

A LANDSCAPE PERSPECTIVE ON THE DISTRIBUTION AND HARVEST OF NORTH
AMERICAN RIVER OTTERS IN MICHIGAN IN RELATION TO PREY AVAILABILITY

By

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ABSTRACT

A LANDSCAPE PERSPECTIVE ON THE DISTRIBUTION AND HARVEST OF NORTH AMERICAN RIVER OTTERS IN MICHIGAN IN RELATION TO PREY AVAILABILITY

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The North American river otter (*Lontra canadensis*) is considered a top predator in many freshwater systems in Michigan and throughout the continent of North America. As a semi-aquatic piscivore, river otters serve a critical role in linking aquatic and terrestrial ecosystems yet the current understanding of river otter distribution is limited to relatively small spatial scales. A landscape analysis was used in this study to assess river otter distribution in Michigan; this approach allowed for broad spatial assessment at the state scale and furthermore assessed the importance of both aquatic and terrestrial habitat components. I designed and evaluated an approach to identify landscape features related to river otter distribution in Michigan at two spatial resolutions with specific attention given to the relationship between river otter occurrence via trapping records and prey availability. A multiple linear regression model identified surface water quantity and wetland configuration, along with percent crop cover, to be effective parameters in predicting river otter harvest at the county scale (adjusted $R^2 = 0.67$). At the local catchment scale, human population density, number of road crossings, percent crop cover, and percent canopy cover explained 62% of a predictive, maximum entropy model of species occupancy (AUC = 0.733). This analysis helps to identify the river otter's large scale habitat needs, highlighting the importance of connectivity between aquatic and terrestrial systems for effective, landscape-based management of fish and wildlife resources.

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INTRODUCTION

A landscape approach to ecology includes the study of how systems function in the context of the physical structure of the landscape at varying spatial scales (Hobbs et al. 1993). Examples of physical landscape structure include land cover characteristics such as the amount of forest cover (composition) or the pattern of forest and nonforest patches (configuration) within a given area. This spatially-explicit perspective is useful in natural resource management because it fosters a systems-based approach that spans disciplines, spatial and temporal scales, and jurisdictional boundaries (Liu and Taylor 2002, Rabeni and Sowa 2002). A landscape perspective of a region's ecology accounts for the highly integrated nature of aquatic and terrestrial landscape elements rather than isolating patches of landscape, such as water from forest, as self-contained ecosystems. Within the landscape ecology framework, the land-water interface is commonly represented as a permeable and dynamic boundary with reciprocal flows of matter and energy (Fausch et al. 2002, Schlosser 1991). Although aquatic-terrestrial ecological linkages are recognized by managers, traditional management practices have failed to overcome barriers that inhibit landscape-based management of the fish and wildlife species that rely on these linked habitats (Dunning 2002, Schneider et al. 2002). For example, Taylor et al. (2002) point out that fisheries managers are often jurisdictionally bound to localized, in-stream habitat enhancement (i.e. placement of woody debris, gravel deposition) despite evidence that large, catchment scale processes (i.e. land use change, groundwater withdrawal) have a greater effect on fish community dynamics.

Semi-aquatic species are particularly vulnerable to extinction when managers do not use a landscape perspective that accounts for the entire spectrum of habitat types and connectivity

that are required through their life cycles (Bowne et al. 2006, Schneider et al. 2002) as these animals spend the majority of their lives in aquatic habitats yet require specific upland conditions in order to reproduce or colonize new areas (Carranza et al. 2012). This research uses a landscape approach toward understanding one semi-aquatic species' habitat needs, the North American river otter (*Lontra canadensis*, Coues 1877) in the State of Michigan, USA. The river otter fills a critical ecological role connecting terrestrial and aquatic landscape components by transporting aquatic-derived nutrients to terrestrial environments (Crait and Ben-David 2007). Until the time of European settlement, river otters exhibited one of the largest geographic ranges of any North American mammal (Anderson 1977). Their range encompassed all but the most arid southwestern deserts of the U.S. or permafrost covered regions of the arctic (Polechla 1988). By the 1960's however, river otters had been extirpated from over 70% of their United States (U.S.) range (Melquist and Dronkert 1987). The reasons for these declines were attributed to habitat loss (particularly wetland draining), water pollution, and overharvest (Deems and Pursley 1983, Polechla 1990, Toweill and Tabor 1982). Populations that remained intact in the conterminous U.S. were found in the Pacific Northwest, the coastal marshlands surrounding the Gulf of Mexico and Atlantic Ocean, and the northern Great Lakes regions of Minnesota, Wisconsin, and Michigan (Deems and Pursley 1983, Feldhamer et al. 2003).

Broadly speaking, these remnant populations were found in regions of the U.S. that had relatively low human population densities and/or abundant precipitation and surface water resources. These trends are purely observational, as no formal assessment of landscape drivers underlying river otter distribution exists at such a large scale (i.e. state, regional, continental). A founding principle of landscape ecology is that biological interactions between an organism its environment are scale-dependant (Levin 1992, Wiens 1989). For example, a tadpole will

perceive landscape features on a relatively small scale, such as the few square meters within an ephemeral pond, compared to an adult frog with the ability to interact with its environment on a scale of kilometers as it moves cross-country to colonize new wetland patches. Generally speaking, larger and more mobile organisms view their environment on broader spatial scales. River otters are highly mobile mammals yet most ecological studies of this organism were executed at small scales (river reach, single watershed). Large scale studies are useful in identifying ecological processes operating at such a scale (Wiens 1989) and therefore have the potential to highlight ecological processes otherwise undetected by smaller scale studies and thus assist in the management and conservation..

River otters are known to use a wide variety of terrestrial and aquatic landscape structures for socializing, denning, and foraging. Previous studies have documented otters foraging in lakes (Reid et al. 1994), wetlands (Newman and Griffin 1994), even man-made farm ponds (Ostroff 2001), but the vast majority of studies emphasize river otter's use of stream resources (Melquist et al. 2003) throughout their range. In Europe and Chile, large scale landscape studies (1500-9900 km²) have found Eurasian river otter (*Lutra lutra*) and Southern river otter (*Lontra provocax*) distribution to be strongly correlated to the amount of prey available in a watershed (Prenda and Granado-Lorencio 1996, Sepulveda et al. 2009). North American otter prey in the Upper Great Lakes region of the U.S. (Minnesota, Wisconsin, Michigan) consists primarily of fish (Knudsen and Hale 1968, Ryder 1955). Advances in remote sensing technology and landscape analysis have enabled fisheries scientists and managers to predict fish population dynamics at a continuous, large spatial scale (Zorn et al. 2011). Frissell et al. (1986) proposed a hierarchical framework to classify stream habitats using nested spatial units ranging in size from the river network (10³ m) down to the microhabitat (10⁻¹ m). Since then, numerous models have

used this hierarchical framework for the purpose of predicting overall fish abundance and assemblage structure in Michigan (Infante et al. 2006, Pace et al. 2004, Steen et al. 2008). These studies used landscape metrics that summarized climate, geology, and land cover in conjunction with historical stream fish sampling data to identify and predict patterns in fish community composition given the landscape features measured. The conceptual framework developed for these studies was adapted for use in the National River Fish Habitat Condition Assessment (Wang et al. 2011), which provides a continuous coverage of spatially nested landscape information on all river catchments in the U.S. My analysis implemented this theoretical framework in order to explore how well landscape features could predict river otter distribution, as fish abundance is considered a major influence on river otter habitat selection and production in smaller scale studies (Blundell et al. 2000, Melquist et al. 2003).

The goal of my study was to explore the distribution and harvest of river otters in Michigan in relation to landscape features and subsequent fish availability. My first objective was to develop a predictive model of river otter harvest at the county scale using landscape metrics relevant to fish resource quantity and quality. This afforded a broad perspective of both landscape composition and configuration features significant to river otter distribution. My second objective was to determine if landscape features known to affect fish habitat could effectively predict river otter distribution at the local catchment scale and if so, identify which of these local features were most useful in modeling river otter harvest. This large scale analysis was aimed to enhance resource managers' ability to understand and more effectively manage semi-aquatic species and the aquatic-terrestrial processes they represent.

METHODS

Study area

This study occurred throughout the state of Michigan, USA (Figure 1). Michigan is comprised of two peninsulas, divided by Lake Michigan and Lake Huron. The Upper Peninsula consists primarily of bedrock and coarse surficial geology which in part drives the cold and cool streams that characterize this portion of the state (Wang et al. 2003). The sand and gravel of the northern Lower Peninsula similarly facilitate high groundwater recharge in this region while more clay and fertile soils in the southern and eastern portions of the state result typically in low gradient, warm water streams. Land use consists primarily of managed forests in the north and agriculture in the south (Wang et al. 2008). Vegetation varies with latitude and geology, ranging from pines and spruces in the north to hardwoods such as sugar maple and oak in the south. The southern Lower Peninsula was originally a large expanse of wetlands that were heavily altered beginning in the mid-1800's for agricultural development (Karr et al. 1985). These patterns in hydrology and land cover have been shown to influence the quality of fish habitat and thus productivity (Hughes et al. 2006, Wang et al. 2008, Zorn et al. 2002) and are considered here in terms of river otter prey requirements across the landscape of Michigan.

Landscape features and river otter harvest at two spatial scales

By focusing on landscape characteristics known to affect fish community dynamics, I developed a state-wide analysis of otter distribution in relation to prey availability using spatially-explicit information on otter harvest and prey resource patches. For this study, I defined prey availability to be a function of the density and dispersion of water bodies (potential patches of prey) and quality of that prey's habitat. I hypothesized that the relative otter habitat suitability

of a location is dependent on the distance between food sources and the potential amount of fish available in each patch.

A patch is a basic unit of landscape structure; in this case it is an element in the landscape that provides otters with food. Patch quality and context (spatial configuration) influence how organisms interact with the landscape (Wiens et al. 2002). Because otters are obligate aquatic predators (Melquist et al. 2003), they must have access to surface water. Beyond this obligatory patch type requirement, there is little evidence to assume otters need anything more specific than water with fish in it. Some studies have suggested that otters select fish species based on their relative vulnerability, a function of prey size, abundance, and swimming ability (Melquist and Hornocker 1983, Serfass et al. 1990, Toweill 1974). Early studies of otter diets determined that these mammals were partial to fish such as minnows (family Cyprinidae, Umbridae) and suckers (Catastomidae) (Field 1970, Knudsen and Hale 1968) and thus otters were not competing directly with anglers for game fish (Ryder 1955). Unfortunately, relative abundance of these fish families in the field have not been measured in conjunction with otter diet analyses. Due to this observed diet plasticity of fish consumption, I broadly defined a resource patch to be any open water (stream, lake, or wetland).

River otter harvest was used as the dependant variable in my analysis of this species' distribution and relative abundance. The Michigan Department of Natural Resources (MDNR) collects otter harvest data on two spatial scales: the county and the township scale. Counties are political boundaries with an average area of 3,051 km². A township is defined as a one square mile unit in a grid covering the entire state; Michigan is comprised of 1,242 townships. Data were available for river otter harvest from 1989-2009. I selected a single trapping season for analysis which ran from October 25, 2006 thru April 15, 2007. This year is

associated with a relatively high price for otter pelts (Dhuey and Olsen 2010), which increased trapping effort and harvest for that season (Figure 2), therefore increasing the likelihood of otter detection (Poole and Mowat 2001). I assumed analyzing a single trapping season would reduce variation in reported harvest numbers due to temporally dynamic effects such as weather, pelt price, and bag limits. Otters are harvested for their pelts using jaw and body grip traps that are partially or fully submerged in shallow water near the banks of water bodies (Frawley 2007). Michigan residents are legally required to obtain a cost free otter harvest tag in order to trap and sell otter pelts. These pelts require inspection by the MDNR, at which time the date and location of harvest is collected. Harvest data were used to infer patterns in relative otter abundance at the county scale and otter occurrence at the local catchment scale; a conceptual diagram can be found in Figure 3.

County scale otter harvest

Michigan is comprised of 83 counties (Figure 1): 15 in the Upper Peninsula and 68 in the Lower Peninsula. In order to identify key landscape features in river otter distribution and harvest, I analyzed 12 land cover and patch configuration metrics summarized at the county scale (Table 1) in order to develop a multiple linear regression model of river otter relative abundance. Relative abundance was defined as the number of otters harvested within a county in the 2006 trapping season. I excluded counties with no reported trapping effort. Effort data was collected by the MDNR via mail-in survey at the end of the season and is reported as the total number of nights traps were set for otter or beaver, as otters are often caught incidentally when beaver are targeted. Poole et al. (2001) found that effort reported by trapper affidavits was not a good indicator of catch per unit effort due to incidental trapping. Based on preliminary analysis of the MDNR harvest data, I believe this to be true in Michigan as well and therefore did not use a

catch per unit effort as a response variable. Percent land use/land cover class (i.e. forest, open water) per county was measured using the satellite-derived National Land Cover Database (Homer et al. 2007). The National Hydrography Dataset Plus (USEPA and USGS 2010) was used to measure the number, type, and density of water bodies present in each county. Although the NLCD has an open water land cover class, NHDPlus has a finer resolution (1:100,000) which was important in differentiating types of open water (e.g. lakes versus streams) and linear, dendritic pattern of streams and associated floodplains demanded this resolution. These layers were analyzed using ArcGIS 10.0 (ESRI 2011). The 17 NLCD land cover classifications were reclassified into eight different categories in order to address the large scale questions at an equally broad resolution. For example, by default NLCD defines three different types of forest cover: deciduous, evergreen, and mixed. These three classifications were combined in to one forest classification. Reclassification also reduced the spatial autocorrelation bias, as evergreen forests are primarily in northern Michigan and deciduous hardwoods are in southern Michigan. Landscape pattern analysis was executed using the statistical program FragStats (McGarigal and Marks 1995) which characterized the relative position of open water and wetland NLCD land cover classes. Specifically, I used the interspersions/juxtaposition index (IJI) to characterize the relative connectivity of prey resources. The IJI measured the amount of waterbody patch adjacencies, yielding a measurement of how well these aquatic land cover classes are intermixed among other classes in the county (McGarigal and Marks 1995). Regardless of patch size (cell adjacencies of same class), interspersions will reach a maximum when water and wetland patch types are equally adjacent to other patch types (Figure 4).

All landscape composition and configuration metrics were transformed for normality and only significant variables ($p < 0.05$), as identified by Pearson's correlation test, were included in

the regression analysis (Appendix A). Variable selection and model comparisons were executed in the R statistical software package (R Core Development Team 2012). The final model was selected using a stepwise comparison analysis using Akaike's Information Criterion (Akaike 1973), run in both directions.

Local catchment scale otter harvest

This portion of the analysis used an occupancy modeling approach to estimate the relationship between otter harvest distribution and fish habitat characteristics. With no effort data available at the township resolution and an average otter harvest per township of less than 0.2, I analyzed township scale harvest as presence-only information: all townships were categorized in a binary fashion as either having otters present or unknown. In order to consider fish habitat characteristics at this resolution, I dissolved all townships into local catchments (Figure 5), the basic spatial unit within the framework of the National Fish Habitat Action Plan (NFHAP, Esselman et al. 2011, Wang et al. 2011). Local catchments were topographically defined as the land area that drains laterally to an individual, confluence to confluence stream reach (USEPA and USGS 2010). There are a total of 32,002 local catchments in Michigan. Fish habitat metrics had been previously assembled by the NFHAP and National River Fish Habitat Condition Assessment (Wang et al. 2011).

I used a maximum entropy analytical approach, adapted from Elith et al. (2011), to generate a predictive occupancy model based on the likelihood of otter harvest in the state of Michigan. This model minimizes the relative entropy (randomness) between two probability densities, a ratio defined by presence sites versus random (background) sites on the landscape (Elith et al. 2011). This raw output is transformed in to the following logistic equation:

$$n(\mathbf{z}) = \log [f_1(\mathbf{z})/f(\mathbf{z})]$$

where $f_1(\mathbf{z})$ is the conditional density of local catchment (i.e. NFHAP) covariates at a site with otter and $f(\mathbf{z})$ is the unconditional (random) density of covariates across Michigan. Thus, the logit score gives a value in which to compare between catchments. The default value I used to compare was set to 0.5, i.e. if there is no relationship between otter harvest versus a given habitat variable, we would expect to see a 50% probability (binary, random probability) that otters are present in that catchment (Elith et al. 2011).

A total of 20 anthropogenic disturbance variables were used as covariates, defined at the local catchment scale as part of the national assessment of fish habitats (Wang et al. 2011, Table 2) in the MaxEnt software package (Phillips and Dudik 2008). Otters were considered present in 1,876 local catchments after dissolving townships in to local catchments. Ten thousand randomly selected local catchments were used as background in the MaxEnt analysis. Background data are random landscape units (local catchments in this case) chosen without regard to otter presence. However, catchments within counties with no trapping effort were ineligible to be selected as background data. No sampling was known to occur in these counties along with catchments in Pictured Rocks National Lakeshore and the Sleeping Bear Dunes National Park, where all trapping was prohibited. Default MaxEnt settings were used for model training and a 10-fold cross-validation was used to measure predictive performance and estimates of uncertainty (Elith et al. 2011). The approach is nearly identical to that done by Elith et al. (2011) in their explanation of MaxEnt application toward modeling fish species distribution at a comparable spatial grain- the river segment.

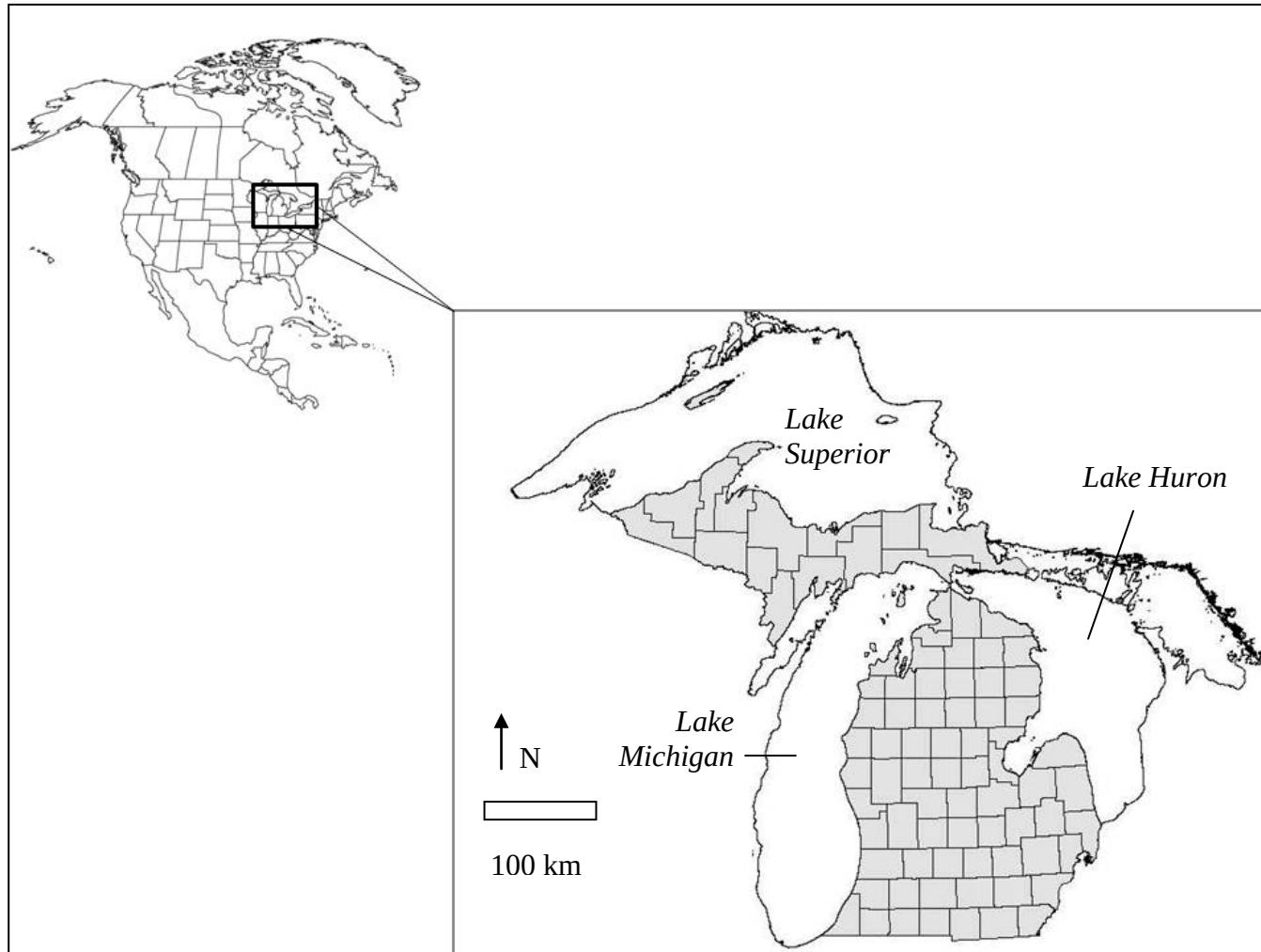


FIGURE 1. Study area for river otters of Michigan, USA (highlighted in grey). Surrounding three Great Lakes are included for reference, along with the political boundaries for the 83 counties that comprise the state of Michigan.

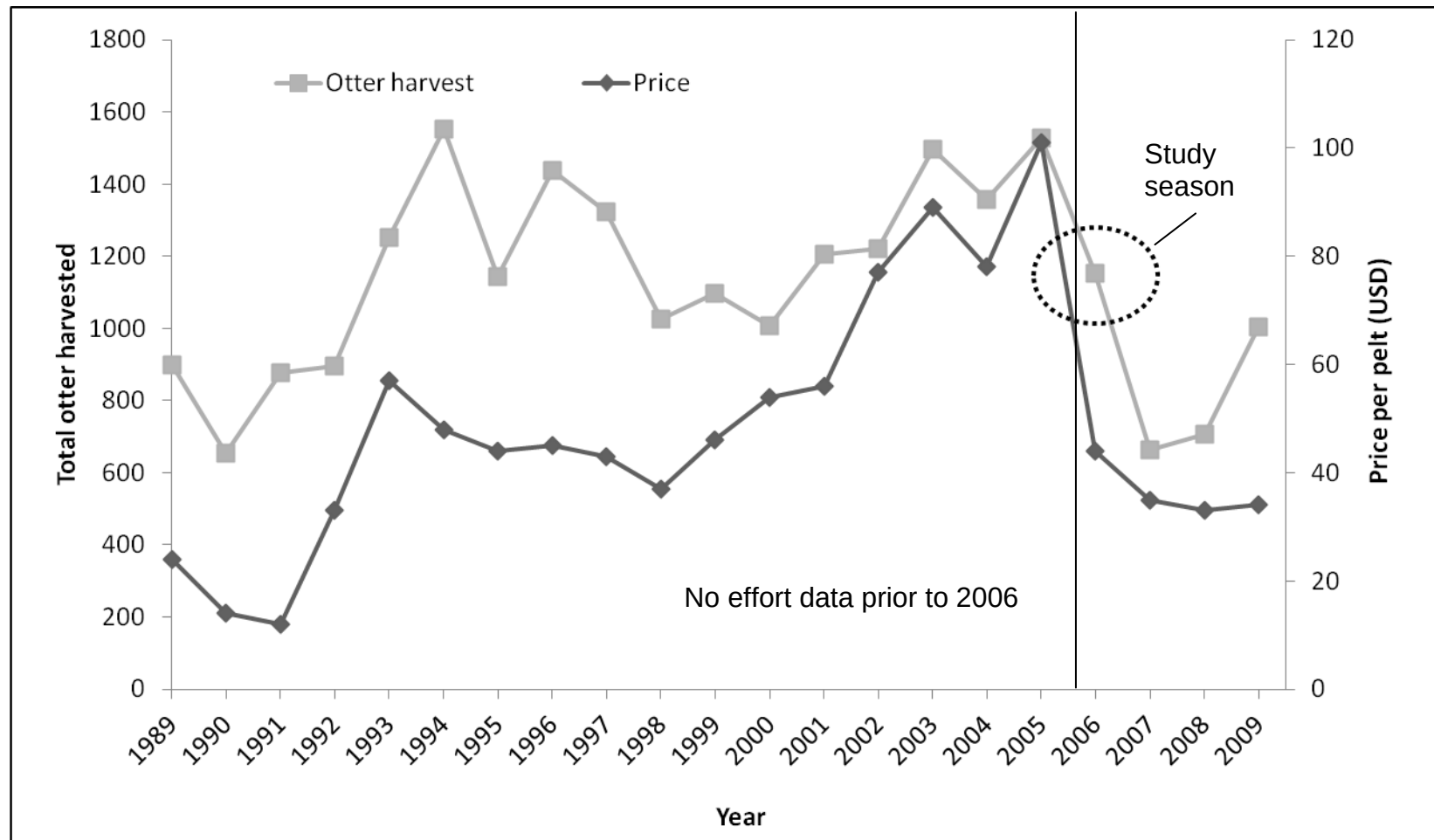


FIGURE 2. Total river otter harvest in Michigan and historical otter pelt price for the upper Great Lakes region of the U.S. (Michigan, Minnesota, Wisconsin). Pelt price was estimated by the Wisconsin Department of Natural Resources (WDNR 2009).

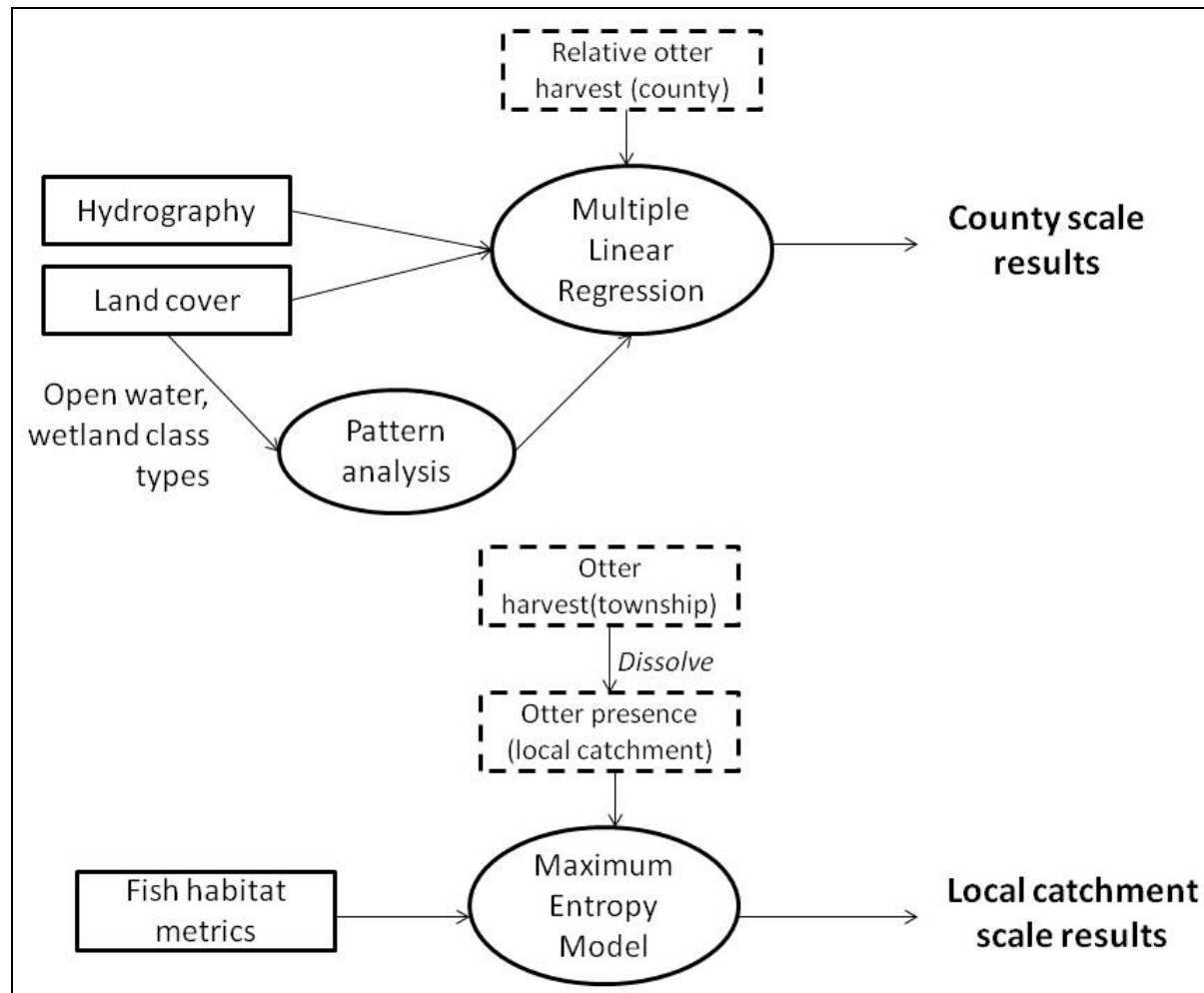


FIGURE 3. Conceptual diagram for river otter harvest analyzed at two spatial scales, the county and the local catchment scale. This approach was used to identify how landscape features affected harvest distribution in relation to fish availability.

TABLE 1. Landscape variables used to model river otter harvest in Michigan, USA at county scale. Landscape spatial data were derived from the National Land Cover Database (abbreviated NLCD 2001), National Hydrography Database Plus (abbreviated NHDPlus).

Category	Abbreviation	Description (units)	Source	Resolution	Mean	Range
Landscape composition						
	Water	Open water (%)	NLCD 2001	30 m	2.8	0.24-12.7
	Dev	Developed (%)	NLCD 2001	30 m	8.6	2.2-32.2
	Forest	Forest (%)	NLCD 2001	30 m	39	6.2-82.1
	Shrub	Shrub/Scrub (%)	NLCD 2001	30 m	1.4	0.05-4.94
	Grass	Grassland/Herbaceous (%)	NLCD 2001	30 m	6.3	0.49-16.6
	Crop	Cultivated crops & Pasture (%)	NLCD 2001	30 m	21.8	0.057-73.2
	WtInd	Woody/Herbaceous Wetland (%)	NLCD 2001	30 m	19.5	7.09-53.116
	stream_st	Stream length/County area (km/km2)	NHDPlus	1:100,000	1.90E-03	9.5E-05-9.91E-03
	wtrbdA_km2	Area of waterbodies/County area	NHDPlus	1:100,000	7.57E-05	8.6E-6-1.00E-3
	numwtrbd_km2	Number waterbodies/County area	NHDPlus	1:100,000	2.94E06	78.7E3-17.6E6
Patch configuration						
	WATER_ IJI	Interspersion / Juxtaposition Index-Open Water	NLCD 2001	30 m	63.99	39.43-88.92
	WTL_ IJI	Interspersion /Juxtaposition Index-Wetlands	NLCD 2001	30 m	61.34	29.6-83.3

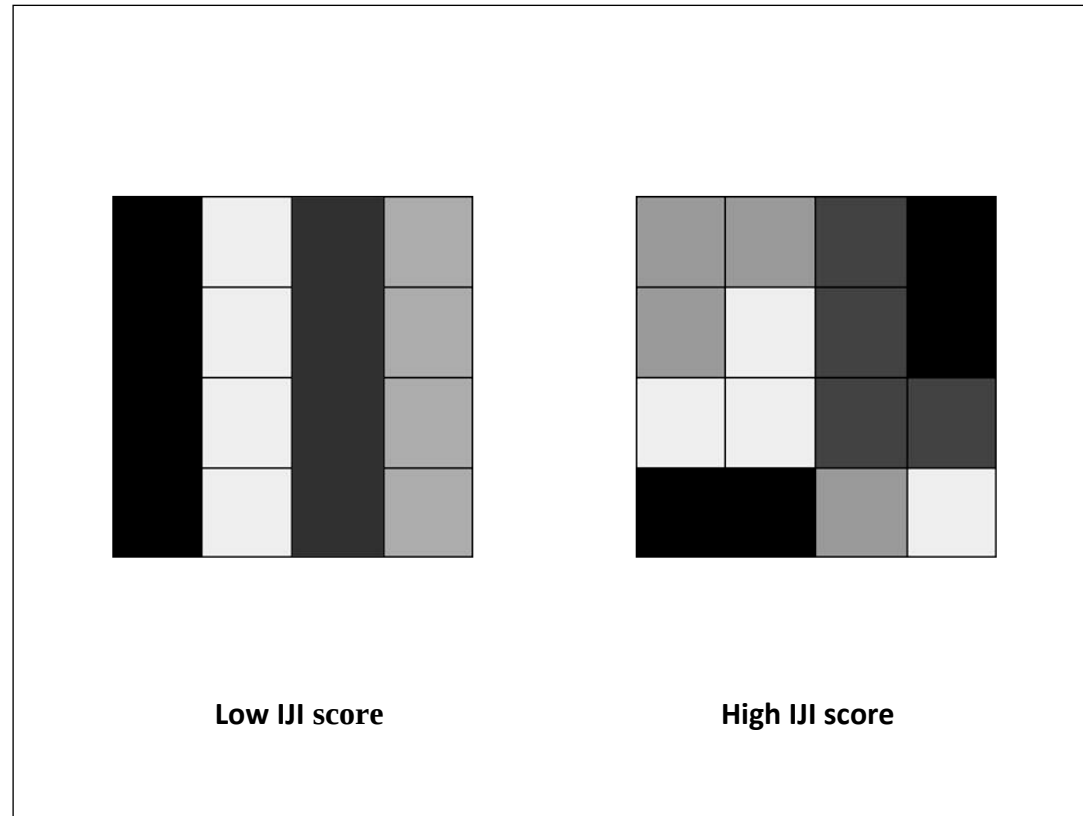


FIGURE 4. Interspersion and juxtaposition index (IJI) comparison for two landscapes with identical numbers of classes and area for each class. IJI reaches a maximum when all classes are equally adjacent to each other. Adapted from Eiden et al. 2012.

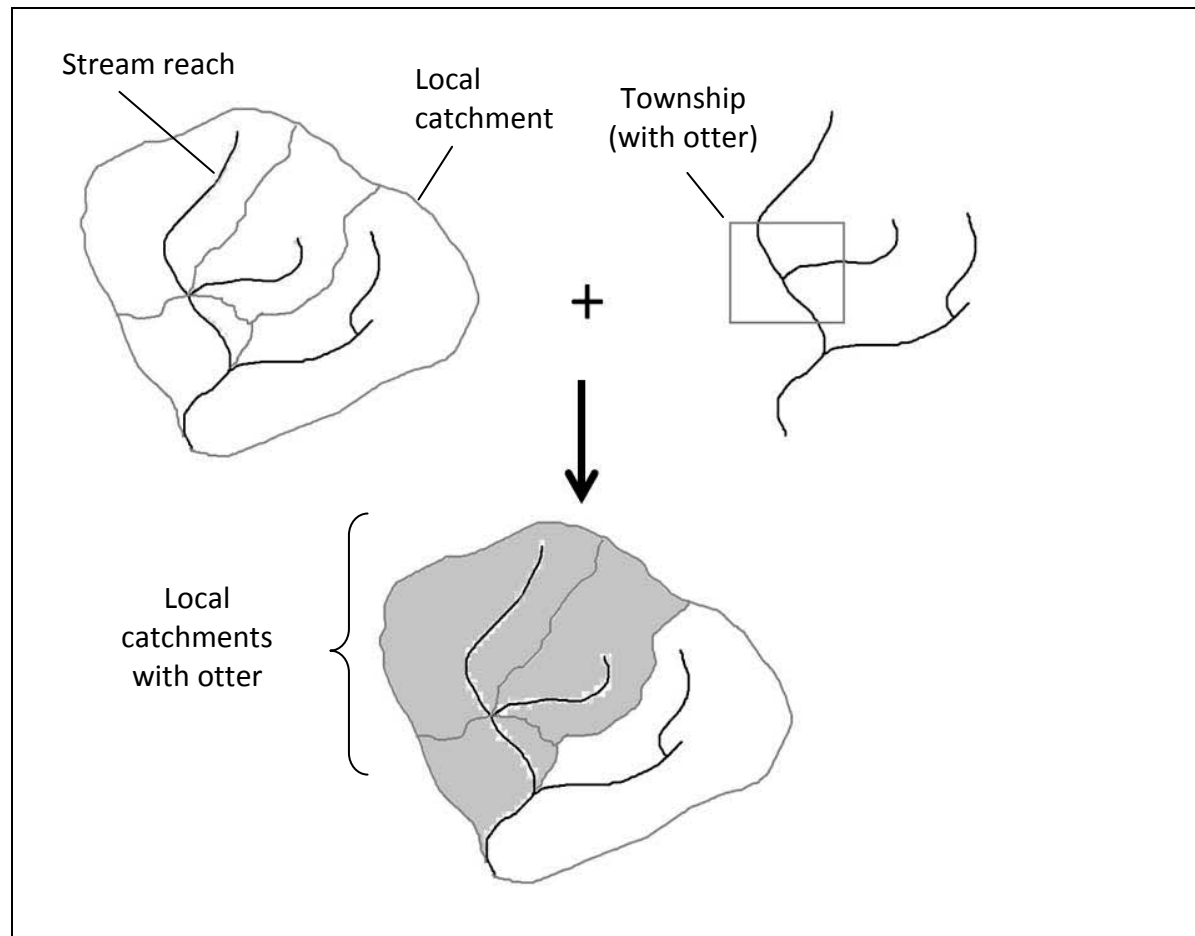


FIGURE 5. Process used to dissolve township (political boundaries) into hydrological boundaries of the local stream catchment for MaxEnt analysis of river otter harvest. All local catchments that intersected a township with river otter harvest were considered an occurrence.

TABLE 2. Landscape variables used in the assessment river otter habitat in Michigan at catchment scale with associated units, resolution, quartile values, means, and source of data. NLCD = National Land Cover Dataset; USGS = US Geological Survey; NHDPlus = National Hydrography Database Plus; USDA = US Department of Agriculture; NOAA = National Oceanic and Atmospheric Administration; USACE = US Army Corps of Engineers; EPA = US Environmental Protection Agency. Adapted from Wang et al. 2011.

Abbreviation	Description	Units	Resolution	Quartile		Mean	Source
				25%	75%		
GWindex	Groundwater index	base flow/total flow * 100%	1:250K	59.00	72.00	63.25	USGS
Canal	Length of streams designated canal/ditch	km	1:100K	0	0	93.32	NHDPlus
Slope	Mean catchment slope	degrees	1:100K	0.36	18.00	1.42	NHDPlus
UrbanL	Developed, open and low % intensity		30 m	0	8.18	7.62	NLCD 2001
UrbanM	Developed, medium intensity	%	30 m	0	0	0.63	NLCD 2001
UrbanH	Developed, high intensity	%	30 m	0	0	0.23	NLCD 2001
Forest	Forest, all classes	%	30 m	11.05	59.99	37.13	NLCD 2001
Shrub	Shrub/Scrub	%	30 m	0	0.77	0.84	NLCD 2001
Grass	Grassland/Herbaceous	%	30 m	0	5.97	4.45	NLCD 2001
Pasture	Pasture/hay	%	30 m	0	7.00	5.41	NLCD 2001
Crops	Cultivated crops	%	30 m	0	24.48	15.10	NLCD 2001
Barren	Bare rock/sand/clay	%	30 m	0	0	0.76	NLCD 2001
WetInd	Wetlands	%	30 m	5.19	32.46	23.17	NLCD 2001
Water	Open water	%	30 m	0	1.22	4.64	NLCD 2001
Canopy	Tree canopy cover	%	1:100K	22.76	66.40	44.82	NHDPlus
Popdens	Human population density	#/km ²	1 km	1.15	14.57	21.42	NOAA
Roadcr	Road crossing density	#/km ²	1:100,000	0	2	1.01	US Census 2000

TABLE 2 (cont'd)

Abbreviation	Description	Units	Resolution	Quartile		Mean	Source
				25%	75%		
Roadlen	Road density	m/km ²	1:100,000	386.7	6603	6032	US Census 2000
Cattle	Cattle density in farms	#/acre * 10,000	1:100,000	684	1317	1035	USDA
Imperv	Impervious surfaces	%	30 m	0.05	1.34	1.78	NLCD 2001
SO	Strahler stream order	NA	1:100,000	1	1	1.28	NHDPlus
Dams	Dam density	#/km ²	NA	0	0	0.02	USACE National Inventory 2005
Mines	Mines or mineral processing plants	#/km ²	NA	0	0	0.005	USGS
EPA	Pollutant Release Sites	#/km ²	NA	0	0	0.04	EPA

RESULTS

County Scale otter harvest

A state total of 1,0171 river otters (SE = 39, $\alpha = 0.05$) were reported captured in Michigan during the 2006 trapping season. Of this total, 1,017 (95%) were catalogued by the MDNR, spatially referenced, and used in this analysis. There was a north-south longitudinal gradient apparent in harvest numbers with northern counties generally reporting more harvested river otters (Figure 6). Over half (64%) of all otters harvested in the 2006 trapping season were captured in the 15 counties of the Upper Peninsula.

The best performing linear regression model that predicted total otter harvest based on the aforementioned landscape metrics selected three parameters as described in the following equation:

$$N = 7.99(\mathbf{Water}) - 2.03(\mathbf{Crop}) - 0.054(\mathbf{Wetland\ IJI}) + 4.8$$

where N is the total number of otter harvested per county (adjusted $R^2 = 0.67$, $p = 1.93 \times 10^{-14}$).

More open water in the catchment was generally associated with an increase in otters harvested while greater crop cover was indicative of fewer otters harvested. The wetland IJI was inversely proportional to otter harvest, meaning that more dispersed wetland patches throughout the county would increase the likelihood of otter harvest. Conversely, fewer and more clumped wetland patches were correlated with lower otter harvest numbers. Inclusion of development, forest, wetland, and stream length variables did not significantly strengthen model performance according to the AIC analysis.

Local catchment scale otter harvest

The maximum entropy analysis generated a predictive model of otter harvest at the local catchment scale, with an area under the curve of 0.733 (sd = 0.016), indicating moderate predictive power (Viña et al. 2010). Of the 24 fish habitat variables used to characterize the local catchment, the top four variables cumulatively explained 62% of the variance in the model (Table 3). In order of percent contribution, these variables were human population density, number of road crossings, percent crop cover, and percent tree canopy cover. The response curves for each of these four variables can be found in Figure 7, which shows that three of these variables, human population density, percent crop cover, and percent tree canopy cover, exhibited an exponential decline in likelihood of otter occurrence as the intensity of human disturbance and canopy cover increased. Conversely, the number of road crossings has an overall positive relationship, with likelihood of otter harvest increasing with an increase in the number of roads. The remaining 19 variables contributed to less than 5.5% of the predictive model of likelihood of otter harvest.

According to the predicted otter habitat suitability map (Figure 8), highly suitable local catchments (HSI score > 0.7) are abundant and relatively dispersed in the Upper Peninsula and the northern Lower Peninsula. These are regions of the state with relatively low human population densities compared to southern regions, and agricultural land use is less prominent. A small number of suitable catchments were predicted in the southeastern region of the Lower Peninsula.

TABLE 3. Relative contribution of fish habitat variables (NFHAP 2006) in analysis of 2006 river otter occupancy in local catchments in Michigan to MaxEnt model. Percent contribution refers to the regularized gain in the model as each variable is added.

Variable	Percent Contribution
PopDens	22.5
Roadcr	19.4
Crops	11.7
Canopy	8.3
Pasture	5.9
Roadlen	5.4
GWindex	5.1
Shrub	4.3
Wetland	4.3
Water	2.9
Cattle	2.4
Barren	1.1
UrbanL	1.0
Stream Order	0.9
Forest	0.9
Slope	0.7
UrbanM	0.6
Imperv	0.6
Dams	0.5
Canal	0.5
Mines	0.4
EPA	0.3
Grass	0.2
UrbanH	0.1

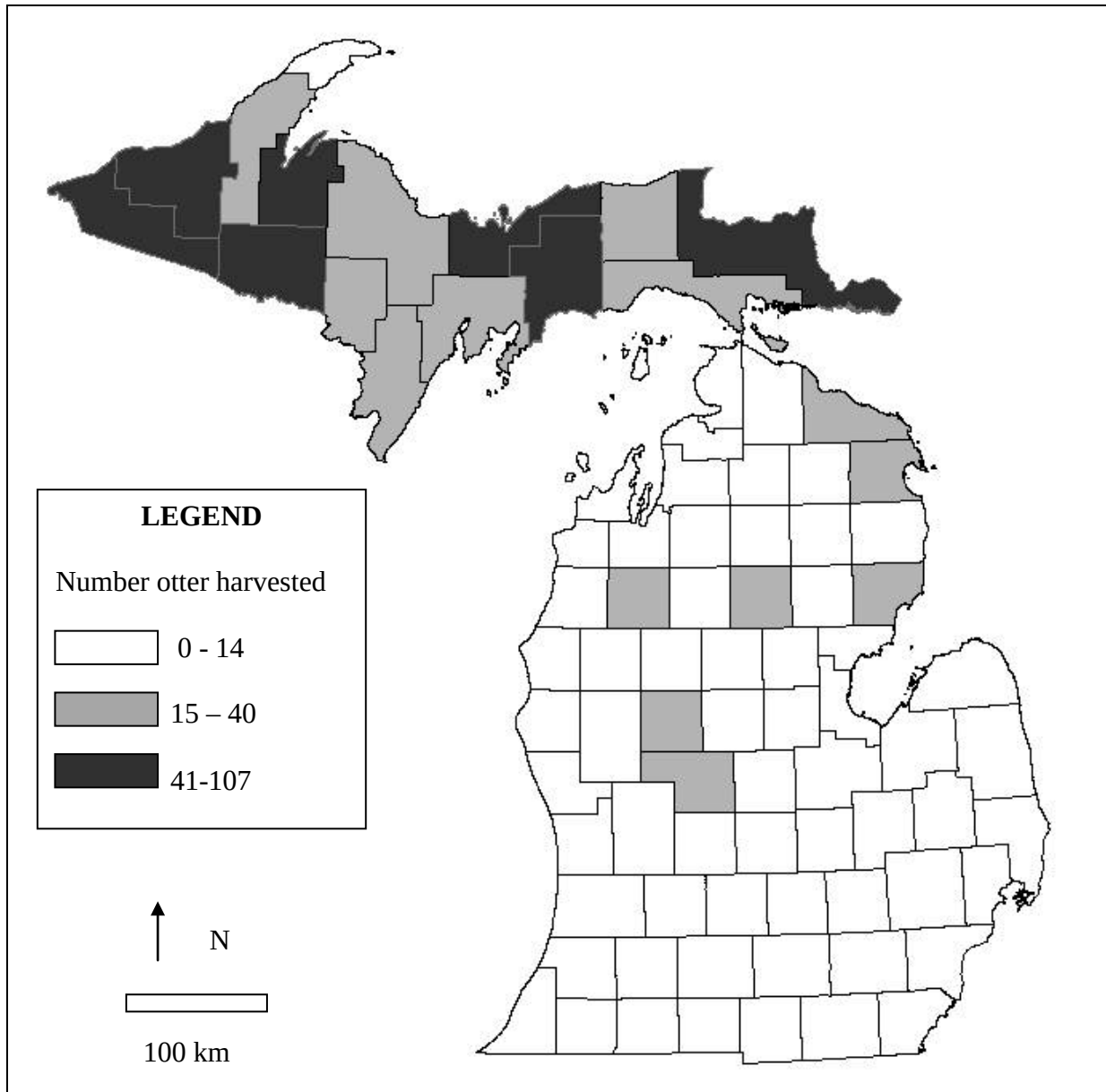


FIGURE 6. River otter harvest by county for 2006 in Michigan. Each county is classified by number of otters registered with the Michigan Department of Natural Resources.

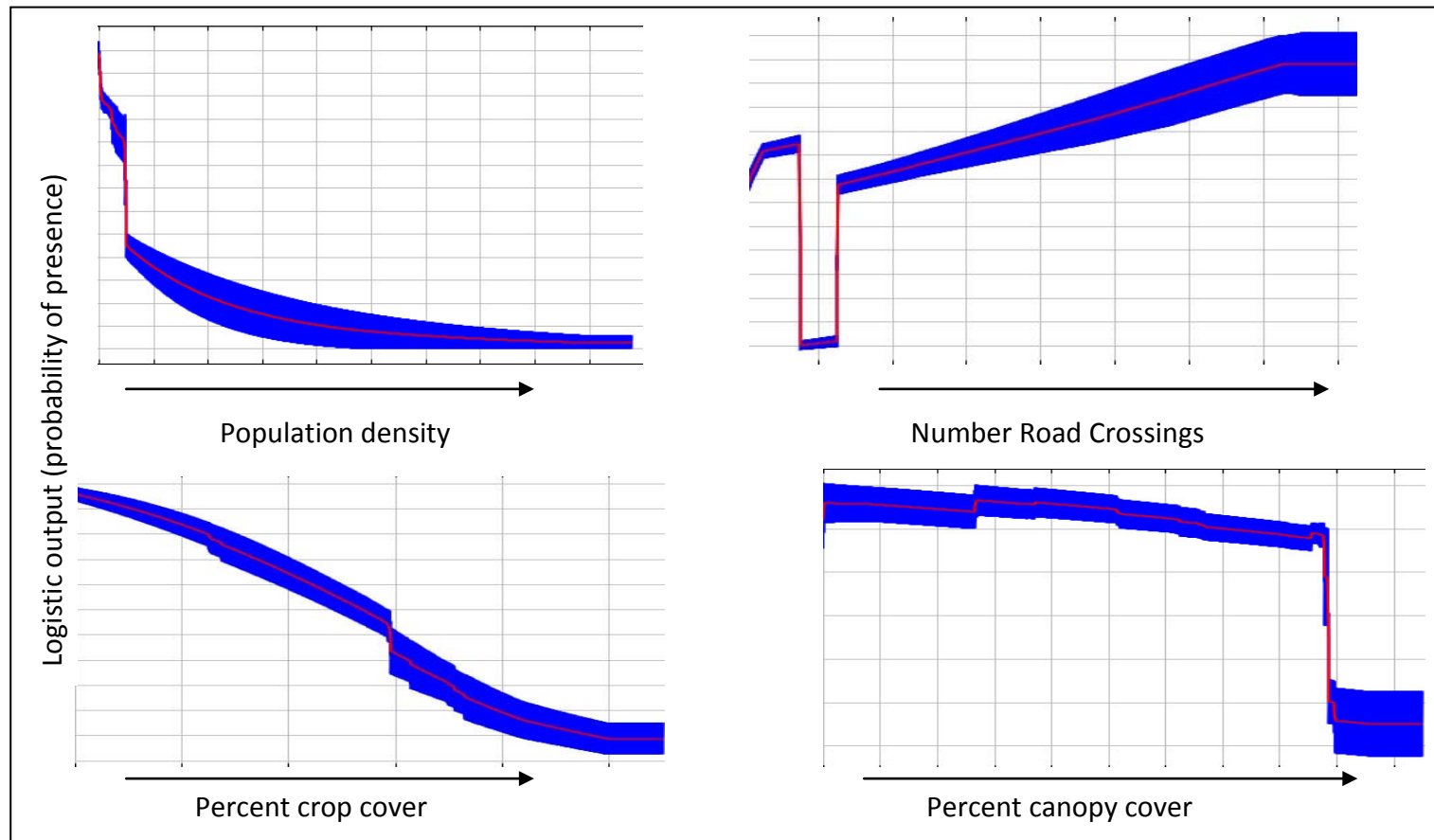


FIGURE 7. Response curves for top four fish habitat variables (NFHAP 2006) used in MaxEnt model of otter occurrence in local catchments in Michigan. The curves show how the logistic prediction changes as each environmental variable is varied, keeping all other environmental variables at their average sample value. Red is the mean response after ten replicate runs and blue is one standard deviation. Variables and their respective percent contribution are human population density (22.5%), number of road crossings per catchment (19.4%) , percent crop cover (11.7%), percent tree canopy cover (8.3%). *For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this thesis.*

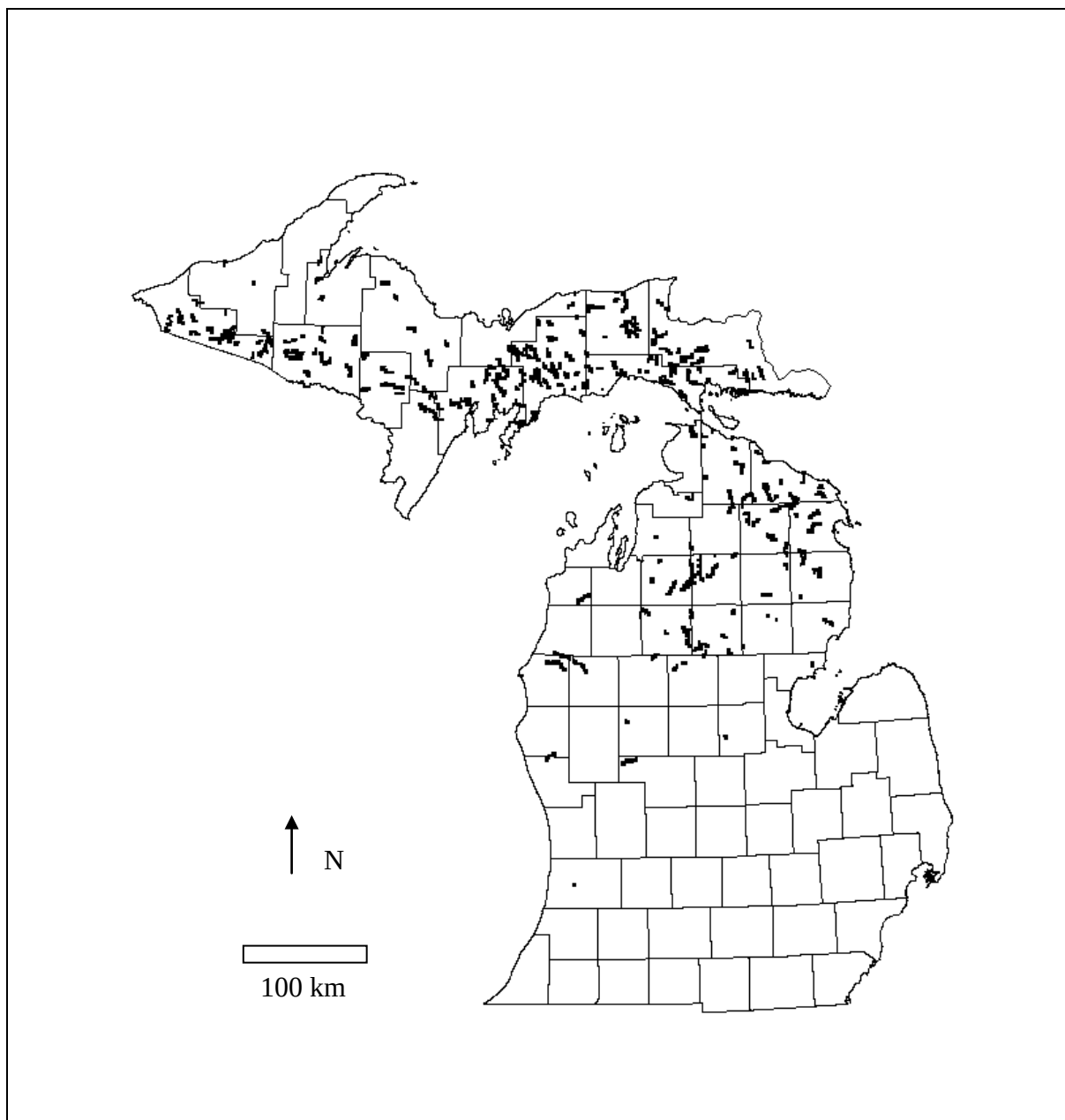


FIGURE 8. Local stream catchments in Michigan predicted to have >70% likelihood of river otter occurrence according to a MaxEnt model of harvest-only location (in bold). 24 landscape variables were used from the National Fish Habitat Action Plan database (Esselman et al. 2011). County delineations are included for reference.

DISCUSSION

The regression model that best predicted the number of river otters harvested per county included percent open water, crop cover, and the wetlands interspersed/juxtaposition index. Because river otters are piscivores (Knudsen and Hale 1968, Reid et al. 1994) I expected to see water and wetland composition and pattern metrics to be important in predicting otter abundance at this scale given the assumption that any water or wetland patch containing fish could serve as a potential food resource. Under this assumption, increased open water would increase the foraging opportunities available to river otters. High interspersed of wetlands equates to less travel time between wetland patch types, which would benefit an otter's high metabolism and their need for readily available prey. Extensive movement between wetland and water patch types would be costly for a carnivore that requires daily replenishment of 20% of its body weight (Dekar et al. 2010) in aquatic-derived prey. Therefore, when one patch is reduced or exhausted of fish, the otter must find a new resource patch in order to satisfy its energetic needs. As such, landscapes with an abundance of readily accessible water and wetlands may support higher densities of otters, assuming that these waters maintain environments that promote fish production.

If total fish abundance was the best, singular predictive variable of river otter distribution as found for river otters in other regions (Blundell et al. 2000), I would have expected higher relative harvest in the southern and eastern portions of the state which generally have more warm water streams and increased nutrient inputs (Wang et al. 2008). Temperature and phosphorus have been determined to have a positive, effect on fish biomass for both streams (Steen et al. 2008, Zorn and Wiley 2006) and lakes (Hanson and Leggett 1982, Kitchell et al. 1974). This

relationship however is nonlinear, as hypereutrophic and anoxic conditions arise when water bodies are too warm or have an excessive amount of primary production.

The local catchment analysis suggests a positive relationship between otter presence and biotic integrity. Biotic integrity is defined as the ability of a system to support and maintain a balanced, integrated, adaptive community of organisms (Karr and Dudley 1981). Indices of biological integrity are multimetric tools used to rapidly assess the health of aquatic resources (Karr 1991). The basic approach compares numbers of indicator functional groups present to those found in the least disturbed reference conditions (Karr and Dudley 1981). The functional groups vary among approaches, such as measuring the number of native fish species present (Angermeier and Karr 1986), percent carnivorous fish species (Stewart et al. 2001), or number lithophilic fish species (Karr and Chu 2000). The NFHAP assessment (Esselman et al. 2011) used indicator fish groups such as these to identify the landscape-based sources of fish habitat degradation. While temperature and nutrient levels may suggest greater productivity in southern Michigan, the lack of river otter harvest in this area may suggest that either the fish are not as abundant or river otters' ability to access prey resources is limited.

Based on county scale results, I would hypothesize that the low wetland interspersions reduces functional connectivity of prey patches for river otters in the southern Lower Peninsula. Alternatively, environmental contaminants may also be limiting river otter population due to the species' susceptibility to bioaccumulation (Bowyer et al. 2003). A study of river otter harvest in the Upper Peninsula and northern lower two-thirds of Michigan concluded that river otter distribution was primarily limited by poly-chlorinated biphenyl pollutants (Kotanchik 1997). If correct, this hypothesis would help explain why river otters were not often detected in the

warmer waters of the southern Lower Peninsula surrounded by increased agriculture and urban development.

Human population density would alter the suitability of a local catchment to otters, fish, and trappers, which may explain why this metric contributed the most to the predictive occupancy model. From a trapping perspective, areas with high human densities, today, likely do not receive high if any trapping pressure as a multitude of diverse land ownership (no trespassing laws) and domestic animals would not be conducive to regular trapping. The NFHAP assessment found urban development to be a dominant disturbance variable in their analysis of fish habitat on a national scale (Esselman et al. 2011). In a similar analysis of disturbance gradients specific to Michigan catchments, Wang et al. (2008) determined that most moderate to severely disturbed streams (based on fish assemblage structure) in Michigan were degraded by urbanization and occurred in the southeast Lower Peninsula of Michigan.

I found that not all forms of fish habitat disturbance affected the likelihood of river otter occurrence, as evidenced by the second-highest ranked local catchment variable, number of road crossings per stream segment. Road crossings fragment fish habitat and add sediment and contaminants directly to the stream (Bouska and Paukert 2010, Warren and Pardew 1998). This form of disturbance has been shown to negatively affect sensitive, stenothermic fish species (Hudy et al. 2008) and ranked highly as a fish habitat disturbance variable in the national assessment (Esselman et al. 2011). According to my results, river otters are still able to inhabit these catchments, otherwise deemed degraded. The trend modeled by the MaxEnt response curve is almost the opposite of the known effects on fish. In terms of fragmentation, river otters have been shown to have an affinity to areas with beaver dams (Gallant et al. 2007, Swimley et al. 1998) speculated to provide both shelter and a stream morphology conducive to foraging. A road

culvert that aggregates fish, either as a barrier or cover, could increase the favorability of otter habitat while at the same time increase the ease of access to trappers. Further evidence of the access bias is found in the parabolic road length response. Probability of otter occurrence increased with the amount of road coverage. This result suggests that this level of road development increases trapper accessibility. The response to canopy cover would further support this hypothesis as existing spatially-explicit river otter habitat research has found forest cover to be an important, positive factor in predicting otter presence and abundance at both a local and landscape scale (Jeffress et al. 2011, Shardlow 2009). I found that there was little effect up to 90% canopy cover, when the likelihood of otter presence significantly decreased. Riparian stream cover typically results in positive effects on fish habitat and productivity by buffering the water body from runoff (Peterjohn and Correll 1984, Rabeni and Smale 1995, Whitley et al. 2006). This canopy cover threshold may indicate restricted trapper access in dense, riparian vegetation rather than a true reduction in otter abundance or fish populations.

Point source pollution sites (abbreviated “EPA”) ranked very highly in predicting fish habitat quality in the national assessment (Esselman et al. 2011, Wang et al. 2008) yet this metric minimally (0.3%) contributed to the MaxEnt model for this analysis. This may indicate the difference between biotic integrity stream health metrics, which include measures of sensitive fish species (Fausch et al. 1990) versus river otter prey requirements that are less species-specific. In consideration of the different responses that fish and otters have to anthropogenic disturbance, river otter presence may be a unique ecological indicator of landscape integrity. Landscape integrity measures the relative health of systems in the context of the structure and function of this landscape mosaic (Liu and Taylor 2002), effectively adding a spatial component, or landscape perspective, to biotic integrity assessments. Indices of biotic integrity are used

because they are believed to integrate the effects of anthropogenic disturbance sources using a limited number of field measurements and environmentally sensitive biota (Fausch et al. 1990). Monitoring otter presence could strengthen aquatic biological index assessments by integrating information currently not represented by measurements in fish communities alone, specifically the functioning of aquatic-terrestrial linkages. As a semi-aquatic top-predator, river otter presence and abundance could be used to assess overall fish productivity in conjunction with connectivity of aquatic and terrestrial landscape components. This would surmount to an integrated signal of reciprocal landscape processes: nutrients are entering aquatic systems, fueling fish production and these nutrients are being cycled back to terrestrial systems via a semi-aquatic piscivore.

Limitations and future research

It is important to recognize the biases inherent in evaluating populations using harvest-only based data, as was used for this analysis. Furbearer experts agree that harvest data can be a useful management tool (Hiller et al. 2011) however these data do not directly represent the actual population dynamics of the species under consideration (Poole and Mowat 2001). Factors affecting river otter harvest include such things as species abundance, trapping season length and bag limits, trap type restrictions, fur prices, weather, socio-economic conditions, trapper skill and motivation, mode of transportation, and access (Erickson 1982). Of these factors, access, season length and bag limits, and trapper motivation are particularly relevant to this analysis as it focuses on road length and crossings, canopy cover, agriculture, and human population density. Bag limits and season length are location dependant in Michigan as the state is divided in to three otter and beaver management units (Figure 9): Unit A (upper peninsula) allowed three otters per person and had the longest season from October 6, 2006 to April 15, 2007 while the

Unit B (northern lower peninsula- two otters per person) went from November 1 to April 15 and finally Unit C (southern lower- one otter per person) was shortest in length from November 10 to March 7. Further confounding these results is the fact that trappers are often targeting beaver and incidentally catch otter (Bailey and Faust 1981). In accordance with state fur-taker regulations, incidentally harvested otter carcasses are relinquished to the MNDR. There is no monetary incentive for trappers to invest time in processing these incidentally harvested otter. Additionally, a response bias may arise in which a trapper could understate, exaggerate, or provide inaccurate harvest locations (Poole and Mowat 2001), however Michigan furbearer biologists believe incidence of this behavior is low in Michigan (Etter and Bump 2011).

Clearly, using harvest-only data to extrapolate otter habitat suitability and relative abundance inherently includes biases in sampling effort and reporting. This analysis however does allow for a broad assessment of the potential link between river otter's prey-based habitat and their presence in the landscape as evidenced in harvest despite the potential biases discussed above. This large scale analysis allows for visualization of the known species distribution and considers river otter's potential in landscape-based management and potentials for its restoration. This analysis, by its very nature, cannot identify the causal process behind the species' occurrence patterns. Nevertheless, I believe there is value in evaluating species from such a large scale perspective, specifically in identifying avenues for future research and potential areas for restoration activities. The Michigan otter harvest dataset currently spans from 1987 to 2009. Inclusion of a temporal component in to this analysis would likely strengthen our ability to identify causal relationships in otter distribution patterns. Additionally, my study only considered the bottom-up effects underlying river otter distribution: landscape composition (i.e. percent crop cover) and configuration (i.e. interspersed and juxtaposition of wetlands) define prey

availability which was hypothesized to influence otter presence and abundance. Bioenergetics research has theorized that otters are capable of altering fish communities based on their predatory demands (Dekar et al. 2010). Isolating and assessing both top-down and bottom-up effects is critical to a complete understanding of otter habitat requirements and their role in influencing the biotic communities of aquatic ecosystems, not to mention a valuable step in linking landscape and trophic ecology research (Polis et al. 1997). In the U.S., 28 states funded reintroduction programs for river otters during the 1980's and 1990's (Raesly 2001), demonstrating the species' importance on the landscape of these states and in the U.S. Understanding river otter habitat needs and trophic interactions would likely further increase the success and acceptance of current and future otter reintroduction and management programs.

Management implications

While this research describes the need for a more in-depth study to understand cause-and-effect relationships between landscape changes and otter distribution, my results do demonstrate that landscape pattern metrics significantly contribute to our ability to predict relative abundance of river otters at a large spatial unit such as a county. Considering the significance of the wetland interspersed/juxtaposition index, I would not recommend a linear home range pattern for otters in Michigan restricted to only streams and riparian zones, as is used in numerous river otter studies in other regions (Blundell et al. 2000, Mack et al. 1994, Melquist and Hornocker 1983). As remote sensing tools continue to gain accuracy and utility in ecological analysis, it is important to consider land pattern metrics, particularly for highly mobile species like river otter. In the field of fisheries research and management, spatial pattern metrics are not widely used when defining aquatic condition from landscape variables. Nevertheless, predators such as river otter and prey such as winged macroinvertebrates are less laterally restricted and therefore the

entire aquatic community can be affected by the spatial arrangement of water bodies across the landscape (Beisner et al. 2006, Chase et al. 2010). If management goals include persistence of river otter populations and their function in linking aquatic and terrestrial ecosystems, land use planning models must take landscape configuration as well as composition in to account.

The loss of top predators such as river otter is considered an indication of ecosystem instability, as cascading effects have resulted in altered biogeochemical cycles, nonnative species invasion, and disease transmission (Estes et al. 2011). From a conservation standpoint, our understanding of the river otter's interaction with the landscape becomes increasingly relevant as freshwater systems prove extremely vulnerable to anthropogenic disturbance (Carpenter et al. 1992, Jelks et al. 2008, Voeroesmarty et al. 2010). The absence of this species could be a critical red flag signaling decoupled aquatic and terrestrial systems. If not corrected, this will result in simplified landscapes incapable of supporting well functioning ecosystems and aquatic community structure. Linked ecosystems require linked management (Wiens et al. 2002). River otter monitoring could serve as a common management tool for linking wildlife, fish, water and land management agencies because their semi-aquatic habitat needs span these organizational boundaries.

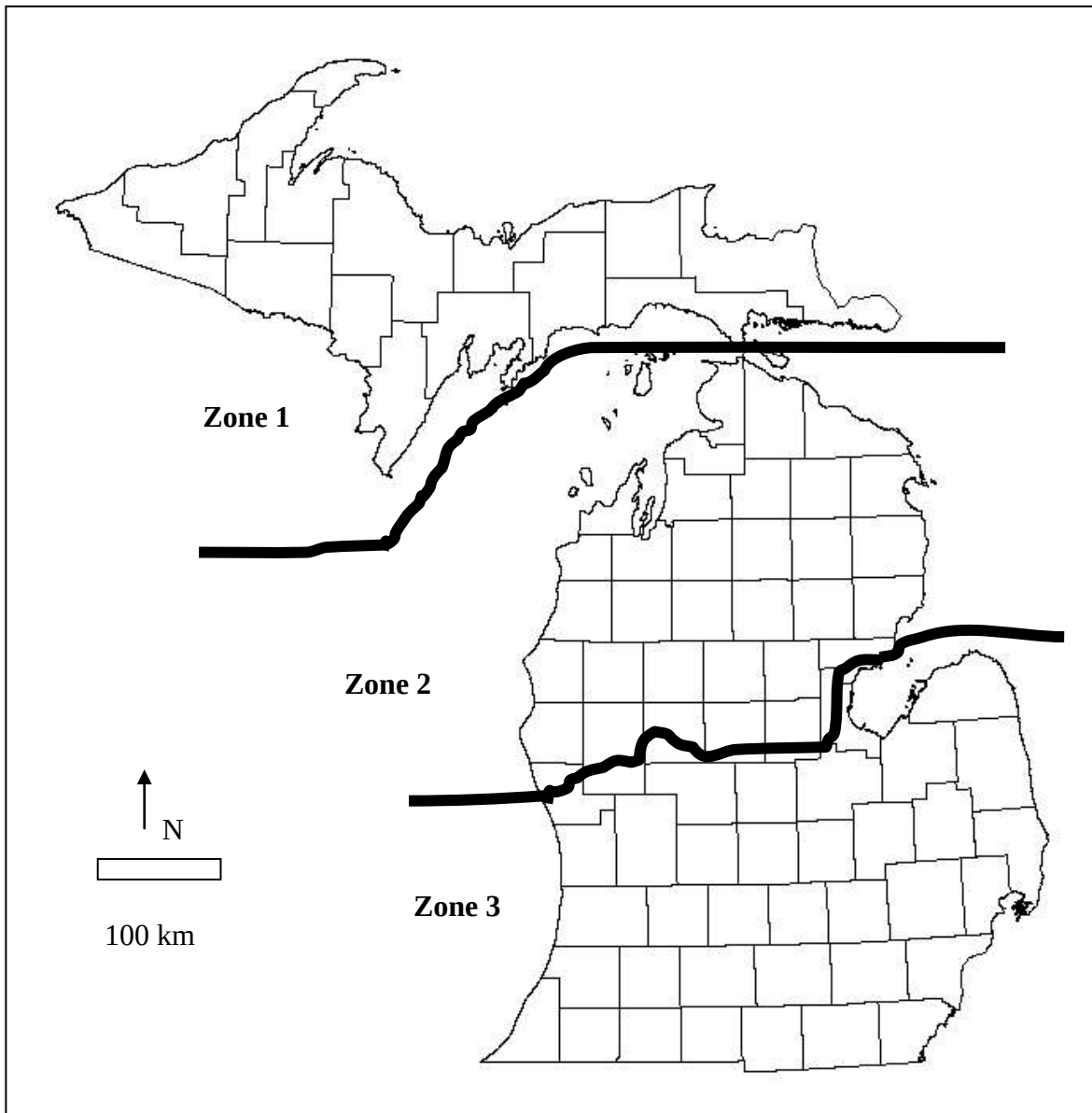


FIGURE 9. River otter and beaver trapping units in Michigan as defined by the Michigan Department of Natural Resources (Adapted from the MDNR Furbearer Harvest Regulations 2006).

APPENDIX

APPENDIX A: County scale correlation results

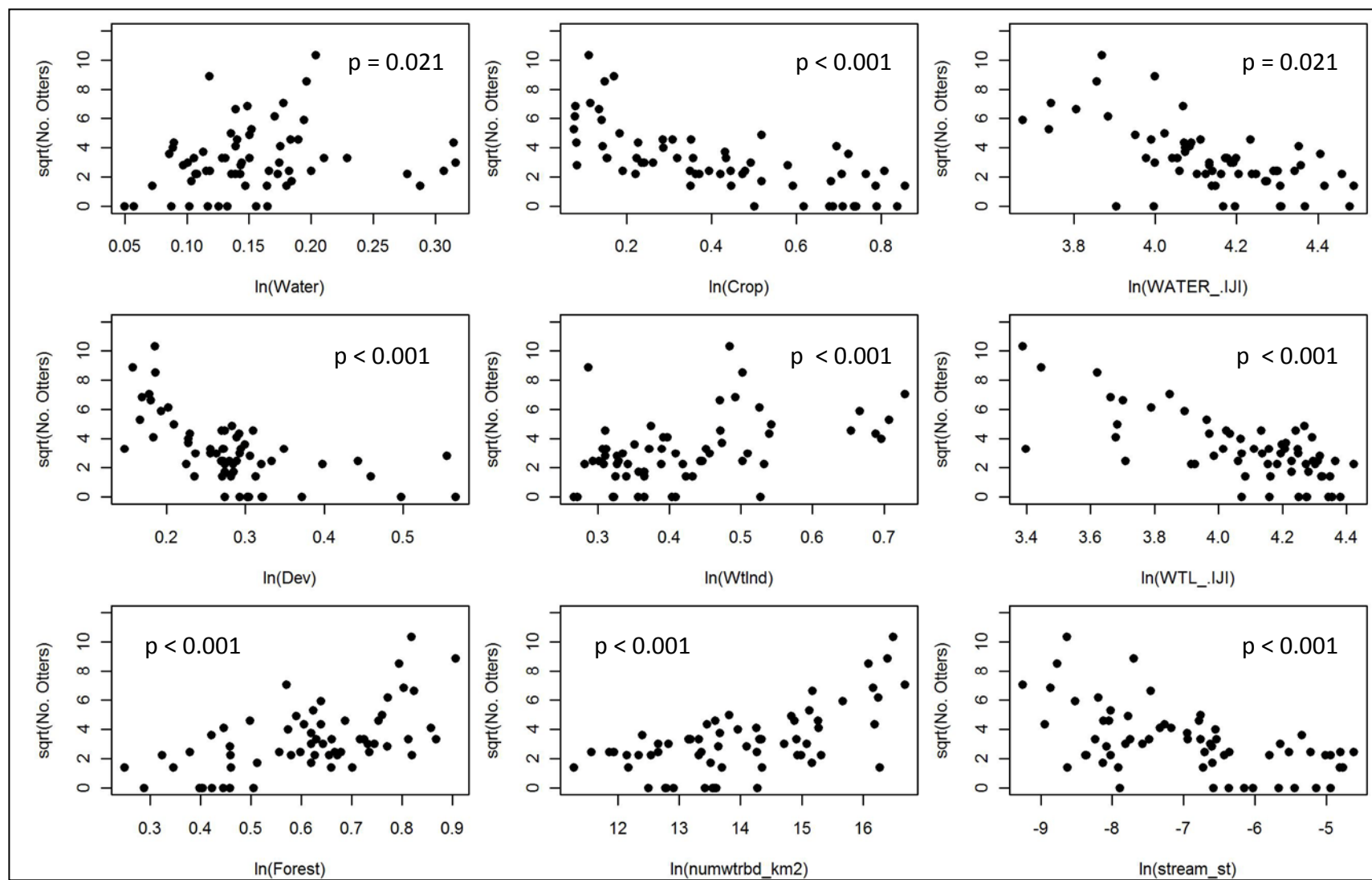


FIGURE 10. Results from Pearson's correlation test on river otter harvest and nine landscape variables measured at the county scale.

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