Predicting mussel species at risk distributions in southwestern Ontario rivers using spatial distribution models and the Aquatic Ecosystem Classification method

Scott M. Reid, Allan H.M. Bell, Anita LeBaron, Bastian J. Schmidt, and Nicholas E. Jones

Ontario and Prairie Region
Fisheries and Oceans Canada
P.O. Box 5050, 867 Lakeshore Road
Burlington, ON
L7S 1A1

2023

Canadian Manuscript Report of Fisheries and Aquatic Sciences 3259

Fisheries and Oceans Canada Pêches et Océans Canada

Canada

Canadian Manuscript Report of Fisheries and Aquatic Sciences

Manuscript reports contain scientific and technical information that contributes to existing knowledge but which deals with national or regional problems. Distribution is restricted to institutions or individuals located in particular regions of Canada. However, no restriction is placed on subject matter, and the series reflects the broad interests and policies of Fisheries and Oceans Canada, namely, fisheries and aquatic sciences.

Manuscript reports may be cited as full publications. The correct citation appears above the abstract of each report. Each report is abstracted in the data base *Aquatic Sciences and Fisheries Abstracts*.

Manuscript reports are produced regionally but are numbered nationally. Requests for individual reports will be filled by the issuing establishment listed on the front cover and title page.

Numbers 1-900 in this series were issued as Manuscript Reports (Biological Series) of the Biological Board of Canada, and subsequent to 1937 when the name of the Board was changed by Act of Parliament, as Manuscript Reports (Biological Series) of the Fisheries Research Board of Canada. Numbers 1426 - 1550 were issued as Department of Fisheries and Environment, Fisheries and Marine Service Manuscript Reports. The current series name was changed with report number 1551.

Rapport manuscrit canadien des sciences halieutiques et aquatiques

Les rapports manuscrits contiennent des renseignements scientifiques et techniques qui constituent une contribution aux connaissances actuelles, mais qui traitent de problèmes nationaux ou régionaux. La distribution en est limitée aux organismes et aux personnes de régions particulières du Canada. II n'y a aucune restriction quant au sujet; de fait, la série reflète la vaste gamme des intérêts et des politiques de Pêches et Océans Canada, c'est-à-dire les sciences halieutiques et aquatiques.

Les rapports manuscrits peuvent être cités comme des publications à part entière. Le titre exact figure au-dessus du résumé de chaque rapport. Les rapports manuscrits sont résumés dans la base de données *Résumés des sciences aquatiques et halieutiques.*

Les rapports manuscrits sont produits à l'échelon régional, mais numérotés à l'échelon national. Les demandes de rapports seront satisfaites par l'établissement auteur dont le nom figure sur la couverture et la page du titre.

Les numéros 1 à 900 de cette série ont été publiés à titre de Manuscrits (série biologique) de l'Office de biologie du Canada, et après le changement de la désignation de cet organisme par décret du Parlement, en 1937, ont été classés comme Manuscrits (série biologique) de l'Office des recherches sur les pêcheries du Canada. Les numéros 901 à 1425 ont été publiés à titre de Rapports manuscrits de l'Office des recherches sur les pêcheries du Canada. Les numéros 1426 à 1550 sont parus à titre de Rapports manuscrits du Service des pêches et de la mer, ministère des Pêches et de l'Environnement. Le nom actuel de la série a été établi lors de la parution du numéro 1551.

Canadian Manuscript Report of
Fisheries and Aquatic Sciences 3259

2023

Predicting mussel species at risk distributions in southwestern Ontario rivers using spatial distribution models and the Aquatic Ecosystem Classification method

by

Scott M. Reid[1], Allan H.M. Bell[1], Anita LeBaron[1], Bastian J. Schmidt[1], and Nicholas E. Jones[1]

Ontario and Prairie Region
Fisheries and Oceans Canada
P.O. Box 5050, 867 Lakeshore Road
Burlington, ON
L7S 1A1

---

[1] Aquatic Research and Monitoring Section, Ministry of Northern Development, Mines, Natural Resources and Forestry. Trent University – DNA Building, 2140 East Bank Drive, Peterborough ON, K9L 1Z8

Cat. No. Fs97-4/3259E-PDF ISBN 978-0-660-47199-0 ISSN 1488-5387

Correct citation for this publication:

Reid, S.M., Bell, A.H.M., LeBaron, A., Schmidt, B.J., and Jones, N.E. 2023. Predicting mussel species at risk distributions in southwestern Ontario rivers using spatial distribution models and the Aquatic Ecosystem Classification method. Can. Manuscr. Rep. Fish. Aquat. Sci. 3259: vii + 26 p.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABSTRACT

Reid, S.M., Bell, A.H.M., LeBaron, A., Schmidt, B.J., and Jones, N.E. 2023. Predicting mussel species at risk distributions in southwestern Ontario rivers using spatial distribution models and the Aquatic Ecosystem Classification method. Can. Manuscr. Rep. Fish. Aquat. Sci. 3259: vii + 26 p.

By identifying relationships with abiotic and biotic factors, output from species distribution models can help to identify the boundaries of aquatic species at risk critical habitat, direct inventories, and define the spatial units for long-term population monitoring. In this study, we tested whether SDMs can be developed from existing southern Ontario occurrence data for five mussel species at risk using MaxEnt software, a program for modelling species distributions with presence-only species records. Models were built using species presence and abiotic attribute data for the Ausable, Bayfield, Grand, Thames, and Sydenham rivers. Abiotic attributes included: channel slope, riparian and catchment forest cover, summer water temperature, surficial geology, and upstream catchment area. Attributes were based on the provincial Aquatic Ecosystem Classification (AEC) scheme. Strongly supported distribution models were developed for all five mussel species, with 2 to 4 influential predictor variables being identified for each species. Predictors identified consistently across species as influencing habitat suitability were summer water temperature and upstream contributing area. Other informative variables (i.e., geology and tree cover) were only identified for more widespread species (e.g., Wavy-rayed Lampmussel). The number of informative predictor variables for rarer species (e.g., Fawnsfoot) may be limited by the small number of species records, which could be addressed through future inventories. Incorporating the influence of anthropogenic stressors and host fish availability would also improve MaxEnt models but does require the compilation of additional databases.

RÉSUMÉ

Reid, S.M., Bell, A.H.M., LeBaron, A., Schmidt, B.J., and Jones, N.E. 2023. Predicting mussel species at risk distributions in southwestern Ontario rivers using spatial distribution models and the Aquatic Ecosystem Classification method. Can. Manuscr. Rep. Fish. Aquat. Sci. 3259: vii + 26 p.

En recensant les relations avec les facteurs abiotiques et biotiques, les résultats des modèles de répartition des espèces peuvent aider à déterminer les limites de l'habitat essentiel des espèces aquatiques en péril, à diriger les comptabilisations des stocks et à définir les unités spatiales pour le suivi à long terme des populations. Dans le cadre de la présente étude, nous avons tenté de déterminer si des modèles de répartition spatiale (MRS) peuvent être élaborés à partir des données d'occurrence existantes dans le sud de l'Ontario pour cinq espèces de moules en péril à l'aide du logiciel MaxEnt, un programme de modélisation des distributions d'espèces avec des enregistrements d'espèces en présence seulement. Les modèles ont été créés au moyen des données sur la présence des espèces et les déterminants abiotiques pour les rivières Ausable, Bayfield, Grand, Thames et Sydenham. Les déterminants abiotiques comprenaient : l'inclinaison du chenal, la couverture forestière riveraine et du bassin versant, la température estivale de l'eau, la géologie de surface et la zone du bassin versant en amont. Les déterminants étaient fondés sur le schéma provincial de classification des écosystèmes aquatiques (CEA). Des modèles de distribution solidement étayés ont été élaborés pour les cinq espèces de moules, 2 à 4 variables prédictives influentes ayant été recensées pour chaque espèce. Les prédicteurs recensés systématiquement à l'échelle des espèces comme ayant une incidence sur les habitats propices étaient la température estivale de l'eau et la zone contributive en amont. D'autres variables informatives (p. ex. la géologie et le couvert arboré) n'ont été recensées que pour les espèces les plus répandues (p. ex. la lampsile fasciolée). Le nombre de variables prédictives informatives pour les espèces plus rares (p. ex. la troncille pied-de-faon) est peut-être limité en raison du petit nombre d'enregistrements d'espèces, ce qui pourrait être traité dans le cadre d'exercices de comptabilisation des stocks à venir. L'intégration de l'incidence des facteurs de stress anthropiques et de la disponibilité des poissons-hôtes améliorerait également les modèles MaxEnt, mais exige la compilation de bases de données supplémentaires.

INTRODUCTION

Southwestern Ontario rivers support the greatest diversity of freshwater mussels in Canada and provide a refuge for riverine mussel species at risk from the adverse impacts of invasive dreissenid mussels. Understanding the spatial distribution of mussel species at risk is essential for delineating critical habitat, designing long-term monitoring programs, and directing on-the-ground recovery actions. However, given the large amount of riverine habitat in southwestern Ontario and practical constraints facing surveyors (e.g., turbid and non-wadeable habitats, securing permission to access private lands), sampling coverage is not extensive across most watersheds. Often aquatic species at risk surveys are directed back to areas of previous species capture. Therefore, gaps exist in the knowledge of species distributions, affecting conservation planning decisions. Spatial-based approaches are needed to define and account for these biases.

By identifying relationships with abiotic factors, species distribution models (SDM) can help assess whether unsampled river reaches are likely to support mussel species at risk, and therefore require targeted surveys to refine the delineation of critical habitats. Additionally, output from SDMs can be used to define the spatial boundaries of sampling frames associated with long-term population monitoring programs. It is also possible to use “stacked” single species distribution model outputs (for multiple species) for the purpose of identifying important sub-watersheds for multi-species recovery actions. Lastly, SDMs developed for primary and secondary host fishes could be used to model the potential spatial overlap/co-occurrence of mussel species at risk with host fishes.

In this study, we tested whether SDMs can be developed from existing mussel species at risk occurrence data using MaxEnt software; a program for modelling species distributions with presence-only species records. MaxEnt is based on the maximum-entropy approach for modelling species niches and distributions (Phillips et al. 2006). The software uses a list of species presence locations as input as well as a set of environmental predictors across a user-defined landscape that is divided into grid cells. From this landscape, MaxEnt extracts a sample of background locations that it contrasts against the presence locations. Presence is unknown at background locations. The model expresses a probability distribution where each grid cell has a predicted suitability of conditions for the species. In the United States, MaxEnt has been used to predict the distributions of imperiled freshwater mussels based on host fish richness, anthropogenic stressors, and abiotic reach and landscape-based variables (Campbell and Hilderbrand 2017, Daniel et al. 2018). As MaxEnt can perform well with a small number of location records (Wisz et al. 2008), the software is potentially suitable for modelling rare species that have limited geographic distributions.

In this report, we present results of MaxEnt species distribution modelling for Fawnsfoot *Truncilla donaciformis* (SARA status: Endangered), Rainbow (*Cambarunio iris*; SARA status: Special Concern), Round Pigtoe (*Pleurobema sintoxia*; SARA status: Endangered), Threehorn Wartyback (*Obliquaria reflexa*; SARA status: Threatened), and Wavy-rayed Lampmussel (*Lampsilis fasciola*; SARA status: Special Concern). The five species represent a range of data availability for modelling, from a small number of records for Fawnsfoot to the more common and widespread Wavy-rayed Lampmussel. Predictor variables were identified from abiotic attributes used in Ministry of Natural Resources and Forestry Aquatic Ecosystem Classification (AEC) scheme (Jones and Schmidt 2017). Models were built using species presence and abiotic attribute data for the Ausable, Bayfield, Grand, Thames, and Sydenham rivers. While the full distributions of all study species in southern Ontario are not covered, the rivers represent extensively surveyed systems and provide a suitable dataset to demonstrate and assess the modelling approach. The project supports the following priority research and monitoring actions for southern Ontario mussel species at risk: (i) improve understanding of species distribution patterns; (ii) characterize critical habitat; and (iii) establish population monitoring programs.

METHODS

MODELLING DATASET

We obtained freshwater mussel species occurrence data (live individuals and fresh shells) from the Fisheries and Oceans Canada lower Great Lakes Unionid database. Species records were primarily from visual/tactile timed-search (Metcalfe-Smith et al. 2000; Wright et al. 2020) and quadrat surveys (Reid and Morris 2017; Sheldon et al. 2020). Surveys were largely limited to wadeable habitats, although occurrence data does include recent sampling of non-wadeable habitats along the lower Grand River (Reid and LeBaron 2020). The time period of records used was 1997 to 2019. We removed duplicates and records without geographic co-ordinates from the dataset. In total, 994 sampling events were included in the dataset (Figure 1). There were 40 sampling events with Fawnsfoot detections, 213 sampling events with Rainbow detections, 165 sampling events with Round Pigtoe detections, 83 sampling events with Threehorn Wartyback detections and 275 sampling events with Wavy-rayed Lampmussel detections. A sampling event was defined as an individual freshwater mussel survey at a given site. We verified the correspondence of site geographic co-ordinates with AEC reach boundaries in ArcGIS®10.3.1 (Esri, Redlands, California).

Habitat suitability at a landscape scale was based on the MNRF Aquatic Ecosystem Classification (AEC). The AEC is a spatial data framework to classify all rivers and streams in Ontario into ecologically homogenous units at several hierarchically nested spatial scales (Jones and Schmidt 2017). The AEC summarizes climatic, geological, hydrological, and land cover variables at four distinct spatial scales: reach contributing area (RCA), upstream catchment (UCA), reach channel (RCh) (30 m raster), and upstream channel for the catchment (UCh) (30 m raster) (**Figure 2**). AEC attributes have been used to successfully model Brook Trout (*Salvelinus fontinalis*) and Brown Trout (*Salmo trutta*) in streams of the Ontario Mixedwood Plains Ecozone (Jones et al. 2020). AEC attributes used as predictor variables of mussel species occurrence are presented in **Table 1** and **Table 2**.

We selected these eight AEC attributes as prior studies have explained landscape-level mussel species distribution patterns in relation to: stream flow (Weber and Schwartz 2011; Walters et al. 2015; Daniel et al. 2018), gradient (Cao et al. 2015), upstream catchment area (Wenger et al. 2009), summer air temperature (Daniel et al. 2018), riparian vegetation and forest cover (Wenger et al. 2009; Weber and Schwartz 2011), and geology (McRae et al. 2004; Weber and Schwartz 2011). For predictor variables representing forest cover and surficial geology, we combined AEC data layers to reduce the number of variables modelled. We recognize this set of attributes is not an exhaustive list of relevant predictors but consider it to be sufficient for evaluating presence-only modelling. Notably absent are fish host richness and variables that represent anthropogenic stressors such as land use (agricultural and urban) and dams.

We converted each AEC layer to raster form using the polyline to raster tool in ArcGIS. Raster grid size was 30 x 30 m with the same coordinate system as the AEC line layer: MNR Lambert Conformal Conic. We snapped all rasters to the Provincial 30m DEM so the lines of the AEC line layer were positioned in the middle of raster cells. By species, reaches with presences were selected from the AEC line layer to create species-specific presence-only layers. We calculated the centroids of these reaches and input into MaxENT. The number of reaches with positive species detections were 20 for Fawnsfoot, 97 for Rainbow, 53 for Round Pigtoe, 27 for Threehorn Wartyback, and 96 for Wavy-rayed Lampmussel.

Prior to modelling, we assessed the correlation of predictor variable rasters using the “layerstats” function in the R package “raster.” We used a variable inclusion threshold of <0.7 for Pearson correlation coefficient values. The highest correlation was between RCh slope and RCh temperature at -0.49. Therefore, all variables were used in MaxEnt models.

MAXENT MODELLING

Species distribution models were developed with MaxEnt Software (version 3.4.4) (Phillips et al. [Internet]). For each species, we first modelled the influence of each predictor variable on habitat suitability independently. Ten-fold cross validation was used, meaning that the data was split differently 10 times with 90% dedicated to model training and 10% dedicated to testing. We used the area-under-curve (AUC) of the receiver operating characteristic (ROC) as the primary diagnostic output to assess individual variables. We only retained variables with an AUC >0.7 to develop the final model (Phillips and Dudík 2008). AUC values at or below 0.5 indicate the model is no more informative than expected from random chance.

To develop the final model for each species, we assessed the importance of retained variables collectively using the following diagnostics: (i) percent contribution, (ii) permutation importance, and (iii) jackknife tests (Phillips 2017). Jackknife tests produce three plots based on regularized training gain, test gain, and AUC, all of which were considered. Selection of variables was in part based on high percent contribution and permutation importance scores. Additionally, jackknife test output identified variables that provided the most explanatory information alone, or that was not already represented by other variables. We also used response curves to visually assess variable suitability. In some cases, the shape of response curves for a variable in the full model would differ dramatically from when run individually. In these cases, we removed variables from full model development. For each species, suitable variables (based on diagnostics) were run in a final comparison analysis. An AUC threshold of 0.7 was used to assess the performance of final models. Final model structure was additive.

RESULTS

Robust habitat suitability models were developed for all five mussel species at risk (overall AUC values >0.83). When run individually for each species, two to six variables were identified as important predictors of habitat suitability (**Table 3**). At the upstream catchment area spatial scale, important predictors were area (all species), combined tree cover (three species) and mean overburden thickness (three species). Combined tree cover was just below the AUC threshold of 0.7 for Wavy-rayed Lampmussel. At the reach contributing area scale, the contributions of gravel (Wavy-rayed Lampmussel) and sand (Fawnsfoot and Round Pigtoe) to surficial geology were identified as important predictors. At the reach channel scale, important predictors were channel slope (three species) and summer water temperature (all species). Except for Wavy-rayed Lampmussel, some variables were dropped from full models due to dramatic changes in response curve shape (**Figure 3**).

For all five species, summer water temperature and upstream catchment area were retained in full MaxEnt models (**Figure 4**). Although important across all species, the relative influence of summer water temperature and upstream catchment area varied for each species (**Table 4**). Jackknife test output from the Fawnsfoot and Round Pigtoe MaxEnt models indicates that summer water temperature was the important informative predicator on its own, and when other variables were included in the model. Upstream catchment area was the important informative predictor on its own for Threehorn Wartyback, and when other variables were included. Jackknife test output indicates that upstream catchment area was the most informative predictor of Rainbow and Wavy-rayed Lampmussel habitat suitability on its own, but that summer water temperature provided the most additional information when other variables are included in the model. For summer water temperature, the shape of the relationship with habitat suitability was the same for all five species. Suitability improved linearly as summer water temperature increased from ~16–19 ^{o}C up to an asymptote of ~25 ^{o}C (Figures 5–8). Response curves for upstream catchment area were similar for Fawnsfoot, Threehorn Wartyback, and Round Pigtoe; increasing rather linearly to an asymptote ~6750 km^2. For Rainbow and Wavy-rayed Lampmussel, the relationship was unimodal with suitability greatest between 2000 and 3000 km^2.

Additional predictors were only included in models for Rainbow (gravel - surficial geology), Round Pigtoe (tree cover) and Wavy-rayed Lampmussel (gravel - surficial geology and overburden thickness). For Rainbow, the relationship between habitat suitability and percent contribution of gravel to surficial geology in the reach contributing area was unimodal with highest values at intermediate values of 30 to 50% (Figure 6). Jackknife test results indicate that gravel provides the most information not already contributed by other predictors. The response curve for tree cover in the upstream catchment area was unimodal for Round Pigtoe with highest habitat suitability values at relatively low values of 10 to 15% (Figure 7). For Wavy-rayed Lampmussel, response curves for gravel (highest at 50 to 60%), and mean overburden depth in the upstream catchment (highest at 40 m) were also both unimodal (Figure 8). For Round Pigtoe and Wavy-rayed Lampmussel, the influence of these predictors on habitat suitability was less than summer water temperature and upstream contributing area.

To illustrate the potential application of MaxEnt modelling output, habitat suitability maps for each species and for all five species combined are provided by Figures 9 to 14. Overall, maps predict suitable mussel habitats are present along reaches upstream and downstream of known locations. In some cases, suitable habitat is predicted in watersheds where the species has not been detected (e.g., Wavy-rayed Lampmussel in the Bayfield River). For Round Pigtoe and Wavy-rayed Lampmussel, a few occupied AEC segments were classified with low suitability: upper Thames River and lower Grand River, respectively. Compared to the other species, the amount of suitable habitat predicted outside known occupied reaches was greatest for Rainbow.

DISCUSSION

Patterns of river mussel distribution have been studied over a wide range of spatial scales from field studies of micro-habitat associations (Allen and Vaughn 2010) to regional-scale studies testing island biogeography theories (Sepkoski and Rex 1974). In this study, we used MaxEnt software to produce geographic models of habitat suitability for five mussel species at risk across five southwestern Ontario rivers. AEC attributes identified consistently across species as influencing habitat suitability were summer water temperature and upstream contributing area. Other informative AEC attributes (geology and tree cover) were only identified for the three more common species. The coupling of the AEC scheme with MaxEnt modelling presents an alternative to the current approach of critical habitat delineation that is based on identifying Aquatic Landscape Inventory Software (ALIS) layer segments occupied by species at risk. Additionally, habitat suitability scores developed for multiple mussel species can be combined to assist in fine-scale identification of “conservation hot-spots.” The current approach, informed by species richness estimates, ranks conservation status at the tertiary watershed scale (Staton and Mandrak 2006).

Unimodal habitat suitability relationships are expected for water temperature and riverine mussel species (Miller et al. 1987). As the physiological processes of mussels are constrained by water temperature, abnormally cold temperatures can limit growth and inhibit reproduction during spring and summer. Extreme maximum summer water temperatures (especially during low-flow events) can be physiologically stressful or result in mussel die-offs (Gates et al. 2015). Daniel et al. (2018) found annual air temperature to be an important predictor of habitat suitability for host fishes, and for Rainbow and Wavy-rayed Lampmussel across Michigan rivers. The relationship was unimodal for both mussel species. In our study, summer water temperature was a strong predictor of mussel species at risk habitat suitability for all species. However, the relationship was largely linear, likely reflective of lack of extreme water temperatures (i.e., >35 ^{o}C) near or above the upper thermal tolerance limits of most species. Although not addressed in this study, air and water temperatures are known to influence the distribution of fishes in southwestern Ontario watersheds (Sharma and Jackson 2007; Chu et al. 2008); and therefore can be expected to have an indirect influence on mussel species distributions.

Upstream catchment area provides an index of stream size and flow volume, which are habitat characteristics well understood to be correlated with mussel species richness and shifts in species distributions (Strayer 2008; Haag 2012). Compared to headwater areas, lower reaches in watersheds are typified by a greater diversity of habitats, greater flow permanence and diversity of host fishes. In Michigan and Texas rivers, flow volume was frequently identified (through MaxEnt models) as influencing habitat suitability of mussel species (Walters et al. 2017; Daniel et al. 2018). Daniel et al. (2018) found median flow volume to be an important predictor of habitat suitability of eight species also found in Ontario rivers, including Rainbow, Round Pigtoe and Wavy-rayed Lampmussel. In Michigan, species-response relationships were positive for Round Pigtoe and negative for Rainbow and Wavy-rayed Lampmussel. In our study, there were positive linear relationships between upstream catchment area and habitat suitability for Fawnsfoot, Round Pigtoe, and Threehorn Wartyback. Habitat suitability for Rainbow and Wavy-rayed Lampmussel was unimodal and greatest at intermediate upstream catchment sizes, reflective of the concentration of distribution records further upstream than the other three species.

Surficial geology has a strong influence on water clarity and temperature, riverbed (substrate) composition, channel morphology, and flow regimes. All these characteristics have been used to explain variation in mussel species richness, abundance, and occurrence of individual species at watershed and regional spatial scales (Strayer 1983; Arbuckle and Downing 2002; Weber and Schwartz 2011; Cao et al. 2015). The composition of the southwestern Ontario surficial geology is spatially complex, with marked differences in the types of glacially deposited materials that locally influence habitat conditions (Chapman and Putnam, 2007). For example, the Sydenham River and the lower reaches of the Grand and Thames rivers flow through landscapes where silts represent a substantial contribution to the surficial geology; these reaches are characterized by poor water clarity and finer riverbed materials. For two of our study species, variables linked to surficial geology are predicted to influence habitat suitability. For Rainbow and Wavy-rayed Lampmussel, the landscape-level association with gravel is consistent with described habitat associations at the local (or instream) level (Metcalfe-Smith et al. 2005; Bouvier and Morris 2010). Overburden thickness (important for Wavy-rayed Lampmussel) represents groundwater recession, and has been found to influence the distribution of trout species in southern Ontario watersheds (Jones et al. 2020). Thick deposits of overburden contain large amounts of groundwater and maintain flow volume during periods of drought. In contrast, thin veneers of overburden may not have much water to supply during dry periods (Buttle et al. 2004; Buttle and Eimers 2009). During such conditions, freshwater mussels are vulnerable to be killed by desiccation, heat and/or mammalian predation (Strayer 1983).

Our MaxEnt modelling pilot study was limited to a small number of species and abiotic predictor variables that could be easily extracted from the AEC. Accuracy of mussel SDM could be improved by including information on fish hosts and anthropogenic stressors. Local presence of mussel species at risk can be expected to be directly (via survival of glochidia) and indirectly (via dispersal) constrained by the availability of suitable host fishes (Strayer 2008; Haag 2012). In southwestern Ontario, a regional-level congruence exists between host fish and mussel community structure (Schwalb et al. 2013). Daniel et al. (2018) found host fish richness in Michigan rivers to be the second most important variable in MaxEnt models for eight mussel species (which included Ontario species: Black Sandshell (*Ligumia nasuta*), Deertoe (*Truncilla truncata*), Elktoe (*Alasmidonta marginata*), Rainbow, Round Pigtoe and Wavy-rayed Lampmussel). Inclusion of a fish host variable in future Ontario models would require: (i) a fish occurrence database that corresponded to AEC segments (as done by Schwalb et al. using Aquatic Landscape Inventory Software (ALIS) segments), or (ii) a fish host metric that was predicted based on a landscape-level SDM (as done by Daniel et al. 2018).

Landscape-level variation in mussel species distributions has been attributed to anthropogenic stressors such as: agriculture (Daniels et al. 2018), impervious cover and urban development (Wenger et al. 2009; Daniels et al. 2018), density of dams (Weber and Schwartz 2011), and pollution (Weber and Schwartz 2011). Generally, these factors have a negative effect on mussel species richness and distribution of sensitive species. In this study, MaxEnt modelling did not directly investigate the influence of stressors on the distribution of mussel species at risk. Although, we expect that forest and riparian cover is negatively correlated with AEC landcover attributes: agricultural and rural, and community and infrastructure. As with fish hosts, the inclusion of stress-related predictor variables requires the development of new metrics to augment the AEC. At the sub-watershed scale, watershed health reports developed by Conservation Authorities (CAs) provide an index of surface water quality. As well, a provincial stress index for Ontario watercourses that includes measures of ecological integrity is being developed (N. Jones pers. comm). Existing information on the barriers to fish movement and dams could be adapted to create indices of river fragmentation and flow regulation. The MNRF Ontario Dam Inventory (ODI) is a location-based inventory of medium and large dams. The ODI does not contain location information on small dams and water control structures and it would need to be augmented with other data sources (e.g., CAs) or field surveys.

While MaxEnt modelling is relatively robust to small sample sizes (i.e., data quantity), results are sensitive to the quality of presence-only data. Species occurrence records suffer from sources of error that may affect the performance and reliability of MaxEnt models, such as: inaccurate spatial locations, biased sampling, and species misidentifications (Aubry et al. 2017). The two primary mussel species at risk survey protocols used in southern Ontario rivers differ in their sampling design, study objectives, and method of collecting mussels. We expect that the risk of imperfect species detection at sampling sites will differ between protocols. Species occurrences are more likely to be underreported from sites surveyed by only the timed-search method, as species detection may require substrate excavation (Reid and Morris 2017) or multiple repeat surveys (Reid 2016).

Additionally, presence-only SDM methods require a random (i.e., unbiased) or at least representative sample of points from the landscape. Sampling sites were widely distributed across our study watersheds (see Figure 1). However, several field data collection practices likely violate this requirement, such as: (i) repeating historical mussel surveys, (ii) targeted site selection based on prior knowledge of local species richness, and (iii) targeted sampling of wadeable habitats. Models built with biased data may correspond more to a model of mussel survey effort than a model of actual species distribution (Phillips et al. 2009). Suitability of AEC segments will be over-estimated for those environments that have been sampled more intensively and underestimated for those sampled less frequently (Guillera-Arroita et al. 2015). As sampling of small watercourses and non-wadeable habitats along larger watercourses has been limited, the degree to which associated environmental conditions are under-represented by MaxEnt output is not known. However, it is reasonable to expect that such bias exists for study species (such as Fawnsfoot and Threehorn Wartyback) more associated with deeper, non-wadeable habitats.

Our study demonstrates the potential for MaxEnt modelling to (i) identify factors influencing the landscape-level distribution of mussel species at risk in southwestern Ontario rivers, (ii) enhance critical habitat mapping with the inclusion of habitat suitability scores, and (iii) identify stream and river reaches with potentially suitable conditions to support undocumented mussel species at risk populations. As with any modelling approach, robust results are dependent on a sufficiently large set of data collected in a manner consistent with statistical assumptions. The breadth of habitat suitability measures for rarer species (e.g., Fawnsfoot and Threehorn Wartyback) could be increased by identifying a greater number of occupied AEC segments through targeted inventories of: (i) adjacent unoccupied AEC segments and (ii) non-wadeable reaches that represent suitable habitat conditions (Reid and LeBaron 2020, Fisheries and Oceans Canada 2020). Segment attributes easily obtainable through the AEC do not encompass the full range of abiotic and biotic factors expected to influence mussel species distributions. Incorporating the influence of anthropogenic stressors and host fish availability into MaxEnt models would require compilation of additional databases.

ACKNOWLEDGEMENTS

Kelly McNichols-O'Rourke assisted with compilation of freshwater mussel sampling records from the Fisheries and Oceans Canada Lower Great Lakes Unionid database. The project was supported by Federal SARA program funding through a research partnership agreement with NDMNRF. An earlier version of the report was improved with comments provided by Cindy Chu and Todd Morris.

REFERENCES

Allen, D.C., and Vaughn, C.C. 2010. Complex hydraulic and substrate variables limit freshwater mussel species richness and abundance. Freshw. Sci. 29: 383–394.

Arbuckle, K.E. and Downing, J.A. 2002. Freshwater mussel abundance and species richness: GIS relationships with watershed land use and geology. Can. J. Fish. Aquat. Sci. 59: 310–316.

Aubry, K.B., Raley, C.M., and McKelvey, K.S. 2017. The importance of data quality for generating reliable distribution models for rare, elusive, and cryptic species. PloS one, 12(6), e0179152. https://doi.org/10.1371/journal.pone.0179152

Bouvier, L. and T. Morris. 2010. Information in support of a Recovery Potential Assessment of Wavy-rayed Lampmussel (*Lampsilis fasciola*) in Canada. DFO Can. Sci. Advis. Sec. Res. Doc. 2010/074.

Buttle, J.M., Dillon, P.J., and Eerkes, G.R. 2004. Hydrologic coupling of slopes, riparian zones and streams: An example from the Canadian Shield. J. Hydrol. 287: 161–177.

Buttle J.M. and Eimers, M.C. 2009. Scaling and physiographic controls on streamflow behaviour on the Precambrian Shield, south-central Ontario. J. Hydrol. 374: 360–372.

Campbell, C. and Hilderbrand, R.H. 2017. Using maximum entropy to predict suitable habitat for the endangered Dwarf Wedgemussel in the Maryland Coastal Plain. Aquat. Conserv.: Mar. Freshw. Ecosyst. 27: 462–475.

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

Chapman, L.J. and Putnam, D.F. 2007. Physiography of southern Ontario. Ontario Geological Survey, Miscellaneous Release--Data 228.

Chu, C., Jones, N.E., Mandrak, N., Piggott, A., and Minns, C.K. 2008. The Influence of Air Temperature, Groundwater Discharge, and Climate Change on the Thermal Diversity of Stream Fishes in Southern Ontario Watersheds. Can. J. Fish. Aquat. Sci. 65. 297–308.

Daniel, W.M., Cooper, A.R., Badra, P.J., and Infante, D.M. 2018. Predicting habitat suitability for eleven imperiled fluvial freshwater mussels. Hydrobiologia 809: 265–283.

Fisheries and Oceans Canada. 2020. Recovery Strategy and Action Plan for the Fawnsfoot (*Truncilla donaciformis*) and Threehorn Wartyback (*Obliquaria reflexa*) in Canada [Proposed]. *Species at Risk Act* Recovery Strategy Series. Fisheries and Oceans Canada, Ottawa. vi + 66 pp.

Franklin, J. 2009. Mapping species distributions: spatial inference and prediction. Cambridge University Press, Cambridge, UK.

Gates, K.K., Vaughn, C.C., and Julian, J.P. 2015. Developing environmental flow recommendations for freshwater mussels using the biological traits of species guilds. Freshw. Biol. 60: 620–635.

Guillera-Arroita, G., Lahoz-Monfort, J.J., Elith, J., Gordon, A., Kujala, H., Lentini, P.E., McCarthy, M.A., Tingley, R. and Wintle, B.A. 2015. Matching distribution models to applications. Glob. Ecol. Biogeogr. 24: 276–292.

Haag, W.R. 2012. North American freshwater mussels: natural history, ecology, and conservation. Cambridge University Press.

Jones, N.E. and Schmidt, B.J. 2017. Aquatic Ecosystem Classification for Ontario's rivers and streams: Version 1. Ontario Ministry of Natural Resources and Forestry, Science and Research Branch, Peterborough, ON. Science and Research Technical Note TN-04. 23 p.

Jones, N.E., Sutton, I.A., Schmidt, B.J., and Ghunowa, K. 2020. Occupancy of brook trout and brown trout in streams of the Mixedwood Plains Ecozone. Ontario Ministry of Natural Resources and Forestry, Science and Research Branch, Peterborough, ON. Science and Research Technical Report TR-34. 18 p. + appendices.

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

Metcalfe-Smith J.L., MacKenzie A., Carmichael I. and McGoldrick D., 2005. Photo field guide to the freshwater mussels of Ontario. St. Thomas Field Naturalist Club, 60 p.

Metcalfe-Smith, J.L., DiMaio, J., Staton, S.K., and Mackie, G.L. 2000. Effect of sampling effort on the efficiency of the timed search method for sampling freshwater mussel communities. J. North Am. Benthol. Soc. 19: 725−732.

Miller, A.C., Payne, B.S., Naimo, T.J., and Russell-Hunter, W.D. 1987. Gravel bar mussel communities: a community model. Technical Report EL-87-13. US Army Corps of Engineers, Wicksburg, MS.

Phillips, S.J. 2017. A brief tutorial on Maxent. Available from url: http://biodiversityinformatics.amnh.org/open_source/maxent/. Accessed on 2022-02-28.

Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J. and Ferrier, S. 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecol. Appl. 19: 181–197.

Phillips, S.J., Dudík, M., and Schapire, R.E. [Internet] Maxent software for modeling species niches and distributions (Version 3.4.1). Available from url: http://biodiversityinformatics.amnh.org/open_source/maxent/. Accessed on 2020-12-01.

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

Phillips, S.J., Anderson, R.P., and Schapire, R.E. 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model.190: 3–4 pp. 231–259.

Reid, S.M. 2016. Search effort and imperfect detection: Influence on timed-search mussel (Bivalvia: Unionidae) surveys in Canadian rivers. Knowl. Manag. Aquat. Ecosyst. 417: 17.

Reid, S.M., and LeBaron, A. 2020. Lower Grand River freshwater mussels: Results from brail sampling of non-wadeable habitats. *in* Morris, T.J., McNichols-O'Rourke, K. A., and Reid, S.M. (Editors). 2020. Proceedings of the 2019 Canadian Freshwater Mollusc Research Meeting: December 3-4, 2019, Burlington, Ontario. Can. Tech. Rep. Fish. Aquat. Sci. 3352: viii + 34 p.

Reid, S.M. and Morris, T. 2017. Tracking freshwater mussel recovery in Ontario rivers: Evaluation of a quadrat-based monitoring protocol. Diversity 9: 5.

Sapna, S.S. and Jackson, D.A. 2007. Fish assemblages and environmental conditions in the lower reaches of northeastern Lake Erie tributaries. J. Great Lakes Res. 33: 15–27.

Schwalb, A.N., Morris, T.J., Mandrak, N.E. and Cottenie, K. 2013. Distribution of unionid freshwater mussels depends on the distribution of host fishes on a regional scale. Divers. Distrib.19: 446–454.

Sepkoski, J. and Rex, M. 1974. Distribution of freshwater mussels: Coastal rivers as biogeographic islands. Syst. Zool. 23: 165–188.

Sheldon, M.N., McNichols-O'Rourke, K.A., and Morris, T.J. 2020. Summary of initial surveys at index stations for long-term monitoring of freshwater mussels in southwestern Ontario between 2007 and 2018. Can. Manuscr. Rep. Fish. Aquat. Sci. 3203: vii + 85 p.

Staton, S. and Mandrak, N.E. 2006. Focusing conservation efforts for freshwater biodiversity. 2005 Parks Research Forum of Ontario Proceedings, Guelph, Ontario. pp.197–204.

Strayer, D.L. 2008. Freshwater mussel ecology: a multifactor approach to distribution and abundance. University of California Press.

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

Walters, A.D., Ford, D., Chong, E.T., Williams, M.G., Ford, N.B., Williams, L.R., and Banta, J.A. 2017. High-resolution ecological niche modelling of threatened freshwater mussels in east Texas, USA. Aquat. Conserv.: Mar. Freshw. Ecosyst. 27:1251–1260.

Weber, T.C. and Schwartz, M. 2011. Maximum entropy habitat modeling of four endangered mussels in the Ohio River basin, USA. Journal of Conservation Planning 7: 13–26.

Wenger, S.J., Hagler, M.M., and Freeman, B.J. 2009. Prioritizing areas of the Conasauga River sub-basin in Georgia and Tennessee for preservation and restoration. Southeastern Fishes Council Proceedings: No. 51. Available at: http://trace.tennessee.edu/sfcproceedings/vol1/iss51/5.

Wisz, M. S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H., Guisan, A., and NCEAS Predicting Species Distributions Working Group. 2008. Effects of sample size on the performance of species distribution models. Divers. Distrib.14: 763–773.

Wright, K.A., McNichols-O'Rourke, K.A., and Morris, T. J. 2020. Timed-search surveys of freshwater mussels in coastal wetland and riverine sites in lakes Ontario, Erie, and St. Clair in 2015. Can. Manuscr. Rep. Fish. Aquat. Sci. 3192: v + 24 p.

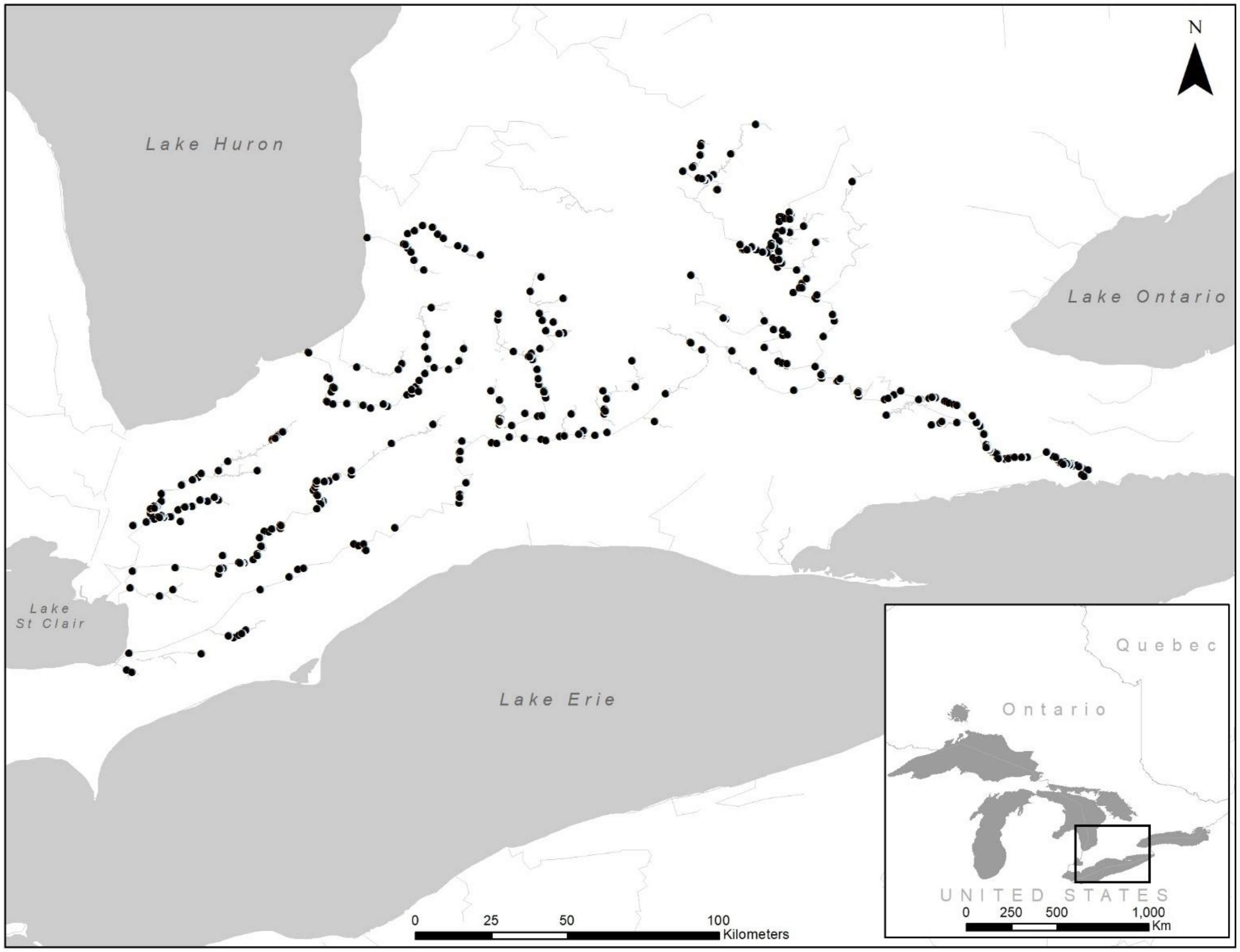

Figure 1. Distribution of mussel species at risk survey records (n = 994) across five southwestern Ontario watersheds (Ausable, Bayfield, Grand, Thames, and Sydenham). Time period for the surveys is 1997–2019. Source: Fisheries and Oceans Canada Lower Great Lakes Unionid database.

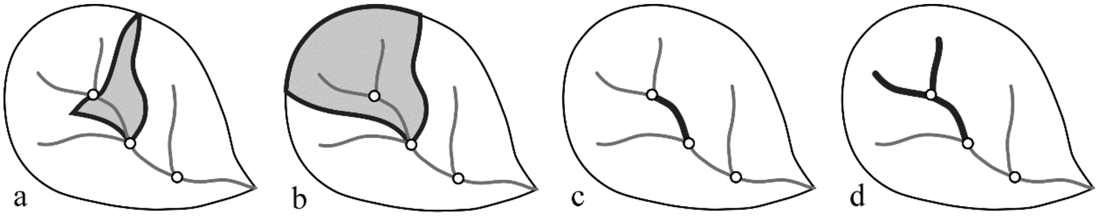

Figure 2. The four scales of AEC landscape summary that were derived using Arc Hydro layers with black polygons/lines illustrating each scale: a) reach contributing area, b) upstream catchment area, c) reach channel, and d) upstream channels.

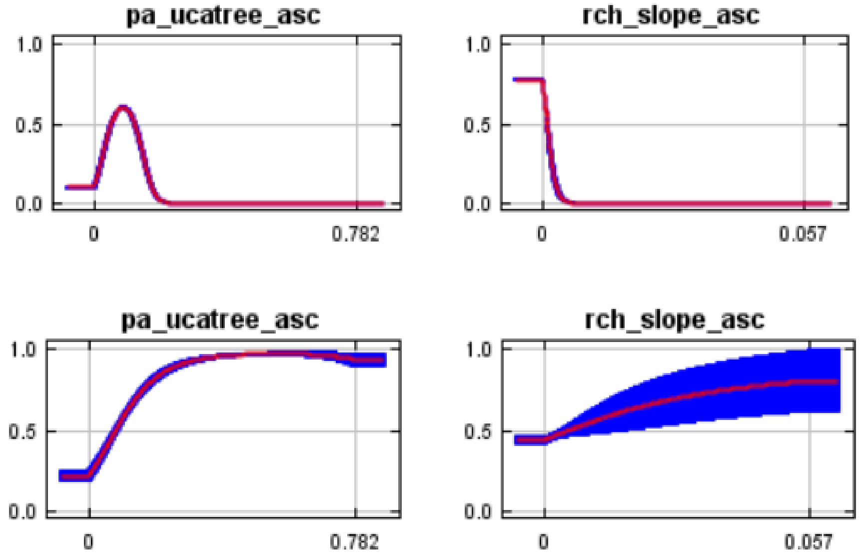

Figure 3. Examples of shifts in response curve shape when predictor variables are modelled independently (upper) or in combination with other variables in the full MaxEnt model (lower). The diagnostic approach was used to exclude suspect variables from full model development. The *x* axis represents the range of values associated with each predictor variable. The *y* axis is the probability of suitable conditions (as given by logistic output function) with all other variables set to their average value over the set of presence localities.

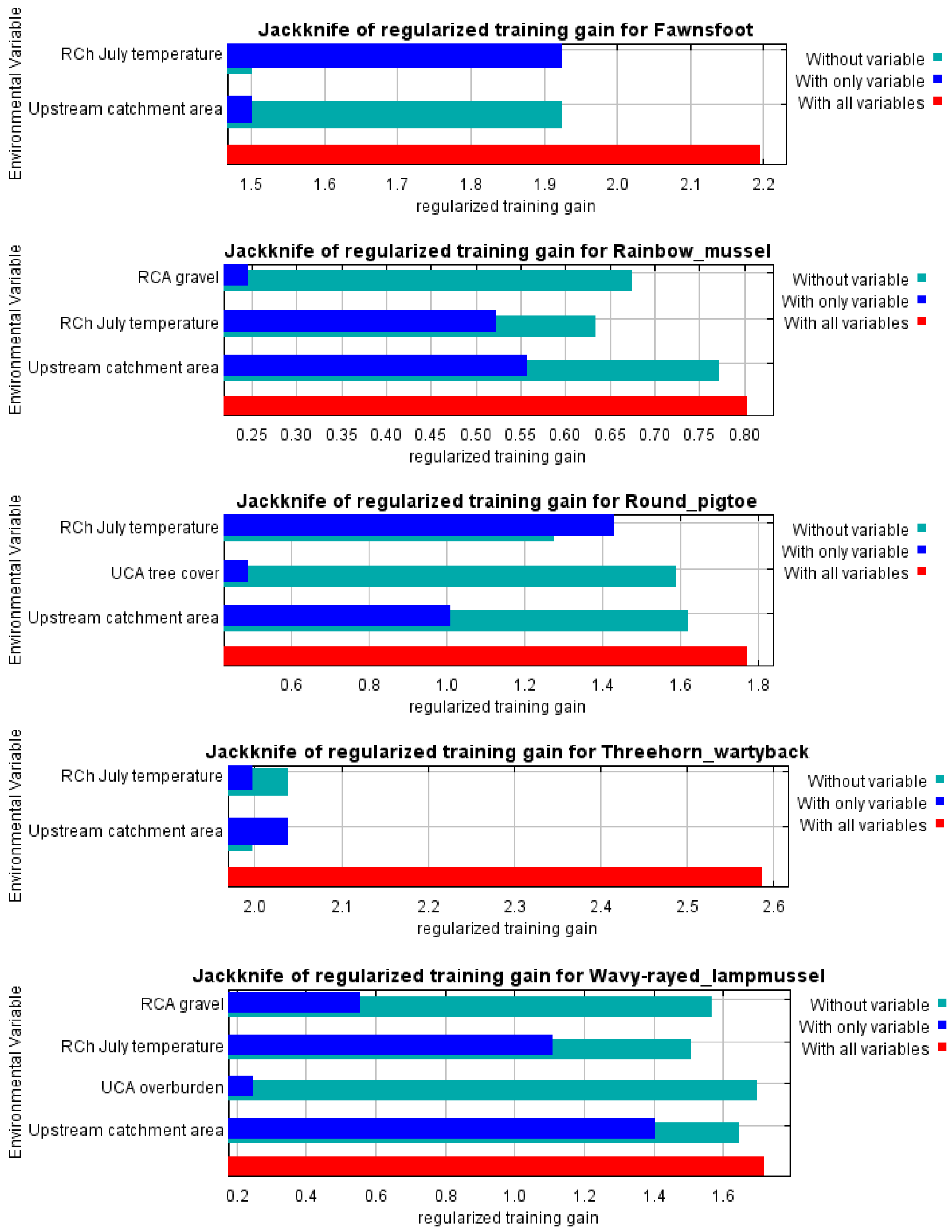

Figure 4. Jackknife test output for AEC predictor variables included in full MaxEnt models for Fawnsfoot, Rainbow, Round Pigtoe, Threehorn Wartyback, and Wavy-rayed Lampmussel.

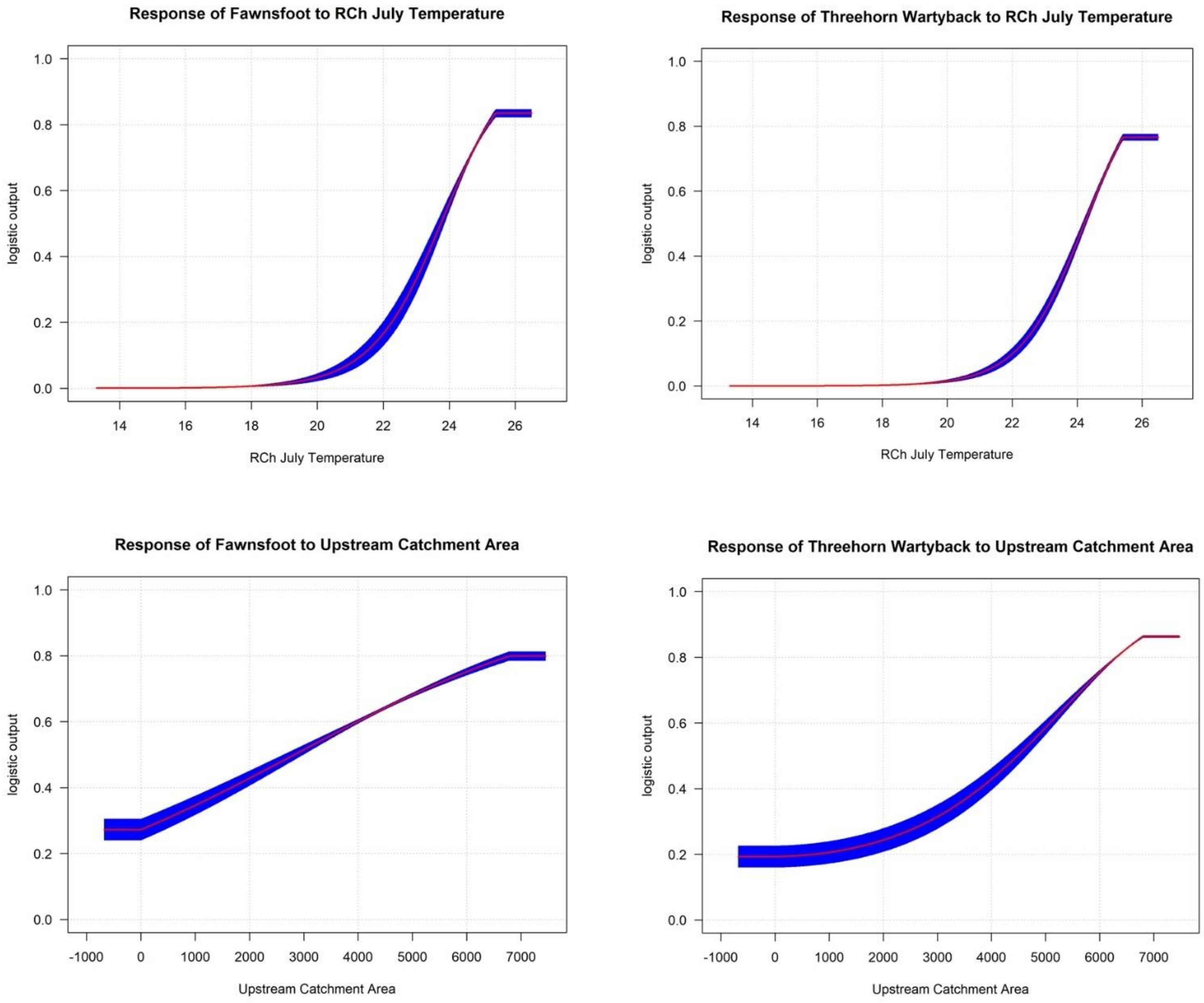

Figure 5. Habitat suitability relationships (i.e., response curves) for Fawnsfoot and Threehorn Wartyback and summer water temperature (upper graphs) and upstream catchment area (lower graphs).

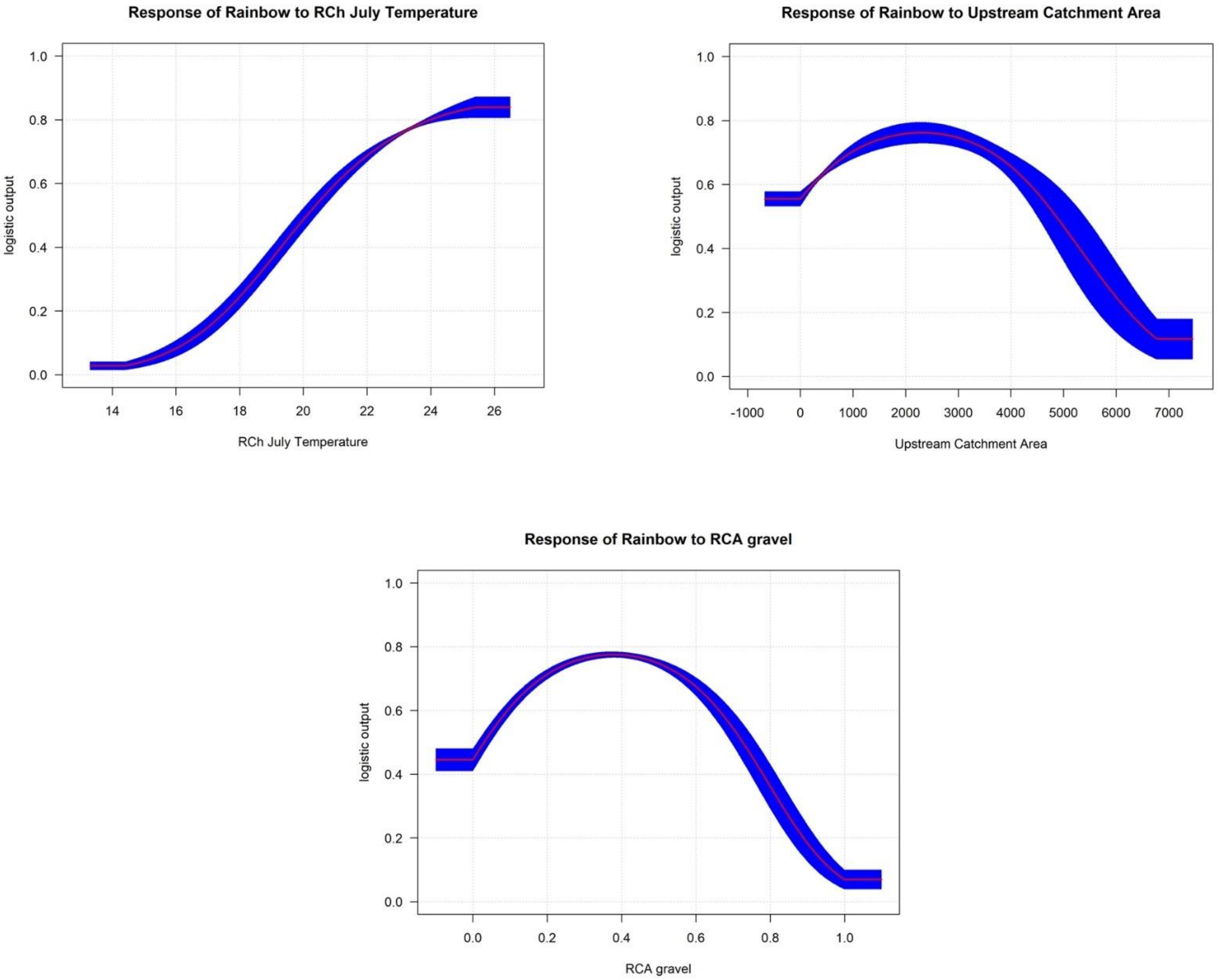

Figure 6. Habitat suitability relationships (i.e., response curves) for Rainbow and summer water temperature (upper left graph), upstream catchment area (upper right graph), and gravel (lower graph).

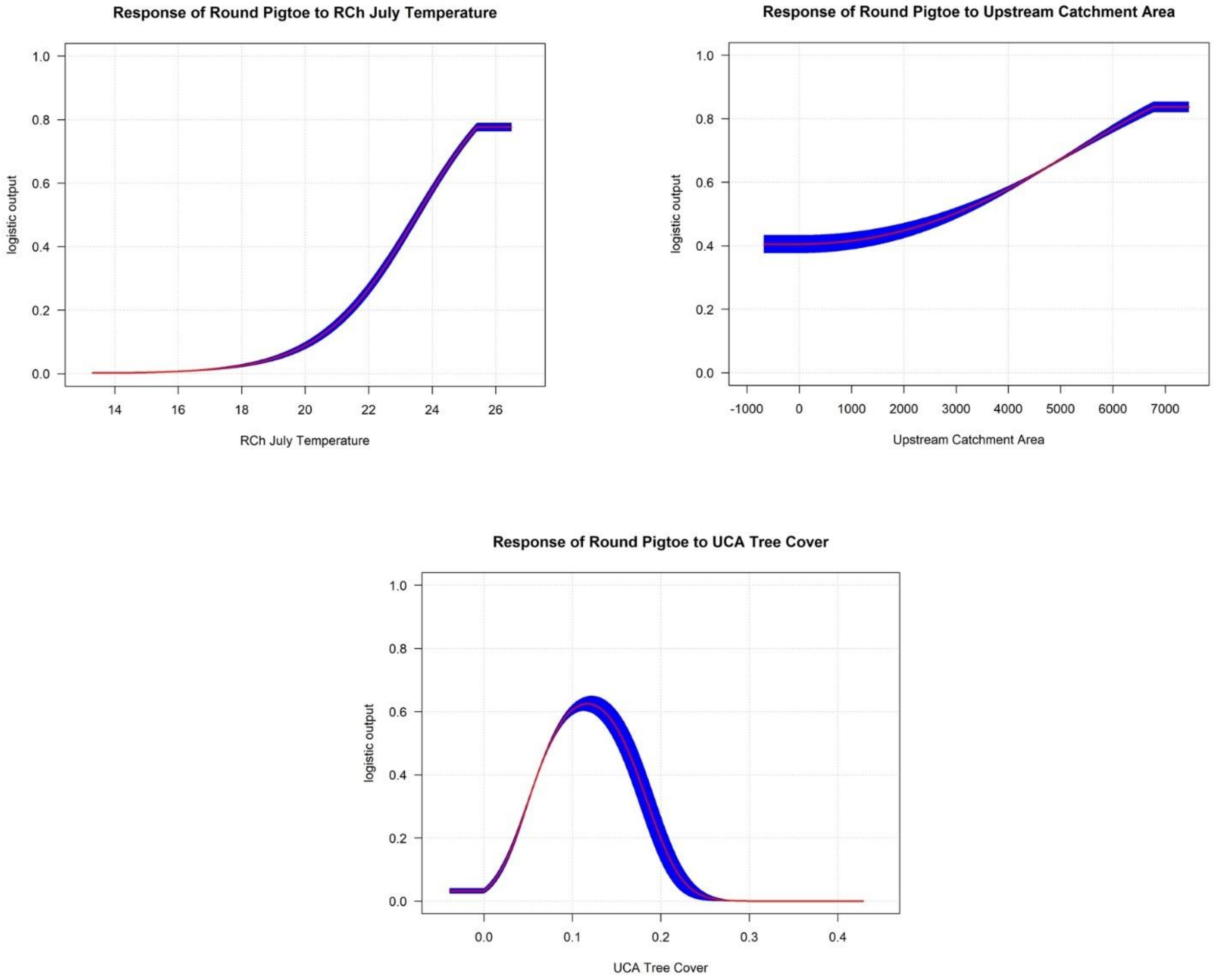

Figure 7. Habitat suitability relationships (i.e., response curves) for Round Pigtoe and summer water temperature (upper left graph), upstream catchment area (upper right graph), and tree cover (lower graph).

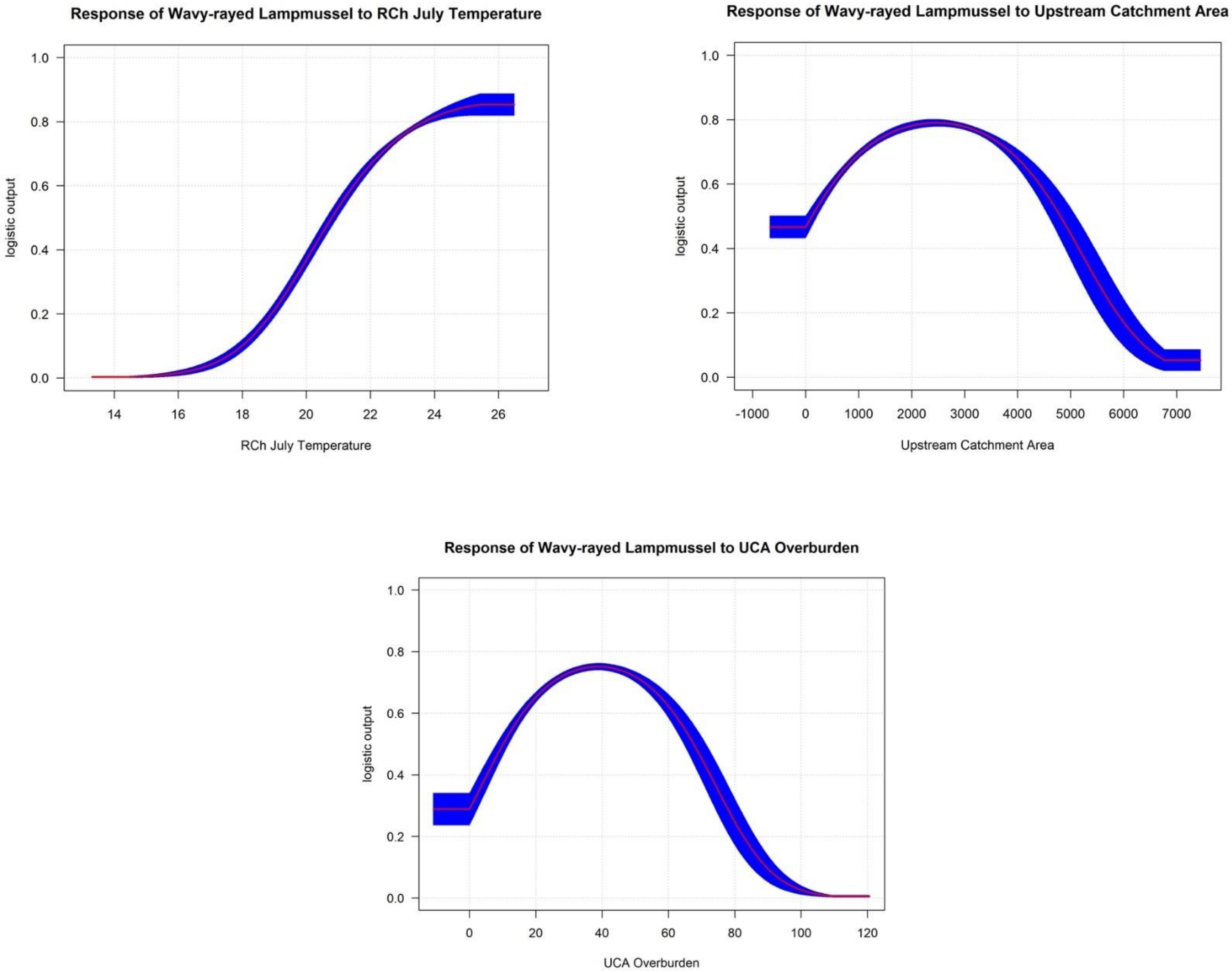

Figure 8. Habitat suitability relationships (i.e., response curves) for Wavy-rayed Lampmussel and summer water temperature (upper left graph), upstream catchment area (upper right graph), gravel (lower left graph), and overburden depth (lower right graph).

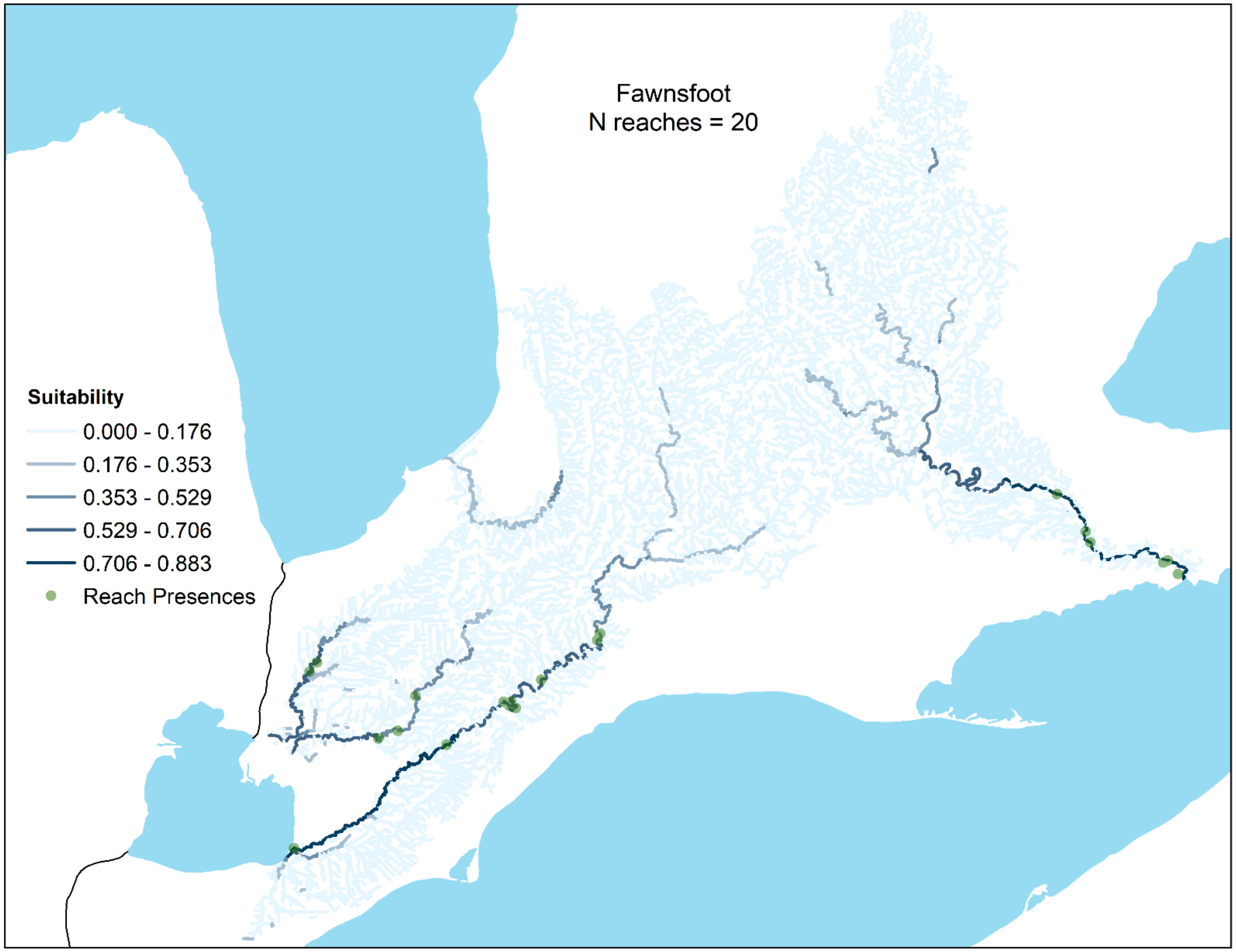

Figure 9. Habitat suitability across southwestern Ontario rivers for Fawnsfoot based on the full MaxEnt model. Locations of past species detections (1997–2019) are identified with green dots (●).

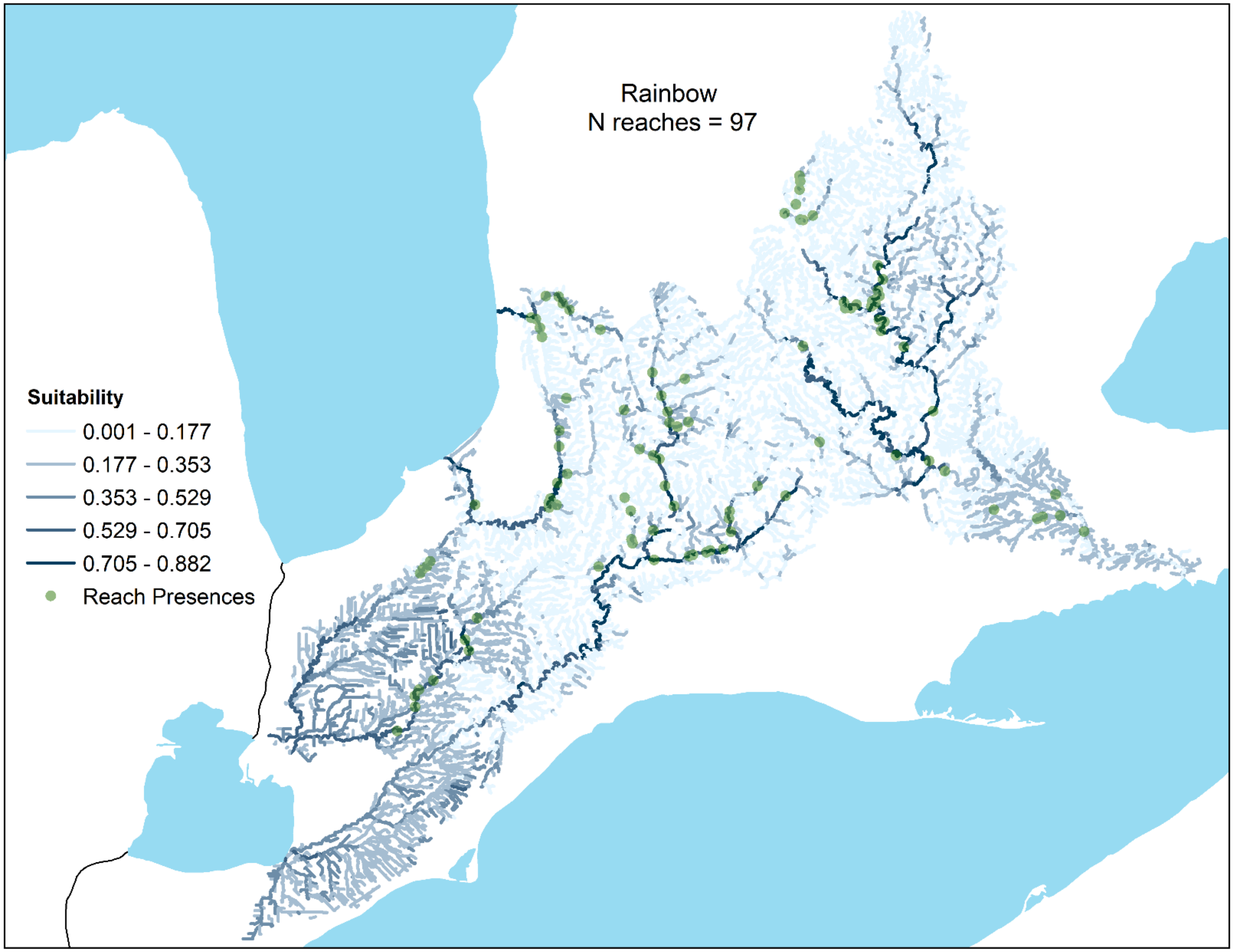

Figure 10. Habitat suitability across southwestern Ontario rivers for Rainbow based on the full MaxEnt model. Locations of past species detections (1997–2019) are identified with green dots (●).

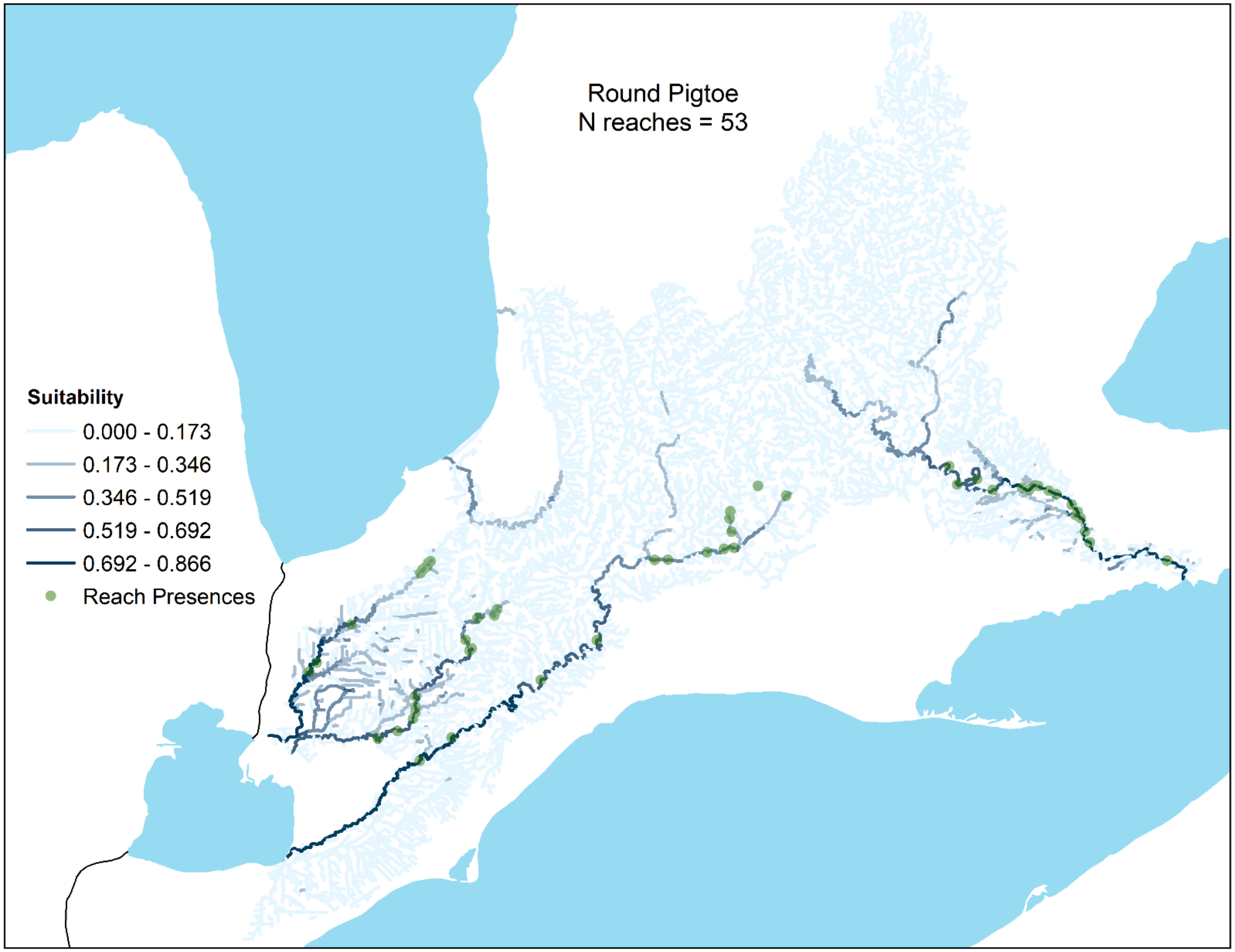

Figure 11. Habitat suitability across southwestern Ontario rivers for Round Pigtoe based on the full MaxEnt model. Locations of past species detections (1997–2019) are identified with green dots (●).

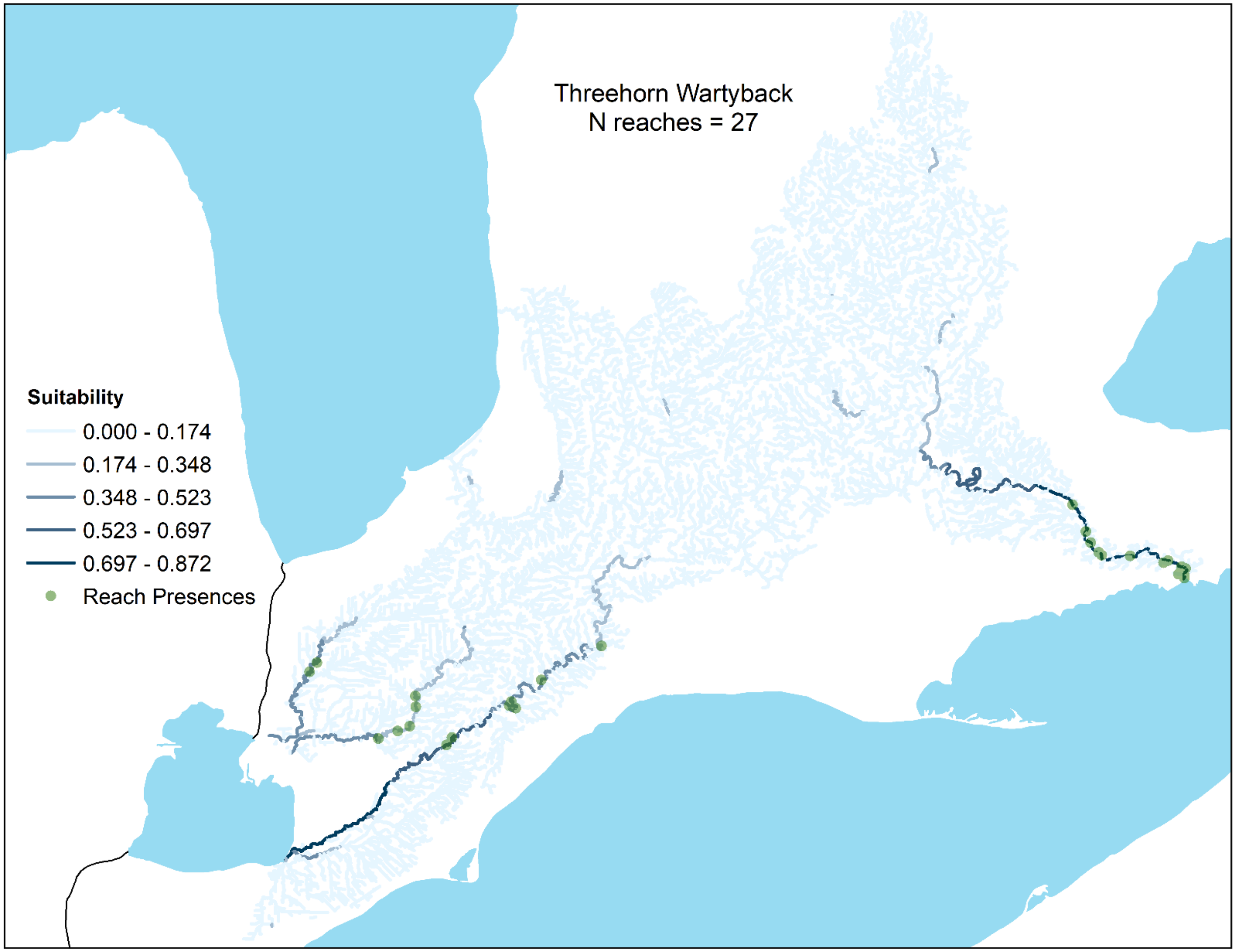

Figure 12. Habitat suitability across southwestern Ontario rivers for Threehorn Wartyback based on the full MaxEnt model. Locations of past species detections (1997–2019) are identified with green dots (●).

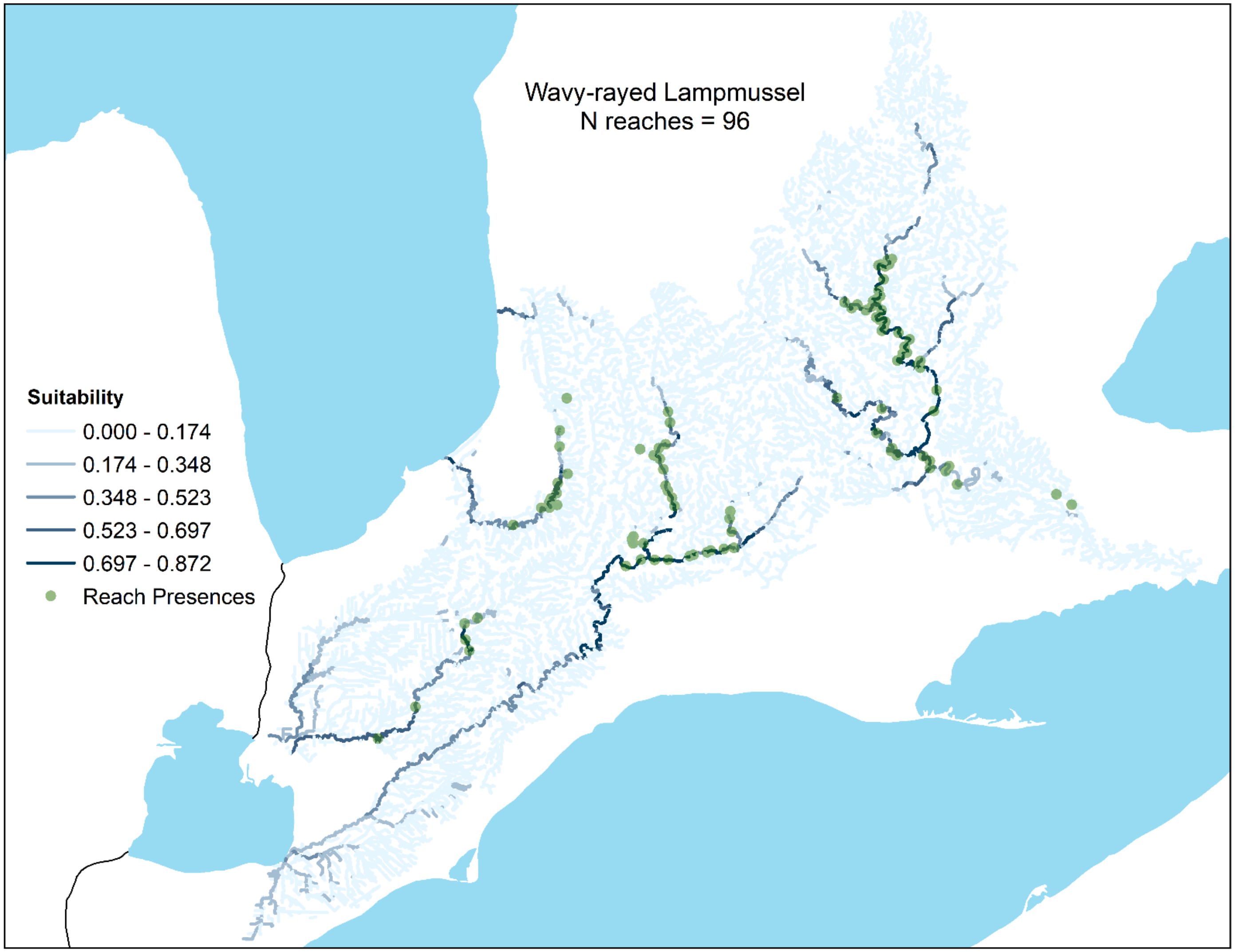

Figure 13. Habitat suitability across southwestern Ontario rivers for Wavy-rayed Lampmussel based on the full MaxEnt model. Locations of past species detections (1997–2019) are identified with green dots (●).

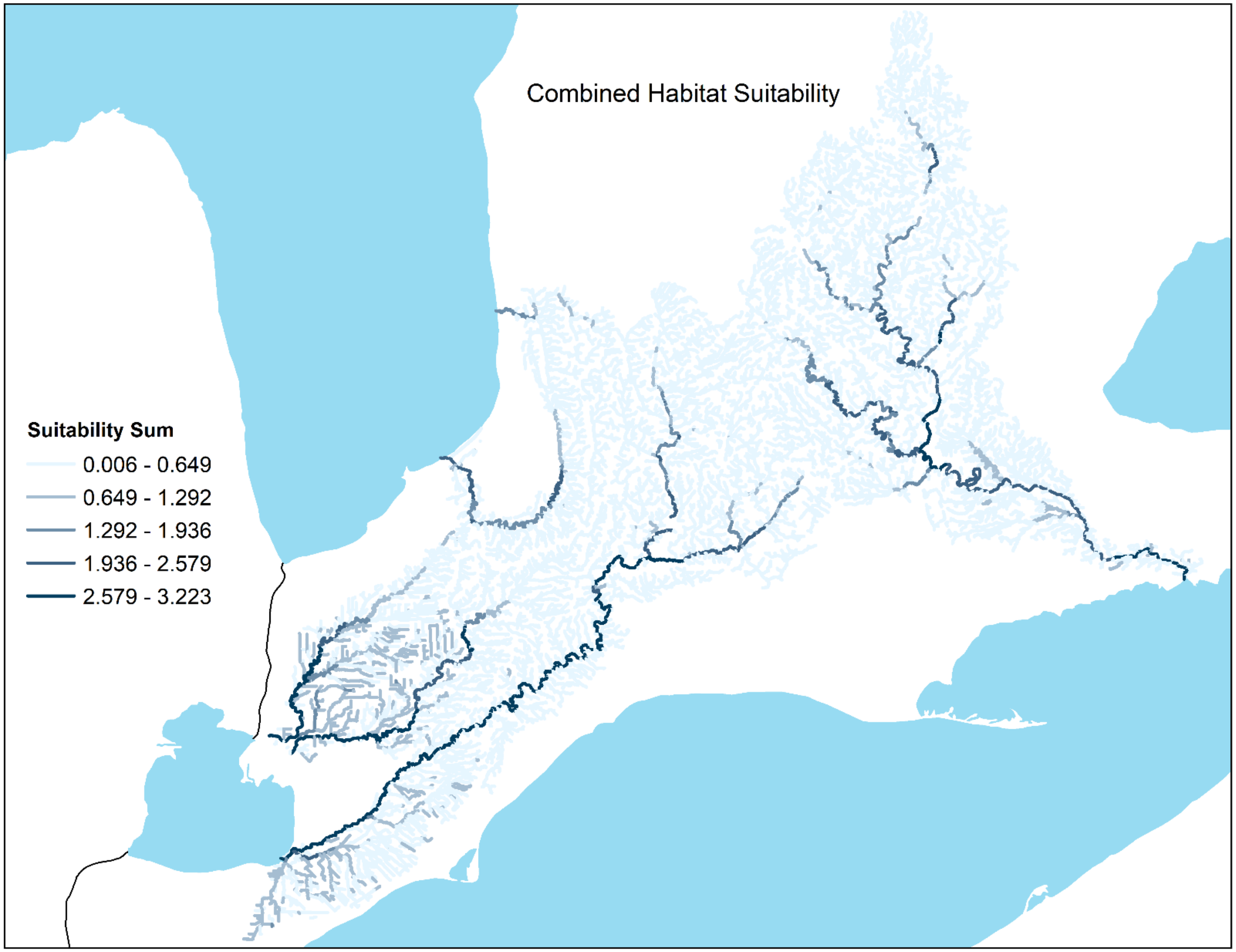

Figure 14. Combined habitat suitability across southwestern Ontario rivers for five mussel species at risk based on scores summed across full MaxEnt models.

Table 1. Description of seven Aquatic Ecosystem Classification (AEC) attributes used as predictor variables to model mussel species at risk distributions in five southwestern Ontario watersheds. Scale acronyms: RCA = reach contributing area; RCh = reach channel; UCA = upstream catchment area.

Variable (AEC attribute)	Scale	Variable unit	Raw AEC layers combined
RCA sand	RCA	Proportion of area (0-1)	RCA_Geology_MRD128mat_sand RCA_Geology_MRD128mat_sand_gravelly RCA_Geology_MRD128mat_sand_silty
RCA gravel	RCA	Proportion of area (0-1)	RCA_Geology_MRD128mat_gravel RCA_Geology_MRD128mat_gravel_sandy
RCh July temperature	RCh	Celsius	No combination
RCh slope	RCh	degrees	No combination
RCh tree cover	RCh	Proportion of area (0-1)	RCh_Landcov_12UplandTreed RCh_Landcov_13DeciduousTreed RCh_Landcov_14MixedTreed RCh_Landcov_15ConiferousTreed RCh_Landcov_17HedgeRow
Upstream catchment area	UCA	km^2	No combination
UCA overburden[1]	UCA	metres	No combination
UCA tree cover	UCA	Proportion of area (0-1)	pArea_UCA_Landcov_12UplandTreed pArea_UCA_Landcov_13DeciduousTreed pArea_UCA_Landcov_14MixedTreed pArea_UCA_Landcov_15ConiferousTreed pArea_UCA_Landcov_17HedgeRow

[1]: areas with thick overburden materials such as moraines contain relatively coarse glaciofluvial and glaciolacustrine deposits, and provide substantial groundwater inputs to streamflow

Table 2. Summary of median values of eight Aquatic Ecosystem Classification (AEC) attributes used as predictor variables to model mussel species at risk distributions in five southwestern Ontario watersheds. Medians were calculated using values for AEC segments occupied by each mussel species at risk. Minimum and maximum values are provided in parentheses.

Variable	Fawnsfoot	Rainbow	Round Pigtoe	Threehorn Wartyback	Wavy-rayed Lampmussel
RCA sand	0.54 (0, 1)	0.21 (0, 0.99)	0.33 (0, 1)	0.26 (0, 1)	0.26 (0, 0.99)
RCA gravel	0 (0, 0.33)	0.06 (0, 0.69)	0 (0, 0.53)	0 (0, 0.13)	0.27 (0, 0.87)
RCh July temperature	24.1 (20.7, 25.3)	22.3 (18.7, 24.6)	23.8 (20.4, 25.3)	23.9 (20.7, 25.3)	23.1 (18.9, 24.6)
RCh slope	0.001 (0, 0.003)	0.002 (0, 0.005)	0.001 (0, 0.007)	0.001 (0, 0.003)	0.002 (0, 0.007)
RCh tree cover	0.19 (0, 0.62)	0.16 (0, 0.93)	0.24 (0, 0.65)	0.13 (0, 0.62)	0.10 (0, 0.93)
Upstream catchment area	4001.5 (5.4, 6714.2)	440.2 (31.1, 6460.4)	1142.8 (82, 6714.2)	4155.5 (5.4, 6793.4)	1115.9 (45.7, 6063.5)
UCA overburden	37.9 (6.5, 42.5)	33.6 (11.9, 59.7)	36.3 (16.8, 61.8)	34.6 (6.5, 42.5)	35.5 (15.3, 59.1)
UCA tree cover	0.07 (0.04, 0.09)	0.046 (0.02, 0.11)	0.068 (0.05, 0.12)	0.067 (0.04, 0.09)	0.045 (0.025, 0.083)

Table 3. Comparison of mean AUC values for individual predictor variables among five mussel species at risk. Variables with AUC values ≥ 0.7 are highlighted in bold.

Variable	Fawnsfoot	Rainbow	Round Pigtoe	Threehorn Wartyback	Wavy-rayed Lampmussel
RCA gravel	0.635	0.675	0.439	0.642	**0.763**
RCA sand	**0.713***	0.641	**0.729***	0.583	0.655
RCh July temperature	**0.954**	**0.800**	**0.924**	**0.960**	**0.891**
RCh slope	**0.825***	0.615	**0.760***	**0.837***	0.624
RCh tree cover	0.597	0.626	0.647	0.407	0.560
Upstream catchment area	**0.925**	**0.881**	**0.946**	**0.946**	**0.909**
UCA overburden	0.490	0.678	**0.733***	**0.769***	**0.704**
UCA tree cover	**0.831***	0.614	**0.808**	**0.846***	0.696

* denotes variables with AUC>0.7 but excluded from comparison analyses due to response curve inconsistencies and poor performance in jackknife tests

Table 4. Summary of diagnostics output (AUC, percent contribution PC and permutation importance PI) used to develop full MaxEnt models. The most influential variables are underlined.

	Fawnsfoot		**Rainbow**		**Round Pigtoe**		**Threehorn Wartyback**		**Wavy-rayed Lampmussel**	
Variable	**PC**	**PI**	**PC**	**PI**	**PC**	**PI**	**PC**	**PI**	**PC**	**PI**
RCA gravel			30.1	20.2					27.7	10.3
RCh July temperature	36.9	96.9	62.8	73.4	39	75	24.5	95.5	49.7	75.5
Upstream catchment area	63.1	3.1	7.1	6.4	50.4	2.6	75.5	4.5	21.4	6
UCA overburden									1.3	8.1
UCA tree cover					10.6	22.4				
Overall Model AUC	**0.957**		**0.831**		**0.952**		**0.969**		**0.929**	