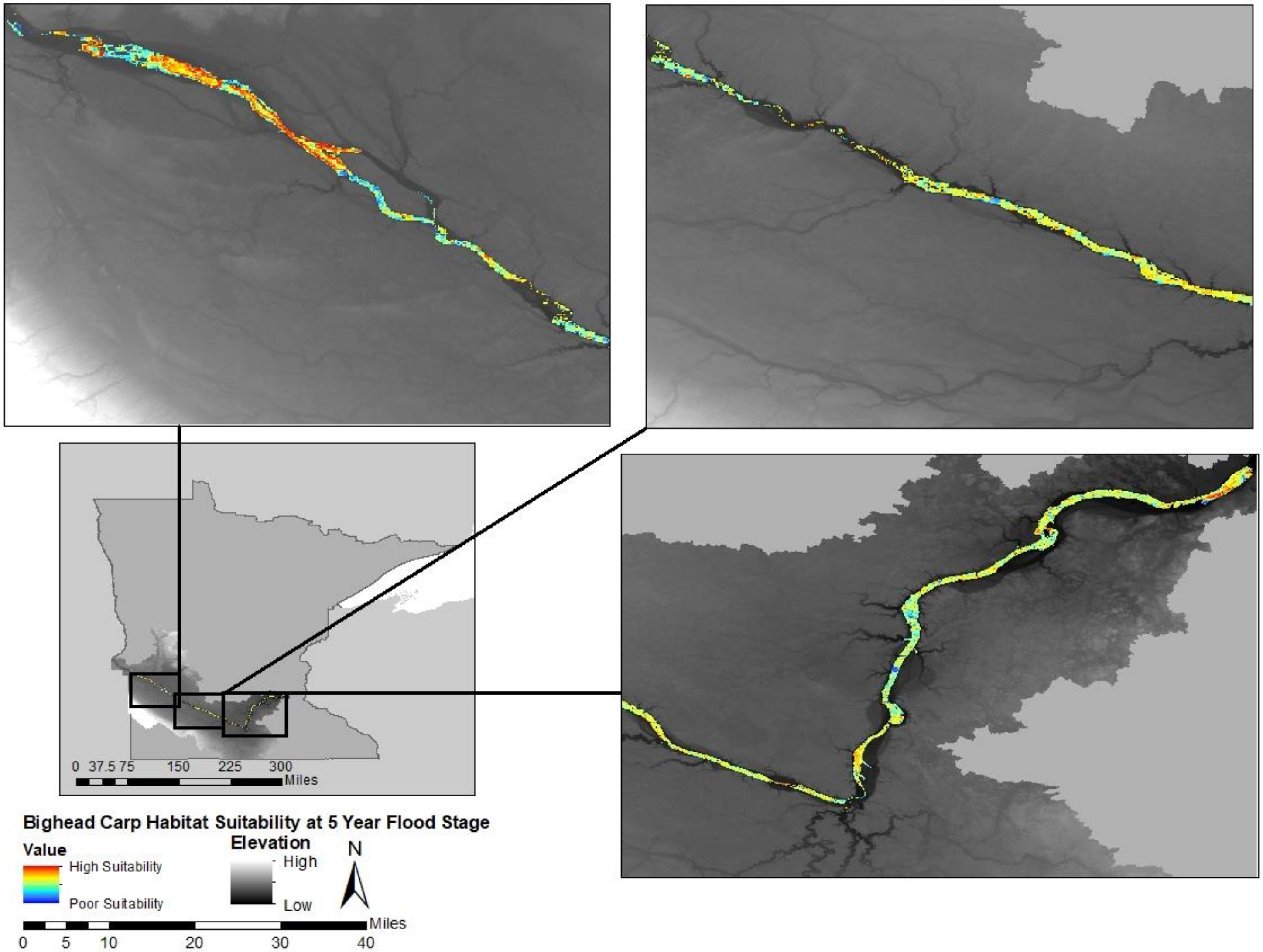


Figure 3.4B. Predicted suitable habitat for bighead carp (H. nobilis) in the Minnesota River during a 10 year flood

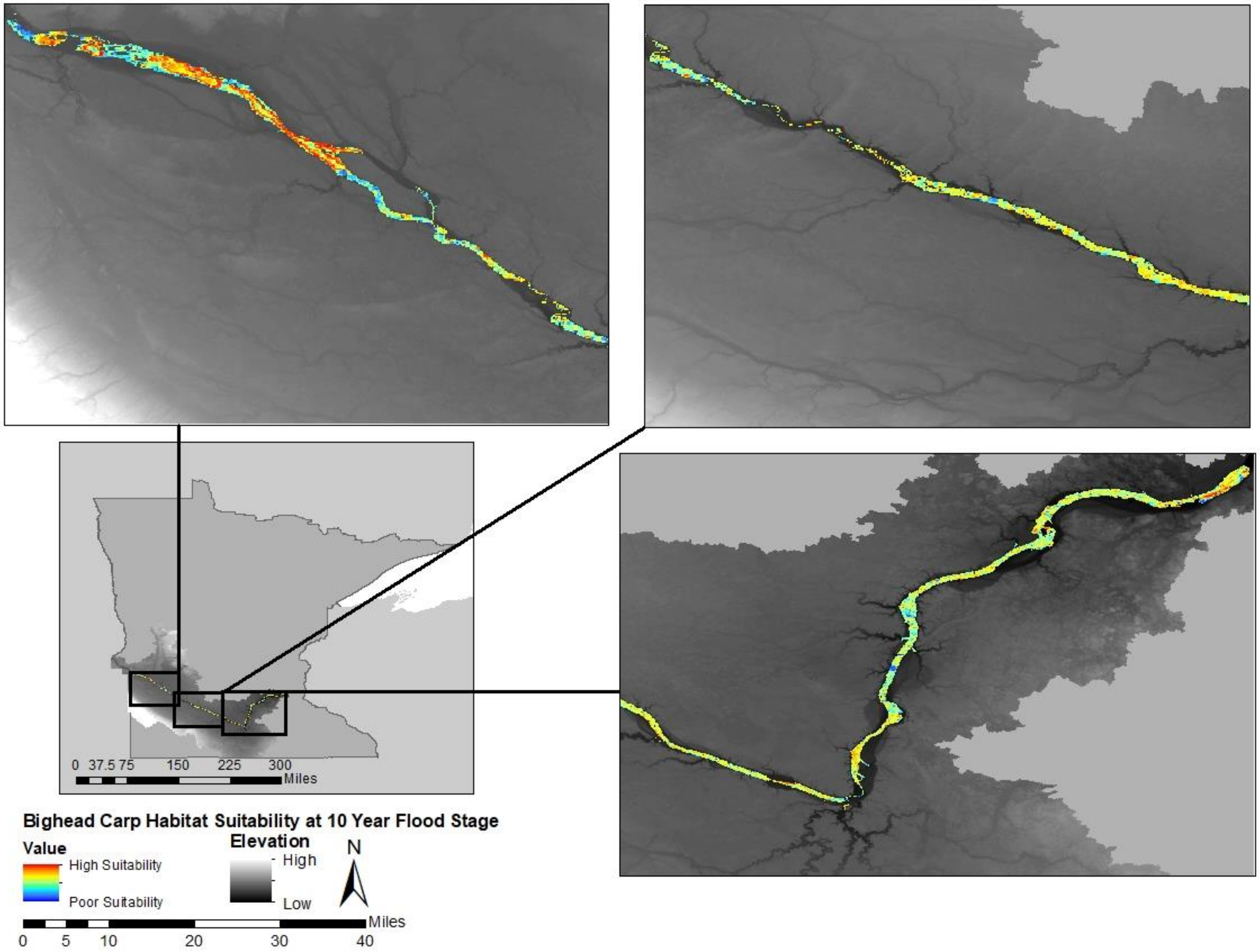


Figure 3.4C. Predicted suitable habitat for bighead carp (H. nobilis) in the Minnesota River during a 25 year flood

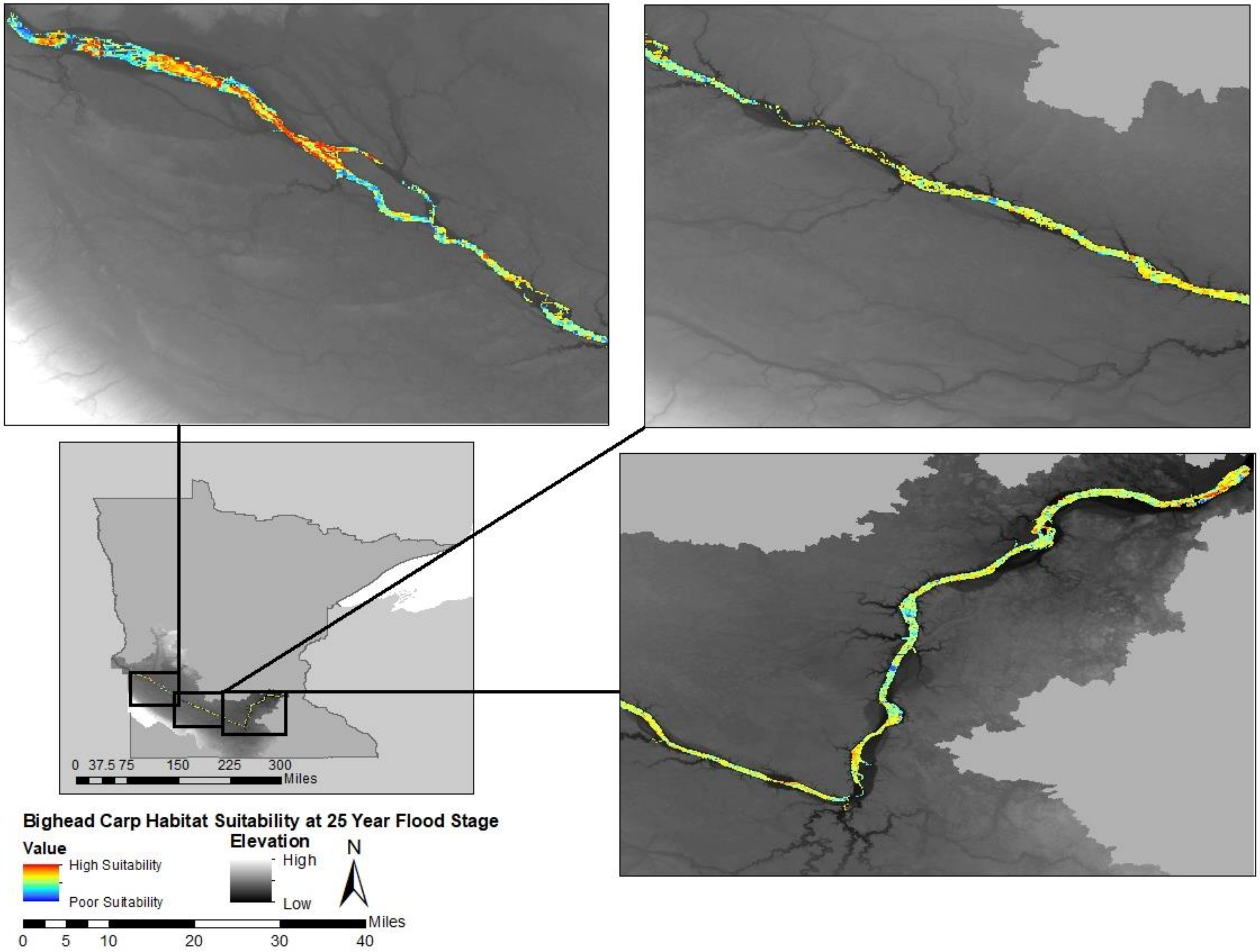


Figure 3.4D. Predicted suitable habitat for bighead carp (H. nobilis) in the Minnesota River during a 50 year flood

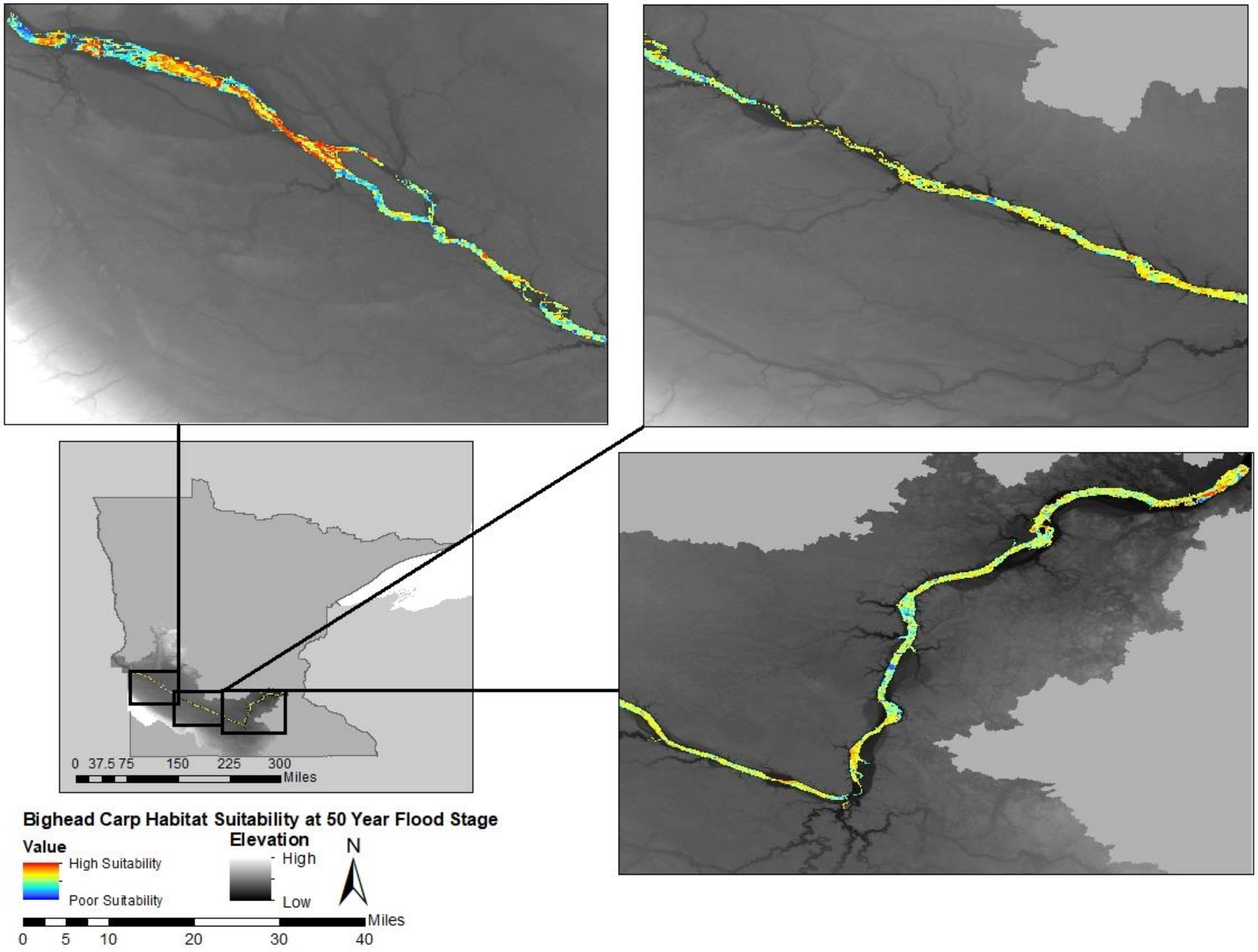
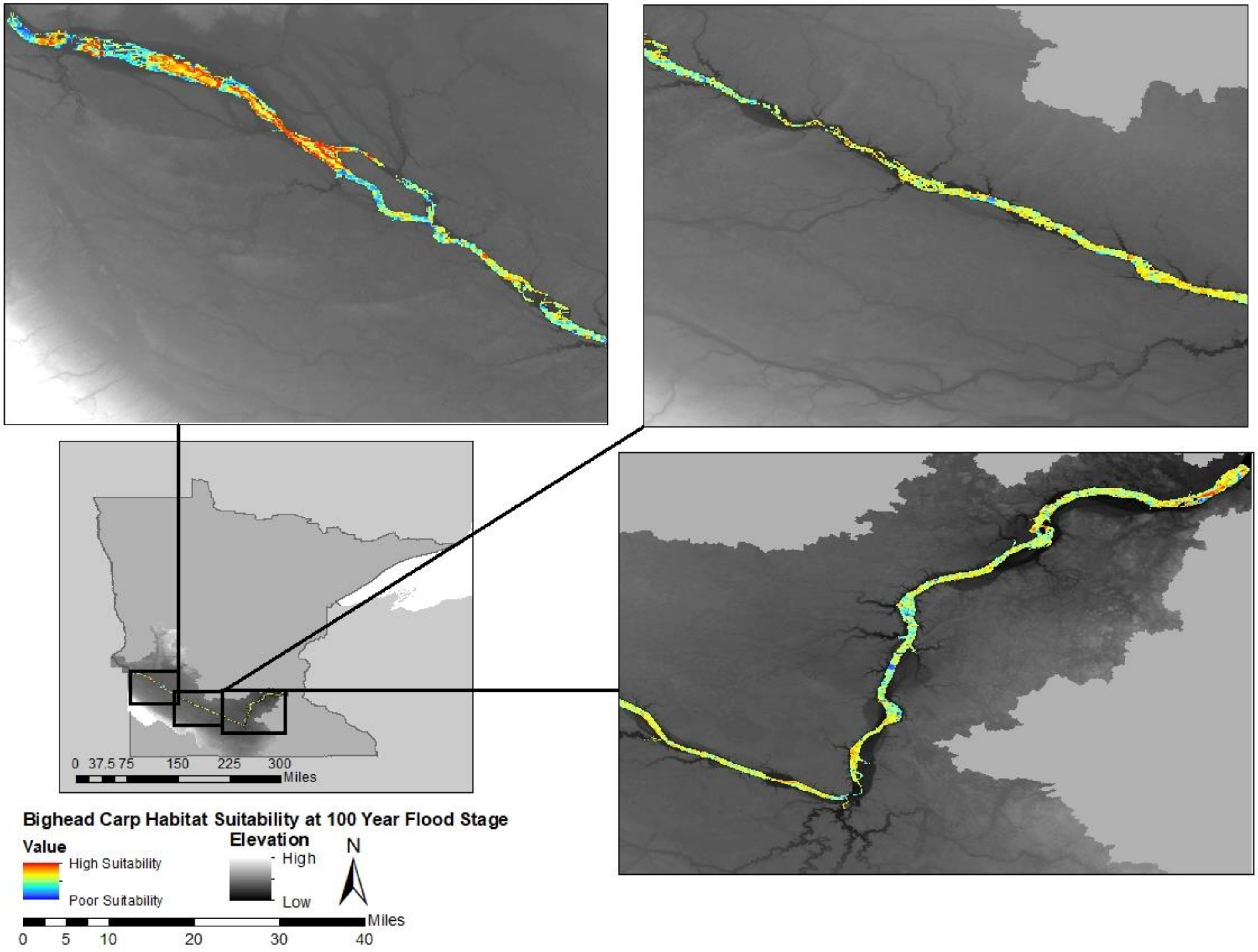


Figure 3.4E. Predicted suitable habitat for bighead carp (H. nobilis) in the Minnesota River during a 100 year flood



Black Carp (M. piceus)

Black carp had the lowest overall suitability in comparison with other invasive carp species, with an average of only 7.3% of the area being highly suitable and 9.1% being moderately suitable (Figures 3.5A-E). Most of the area, an average of 47.6%, was classified as having low suitability. Black carp had the highest percentage, 36.9%, of poorly suited habitat. Black carp did not experience the same trend as the other invasive carp species. Instead, the percent of poorly suited habitat increased, while high, moderate, and low suitability decreased by less than 1.0%. The black carp model had an AUC of 0.847.

Figure 3.5A. Predicted suitable habitat for black carp (M. piceus) in the Minnesota River during a 5 year flood

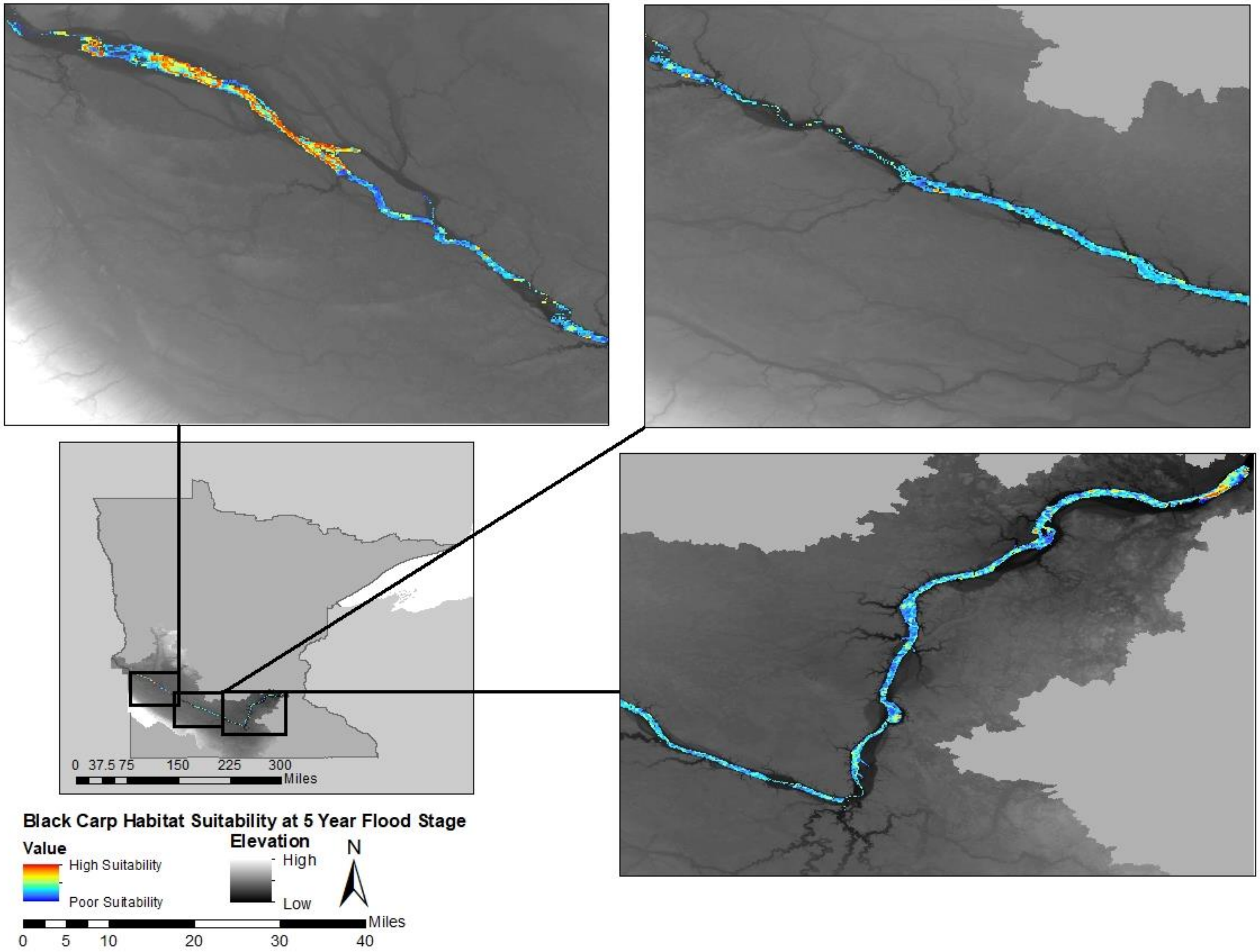


Figure 3.5B. Predicted suitable habitat for black carp (M. piceus) in the Minnesota River during a 10 year flood

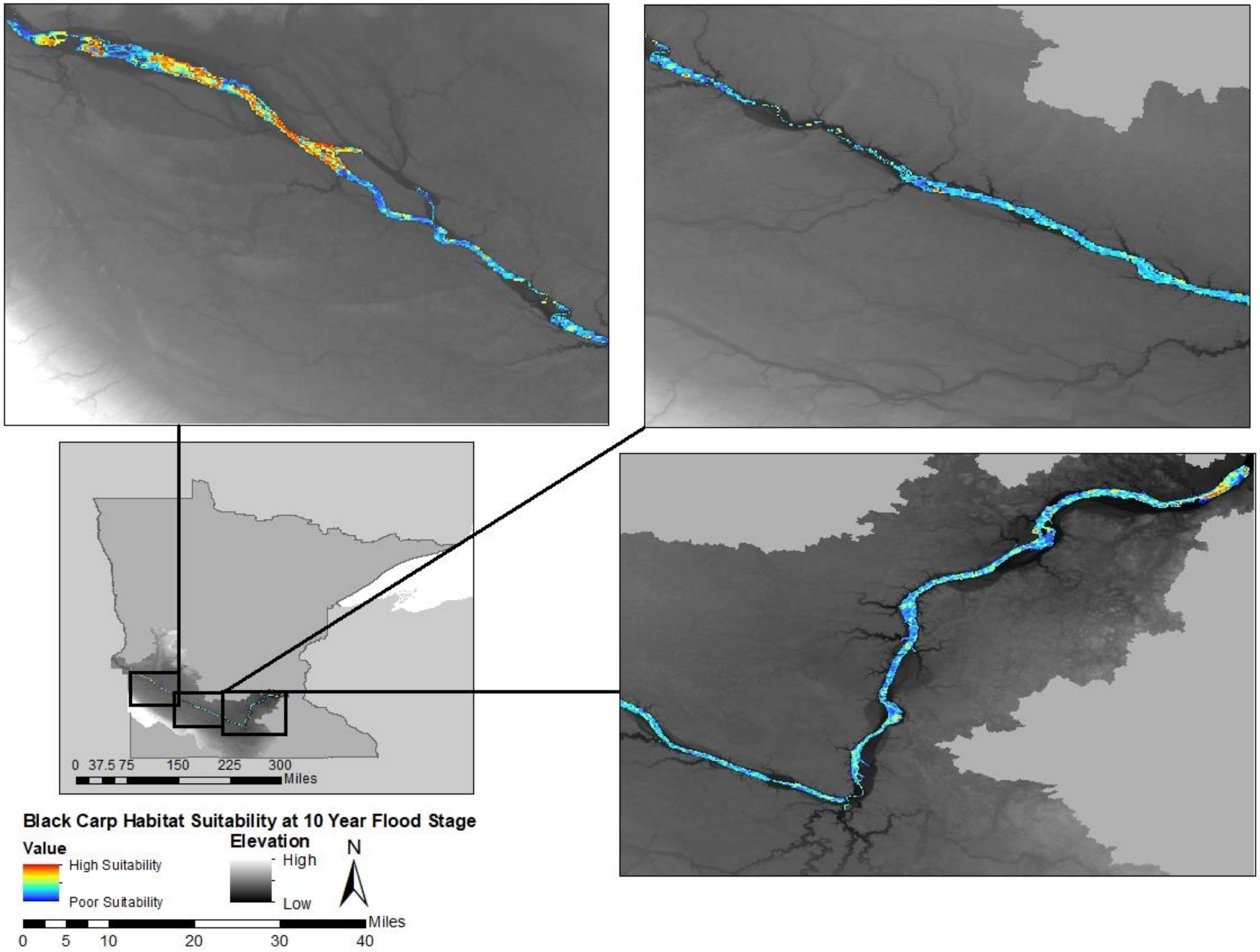


Figure 3.5C. Predicted suitable habitat for black carp (M. piceus) in the Minnesota River during a 25 year flood

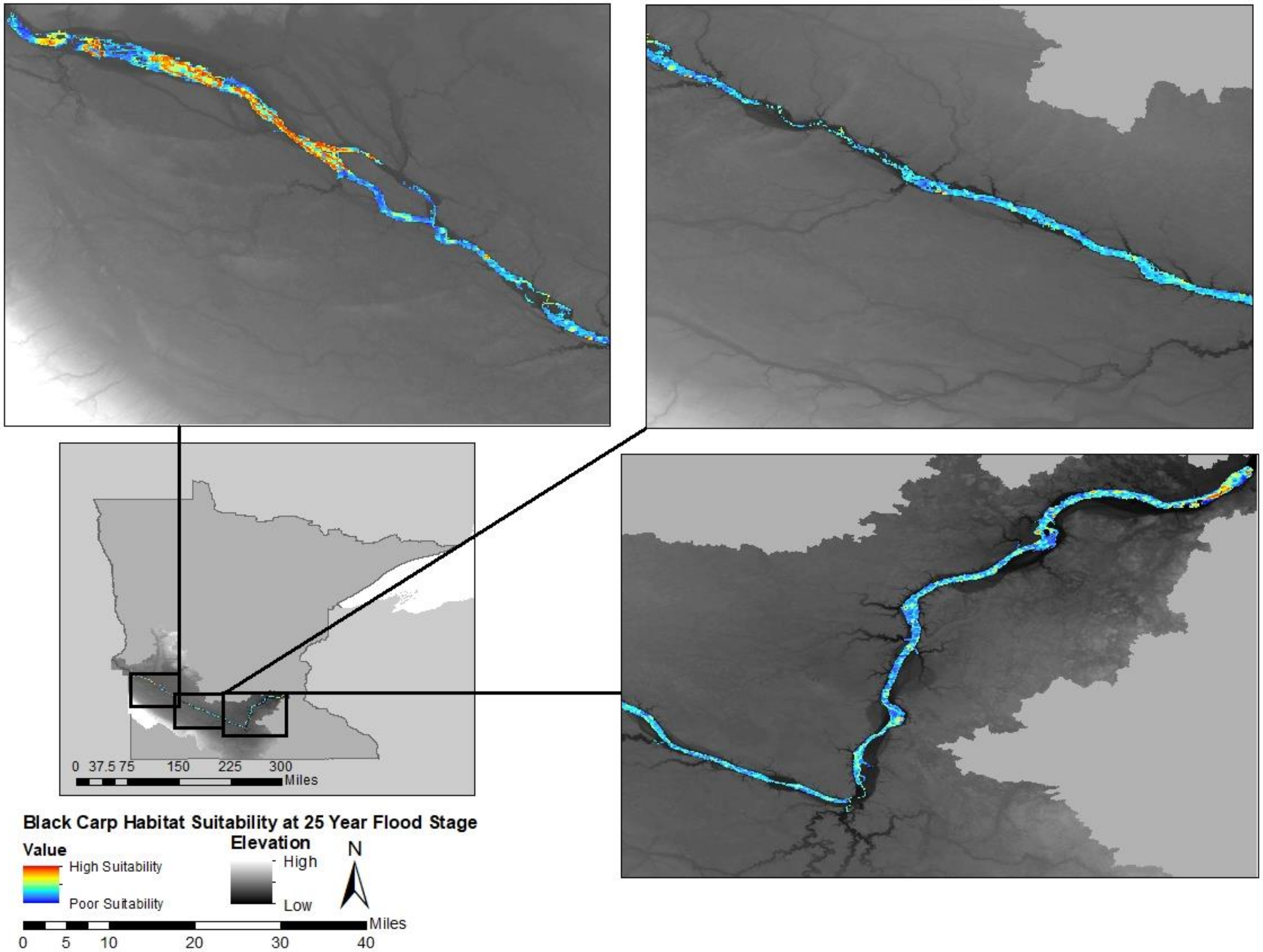


Figure 3.5D. Predicted suitable habitat for black carp (M. piceus) in the Minnesota River during a 50 year flood

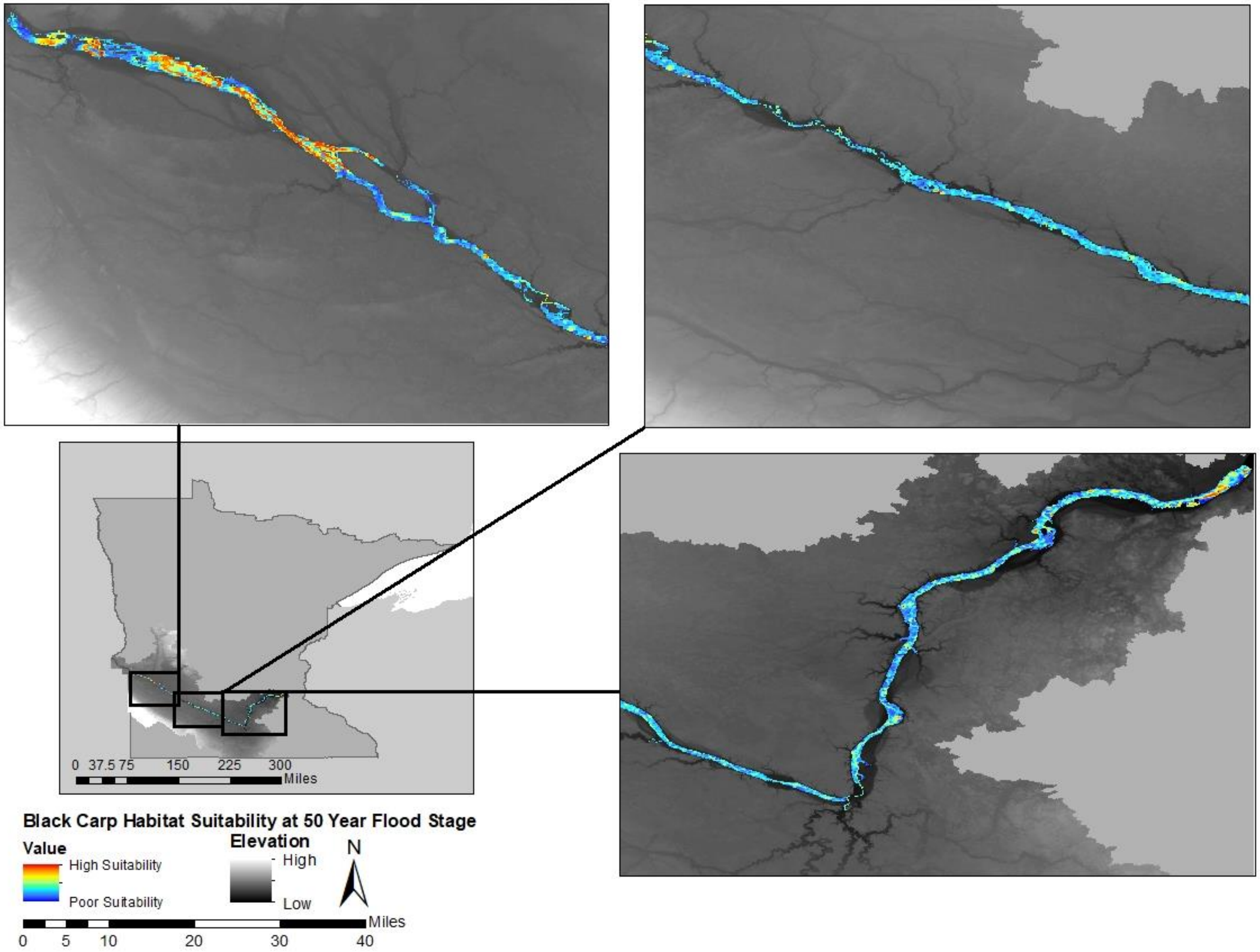
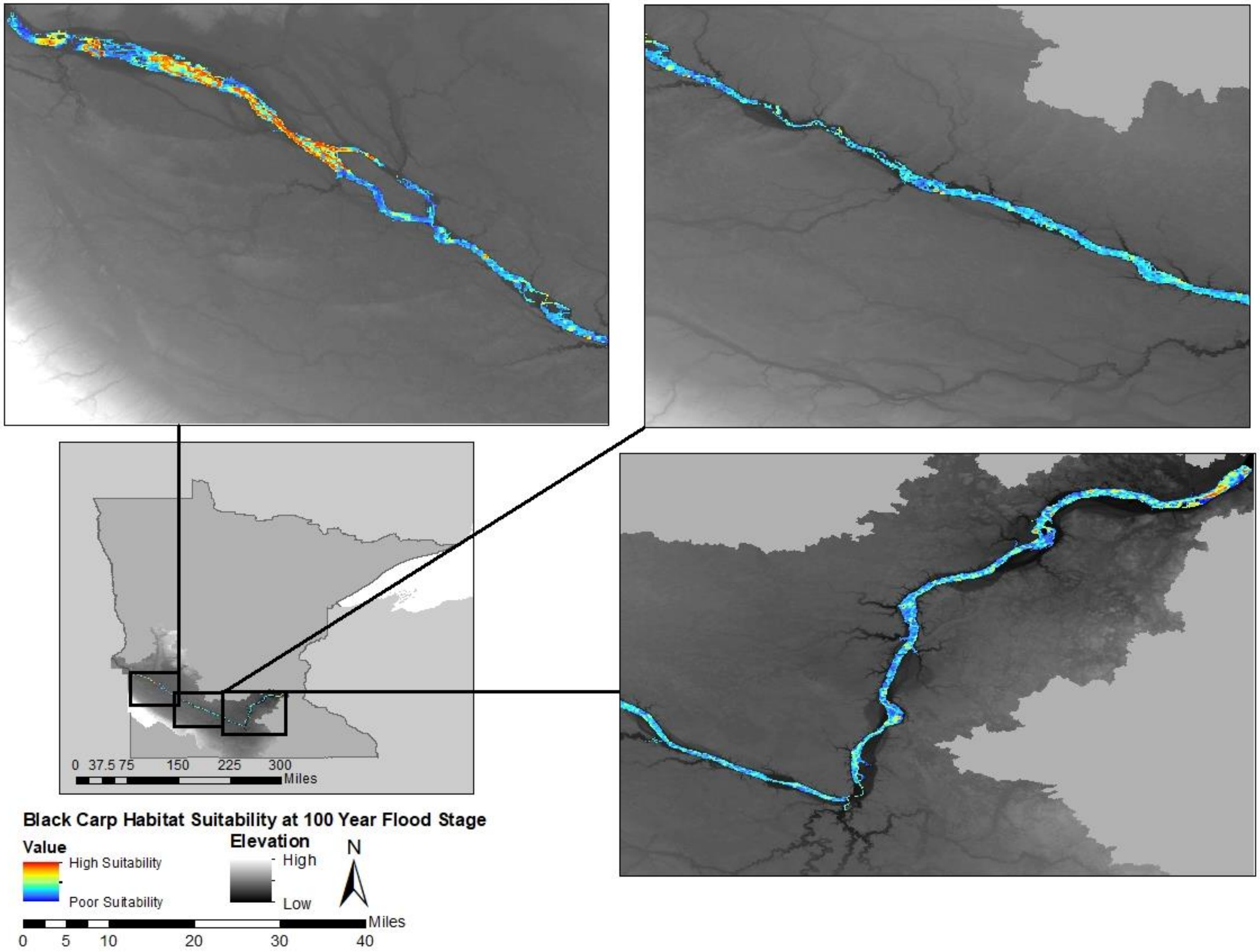


Figure 3.5E. Predicted suitable habitat for black carp (M. piceus) in the Minnesota River during a 100 year flood



Discussion

The MaxEnt results show that the Minnesota River is not equally suitable for all species (Figures 3.2-3.5). According to the model, the Minnesota River was most highly suited for the bighead head carp, with 70% of the area being moderately suitable or higher. Grass carp also had large amounts of suitable area within the river, with 64% of the area being classified as moderately suitable or above. Silver carp had 43% of area moderately suitable or above on average. These results do not support NicheA models that suggested the risk may be highest for grass and silver carp and lower for bighead carp. The model results for black carp did, however, support NicheA models showing low suitability within the Minnesota River. On average, only 17% of area was classified as moderately suitable or higher. This means while highly suitable areas existed within the river, they were less common and more localized.

Moderately suitable habitat was most abundant throughout the river, with the exception of black carp. High suitability did not have the greatest percentage of area for any of the species, but was present in localized hot spots. A majority of the highly suitable areas for invasive carp was near the headwaters where the river is impounded or near backwaters along the river. Areas of highest suitability closely resemble conditions on the Mississippi River (*e.g.* slow moving water, wide channel, pools). This is not unexpected however, as a majority of occurrences used to calibrate the models were in the Mississippi River Basin. The similarities are relevant to the life histories of invasive carp. Adult invasive carp often times remain in slow moving waters or pools when not spawning. Areas of highly suitable habitat could be places to increase sampling efforts to detect adult founder population. Backwaters that were predicted as highly suitable, on the other hand, could be used to target invasive carp in early life stages (e.g. larval, juvenile). However, the abundance of moderately suitable habitat suggests monitoring throughout the river is likely needed.

The MODIS vegetation index used to calibrate the MaxEnt models may have underpredicted the suitability of the Minnesota River for invasive carp. The areas predicted as highly suitable often matched with areas of open water, away from vegetation. This could calibrate the model to predict areas of the river enclosed in terrestrial vegetation as less suitable, despite suitable river conditions.

In order to create a more robust risk assessment, conditions in the Minnesota River need to be considered (*e.g.* water temperature, pH, turbidity, flow velocity). Understanding fine scale patterns could help identify reaches of the river that are more vulnerable to invasive carp. The Minnesota River can be very dynamic in the short term. For example, after a rain storm in June of 2016 the amount of total suspended solids (TSS), or the amount of sediment and other materials in the water, spiked from 244 mg/L to 628 mg/L in five days. Research on invasive carp has suggested spikes in turbidity, a metric related to TSS, could trigger spawning activities. Tracking spikes in TSS in the Minnesota River could help managers isolate portions of the river that would be more prone to invasive carp spawning, but additional research on flow, temperature, and discharge patterns would also be needed. Unfortunately, available long-term Minnesota River data currently does not capture the full variability of water conditions because there are only a few sampling locations. Success of any of the invasive carp species would also be dependent on interspecies interactions (*e.g.* food availability, predation on young carp, pathogens). Further research on the Minnesota River's ecosystem is warranted to provide the data needed to assess these interactions. Examples of studies that would benefit invasive carp risk include topics such as plankton densities and native mussel populations.

The modeling framework used to complete the study also has room for improvement. Default settings in MaxEnt were utilized due to computing limitations. In future studies, customized settings for each species should be used. Moreover, multiple algorithms should have been tested for each species prior to selection. MaxEnt may have not been the best option for all species. The addition of multiple algorithms and trials would have allowed a stronger evaluation metric like akaike information criterion (AIC). Research conducted examining the effectiveness of evaluation metrics suggests the AUC may not be ideal in studies using presence only data and highlights the importance of multiple evaluation metrics (Lobo, Jimenez-Valverde, and Real 2007; Escobar et al. 2018).

Conclusion

The MaxEnt modeling algorithm calibrated with high resolution vegetation indices produced results suggesting the Minnesota River is suitable for invasive carp. Bighead, silver, and grass carp had the greatest area of well suited habitat and may be at greatest risk for establishment, but habitat may not be ideal for black carp, with results showing a majority of area having low suitability. The data produced in this study can be used to preliminarily predict risk of invasion for invasive carp. However, continued research on the Minnesota River and invasive carp is merited to further analyze risk.

Tables

Table 2.1 Variables obtained from Ecoclimate.org

Variable	**Units**
Annual mean temperature	°C
Mean diurnal range	°C
Isothermality	%
Temperature seasonality	%
Max temperature of warmest month	°C
Min temperature of coldest month	°C
Temperature annual range	°C
Temperature annual range	°C
Mean temperature of wettest quarter	°C
Mean temperature of driest quarter	°C
Mean temperature of warmest quarter	°C
Mean temperature of coldest quarter	°C
Annual precipitation	mm/ m^2
Precipitation of driest quarter	mm/ m^2
Precipitation of driest month	mm/ m^2
Precipitation seasonality	%
Precipitation of wettest quarter	mm/ m^2
Precipitation of driest quarter	mm/ m^2
Precipitation of warmest quarter	mm/ m^2
Precipitation of coldest quarter	mm/ m^2

Table 2.2 Results of NicheA model evaluations

Species Name	**Environmental Range**	**Trial**	**% Predicted Correctly**	**P-Value**
Silver Carp	Native Range	CAL	54.65%	< 0.0001
Silver Carp	Native Range	EVL	64.24%	< 0.0001
Silver Carp	United States	CAL	71.55%	< 0.0001
Silver Carp	United States	EVL	81.85%	< 0.0001
Silver Carp	Europe	CAL	67.85%	< 0.0001
Silver Carp	Europe	EVL	80.56%	< 0.0001
Silver Carp Average			**70.12%**	**< 0.0001**
Bighead Carp	Native Range	CAL	22.14%	< 0.0001
Bighead Carp	Native Range	EVL	22.14%	< 0.0001
Bighead Carp	United States	CAL	35.15%	< 0.0001
Bighead Carp	United States	EVL	22.26%	< 0.0001
Bighead Carp	Europe	CAL	33.38%	< 0.0001
Bighead Carp	Europe	EVL	40.42%	< 0.0001
Bighead Carp Average			**29.25%**	**< 0.0001**
Grass Carp	Native Range	CAL	50.71%	< 0.0001
Grass Carp	Native Range	EVL	62.28%	< 0.0001
Grass Carp	United States	CAL	61.51%	< 0.0001
Grass Carp	United States	EVL	73.60%	< 0.0001
Grass Carp Average			**62.03%**	**< 0.0001**
Black Carp	Native Range	CAL	14.76%	0.0122
Black Carp	Native Range	EVL	14.76%	< 0.0001
Black Carp	United States	CAL	32.52%	0.6595
Black Carp	United States	EVL	32.52%	< 0.0001
Black Carp Average			**23.64%**	**0.1680**
Total Average			**46.94%**	

Table 3.1A. Invasive carp MaxEnt model results quantified

Species	Flood Stage	Area of High Suitability (m^2)	% Area of High Suitability	Area of Moderate Suitability (m^2)	% Area of Moderate Suitability	Area of Low Suitability (m^2)	% Area of Low Suitability	Area of Poor Suitability (m^2)	% Area of Poor Suitability
Silver Carp	5	5,687,500	1.3%	182,437,500	42.0%	226,312,500	52.1%	20,750,000	4.8%
Silver Carp	10	6,125,000	1.3%	196,562,500	41.9%	248,750,000	53.0%	24,000,000	5.1%
Silver Carp	25	6,375,000	1.3%	209,250,000	41.3%	265,562,500	52.5%	27,562,500	5.5%
Silver Carp	50	6,375,000	1.2%	213,437,500	41.9%	277,750,000	53.2%	28,187,500	5.4%
Silver Carp	100	6,437,500	1.2%	219,437,500	40.5%	289,437,500	53.4%	29,500,000	5.4%
Average Silver Carp			**1.3%**		**41.3%**		**52.8%**		**5.2%**
Bighead Carp	5	70,375,000	16.2%	236,187,500	54.4%	112,812,500	26.0%	18,125,000	4.2%
Bighead Carp	10	76,875,000	16.4%	252,187,500	53.7%	119,687,500	25.5%	20,937,500	4.5%
Bighead Carp	25	79,937,500	15.8%	272,187,500	53.8%	134,875,000	27.0%	23,375,000	4.6%
Bighead Carp	50	81,062,500	15.5%	281,187,500	53.9%	141,062,500	27.0%	23,750,000	4.6%
Bighead Carp	100	83,187,500	15.3%	290,562,500	53.6%	147,937,500	27.3%	24,937,500	4.6%
Average Bighead Carp			**15.9%**		**53.9%**		**26.5%**		**4.5%**

Table 3.1B. Invasive carp MaxEnt model results quantified

Species	**Flood Stage**	**Area of High Suitability (m^2)**	**% Area of High Suitability**	**Area of Moderate Suitability (m^2)**	**% Area of Moderate Suitability**	**Area of Low Suitability (m^2)**	**% Area of Low Suitability**	**Area of Poor Suitability (m^2)**	**% Area of Poor Suitability**
Grass Carp	5	10,500,000	2.4%	272,375,000	62.7%	147,750,000	34.0%	6,000,000	1.4%
Grass Carp	10	11,125,000	2.4%	292,000,000	62.2%	162,312,500	34.6%	6,500,000	1.4%
Grass Carp	25	11,500,000	2.3%	315,187,500	62.3%	176,312,500	34.8%	6,5625,00	1.3%
Grass Carp	50	11,500,000	2.2%	324,812,500	62.2%	183,312,500	35.1%	6,625,000	1.3%
Grass Carp	100	11,500,000	2.1%	336,312,500	62.0%	191,812,500	35.4%	6,875,000	1.3%
Average Grass Carp			**2.3%**		**62.3%**		**34.8%**		**1.3%**
Black Carp	5	33,312,500	7.7%	39,875,000	9.2%	208,937,500	48.1%	157,250,000	36.2%
Black Carp	10	35,250,000	7.5%	44,250,000	9.4%	224,000,000	47.7%	171,687,500	36.6%
Black Carp	25	36,687,500	7.3%	46,500,000	9.2%	240,000,000	47.4%	186,562,500	36.9%
Black Carp	50	36,875,000	7.1%	47,250,000	9.1%	248,125,000	47.5%	194,875,000	37.3%
Black Carp	100	37,125,000	6.9%	48,937,500	9.0%	257,187,500	47.4%	203,437,500	37.5%
Average Black Carp			**7.3%**		**9.1%**		**47.6%**		**36.9%**

Appendices

Appendix A. R script to divide data into cal and evl groups

```
library(ENMeval)#dismo, raster, rgdal

occ<-read.table("BHC_Combined.csv", head=T, sep=",")
occ<-occ[,c(2,3)]
env<-raster("Bio1b.tif")
plot(env)

#calibration
bg<-as.data.frame(env, xy=T)
block_df<-get.block (occ, bg)
occ$group<-block_df$occ.grp

cal<-occ[which(occ$group %in% c(1,4)),]
evl<-occ[which(occ$group %in% c(2,3)),]
write.table(cal, "cal.csv", row.names = F, sep=",")
write.table(evl, "evl.csv", row.names = F, sep=",")

plot(occ$DecimalLongitude, occ$DecimalLatitude, pch=".", col=rainbow(7)[occ$group])
```

Appendix B. R script used to download MODIS data

```
# MODIS auto-time series download
install.packages("gWidgetsRGtk2")
library(gWidgetsRGtk2)
install.packages("MODIStsp")
library(MODIStsp)
MODIStsp()
```

Bibliography

Abdusamadov, A.S. 1987. Biology of the white amur (*Ctenopharyngodon idella*), silver carp (*Hypophthalmichthys molitix*), and bighead (*Aristichthysnobilis*), acclimatized in the Terek region of the Caspian Basin. *Journal of Ichthyology* 26(4):41-49.

Aguiar, F.C., M.T. Ferreira, and I. Moreira. 2001 Exotic and native vegetation establishment following channelization of a western Iberian river. *Regulated Rivers: Resource Managament* 17: 509-526.

Aliyev, D.S. 1976. The role of phytophagous fishes in the reconstruction of commercial fish fauna and the biological improvement of water. *Journal Ichthyology* 16(2): 216-29.

Anderson, R.P. and A. Raza. 2010. The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents (genus *Nephelomys*) in Venezuela. *Journal of Biogeography* 37(7):1378-1393.

Barve, N., V. Barve, A. Jiménez-Valverde, A. Lira-Noriega, S.P. Maher, A.T. Peterson, J. Soberón, and F. Villalobos. 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecological Modelling* 222(11):1810-1819.

Bain, M.B., D.H. Webb, M.D. Tangedal, and L.N. Mangum. 1990. Movement and habitat use by grass carp in a large mainstream reservoir. *Transactions of the American Fisheries Society* 119(3):553-561.

Belmont, P., K.B. Gran, S.P. Schottler, P.R. Wilcock, S.S. Day, C. Jennings, J.W. Lauer, E. Viparelli, J.K. Willenbring, D.R. Engstrom, and G. Parker. 2011. Large Shift in Source of Fine Sediment in the Upper Mississippi River. *Environmental science & technology* 45(2):8804-8810.

Berg, L.S. 1964. *Freshwater Fishes of the USSR and Adjacent Countries* 2(4). Washington D.C.: The Smithsonian Institution and the National Science Foundation.

Bettoli, P.W., W.H. Neill, S.W. Kelsch. 1985. Temperature preference and heat resistance of grass carp, *Ctenopharyngodon idella* (Valenciennes), bighead carp, *Hypophthalmichthys nobilis* (Gray), and their F1 hybrid. *Journal of Fish Biology* 27(3):239-247.

Blossey, B., L.C. Skinner, and J. Taylor. 2001. Impact and management of purple loosestrife (*Lythrum salicaria)* in North America. *Biodiversity and Conservation* 10(10):1787-1807.

Byers, J. E. 2002. Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. *Oikos* 97(3):449-458.

Carlton, J.T. 2001. *Introduced Species in U.S. Coastal Waters: Environmental Impacts and Management Priorities*. Arlington, VA: Pew Oceans Commission.

Carpenter, S.R. and D.M. Lodge. 1986. Effects of submersed macrophytes on ecosystem processes. *Aquatic Botany* 26:341-370.

Chapman, D.C., J.J. Davis, J.A. Jenkins, P.M. Kocovsky, J.G. Miner, J. Farver, and P.R. Jackson. 2013. First evidence of grass carp recruitment in the Great Lakes Basin. *Journal of Great Lakes Research* 39(4):547-554.

Chen, P., E.O. Wiley, and K.M. Mcnyset. 2007. Ecological niche modeling as a predictive tool: silver and bighead carps in North America. *Biological Invasions* 9:43-51.

Chick, J.H., R.J. Maher, B.M. Burr, and M.R. Thomas. 2003. First black carp captured in U.S.. *Science* 300(5627):1876-1877.

Chilton III, E.W. and M.I. Muoneke. 1992. Biology and management of grass carp (*Ctenopharyngodon idella*, Cyprinidae) for vegetation control: a North American perspective. *Reviews in Fish Biology and Fisheries* 2(4):283-320.

Coetzee, J. A., M. P. Hill, and D. Schlange. 2008. Potential spread of the invasive plant *Hydrilla verticillata* in South Africa based on anthropogenic spread and climate suitability. *Biological Invasions* 11(4):801-812.

Cremer, M.O. and R.O. Smitherman. 1980. Food habits and growth of silver and bighead carp in cages and ponds. *Aquaculture* 20(1):57-64.

Crossman, E.J., S.J. Nepszy, and P. Krause. 1987. The first record of grass carp, *Ctenopharyngodon idella*, in Canadian waters. *Canadian Field-Naturalist* 101(4):584-586.

Cudmore, B. and N.E. Mandrak. 2004. Biological synopsis of grass carp (*Ctenopharyngodon idella*). *Canadian Manuscript Report of Fisheries and Aquatic Sciences*.

DeGrandchamp, K.L., J.E. Garvey, and L.A. Csoboth. 2007. Linking adult reproduction and larval density of invasive carp in a large river. *Transactions of the American Fisheries Society* 136(5):1327-1334.

Deters, J.E., D.C. Chapman, and B. Mcelroy. 2013. Location and timing of Asian carp spawning in the Lower Missouri River. *Environmental Biology of Fishes* 96(5):617-629.

Dibble, E.D. and K. Kovalenko. 2009. Ecological impact of grass carp: a review of the available data. *Journal of Aquatic Plant Management* 47:1-15.

Ehrlich, P.R. 1984. Which animal will invade?. *Ecology of Biological Invasions of North America and Hawaii*: 79-95. New York, NY: Springer.

Elith, J., C. Graham, R. Anderson, M. Dudík, S. Ferrir, A. Guisan, R. Hijmans, F. Huettmann, J.R. Leathwick, A. Lehmann, J. Li, L.G. Lohmann, B.A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. McOverton, A.T. Peterson, S.J. Phillips, K. Richardson, R. Scachetti-Pereira, R.E. Schapire, J. Soberón, S. Williams, M.S. Wisz, N.E. Zimmermann and M. Araujo. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29(2):129-151.

Escobar, L.E. and M.E. Craft. 2016. Advance and limitations of disease biogeography using ecological niche modeling. *Frontiers in Biogeography* 7:1174.

Escobar, L.E., H. Qiao, C. Lee, and N.B. Phelps. 2017. Novel methods in disease biogeography: A case Study with heterosporosis. *Frontiers in Veterinary Science* 4(105).

Escobar, L.E., S. Mallez, M. McCartney, C. Lee, D.P. Zielinski, R. Ghosal, P.G. Bajer, C. Wagner, B.Nash, M. Tomamichel, and P. Venturelli. 2018. Aquatic invasive species in the Great Lakes region: an overview. *Reviews in Fisheries Science & Aquaculture* 26(1): 121-138.

Executive Order No. 13112. 1999. *Federal Register* 64(25).

Fedorenko, A.Y., and F.J. Fraser.1978. A review of the biology of grass carp (*Ctenopharyngodon idella*, Val.) and its evaluation as a potential weed control agent in British Columbia. Technical Report. *Fisheries and Marine Service of Canada* 786.

Ferber, D. 2001. Will black carp be the next zebra mussel?. *Science Magazine*, 13 April: 292.

Fischenich, M. Invasive carp found in river. *The Free Press*, February 25, 2016.

Fisher, T.G. 2004. River Warren boulders, Minnesota, USA: Catastrophic paleoflow indicators in the southern spillway of glacial Lake Agassiz. *Boreas* 33:349-358.

Fukushima, M., N. Takamura, L. Sun, M. Nakagawa, K. Matsushige, and P. Xie. 1999. Changes in the plankton community following introduction of filter- feeding planktivorous fish. *Freshwater Biology* 42(4):719-735.

Garcia, A.M., D. Loebmann, J.P. Vieira, and M.A. Bemvenuti. 2004. First records of introduced carps (Teleostei, Cyprinidae) in the natural habitats of Mirim and Patos Lagoon estuary, Rio Grande do Sul, Brazil. *Revista Brasileira de Zoologia* 21(1).

Garcia, L.M., C.M. Garcia, A.F. Pinedam E,A, Gammad, J. Canta, S.P. Simon, G.V. Hilomen-Garcia, A.C. Gonzal, and C.B. Santiago. 1999. Survival and growth of bighead carp fry exposed to low salinities. *Aquaculture International* 7(4):241-250.

Goldschmidt, Y., F. Witte, and J. Wanink. 1993. Cascading effects of the introduced nile perch and the detritivorous/phytoplanktivorous species in the sublittoral areas of Lake Victoria. *Conservation Biology* 7(3):696-700.

Gorbach, E.J. 1961. Age composition, growth and age of onset of sexual maturity of white Ctenopharyhgodon idella (Val) and bleck Mylopharyngodon pisceus (Rich amur) in the Amur river basin. *Voprosy Ikhtiologii* 1(18):119-126.

Gorbach, E.I. 1970. Condition and fatness of the grass carp [*Ctenopharyngodon idella* (Val.)] in the Amur basin. *Journal of Ichthyology* 1(1):880-890.

Gran, K.B., P. Belmont, S.S. Day, C. Jennings, A. Johnson, L. Perg, and P.R. Wilcock. 2009. Geomorphic evolution of the Le Sueur River, Minnesota, USA, and implications for current sediment loading. *Management and restoration of fluvial systems with broad historical changes and human impacts: Geological Society of America Special Paper* 451:119-130.

Gran, K.B., N. Finnegan, A.L. Johnson, P. Belmont, C. Wittkop, and T. Rittenour. 2013. Landscape evolution, valley excavation, and terrace development following abrupt postglacial base-level fall. *Bulletin of the Geological Society of America* 125:1821-1894.

Herborg, L., C.L. Jerde, D.M. Lodge, G.M. Ruiz, and H.J. MacIssac. 2007. Predicting invasion risk using measures of introduction effort and environmental niche models. *Ecological Applications* 17(3):663-674.

Hermann, K.K. and R.E. Sorensen. 2009. Seasonal dynamics of two mortality-related trematodes using an introduced snail. *Journal of Parasitology* 95(4):823-828.

Horsch, E.J. and D.J. Lewis. 2009. The effects of aquatic invasive species on property values: evidence from a quasi-experiment. *Land Economics* 85(3):391-409.

Illinois Department of Natural Resources. 2016. *2016 Interim Summary Report: Asian Carp Monitoring and Response Plan*.

Illinois Department of Natural Resources. 2017. *2017 Asian Carp Monitoring and Response Plan*.

Irons, K.S., G.G. Sass, M.A. McClelland, and J.D. Stafford. 2007. Reduced condition factor of two native fish species coincident with invasion of non-native Asian carps in the Illinois River, U.S.A. Is this evidence for competition and reduced fitness?. *Journal of Fish Biology* 71:258-273.

Jennings, C.E. 2007. Overview of the quaternary geological history of the Minnesota River watershed. *Native Plant Communities and Rare Species of the Minnesota River Valley Counties: Minnesota County Biological Survey Biological Report* 89.

Jennings, D.P. 1988. *Bighead carp (Hypophthalmichthys nobilis): A Biological Synopsis* FWS-88 (29). Gainesville, FL: National Fisheries Research Center.

Jhingran, V.G., and R.S.V. Pullin. 1985. *A Hatchery Manual for the Common, Chinese, and Indian Major Carps* 252. WorldFish.

Jiménez-Valverde, A., A.T. Peterson, J. Soberón, J.M. Overton, P. Aragón, and J.M. Lobo. 2011. Use of niche models in invasive species risk assessments. *Biological invasions* 13(12):2785-2797.

Johnson, P.T.J., J.D. Olden, and M.J. Vander Zanden. 2008. Dam invaders: impoundments facilitate biological invasions into freshwaters. *Frontier in Ecology and the Environment* 6(7):357-363.

Kamilov, B.G. and T.V. Salikhov. 1996. Spawning and reproductive potential of the silver carp *Hypophthalmichthys molitrix* from Syr Darya River. *Journal of Ichthyology* 36(8):600-606.

Kirkagac, M. and N. Demir. 2004. The effects of grass carp on aquatic plants, plankton and benthos in ponds. *Journal of Aquatic Plant Management* (42):32-39.

Kokotovich, A. and D. Andow. *Potential adverse effects and management of Silver and Bighead carp in Minnesota: Findings from focus groups* (Working paper).

Kolar, C.S., D.C. Chapman, W.R. Courtenay Jr., C.M. Housel, J.D. Williams, and D.P. Jennings. 2007. *Bigheaded carps: A Biological Synopsis and Environmental Risk Assessment*. Bethesda, MD: American Fisheries Society.

Konradt, A.G. 1965. Methods of breeding the grass carp, *Ctenopharyngodon idella* and the silver carp, *Hypophthalmichthys molitrix*. *FAO Fisheries Report* 4(9):195-204.

Krykhtin, M.L. and E.I. Gorbach. 1981. Reproductive ecology of the grass carp, *Ctenopharyngodon idella*, and the silver carp, *Hypophthalmichthys molitrixi*, in the Amur. *Basin Journal of Ichthyology* 21(2):109-123.

Kucklentz, V. 2017. Rstoration of a small lake by combined mechanical and biological methods. *SIL Proceedings* 22(4):2314-2317

Kulhanek, S.A., A. Ricciardi, and B. Leung. 2011. Is invasion history a useful tool for predicting the impacts of the world's worst aquatic invasive species?. *Ecological Applications* 21(1):189-202.

Lager, W. 2015. Upper St. Anthony lock closing after half a century; blame the carp. *MPR News*, June 08.

Lee, D.P. 2001. Northern Pike Control at Lake Davis, California. *Rotenone in fisheries: Are the rewards worth the risk*: 55-61.

Levine, S. 2017. Possible connectivity of the Little Minnesota River and Lake Traverse. Unpublished manuscript.

Lima-Ribeiro, M.S., S. Varela, J. Gonzalez-Hernandez, G. de Oliveira, J.A.F. Diniz-Filho, L.C. Terribile. 2015. EcoClimate: a database of climate data from multiple models for past, present, and future for macroecologists and biogeographers. *Biodiversity Informatics* 10.

Lobo, J. M., A. Jiménez- Valverde, and R. Real. 2007. AUC: a misleading measure of the performance of predictive distribution models. *Global ecology and Biogeography* 17(2):145-151.

Lodge, D.M. 1993. Biological invasions: lessons for ecology. *Treands in ecology & evolution* 8(4):133-137.

Lohmeyer, A.M. and J.E. Garvey. 2009. Placing the North American invasion of Asian Carp in a spatially explicit context. *Biological Invasions* 11(4):905-916.

Lovell, S.J., S.F. Stone, and L. Fernandez. 2006. The economic impacts of aquatic invasive species: a review of the literature. *Agricultural and Resource Economics Review* 35(1):195-208.

Matsch C.L. and H.E. Wright. 1967. The southern outlet of Glacial Lake Agassiz. *Glacial Lake Agassiz*: 231-244.

McKnight, S.K. and G.R. Hepp. 1995. Potential effect of grass carp herbivory on waterfowl foods. *The Journal of Wildlife Management*: 720-727.

McMahon, R.F. 2002. Evolutionary and physiological adaptations of aquatic invasive animals: r selection versus resistance. *Canadian Journal of Fisheries and Aquatic Sciences* 59 (7):1235-1244.

Minnesota Department of Natural Resources (MN DNR). 2011. *Fishing creates 43,000 Minnesota jobs, $2.8 billion in retail spending*. Available at http://news.dnr.state.mn.us/2011/05/05/fishing-creates-43000-minnesota-jobs-28-billion-in-retail-spending/ (last accessed 21 April 2018).

Minnesota Department of Natural Resources (MN DNR). 2014. *Minnesota Invasive Carp Action Plan*.

Minnesota Department of Natural Resources (MN DNR). 2017. *Minnesota River listed for zebra mussels, invasive carp*. Available at https://www.dnr.state.mn.us/invasive-carp/index.html (last accessed 21 April 2018).

Minnesota Department of Natural Resources (MN DNR). 2018a. *Fish and fishing*. Available at https://www.dnr.state.mn.us/faq/mnfacts/fishing.html. (last accessed March 18, 2018).

Minnesota Department of Natural Resources (MN DNR). 2018b. *Fishes of Minnesota*. Available at https://www.dnr.state.mn.us/fish/index.html. (last accessed March 18, 2018).

Minnesota Department of Natural Resources (MN DNR). 2018c. *Invasive carp*. Available at https://www.dnr.state.mn.us/invasive-carp/index.html. (last accessed March 20, 2018).

Minnesota Department of Natural Resources (MN DNR). 2018e. *Rare Species Guide*. Available at https://www.dnr.state.mn.us/rsg/filter_search.html. (last accessed April 4, 2018).

Morrison, B.J., J.C. Casselman, I.B. Johnson, and D.L. Noakes. 2004. New Asian carp genus (*Hypopthalmichthys*) in Lake Erie. *Fisheries* 29(8):6-7.

Moy, P.B., I. Polls, J.M. Dettmers, D. Chapman, and M. Hoff. 2011. The Chicago sanitary and ship canal aquatic nuisance species dispersal barrier. *American Fisheries Society Symposium* 74:121-137.

MPR News. 2017. DNR: Minnesota's largest invasive carp captured near Redwood Falls. *MPR News*.

Mukhamedova, A.F. 1977. The level of standard metabolism of young silver carp, *Hypophthalmichthys molitrix*. *Journal of Ichthyology* 17:292-298.

Murphy, E.A. and P.R. Jackson. 2013. *Hydraulic and Water-quality Data Collection for the Investigation of Great Lakes Tributaries for Asian Carp Spawning and Egg-transport Suitability*. Reston, VA: U.S. Geological Survey.

Musser, K., S. Kudelka, and R. Moore. 2009. *Minnesota River Basin trends*. Minnesota State University, Mankato, Water Resources Center.

Nagaraju, S.K., R. Gudasalamani, N. Barve, J. Ghazoul, G.K. Narayanagowda, and U.S. Ramanan. 2013. Do ecological niche model predictions reflect the adaptive landscape of species?: a test using *Myristica malabarica* Lam., an endemic tree in the Western Ghats, India. *PLoS One* 8(11):e82066.

Nico, L.G., J.D. Williams, and H.L. Jelks. 2005. *Black carp: Biological Synopsis and Risk Assessment of an Introduced Fish*. Bethesda, MD: American Fisheries Society.

Nico, L.G., and H.L. Jelks. 2011. The black carp in North America: an update. *American Fisheries Society Symposium 74*. Bethesda, MD: American Fisheries Society.

Nikolsky, G.V. 1963. *The ecology of fishes*. New York, NY: Academic press.

Noatch, M.R. and C.D. Suski. 2012. Non-physical barriers to deter fish movements. *Environmental Reviews* 20(1):71-82.

Opuzynski, K. 1967. Comparision of temperature and oxygen tolerance in grass carp (*Ctenopharyngodon idella Val*.), silver carp (*Hypophthalmichthys molitrix Val*.) and mirror carp (*Cyprinus carpio L*.). Państwowe Wydawnictwo Naukowe. Oddział

Opuszynski, K. 1981. Comparison of the usefulness of the silver carp and the bighead carp as additional fish in carp ponds. *Aquaculture* 25(2):223-233.

Opuszynski, K., A. Lirski, L. Myszkowski, and J. Wolnicki. 1989. Upper lethal and rearing temperatures for juvenile common carp, *Cyprinus carpio* L., and silver carp, *Hypophthalmichthys molitrix* (Valenciennes). *Aquaculture Research* 20(3):287-294.

Opuszynski, K. and J.V. Shireman. 1995. *Herbivorous Fishes: Culture and Use for Weed Management*. Boca Raton, FL: CRC Press.

Page, L.M. and B.M. Burr. 1991. *A Field Guide to Freshwater Fishes*. Boston, MA: Mifflin Company.

Perea, J. P. 2002. Asian carp invasion: fish farm escapees threaten native river fish communities and boaters as well. *Outdoor Illinois* 10(5):8.

Peters, L. M., M. A. Pegg, and Ulrich G. Reinhardt. 2006. Movements of adult radio-tagged bighead carp in the Illinois River. *Transactions of the American Fisheries Society* 135(5): 1205-1212.

Peterson, A.T. 2003. Predicting the geography of species' invasions via ecological niche modeling. *The Quarterly Review of Biology* 78(4):419-433.

Peterson, A.T., and C.R. Robins. 2003. Using ecological- niche modeling to predict barred owl invasions with implications for spotted owl conservation. *Conservation Biology* 17(4):1161-1165.

Peterson, A.T., and Y. Nakazawa. 2008. Environmental data sets matter in ecological niche modelling: an example with *Solenopsis invicta* and *Solenopsis richteri*. *Global ecology and Biogeography* 17(1):135-144.

Peterson, A.T., J. Soberón, R.G. Pearson, R.P. Anderson, E. Martínez-Meyer, M. Nakamura, and M.B. Araújo. 2011. *Ecological Niches and Geographic Distributions*. Princeton, NJ: Princeton University Press.

Pflieger, W.L. 1978. Distribution and Status of the Grass Carp (*Ctenopharyngodon idella*) in Missouri Streams. *Transactions of the American Fisheries Society* 107(1):113-118.

Phillips, S.J. 2005. A brief tutorial on MaxEnt. *AT&T Research*.

Phillips, S.J. and M. Dudík. 2006. Modeling species distributions with MaxEnt: New extension and a comprehensive evaluation. *Ecography* 31(2):161-175.

Pimentel, D., L. Lach, R. Zuniga, D. Morrizon. 2000. Environmental and economic costs of nonindigenous species in the United States. *Bioscience* 50(1):53-56.

Pyron, R.A., F.T. Burbrink, and T.J. Guiher. 2008. Claims of potential expansion throughout the US by invasive python species are contradicted by ecological niche models. *PloS One* 3(8):e2931.

Qiao, H., A.T. Peterson, L.P. Campbell, J. Soberón, L. Ji, and L.E. Escobar. 2016. NicheA: creating virtual species and ecological niches in multivariate environmental scenarios. *Ecography* 39(8):805-813.

Qiao, H., J. Soberón, and A.T. Peterson. 2015. No silver bullets in correlative ecological niche modelling: insights from testing among many potential algorithms for niche estimation. *Methods in Ecology and Evolution* 6(10):1126-1136.

Radke, R.J. and U. Kahl. 2002. Effects of a filter-feeding fish [silver carp, *Hypophthalmichthys molitrix* (Val.)] on phyto- and zooplankton in a mesotrophic reservoir: results from an enclosure experiment. *Freshwater Biology* 47:2337-2344.

Raibley, P.T., D. Blodgett, and R.E. Sparks. 1995. Evidence of Grass Carp (*Ctenopharyngodon idella*) Reproduction in the Illinois and Upper Mississippi Rivers. *Journal of Freshwater Ecology* 10(1):65-74.

Rasmussen, J.L. 2002. *The Cal-Sag and Chicago Sanitary and Ship Canal: A Perspective on the Spread and Control of Selected Aquatic Nuisance Fish Species*. Rock Island, IL: U.S. Fish and Wildlife Service, Region 3 White Paper, Fisheries Resources Office.

Ray, W.J. and L.D. Corkum, 1997. Predation of zebra mussels by round gobies, *Neogobius melanostomus*. *Environmental Biology of Fishes* 50(3):267-273.

Robison, H.W. and T.M. Buchanan. 1988. *Fishes of Arkansas*. Fayetteville, AR: University of Arkansas Press.

Romero-Alvarez, D., L.E. Escobar, S. Varela, D.J. Larkin, and N.B. Phelps. 2017. Forecasting distributions of an aquatic invasive species (*Nitellopsis obtusa*) under future climate scenarios. *PloS one* 12(7):e0180930.

Ruebush, B.C. 2011. In-situ tests of sound-bubble-strobe light barrier technologies to prevent the range expansions of Asian carp. PhD diss., University of Illinois at Urbana-Champaign.

Sampson, S.J., J.H. Chick, and M.A. Pegg. 2009. Diet overlap among two Asian carp and three native fishes in backwater lakes on the Illinois and Mississippi rivers. *Biological Invasions* 11(3):483-496.

Sass, G.G, C. Hinz, A.C. Erickson, N.N. McClelland, M.A. McClelland, and J.M. Epifanio. 2014. Invasive bighead and silver carp effects on zooplankton communities in the Illinois River, Illinois, USA. *Journal of Great Lakes Research* 40(4):911-921.

Schramm Jr, H.L. 2017. The fishery resources of the Mississippi River: A model for conservation and management. *Fisheries* 42(11):574-585.

Schrank, S.J. and C.S. Guy. 2003. Competitive interactions between age-0 bighead carp and paddlefish. *Transactions of the American Fisheries Society* 132:1222-1228.

Schrank, S.J., P.J. Braaten, and C.S. Guy. 2001. Spatiotemporal variation in density of larval bighead carp in the lower Missouri River. *Transactions of the American Fisheries Society* 130(5):809-814.

Schroeder, G.L. 1978. Autotrophic and heterotrophic production of micro-organisms in intensely-manured fish ponds, and related fish yields. *Aquaculture* 14(4):303-325.

Semmens, B.X., E. R. Buhle, A. K. Salomon, and C.V. Pattengill-Semmens. 2004. A hotspot of non-native marine dishes: evidence for the aquarium trade as invasion pathway. *Marine Ecology Progress Series* 266:239-244.

Shelton, W.L. and R.O. Smitherman. 1984. Exotic fishes in warmwater aquaculture. *Distribution, biology, and management of exotic fishes*. The Johns Hopkins University Press, Baltimore, Maryland.

Shireman, J.G. and C.R. Smith. 1983. Synopsis of biological data on the grass carp, *Ctenopharyngodon idella* (Cuvier and Valenciennes, 1844). *Food and Aquaculture Organization Synopsis* 135.

Simberloff, D. 1989. Which insect introductions succeed and which fail. *Biological invasions: a global perspective*: 61-75.

Singh, W. 1989. Fecundity of silver carp, *Hypophthalmichthys molitrix* (Val.). *Indian Journal of Animal Sciences*.

Smith, C. 2016. Testing a semi-automated geospatial methodology for floodplain inundation mapping: Case study of the Minnesota River valley. M.S. app, Department of Geography, Minnesota State University, Mankato.

Sobolev, Y.A. 1970. Food interrelationships of young grass carp, silver carp and carp reared jointly in ponds in Belorussia. *Journal of Ichthyology* 10(4): 528-533.

Sparks, R.E., T.L. Barkley, S.M. Creque, J.M. Dettmers, and K.M. Stainbrook. 2010. Evaluation of electric fish dispersal barrier in the Chicago Sanitary and Ship Canal. *American Fisheries Society Symposium* 74:139-161.

Spataru, P., G.W. Wohlfarth, and G. Hulata. 1983. Studies on the natural food of different fish species in intensively manured polyculture ponds. *Aquaculture* 35:283-98.

Spataru, P. and M. Gophen. 1985. Feeding behaviour of silver carp *Hypophthalmichthys molitrix* Val. and its impact on the food web in Lake Kinneret, Israel. *Hydrobiologia* 120(1):53-61.

Stanley, J.G., W.W. Miley II, and D.L. Sutton. 1978. Reproductive requirements and likelihood for naturalization of escaped grass carp in the United States. *Transactions of the American Fisheries Society* 107(1):119-128.

U.S. Fish and Wildlife Service (USFWS). 2012. *The Cost of Invasive Species*.

U.S. Fish & Wildlife Service (USFWS). 2018. *Minnesota: County distribution of federally-listed threatened, endangered, proposed, and candidate species*. Available at https://www.fws.gov/midwest/endangered/lists/minnesot-spp.html (last accessed 21 April 2018).

USGS. 2016. *NAS-Nonindigenous Aquatic Species*. Available at https://nas.er.usgs.gov/viewer/omap.aspx (last accessed 6 December 2016).

Van Dyke, J.M., A.J. Leslie Jr., and J.E. Nall. 1984. The effects of the grass carp on the aquatic macrophytes of four Florida lakes. *Journal of Aquatic Plant Management* 22:87-95.

Verigin, B.V., A.P. Makeyeva, and M.Z. Mokhamed. 1978. Natural spawning of the silver carp *Hypophthalmichthys molitrix*, the bighead carp *Aristichthys nobilis*, and the grass carp *Ctenopharyngodon idella*, in the Syr-Dar'ya River. *Journal of Ichthyology* 18(1):143-146.

Vitousek, P.M., HA. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* 277(5325):494-499.

Weber, M.J. and M.L. Brown. 2009. Effects of common carp on aquatic ecosystems 80 years after "carp as a dominant": Ecological insights for fisheries management. *Reviews in Fisheries Science* 17(4):524-537.

Wiley, M.J., P.P. Tazik, and S.T. Sobaski. 1987. Controlling aquatic vegetation with triploid grass carp. *Illinois Natural History Survey Circular* 57.

Williamson, C.J. and J.E. Garvey. 2005. Growth, fecundity, and diets of newly established silver carp in the middle Mississippi River. *Transactions of the American Fisheries Society* 134(6):1423-1430.

Wisz, M.S., R.J. Hijmans, J. Li, A.T. Peterson, C.H. Graham, A. Guisan, and NCEAS Predicting Species Distributions Working Group. 2008. Effects of sample size on the performance of species distribution models. *Diversity and distributions* 14(5):763-773.

Xie, P. and Y. Chen. 2001 Invasive carp in China's plateau lakes. *Science* 224(5544):999-1000.

Yi, Y., Z. Wang., and Z. Yang. 2010. Impact of the Gezhouba and Three Gorges Dams on habitat suitability of carps in the Yangtze River. *Journal of Hydrology* 387(3):283-291.

Zhang, H., E.S. Rutherford, D.M. Mason, J.T. Breck, M.E. Wittmann, R.M. Cooke, D.M. Lodge, J.D. Rothlisberger, X. Zhu, and T.B. Johnson. 2016. Forecasting the impacts of silver and bighead carp on the Lake Erie food web. *Transactions of the American Fisheries Society* 145(1):136-162.

Zielinski, D.P. and P.W. Sorensen. 2016. Bubble curtain deflection screen diverts the movement of both Asian and common carp. *North American Journal of Fisheries Management* 36(2):267-276.

Zielinski, D.P. and P.W. Sorensen. 2017. Silver, bighead, and common carp orient to acoustic particle motion when avoiding a complex sound. *PloS one* 12(6).