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Predicting habitat suitability for eleven imperiled fluvial freshwater mussels

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Abstract Understanding patterns in freshwater mussel distributions and habitat use, particularly for imperiled species, is critical for their conservation. To aid in management of imperiled mussels, and to demonstrate the utility using both landscape-based and biotic predictors in assessing species habitat suitability, we modeled 11 imperiled mussels in rivers of Michigan, USA. Models were developed with MaxEnt using a combination of host fish richness, natural abiotic reach variables, and landscape-based natural and anthropogenic variables. Because potential host fishes are important biological determinants of mussel distributions, fluvial host fish distributions ($n = 37$) were modeled and integrated as a predictor in mussel models. Key predictors determining habitat suitability for mussels included host fish richness, a strong positive predictor for 8 of 11 mussel species, stream discharge, urban land use, and upstream dam density. Models predicted 853 to 10,138 stream km of suitable habitat (1.1 to 13.6% of the state's stream length) for the 11 mussel species, with 54 to 1,382 km (0.1 to 1.8%) being considered highly suitable habitat. Mapping of suitable habitats identified streams with available habitat for multiple listed species, allowing for more informed decisions in conservation planning and management of Michigan's listed freshwater mussels and their fish hosts.

Keywords Unionid mussels · Host fish richness · Habitat suitability · Conservation · MaxEnt · Michigan

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Introduction

Unionid freshwater mussels are one of the most imperiled aquatic families in North America (Williams et al., 1993; Strayer, 2008) and Europe (Lopes-Lima et al., 2016). Of 297 native fauna to North America, more than 70% are considered threatened (Williams et al., 1993). Freshwater mussels are particularly sensitive to habitat disturbances due to their limited mobility (Daniel & Brown, 2014), complex life cycles (Strayer, 2008), and long life spans (Haag, 2012). The decline of freshwater mussels has been attributed to a suite of anthropogenic landscape-scale stressors. The most commonly cited causes of decline (Downing et al., 2010) include water pollution, which may result from inputs of toxic substances or excess sediments to stream channels (Naimo, 1995; Strayer et al., 2004; Newton & Bartsch, 2007), habitat destruction or reduced suitability from urban and agricultural land uses (Watters, 1999; Brown et al., 2010; Daniel & Brown, 2013), and dams that impound and fragment freshwater habitats (Watters, 1996; Vaughn & Taylor, 1999).

Freshwater mussel distributions are also influenced by distributions of fish species (Vaughn & Taylor, 2000; Strayer, 2008). Fishes are essential in structuring mussel assemblages and determining mussel habitat suitability because most freshwater mussel recruitment and dispersal ceases with loss of suitable host fishes (Haag, 2012). In addition to direct effects of anthropogenic landscape-scale stressors on freshwater mussels and their habitat quality, they may have equally important influences on mussels' obligate host fishes (Vaughn & Taylor, 2000; Strayer, 2008). This can magnify effects of landscape-scale stressors on freshwater mussel recruitment due to potential influences on suitable host fishes (Haag, 2012). Multiple studies conducted throughout North America have shown how distributions and abundances of fishes change with urban and agricultural land uses (Wang et al., 2000; Utz et al., 2010), dams (Watters, 1995; Cooper et al., 2016), and other human stressors (Gido et al., 2010).

Imperiled freshwater mussel species are often difficult to manage due to their sensitivities to multiple threats (FMCS, 2016), their low prevalence and declining populations compared to other freshwater mussels, and poorly understood ecology (Clark & Harvey, 2002; FMCS, 2016). This underscores the need to better understand the complex relationships between host fish richness and distribution, natural reach and landscape variables, and anthropogenic landscape stressors, all of which influence mussel species' habitat suitability. Previous studies have shown that reach characteristics of stream habitat such as sediment type and flow conditions alone were not good predictors of freshwater mussel distributions (Strayer & Ralley, 1993; McRae et al., 2004) and suggested that a combination of stream reach-level, host fish, and landscape-scale variables are better suited to understand and predict habitat use by mussels (Strayer, 2008). Further, an approach that considers landscape-scale influences is required to understand potential habitat suitability over large geographic extents such as an entire region (Roth et al., 1996; Allan, 2004), matching the spatial scales at which these species are typically evaluated in region-wide management initiatives for more effective conservation and management (Strayer, 2008; Newton et al., 2011).

Despite the imperiled status of many freshwater mussels, species' habitat suitability models for freshwater mussels have been primarily applied to predict distributions of invasive species (e.g., Oliveira et al., 2010; Gallardo et al., 2013; Quinn et al., 2014). Fewer studies have generated species' habitat suitability models for native mussels, particularly those that are imperiled (but see Hopkins, 2009; Prié et al., 2014; Cao et al., 2015). Recent advancements in developing species' habitat suitability models for imperiled native freshwater mussels have mainly focused on either a single species (e.g., Wilson et al., 2011) or have been applied within single river basins (Dunithan, 2012; Heffentrager, 2013), despite the ability of a landscape approach to aid in efforts to assess freshwater mussel's habitat suitability across much larger extents. Only a few species' habitat suitability models developed for freshwater mussels have incorporated host fish distributions as a predictor variable (Cao et al., 2013; Lois et al., 2015; Inoue et al., 2016). Instead, most approaches have relied solely upon abiotic variables. The development of species' habitat suitability models for multiple imperiled mussels across a broad geographic region that accounts for host fish distributions, natural reach and landscape variables, and anthropogenic landscape variables could significantly improve species' habitat suitability models over those that do not consider hosts or landscape variables. Ultimately, the products of freshwater mussel habitat suitability modeling can provide utility to mussel conservation efforts by identifying highly suitable habitats within a region that can be protected or restored to the benefit of the imperiled species, including aiding in efforts to identify populations that may exist outside of species' known biogeographic ranges (FMCS, 2016).

The goal of this study was to characterize suitable fluvial habitat for imperiled freshwater mussels throughout the state of Michigan, USA using host fish richness, natural reach and landscape variables, and anthropogenic landscape variables in the development of habitat suitability models over a large spatial extent.

We took a statewide approach to potentially identify populations of imperiled Michigan freshwater mussels that may exist outside of species' known biogeographic ranges. We address four questions in our study. First, what are the important abiotic variables in determining host fish habitat suitability? We modeled habitat suitability for 37 fishes known to be hosts for imperiled freshwater mussels, developing species-specific mussel host richness distributions throughout Michigan and identifying abiotic variables influencing fluvial host fish habitat suitability. Second, what are the important abiotic and biotic variables in determining mussel habitat suitability? We developed species' habitat suitability models for 11 imperiled fluvial freshwater mussel species using the same pool of abiotic variables as the host fishes but also utilizing modeled host fish richness as a predictor. Third, how much suitable habitat is predicted for each mussel species, and will that suitable habitat be outside their known biogeographic range? For each freshwater mussel species, we quantify the amount of suitable habitat both within and outside the species' known biogeographic ranges. Lastly, which fluvial habitats in Michigan are suitable for multiple imperiled freshwater mussels? We combine all mussel model results to create a multi-species habitat suitability map for the state, combining this map with future climate projections of stream temperature, current fish habitat conditions, and locations of protected landscapes to provide additional insights about current and future risks to rivers with high co-occurrence of imperiled freshwater mussels in Michigan.

Methods

Study area and spatial framework

The scope of our study encompassed the Upper and Lower Peninsulas of Michigan, USA, a region containing 74,775 km of streams (Upper Peninsula with 19,302 km and Lower Peninsula with 55,473 km; NHDPlusV1, 2008) with a range of thermal conditions, including warm, transitional, and cold water habitats (Lyons et al., 2009). The base data layer for the spatial framework (called NRiSD, National River Spatial Database; Wang et al., 2016) was developed from the National Hydrography Dataset Plus Version 1 (NHDPlusV1, NHDPlus, 2008), which includes 1:100,000 scale river arcs referred to as stream reaches. Stream reaches represent a delineated length of stream arc defined by stream confluences and representing the smallest spatial unit for summarizing and analyzing data in this study (Wang et al., 2011a). This spatial framework has shown to facilitate low amounts of spatial autocorrelation between units in past studies (Daniel et al., 2015; Crawford et al., 2016). Due to a lack of comparable freshwater mussel and stream data for Canada, rivers bordering the USA and Canada (e.g., Saint Clair and Detroit Rivers) were not evaluated in this study. Major river basin boundaries corresponding to Michigan's Great Lakes tributaries (Supplementary Figure A1) were used to delineate species' biogeographic ranges and to evaluate model results both inside and outside of these biogeographic ranges.

Mussel data

Statewide freshwater mussel occurrence data for 45 species were obtained from the Michigan Natural Features Inventory. Contemporary occurrences used for modeling (spanning 1990 to 2013) were obtained primarily using semi-quantitative sampling methods (see Badra & Goforth, 2003). In wadeable stream habitats (average depth less than approximately 70 cm), live freshwater mussels and shells were located with a combination of visual inspections using glass bottom buckets and tactile searches through the substrate. The search area was typically 128 m^2 per survey site. When possible, search areas spanned the river from bank to bank. Surveys were conducted in transects using SCUBA in non-wadable habitats, with transects being set side by side approximately 3–8 m apart and 10 m in length. Transects were searched for 80 cm on each side and 5 cm deep into the substrate by hand. Live individuals were identified to species, and planted back into the substrate anterior end down (siphon end up) near where they were found. We linked the mussel sample sites to stream reaches of NRiSD. Many stream reaches had multiple mussel samples available; we only used a single sample that was the most recent sample to represent a reach. A total of 323 sites were included in the contemporary occurrences used for modeling.

In Michigan, USA, 31 of 45 native freshwater mussel species are currently listed by the state as endangered or threatened or are considered species of special concern. Of those 31 species, we selected 11 that fit three criteria for inclusion in this study included: *Alasmidonta marginata* (Say, 1818) elktoe, *Alasmidonta viridis* (Rafinesque, 1820) slippershell, *Cyclonaias tuberculata* (Rafinesque, 1820) purple wartyback, *Epioblasma triquetra* (Rafinesque, 1820) snuffbox, *Lampsilis fasciola* (Rafinesque, 1820) wavy-rayed lampmussel, *Ligumia recta* (Lamarck, 1819) black sandshell, *Pleurobema sintoxia* (Rafinesque, 1820) round pigtoe, *Ptychobranchus fasciolaris* (Rafinesque, 1820) kidneyshell, *Truncilla truncata* (Rafinesque, 1820) deertoe, *Venustaconcha ellipsiformis* (Conrad, 1836) ellipse and *Villosa iris* (Lea, 1829) rainbow. First, we only considered fluvial (vs. lentic) freshwater mussel species, and we required a minimum of 10 fluvial species occurrences to develop habitat suitability models. Last, we required that freshwater mussels chosen for modeling have known host fish species that were identified via laboratory experiments (as opposed to expert opinion; following Keller & Ruessler, 1997).

Occurrences were summarized within major river basin boundaries to generate individual maps of river basins with known historical and contemporary occurrences (1890 to 2013) for each mussel species (Fig. 1). These range maps were used to summarize habitat suitability model predictions within known biogeographic ranges (as compared to extending modeling results statewide) and to map the co-occurrence of the 11 study freshwater mussel species in Michigan's river basins.

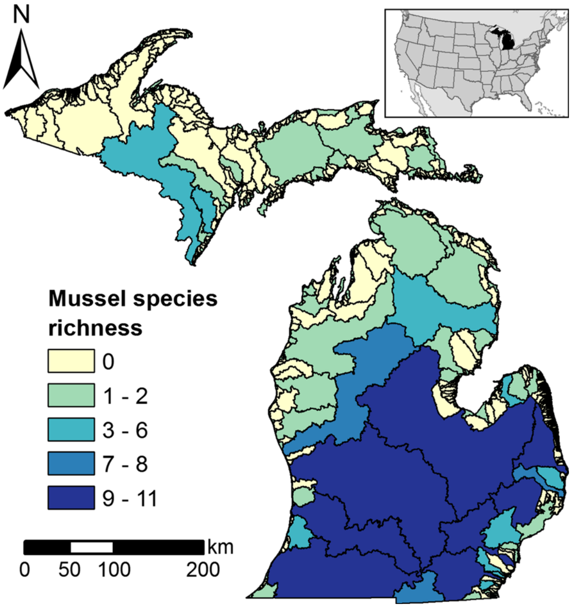

Fig. 1 Species richness of 11 study mussel species within Michigan river basins based on historical and contemporary occurrences (1890 to 2013). Mussel species richness is calculated per river basin. River basin names are included in Supplementary Figure A1

Host fish data

Known host fishes for the 11 freshwater mussel species in this study were identified from three sources: Ohio State University's Division of Molluscs (http://www.biosci.ohio-state.edu/~molluscs/OSUM2/), Michigan State University's Michigan Natural Features Inventory (http://mnfi.anr.msu.edu/), and University of Michigan's Animal Diversity Web (http://animaldiversity.org/). From these sources, 37 laboratory-verified host fishes were identified. Data characterizing contemporary occurrences (1990–2013) of these host fishes were compiled from the Michigan Department of Natural Resources (MDNR, unpublished data) and Michigan Fish Atlas (Bailey et al., 2004). All survey locations were spatially referenced to corresponding stream reaches of the NRiSD, with a single, most recent fish sample being used to represent a host occurrence within a stream reach. The number of identified fish hosts ranged from 1 to 13 among mussel species, and included elktoe with 5 hosts, slippershell (2 hosts), purple wartyback (4 hosts), snuffbox (3 hosts), wavy-rayed lampmussel (4 hosts), black sandshell (13 hosts), round pigtoe (5 hosts), kidneyshell (3 hosts), deertoe (1 host), ellipse (9 hosts), and rainbow (10 hosts) (Supplementary Table A1).

Host fishes predictor variable

Host fish richness as a biotic predictor variable was created based on habitat suitability results from the 37 known host fishes (see below and Table 1 for further description of this predictor variable). Only the freshwater mussel's known host fishes were used to build each mussel species' predicted stream reach-level host richness (see Supplementary Table A1).

Natural reach and landscape predictor variables

Natural reach and landscape predictor variables used in this study are described in Table 1; along with

Table 1 Natural and anthropogenic predictors used in freshwater mussel and host fish habitat suitability modeling

Type	Variable	Description	Units	Scale/resolution	Source
Natural					
Reach					
	QA50	Annual 50% exceedance stream flow (median annual stream flow)	cms	1:100,000	FishVis (2013)
	QY10	April 10% exceedance flow yield (high flow yield)	cms/km^2	1:100,000	FishVis (2013)
	QY90	August 90% exceedance flow yield (low flow yield)	cms/km^2	1:100,000	FishVis (2013)
	JST	July mean stream temperature	degrees C	1:100,000	FishVis (2013)
	Elev	Minimum stream segment elevation	msl	1:100,000	NHDPlus V1 (2008)
	Grad	Gradient of the stream reach	m/m	1:100,000	NHDPlus V1 (2008)
Landscape					
	AAT	Mean annual air temperature within local catchment	degrees C	4 km	OCS (2014)
	PPT	Mean annual precipitation with network catchment	mm/year	4 km	OCS (2014)
	Glacial	Extent of last glaciation in Michigan	%	NA due to various scales	Schaetzl (personal commutation 2015)
	Fine	Fine-textured surficial lithography within network catchment	%	1 km	USGS (2010)
	Soil	Soil permeability rate within network catchment	mm/hour * 100	1:250,000	USGS (1995)
	Wetland	Woody and emergent herbaceous wetland within network catchment	%	30 m	NLCD (2006)
Anthropogenic					
Landscape					
	UrbanL	Low intensity urban within network catchment	%	30 m	NLCD (2006)
	UrbanM	Medium intensity urban within network catchment	%	30 m	NLCD (2006)
	UrbanH	High intensity urban within network catchment	%	30 m	NLCD (2006)
	RowCrop	Row crop agriculture within network catchment	%	30 m	NLCD (2006)
	Pasture	Pasture within network catchment	%	30 m	NLCD (2006)
	Imperv	Imperviousness within network catchment	%	30 m	NLCD (2006)
Fragmentation					
	RoadCrDens	Road/stream crossing density within upstream river network	#/km	1:100,000	TIGER (2006)
	UNDR	Upstream network dam density within upstream river network	#/100 km	1:100,000	Cooper et al.2017
	UMO	Percentage of open upstream mainstem based on dam locations	%	1:100,000	Cooper et al. (2017)
	DMD	Downstream mainstem dam density per unit downstream river mainstem length	#/100 km	1:100,000	Cooper et al. (2017)
	DMO	Percentage of open downstream mainstem based on dam locations	%	1:100,000	Cooper et al. (2017)
Biotic					
Reach					
	HostRich[a]	Stream reach-level host richness	#	1:100,000	Current study

[a] Mussel habitat suitability models only

abbreviations for each variable. Methods for summarizing information in spatial units described in Tsang et al. (2014). To represent important reach habitat characteristics, we used model estimates of stream flow variables including annual 50% exceedance stream flow representing median annual stream flow, April 10% exceedance flow yield representing seasonal high flow yield, and August 90% exceedance flow yield representing seasonal low flow yield. July mean stream temperature (FishVis, 2013) was used to represent predicted instream temperatures during summer that could be limiting to aquatic organisms (following Wehrly et al., 2003). Two additional reach-based variables, minimum stream reach elevation (abbreviation Elev) and gradient of the stream reach, were obtained from the NHDPlusV1. Often, catchment area has been used in predicting aquatic species habitat suitability (e.g., Cao et al., 2015), but for this study we utilized stream flow, which is highly correlated with catchment area within the region (Zorn et al., 2002) and suggests a more mechanistic characterization of habitat availability compared to catchment area.

To represent major climatic influences on habitat suitability, two variables were developed from climate data (Oregon Climate Service, 2014) spanning 1990 to 2010; mean annual air temperature within the local catchment and mean annual precipitation within the network catchment. Because glaciation within the study region has had strong influences on stream flow, temperature, and aquatic species distributions (Provan & Bennett, 2008), a map of the Wisconsin glacial period (Schaetzl, 2015, personal communication) was used to determine the percent of a local catchment that was covered in glacial ice during the most recent glaciation. Variables characterizing geology and soil characteristics were also used, including percent of network catchment with fine-textured surficial lithography (USGS, 2010) and soil permeability rate within the network catchment (USGS, 1995). Lastly, we calculated the percent wetland land cover within the network catchment from the 2006 National Land Cover Dataset (NLCD 2006; Xian et al., 2009).

Anthropogenic landscape predictor variables

Eleven anthropogenic landscape predictor variables were selected from two primary sets of known stressors to freshwater mussels and host fishes, human land use and stream fragmentation (Wang et al., 2011b; Cooper et al., 2017; Table 1). Percentages of urban and agricultural land uses and impervious surfaces were summarized within network catchments (NLCD 2006; Xian et al., 2009). These land uses were summarized as individual land uses classes, including low, medium, and high intensity urban land uses, as well as and row crop, and pasture/hay classes for agriculture. Although these land use classes can be correlated, retaining individual classes (as opposed to combining them into one broad category) allows for evaluating differing anthropogenic intensities. Further, the habitat suitability modeling approach used (described below) can accommodate for multicollinearity among predictor variables (Elith et al., 2011).

To account for fragmentation by dams and roads within the stream network, we included four dam variables developed using the spatial location of large dams (generally > 2 m in height) from the 2013 National Anthropogenic Barrier Dataset (NABD) within stream networks of the NHDPlusV1 (Cooper et al., 2017) and stream/road crossing densities along the stream network developed from the 2006 TIGER U.S. Census roads layer (Table 1). Two distance-based dam variables, upstream mainstem openness and downstream mainstem openness, were used to represent the percentage of accessible upstream or downstream mainstem length based on locations of dams as barriers. Upstream mainstem pathways were defined as the longest route upstream of a reach within the upstream network, whereas downstream mainstem pathways were defined as the shortest path below a stream reach to a Great Lake outlet (Cooper et al., 2017). We also included two density-based dam variables, upstream network dam density along all upstream flow paths and dam density along the downstream mainstem flow path to account for landscape-scale cumulative dam effects (e.g., upstream flow alteration).

Habitat suitability modeling

Habitat suitability modeling was conducted using maximum entropy method (MaxEnt: Phillips et al., 2006), a presence-only species modeling approach that uses species occurrences to fit a variety functions (e.g., linear, product, quadratic, threshold; see Phillips & Dudík, 2008) in modeling species' responses to environmental predictors. Because the base spatial units in our study area are individual stream reaches, we used the 'samples with data' option within MaxEnt, utilizing 10,000 randomly selected stream reaches as background points and projecting model results to all stream reaches within the study region. Here, we use relative predictor contributions from MaxEnt to identifying key predictors for host fishes and mussels, using variable contributions of $\geq$ 10% as the criterion for identifying key predictors. The response relationship type (positive, negative, or unimodal; e.g., Cao et al., 2015) between each species and key predictor variables was assessed from response curves representing MaxEnt models created using each predictor variable individually. We first modeled habitat suitability of 37 known host fishes using 23 environmental predictor variables (described above) generating a stream reach-level predicted host richness metric incorporated into habitat suitability models for each mussel species. To establish reach-level host presence, we converted the logistic output from MaxEnt to presence/absence using logistic cutoff values identified based on maximizing the sum of sensitivity and specificity (max SSS; Jiménez-Valverde & Lobo, 2007; Liu et al., 2013). This max SSS logistic cutoff was used to represent suitable habitat and logistic values corresponding to the 50th percentile training occurrence cutoff to identify highly suitable habitats in summarizing model predictions. Results are shown for suitable and highly suitable habitats both statewide and for stream reaches that fell inside the known biogeographical range for each species. For all MaxEnt models, we used AUC values developed with a fivefold cross-validation approach in evaluating model performance (Elith et al., 2011), and utilized a 0.75 AUC threshold as the point in which models are considered useful (Elith, 2000; Phillips & Dudík, 2008).

Multi-species habitat suitability

A single combined map was created from the 11 individual freshwater mussel species results identifying river basins that have suitable habitat for multiple imperiled mussel species. In developing this map, model results at the reach level were binned into five groups of co-occurring species counts. The five groups included no suitable habitat (0 species); single mussel species habitat; and habitat for 2–4, 5–7, and 8–10 imperiled mussel species. This output aids in identification of which river basins have the best habitats for multiple freshwater mussel species.

To illustrate current and future risks to rivers with high mussel co-occurrence, the multi-species habitat suitability map was combined other pre-existing datasets. These datasets included the following: the risk of stream temperature alteration with projected future climate change, the risk of fish habitat degradation from current stressors, and locations of protected landscapes. These variables were summarized for the co-occurring mussel species groups by the total stream length and relative percent of streams in Michigan. To understand how climate change may affect mussel habitat into the future, models of projected changes in water temperature classes for rivers in Michigan were incorporated. These changes in water temperature classes were derived from a project that considered changes in air temperature expected to occur by mid-century (2046–2065, FishVis, Stewart et al., 2016). Temperature classes include cold, cold transitional, warm transitional, and warm streams. For this project, we only assessed warming temperatures, because increased water temperature can affect individual mussel growth, longevity, and reproductive success of populations (Hastie & Young, 2003). To understand potential host fish habitat conditions, we used an index that scores relative condition of stream fish habitats across Michigan (National Fish Habitat Partnership 2015 river assessment results; Crawford et al., 2016). This index was developed based on stream fish responses to numerous landscape disturbances. Condition is represented in five classes of fish habitat degradation (very low, low, moderate, high, and very high), and for this study, the low and very low groups were binned together to form the low habitat degradation group, and high and very high groups were binned together to form the high habitat degradation group. These results can show how current stream conditions can influence freshwater mussels' potential for recruitment and dispersal by influencing host fish availability (Haag, 2012). Lastly, we incorporated a protected lands database (USGS, 2016) that provides an inventory of public lands held in trust by federal, state, and local governments and by nonprofit conservation organizations. Streams that occur in protected areas should have less risk of alteration from anthropogenic disturbance and may be more likely to be maintained into the future in their current state.

Results

Host fish habitat suitability models

Host fish habitat suitability model AUC values ranged from 0.76 to 0.99 with an average of 0.89 (Table 2). Models demonstrated that natural reach and landscape predictor variables contributed more to habitat suitability model development for 32 of 37 host fish species (Supplementary Table A2), while anthropogenic variables contributed more for the five remaining species. Important predictor variables for host fishes included median annual stream flow, stream gradient, mean annual air temperature, upstream dam openness, and medium and high urban land uses (Supplementary Tables A2 and A3). For individual host fishes, predicted statewide habitat suitability ranged from 364 km (0.5% of total statewide stream length) for freshwater drum to 22,670 km (30.3%) for white sucker (Table 2).

Freshwater mussel habitat suitability models

Mussel habitat suitability models had AUC values ranging from 0.91 to 0.99 with an average of 0.96 (Table 3). Host fish richness was a key predictor variable for 8 of 11 freshwater mussel species, having a positive influence on habitat suitability in all eight cases. Host fish richness also had the second highest average model contribution (14.3%) among all predictor variables, behind median annual stream flow (28.9%). For abiotic predictors, natural reach and landscape predictors had greater overall model contributions for 10 of 11 mussel species when compared to anthropogenic predictors. Key natural predictors that contributed $\geq$ 10% in mussel habitat suitability models included median annual stream flow, mean annual air temperature, and minimum stream reach elevation (Table 4). Median annual stream flow had a mixture of negative (4 species), positive (5 species), and unimodal (1 species) associations, suggesting possible stream size preferences among mussel species.

Important anthropogenic landscape predictors included network high urban land use, pasture land use, row crop land use, upstream mainstem openness, and upstream dam density. These predictors had negative associations with habitat suitability with the exception of row crop land use, which had a positive association for the ellipse. The snuffbox was the only mussel species with anthropogenic variables contributing more to the habitat suitability model then natural predictor variables (Table 5), being negatively associated with upstream network dam density and high intensity urban land use. Among anthropogenic landscape predictors, high intensity urban land use was a key predictor for the most species, including elktoe, purple wartyback, snuffbox, kidneyshell, and deertoe. For the stream fragmentation predictors, only upstream-oriented variables (upstream mainstem openness and upstream dam density) were key predictors, both having negative associations with habitat suitability for 6 of 11 mussel species combined.

When looking at the three intensities of urban land uses in network catchments in Michigan, you can see a lot of variation across the 25 major basins (see Supplementary Table A4). The statewide minimum percent urban land use of all three intensities was 0% of the network catchment. The exceptions were the minimum low intensity urban in the Raisin (0.3%) and Rouge (3.3%) basins. The statewide maximum percent urban land use of the network catchment was 100% for low intensity (Clinton and Saginaw basins), 57.7% for medium intensity (Rouge basin) and 32.6% (Raisin basin) for high intensity. The statewide urban land use mean was 8.3% for low intensity, 0.9% for medium intensity, and 0.3% for high intensity.

Predicted statewide suitable habitat for freshwater mussels ranged from 853 km (1.1% of total statewide stream length) for the deertoe to 10,138 km (13.6%) for the slippershell (see Table 3). When considering only highly suitable habitats, these values drop to 54 km (0.1% of total statewide stream length) for deertoe and 1,382 km (1.8%) for slippershell. For all mussel species, highly suitable habitat accounted for 10% of total suitable habitat on average. The amount of suitable habitat found within each specie's biogeographical range varied from 67% for the deertoe to 99.6% for rainbow (Fig. 2), and when considering only highly suitable habitats, eight species had > 99% of predicated habitat within their known biogeographical range (Supplementary Figures A2–A4). Wavy-rayed lampmussel had the lowest amount of highly suitable habitat found within its biogeographical range at 87.9%. Multi-species habitat suitability.

When evaluating the combined results for the 11 freshwater mussel habitat suitability models, many of

Table 2 Host fish number of occurrences, model test AUC values, and predicted habitat length considered suitable and highly suitable

Genus and species	Common name	Occur.	Test AUC	Suitable		Highly suitable	
				Length (km)	State (%)	Length (km)	State (%)
Ambloplites rupestris	Rock bass	270	0.88	15144	20.3	3109	4.2
Ameiurus melas	Black bullhead	54	0.85	12331	16.5	1954	2.6
Ameiurus natalis	Yellow bullhead	66	0.90	8029	10.7	1261	1.7
Aplodinotus grunniens	Freshwater drum	20	0.99	364	0.5	62	0.1
Campostoma anomalum	Central stoneroller	138	0.92	8408	11.2	1150	1.5
Catostomus commersonii	White sucker	633	0.84	22670	30.3	7557	10.1
Chrosomus eos	Northern redbelly dace	65	0.86	17467	23.4	2980	4.0
Cottus bairdii	Mottled sculpin	304	0.87	17350	23.2	3690	4.9
Cottus cognatus	Slimy sculpin	34	0.94	8558	11.4	485	0.6
Culaea inconstans	Brook stickleback	145	0.81	13401	17.9	1995	2.7
Cyprinella spiloptera	Spotfin shiner	77	0.93	7077	9.5	1213	1.6
Etheostoma blennioides	Greenside darter	74	0.94	7401	9.9	1272	1.7
Etheostoma caeruleum	Rainbow darter	168	0.90	10574	14.1	1273	1.7
Etheostoma exile	Iowa darter	27	0.76	10119	13.5	892	1.2
Etheostoma flabellare	Fantail darter	30	0.91	9548	12.8	300	0.4
Etheostoma nigrum	Johnny darter	444	0.84	21289	28.5	5543	7.4
Fundulus diaphanus	Banded killifish	13	0.81	3931	5.3	1345	1.8
Hypentelium nigricans	Northern hog sucker	197	0.92	10231	13.7	1742	2.3
Ictalurus punctatus	Channel catfish	29	0.97	1653	2.2	200	0.3
Lepomis cyanellus	Green sunfish	317	0.88	13503	18.1	3082	4.1
Lepomis gibbosus	Pumpkinseed	193	0.84	16774	22.4	2584	3.5
Lepomis gulosus	Warmouth	19	0.86	5128	6.9	336	0.4
Lepomis macrochirus	Bluegill	291	0.86	14239	19.0	3165	4.2
Lepomis megalotis	Longear sunfish	31	0.94	4560	6.1	441	0.6
Luxilus chrysocephalus	Striped shiner	14	0.80	7393	9.9	1583	2.1
Lythrurus umbratilis	Redfin shiner	43	0.95	3069	4.1	364	0.5
Micropterus dolomieu	Smallmouth bass	171	0.92	10405	13.9	1486	2.0
Micropterus salmoides	Largemouth bass	236	0.87	13312	17.8	2514	3.4
Morone americana	White perch	14	0.96	1597	2.1	124	0.2
Moxostoma macrolepidotum	Shorthead redhorse	60	0.96	6643	8.9	603	0.8
Notropis rubellus	Rosyface shiner	34	0.93	5635	7.5	703	0.9
Perca flavescens	Yellow perch	146	0.87	11806	15.8	1686	2.3
Percina caprodes	Logperch	99	0.89	11255	15.1	1993	2.7
Percina maculata	Blackside darter	235	0.89	12901	17.3	2854	3.8
Pimephales notatus	Bluntnose minnow	259	0.85	16283	21.8	3339	4.5
Pylodictis olivaris	Flathead catfish	10	0.99	490	0.7	202	0.3
Sander vitreus	Walleye	44	0.90	4887	6.5	362	0.5

Habitat lengths are presented both as a total (km) and as a percentage of all streams within the state (%). See methods for a description of suitable and highly suitable habitat

Michigan's rivers are predicted as being suitable for multiple species, with an overall range of 0–10 mussel species co-occurring within stream reaches for the state (Fig. 3a). Among individual river basins, rivers containing the highest number of co-occurring species included the Black, Belle, Clinton, and Huron Rivers

Table 3 Freshwater mussel number of occurrences in the state of Michigan, model test AUC values, and predicted habitat length considered suitable and highly suitable habitat

Genus and species	Common name	Occur.	Test AUC	Suitable			Highly suitable		
				Length (km)	State (%)	Bio. (%)	Length (km)	State (%)	Bio. (%)
Alasmidonta marginata[c]	Elktoe	140	0.96	3908	5.2	96.9	562	0.8	100.0
Alasmidonta viridis[b]	Slippershell	72	0.91	10138	13.6	90.5	1382	1.8	95.7
Cyclonaias tuberculata[b]	Purple wartyback	25	0.98	1220	1.6	98.1	124	0.2	100.0
Epioblasma triquetra[a,d]	Snuffbox	43	0.99	1506	2.0	91.5	145	0.2	100.0
Lampsilis fasciola[b]	Wavy-rayed lampmussel	61	0.98	1636	2.2	67.8	164	0.2	87.9
Ligumia recta[a]	Black sandshell	42	0.97	2147	2.9	84.6	117	0.2	96.5
Pleurobema sintoxia[c]	Round pigtoe	113	0.96	4287	5.7	98.5	512	0.7	100.0
Ptychobranchus fasciolaris[c]	Kidneyshell	47	0.97	2351	3.1	91.3	204	0.3	100.0
Truncilla truncata[c]	Deertoe	23	0.95	853	1.1	67.0	54	0.1	100.0
Venustaconcha ellipsiformis[c]	Ellipse	72	0.96	4295	5.7	86.6	450	0.6	99.0
Villosa iris[c]	Rainbow	151	0.95	4566	6.1	99.6	506	0.7	100.0

Habitat lengths are presented both as a total (km) and as a percentage of all streams within the state (State) and within the known biogeographic range of the species (Bio.). See methods for a description of suitable and highly suitable habitat

[a] State listed as endangered (MDNR, 2015)

[b] State listed as threatened (MDNR, 2015)

[c] State designated species of concern (MDNR, 2015)

[d] Federally listed as endangered (USFWS, 2011)

in the Lake Erie Basin, the Saginaw River and many of its major tributaries in the Lake Huron Basin, and the Grand and St. Joseph Rivers in the Lake Michigan Basin (Fig. 3 and Supplementary Fig. A1). A total of 4,417 km (5.9% statewide stream length) was considered suitable, and 1,461 km (2.0%) was considered highly suitable habitat for a single freshwater mussel species. These suitable and highly suitable levels drop to 3,075 km (4.1%) and 894 km (2.0%) for streams predicted to contain 2–4 imperiled mussel species (Fig. 3a), while streams with 5–7 imperiled mussel species total 2,583 km (3.5%) and 56 km (0.1%). Lastly, stream reaches supporting 8–10 imperiled mussel species totaled 1,012 km of suitable habitat (1.4%), with no streams considered highly suitable for this species group.

Of the streams predicted to have at least one mussel species, 3.7% is expected to change from cold water to cold transitional habitat by mid-century, 29.5% from cold transitional to warm transitional habitat, and 27.9% from warm transitional to warm water habitat (Fig. 3b; Table 6). Only 38.9% of streams predicted to have one or more mussel species are not expected to change temperature classes by mid-century. Based on results of the National Fish Habitats Partnerships' 2015 assessment of fish habitat condition, 64.2% of stream length predicted to have one or more mussels has moderately to highly degraded fish habitat. Although the remaining 35.8% of stream length is considered low degradation, very little coincides with streams predicted to have five or more imperiled mussel species (Table 6). Lastly, a majority of the protected lands in Michigan occur in the Upper Peninsula and northern Lower Peninsula, while many of the streams containing a high number of co-occurring imperiled freshwater mussel species occur in the southern Lower Peninsula (Fig. 3d). This results in only 230 km of streams suitable for one or more imperiled mussel species that occur in protected areas, with very little (6 km) coinciding with streams expected to have 8–10 imperiled mussel species.

Discussion

Host fishes are important in determining habitat suitability for freshwater mussels in Michigan. Host fish richness was the second most important predictor

Table 4 Freshwater mussel natural variable relative importance percentage and species response type [denoted as positive (+), negative (−), or unimodal (*)] for key predictors shown in bold with variable contributions of ≥ 10% to the habitat suitability model

Common name	HostRich	QA50	QY10	QY90	JST	AAT	PPT	Elev	Grad	Glacial	Fine	Soil	Wetland
Elktoe	**14.0**(+)	**33.9**(+)	0.5	0.3	5.8	4.2	4.0	1.9	0.3	0.0	0.3	3.8	0.3
Slippershell	**15.4**(+)	**38.0**(+)	0.2	0.7	1.4	0.4	0.6	1.3	0.6	1.9	4.2	2.1	2.8
Purple wartyback	6.7	**41.1**(+)	0.8	0.1	4.0	0.3	0.1	0.0	0.6	0.3	3.4	0.6	0.2
Snuffbox	0.3	**12.5**(+)	0.4	0.1	0.7	1.1	1.5	0.0	0.7	0.1	1.8	3.2	0.3
Wavy-rayed lampmussel	**20.4**(+)	**10.6**(−)	1.3	0.0	0.0	**13.2**(*)	0.3	0.1	1.8	1.1	0.6	0.5	0.8
Black sandshell	**12.3**(+)	**32.8**(*)	0.4	0.2	1.9	1.0	2.0	0.0	0.4	2.3	1.8	0.6	0.0
Round pigtoe	**17.8**(+)	**35.8**(+)	1.6	0.3	5.1	6.7	2.0	2.2	0.9	0.2	1.4	2.9	2.5
Kidneyshell	0.9	**50.4**(−)	0.7	0.6	0.7	9.4	2.9	0.3	1.7	0.6	0.8	1.8	0.2
Deertoe	**19.1**(+)	0.0	0.5	0.4	1.8	2.9	0.6	**12.1**(−)	6.4	0.1	6.9	1.1	0.2
Ellipse	**10.0**(+)	**44.8**(−)	0.2	0.4	0.1	0.8	0.6	1.2	1.5	0.7	5.6	0.6	0.6
Rainbow	**40.4**(+)	**17.5**(−)	1.4	1.6	1.8	**12.1**(*)	4.2	1.6	0.3	0.7	0.4	1.8	3.5
Average	14.3	28.9	0.7	0.4	2.1	4.7	1.7	1.9	1.4	0.7	2.5	1.7	1.0

See Table 1 for full description of the variables

Table 5 Mussel anthropogenic variable relative importance percentage and species response type [denoted as positive (+), negative (−), or unimodal (*)] for key predictors shown in bold with contributions of ≥ 10% to the habitat suitability model

Common name	UrbanL	UrbanM	UrbanH	RowCrop	Pasture	Imperv	RoadCrDens	UNDR	UMO	DMD	DMO
Elktoe	0.6	0.2	**10.8**(−)	0.4	1.5	0.1	1.1	0.2	**14.1**(−)	0.7	0.9
Slippershell	0.2	4.0	0.1	2.5	**14.7**(−)	0.0	1.2	3.6	2.4	1.3	0.4
Purple wartyback	0.0	0.1	**11.2**(−)	0.1	0.4	0.0	0.0	0.1	**27.6**(−)	2.0	0.1
Snuffbox	3.0	4.6	**13.2**(−)	0.7	1.2	6.5	0.2	**40.2**(−)	1.9	2.0	3.6
Wavy-rayed lampmussel	1.6	3.7	8.0	1.3	0.6	0.2	0.0	**30.4**(−)	2.2	0.3	1.0
Black sandshell	0.2	0.6	7.6	0.5	0.2	0.0	0.0	**17.8**(−)	**16.3**(−)	0.0	1.2
Round pigtoe	0.2	0.7	9.1	1.0	2.6	0.1	0.4	1.9	3.1	0.4	1.3
Kidneyshell	0.5	0.6	**18.3**(−)	0.6	2.5	0.0	2.4	1.8	1.0	0.3	1.1
Deertoe	0.0	0.3	**20.3**(−)	2.7	0.5	0.3	0.4	0.0	**16.7**(−)	0.0	6.7
Ellipse	0.2	0.3	9.3	**17.7**(+)	1.9	0.0	0.0	0.1	2.5	0.3	0.7
Rainbow	0.5	0.4	4.1	0.4	1.0	1.1	0.9	0.1	2.9	0.9	0.3
Average	0.6	1.4	10.2	2.5	2.5	0.8	0.6	8.7	8.2	0.7	1.6

See Table 1 for full description of the variables

in mussel habitat suitability models; it was a key contributor to suitability for 8 of 11 species assessed. Other regional or broad scale studies have found host fish variables were less important in determining mussel habitat use then abiotic variables. Inoue et al. (2016) concluded that a lack of concordance in central and northern European mussels and their obligate host fishes was due to the importance of abiotic (natural and anthropogenic variables) determining mussel local habitat use instead of host fish presence. Daniel and Brown (2013) found that host fishes were not a limiting resource for most mussel species of eastern Louisiana, so were also less important in determining local habitat suitability. While these studies concluded

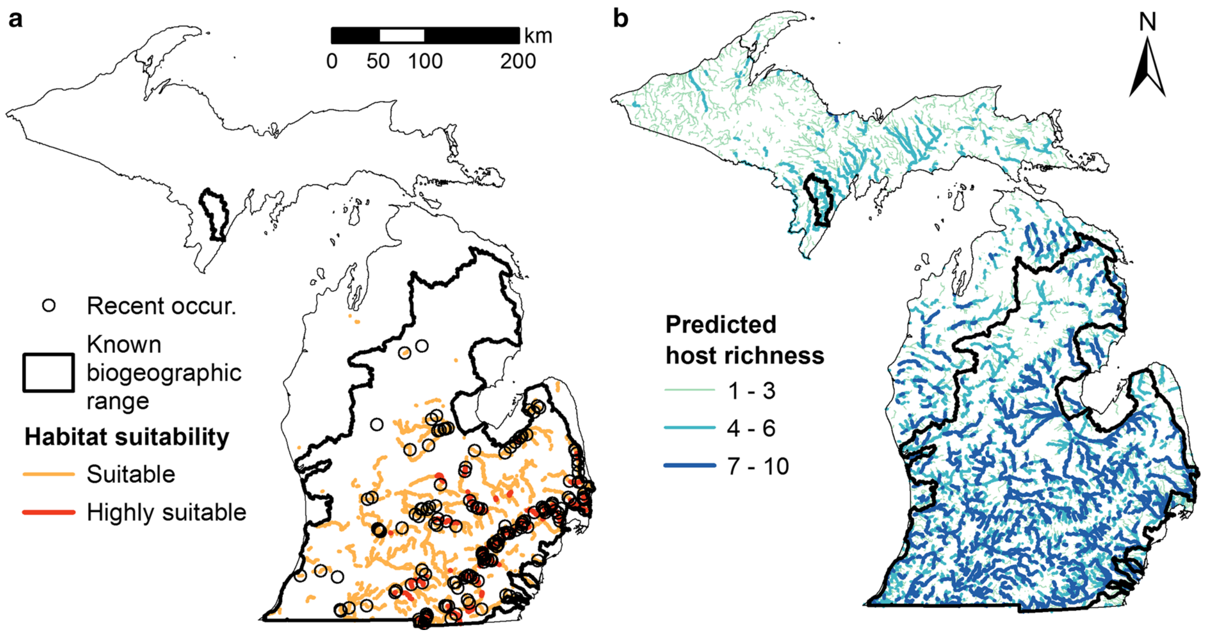

Fig. 2 Predicted habitat suitability (**a**) and host richness (**b**) compared with the known biogeographic range for *villosa iris* (rainbow)

that host fishes have a diminished role in determining small-scale mussel occurrence, we have shown that mussel distributions over Michigan are strongly tied to host fish distributions, and those mussel distributions are constrained hierarchically by host fish ranges.

The reliance of freshwater mussels on host fishes for juvenile development and dispersal underscores the importance of accounting for host fishes when considering mussel distributions (Strayer, 2008). While relationships between mussel distributions and host fish abundance measures have been described in previous studies (Vaughn & Taylor, 2000; Haag & Warren, 1998), our results demonstrate an approach for using predicted presence of host fishes to assess distributions of mussels across a large and heterogeneous region compared to smaller scaled studies within a single watershed. This approach shows promise for large-scale efforts to effectively conserve freshwater mussels and their fluvial habitats and suggests the value of incorporating host richness in modeling habitat suitability of imperiled freshwater mussels.

Development of host habitat suitability models allows for evaluation of relationships between individual hosts and mussel species at broad geographic scales. For example, the slippershell has two ubiquitous fish hosts (johnny darter and mottled sculpin; Clarke, 1981) and the highest amount of predicted suitable habitat in this study. Johnny darter has the second most predicted suitable habitat among host fishes, and this may be one of the key variables in the higher amount of suitable habitat identified for slippershell. Alternatively, the deertoe had the lowest amount of predicted suitable habitat in this study, potentially driven by the species' use of only two very rare fish species as hosts in Michigan, freshwater drum and sauger (Wilson, 1916). The freshwater drum had the lowest amount of suitable habitat of all modeled host fishes in the state and is often limited to large rivers and their tributaries (Etnier & Starnes, 1993). The sauger was not modeled due to the low number of fluvial records within the state, suggesting its limited distribution in riverine habitats. Low host availability for deertoe is a likely variable contributing to the species' threatened status in Michigan.

Natural landscape variables

Natural reach and landscape predictors contributed the most to explaining habitat suitability in 10 of 11 mussel habitat suitability models. This outcome is expected, as natural variables are known to be important determinants of mussel distributions based on results from numerous studies (e.g., Smith, 2001;

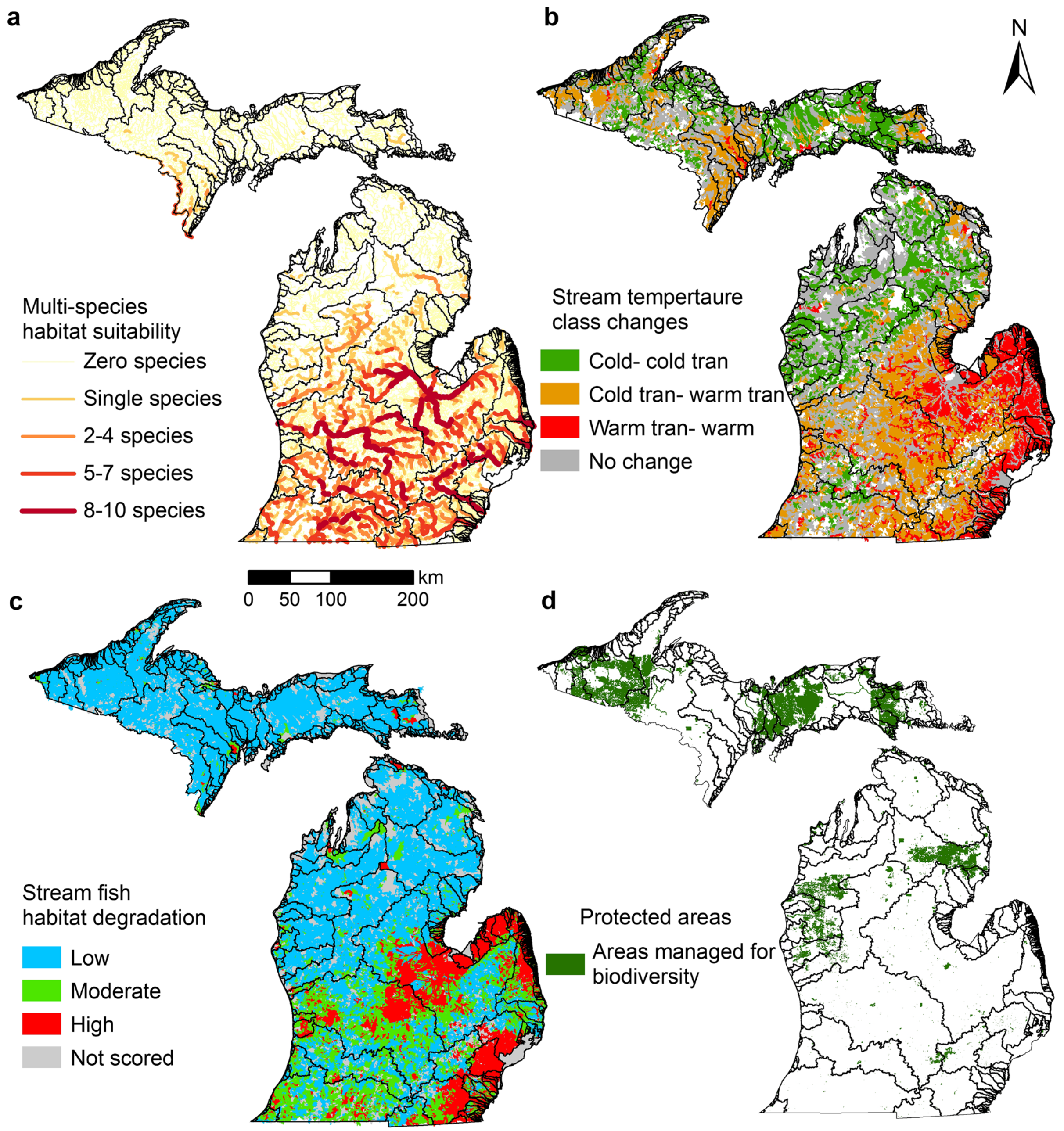

Fig. 3 Maps depicting suitable habitats for multiple imperiled mussel species (**a**), stream temperature class changes to occur with changes in climate (**b**), stream fish habitat condition estimates (**c**), and protected areas (**d**). Stream temperature class changes include the following: cold–cold transitional, cold transitional–warm transitional, and warm transitional–warm

McRae et al., 2004; Strayer, 2008; Daniel & Brown, 2013). Although the resolution of the study's variables and maps do not allow for the identification of individual freshwater mussel habitat patches within a stream, our landscape approach does allow for the determination of continuous variables across the state that contribute to explaining habitat suitability of mussels. Providing a statewide view of significant biotic and abiotic variables which would not be possible with finer scale variables associated with local habitat patches. In our study, median annual stream discharge was the main predictor of mussel

Table 6 Co-occurring mussel species groups at reach-level suitable habitats for the 11 modeled mussel species

Co-occurring mussel species group	No change in temperature class		Change from cold to cold transitional		Change from cold transition to warm transition		Change from warm transition to warm		Low-risk of fish habitat degradation (km)		Moderate risk of fish habitat degradation (km)		High-risk of fish habitat degradation (km)		Protected areas (km)	
	Length (km)	State (%)	Length (km)	State (%)	Length (km)	State (%)	Length (km)	State (%)	Length (km)	State (%)	Length (km)	State (%)	Length (km)	State (%)	Length (km)	State (%)
1 species	1236.9	1.7	374.7	0.5	1784.8	2.4	942.5	1.3	2869.4	3.8	1199.6	1.6	765.6	1.0	167.0	0.2
2–4	955.7	1.3	25.9	0.0	1101.7	1.5	895.4	1.2	1235.1	1.7	1332.3	1.8	728.5	1.0	47.2	0.1
4–7	1216.2	1.6	0.0	0.0	286.0	0.4	985.0	1.3	132.9	0.2	1810.4	2.4	758.5	1.0	9.3	0.0
8–10	798.0	1.1	0.0	0.0	16.9	0.0	194.3	0.3	20.6	0.0	527.3	0.7	523.3	0.7	6.2	0.0

Temperature class changes were developed from FishVis mid-century (2046–2065) models, risk of fish habitat degradation was developed from National Fish Habitat Partnership's (NFHP) 2015 inland assessment, and protected areas developed from the USGS protected lands managed for biodiversity dataset. Low risk of fish habitat degradation was created by combining the low- and very low-risk groups; high risk of fish habitat degradation was created by combining the high- and very high-risk groups from the NFHP 2015 inland assessment results. Habitat lengths are presented both as a total (km) and as a percentage of all streams within the state (%)

habitat suitability. This measure is known to be highly correlated with stream size in the study area (e.g., Zorn et al., 2002), with previous studies showing that mussel richness and diversity increase with increasing stream size (Strayer, 1983; Watters, 1995; Daniel & Brown, 2013). Stream discharge has been shown to determine habitat availability, an important variable for mussels (Layzer & Madison, 1995; Strayer, 1999; Arbuckle & Downing, 2002; Strayer, 2008; Daniel & Brown, 2013). Cao et al. (2015) found stream size measures (catchment area and stream link number) to be dominant variables in the species distribution models of 29 mussels in Illinois, USA. Mussels negatively associated with stream discharge in our study include wavy-rayed lampmussel, kidneyshell, ellipse, and rainbow. While wavy-rayed lampmussel can be found in large rivers (Burch, 1975), the other three species are primarily considered small to medium river specialists (van der Schalie, 1938; Burch, 1975; Cummings & Mayer, 1992; Watters, 1995). Mussel species with positive associations with discharge (elktoe, slippershell, purple wartyback, snuffbox, and round pigtoe) are more commonly found in riffles and runs of mainstem streams and large rivers, with slippershell being an exception as it is also founds in headwater streams (Cummings & Mayer, 1992).

Anthropogenic landscape variables

This study has also showed that anthropogenic landscape variables contributed less than natural variables in determining habitat suitability for most of the mussel species. Agricultural land use is the dominant land use south of the Muskegon and Rifle River basins within the Lower Peninsula of Michigan (Wang et al., 2008), and it contributed little to explaining habitat suitability. Pervasiveness of agricultural land use across the study region may contribute to the fact that it did not have an important role in the models. This finding aligns with that of Cao et al. (2015) who found limited agricultural influences in habitat suitability models of 29 mussel species in Illinois, USA, a study region that contains very high levels of agricultural land use. Urban land use was more variable across the study region, and it had a more consistent negative influence on freshwater mussels than agricultural land use. Urbanization in a watershed can lead to major hydrological, chemical, physical, and geomorphic changes to streams (Watters, 1999; Morgan & Cushman, 2005), and it has been shown to negatively influence mussel populations in previous studies (Watters, 1999; Brown et al., 2010). In this study, five mussel species had negative associations with urban land use. Dams have historically been viewed as one of the major disturbances leading to declines in abundances of freshwater mussels and to species loss (Watters, 1996; Vaughn & Taylor, 1999). Dams alter mussel stream habitat both upstream due to creation of impoundments and downstream by changing fish assemblages, flow conditions, water depth, temperature, dissolved oxygen, and substrate (Watters, 1996; 1999). Within this study, six mussels had dam variables (greater upstream dam densities and decreased upstream mainstem openness) as key predictors for determining habitat suitability.

Modeled suitable and highly suitable habitats as compared to biogeographic ranges

To characterize the full potential extent of suitable habitat statewide, we modeled potential habitats for mussel species both inside and outside of mussels' known biogeographic ranges. The majority of suitable and highly suitable habitats were predicted to occur inside the known biogeographical range for all 11 mussel species. On average, mussels had 93.1 and 95% of suitable and highly suitable, respectively, inside the species known biogeographic range but the exceptions were wavy-rayed lampmussel and deertoe. Wavy-rayed lampmussel and deertoe only had 67.8 and 67.0%, respectfully, of their suitable habitat in their historical biogeographical range. This suggests some potential conclusions about wavy-rayed lampmussel and deertoe. These species are considered habitat generalists, and this fact may have resulted in more habitats being modeled as suitable outside of their existing biogeographic range. Second, host fish mobility might be a limiting variable to wavy-rayed lampmussel and deertoe range expansion instead of the lack of suitable habitat. Deertoe's host fishes were discussed earlier (i.e., freshwater drum and sauger have limited distributions in the state), and wavy-rayed lampmussel hosts include sunfishes and black basses which are abundant through the state, but often have small home ranges, potentially limiting mussel transport to new habitats (Funk, 1957).

For remaining species, a high level of congruence between locations of suitable habitats inferred by the models and species' known biogeographic ranges suggests that these species have occupied many of the basins within the state that have abiotic conditions that are suitable. Although most species had high level of congruence with suitable habitat and historic ranges, the habitat suitability models can inform survey efforts to find additional populations inside of mussel species' known biogeographic range, particularly from basins that have been under-sampled. Further, statewide model results can be useful in cases when managed relocation of a species may become necessary due to habitat degradation within their biogeographic range (Cope & Waller, 1995; Cosgrove & Hastie, 2001).

Multi-species habitat suitability

The stream water temperature changes in Michigan that could occur by mid-century will not, to any great degree, influence the imperiled mussel species directly, but water temperature changes may have the potential to alter host fish habitat suitability. Michigan has a strong north to south stream temperature gradient (Wehrly et al., 2003; Lyons et al., 2009), with most of the freshwater mussel suitable habitat found in the southeastern portion of the Lower Peninsula in warm water habitats. Some of the host fishes of the imperiled mussels are considered cool or cold water species (Lyons et al., 2009), and may have less suitable habitat into the future, leading to possible indirect impact of water temperature changes on mussels. The highly suitable habitat identified by this study that occurs in areas that are not projected to change temperature class could be considered for establishments of new populations as part of adaptive management strategies to address potential changes in climate (Schwartz et al., 2012). Based on stream water temperature changes, many of the streams of the Upper Peninsula and northern Lower Peninsula are projected to change temperature classes. This might open up more suitable habitat in the future for the imperiled mussels, and could be considered for managed relocations in the future, provided they remain suitable for host fishes.

Anthropogenic landscape variables can affect different groups of aquatic organisms differently depending on the scale and intensity of the disturbance (Allan, 2004; Wang et al., 2006). When considering highly degraded fish habitats, it becomes evident that areas that might be suitable for many imperiled freshwater mussels based off our results may be poor habitat for their host fishes. This does not suggest that those fish species may not occur in those locations; however, it does indicate that there are anthropogenic conditions within the basin that have shown to be detrimental to fish abundances. These are areas that need to be considered for restoration activities within the state as they support numerous imperiled mussel species. Further, there is a limited amount of protected lands in Michigan that contain streams with 8–10 imperiled mussel species. This limits the current protection of many of the most suitable habitats for those freshwater mussels in the state. Future conservation actions should take this information into account and look towards protecting mussel habitat that is suitable for multiple imperiled fluvial mussel species.

Conservation implications

Conservation of Michigan's imperiled freshwater mussels may be difficult in the future due to the low amount of stream habitats that contain multiple co-occurring imperiled freshwater mussel species in protected areas and that will not change temperature class with projected climate changes. These streams should be a focus of future conservation efforts until more prioritization of conservation efforts is made, but other areas in Michigan may remain important to focus on due to other reasons. For example, while the Lower Peninsula contains a much higher amount of highly suitable habitat according to our results, anthropogenic disturbances to aquatic habitats tend to be much greater (Wang et al., 2008; Esselman et al., 2011). As a result, smaller pockets of habitat in the Upper Peninsula may provide least-disturbed conditions for certain mussels, such as black sandshell, elktoe, and round pigtoe, and their hosts. Streams in the Lower Peninsula that contain suitable habitat and are only moderately disturbed would provide potential restoration opportunities for mussels, especially in areas that are currently protected or are unlikely to have large stream temperature shifts in the future.

This study has demonstrated the importance of fish hosts to many freshwater mussels' habitat suitability. Because of this, continued efforts to identify host fishes are essential, and our knowledge of host fishes for freshwater mussels is incomplete both in the USA (Strayer, 2008) and globally (Bogan, 2008). With the addition of more host fish species not currently known to science, habitat suitability predictions for the mussels in this study would change. As a result, current habitat suitability predictions may be underestimating potential habitat due to the exclusion of host fishes for certain mussels.

Global conservation of imperiled freshwater mussels can begin with mapping habitat suitability and identifying important variables related to their distribution to help inform decisions in conservation planning and management. Streams with suitable habitat for several co-occurring mussels yield locations with high potential for conserving multiple imperiled species, and provide a starting point for regional conservation efforts, stimulating further field sampling efforts and in-stream habitat evaluations. Our study has also demonstrated the need for larger scale models of habitat suitability for freshwater mussels that expand across political boundaries and represent the species' entire native range. We propose development of a large-scale, integrated database characterizing current freshwater mussel distributions at national or continental scales, an effort that can only be possible by coordination and cooperation among numerous agencies, scientists, and environmental organizations. A large-scale assessment of freshwater mussels would improve opportunities to conserve freshwater habitats and the mussels that inhabit them.

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References

Allan, J. D., 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. Annual Review of Ecology, Evolution, and Systematics 35: 257–284.

Arbuckle, K. E. & J. A. Downing, 2002. Freshwater mussel abundance and species richness: GIS relationships with watershed land use and geology. Canadian Journal of Fisheries and Aquatic Sciences 59: 310–316.

Badra, P. J. & R. R. Goforth, 2003. Freshwater mussel surveys of Great Lakes tributary rivers in Michigan. Michigan Natural Features Inventory report number 2003-15.

Bailey, R. M., W. C. Latta, & G. R. Smith. 2004. An atlas of Michigan fishes with keys and illustrations for their identification. Museum of Zoology, University of Michigan, Miscellaneous Publications No. 192. Ann Arbor.

Bogan, A. E., 2008. Global diversity of freshwater mussels (Mollusca, Bivalvia) in freshwater. Hydrobiologia 595: 139–147.

Brown, K. M., G. George & W. Daniel, 2010. Urbanization and a threatened freshwater mussel: evidence from landscape scale studies. Hydrobiologia 655: 189–196.

Burch, J., 1975. Freshwater unionacean clams (Mollusca: Pelecypoda) of North America. Malacological Publications, Hamburg.

Cao, Y., J. Huang, K. S. Cummings & A. Holtrop, 2013. Modeling changes in freshwater mussel diversity in an agriculturally dominated landscape. Freshwater Science 32: 1205–1218.

Cao, Y., A. Stodola, S. Douglass, D. Shasteen, K. Cummings & A. Holtrop, 2015. Modeling and mapping the distribution, diversity, and abundance of freshwater mussels (Family Unionidae) in wadeable streams of Illinois, U.S.A. Freshwater Biology 60: 1379–1397.

Clarke, A. H., 1981. The freshwater mollusks of Canada. National Museum of Natural Sciences, Ottawa.

Clark, J. A. & E. Harvey, 2002. Assessing multi-species recovery plans under the Endangered Species Act. Ecological Applications 12: 655–662.

Cooper, A. R., D. M. Infante, K. E. Wehrly, L. Wang & T. O. Brenden, 2016. Identifying indicators and quantifying large-scale effects of dams on fishes. Ecological Indicators 61: 646–657.

Cooper, A. R., D. M. Infante, W. M. Daniel, K. E. Wehrly, L. Wang & T. O. Brenden, 2017. Assessment of dam effects on streams and fish assemblages of the conterminous USA. Science of the Total Environment. 586: 879–889.

Cope, W. G. & D. L. Waller, 1995. Evaluation of freshwater mussel relocation as a conservation and management strategy. Regulated Rivers: Research & Management 11: 147–155.

Cosgrove, P. J. & L. C. Hastie, 2001. Conservation of threatened freshwater pearl mussel populations: river management, mussel translocation and conflict resolution. Biological Conservation 99: 183–190.

Crawford, S., G. Whelan, D. M. Infante, K. Blackhart, W. M. Daniel, P. L. Fuller, T. Birdsong, D. J. Wieferich, R. McClees-Funinan, S. M. Stedman, K. Herreman & P. Ruhl, 2016. Through a Fish's Eye: The Status of Fish Habitats in the United States 2015. National Fish Habitat Partnership [available at http://assessment.fishhabitat.org/].

Cummings, K. S. & C. A. Mayer, 1992. Field Guide to Freshwater Mussels of the Midwest. Illinois Natural History Survey Manual 5, Champaign.

Daniel, W. M. & K. M. Brown, 2013. Multifactorial model of habitat, host fish, and landscape effects on Louisiana freshwater mussels. Freshwater Science 32: 193–203.

Daniel, W. M. & K. M. Brown, 2014. The role of life history and behavior in explaining mussel distributions. Hydrobiologia 734: 57–68.

Daniel, W. M., D. M. Infante, R. M. Hughes, P. C. Esselman, Y. P. Tsang, D. Wieferich, K. Herreman, A. R. Cooper, L. Wang & W. Taylor, 2015. Coal and mineral mines as a regional source of stress to stream fish assemblages. Ecological Indicators 50: 50–61.

Downing, J. A., P. Van Meter & D. A. Woolnough, 2010. Suspects and evidence: a review of the causes of extirpation and decline in freshwater mussels. Animal Biodiversity and Conservation 33: 151–185.

Dunithan, A., 2012. Using Ecological Niche Modeling to Predict Occurrence of Rare Fish and Unionid Mussels in East Texas. The University of Texas at Tyler. Master's thesis.

Elith, J., 2000. Quantitative methods for modeling species habitat: comparative performance and an application to Australian plants. In Ferson, S. & M. Burgman (eds), Quantitative Methods for Conservation Biology. Springer, New York: 39–58.

Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee & C. J. Yates, 2011. A statistical explanation of MaxEnt for ecologists. Diversity and Distributions 17: 43–57.

Esselman, P. C., D. M. Infante, L. Wang, D. Wu, A. R. Cooper & W. W. Taylor, 2011. An index of cumulative disturbance to river fish habitats of the conterminous United States from anthropogenic activities in landscapes. Ecological Restoration 29: 133–151.

Etnier, D. A. & W. C. Starnes, 1993. The fishes of Tennessee. The University of Tennessee Press, Knoxville.

FishVis, 2013. Regional decision support tool for identifying vulnerabilities of riverine habitat and fishes to climate change [available at https://www.sciencebase.gov/catalog/item/5113e594e4b0a9ee4115bb08].

FMCS (Freshwater Mollusk Conservation Society), 2016. A national strategy for the conservation of native freshwater mollusks. Freshwater Mollusk Biology and Conservation 19: 1–21.

Funk, J. L., 1957. Movement of fishes in Missouri. Transactions of the American Fisheries Society 85: 39–57.

Gallardo, B., P. S. E. Ermgassen & D. C. Aldridge, 2013. Invasion ratcheting in the zebra mussel (*Dreissena polymorpha*) and the ability of native and invaded ranges to predict its global distribution. Journal of Biogeography 40: 2274–2284.

Gido, K. B., W. K. Dodds & M. E. Eberle, 2010. Retrospective analysis of fish community change during a half-century of landuse and streamflow changes. Journal of the North American Benthological Society. 29: 970–987.

Haag, W. R., 2012. North American Freshwater Mussels: Natural History, Ecology, and Conservation. Cambridge University Press, New York.

Haag, W. R. & M. L. Warren, 1998. Role of ecological factors and reproductive strategies in freshwater mussel communities. Canadian Journal of Fisheries and Aquatic Sciences 55: 297–306.

Hastie, L. C. & M. R. Young, 2003. Timing of spawning and glochidial release in Scottish freshwater pearl mussel (Margaritifera margaritifera) populations. Freshwater Biology 48: 2107–2117.

Heffentrager, K. B., 2013. Utilizing MAXENT to Improve and Explain a Species Distribution Model for Freshwater Mussel Species in East Texas. The University of Texas at Tyler. Master's thesis.

Hopkins, R. L., 2009. Use of landscape pattern metrics and multiscale data in aquatic species distribution models: a case study of a freshwater mussel. Landscape Ecology 24: 943–955.

Inoue, K., K. Stoeckl & J. Geist, 2016. Joint species models reveal the effects of environment on community assemblage of freshwater mussels and fishes in European rivers. Diversity and Distribution 23: 284–296.

Keller, A. E. & D. S. Ruessler, 1997. Determination or verification of host fish for nine species of unionid mussels. American Midland Naturalist 138: 402–407.

Jiménez-Valverde, A. & J. M. Lobo, 2007. Threshold criteria for conversion of probability of species presence to either-or presence-absence. Acta Oecologica 31: 361–369.

Layzer, J. B. & L. M. Madison, 1995. Microhabitat use by freshwater mussels and recommendations for determining their instream flow needs. Regulated Rivers: Research & Management 10: 329–345.

Liu, C., M. White & G. Newell, 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. Journal of Biogeography 40: 778–789.

Lois, S., D. E. Cowley, A. Outeiro, E. San Miguel, R. Amaro & P. Ondina, 2015. Spatial extent of biotic interactions affects species distribution and abundance in river networks: the freshwater pearl mussel and its hosts. Journal of Biogeography 42: 229–240.

Lopes-Lima, M., R. Sousa, J. Geist, D. C. Aldridge, R. Araujo, J. Bergengren, et al., 2016. Conservation status of freshwater mussels in Europe: state of the art and future challenges. Biological Reviews 92: 572–607.

Lyons, J., T. Zorn, J. Stewart, P. Seelbach, K. Wehrly & L. Wang, 2009. Defining and characterizing coolwater streams and their fish assemblages in Michigan and Wisconsin, USA. North American Journal of Fisheries Management 29: 1130–1151.

McRae, S. E., J. D. Allan & J. B. Burch, 2004. Reach- and catchment-scale determinants of the distribution of freshwater mussels (Bivalvia: Unionidae) in south-eastern Michigan, U.S.A. Freshwater Biology 49: 127–142.

MDNR, 2015. Appendix 1- Species of Greatest Conservation Need: Michigan's wildlife action plan. Michigan Department of Natural Resources, Lansing, Michigan, USA. (Draft)

Morgan, R. P. & S. F. Cushman, 2005. Urbanization effects on stream fish assemblages in Maryland, USA. Journal of the North American Benthological Society 24: 643–655.

Naimo, T. J., 1995. A review of the effects of heavy-metals on fresh-water mussels. Ecotoxicology 4: 341–362.

Newton, T. J. & M. R. Bartsch, 2007. Lethal and sublethal effects of ammonia to juvenile Lampsilis mussels (Unionidae) in sediment and water-only exposures. Environmental Toxicology and Chemistry 26: 2057–2065.

Newton, T. J., S. J. Zigler, J. T. Rogala, B. R. Gray & M. Davis, 2011. Population assessment and potential functional roles of native mussels in the Upper Mississippi River. Aquatic Conservation: Marine and Freshwater Ecosystems. 21: 122–131.

Oliveira, M. D., S. K. Hamilton & C. M. Jacobi, 2010. Forecasting the expansion of the invasive golden mussel *Limnoperna fortune* in Brazilian and North American rivers based on its occurrence in the Paraguay River and Pantanal wetland of Brazil. Aquatic Invasions 5: 59–73.

Phillips, S. J. & M. Dudík, 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31: 161–175.

Phillips, S. J., R. P. Anderson & R. E. Schapire, 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190: 231–259.

Prié, V., Q. Molina & B. Gamboa, 2014. French naiad (Bivalvia: Margaritiferidae, Unionidae) species distribution models: predication maps as tools for conservation. Hydrobiologia 735: 81–94.

Provan, J., & K. D. Bennett, 2008. Phylogeographic insights into cryptic glacial refugia. Trends in Ecology & Evolution 23: 564–571.

Quinn, A., B. Gallardo & D. C. Aldridge, 2014. Quantifying the ecological niche overlap between two interacting invasive species: the zebra mussel (*Dreissena polymorpha*) and the quagga mussel (*Dreissena rostriformis bugensis*). Aquatic Conservation: Marine and Freshwater Ecosystems 24: 324–337.

Roth, N. E., J. D. Allan & D. L. Erickson, 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecology 11: 141–156.

Schwartz, M. W., J. J. Hellmann, J. M. McLachlan, D. F. Sax, J. O. Borevitz, J. Brennan, A. E. Camacho, G. Ceballos, J. R. Clark, H. Doremus & R. Early, 2012. Managed relocation: integrating the scientific, regulatory, and ethical challenges. BioScience 62: 732–743.

Stewart, J. S., S. A. Covert, D. Krueger, M. T. Slattery, D. J. Wieferich, S. M. Westenbroek, D. M. Infante, J. E. McKenna & J. D. Lyons, 2016. FishVis: predicted occurrence and vulnerability for 13 fish species for current (1961 - 1990) and future (2046 - 2100) climate conditions in Great Lakes streams: U.S. Geological Survey data.

Smith, D., 2001. Pennak's Freshwater Invertebrates of the United States: Porifera to Crustacea, 4th ed. Wiley, New York.

Strayer, D., 1983. The effects of surface geology and stream size on freshwater mussel (Bivalvia, Unionidae) distribution in southeastern Michigan, USA. Freshwater Biology 13: 253–264.

Strayer, D. L., 2008. Freshwater Mussel Ecology: A Multifactor Approach to Distribution and Abundance. University of California Press, Berkeley.

Strayer, D. L. & J. Ralley, 1993. Microhabitat use by an assemblage of stream-dwelling unionaceans (Bivalvia), including two rare species of Alasmidonta. Journal of the North American Benthologial Society 12: 247–258.

Strayer, D. L., N. F. Caraco, J. J. Cole, S. Findlay & M. L. Pace, 1999. Transformation of freshwater ecosystems by bivalves: a case study of zebra mussels in the Hudson River. BioScience 49: 19–27.

Strayer, D. L., J. A. Downing, W. R. Haag, T. L. King, J. B. Layzer, T. J. Newton & J. S. Nichols, 2004. Changing perspectives on pearly mussels, North America's most imperiled animals. BioScience 54: 429–439.

Tsang, Y. P., D. Wieferich, K. Fung, D. M. Infante & A. R. Cooper, 2014. An approach for aggregating upstream catchment information to support research and management of fluvial systems across large landscapes. SpringerPlus 3: 1.

USFWS (U.S. Fish and Wildlife Service), 2011. Endangered and Threatened Wildlife and Plants; Permits. U.S. Fish and Wildlife Service, Federal Register 76(110):33334–33336.

USGS, 1995. Soils data for the Conterminous United States Derived from the NRCS State Soil Geographic (STATSGO) Data Base [available at https://water.usgs.gov/GIS/metadata/usgswrd/XML/ussoils.xml].

USGS, 2010. Terrestrial Ecosystems – Surficial Lithology of the Conterminous United States [available at https://rmgsc.cr.usgs.gov/ecosystems/datadownload.shtml].

USGS, 2016. National Gap Analysis Program (GAP), Protected Areas Data Portal [available at http://gapanalysis.usgs.gov/padus/]. Accessed May 2015.

Utz, R., R. Hilderbrand & R. Raesly, 2010. Regional differences in patterns of fish species loss with changing land use. Biological Conservation 143: 688–699.

Van der Schalie, H., 1938. The naiad fauna of the Huron River, in southeastern Michigan. Miscellaneous Publications of the Museum of Zoology, University of Michigan 40: 1–83.

Vaughn, C. C. & C. M. Taylor, 1999. Impoundments and the decline of freshwater mussels: a case study of an extinction gradient. Conservation Biology 13: 912–920.

Vaughn, C. C. & C. M. Taylor, 2000. Macroecology of a host-parasite relationship: distribution patterns of mussels and fishes. Ecography 23: 11–20.

Wang, L., P. W. Seelbach & R. M. Hughes, 2006. Introduction to landscape influences on stream habitats and biological assemblages. In American Fisheries Society Symposium, Vol. 48, p. 1. American Fisheries Society.

Wang, L., J. Lyons, P. Kanehi, R. Bannerman & E. Emmons, 2000. Watershed urbanization and changes in fish communities in southeastern Wisconsin streams. Journal of the American Water Resources Association 36: 1173–1189.

Wang, L., T. Brenden, P. Seelbach, A. Cooper, D. Allan, R. Clark, & M. Wiley, 2008. Landscape based identification of human disturbance gradients and reference conditions for Michigan streams. Environmental Monitoring and Assessment 141: 1–17.

Wang, L., D. Infante, P. Esselman, A. Cooper, D. Wu, W. Taylor, D. Beard, G. Whelan, et al., 2011a. A hierarchical spatial framework and database for the national river fish habitat condition assessment. Fisheries 36: 436–449.

Wang, L., D. Infante, J. Lyons, J. Stewart & A. Cooper, 2011b. Effects of dams in river networks on fish assemblages in non-impoundment sections of rivers in Michigan and Wisconsin, USA. River Research and Applications 27: 473–487.

Wang, L., D. Infante, C. Riseng & K. Wehrly, 2016. Advancement of geospatial capability by NRiSD and GLAHF in enhancing aquatic ecosystem research and management. Geoinformatics & Geostatistics: An Overview 4: 2.

Watters, G., 1995. A Guide to the Freshwater Mussels of Ohio. Ohio Department of Natural Resources, Columbus.

Watters, G. T., 1996. Small dams as barriers to freshwater mussels (Bivalvia, Unionoida) and their hosts. Biological Conservation 75: 79–85.

Watters, G. T., 1999. Freshwater mussels and water quality: A review of the effects of hydrologic and instream habitat alterations. Proceedings of the First Freshwater Mollusk Conservation Society Symposium: 261–274.

Wehrly, K. E., M. J. Wiley & P. W. Seelbach, 2003. Classifying regional variation in thermal regime based on stream fish community patterns. Transactions of the American Fisheries Society 132: 18–38.

Williams, J. D., M. L. Warren, K. S. Cummings, J. L. Harris & R. J. Neves, 1993. Conservation status of freshwater mussels of the United States and Canada. Fisheries 18: 6–22.

Wilson, C., 1916. Copepod parasites of fresh-water fishes and their economic relations to mussel glochidia. Bulletin of the Bureau of Fisheries 34: 333–374.

Wilson, C. D., D. Roberts & N. Reid, 2011. Applying species distribution modelling to identify areas of high conservation value for endangered species: A case study using *Margaritifera margaritifera* (L.). Biological Conservation 144: 821–829.

Xian, G., C. Homer & J. Fry, 2009. Updating the 2001 National Land Cover Database land cover classification to 2006 by using Landsat imagery change detection methods. Remote Sensing of Environment 113: 1133–1147.

Zorn, T. G., P. W. Seelbach & M. J. Wiley, 2002. Distributions of stream fishes and their relationship to stream size and hydrology in Michigan's Lower Peninsula. Transactions of the American Fisheries Society 131: 70–85.