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Combining historic records and multi-criteria habitat suitability analysis for the potential reintroduction of Lake Sturgeon (Acipenser fulvescens Rafinesque) into tributaries of Lake Erie

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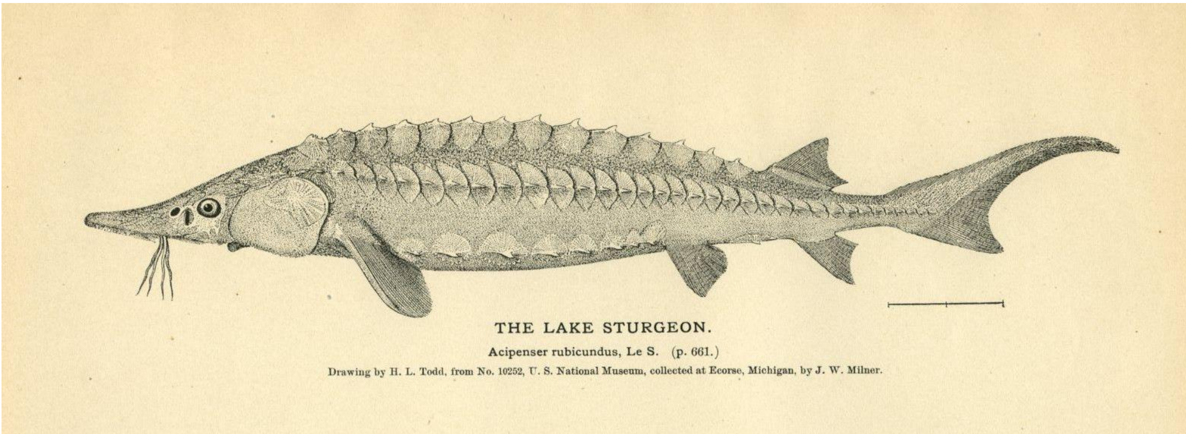

Combining historic records and multi-criteria habitat suitability analysis for the potential reintroduction of Lake Sturgeon (*Acipenser fulvescens* Rafinesque) into tributaries of Lake Erie

A Thesis

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Abstract

Predicting the location and quality of habitat for imperiled species is an increasingly important application of modeling technology. The Lake Sturgeon *(Acipenser fulvescens)* is a widely-extirpated fish of the Laurentian Great Lakes whose recovery is dependent on the availability and connectivity of suitable stream habitat today. This is especially true in Lake Erie, where the largest Lake Sturgeon fishery was once found. I predicted that modern habitat suitability would be dependent on land use legacies from the past 200 years, with western Lake Erie tributaries having less suitable habitat compared to the eastern Lake Erie tributaries. I developed a multi-criteria habitat suitability analysis framework that was applied to two different spatial scales (watershed and stream segment) to predict the location and quality of habitat for spawning adults and juveniles in historically-used U.S. tributaries of Lake Erie. I also tested the transferability of the model framework by applying it to a stream where extant Lake Sturgeon spawn currently: the Black River in northern Michigan. My results suggest that a broad range of habitat qualities exist across the study region, with predictions aligning with several smaller-scale habitat suitability projects in the past in several of the watersheds analyzed here. Most low-scoring watersheds were located to the west, while the highest-scoring watersheds were located to the east, as predicted. The model found a high degree of agreement between the watershed scale and reach scale, suggesting that the framework could be applied at either scale accurately depending on input data availability. The model predicted that the Black River watershed is fairly suitable (40-50% suitable) for Lake Sturgeon, which warrants further investigation and ground-truthing of the model's real-world accuracy given that the Black River is known to be highly suitable for the species. Additional spatially-explicit analysis of these results in the future will aim to reveal patterns in habitat connectivity from river mouth upstream for each watershed. My results can be used on the fine scale by managers seeking to develop local Lake Sturgeon reintroduction and restoration projects but also at the large scale for the purpose of communication and habitat connectivity for the benefit of multiple populations of Lake Sturgeon.

Habitat suitability analysis for the reintroduction of Lake Sturgeon

Introduction

The presence and persistence of a species requires available habitat that provides the needed resources for every stage of its life cycle. Resource managers, ecological researchers, naturalists, and indigenous peoples have assessed and maintained habitat quality for countless species for hundreds of years, with ultimate goals including improved recreational opportunities, preserving a means of sustenance, predicting the impacts of a project, or planning species recoveries and reintroductions for ecological wellbeing. Today, imperiled species are being lost at a staggering rate, and 28% of all assessed species are currently threatened with extinction (IUCN 2022). As global environmental change impacts the distribution of species, habitat modeling (the prediction of habitat conditions using limited data in a model environment) is becoming increasingly important for its capabilities in tackling large spatial scales as well as multiple interacting variables. Researchers and managers are tasked with quickly assessing current environmental trends, and predicting future ones, to make decisions about safeguarding species and their ecosystems, sometimes even in the absence of previous data related to the species' habitat use. As such, developing, assessing, and reporting on modeling methods is tantamount to keeping up with the changing world.

The Lake Sturgeon (Acipenser fulvescens)

The Lake Sturgeon (*Acipenser fulvescens*, Rafinesque 1817) is the largest fish species found in the Great Lakes, with mature adults reaching over two meters in length and nearly 70 kilograms in weight (Egerton 2018). Lacking scales, it has a smooth, streamlined body that is lined with five rows of bony scutes, which decrease in size as the fish grows. Like all Acipenserids, the Lake Sturgeon is a benthivore that feeds on a varied diet of primarily invertebrates (Beamesderfer and Farr 1997, Peterson *et al.* 2007), but in the Great Lakes it also feeds opportunistically on invasive Round Goby and Dreissenid mussels (Bruestle et al. 2019). It can take upwards of 15 to 20 years for adult fish to reach sexual maturity, after which they will migrate from lake to stream habitat to spawn and lay eggs every few years (Bruch *et al*. 2016). Individuals can live well over 100 years if conditions are suitable, though estimating the exact age of a large Lake Sturgeon is difficult (Bruch et al. 2016).

The Lake Sturgeon has a Holarctic lineage with many sister and cousin species distributed across the Northern Hemisphere, including the White Sturgeon (*Acipenser transmontanus*) in the Pacific Northwest and the Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) which sometimes co-occurs with the Lake Sturgeon to the south of its range (Peterson *et al.* 2007). The last glacial retreat and shifting of the giant water bodies that were left behind isolated the Lake Sturgeon to the northeastern portion of North America. Its historic range stretched as far north as the Hudson Bay, as far west as some systems in Alberta, as far east as the outlet of the St. Lawrence River, and as far south as the Mississippi River's mainstem in Louisiana (Baril *et al.* 2017). The Great Lakes have historically served as the center of the Lake Sturgeon's range.

The Lake Sturgeon's varied diet, far-reaching distribution, and status as the largest fish to have ever lived in the Laurentian Great Lakes make it a prime candidate for conservation, and under protection it can serve as an umbrella species for other threatened species in the region (e.g. spawning reefs constructed for Lake Sturgeon have been used by 17 other species of fish: Bennion and Manny 2014). This potential is doubly important given the tumultuous last two centuries for the Lake Sturgeon.

Lake Sturgeon history and conservation

Prior to the colonization of the Americas by Europeans, the people of the Great Lakes region harvested Lake Sturgeon sustainably for more than 2,000 years for its meat, eggs, bones, bladders, oil, and skin (Needs-Howarth 1996, Holzkamm and Waisberg 2004). The Potawatomi, Menominee, Cree, Anishinaabe, and others utilized Lake Sturgeon for practical uses as well as economical purposes, comparable in importance to the fur trade, even well past the 1600s when European trade and colonization began (Holzkamm and Waisberg 2004).

As the domination of the fishery in the Great Lakes "traded" hands from the native peoples to the Europeans, industrialization of the region allowed harvests of many species to skyrocket. However, the Lake Sturgeon was not initially a target catch. Although there had previously been a strong European demand for Lake Sturgeon isinglass for glue, paints, and other uses, the meat and roe were not fashionable foods, and the largest adult sturgeon had the ability to tear holes in fishing nets and release entire hauls (Egerton 2018). In the infancy of the industrialized Great Lakes Region, the Lake Sturgeon was quickly considered a nuisance species. In fact, some bands of fishermen would purposely catch sturgeon simply to pile them on the shore and light them on fire (Peterson *et al.* 2007, Egerton 2018).

By the mid-1800s, more eastern-European immigrants had come to the region, and they brought with them knowledge of how to prepare the meat and eggs of European sturgeon species in ways that were more palatable to the colonials and which benefited from recent advancements in refrigeration that kept raw fish fresh. The Lake Sturgeon was now a desirable catch, but this time the commercialization of the fishery allowed for less-than-sustainable harvests. In the span of approximately two decades, the Lake Sturgeon population of the Great Lakes was fished to near-total extinction, with an annual 4 million lbs. brought to market across the entire Lake Sturgeon range (Regier and Hartman 1973, Baker and Auer 2013, Haxton *et al.* 2014). The transition into the 1900s saw the Lake Sturgeon as an increasingly rare but extremely valuable fish.

People first began to take note of the Lake Sturgeon's decline with concern in the early 1900s. For example, established fisheries expert Livingston Stone published a paper in 1900 detailing his travels to study the spawning habits of the Lake Sturgeon, focusing mainly on the Missisquoi River of Vermont. In this paper, he recounted meetings with fishermen regarding their perceptions of the fish and observations of the types of habitats where Lake Sturgeon have spawned. Additionally, Stone described a study in the Detroit River, Michigan, in which eggs were successfully taken and fertilized but were not successfully reared. Stone concluded that conservation of the Lake Sturgeon fishery should be prioritized now that the population had been thoroughly diminished (Stone 1900). By 1928, commercial fishing of Lake Sturgeon had been banned everywhere except for one area in Canada on Lake St. Clair and within Lake Huron (Peterson *et al*. 2007). Just two hundred years prior, one could supposedly walk along the backs of these large and plentiful fish as their spawning runs jammed streams (Goodman 2019); now, fishermen told stories of lingering, "legendary" monster-sized sturgeon breaking lines and crashing into boats, but only rarely (The Associated Press 1937).

Even in the wake of the fishery's major ban, a new swathe of challenges came with the new century for Lake Sturgeon. Development around the Great Lakes had been occurring since the 1600s, but industrialization had increased more rapidly around this time. Paper mills and other operations polluted waterways, wetlands and marshes were drained for agriculture, and the dredging, damming, and channelization of the lakes and their tributaries all but eliminated habitat for the Lake Sturgeon's entire life cycle (Regier and Hartman 1973). As a result, the Lake Sturgeon did not recover once the fishery was banned; instead, it continued to decline across most of its range even through the mid-1900s (Hartman 1972).

Research improved understanding of the Lake Sturgeon throughout the 1900s but increased in earnest towards the second half of the century, as the mainstream anti-pollution and pro-conservation environmental movements gained steam post-1969. Progress was quick; for example, the first extensive watershed surveys of fish distribution and relative abundance in New York began around the mid-1900s (Carlson 1996), and a restorative management program for Lake Sturgeon was instituted in New York in 1995 (Chalupnicki *et al*. 2011). Harkness and Dymond (1961) published a pivotal comprehensive study on Lake Sturgeon, and this study is still heavily cited in Lake Sturgeon investigations 60 years later (Harkness and Dymond 1961; see Hughes 2002, Collier *et al.* 2021). By 2000, the Lake Sturgeon's ecological status in the Great Lakes was well-documented (Beamesderfer and Farr 1997, Baker and Auer 2013).

Status of the Lake Sturgeon today

The Lake Sturgeon has still not experienced substantial recovery in the Great Lakes as a whole, two decades into the 21st century. It remains listed as threatened, endangered, or extinct across the Great Lakes, particularly in Lake Erie, where the peak of the fishery once was (Bruch et al. 2016). A comparison of conservation designations across all Great Lakes fish species resulted in the Lake Sturgeon receiving the highest number of conservation rankings; it was the only species on a list of 83 to receive rankings in every U.S. state covering its range, as well as Ontario, from both NatureServe and the local jurisdictions (Mandrak and Cudmore 2013). This level of concern was attributed to historic overexploitation and, more-contemporarily, habitat fragmentation and the effects of lampricide on juveniles.

Many other studies have concluded that habitat availability and quality are the main remaining limitations to Lake Sturgeon repopulation, based on habitat use patterns by remnant populations and the accessibility of these habitats across the region (e.g., Koonce *et al*. 1996, Auer 1996, Holtgren and Auer 2004). According to historic fishery records, the Lake Sturgeon had first declined in marsh and stream habitats, with lingering populations remaining in certain areas of the main Lakes, such as a population in eastern Lake Erie that continued to spawn through the end of the 1800s (Regier and Hartman 1973). However, no contemporary in-lake hotspots for non-spawning Lake Sturgeon have been identified in Lake Erie despite at least two spawning populations existing there today (Welsh *et al.* 2017). This may suggest that habitat-use in tributaries is comparatively important for these remaining populations in Lake Erie, and possibly beyond, though perhaps in insufficient amounts to improve numbers over time (Baker and Auer 2013). Regardless of where remaining Lake Sturgeon (and their habitats) exist, depletion-based stock-reduction analysis has estimated that enough time has passed since the fishery ban for the species to have been able to repopulate to levels that would allow fishing at maximum sustainable yield (in Lake Erie), yet the Lake Sturgeon remains rare, and thus habitat availability is most likely the culprit (Sweka *et al.* 2018).

Knowns and unknowns: movement and habitat use

Remaining Lake Sturgeon populations in the Great Lakes have allowed us to learn much about their needs and how they interact with available resources in modern times, including other populations. The Lake Surgeon is potamodromous, and populations maintain a wide range of movement within their ranges, yet a degree of spawn-site fidelity has been repeatedly reported (Auer 1996, Barth *et al*. 2011, Boase *et al.* 2014). This homing trait is beneficial for the growth and recovery of populations in between spawning events, especially since individuals go several years between spawning events; however, some straying in sturgeon populations is important for the metapopulation genetics of the region and allows for the colonization of new or previously-extirpated tributaries (Smith *et al.* 2002, Donofrio *et al.* 2017). Analysis of the greater Lake Michigan Lake Sturgeon populations has suggested that historic gene flow and contemporary straying rates were nonrandom in Lake Michigan, and those individuals that did stray successfully reproduced (Homola *et al.* 2012 in Donofrio *et al.* 2017). Analysis of Lake Erie populations has shown that, currently, the populations are genetically semi-independent, with the two “end” populations (Detroit, MI, and Niagara, NY) preferring to spawn in the rivers (or Lake St. Clair/St. Clair River in the case of the Detroit population) rather than in the main body of Lake Erie (Nichols *et al.* 2003, Kessel *et al.* 2017), in agreement with the Lake Erie hotspot investigation published around the same time that found no habitat hotspots in the lake proper (Welsh *et al.* 2017). This means that the two Lake Erie populations do not exchange genetic information between each other, which is atypical of other nearby populations. Intrapopulation variation in movement behavior seems to be a general Lake Sturgeon feature in unfragmented landscapes (Kessel *et al.* 2017), so “de-fragmenting” the available habitat in Lake Erie may be the solution to the lack of interpopulation mingling of the two Lake Erie groups.

Lake Sturgeon also interact with different habitat resources at different life stages (Auer, 1996; Koonce *et al.* 1996; Holtgren and Auer 2004). Water temperature is the main cue that triggers adults to migrate and spawn in the Spring, usually in April or May in the Great Lakes (Harkness and Dymon 1961, Baril *et al*. 2017). Spawning adults in rivers select coarse substrate beds, with large interstitial spaces to provide refugia for eggs and larvae (Holtgren and Auer 2004, Baril *et al.* 2017). Some months later, larvae drift downstream (also cued by temperature; Smith and King 2005) and settle on mixed sand and gravel beds, where they remain until large enough to leave the natal stream and enter the lake body (though some populations remain in the streams their entire life cycles; Baker and Auer, 2013; Holtgren and Auer, 2004). Immature adult Lake Sturgeon will spend time moving between the lake and the rivers until sexual maturity, which can take up to a decade (Holtgren and Auer 2004, Baker and Auer 2013). Prior to spawning, winter staging occurs, in which adults linger at the mouth of the spawning stream; this stage is the least-utilized part of the Lake Sturgeon life cycle in terms of quantifying habitat needs (Daugherty *et al*. 2007). At all stages except egg and larva, the sturgeon feed on benthic macroinvertebrates found in the substrate (Holtgren and Auer 2004).

Studies of the interplay between life stages and habitat use have revealed patterns. For example, it seems that not all habitat characteristics are consistently necessary for all life stages of the Lake Sturgeon (Daugherty *et al.* 2007); specifically, depth, velocity, and substrate use tend to be similar between older juvenile (ages 3 to 9 years old) and adult Lake Sturgeon (older than 10), though older juveniles used slightly shallower depths and slightly slower velocities than the adults (eddy refugia) in one study (Hughes 2002). The main difference in habitat use between young juveniles ("young-of-year," <500 mm in length) and adults appears to be substrate size more than any other habitat parameter (Baril *et al*. 2017). With this in mind, the presence of abundant spawning habitat does not indicate or facilitate an abundance of juvenile habitat, and vice-versa. For example, an abundance of suitable habitat for young Lake Sturgeon was found in the North Channel of the St. Clair River, but very little suitable spawning adult habitat was found (Kreiger and Diana 2017). A similar trend was found for multiple tributaries of Lake Michigan (Daugherty *et al.* 2007); as a result, initial recruitment is low in these systems.

The gestalt of habitat knowledge for Lake Sturgeon is that several key habitat parameters are important across their lives: repeatedly, the "big four" habitat needs are substrate size, water temperature, channel discharge or velocity, and channel depth (Boase *et al*. 2014, Baril *et al.* 2017). Substrate size has already been discussed here as important for various life stages, and temperature has already been described to be the most important cue for phenological events. Like salmonids, Lake Sturgeon spawn and drift in dynamic, fast-flowing waters (Holtgren and Auer 2004, Smith and King 2005, Baril *et al.* 2017), which is another reason why coarse substrates with large interstitial spaces are required for the security of eggs. Finally, depth is the variable with the most contention of the big four, since high variability is seen across populations (Chiotti *et al.* 2008 in Baker and Auer 2013, Boase *et al.* 2014, Baril *et al*. 2017, Dimitry Gorsky, personal comm.); in fact, while Lake Sturgeon can reach huge sizes such that shallow water would not facilitate easy travel, Lake Sturgeon have been found in waters as shallow as one meter deep or less (Hughes 2002, Manny and Kennedy 2002; Baril *et al.* 2017).

Other habitat parameters are only rarely investigated or reported as important indicators of Lake Sturgeon success. For example, water "quality" (related to either water chemistry parameters or turbidity) seems to be comparatively unimportant to Lake Sturgeon, as stream populations occur in habitats with a variety of chemical quality (see Manny and Kennedy 2002). Similarly, benthic community quality (i.e., diversity or quality of macroinvertebrate foodstock) is less explored as a predictor of suitable Lake Sturgeon habitat, likely because Lake Sturgeon are diet generalists that will feed on a variety of prey (Holtgren and Auer 2002).

Many studies have focused on the habitat use of individual populations of Lake Sturgeon across its modern distribution, but few have collated these ranges of habitat parameters into a summary for the entire species. Baril *et al*. (2017) published the most comprehensive habitat summary for Lake Sturgeon, with ranges and averages of various habitat parameters for several regions, including the Great Lakes, and showed that regional differences exist for the habitat ranges of populations. The authors designed their study for the explicit purpose of aiding in the development of habitat suitability models for Lake Sturgeon, which involve using spatial data on habitat parameters to identify locations that may be highly suitable for a particular species' needs (Baril *et al.* 2017). As it is increasingly clear that habitat quality and connectivity are the roadblocks to Lake Sturgeon recovery, the next step for many managers and researchers is to use habitat suitability modeling techniques to locate suitable habitats in the real world.

Habitat suitability analysis

As briefly mentioned already, habitat modeling is the prediction of real-world habitat conditions based on limited data in a digital (but still often spatially-explicit) workspace. One form of habitat modeling employs Ian McHarg's suitability assessment framework, which is a means of mapping the forms of relevant environmental factors and then overlaying them to locate areas with the greatest potential (or risk) for a given ecological goal, such as installing a low-harm wind farm, developing a green space for a metropolitan area, or reintroducing an extirpated species to a region (Daniels 2019). Habitat suitability modeling (HSM) has several benefits for those with limited time and funding to locate, assess, and potentially improve site(s) for the reintroduction of species. For one, most HSM techniques are based upon multi-criteria decision-making methods, allowing for the consideration of several important factors at once (Saaty 1996; Malczewski 2000). Further, since the framework is built before the analysis is run, each individual input (or factor criterion) in an HSM can be altered while leaving the others constant, such that the relative impact of each input on the results can be investigated and changed through different runs of the model, based on the goal and what is known about habitat requirements (Collier *et al*. 2021). Finally, HSM modeling is spatially-explicit, which means that both the inputs and the output of the model can be mapped for ease of final interpretation; features such as total suitable patch area (or simply "habitat availability") and the proximity of suitable patches to one another (or "habitat connectivity or accessibility") can be visualized (Malczewski 2000, Lord *et al.* 2019, Collier *et al.* 2021).

The spatial aspect of HSMs is also important for the freedom of project scaling and transferring; only spatially-explicit HSMs allow for empirical assessment of the predictive performance of the model across spatial scales (Haxton *et al.* 2008). Further, studies have demonstrated how erroneous inferences can be made when there is a mismatch between study scale and the scale at which Lake Sturgeon populations are naturally structured (Haxton *et al*. 2015). Dittman *et al.* (2015) hypothesized that the scale of their HSM in the St. Regis River of New York was of a different scale compared to the dynamic-habitat selection of an individual Lake Sturgeon, and they would have been able to alter the scale of their model based on fish habitat selection were it not for the small sample size of Lake Sturgeon caught in their study. Other studies have been able to successfully scale-down their HSMs using habitat-use data from the local extant Lake Sturgeon population (Haxton *et al*. 2008, Daugherty *et al.*, 2007), and, overall, large-scale habitat suitability indices that have been parameterized for specific regions or systems can also be accurately transferable to other locations in lieu of local Lake Sturgeon populations (Kreiger *et al*. 2018, Baril *et al.* 2017). The robustness of HSMs for spatial scaling and transferring is quite a boon, particularly given that experts have long suggested that habitat connectivity or adjacency should be stressed over individual habitat enhancement for Lake Sturgeon (Auer 1996).

HSMs for Lake Sturgeon around Lake Erie

Lake Sturgeon-focused habitat suitability modeling has already been applied across the Great Lakes, including the U.S. states bordering Lake Erie. In New York, Hughes (2002) completed the first assessment of Lower Niagara River Lake Sturgeon, whereas previously the only means of assessing this remnant population was via anecdotal information. That study involved quantifying habitat use (depth, current velocity, and substrate) by the population for the purpose of developing an HSM. Later, Neunhoff *et al*. (2018) used casual, qualitative habitat suitability assessment based on another HSM to search for a Lake Sturgeon spawning bed in eastern Lake Erie and the headwaters of the Niagara River, with focus on depth, velocity, and substrate; in doing so, they discovered a population of spawning adults and viable egg beds. As already discussed, Dittman *et al*. (2015) completed a post-reintroduction assessment of habitat use in the St. Regis River of New York, which is a tributary of the St. Lawrence River connecting Lake Ontario to the Gulf of St. Lawrence; they took note of, specifically, the depth and substrate type occupied by each individual they caught, as well as the biometrics of each individual to assess how they had adjusted to the system post-reintroduction.

In Michigan, the St. Clair-Detroit River (SC-DR) System has the largest remaining population of Lake Sturgeon in the Great Lakes, a legacy of retaining access to most if not all of its historic range (Kessel *et al*. 2017). As such, the system has been the subject of several habitat based investigations. Boase *et al.* (2014) assessed habitat use versus availability in the North Channel of the St. Clair River (using depth and substrate). Kreiger and Diana (2017) assessed the North Channel of the St. Clair River using four criteria: substrate, invertebrate density, depth, and benthic velocity. Bennion and Manny (2014) completed an HSM for the general SC-DR system, focusing on only depth and velocity for the purpose of identifying substrate beds that could be improved. Outside of the SC-DR system, few other Michigan tributaries have been investigated; Daugherty *et al.* (2007) quantified the habitat availability in five tributaries of Lake Michigan, using three criteria: substrate, depth, and gradient. Dean *et al.* (2020) also investigated various tributaries of Lake Michigan for Lake Sturgeon and other migratory species, though the final report has not yet been published.

While Ohio has the largest U.S. portion of Lake Erie shoreline, fewer HSMs have been developed for Ohio tributaries. Collier's thesis (2018) was a habitat suitability index (HSI) developed for the Maumee River, where Lake Sturgeon are extirpated, and it was the first study to evaluate habitat for the reintroduction of Lake Sturgeon into any Lake Erie tributary. This HSI considered three criteria: substrate, depth, and velocity. Since then, managers of other locales in Ohio have developed interest in reintroduction into other historically-used tributaries, including the Cuyahoga River and the Sandusky River, while managers of the Maumee have already released two cohorts of juvenile Lake Sturgeon (Markey 2018).

Finally, Pennsylvania has the smallest portion of Lake Erie shoreline of the four U.S. bordering states, and it is generally considered inaccessible to Lake Sturgeon (Timothy Wilson, personal comm.). No HSMs have been completed within Pennsylvania tributaries, but some nearshore habitat has been assessed, with poor findings (Regional Science Consortium 2013).

Lake Sturgeon HSM gaps in knowledge, synthesis

There are still several gaps in the Lake Sturgeon HSM literature. Despite the number of studies described thus far, less than 25% of all sturgeon research models published between 1996 and 2012 were spatially-explicit, and the highest percentage of the spatially-explicit sturgeon models were designed for the northwest region of North America, for the White Sturgeon (Jaric *et al*. 2014). Of the published habitat studies for Lake Sturgeon, smaller spatial scales (focused on one or multiple portions of an individual river) have been considered more often than larger spatial scales (Daugherty *et al.* 2007, Haxton *et al.* 2008). Habitat assessments at the whole-watershed have been described as “large-scale mapping investigations” (Bennion and Manny 2014), while very few multi-system investigations or regional summaries have been published (but see Daugherty *et al.* 2007 and Baril *et al*. 2017). Finally, although HSMs consider multiple habitat needs, most Lake Sturgeon HSIs have focused on locating habitat for specifically the juvenile life stage, with focus only recently shifting towards spawning habitat for reintroduction projects, now that it is clear that there are few active juvenile sites (Baril *et al*. 2017).

Baril’s thesis (2017) found that, after completing a habitat suitability index, the previously-placed artificial spawning sites were in unsuitable areas for Lake Sturgeon, underpinning a potential drawback of not completing a spatially-explicit habitat assessment prior to selecting locations for restoration. Similarly, several studies have observed some degree of correspondence between HSM suitability scores and Lake Sturgeon catch rate post-reintroduction into study streams (Haxton *et al*. 2008, Dittman *et al.* 2015). With these findings in mind, a knowledge gap can be filled; there is a need for a multi-criteria, multi-scale, and multi-life stage habitat suitability model for Lake Sturgeon that summarizes suitability across a larger spatial scale, such as a lake-wide scale. There is also a need to develop a framework for a Lake Sturgeon habitat suitability model framework that can be scaled-up or scaled-down depending on the research need, with minimal loss of predictive accuracy. Completing such a project would have the benefit of aiding in the prioritization of systems and sites for connective restoration, with the goal of successfully reintroducing Lake Sturgeon into several locations across the region, to increase gene flow and the colonization of habitats.

Objectives

The goal of this thesis was to design and complete a multi-criteria, multi-scale habitat suitability analysis for tributaries historically used by Lake Sturgeon in Lake Erie, USA. This project was completed using spatially-explicit criteria in a Geospatial Information System (GIS) environment; the criteria selected were based on the most well-documented habitat needs for Lake Sturgeon. An additional goal was to assess the suitability of habitat for needs at multiple life stages of the Lake Sturgeon, namely both juvenile and spawning adult, as these are the life stages that are found most often in tributaries.

Once a habitat suitability analysis was completed for all of the tributaries of interest, the results were compared on a watershed-by-watershed basis. The watersheds were ranked on a scale of highest total suitability to lowest total suitability to make recommendations to local managers aiming to design Lake Sturgeon reintroduction projects. Watersheds with high total suitability may require little habitat restoration prior to reintroduction, whereas watersheds with low total suitability may require targeted restoration to improve habitat quality and connectivity prior to reintroduction, though the spatially-explicit results would also allow managers to investigate specific areas within their watersheds to see where (and why) certain suitability scores are assigned.

Predictions

Generally, an HSM is designed to output a range of predicted suitability or “feasible alternatives.” I expected to see a range of suitability, even within this collection of historically-suitable tributaries, based on current and legacy effects of land use in this region. Legacy effects of historic land use likely limit the suitability of watersheds in Lake Erie today. I expected that the Ohio tributaries would be less suitable than New York tributaries, since the eastern portion of Lake Erie avoided much of the agricultural and industrial development that occurred in coastal Ohio. I also expected that, overall, the watersheds in this study region would be less suitable than another reference system that currently has a spawning Lake Sturgeon population, the Black River in northern Michigan, which flows into Lake Huron.

Methods

Literature search and model development

The first facet of this project involved a historic records search to identify all U.S. tributaries of Lake Erie that were previously documented as providing habitat for Lake Sturgeon. Using library databases and internet browser searches, I obtained newspaper articles, government reports, blog posts, and personal communications with experts referencing known or suspected Lake Sturgeon sightings or catches in tributaries of Lake Erie. A total of 22 tributaries across all four U.S. states bordering Lake Erie were initially isolated as potential watersheds of interest (Appendix 1). After further investigation and communication with experts, three tributaries were removed from the list due to the low confidence in their historic and contemporary suitability: Walnut Creek (PA), Twelvemile Creek (PA), and Sixteenmile Creek (PA). Further, the inlet (Detroit River, MI) and outlet (Niagara River, NY) of Lake Erie were removed, since much of the influence on the instream habitat of their systems comes from Lake St. Clair and Lake Erie, respectively, more so than from the surrounding watershed (Kessel *et al*. 2017). Thus, a total of 16 Lake Erie watersheds were used (Figure 1). Using this list, all relevant watersheds and subwatersheds (HU10) were extracted from the United States Geological Survey's national Watershed Boundary Dataset (WBD; USGS, 2013). All streams within these watersheds were represented by pre-digitized vector-line data developed by McKenna *et al.* (2014).

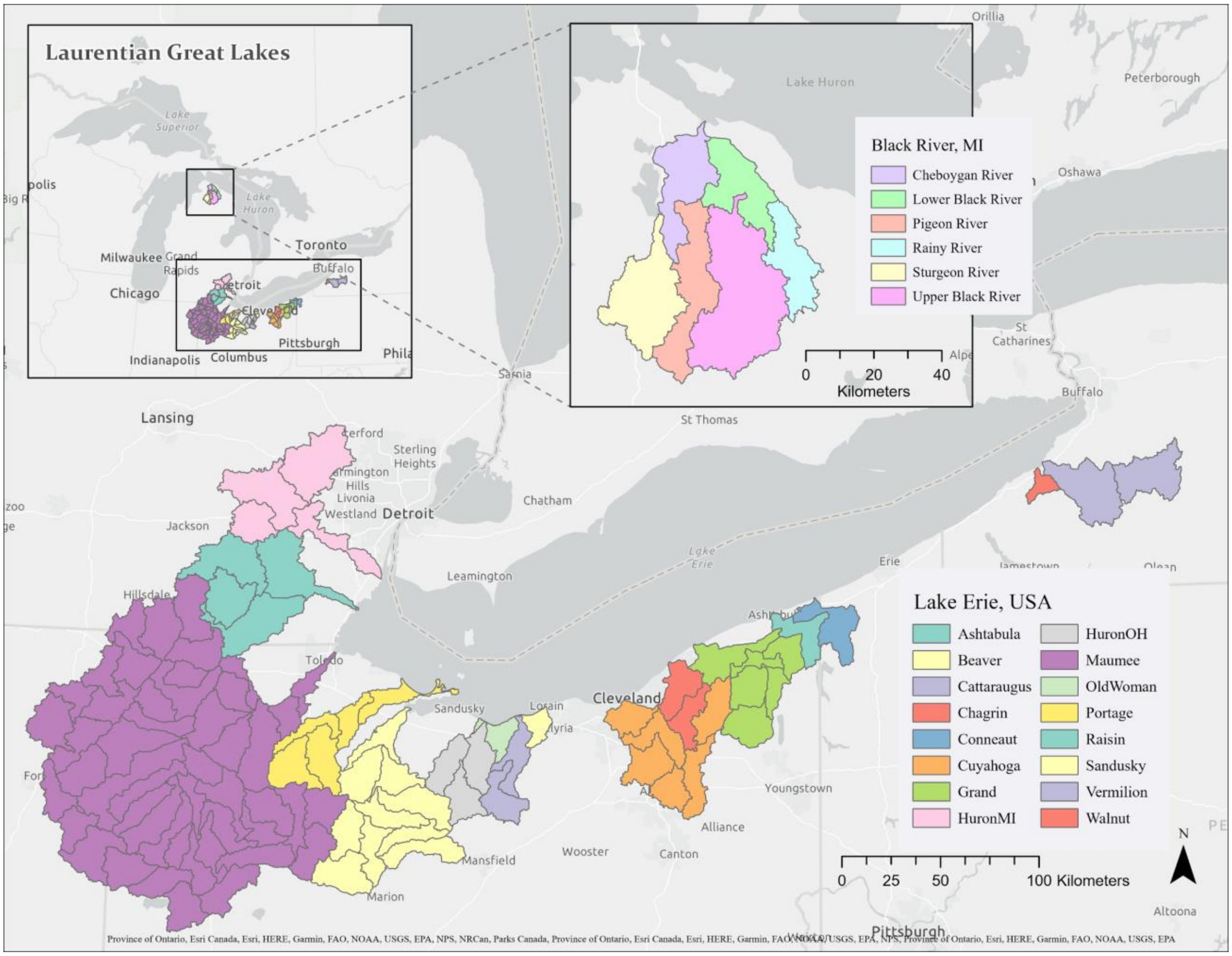


Figure 1. Historically-used U.S. tributaries of Lake Erie considered in this analysis, with the reference system, the Black River in northern Michigan (Lake Huron) inset.

A second literature review was completed to make a list of potential habitat needs to be used as criteria in the analysis. The most widely-documented habitat parameters of Lake Sturgeon in this literature search were collated and preliminarily ranked in terms of importance and/or level of documented knowledge (Appendix 2). Since one facet of this project is considering multiple spatial scales, part of this literature search was dedicated to finding documented watershed-scale surrogates to (or factors that inform) stream-scale habitat parameters (Appendix 3). From this set of relationships, large-scale data sources could be identified to represent stream-scale habitat needs for the entire study region. Spatial data representing the Lake Sturgeon habitat needs at two different scales (watershed/landscape and reach/stream segment) were mined or derived from preexisting data sources (Appendix 4). In particular, the reach-level data were provided by the authors McKenna *et al.* (2014) while most of the watershed-level data were downloaded from the

Habitat suitability analysis for the reintroduction of Lake Sturgeon

United States Geological Survey (USGS), United States Fish and Wildlife Service (US FWS), and the Multi-Resolution Land Characteristics Consortium (MRLC) data repository sites. To reduce redundancy, only one dataset was used for each habitat criterion, and no derived dataset was used twice.

Habitat suitability analysis workflow

Once the derived datasets were obtained, they were loaded into a GIS environment (ArcGIS Pro ver. 2.7, *Esri*, Badlands, CA, USA) and given the same projected coordinate system (NAD 1987 UTM Zone 17N). Per best practice in spatial MCDM analysis, input criteria datasets should not be reclassified into suitability ranks until all unusable or restricted values are removed (Malczewski 2000). In this case, the dataset areas outside of the watersheds of interest contributed values to the dataset that would not be investigated, so those values were removed by clipping each input dataset to the extent of the watersheds of interest using the trimmed USGS Watershed Boundary Dataset (WBD) as a mask.

The clipped datasets were then explored using univariate statistics to determine the ranges of values for each input criterion. A rank table was developed based on those ranges as well as knowledge of Lake Sturgeon population ranges in other areas of the Great Lakes (Appendix 6; Figs. 2-3; Baril *et al.* 2017). A common ranking scale of 1 (least suitable) to 5 (most suitable) was used because the intermediate values 2, 3, and 4 could illustrate the gradient of suitability seen in real-world environments (i.e., 1 = very unsuitable, 2 = slightly unsuitable, 3 = moderately suitable, 4 = slightly suitable, 5 = very suitable). I felt that this was more realistic than a Boolean scale (0 = unsuitable, 1 = suitable) or shorter ranking scale (1 = unsuitable, 2 = neutral, 3 = suitable). The ranking scheme was applied to the input criteria using a reclassification tool and geometric intervals in the GIS environment; geometric interval was chosen as the scaling method since the input data ranges were not normally-distributed and were skewed by an abundance of replicate values (Frye 2007), so each rank had approximately the same number of values once the scaling was applied.

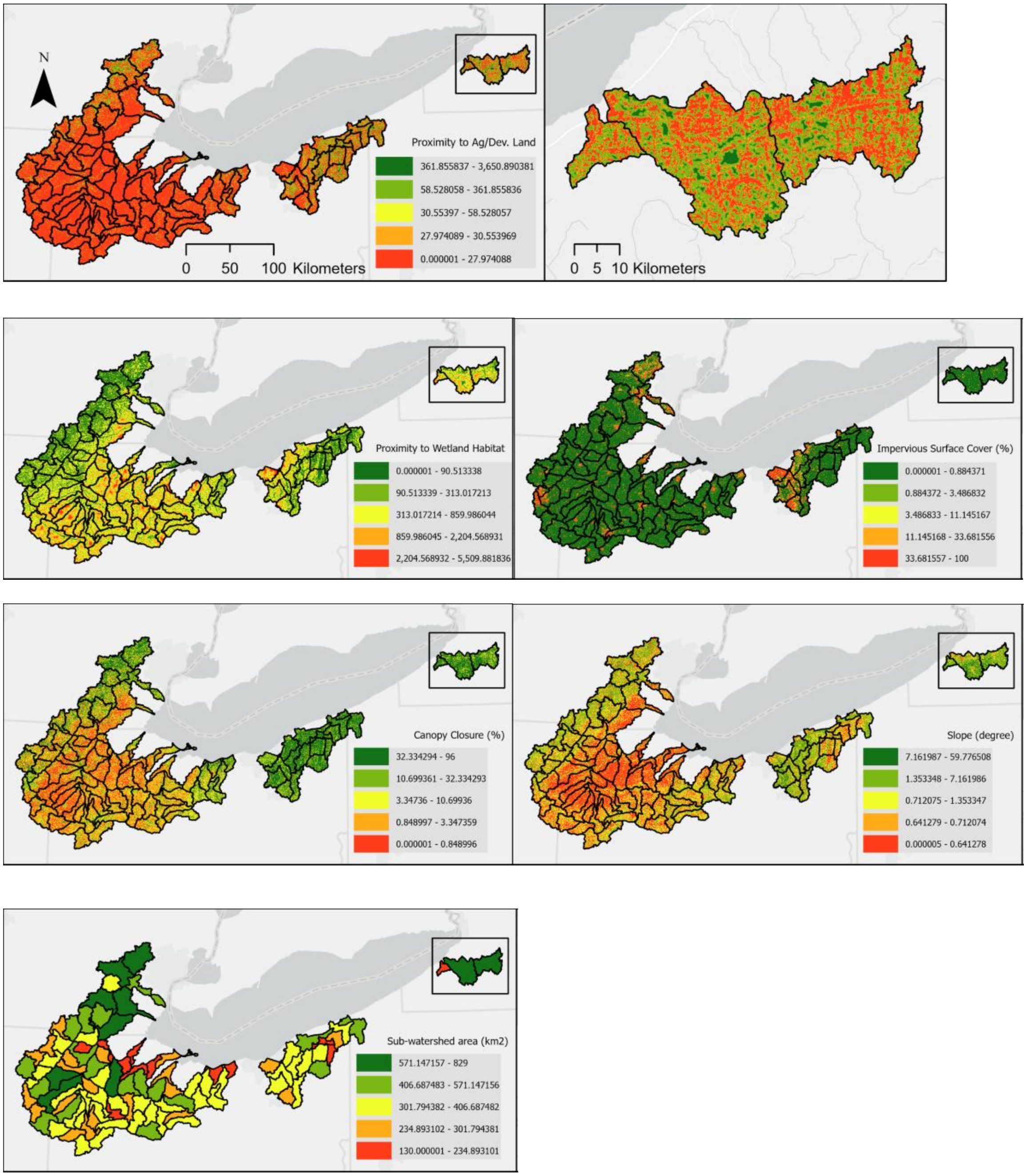


Figure 2. Ranked input criteria at the watershed level with inset of NY tributaries (Cattaraugus, Walnut) at closer scale.

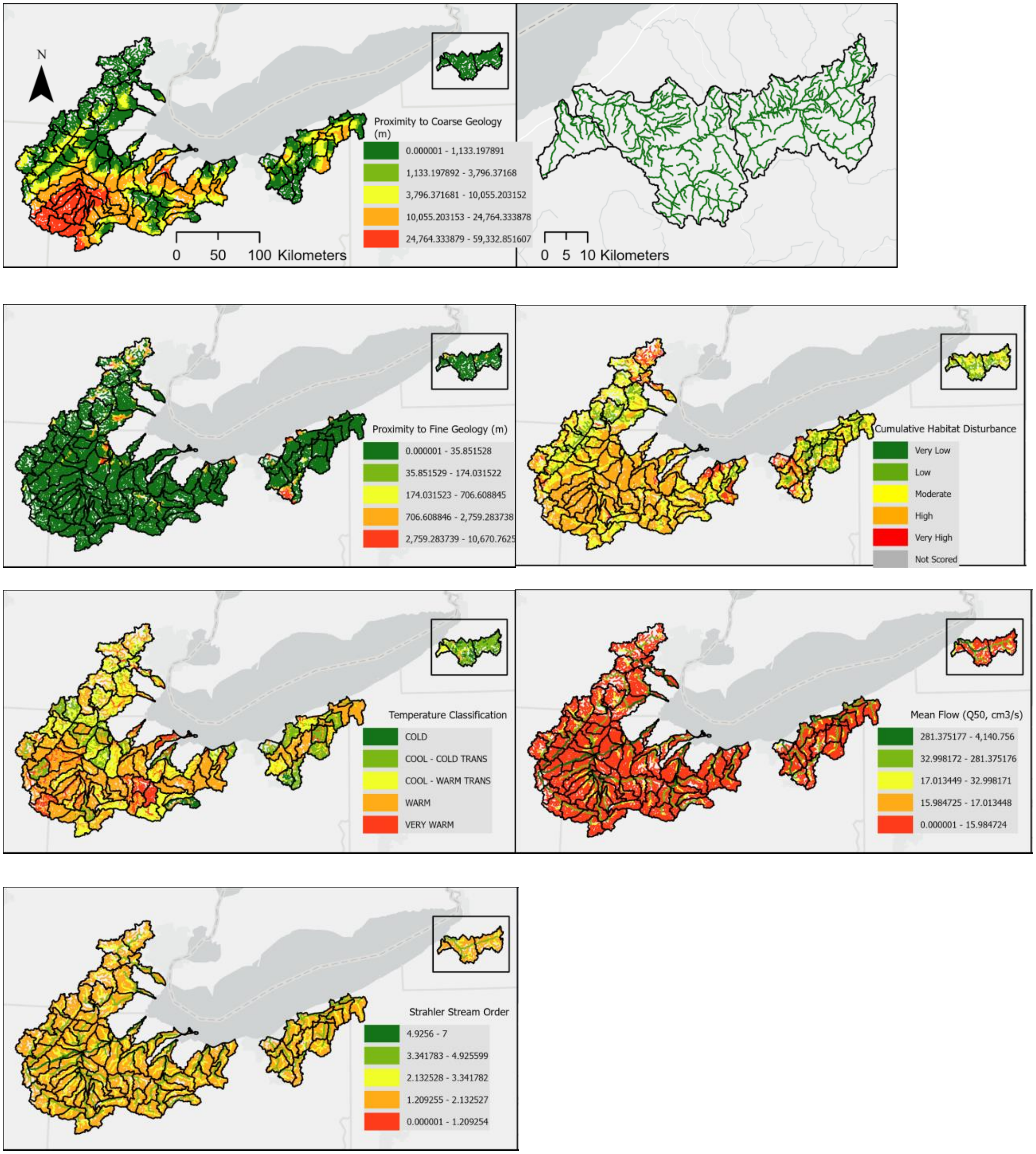


Figure 3. Ranked input criteria at the reach level with inset NY tributaries (Cattaraugus, Walnut) at closer scale.

To account for differences in relative importance among the habitat criteria, a survey was administered to Lake Sturgeon habitat experts that asked respondents to list the six habitat criteria in order of least to most important for Lake Sturgeon success. The responses to this survey were collated and used to determine a “master order of importance.” This list was used as reference as the criteria weights were calculated using a pairwise comparison matrix, following the framework of analytical hierarchy process (AHP) in multi-criteria decision-making (MCDM; Saaty 1996; Malczewski 2000) (Appendix 5). Several versions of the matrix were created, all with consistency ratios (CRs) below the ideal threshold of 1.24 for a matrix of six (Saaty 1996).

Each weight scheme was combined with the ranked input criteria using weighted linear combination (WLC) as follows: each input criterion was multiplied by its respective weight in decimal form, and then all weighted inputs were combined by simple addition (Saaty 1996; Malczewski 2000). This process is shown in the equation:

$$HSA = ((weight\ of\ crit1/100) * ranked\ crit1) + \ldots ((weight\ of\ crit6/100) * ranked\ crit6)$$

The HSA model was run separately for the watershed level and the reach level, but the same process was used for both scales (i.e., the watershed-level data were combined in one version, and the reach-level data were combined in another version, though the latter involved first converting all input criteria from vector-lines to raster-lines before ranking, weighting, and combining). The first passes of the models applied equal weights to all criteria (16.6%), meaning each input variable had equal influence on the results, and subsequent passes applied the weighing scheme shown in Appendix 6. The final weight scheme developed had the best CR value, 0.037, and was therefore selected to be the final version of the weighted model. A “reversed” version of this final weight scheme (the highest-weighted variable instead being weighed the least, and vice versa) was also applied to one version of the model as a form of sensitivity analysis.

The output from the WLC process is a composite map showing the combined suitability scores of each 30 x 30 m pixel in the study region (Figs. 6-10). These final scores were then converted back into the common integer scale of 1 through 5 using geometric intervals for ease of interpretation. A log-likelihood G-test was used to compare the proportion representations for the final scores at the reach vs. watershed scale for the equally-weighted and relative-weighted outputs, and to compare the distribution of final scores for the equally-weighted and relative-weighted outputs within the reach or watershed scale (i.e., four distribution comparisons).

Comparing to the Black River, MI

The results were compared to a non-Erie system that is known to have a spawning Lake Sturgeon population: the Black River in northern Michigan. The same methods were applied to the Black River watershed, first constructing the ranking table based on the data ranges in the Black River (Fig. 4, Appendix 7), and then a second pass using the same ranking schemes as were used from the Lake Erie data ranges (Appendix 6, 8), in order to determine whether the “high suitability” results that were meant to predict high Lake Sturgeon success in Lake Erie would reflect real-world Lake Sturgeon success; in other words, the goal was to assess whether the Erie model correctly predicted that the Black River watershed is highly suitable for Lake Sturgeon. Note that the shapes of the two large lakes in the watershed, one being Black Lake, were removed from the input watershed-level datasets to avoid ranking data that did not truly contribute to the landscape data for the watershed.

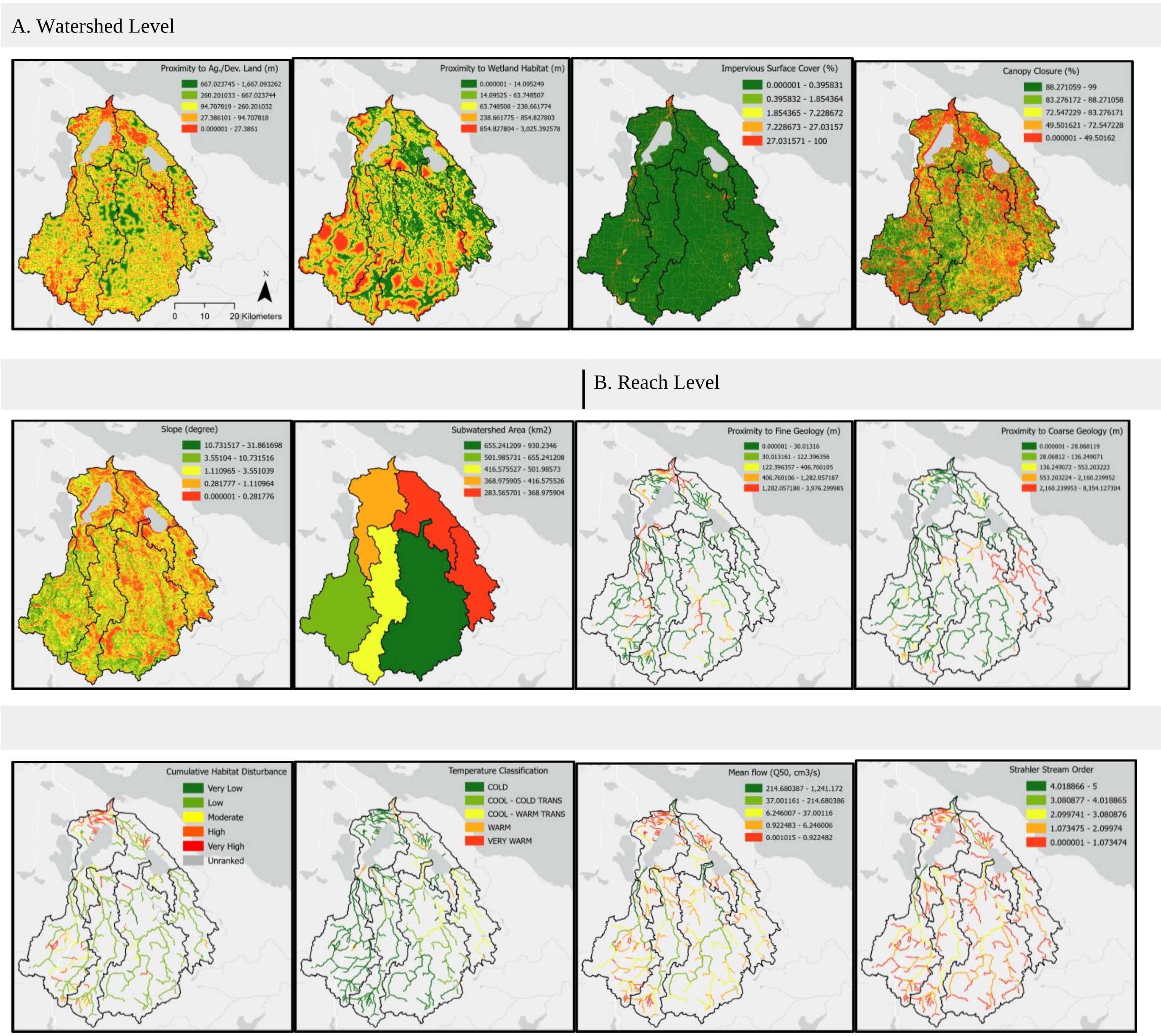


Figure 4. Ranked input criteria at the watershed (A) and reach (B) levels for the Black River, MI, based on Black River data ranges.

Comparing between watershed- and reach- level

To assess the power of the model for transferring across spatial scales, the final scores at the watershed-level and reach-level models were compared by taking the absolute value of the difference between the scores of each reach and the watershed pixel overlaying each reach. Differences of 0, 1, or 2 implied that there was agreement between the watershed-level results and the reach-level results, while differences of 3 or 4 implied that there was disagreement in the watershed- and reach-level results.

Results

Weighted versus unweighted model - Erie

The proportions of the final suitability scores (1-5) differed between the equally-weighted and relatively-weighted models (Fig. 5). Applying the relative weight scheme increased the amount of overall highly-suitable habitat (score 5) slightly at both scales (14.7% → 15.9% at the watershed level; 15.6% → 18.7% at the reach level; Fig. 5.) but also had varying effects on the proportions of the four other rank scores (scores 1-4). The output distributions for equally-weighted vs relatively-weighted scores at the watershed scale were significantly different ($G = 35.6$, $df = 4$, $P < 0.001$), but the output distributions were not significantly at the reach scale ($G = 3.8$, $df = 4$, $P = 0.436$). In other words, the identity of the weight scheme (whether equally weighted or relatively-weighted) did not have a significant effect on the final score proportions for the reach scale, but it did influence the final score proportions at the watershed scale.

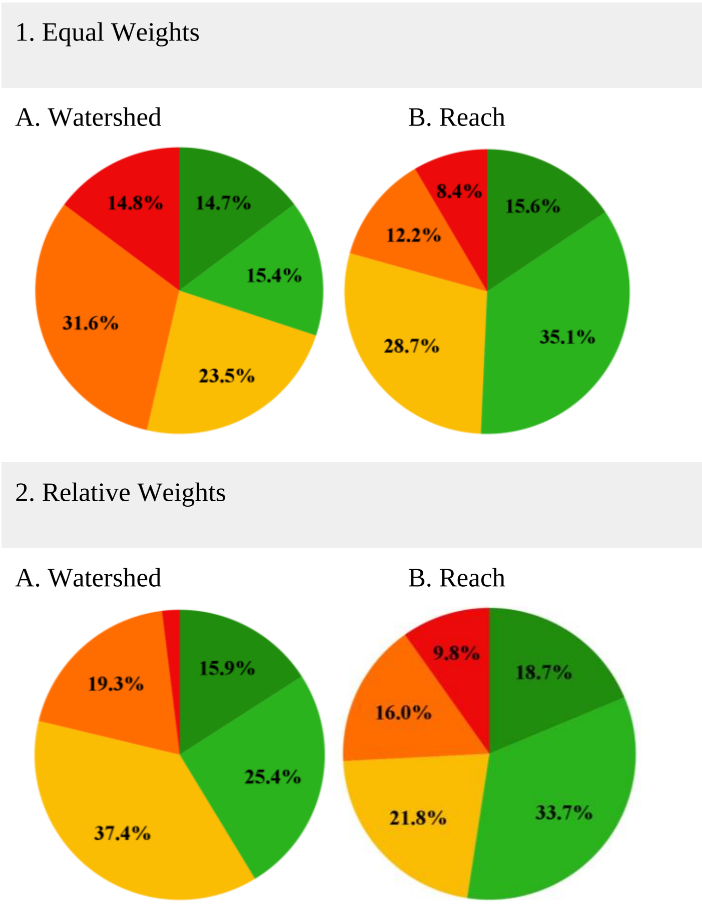
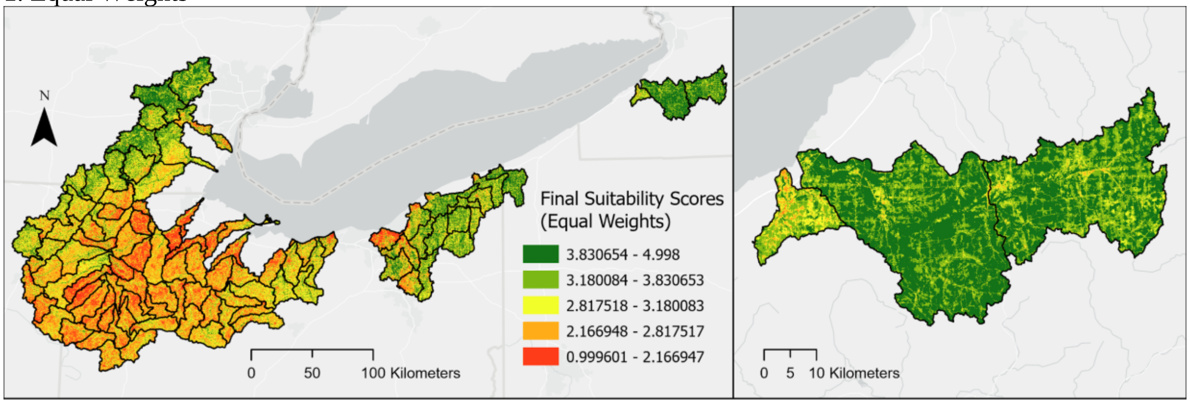


Figure 5. Proportions of final suitability rankings for the total Lake Erie study region at two scales (watershed and reach), from an equal-weight and a relative-weight model.

The spatial distribution of the final scores between the equally-weighted and relatively weighted models were more similar to each other. For both weights schemes and both scales, the lowest suitability scores were mostly aggregated around the Ohio tributaries to the southwest at both scales and both weight schemes, while the Michigan and New York tributaries to the north and east had overall higher suitability scores (Figs. 6, 7).

1. Equal Weights



2. Relative Weights

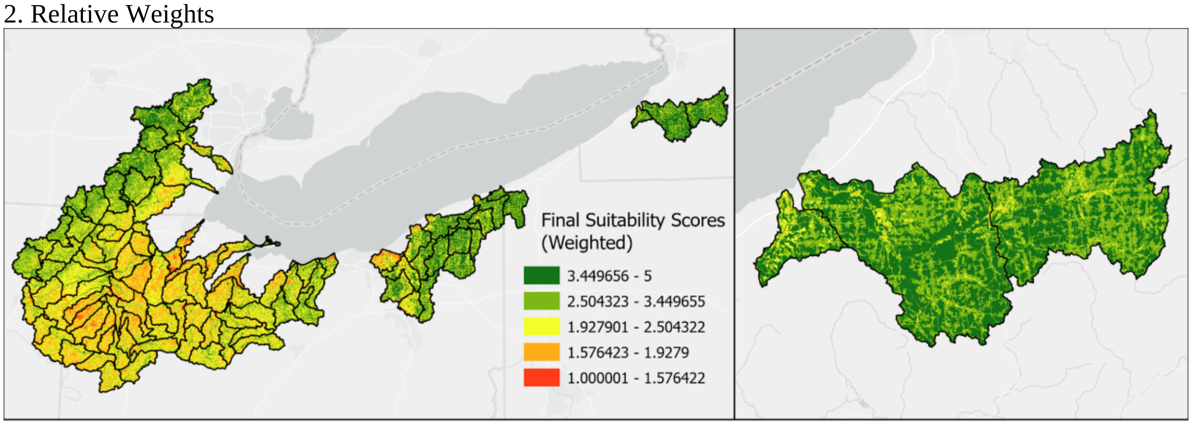


Figure 6. Final suitability scores at the watershed level for Lake Erie, with equal weights applied (1) and the relative weight scheme applied (2).

When comparing between the results of the two spatial scales by using a visual inspection of the maps, it appears that the final scores are much more distinctly aggregated at the reach level (Fig. 7) compared to at the watershed level (Fig. 6), likely owing to the high weight (38.3%) of the highly-segregated coarse geology input criterion, whereas the ranks of the corresponding watershed input criterion (ag./dev. land) were less distinctly segregated (Fig. 3).

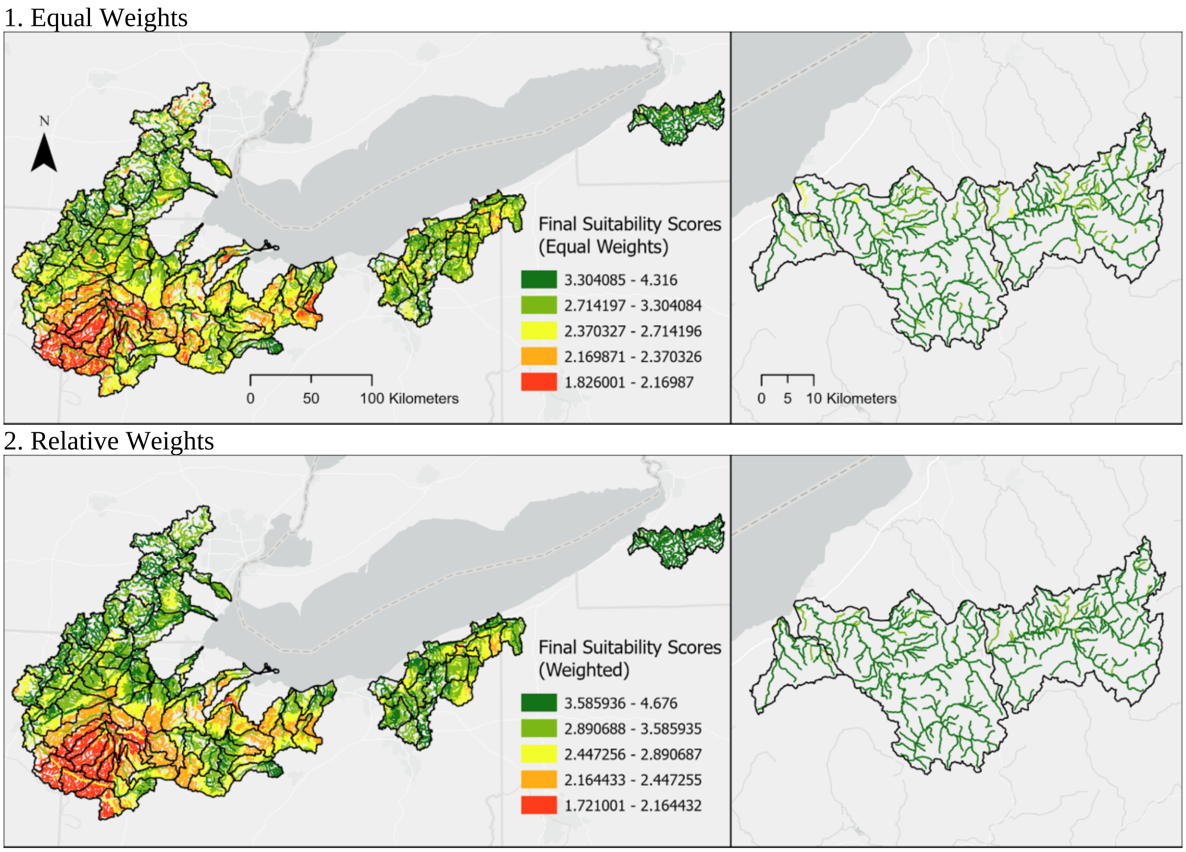
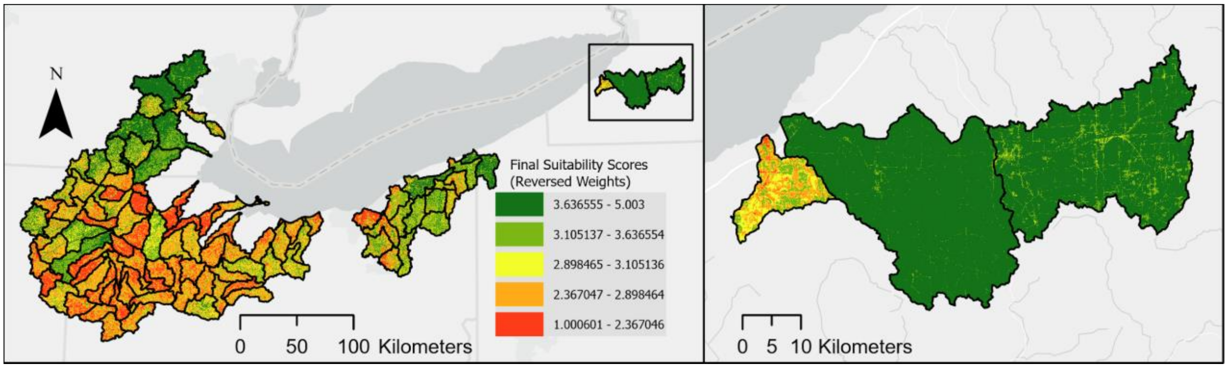


Figure 7. Final suitability scores at the reach level for Lake Erie, with equal weights applied (1) and the relative weight scheme applied (2).

When the relative weight scheme was reversed, the distribution of the final scores was more clustered by subwatershed at the watershed scale, owing to the higher weight on the subwatershed input criterion (5.7% → 38.3%) compared to both the equally-weighted and relatively-weighted models, though a similar pattern can still be seen where low scores are congregated in the southwestern Ohio tributaries and higher scores are congregated to the north and east (Fig. 8). The same can be true for the reach-level results of the reverse-weight model (Fig. 8).

A. Watershed



B. Reach

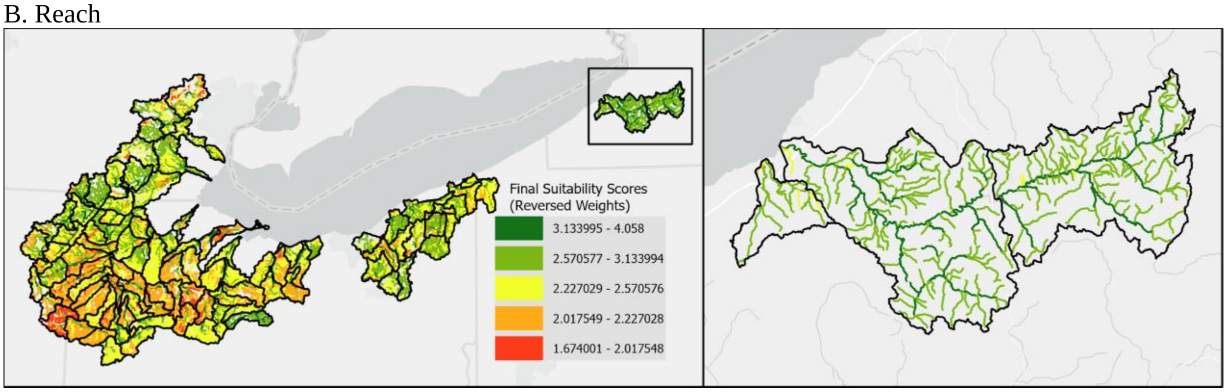


Figure 8. Final suitability scores for the watershed (A) and reach (B) scales in 16 Lake Erie tributaries when the relative weight scheme was reversed.

The distribution of final score proportions was quite different between the watershed and reach scales under the reserved weight scheme (Fig. 9, Table 1; G = 31.4, df = 4, P <0.001), with score 5 habitat (highest suitability) comprising 9.2% of the study region at the watershed scale but 19.2% at the reach scale.

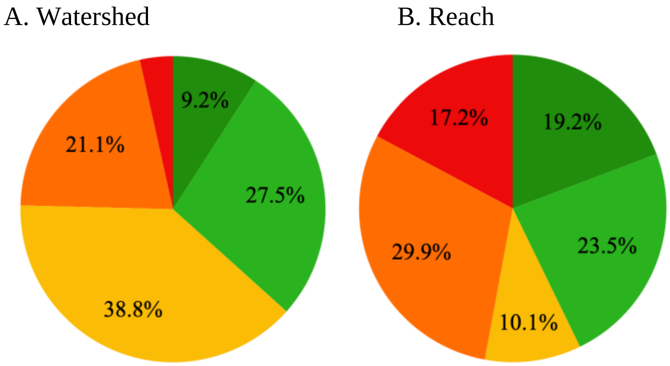


Figure 9. Proportions of final suitability rankings for the total Lake Erie study region at two scales (watershed and reach), from the reversed relatively-weighted model.

Final weighted model results - individual tributaries

Breaking down the final suitability scores at both scales using the relatively-weighted model results showed a range of total suitable (scores 4 and 5 together) and highly-suitable (score 5 only) habitat availability by area (Table X). The watershed with the highest overall suitability across both scales was Cattaraugus Creek, NY, which was predicted to have 93.7% suitability (52.9% highly suitable) at the watershed level and 100.0% suitability (92.9% highly suitable) at the reach level. The watershed with the lowest overall suitability across both scales was the Portage River, which was predicted to have 14.9% suitability (5.2% highly suitable) at the watershed level and 30.3% suitability (2.3% highly suitable) at the reach level. Notable deviations from the agreement between reach and watershed suitability included Old Woman Creek (13.7% highly suitable at the watershed level vs 0.0% highly suitable at the reach level), the Ashtabula River (78.7% suitable at the watershed level but only 33.8% suitable at the reach level), and the Cuyahoga River (56.3% suitable at the watershed level but 93.1% suitable at the reach level).

Table 1. Summary of suitable (scores 4 and 5) and highly-suitable (score 5 only) habitat coverage by watershed in Lake Erie.

A. Relatively-weighted scheme results

		Watershed Level		Reach Level	
State	Watershed	% Suitable (4+5)	% Highly Suitable (5)	% Suitable (4+5)	% Highly Suitable (5)
	Total (16 tributaries)	41.3	15.9	52.4	18.7
NY	Cattaraugus Creek	93.7	52.9	100	92.9
OH	Conneaut Creek	90.1	51.6	84.2	23.1
NY	Walnut/Silver Creek	79.8	46.9	100	87.8
OH	Ashtabula River	78.7	43.8	33.8	11.0
OH	Grand River	78	43.2	52	8.2
MI	Huron River (MI)	75.4	34.9	94.9	38.8
OH	Chagrin River	63	32.4	77.4	29.0
OH	Cuyahoga River	56.3	26.9	93.1	35.8
MI	River Raisin	55.8	16.8	88.6	39.8
OH	Vermilion River	55.1	17.3	24.0	5.9
OH	Old Woman Creek	41	13.7	53.8	0.0
OH	Beaver Creek	40.5	16.5	97.5	25.9
OH	Huron River (OH)	37.9	9.9	22.7	1.9
OH	Maumee River	25.8	6.3	40.5	12.1
OH	Sandusky River	24	5.6	41.2	10.5
OH	Portage River	14.9	5.2	30.3	2.3

B. Reverse-weighted scheme results for the whole study region

	Watershed Level		Reach Level	
	% Suitable (4+5)	% Highly Suitable (5)	% Suitable (4+5)	% Highly Suitable (5)
Total (16 tributaries)	42.8	19.2	36.64	9.2

Black River - results, model assessments, and comparisons to Lake Erie

Habitat suitability analysis for the reintroduction of Lake Sturgeon

Using the same methods as were used to develop the model for Lake Erie, while using the data ranges from the Black River, yielded similar results as the Lake Erie model. A range of habitat qualities were predicted across the subwatersheds of the Black River. The Upper Black River and Lower Black River subwatersheds (see Fig. 1), where the Black River Lake Sturgeon population spawns, had differing amounts of suitable scores between them, with the upper subwatershed having large clusters of highly-suitable habitat and the lower subwatershed having more clusters of less-suitable habitat (Fig. 10). Also notable was the fact that the outlet of the watershed was ranked poorly in all four versions of the Black River model (Fig. 10).

Comparing final score proportions for each spatial scale (watershed-to-watershed and reach-to-reach) between the two weight schemes showed that the watershed-level score proportions were significantly different from each other ($G = 11.59$, $df = 4$, $P = 0.021$), whereas the reach-level score proportions were similar to each other ($G = 7.18$, $df = 4$, $P = 0.126$). In other words, the identity of the weight scheme applied had a significant effect on the final score proportions at the watershed level but not the reach level.

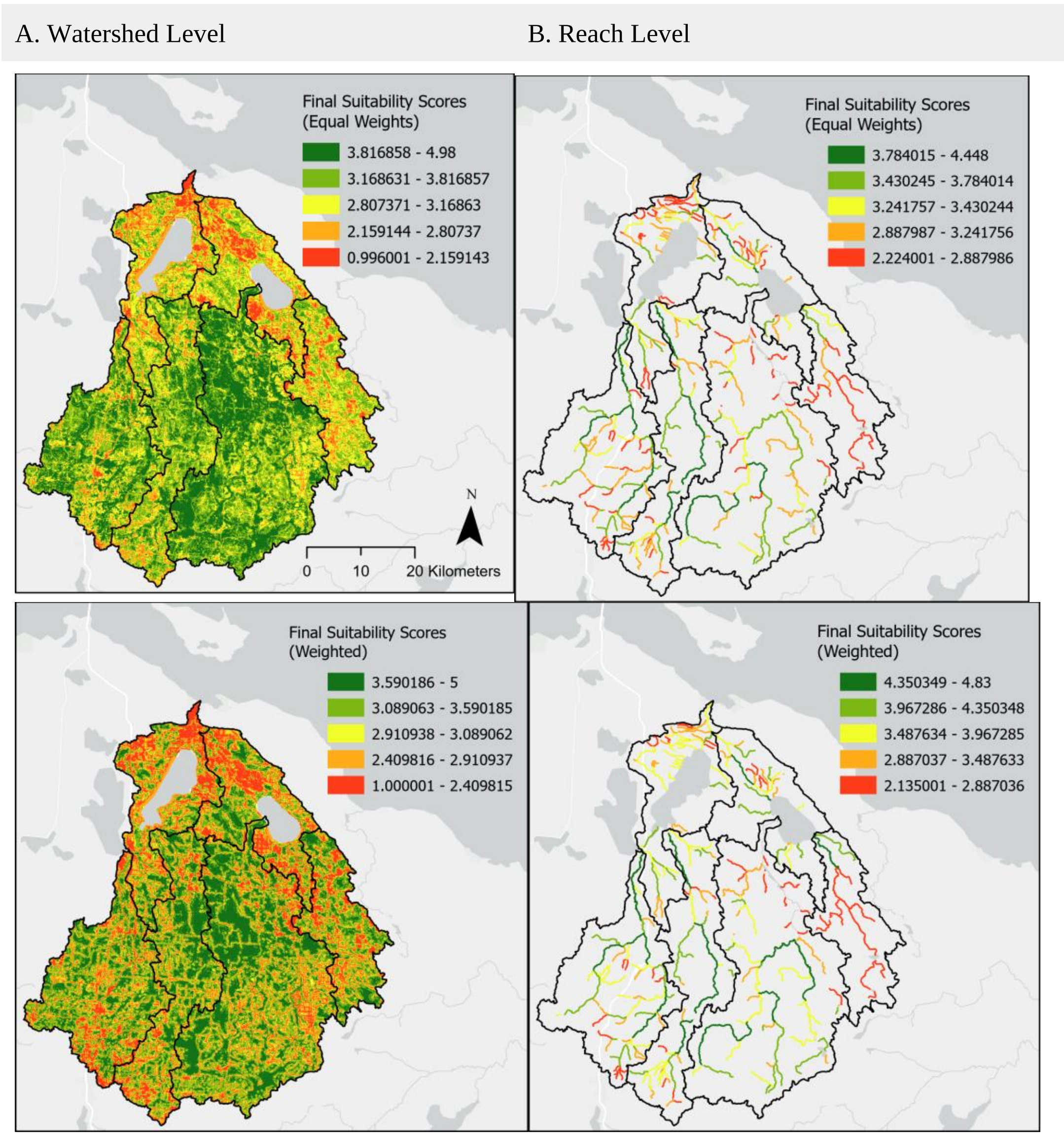


Figure 10. Final suitability scores (equally-weighted and relatively-weighted) at the watershed (A) and reach (B) level for the Black River, MI, based on Black River data ranges.

Using the ranking ranges from the Lake Erie tributaries on the Black River did not significantly change the final suitability score distributions, spatially. As in the original Black River models, the outlet of the watershed was ranked poorly in all four versions using the Lake Erie ranks (Fig. 11). Further, the Upper Black River subwatershed had large congregations of highly-suitable patches and reach-segments in all four models, while the Lower Black River subwatershed had more apparent regions of unsuitable patches and segments (though the mainstem appears highly suitable at the reach level compared to its surrounding landscape suitability; discussed later).

A. Watershed Level B. Reach Level

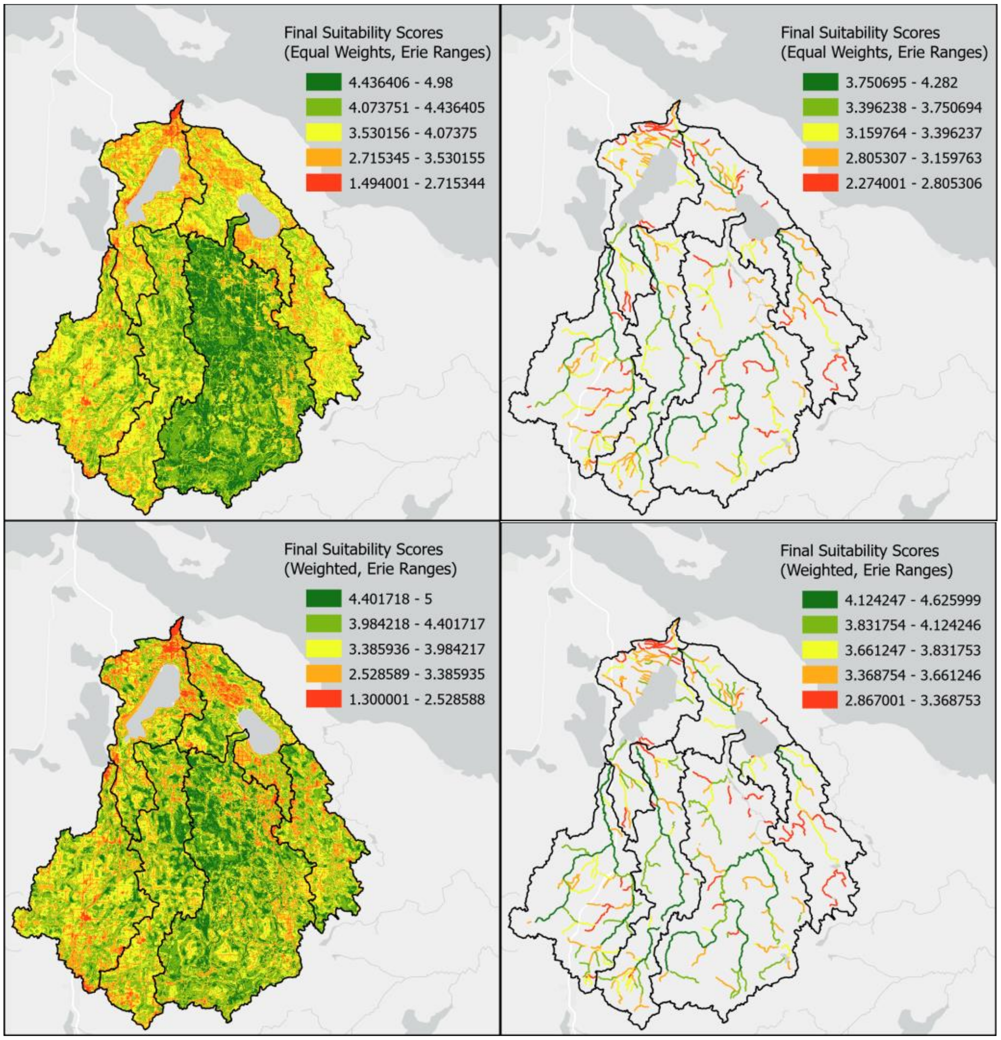


Figure 11. Final suitability scores (equally-weighted and weighted) at the watershed (A) and reach (B) levels for the Black River, MI, based on Lake Erie input ranks.

The original Black River-range model predicted a greater proportion of suitable habitat compared to the Lake Erie-range model for the same study region, comparing between either spatial scale or weight scheme (Fig. 12) The Lake Erie version of the Black River model had similar final score proportions when the two weight schemes (equally-weighted versus relatively weighted) were compared to each other, at both the watershed scale (G = 2.34, df = 4, P = 0.674) and reach scale (G = 6.97, df = 4, P = 0.137).

Figure 12. Summary of final suitability scores for the Black River watershed, based on the model created using Black River data ranges (top) and the model using Lake Erie data ranges (bottom).

The final weighted Black River suitability models were both comparable to moderately ranked watersheds in the Lake Erie model, such as the Cuyahoga River, the River Raisin, and the Vermilion River (Tables 1, 2). Total watershed suitability somewhat agreed with total reach suitability for both the Black River-range model (54.2% suitable watershed vs. 39.9% suitable reach; 22.1% highly suitable watershed vs. 18.5% highly suitable reach) and the Lake Erie-range version of the Black River model (47.4% suitable watershed vs. 45.1% suitable reach; 12.6% highly suitable watershed vs. 22.7% highly suitable reach) (Table 2). For specifically the Upper and Lower Black River subwatersheds (relatively-weighted, BR ranges), suitability was higher across the board for the Upper Black River at both scales and lower across the board (except for 4+5 suitability at the reach level) for the Lower Black River (Table 2).

Table 2. Summary of suitable (scores 4 and 5) and highly-suitable (score 5 only) habitat coverage in the Black River watershed based on Black River data ranges and Lake Erie data ranges (both relatively-weighted), as well as specifically the Upper and Lower Black River subwatersheds (BR ranges, relatively-weighted only).

Model	Watershed level		Reach level	
	% Suitable (4+5)	% Highly Suitable (5)	% Suitable (4+5)	% Highly Suitable (5)
Black River - BR ranges	54.2	22.1	39.9	18.5
Black River - Erie ranges	47.4	12.6	45.1	22.7
Upper Black River only	64.6	31.2	42.9	22.9
Lower Black River only	37.3	11.2	42.3	9.25

Comparing between spatial scales

For the Lake Erie tributaries, the (aspatial) G-test on the distribution of final score proportions showed that, for both the equally-weighted and relatively-weighted models, the score proportions were not the same between the watershed and reach scales (equally-weighted: G = 19.13, df = 4, P = 0.0007; relatively-weighted: G = 11.48, df = 4, P = 0.0216) (Fig. 5). In other words, under both weight schemes, the watershed and reach final score proportions were significantly different from each other. However, comparing the final suitability scores between the reach and watershed scales in a spatially-explicit manner showed high agreement for both the equally-weighted and the relatively-weighted model (Fig. 13). The areas with the lowest agreement between scales appear to be in the Ohio tributaries, namely in the Maumee watershed and to some degree in the eastern Ohio tributaries, such as the Grand and Ashtabula Rivers. Unranked reaches (those that could not be compared between reach and watershed scale due to model error) accounted for only 19 of the 188,218 stream segments assessed in both models.

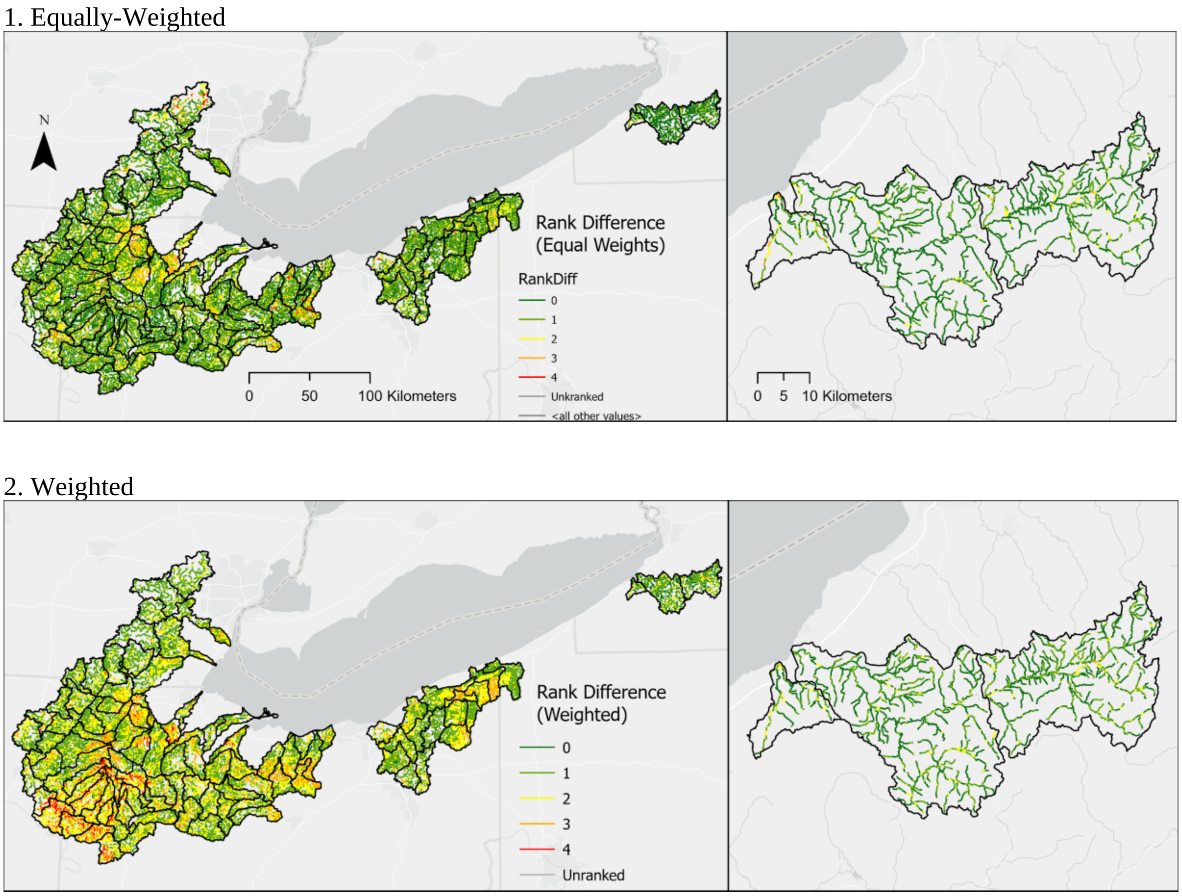


Figure 13. Difference in watershed- and reach-level suitability scores for equally-weighted (A) and weighted (B) Lake Erie model.

The mean difference in ranks between scales was 0.975 for the equally-weighted model and 0.983 for the relatively-weighted model. A difference of 1 was the most common occurrence for both models, and a difference of 0 (total agreement) was the second-most common occurrence for both models (Fig. 14).

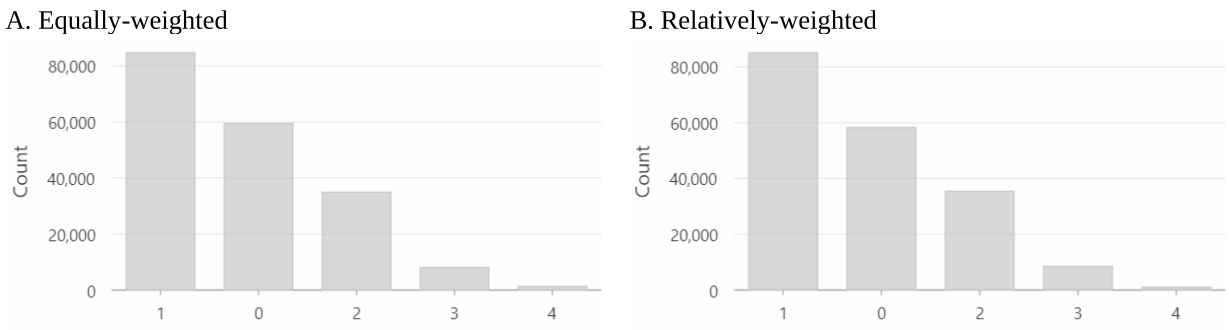


Figure 14. Histograms of rank differences for the total Lake Erie study region for the equally weighted (A) and relatively-weighted (B) models. Count refers to the number of stream segments in the total study region.

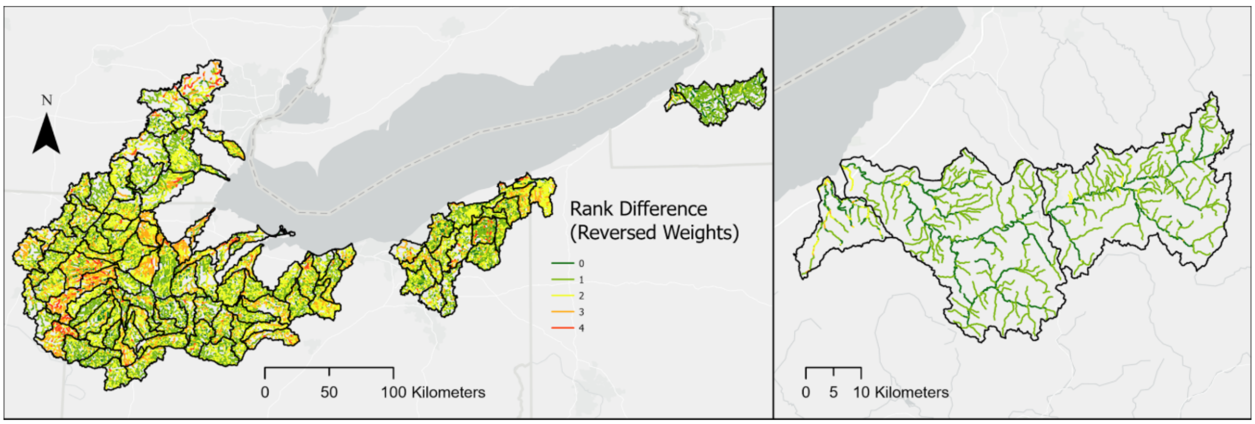


Figure 15. Difference in watershed- and reach-level suitability scores for the reversed relatively-weighted model for Lake Erie model.

As in the equally-weighted and relatively-weighted models, the reverse-weighted model mainly differed by a score of 1 in terms of final scores for the watershed and reach scales, while a difference of 0 (total agreement) lagged far behind as the second-largest proportion of the study region (Fig. 16). The mean difference in final scores between the two spatial scales in this model was 1.09, slightly greater than those of both the equal and relative models.

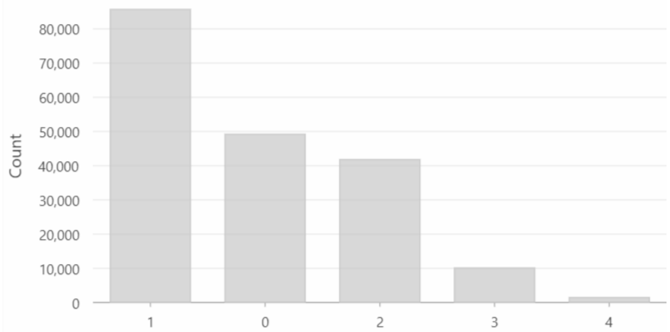


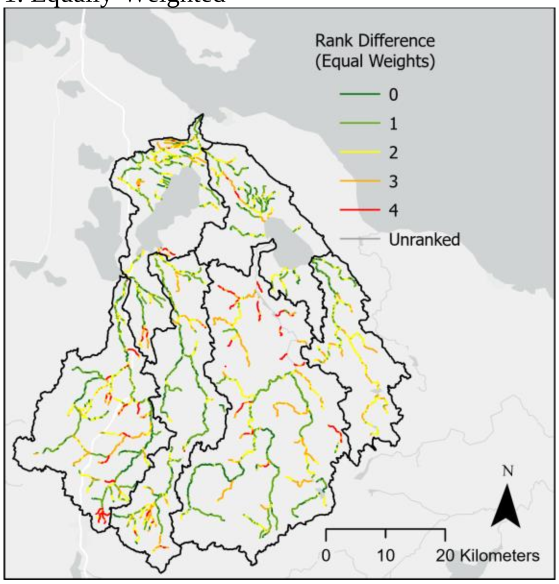
Figure 16. Histogram of rank differences for the total Lake Erie study region for the reversed relatively-weighted model. Count refers to the number of stream segments in the total study region.

For the Black River, the proportions of final suitability scores were again significantly different between scales for both the equally-weighted and relatively-weighted models according to the (aspatial) G-test (equally-weighted: $G = 19.01$, $df = 4$, $P < 0.001$; relatively-weighted: $G = 11.58$, $df = 4$, $P = 0.021$; Fig. 12). Spatially, rank agreement between scales was moderate in the Black River model (Fig. 17). Most of the low-agreement areas are seen in the lower (northern) portion of the Upper Black River subwatershed in both the equally-weighted and relatively-weighted model as well as the mainstem of the Lower Black River subwatershed (Fig. 17.A). Unranked reaches accounted for 8 of the 7,188 stream segments assessed.

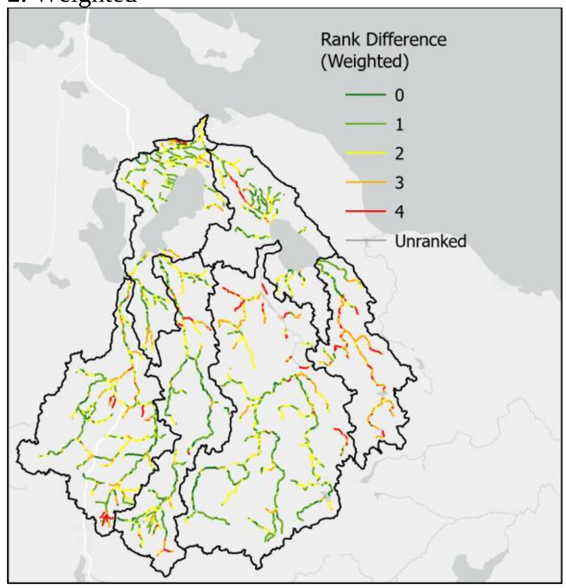
The model created for the Black River using the ranking ranges from the Lake Erie tributaries had similar trends in scale-versus-scale agreement. First, according to the (aspatial) G test, the final score proportions were significantly different between scales in both the equally weighted ($G = 26.68$, $df = 4$, $P <0.001$) and relatively-weighted ($G = 14.16$, $df = 4$, $P = 0.007$) model runs. Spatially, the reach segments that were red (a difference of 4) in the original Black River model (Fig. 17.A) were instead orange (difference of 3), yellow (a difference of 2), or even light green (a difference of 1) in the Lake Erie-range version (Fig.17.B; note Lower Black River, Upper Black River, and Rainy River subwatersheds). However, overall, there were now far more yellow segments (score difference 2) across the Black River study region.

A. Black River Data Ranges

1. Equally-Weighted

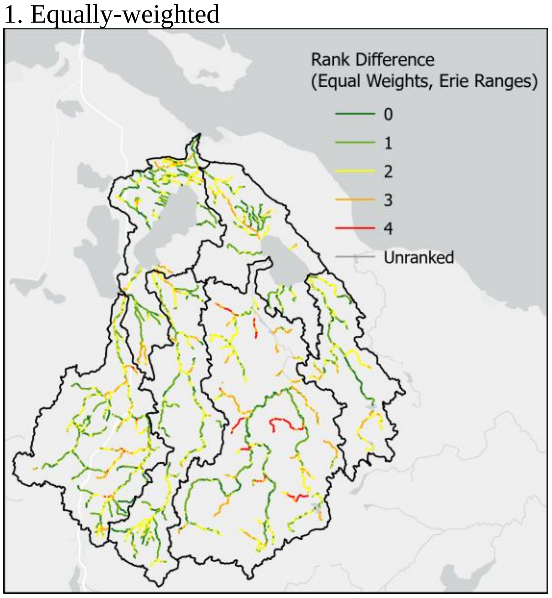


2. Weighted



B. Lake Erie Data Ranges

1. Equally-weighted



2. Weighted

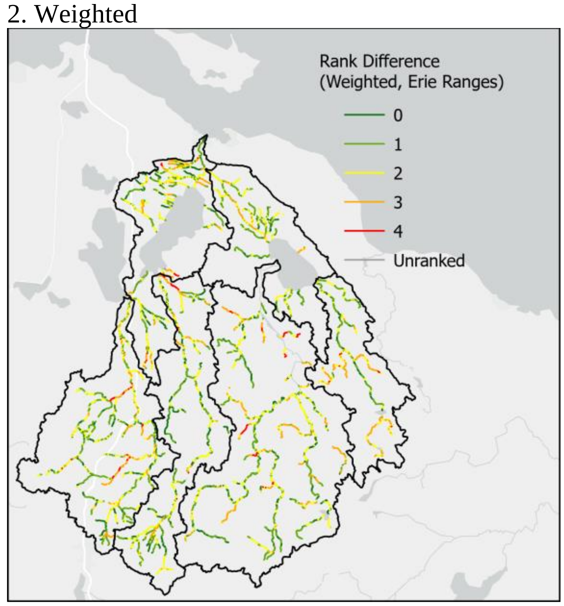


Figure 17. Difference in watershed- and reach-level suitability scores for the equally-weighted (1) and weighted (2) Black River models, based on Black River (A) and Lake Erie (B) data rankings.

For the Black River model created with the Black River data ranges, the mean difference in ranks across the two spatial scales was 1.409 for the unweighted model and 1.364 for the relatively-weighted model. A difference of 1 was the most common occurrence, while a difference of 0 was the second-most common, for both weighted and unweighted runs (Fig. 18.1). For the Black River model created with the Lake Erie ranges, the mean difference in ranks was 1.297 for the unweighted model and 1.275 for the relatively-weighted model. A difference of 1 was again the most common occurrence, but in this version of the model a difference of 2 was the second most common occurrence, with a difference of 0 being the third-most common occurrence for both the unweighted and weighted runs (Fig. 18.2).

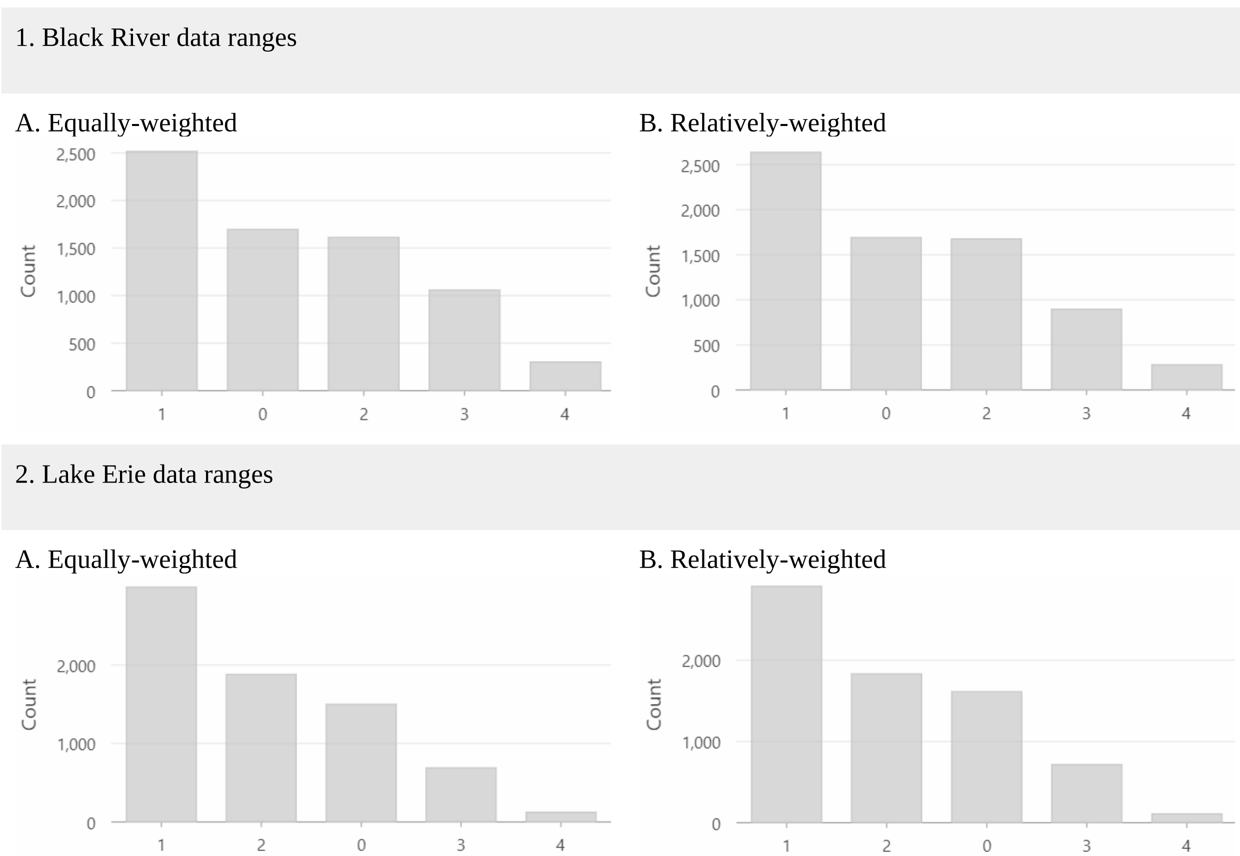


Figure 18. Histograms of rank differences for the Black River watershed for the equally-weighted (A) and relatively-weighted (B) models using the Black River and Lake Erie data ranges. Count refers to the number of reach segments out of the total Black River study region.

Discussion

Results overview - total study region suitability (Lake Erie)

This habitat suitability analysis had highly varied results, allowing for a high degree of discrimination across the study region, though certain aspects of the model framework should be kept in mind before the results are discussed at length. First, no values in the input criteria were labeled as “restricted” or removed from the analysis, since the goal was to rank the entire study region of each watershed and identify feasible alternatives for the particular goal of restoring habitat for the reintroduction of Lake Sturgeon; segments of streams or patches of landscape that are severely unsuitable in terms of a particular environmental factor *could* potentially be improved by local restoration projects, so being able to see the scores at each scale and for each input criterion is more important than removing values (and therefore habitats) that are currently unfeasible for Lake Sturgeon. Second, the total amount of suitable habitat identified in a region is an appropriate first step in assessing an HSM’s results, but the spatial aspect of these results is much more informative for interpretation. Habitat suitability models often output highly-restricted results in terms of suitability. For example, in one habitat assessment, Kreiger and Diana (2017) found that only 29.1% of the North Channel of the St. Clair River comprised suitable nursery habitat for Lake Sturgeon. Similarly, Daugherty *et al.* (2007) found that only 0-23% of the three Michigan tributaries in the study were highly suitable habitat for spawning adults, and only 0-9% of the tributaries were highly suitable habitat for winter staging adults (with a surprising 39-99% highly suitable for juveniles across the three study tributaries, emphasizing the potential for variability in this region). Total reach suitability for the entire study region in my analysis was 52.4% suitable (scores 4+5, a liberal interpretation of the results) or 18.7% highly-suitable (score 5 only, a more conservative interpretation) (Table 1), both of which are fairly on-trend with other finer-scale assessments in Great Lakes tributaries. However, looking at the spatial distribution of these scores reveals watershed-specific differences in habitat availability as well as finer-scale patterns that warrant further study.

Habitat suitability model - spatial interpretations

In this analysis, the suitability of eastern Lake Erie watersheds was higher than western Lake Erie watersheds, as predicted, which makes sense given the legacy effects of historic land development across the lake (Regier and Hartman 1973); however, differences in habitat quality within the lower-scoring watersheds could still provide valuable potential for Lake Sturgeon reintroduction projects. For example, the Maumee River had higher suitability near its outlet into Lake Erie compared to much of its headwaters (Figs. 7-8), and in a watershed of its size, the mainstem alone may provide adequate abundance of habitat for a population of Lake Sturgeon (Collier *et al.* 2021; discussed further later). Within-watershed interpretation for every watershed assessed here was largely outside of the scope of this study, but the framework itself was designed to be interpreted by local managers on a watershed-by-watershed or even subwatershed-by-subwatershed basis, and specific areas of certain watersheds such as the Maumee's outlet allowed for a form of validation against previous small-scale studies. Had this spatially-explicit aspect of the results been ignored, the Maumee River would not be recognized as a potential reintroduction location based on total suitability percentage alone.

The relative weight scheme was applied to represent real-world differences in importance between the various habitat criteria for Lake Sturgeon, but relative weight schemes seem to be an uncommon practice in previous Lake Sturgeon habitat suitability analyses. The use of multiple weight schemes (differently-weighted versus equally-weighted) was intended to serve as a sensitivity analysis, which investigates how sensitive the results are to a model's parameters. Significant changes in the results between model versions (in this case, the two weight schemes) would indicate high sensitivity of the results to the parameters of the model (hard-cut boundaries) rather than to the gentle variation seen in real-world habitat use by different populations of the same species (see Baril 2017). Between the equally-weighted and the relatively-weighted models, there were no major changes in terms of proportion distribution (total percentages of each score classification) as well as spatial distribution (visual interpretation of the maps), suggesting that the results were not highly sensitive to the application of weights compared to weighing everything equally (Figs. 13-14). This can also be said for the reverse-weighted model, as the same general distribution of suitability scores can be seen (Figs. 15-16). It is worth noting that in the unweighted watershed results of both study regions, individual subwatersheds have apparent "shades" of suitability, which is a result of the subwatershed area input criterion being weighed at 16.6% (Fig. 6A). However, in the weighted watershed results, that effect is removed due to the input being weighed at only 4.7% (Fig. 6B). The effect is again present when the weight order is reversed, giving subwatershed size a weight of 51.4%, the highest weight rather than the lowest (Fig. 8).

Thus, the results are somewhat sensitive to the *order* of the weights; however, the goal of this analysis was not to maximize the total suitability, but rather to achieve a realistic prediction of suitability. Reversing the weight order or even forgoing the use of the different weights would be unrealistic of real-world Lake Sturgeon habitat needs, so weighing the habitat criteria and selecting the scheme with the lowest CR value was best-practice (Saaty 1996, Malczewski 2000), even if it resulted in lower habitat suitability in total; this is doubly true given that this analysis involved six criteria, whereas many habitat suitability analyses for Lake Sturgeon have accounted for differences in the importance of habitat needs by only working with a few (2-4) highly-important criteria (i.e., the "big four" as previously discussed here).

Using two spatial scales was also an important consideration during the development of this model, since surrogate data availability looked drastically different between the landscape and stream levels. In the end, the two-scaled models showed a close agreement between the final scores of the watershed level and reach level in both Lake Erie and the Black River, based on low average differences between scales (Figs. 13-18). This implies that the frameworks of the models at both scales were parameterized with appropriate data surrogates, such that they represented the habitat criteria similarly between the two scales (see Appendix 3). Scale agreement was similar and only slightly lower (i.e., had a slightly higher mean score difference) when the weight scheme was reversed entirely (Figs. 14-15). This is an important finding given that HSMs are generally built on classifications of data inputs that are not directly comparable to other data classification schemes (McKenna *et al*. 2014). As such, either scale (and thus either set of spatial datasets) could be used to predict habitat suitability alone, and the findings would be similar to if the other were used.

Besides specific small-scale habitat studies found within the same Lake Erie watersheds that were considered here, I wanted to compare this model's results to a real-world reference that was both (a) outside of the Lake Erie study region and (b) still a present-day host to a Lake Sturgeon population, so the Black River in northern Michigan was used. As already mentioned, the model predicted that the Black River watershed as a whole is "fairly suitable" (40-54% suitable at both scales) for Lake Sturgeon at both spatial scales when relatively-weighted (Table 2), suggesting that the model has at least some degree of accuracy in depicting the real-world suitability of the watersheds, though real-world suitability may be higher (discussed further below, and see Smith and King 2005). Applying the Lake Erie data ranges did not predict higher suitability in the Black River watershed compared to the results of the model using the Black River input ranges, and this is likely due to key differences in flow, stream order, and subwatershed size between the two groups of watersheds. Specifically, since many of the Lake Erie tributaries are larger than the Black River watershed, the ranges of Strahler stream orders, mean flows, and subwatershed areas were larger, which penalized much of the Black River in the model (see Appendix 8).

Further, the Lake Erie data ranges, when applied to the Black River, showed slightly lower agreement between spatial scales, such that a difference of 2 accounted for the second-largest proportion of the scores compared to a score of 0 in the other models (Fig. 18). I believe that using the actual data ranges for the Black River study region in the model, rather than the ranges developed for the Lake Erie watersheds, was more accurate as well as a more feasible (and less confusing) technique for transferring this HSM framework to a new location. HSM frameworks can be transferable between study regions, but the accuracy depends on the uniqueness of the system (and population) for which the HSM was originally built (Haxton 2008). Overall, this HSM seems to be accurately transferable to a tributary outside the Lake Erie system, with minimal loss in output feasibility as seen in the final scale difference assessment as well as the differences between the Black River-range results and the Lake Erie-range results (Fig. 17). It is promising that several of the Lake Erie watersheds are comparable to a system that is currently habitable to a Lake Sturgeon population (i.e., ≥ 40% suitable (score 4+5) at either scale), as this system can serve as a reference for both restoration and reintroduction goals. While it is concerning that a higher total suitability was not found for the Black River watershed as a whole, we have already shown that subwatershed and even by-the-segment suitability can vary widely within one system. Looking specifically at the Upper Black River watershed (see Fig. 1 inset) results for the relatively-weighted model, the watershed level is 64.6% suitable and 31.2% highly-suitable, while the reach level is 42.9% suitable and 22.9% highly-suitable (Fig. 10, bottom, and Table 2). On the other hand, the Lower Black River is only 37.3% suitable and 11.2% highly-suitable at the watershed scale and 42.3% suitable and 9.25% highly-suitable at the reach level (Fig. 10, bottom, and Table 2). The Upper Black River is the specific subwatershed in which the Black River Lake Sturgeon population lives and spawns (Smith and King 2005), so the fact that this study found habitat suitability coverage as high as 64.6% and high-suitability coverage as high as 31.2% is comforting compared to the total watershed. An even deeper look at the spatially-explicit patterns of suitability in this subwatershed could support this finding.

Criticism of the framework

Some aspects of the framework of this analysis could be revisited to improve prediction accuracy and(or) streamline the workflow. For example, to compare the reach-level suitability scores to watershed-level suitability scores, only the score of the watershed pixel directly above the center point of each reach segment was used, rather than the watershed suitability scores overlaying the entire reach segment or even the entire drainage area of the segment. This technique likely decreased the accuracy of rank matches for longer stream segments that crossed a diversity of watershed suitability pixels, especially given that each watershed pixel represents only a 30 x 30-meter tract of land. A more detailed part of this workflow could be developed to consider the true range of watershed suitability scores crossed by each stream segment.

Another example of a pitfall in the model's framework is that the relatively-weighted model decreased the total amount of suitable habitat, which was expected and not indicative of a problem, but also slightly decreased scale-to-scale final rank agreement, which was unexpected. This effect is seen in the histograms of rank differences between the equal and relative models (Fig. 14); although the histograms look almost identical, the mean score difference in the weighted model is just slightly higher (0.983 vs. 0.975), indicating that the models agreed *less* when the relative weight scheme was applied. This small difference in agreement is not concerning enough to warrant the removal of the relatively-weighted model, but it does point to potential issues related to data surrogate matching between scales as well as the distribution of the weights.

Specifically, the above finding may imply that there was an overrepresentation of a less-accurate data surrogate pairing (such as proximity to ag./dev. land and proximity to coarse surficial geology, which were weighted 38.3% in the final model, compared to 16.6% in the equally-weighted model) and(or) a de-emphasis of the more-accurate surrogate pairs (e.g. canopy closure and reach temperature, which were weighted 7.7% in the final model, compared to 16.6%). Indeed, certain data inputs for the habitat criteria could have been a source of redundancy or poor surrogacy. For example, impervious surface cover at the watershed level and cumulative habitat disturbance at the reach level may not be the most intuitive surrogates to represent benthos quality as a criterion; however, no large-scale dataset representing benthic community composition exists for the entirety of the study region in this analysis. The proximity datasets (proximity to ag./dev.

land, watershed habitat, coarse surficial geology, fine surficial geology) were derived from two base datasets, and the "proximity to" aspect was applied to not only eliminate the redundancy of using one dataset for two input criteria (e.g., the same NLCD base dataset for ag./dev. and wetland) but also to eliminate the problem of canceling each other out (e.g., a reach segment scoring suitably for being on coarse surficial geology but also scoring unsuitably for NOT being on fine surficial geology, canceling both criteria scores out). Instead, the two derived datasets would both provide new information about the suitability of the point of interest (e.g., ranking suitable for being in close proximity to coarse geology as well as ranking suitable for being in close proximity to fine geology). This probably reduced redundancy in that regard, but the fact remains that the impervious surface cover input was adapted by the originators (MRLC) based on the intensity and type of developed (namely urban) land cover, which again highlights the possibly counterintuitive use of ISC as a criteria surrogate in this analysis, though no feasible alternatives immediately come to mind.

Further to the above, the *distribution* of weights in the relative weight scheme could have compounded the impact of mismatch and(or) under/over-representation of data surrogates on scale agreement in the weighted model results. Although the CR for the weighted scheme was below the suggested threshold of 1.24 for a matrix of six criteria (Appendix 5), the difference between the highest weight (51.4%, for coarse substrate) and the lowest weight (4.7%, for depth) was 46.7 -- nearly fifty. The order and magnitude of difference among the weights was determined using feedback from multiple Lake Sturgeon researchers and other best practices for analytical hierarchy process and multi-criteria decision-making (Saaty 1996, Malczewski 2000), but quantifying *exactly* how much more important one criterion is over another criterion for Lake Sturgeon success is challenging and subjective, especially while considering all the other input criteria at the same time. Making the claim that coarse substrate is "about" 10 times more important for Lake Sturgeon than channel depth is dubious, even if it is supported by expert feedback and an acceptable CR. As already discussed, the relative weight scheme was important for this study's framework, but the scheme could be reworked to reflect a more realistic distribution of criteria importance if more feedback was obtained.

Spatial results in context - state by state

Habitat suitability analysis for the reintroduction of Lake Sturgeon

While comparing the results of this analysis to the Black River is beneficial, it is also important to compare these results to previous Lake Erie-based habitat assessments for the four states involved.

The Lake Sturgeon has been listed as threatened in New York since 1983 (Carlson and Daniels 2004). My literature review of Lake Sturgeon habitat assessments found no studies of Lake Erie tributaries in New York other than the Niagara River, which has been heavily investigated since 2002 (Hughes 2002). While the Niagara River's Lake Sturgeon population is important as one of the only two in Lake Erie, assessments suggest that habitat is limited and the population remains small (Nuenhoff et al. 2018, Chalupniki *et al*. 2011). Meanwhile, the Lake Sturgeon population in the Upper St. Lawrence River has recently exceeded crucial metrics for recruitment of spawning adults and juveniles, underpinning the localized effectiveness of New York's Lake Sturgeon Recovery Plan (NYS DEC 2022). Attention on Lake Sturgeon populations that have been reintroduced to other systems in New York have provided crucial information on habitat use (see Dittman *et al.* 2015), but overall habitat assessment information across New York is lacking. The two New York tributaries considered here, Walnut/Silver Creek and Cattaraugus Creek, appear to be highly suitable for Lake Sturgeon across both spatial scales (Table 1), and local ground-truthing to create a habitat suitability index for each of these watersheds may reveal that little to no restoration or alteration is needed to prepare for a Lake Sturgeon reintroduction. However, the extreme positivity of the results (up to 100% suitable, Table 1) across the various forms of this analysis is unrealistic given the typical results of HSMs, as discussed above; it would not be surprising if real-world ground-truthing of these watersheds' reaches reveals less than-perfect conditions for Lake Sturgeon (although, total suitability up to 99% in one stream has been estimated for larval habitat needs; see Daugherty *et al.* 2007).

Similarly to New York state, Michigan's library of Lake Erie Lake Sturgeon habitat assessment has been focused on the system currently inhabited by Lake Sturgeon: the St. Clair Detroit River system. Studies quantifying habitat suitability have found varying results at different points within the SC-DR system even while considering similar sets of habitat criteria (e.g., substrate, depth, and gradient by Daugherty *et al.* (2007); substrate, depth, benthic velocity, and invertebrate density by Krieger and Diana (2017); depth and velocity by Bennion and Manny (2014); discussed previously here). Although the SC-DR system has the largest remaining population of Lake Sturgeon in the entire Great Lakes, which has been attributed to maintaining access to most or all of its historic range (Kessel *et al.*, 2017), the Detroit River appears to be considerably less suitable than the St. Clair River, with reports that no spawning grounds exist in all of the Detroit River (Nichols *et al*. 2003, Hartig *et al*. 2009). In this analysis, two Michigan tributaries of Lake Erie were assessed, and both appear worthy of further investigation for Lake Sturgeon reintroduction (River Raisin: 55.8% suitable watershed, 88.6% suitable reach; Huron River: 75.4% suitable watershed, 94.9% suitable reach; Table 1). Reintroducing Lake Sturgeon to this region of Lake Erie would benefit the whole system given that the Detroit population has a low (partial) migration rate out of the river (Kessel *et al.* 2017), meaning that remnant Lake Sturgeon are essentially absent from western Lake Erie proper.

Ohio has the largest portion of Lake Erie's U.S. shoreline, and thus 12 of the 16 watersheds assessed in this study were located in Ohio (Fig. 1). As predicted, many of these tributaries accounted for the lowest total suitability scores at both the watershed and reach levels (Table 1). While both New York and both Michigan tributaries had total suitability scores above 50%, six of the Ohio tributaries had less than 50% suitable habitat at the watershed level (though one such tributary, Beaver Creek, had an anomalous 97.5% suitability at the reach level compared to its 40.5% watershed suitability, which should be explored further along with the 100% suitable New York tributaries). Other Ohio tributaries had high suitability scores, including the Huron River, the Chagrin River, and the Cuyahoga River (Table 1), the latter of which has been a watershed of interest for the potential reintroduction of Lake Sturgeon for several years by multiple entities such as the Cuyahoga Valley National Park (Spectrum News Staff, 2021). Similarly, reintroduction of juvenile Lake Sturgeon has already occurred in the Maumee River, the largest watershed in this analysis (Markey 2018). This analysis found that the Maumee River has about 25.8% suitable habitat at the watershed level and 40.5% suitable habitat at the reach level, but again it is worth noting that the bulk of the low suitability scores are congregated in the headwaters of the Maumee, which makes up a majority of the shed's total area. The mainstem of the tributary, especially near the outlet into Lake Erie, appears to be much more highly suitable at the reach scale despite low suitability at the watershed scale (Figs. 6, 7). Not only does this finding indicate the possibility of a local, large-scale (landscape-scale) habitat improvement opportunity to safeguard the higher-quality reach-scale habitat, it also supports the findings of an HSI of the lower Maumee River by Collier *et al.* (2021), which was the first study designed to evaluate the potential for Lake Sturgeon reintroduction into any Lake Erie tributary (also see Collier 2018). Collier's HSI found that suitable habitat (depth, substrate, and velocity) is not limiting for Lake Sturgeon at different life stages (namely the spawning adult and age-0 stages), and the study's framework was also designed to consider connectivity between life stage habitats (distances of juvenile habitats downstream of spawning habitats), which was not assessed in the present study. Given Ohio's history of development along Lake Erie's shoreline, the presence of several suitable watersheds (>50% suitable at either scale) for the potential (and already-successful) reintroduction of Lake Sturgeon is promising for the future of Lake Erie's populations, especially for their potential for serving as connecting habitats between the two remnant populations, which should not be overlooked (Auer 1996).

Pennsylvania has the shortest portion of the U.S.'s Lake Erie shoreline, and the confidence of experts in the historic use of Pennsylvania waters by Lake Sturgeon is equally slim. Assessments of nearshore habitat in Pennsylvania have found minimally-feasible spawning grounds (Regional Science Consortium 2013), and the tributaries are unlikely to ever be accessible to Lake Sturgeon due to the condition of the outlets. One of the Ohio tributaries considered here, Conneaut Creek, crosses the Pennsylvania border. Conneaut Creek had high suitability at both scales (90.1% suitable watershed and 84.2% suitable reach). Managers of the Conneaut Creek watershed from both Ohio and Pennsylvania may need to collaborate on a Lake Sturgeon reintroduction given that about half of the watershed sits on either side of the state border.

Notes for managers

As already mentioned, habitat access (and connectivity) should be stressed over habitat enhancement for the restoration of Lake Sturgeon populations, given that population resilience in Lake Erie would be bolstered significantly by both access to multiple suitable spawning river options as well as lake-wide genetic exchange among populations (Auer 1996). This study revealed several suitable tributaries that could prove to be feasible for Lake Sturgeon reintroduction, and the adjacency of these watersheds warrants communication and collaboration between local management organizations for multiple projects. Fortin *et al.* (2002) suggested that an average female Lake Sturgeon would require 13 - 48 m^2 of spawning area to maximize spawning success, though in linear terms Lake Sturgeon will reportedly use 250 - 300 km of combined river and lake range at a minimum, with 750 - 1,000 km being typical (Auer 1996). Although maximum suitable habitat length was not assessed here, the adjacency of suitable watersheds reported here is a gateway into such an investigation. Communication between Lake

Sturgeon groups across Lake Erie is already extensive, as the Lake Erie Lake Sturgeon Working Group meets multiple times a year and periodically puts out reports summarizing ongoing work (e.g., Aloisi *et al*. 2019).

Another means of addressing the connectivity of habitat for Lake Sturgeon involves removing barriers within stream systems. Barriers are present in several of the tributaries considered here, but presence of a barrier was not considered a constraint since they can technically be removed. In fact, the Brecksville diversion dam on the Cuyahoga River has been in the process of being removed since 2020, which will add to the reintroduction potential of the Cuyahoga River as a whole (National Park Service 2022). The presence of large barriers that significantly alter flow regimes, such as hydroelectric power generating facilities, has been identified as the primary factor affecting the variation in relative abundance of Lake Sturgeon in Ontario rivers (Haxton *et al*. 2015). Specifically, that study found that relative abundance of Lake Sturgeon was significantly greater in unregulated (natural-flowing) rivers than in regulated (controlled-flow) rivers; individual growth was faster, and body condition was significantly greater, in natural-flowing systems than in controlled-flow systems. Finally, recruitment of Lake Sturgeon was highly variable in both regulated and unregulated systems, but recruitment failure was more evident in regulated systems. In the Ottawa River, Canada, Lake Sturgeon were relatively more abundant in natural reaches compared to impounded reaches, and no lake sturgeon were sampled in three reaches, two of which were subject to annual winter drawdown (Haxton 2002). The impacts of barriers on habitat use are not limited to streams; a study on Lake Sturgeon movement in a large hydroelectric reservoir in the Nelson River of Canada led the authors to suggest that factors other than habitat suitability influence Lake Sturgeon movement and utilization patterns, such as core area affinity and natural versus disturbed or altered systems (Hrenchuk *et al*. 2017). While Lake Sturgeon can use certain types of fish passages, due to their large body sizes as adults they are not as capable as salmonids at using these passages (Pandit *et al*. 2016). Further, Lake Sturgeon are capable of going over dams to move downstream, but the barrier will still impede them when they return, guided by their natal site fidelity (Thuemler 1985). Removing barriers has the dual benefit of not only directly allowing access to habitat but also potentially facilitating different movement behaviors in Lake Sturgeon populations, including straying behavior and more natural use patterns of available habitat (Kessel *et al*. 2017). Removing barriers in highly suitable watersheds would improve the connectivity of suitable habitats at both the small scale and the large scale. A preliminary look at an overlay of the USGS's National Anthropogenic Barrier Dataset (2012; obtained from: https://www.sciencebase.gov/catalog/item/56a7f9dce4b0b28f1184dabd) shows that 299 anthropogenic barriers are present in the 16 Lake Erie watersheds assessed in the present study, each watershed has at least one barrier, and most of the barriers are found in the Michigan and eastern-Ohio watersheds (Appendix 9). Assessing accessibility quantitatively using barrier datasets like this one is a major next step of the research presented here; could there be any patterns linking currently-unused yet highly-suitable habitat to the presence of barriers, or is some other factor preventing sturgeon from accessing these habitats?

Further research directions

Besides connectivity of habitats as a broad metapopulation factor, connectivity on an even smaller scale is important for Lake Sturgeon. Haxton *et al.* (2015) found a spatial segregation of life stages in the Attawapiskat River system of Ontario; there was a significant difference in the mean total length of the Lake Sturgeon caught within the stream, with larger sturgeon in the upstream sites and smaller sturgeon in the downstream sites (avg. study stream length = 37 river kilometers). Adjacency of habitat types also impacts survivorship; one study suggested that the amount and location of nursery habitat in relation to sources of young Lake Sturgeon (i.e., larvae drifting downstream from spawning beds) shapes early behavior and distribution of the juvenile Lake Sturgeon as well as subsequent survival rates (Kreiger *et al.* 2018). Considering the impacts of flow direction and adjacency of habitats for different life stages was generally beyond the timeline of this report, but these warrant investigation using this project's framework and data, and thus the next steps for this research will focus on these topics. Some preparation of the datasets would need to occur first, namely to rectify the fact that the reach-level base dataset (i.e., the vector reach segments) were not consistently linked to each other across the study region. In particular, connective lakes and ponds dividing stream segments were not digitized, so some gaps are present. Individually checking the digitization of all segments in the study region would take much time, but the GIS environment offers tools capable of assessing the flow or connectivity of stream (polyline vector) datasets at small and whole-system scales. Assessing connectivity would not necessarily have to be completed for every segment of the study region. Generally, mainstem suitability is important before headwater suitability, even given the fact that Lake Sturgeon have far-reaching ranges (Auer 1996); encountering unsuitable habitat in the mainstem may lead to low recruitment in the entire system, even if better habitat exists upstream. Some *in-situ* HSIs have assessed connectivity by starting at the mouth of the stream where Lake Sturgeon would enter and work upstream until the first major stretch of unsuitable habitat is encountered, which would likely be an indirect barrier to Lake Sturgeon moving further inland (Daugherty *et al*. 2007).

Another factor that could be investigated using this study's framework is an assessment of non-historic watersheds. Other tributaries of Lake Erie that have never had documented use by Lake Sturgeon could still be suitable for populations today, such as the Buffalo River in New York, the outlet of which is in close proximity to the Niagara River inlet. As discussed, the transferability of an HSM depends on the uniqueness of the region for which it was developed, as well as the proximity of the new study region of interest in relation to the original (though even then it is still not guaranteed to be accurate; Haxton *et al.* 2008). The model used here was transferable to the Black River of Lake Huron, so it could certainly be transferable to other tributaries of Lake Erie. Though legacy effects have been important for the lingering populations of Lake Sturgeon in the Great Lakes (Kessel *et al*. 2017, Regier and Hartman 1972), historic suitability does not necessarily imply contemporary suitability, especially given the rapid and diverse landscape changes in the Great Lakes region over time (Wehrly *et al.* 2013).

Some factors that were not considered here could be investigated in a sister study, though some may prove redundant. One example of a possibly-redundant topic is the consideration of winter staging habitat suitability. This was not considered for two reasons, one being the fact that winter staging is the least-studied life stage of Lake Sturgeon, likely due to the lack of major ontogenetic events that occur in this season (Daugherty *et al*. 2007), and the other reason being that spawning habitat quality generally correlates with the quality of habitat for other life stages of Lake Sturgeon (though abundance and distribution of these various habitats is another story; Bennion and Manny 2014), so it is possible that watersheds that are highly suitable for spawning and juvenile habitat according to this analysis are also highly suitable for winter staging. Another factor not considered here, which could instead be beneficial, is the presence of invasive species prey items in the study region, namely Dreissenid mussels and the Round Goby. This factor is still contentious in terms of determining habitat suitability for Lake Sturgeon, since adults will feed on these organisms in certain systems, but doing so can introduce bioaccumulative toxins (Boase *et al.* 2014). Further, the Round Goby can predate Lake Sturgeon eggs (Nichols *et al*. 2003), and Dreissenid mussel beds have shown low use by juvenile Lake Sturgeon compared to other available habitat (Hughes 2002). The prevalence of these nonnative species in particular systems may warrant their consideration for Lake Sturgeon habitat suitability studies, especially as they spread, though whether to consider them as factors that negatively influence or *entirely* eliminate habitat suitability is a difficult decision. Finally, combining the results of this study (or the framework of this study) with environmental DNA (eDNA) detection of Lake Sturgeon could help validate the model's predictive power. The capability of detecting Lake Sturgeon with eDNA technology has already been employed (Pfleger *et al*. 2016; Farrington and Lance 2014) and doing so in Lake Erie may be on the horizon (Silverbrand, personal comm.).

Conclusions

I successfully developed a multi-scale, multi-life-stage, and multi-criteria habitat suitability analysis for Lake Sturgeon in historically-used tributaries of Lake Erie. I found a range of suitability levels for the tributaries in question, which allowed me to rank them and make specific recommendations to managers with the goals of collaborative restoration and reintroduction of Lake Sturgeon in mind. My framework can be adapted to other watersheds in Lake Erie and other regions of the Great Lakes, and the results can be interpreted at finer scales using ground-truthing assessments. Further research using these findings will include assessment of habitat connectivity given the presence of barriers and proximity to other areas of suitable habitat. At least 17 Lake Sturgeon habitat restoration projects have been completed in the past 20 years for spawning adults alone (Baril 2017), and habitat suitability analysis prior to starting such projects can be used to focus that momentum towards the areas of highest priority so that resources are not wasted and impacts are substantial. My study adds to the growing library of work that shows that the use of spatially-explicit habitat suitability models is a beneficial tool in the safeguarding of imperiled species.

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Appendix

Appendix 1. U.S. tributaries of Lake Erie believed or known to have been used by Lake Sturgeon, 1600-current.

State	Name	Status	Sources
MI	Detroit River	Extant	Bennion and Manny 2014 Goodyear *et al.* 1982
MI	River Raisin	Extirpated	Aloisi *et al*. 2019
MI	Huron River	Extirpated	Goodyear *et al*. 1982
OH	Ashtabula River	Unknown	Rice and Zimmerman 2019
OH	Beaver Creek	Unknown	Rice and Zimmerman 2019
OH	Chagrin River	Unknown	Rice and Zimmerman 2019
OH/ PA	Conneaut Creek	Unknown	Rice and Zimmerman 2019 Goodyear *et al*. 1982
OH	Cuyahoga River	Extirpated	Weimer 2020 Zimmerman 2019 Goodyear *et al.* 1982
OH	Grand River	Unknown	Rice and Zimmerman 2019
OH	Huron River	Unknown	Rice and Zimmerman 2019
OH	Maumee River	Reintroduced	Rice and Zimmerman 2019 Goodyear *et al*. 1982
OH	Old Woman Creek	Unknown	Rice and Zimmerman 2019
OH	Portage River	Unknown	Rice and Zimmerman 2019 Aloisi *et al.* 2019 Goodyear *et al.* 1982
OH	Sandusky River	Extirpated	Rice and Zimmerman 2019 Goodyear *et al*. 1982
OH	Vermilion River	Unknown	Rice and Zimmerman 2019
PA	Sixteenmile Creek	Unknown	Henry and Hayes 2015 Klingensmith 2009
PA	Twentymile Creek	Unknown	Henry and Hayes 2015 Weisberg 1999
PA	Walnut Creek	Unknown	Henry and Hayes 2015 Weisberg 1999 Goodyear *et al*. 1982
NY	Niagara River	Extant	Neuenhoff *et al.* 2018 Hughes 2002
NY	Cattaraugus Creek	Extirpated	Aloisi *et al.* 2019
NY	Walnut / Silver Creek	Unknown	Goodyear *et al.* 1982

Appendix 2. Lake Sturgeon habitat criteria that have been most often included in HSIs, with general suitability classifications.

Habitat criterion	Life stage	High suitability	Low suitability	Importance	Key sources
Substrate size	Sp, Eg L, J, Ad	Coarse (Sp, Eg) Fine (L, J)	Coarse absent Fine absent	High	Neuenhoff *et al.* 2018 Baril *et al.* 2017
Temperature (ºC)	Sp, Eg, J	Cooler (13-14)	Warmer (>14)	High	Baril *et al.* 2017
Flow velocity (m/s)	Sp	Fast (> 0.5)	Slow (< 0.5)	High	Neuenhoff *et al.* 2018 Baril *et al.* 2017 Bennion and Manny 2014
Channel depth (m)	Sp, Ad	>0.5 (high variability)	<0.5 (high variability)	Moderate	Baril *et al.* 2017 Bennion and Manny, 2014 Manny and Kennedy, 2002
Gradient (impacts on flow stability)	L, J	Low	High	Moderate	Kreiger and Diana 2017
Water quality*	All	Varies	Varies	Low	Manny and Kennedy 2002
Water chemistry	All	??? (high variability)	??? (high variability)	???	Dimitry Gorsky, personal communication
Presence of predator species	Eg, L	Not present	Present	???	Manny and Kennedy 2002
Benthic macroinvertebrate community composition	J, Ad	Present: Chironomidae, Gammaridae, Ephemeroptera (Hexagenia), Hirudinea, Gastropoda, Dreissenidae	???	???	Kreiger and Diana 2017
Presence of Round Goby (*Neogobius melanostomus*)	J, Ad, Sp	??? (potential prey item)	??? (can introduce toxins and predate on LS eggs)	???	Chalupnicki *et al.* 2011

For life stages: Sp = Spawning adult, Eg = Egg, L = Larvae, J = Juvenile, Ad = Adult (not spawning). Criteria with “???” importance labels either have rarely been considered in habitat studies or may not be able to be mapped at a large scale.

(* = “Water quality” in this instance was defined as “percent of surface light reaching the bottom (range: 0.05–8.7%), Secchi disc depth (range: 2.5–6.5 m), and water current velocity (range: 0.35–0.98 m/s)” by Manny and Kennedy (2002) and was found to vary threefold across the habitats used by Lake Sturgeon in the study.)

Appendix 3. Lake Sturgeon habitat needs matched to feasible, large-scale data surrogates at the watershed and reach levels.

Habitat need	**Watershed (landscape) surrogate**	**Explanation**	**Reach (in-stream) surrogate**	**Explanation**
Coarse substrate (spawning stage)	Proximity to agricultural / developed land	Presence of agricultural and developed land increases embeddedness (reduces abundance of clear, coarse substrate beds; unfavorable for spawning grounds)	Proximity to coarse surficial geology	Streams overlaying coarse surficial geology are more likely to have coarse bed habitat; habitats near both coarse and fine substrate favorable for larval drift
Fine substrate (juvenile stage)	Proximity to wetland habitat	Presence of fluvial wetland habitat maintains riffle/run/pool (RRP) sequence and increases (interval) abundance of fine substrate beds (favorable for juvenile grounds)	Proximity to fine surficial geology	Streams overlaying fine surficial geology are more likely to have fine bed habitat; habitats near both coarse and fine substrate favorable for larval drift
Temperature	Canopy closure	Increased canopy closure reduces stream temperature via shading (favorable for spawning and drift cues)	Temperature classification	Cold-class streams are most likely to reach the target seasonal temperature cue (14ºC) that triggers spawning
Flow	Slope	Increased slopes (gradient) lead to increased flows (velocity in particular)	Mean flow (Q50)	Higher mean flow is more favorable for LS at both spawning and juvenile stages
Channel depth	Subwatershed area	Larger subwatersheds are more likely to have deeper mainstem channels	Strahler stream order	Larger-ordered streams are more likely to have deeper mainstem channels than headwaters
Benthos	Impervious surface cover (ISC)	Increased impervious surface cover leads to a benthic community shift towards warm-water, pollution-tolerant species (unfavorable for LS diet)	Cumulative habitat disturbance index	Disturbed habitats are more likely to have pollution-tolerant/ facultative rather than sensitive/indicator communities (unfavorable for LS diet)

Appendix 4. Spatial data sources for all input criteria used in this analysis.

Name	Date	Originator	Use
National Watershed Boundary Dataset	2013	USGS (via The National Map)	Study region delineation (watershed) and subwatershed delineation (depth surrogate at watershed scale)
National Landcover Dataset (NLCD)	2019	Multi-Resolution Land Characteristics Consortium (MRLC)	Derive proximity datasets for ag./dev. land (coarse substrate surrogate at watershed scale) and wetland habitat (fine substrate surrogate at watershed scale)
CONUS Tree Canopy Closure Dataset	2016	USFS, MRLC	Canopy closure (temperature surrogate at watershed scale)
Urban Impervious Surface Cover (ISC)	2019	MRLC	Impervious surface cover (benthic community surrogate at watershed scale)
⅓ arc-second Digital Elevation Models	2021	USGS (via The National Map)	Derive slope (flow surrogate at watershed scale)
Great Lakes Regional Aquatic Gap Analysis datasets	2014	USGS, McKenna *et al.* (2014)	Study region delineation (stream segments) and all data surrogates at reach level (temperature, flow, Strahler order, proximity to fine and coarse surficial geology, and cumulative habitat disturbance index)

Appendix 5. Process of creating a consistent weight scheme for a habitat suitability analysis using expert feedback on input criteria (A) and a pairwise comparison matrix (B).

A. Summary of ranking feedback from Lake Sturgeon expert survey for six input criteria, on a scale of 1 (most important to Lake Sturgeon) to 6 (least important). The final ranking order was determined based on the sum of responder rankings for each criterion, with a lower sum implying higher importance (higher ranking overall). Relativity, or the closeness of each criterion sum to other criterion sums, was also used to loosely guide the magnitude of differences between the weights in the pairwise comparison matrix (B).

	Input criteria ranks					
Responder	**Embeddedness (coarse substrate)**	**Fine substrate**	**Water temperature**	**Channel depth**	**Mean flow**	**Benthos quality**
J. Collier	1	2	5	6	3	4
D. Daugherty	1	3	2	6	5	4
J. Sweka	1	3	5	4	2	6
J. Diana	1	5	6	4	2	3
J. Krieger	1	3	6	5	2	4
J. Chiotti, J. Boase	1	3	5	6	2	4
Sum of ranks	6	19	29	31	16	25
Final ranking order	1	3	5	6	2	4
Relativity (closeness)	A	B	C	C	B	C

B. Pairwise comparison matrix for a Lake Sturgeon using an intensity of importance scale modified from Thomas Pyzdek (Source: https://www.pyzdekinstitute.com/blog/six-sigma/ahp-spreadsheet.html) and Saaty (1980). Final consistency ratio (CR) = 0.04 < constant 1.24 for a 6-way matrix.

Intensity of importance...		
if Criterion A > B	**if Criterion B > A**	**Definition**
1	1.000	Equal importance
2	0.500	Equal to moderate importance
3	0.333	Moderate importance
4	0.250	Moderate to strong importance
5	0.200	Strong importance
6	0.167	Strong to very strong importance
7	0.143	Very strong importance
8	0.125	Very to extremely strong importance
9	0.111	Extreme importance

Pairwise comparisons							
Item No.	Item No.	1	2	3	4	5	6

Habitat suitability analysis for the reintroduction of Lake Sturgeon

	Item Description	Coarse substrate	Flow	Fine substrate	Benthos	Temperature	Depth
1	Coarse substrate	1.00	5.00	6.00	6.00	7.00	7.00
2	Flow	0.20	1.00	2.00	3.00	3.00	3.00
3	Fine substrate	0.17	0.50	1.00	2.00	3.00	3.00
4	Benthos	0.17	0.33	0.50	1.00	2.00	2.00
5	Temperature	0.14	0.33	0.33	0.50	1.00	2.00
6	Depth	0.14	0.33	0.33	0.50	0.50	1.00
	Sum	1.82	7.50	10.17	13.00	16.50	18.00

Standardized matrix								
		Coarse substrate	Flow	Fine substrate	Benthos	Temperature	Depth	Weight
1	Coarse substrate	0.55	0.67	0.59	0.46	0.42	0.39	51.4%
2	Flow	0.11	0.13	0.20	0.23	0.18	0.17	17.0%
3	Fine substrate	0.09	0.07	0.10	0.15	0.18	0.17	12.6%
4	Benthos	0.09	0.04	0.05	0.08	0.12	0.11	8.2%
5	Temperature	0.08	0.04	0.03	0.04	0.06	0.11	6.1%
6	Depth	0.08	0.04	0.03	0.04	0.03	0.06	4.7%

CI and CR worksheet									
		Coarse substrate	Flow	Fine substrate	Benthos	Temperature	Depth	SUM	SUM/Weight
1	Coarse substrate	0.51	0.85	0.76	0.49	0.43	0.33	3.37	6.56
2	Flow	0.10	0.17	0.25	0.25	0.18	0.14	1.10	6.45
3	Fine substrate	0.09	0.08	0.13	0.16	0.18	0.14	0.78	6.20

4	Benthos	0.09	0.06	0.06	0.08	0.12	0.09	0.50	6.11
5	Temperature	0.07	0.06	0.04	0.04	0.06	0.09	0.37	6.03
6	Depth	0.07	0.06	0.04	0.04	0.03	0.05	0.29	6.22
									Count 6.00 λ max 6.263 CI 0.053 **CR 0.04** Constant 1.24

Appendix 6. Rank and weight table for watershed (A) and reach (B) input criteria datasets for the Lake Erie study region.

A. Watershed-level data ranks

	Criteria (Watershed Surrogate)					
	Abundance of Coarse Substrate	Abundance of Fine Substrate	Temperature	Flow	Depth	Benthos Quality
Rank	Proximity to Ag./Dev. Land (m)	Proximity to Wetland Habitat (m)	Canopy Closure (%)	Slope (degree)	Subwatershed Area (km^2)	Impervious Surface Cover (%)
5 (most suitable)	361.8-3650.9	0.0-90.5	32.3-96.0	7.2-59.8	571.1-829.0	0.0-0.9
4	58.5-361.8	90.5-313.0	10.7-32.3	1.4-7.2	406.7-571.1	0.9-3.5
3	30.5-58.5	313.0-859.9	3.3-10.7	0.7-1.4	301.8-406.7	3.5-11.1
2	27.9-30.5	859.9-2204.6	0.8-3.3	0.6-0.7	234.9-301.8	11.1-33.7
1 (least suitable)	0.0-27.9	2204.6-5509.9	0.0-0.8	0.0-0.6	130.0-234.9	33.7-100.0
Equal Weights (%)	16.6	16.6	16.6	16.6	16.6	16.6
Final Weights (%)	38.3	16.6	7.7	20.4	5.7	11.3

B. Reach-level data ranks

	Criteria (Reach Surrogate)					
	Abundance of Coarse Substrate	Abundance of Fine Substrate	Temperature	Flow	Depth	Benthos Quality
Rank	Proximity to Coarse Geology (m)	Proximity to Fine Geology (m)	Temperature Classification	Mean Flow (Q50) (cm^3/s)	Strahler Stream Order	Cumulative Habitat Disturbance
5	0.00-1133.19	0.0-35.85	COLD	281.38-4140.76	4.93-7	Very Low
4	1133.19-3796.37	35.85-174.03	COOL-COLD TRANS.	32.99-281.38	3.34-4.93	Low
3	3796.37-10055.20	174.03-706.61	COOL-WARM TRANS.	17.01-32.99	2.13-3.34	Moderate
2	10055.2-24764.33	706.61-2759.28	WARM	15.98-17.01	1.21-2.13	High
1	24764.33-59332.85	2759.28-10670.76	VERY WARM	0.00-15.98	0-1.21	Very High
Equal Weights (%)	16.6	16.6	16.6	16.6	16.6	16.6
Final Weights (%)	38.3	16.6	7.7	20.4	5.7	11.3

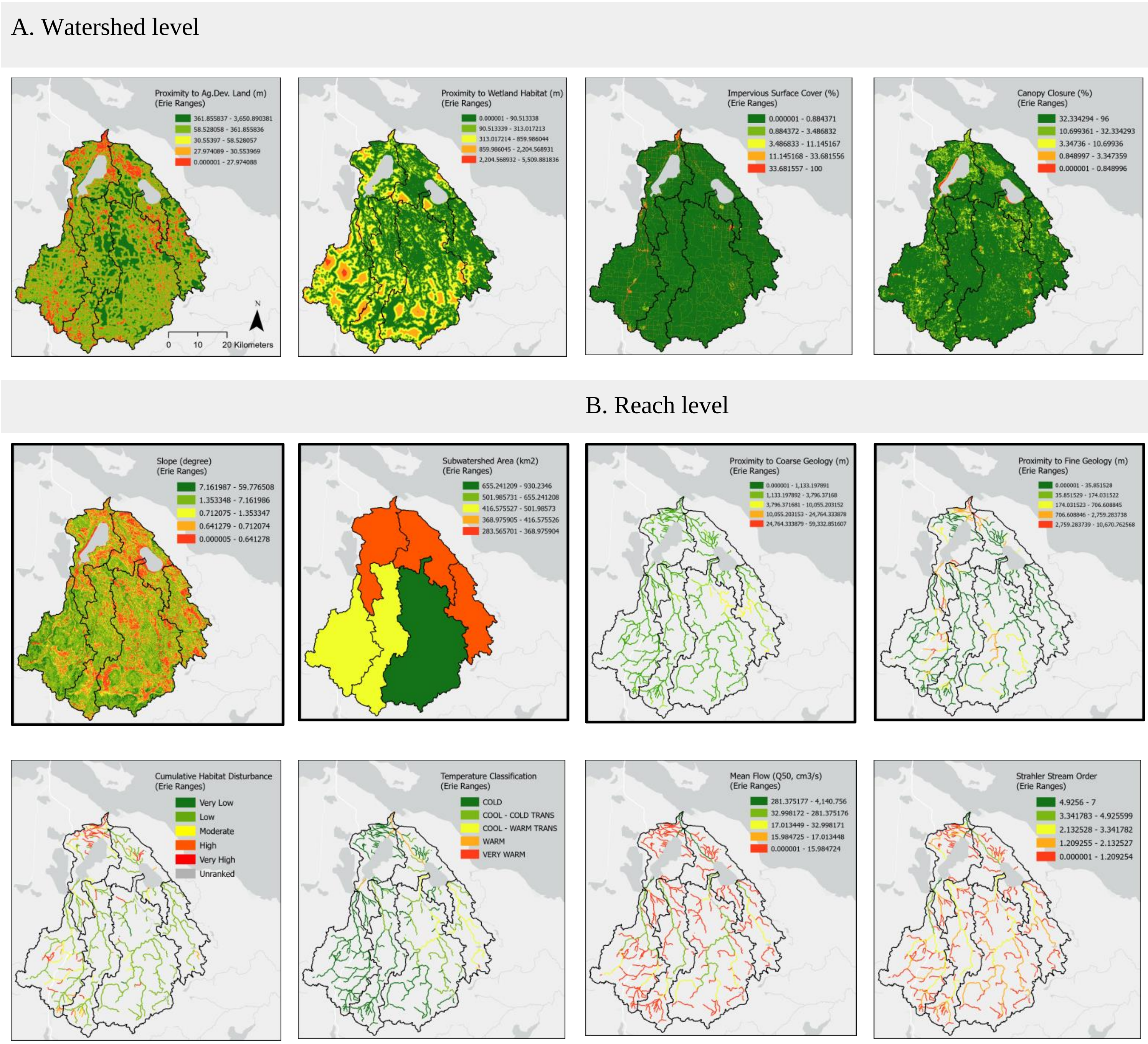
Appendix 7. Rank and weight table for watershed (A) and reach (B) input criteria datasets for the Black River watershed.

A. Watershed-level data ranks

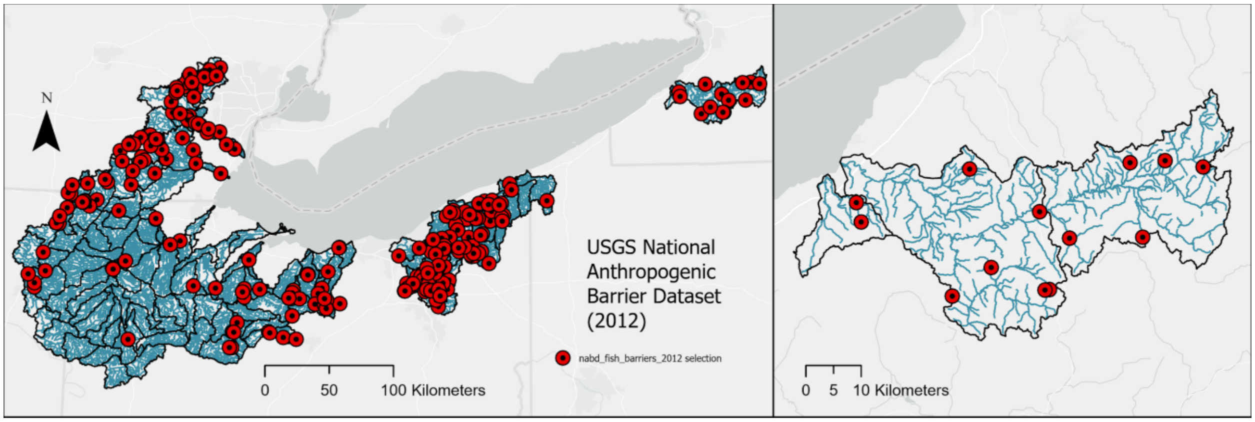
	Criteria (Watershed Surrogate)					
	Abundance of Coarse Substrate	Abundance of Fine Substrate	Temperature	Flow	Depth	Benthos Quality
Rank	Proximity to Ag./Dev. Land (m)	Proximity to Wetland Habitat (m)	Canopy Closure (%)	Slope (degree)	Subwatershed Area (km^2)	Impervious Surface Cover (%)
5 (most suitable)	667.02-1667.09	0.00-14.09	88.27-99.00	10.73-31.86	655.24-930.23	0.00-0.39
4	260.20-667.02	14.09-63.75	83.27-88.27	3.55-10.73	501.99-655.24	0.39-1.85
3	94.70-260.20	63.75-238.66	72.55-83.27	1.11-3.55	416.58-501.99	1.85-7.22
2	27.39-94.70	238.66-854.83	49.50-72.55	0.28-1.11	368.98-416.58	7.22-27.03
1 (least suitable)	0.00-27.39	854.83-3025.39	0.00-49.50	0.00-0.28	283.57-368.98	27.03-100.00
Equal Weights (%)	16.6	16.6	16.6	16.6	16.6	16.6
Final Weights (%)	38.3	16.6	7.7	20.4	5.7	11.3

B. Reach-level data ranks

	Criteria (Reach Surrogate)					
	Abundance of Coarse Substrate	Abundance of Fine Substrate	Temperature	Flow	Depth	Benthos Quality
Rank	Proximity to Coarse Geology (m)	Proximity to Fine Geology (m)	Temperature Classification	Mean Flow (Q50) (cm^3/s)	Strahler Stream Order	Cumulative Habitat Disturbance
5	0.00-28.07	0.00-30.01	COLD	214.68-1241.17	4.02-5	Very Low
4	28.07-136.25	30.01-122.39	COOL-COLD TRANS.	37.00-214.68	3.08-4.02	Low
3	136.25-553.20	122.39-406.76	COOL-WARM TRANS.	6.25-37.00	2.09-3.08	Moderate
2	553.20-2160.24	406.76-1282.06	WARM	0.92-6.25	1.07-2.09	High
1	2160.24-8354.13	1282.06-3976.29	VERY WARM	0.00-0.92	0.00-1.07	Very High
Equal Weights (%)	16.6	16.6	16.6	16.6	16.6	16.6
Final Weights (%)	38.3	16.6	7.7	20.4	5.7	11.3



Appendix 8. Ranked input criteria at the watershed and reach levels for the Black River, MI, based on ranking schemes developed for the 16 Lake Erie watersheds as reported in Figures 2-3 and Appendix 6.



Appendix 9. Overlay of the USGS National Anthropogenic Barrier Dataset (2012) on all river segments in the 16 Lake Erie tributaries assessed in this study.