

STREAM HABITAT MODELLING FOR CONSERVING A THREATENED HEADWATER FISH IN THE UPPER CUMBERLAND RIVER, KENTUCKY

L. LIANG,^{a*} S. FEI,^b J. B. RIPPY,^c B. L. BLANDFORD^c and T. GROSSARDT^c^a Department of Geography, University of Kentucky, Lexington, KY, USA^b Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN, USA^c Kentucky Transportation Center, University of Kentucky, Lexington, KY, USA

ABSTRACT

The conservation of stream biodiversity requires more explicit knowledge on the distribution of aquatic species within the context of their specific environmental settings and stresses. Although species distribution models (SDMs) have been widely used for organisms occupying contiguous spatial extents, the implementation of SDMs in relatively complex and segmented riverine networks is still at its early stage. In this study, we explicitly modelled the headwater stream habitat for the threatened blackside dace (*Phoxinus cumberlandensis*) endemic to the upper Cumberland River, Kentucky, USA. An occurrence record data set, along with variables describing stream properties and land use impacts, was used to predict the fish habitat suitability at the stream segment level. An approach combining geographic information systems and the maximum entropy species distribution modelling (MaxEnt) was adopted. Results demonstrated that natural conditions and land use disturbances, respectively, form the primary and secondary environmental constraints on the species' habitat. We generated regional-scale management-friendly maps showing subwatershed habitat suitability and locations of the clustered suitable habitats (hotspots) and thus set an example for spatially explicit management of threatened and endangered riverine species. This study demonstrates the usefulness of SDMs for stream network-based environments in the facilitation of biogeographic conservation efforts and studies. Copyright © 2012 John Wiley & Sons, Ltd.

KEY WORDS: species distribution models; river systems; conservation; biodiversity; freshwater fish; blackside dace; Appalachia; human impacts

Received 14 March 2012; Revised 29 May 2012; Accepted 31 July 2012

INTRODUCTION

Knowledge about how a geographic distribution of species interacts with the changing habitat conditions forms a necessary basis for biodiversity conservation. The application of biogeographic principles in monitoring and protecting endangered and imperiled species has become increasingly important (Richardson and Whittaker, 2010). Such integration of geography and biological conservation has fostered the development of conservation biogeography, which associates interests in environmental stewardship and scientific inquiry (Ladle and Whittaker, 2011). Because of often very limited field survey data of species occurrence as described in the notion of the 'Wallacean shortfall' (Whittaker *et al.*, 2005), tools such as species distribution models (SDMs; also referred to as ecological niche models or habitat models) have been widely used to infer potential habitat extent of species that require conservation (Peterson, 2001; Marcot, 2006).

Among a wide span of taxa within diverse ecosystems, freshwater fish draw particular attention as their conservation faces unique challenges because of their exceptionally

high vulnerability to anthropogenic threats to watersheds and the embedded complexity in aquatic environments (Richardson and Whittaker, 2010; Olden *et al.*, 2010). There have been works testing various statistical methods to model riverine habitat suitability using related stream properties (Ahmadi-Nedushan *et al.*, 2006; Oakes *et al.*, 2005; Buisson *et al.*, 2008). However, spatially explicit prediction for stream networks that can be useful for conservation planning or other management applications is still at a very early stage (Joy and Death, 2004; McAbee *et al.*, 2008). One particular challenge for modelling species distribution in riverine systems, as different from that of the freshwater lakes (Olden and Jackson, 2002), is the need to incorporate unique spatial arrangements of fish habits. Specifically, the riverine habitats are characterized, at the same time, by both connectivity and isolation because of the longitudinal and directional streamflow patterns as well as by watershed segmentations. These unique spatial situations hinder the movement of certain species such as the headwater minnow and make a population more susceptible to extinction from habitat degradation or destruction. Hence, it is even more important to better understand and monitor the distribution of threatened and endangered fish species in river systems as influenced by natural conditions and pressing anthropogenic influences.

*Correspondence to: L. Liang, Department of Geography, University of Kentucky, Lexington, KY 40506, USA.
E-mail: liang.liang@uky.edu

In this study, we predict habitat suitability for a threatened headwater fish species, blackside dace (*Phoxinus cumberlandensis*) at the stream segment level in the context of existing occurrences, habitat requirements and land use disturbances. In addition to a spatially explicit understanding of environmental factors influencing riverine habitat of the species, better-informed regional conservation planning is also intended.

MATERIALS AND METHODS

Study species and environment

The blackside dace is a threatened aquatic species identified by the US Fish and Wildlife Service on 12 June 1987 (52 FR 22580–22585, US Fish and Wildlife Service 1988) and is on the red list of the International Union for Conservation of Nature (2010). This species has a very limited geographic range, which is confined in the Cumberland River drainage of southeastern Kentucky and northeastern Tennessee, USA (Starnes and Starnes, 1981), with a possibly introduced outlying population in a tributary of the North Fork Powell River in Virginia (www.natureserve.org).

The blackside dace inhabits small, cool and clear upland stream waters with moderate flow and silt-free substrates (Starnes and Starnes, 1981; Starnes and Starnes, 1978). Stream properties such as turbidity/conductivity (proxies of siltation and pollution levels), summer temperature (related to shaded environment) and gradient and link magnitude (proxies of flow velocity) appear to directly affect the habitat quality of the fish (Jones, 2005; McAbee *et al.*, 2008; Mattingly, 2005; Black, 2007). Studies by Jones (2005) and Mattingly (2005) confirmed correlations of these environmental factors with blackside dace occurrence and distribution. Black (2007) used logistic regression models to predict blackside dace habitat and found that summer water temperature and water conductivity were most influential. Further, it was noted that different land management and land use patterns, in addition to ecological factors, may affect the blackside dace habitat in a spatially explicit manner (McAbee *et al.*, 2008). Therefore, spatial modelling incorporating both stream attributes and regional land use variables is important for a more comprehensive understanding of the fish's distribution for conservation purposes.

More specifically, in the coal and timber-rich Appalachian Mountain region, stream siltation and pollution caused by human activities such as surface coal mining, logging, agriculture and construction/use of transportation corridors have led to severe habitat loss and subsequent population decline of the species (O'Bara, 1985; Starnes and Starnes, 1978; Black and Mattingly, 2007). Human-induced stream alterations are also believed to have facilitated the displacement of the blackside dace by a demonstrably secure species,

redbelly dace (*Phoxinus erythrogaster*), which has competitive advantages in disturbed stream environments (Starnes and Starnes, 1981; www.natureserve.org).

Data sources and environmental variables

We were able to acquire observed occurrence data of the blackside dace in southeastern Kentucky portion of the upper Cumberland River basin from the Kentucky State Nature Preserves Commission, covering 8 of 13 counties where the species are naturally found, not including the portion in Tennessee. The data set consists of an accumulative assemblage of multiple field observations up to 2010 with historical data dating back to 1883. To better represent the relatively current status, we removed records obtained before 1990s (approximately when the conservation efforts commenced), leaving 179 observations to use for subsequent modelling. Locations of all the occurrence records were georeferenced with a radius precision below 30 m.

Both stream properties and regional land use factors were considered for building habitat suitability models and hence predicting potential habitat of the species. From the Kentucky Geography Network (<http://kygeonet.ky.gov>), we downloaded the latest statewide environmental data sets covering (i) 30 ft (9 m) digital elevation model, (ii) 14-digit hydrological units (HUC14), (iii) 3 ft (0.6 m) aerial imagery (natural colour orthophotos, acquired in 2006), (iv) map of mined areas, (v) national hydrography data set (1:24,000) and (vi) map of state-maintained roads. In addition, we acquired US Geological Survey Gap Analysis Program (GAP) land cover map (level III) for Kentucky (<http://www.gap.uidaho.edu/landcoverviewer.html>). All data layers were cropped to the study region using the boundary of the upper Cumberland River watershed.

These data were further processed to derive corresponding environmental variables (Table I). For stream properties, we calculated stream order and gradient using both national hydrography data set stream feature and digital elevation model for all stream segments with ArcGIS Hydrology Tools. To derive fractional canopy cover along the streams, both aerial imagery and land cover map were used. Blue band from the visible colour aerial imagery was empirically found to be most predictive in determining canopy. A band comparison criterion, blue > red and blue > green and green > red, was applied on aerial imagery to extract canopy shaded areas. Ponds, lakes and non-vegetation were masked out using GAP level III land cover map. Then for each remaining pixel in the area, a fractional coverage estimate was calculated using the ratio of the blue band digital number (8 bits, 0–255) to the maximum value (255) present in the area. Mine density (ratio of mined area over total area) was calculated for each HUC14 unit. Both surface mines and underground mines were included, yielding mine density ratios greater than 1 for some watersheds where more than one layer of coal seams were

Table I. Environmental variables used for predicting blackside dace habitat suitability; the data sources and variable descriptions are included

Variable	Data source	Description
Stream order	NHD	Strahler's ranks
Stream gradient	NHD, DEM	Stream segment gradient
Mine density	KY mined area, HUC14	Ratio of area mined within HUC14
Stream–road intersection	NHD, state roads	Number of intersections per unit area
Elevation	DEM	Elevation in meter
Canopy cover	Air Photo, GAP land cover	Ratio of area covered with canopy

NHD, National Hydrography Data set; DEM, digital elevation model; HUC, hydrologic unit code.

mined. Further, stream–road intersections were extracted using stream feature and state-maintained roads data. The density of stream–road intersections was calculated as the number of crossings per unit area. Geospatial data processing tasks were primarily performed using ArcGIS 9.3 (Environmental Systems Research Institute, 2009) and third party extensions: XTools Pro (Data East, 2010) and HawthTools (Beyer, 2004).

Modelling approach

We used the maximum entropy method (MaxEnt) to model blackside dace habitat suitability with the abovementioned species occurrence data and environmental variables derived therein (Phillips *et al.*, 2006; Elith *et al.*, 2011). MaxEnt is a presence-only species distribution modelling approach derived from the use of a machine learning method with a simple and precise mathematical formulation (Phillips *et al.*, 2006). According to the principle of maximum entropy, the best approximation of a target distribution is one with maximum entropy (most uniform) over the geographic area of interest as restrained by a set of currently known environmental variables. In MaxEnt, these variables (covariates) are transformed into features to account for complex nonlinear species–environment relationships. From a statistical point of view, MaxEnt selects the covariate probability density function of presence data that is closest to the probability density function derived for the background (Elith *et al.*, 2011). The species' distribution is thus estimated by minimizing the distance between the two probability density functions subject to constraining each covariate's mean across predicted locations to that of observed presence locations. Hence, the maximization of the entropy over the geographic space is realized through minimizing the relative entropy (distance) between the two probability density functions (presence and background) within the environmental space (as defined by a set of features [transformed covariates]). The application of MaxEnt for habitat modelling with presence-only data (as in our case) has been improved since its emergence, and the technique is among the available techniques with highest performance (Phillips and Dudík, 2008; Phillips, 2008; Peterson *et al.*, 2007; Pearson *et al.*,

2007). A MaxEnt program (v.3.3.3 k) implementing the modelling approach is available at no cost from the authors' web site (<http://www.cs.princeton.edu/~schapire/maxent/>).

A total of six derived variables covering the upper Cumberland River drainage—stream order, stream gradient, canopy cover, elevation, mine density and stream–road intersection (see Table I)—were used to run the models. For each location with blackside dace occurrence, values of the environmental variables were extracted (for cases when a location offsets from the stream, manual matching was performed). Along the vector-based stream features, we performed an equal-distance point sampling at a 30-m interval, the smallest meaningful sampling unit given the geolocation accuracy of occurrence records (30 m). Outlier points from small gullies and steep slopes that lead to unreasonable stream order and gradient calculation were removed using empirical rules (Cumberland River maximum stream order = 7; stream gradient ≤ 300 m/km). These provided background points representing all primary stream segments in the study area. A total of 46,287 background points were sampled, and the corresponding environmental values were extracted. For model construction and evaluation, the observed blackside dace records were partitioned into training data set and testing data set according to a heuristic “rule of thumb” (Huberty, 1994), which prescribed the partition ratio of 30% for testing subset in our case. Hence, 30% of the data were reserved for model performance assessment for each model run. We performed 10 replicate runs with samples randomly repartitioned each time according to the specified ratio (each partition was composed of 119 training localities and 51 testing localities; with nine outliers removed). Data were fed into the MaxEnt program in the format of samples with data. Each model was applied to the background points using their environmental attributes to predict blackside dace habitat suitability (in logistic output format as represented with a 0–1 ratio) for all stream segments. All predictions were then averaged to generate a “final” habitat suitability estimate, available at the stream segment level at a 30-m linear resolution.

Further, to facilitate watershed-level management, average habitat suitability was computed for each subwatershed as

identified with a unique hydrologic unit code (HUC14). A map was then created showing potential habitat suitability for the fish in all subwatersheds of the area. Lastly, we assessed the clustering patterns of predicted habitats of the species using Moran's I and Geti's G_i^* statistics (Rogerson, 2010), available in ArcGIS Spatial Statistics Tools, to identify areas that have the concentrated quality habits and therefore entail more imminent conservation concerns.

RESULTS

Model evaluation

Model performance was evaluated with receiver operating characteristic (ROC) analysis, which has been widely useful for SDMs with threshold independent outputs (Zweig and Campbell, 1993; Fielding and Bell, 1997). A typical ROC curve plots true positive rate (sensitivity) against false-positive rate (1 - specificity) for the entire range of possible thresholds, therefore providing a unified representation for assessing the overall model performance. In the case of a presence-only model, MaxEnt defines specificity as the fractional predicted area. The area under the curve (AUC) was used as a single performance measure to decide whether the model prediction was better than random (0.5). A perfect model would yield an AUC value of 1. Training AUC values (>0.892) are fairly high across models and are higher than the testing AUC values as anticipated (Phillips, 2010). The testing AUC values, which demonstrate the actual model predictive powers, are consistently higher than 0.834 across the models. This suggests that all model predictions are far from random. The ROC curve for the average model prediction with a mean test AUC value (0.864) and corresponding standard deviation (0.020) is provided in Figure 1.

Environmental factors assessment

The response of environmental variables to blackside dace habitat suitability generally agreed with existing knowledge about stream characteristics and land use impacts, suggesting that slow-flowing headwater streams that are least impacted by mining and roads are best for the species' subsistence. The MaxEnt program provided a marginal response curve for each variable, respectively, while holding other variables at their average levels (Figure 2). Each curve shows how the predicted habitat suitability changes with value of a selected variable. This is mainly to demonstrate the range of effect of a predictor on the suitability estimate and does not suggest a direct causal relationship between each individual environmental variable and the suitability value. We also visually compared the environment of occurrence samples and the environment of background using a bar chart (for stream order) and box plots (Figure 3). In particular,

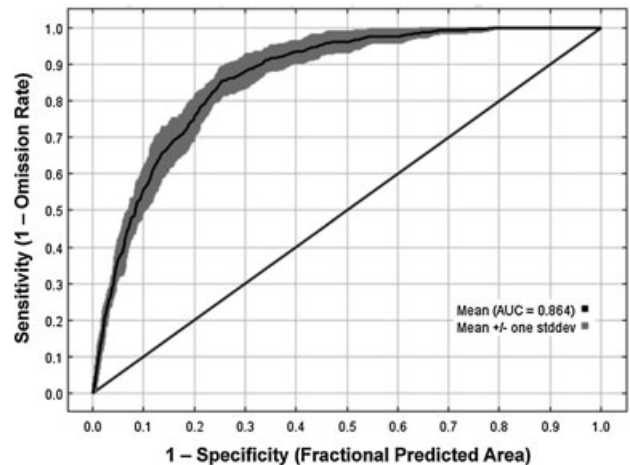


Figure 1. ROC curve for the MaxEnt model prediction averaged on 10 replicate runs. The average test AUC is 0.864, and the standard deviation is 0.020. The 1:1 line indicates the condition if the prediction is completely out of random chance (AUC=0.5).

headwater streams with orders 2 and 3 appear to support the highest quality habitat, with the second-order streams being most prevalent (0.77). Other stream orders do not seem to contribute any increase of suitability. Further, optimum habitat is found with a relatively low stream gradient, and habitat suitability decreases gradually with increased gradient values. Predicted suitability touches the base line (0) when gradient increases to 150 m/km and remains no change afterwards. The sharp increase of suitability with stream gradient between values of 0 up to approximately 10 m/km reflects the lack of blackside dace presence in stream channels with extremely low gradients. A similar pattern is seen with the case of total mine density. As anticipated, better habitat for the blackside dace is associated with lower mine density, and with the increase of mine density beyond a minimum realistic value (slightly higher than 0 as the subwatersheds were more or less influenced by coal mining), habitat suitability drops consistently. This relationship is not clearly shown in the corresponding box plot, perhaps because the background had higher areal proportion with lower mine density than the samples over the entire region. Stream-road intersection density (approximately $<3/\text{km}^2$; see Figure 2) is negatively correlated with blackside dace habitat suitability. Although in general elevation is shown to be positively correlated with habitat suitability (the higher the elevation, the better the habitat), a 500- to 600-m window seems to offer peak habitat suitability. For the most part canopy coverage is positively associated with blackside dace habitat quality, also as anticipated. Among the six variables, stream gradient and stream order contributed the most to the average model prediction (33.5% and 21.9%, respectively) among the natural variables;

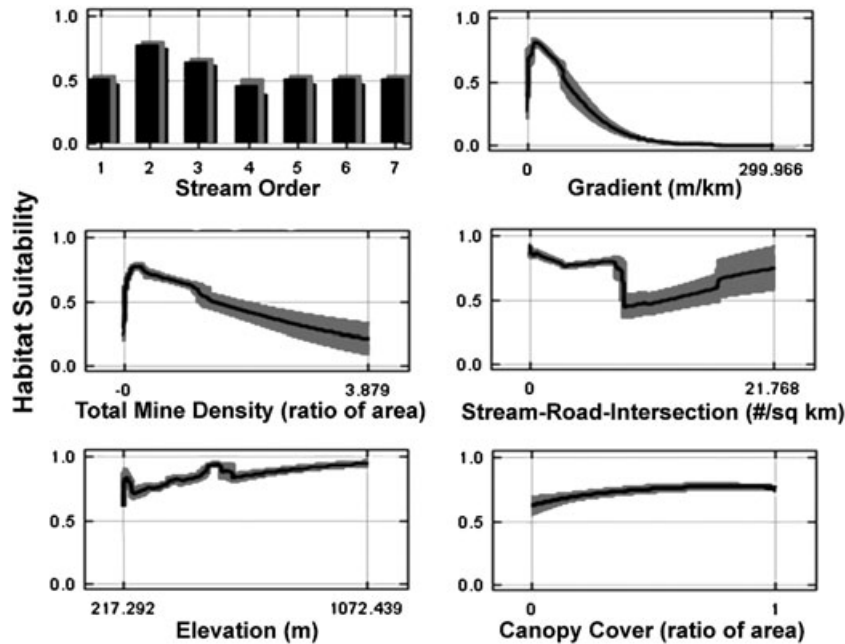


Figure 2. Partial dependence plots showing the marginal responses of blackside dace to the environmental variables. The response of habitat suitability to each single variable is illustrated when all other variables are kept constant at their average level. In the bar chart for stream order, the standard deviation values from the mean are provided as additional bars with variant shades. Two vertical lines in each response graph mark the range of the environmental variable, and the shaded areas indicate the standard deviation.

followed by the human impact variables—mine density (24.8%) and stream–road intersection (12.2%). Elevation and canopy cover had the least relative importance in models with the former contributing 6.5% and the latter 1.2%, respectively.

Distribution maps

A predicted blackside dace distribution map showed habitat suitability by subwatersheds for the upper Cumberland River drainage in Kentucky (Figure 4). Areas with higher predicted habitat suitability generally matched the distribution of recently observed (1990–2010) blackside dace occurrences. Most occurrence locations were located in areas with relatively high habitat suitability. In areas where the species has not been reported, the predicted habitat suitability appeared to be consistently low. Highly suitable habitats were predicted within gaps between existing occurrence locations. Further, Moran’s *I* index, which was 0.35 (*Z* score = 26.5, *p* < 0.01), suggested that subwatersheds with suitable habitats were strongly clustered. Geti’s *G_i^{*}* statistics supported mapping the hot spots (spatial clusters with higher suitability) as well as cold spots (spatial clusters with lower suitability) in the study region (Figure 5). Five major hot spot areas were identified (*Z* score 2.58, *p* < 0.05), which were mainly distributed to the south

of the upper Cumberland River basin, close to the border with Tennessee. Cold spots were primarily found in the north of the Upper Cumberland Drainage basin, where no blackside dace occurrence has yet been reported.

DISCUSSION

Understanding spatial patterns of fish habitat at the regional scale is crucial for science-based management of fluvial ecosystems for species conservation. Using advanced modelling tools and geospatial techniques, we were able to effectively predict potential stream habitat distribution for a threatened fish species, the blackside dace. Presence data were linked to environmental variables that characterized both streams’ natural properties and regional-scale land use influences. A modelling algorithm in line with the second law of thermodynamics (MaxEnt) was used, and the overall results were coherent and informative.

To our knowledge, this study is among the first to explicitly map vector-characterized fish habitat in riverine systems and with land use factors effectively incorporated in addition to the natural variables (Elith *et al.*, 2011; Buisson *et al.*, 2008). The habitat of blackside dace shows unique and narrow range of environmental requirements/sensitivity and is evidently influenced by both natural and

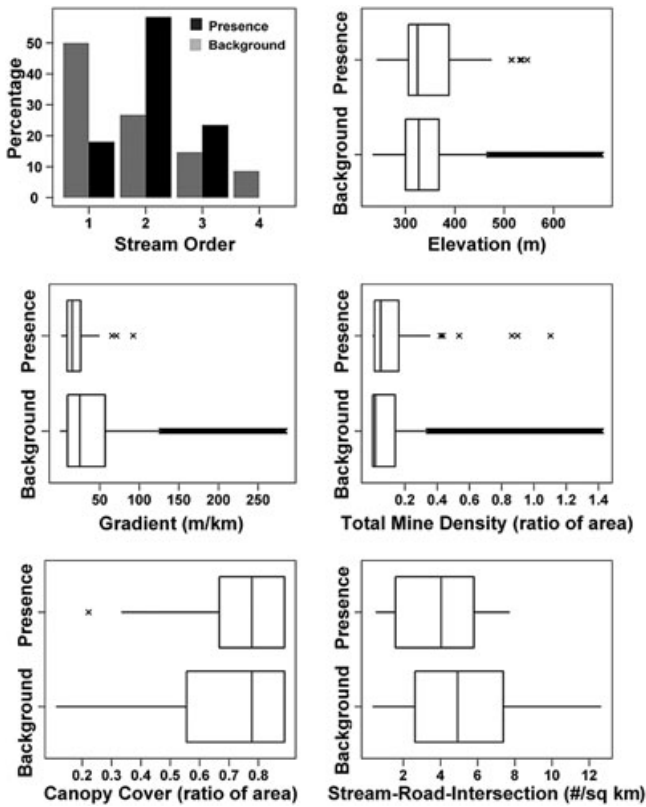


Figure 3. Box plots of environmental variable values used for known blackside dace locations and systematic samples of the background for the entire study area. Because of far ranges of extreme values, a 2.5% stretching was applied (retaining data between the 2.5% and the 97.5% percentiles). For stream orders, the percentages of occurrence within presence sample and background, respectively, were calculated. Each box is composed of the first quartile (lower hinge), the median and the third quartile (upper hinge). The whiskers extend to the largest and smallest observations that fall within a distance of 1.5 times the interquartile range (box size) from the nearest hinge. Extreme values are shown as separate points.

anthropogenic factors. In particular, our study further confirmed that headwater streams with adequate flow volume (indicated with stream order rankings) and low flow velocity (indicated with gentle stream gradients) are characteristic in favourable conditions for the species and form the baseline of its physical habitat. In addition, the negative effects on the fish's habitat from mining and road construction/use were clear. The densities of coal mine and road-stream crossings were effective proxies to stream degradation in relation to expected water siltation and pollution, agreeing with lessons learned in this and other areas (Lindberg *et al.*, 2011). According to a relative contribution assessment of each predictor variable to the models, two natural factors (stream order and stream gradient) formed a first-order constraint to the fish habitat; mine density and stream-road intersection density formed a second-order stress group. Two additional natural factors

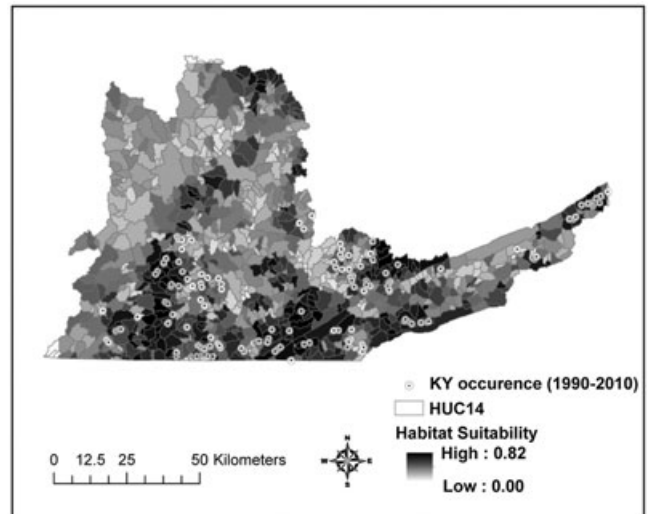


Figure 4. Predicted habitat suitability for blackside dace in the upper Cumberland River drainage area, southeastern Kentucky; occurrence records taken between 1990 and 2010 (used in the models) are shown, and the polygons are HUC14 subwatersheds.

(elevation and canopy cover) tested in the study contributed minimally to models, but their predictive relationships were consistent with prior knowledge. Elevation may generally reflect the topographic locations of the headwater streams that met the abovementioned natural constraints in the study region and therefore do not necessarily impose limits to the fish habitat. Canopy cover's influence further implies that the fish prefers ample shades to maintain cool water temperatures in the summer, although it was not a significant predictor in the models. The lesser role of canopy cover

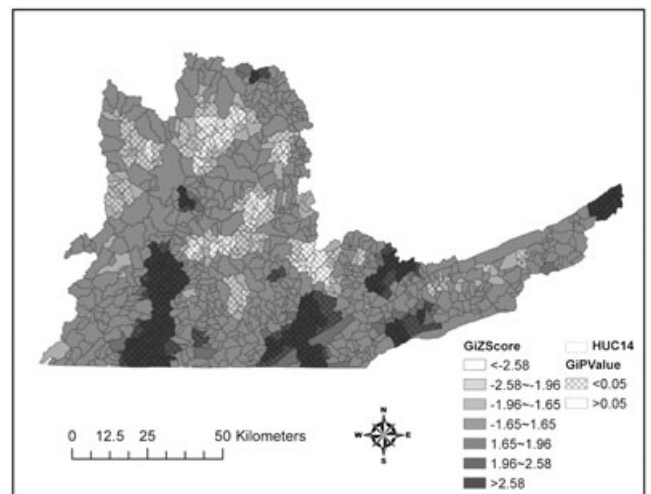


Figure 5. Hot spots (darker colour) according to Geti's G_i^* statistics based on predicted habitat suitability for blackside dace in the upper Cumberland River drainage, southeastern Kentucky; the polygons are HUC14 subwatersheds.

estimate may be due to difficulty in precisely matching the canopy estimates with stream water locations, given complex variations of tree covers along creeks, and limitations of the data and methods used to derive the variable.

Our study presented a successful example of generating management-friendly end products with stream habitat modelling, and the approach should be transferrable to study and conservation of other riverine species. Prediction results are presented primarily at the subwatershed level, which offers a convenient view to facilitate direct access for management purposes. Hence, the derived map showing small watersheds with corresponding blackside dace habitat suitability may serve as an essential reference for planning and prioritizing conservation efforts. To proactively protect potential habitat loss due to human activities, such explicit knowledge of the spatial distribution of the species' suitable habitats is a pressing need for this and other fish species under threat. The information derived from our models is also available for every stream segment (not presented in this article) to therefore allow more precise applications when landscape-scale details within selected subwatersheds are required. The identified hotspots may be used as basis to delineate protected regions for preventing further habitat destruction, informing government agencies for mining and transportation regulations/construction planning as well as educating private landowners who hold properties within the affected region. Moreover, in view of restoring blackside dace populations for the future, the predicted habitat distribution may be used as guidance for reintroducing the species into healthy streams where it is not currently present (Polak and Saltz, 2011). Of course, local biotic constraints such as competition from other species should be monitored and, if necessary, moderated within the targeted subwatersheds.

Using a modelling approach was a necessity given the impossibility of conducting an exhaustive survey over the concerned region. Unavoidable uncertainties may hence be introduced from biases within species presence data and environmental data as well as due to the inadequacies of models used. In our study, known limitations in this regard include the following: (i) the occurrence records are an accumulation during a two-decade long period (from 1990 to 2010), yet the environmental data are relatively recent (2005 and later). This was necessary to allow a large enough sample size (179 cases in total; only 49 cases are available after 2005) but may have led to an underestimation of the more recent human land use effect on the species' habitat. Further work with a more concentrated survey of the area over a short time period may eliminate this uncertainty. (ii) Environmental data used in the study did not reflect known biological interactions such as the presence of the competitive redbelly dace or direct habitat disruption by beaver colonization (McAbee *et al.*, 2008); only the former

is partly accounted for by the properties related to water quality, given that the blackside dace does better than the competing fish in clean waters. Regardless, the lack of data has made incorporating these factors impracticable at this point. In addition, large-scale factors such as climate change may also come into play (Harley, 2011), but its role in the case is still unclear. (iii) In relation to the modelling method, we chose the well-tested presence-only MaxEnt algorithm (Elith *et al.*, 2011) to perform the work but would expect potential improvement as the model further refines. Also, the ensemble forecasting approach, testing multiple model types, could more comprehensively define the base line of prediction results and therefore may be considered a follow-up effort for the future.

In conclusion, our results demonstrated the usefulness of stream habitat modelling for conserving a threatened fish species in a disturbed drainage area. Prediction results showed that both physical and anthropological factors are combined to influence the fish habitat suitability. Currently, suitable habitats of the blackside dace are arranged in several groups of subwatersheds, but these groups (clusters) are isolated from one another, suggesting that possible population segregations may have occurred over time (either naturally or due to disturbances) and calling for more attention for conservation efforts. Given that the scarcity of field records will continue to be a limitation in the coming decades, we anticipate that improved application of SDMs in riverine environments incorporating natural and human influences will continue to provide explicit biogeographic guidance for conserving stream biodiversity.

ACKNOWLEDGEMENTS

The authors acknowledge the valuable support provided by Ryan Evans and Sarah Hines of the Kentucky State Nature Preserves and John Brumley of the Kentucky Department for Environmental Protection. They also thank Jonathan Phillips for reviewing the manuscript and Hannah LeGris for copy editing support. Lastly, they thank the two anonymous reviewers for taking time to review the manuscript and the constructive comments.

REFERENCES

- Ahmadi-Nedushan B, St-Hilaire A, Bérubé M, Robichaud É, Thiémonge N, Bobée B. 2006. A review of statistical methods for the evaluation of aquatic habitat suitability for instream flow assessment. *River Research and Applications* **22**: 503–523.
- Black T, Mattingly H. 2007. Impacts of logging disturbance on blackside dace (*Phoxinus cumberlandensis*) reproductive ecology. The Nature Conservancy, Tennessee Chapter, Nashville, Tennessee.
- Black TR. 2007. Population densities and performance of predictive habitat models for the threatened blackside dace (*Phoxinus cumberlandensis*). Master Thesis. Tennessee Technological University, Cookeville, Tennessee.

- Buisson L, Blanc L, Grenouillet G. 2008. Modelling stream fish species distribution in a river network: the relative effects of temperature versus physical factors. *Ecology of Freshwater Fish* **17**: 244–257.
- Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* **17**: 43–57.
- Fielding AH, Bell JF. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* **24**: 38–49.
- Harley CDG. 2011. Climate change, keystone predation, and biodiversity loss. *Science* **334**: 1124–1127. DOI:10.1126/science.1210199.
- Huberty C. 1994. *Applied Discriminant Analysis*. Wiley-Interscience: New York.
- Jones BK. 2005. Predictive habitat models for conservation of the threatened blackside dace (*Phoxinus cumberlandensis*). Master Thesis. Tennessee Technological University, Cookeville, Tennessee.
- Joy MK, Death RG. 2004. Predictive modelling and spatial mapping of freshwater fish and decapod assemblages using GIS and neural networks. *Freshwater Biology* **49**: 1036–1052.
- Ladle RJ, Whittaker RJ. 2011. *Conservation Biogeography*. Wiley-Blackwell: West Sussex, UK.
- Lindberg TT, Bernhardt ES, Bier R, Helton AM, Merola RB, Vengosh A, Di Giulio RT. 2011. Cumulative impacts of mountaintop mining on an Appalachian watershed. *Proceedings of the National Academy of Sciences* **108**: 20929–20934. DOI:10.1073/pnas.1112381108.
- Marcot BG. 2006. Habitat modeling for biodiversity conservation. *Northwestern Naturalist* **87**: 56–65.
- Mattingly HT. 2005. Factors affecting the distribution and recovery of the threatened blackside dace in Kentucky and Tennessee. Final project report. Cookeville Field Office, Cookeville, Tennessee.
- McAbee K, Albeke S, Nibbelink N. 2008. Improving imperiled species management through spatially-explicit decision tools. *Proceedings of the 6th Southern Forestry and Natural Resources GIS Conference*: 196–209.
- O'Bara C. 1985. A status survey of the blackside dace, *Phoxinus cumberlandensis*. Unpublished Report to USFWS Asheville, North Carolina.
- Oakes R, Gido K, Falke J, Olden J, Brock B. 2005. Modelling of stream fishes in the Great Plains, USA. *Ecology of Freshwater Fish* **14**: 361–374.
- Olden JD, Jackson DA. 2002. A comparison of statistical approaches for modelling fish species distributions. *Freshwater Biology* **47**: 1976–1995.
- Olden JD, Kennard MJ, Leprieux F, Tedesco PA, Winemiller KO, García-Berthou E. 2010. Conservation biogeography of freshwater fishes: recent progress and future challenges. *Diversity and Distributions* **16**: 496–513.
- Pearson RG, Raxworthy CJ, Nakamura M, Townsend Peterson A. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography* **34**: 102–117.
- Peterson AT. 2001. Predicting species' geographic distribution based on ecological niche modeling. *Condor* **103**: 599–605.
- Peterson AT, Papeş M, Eaton M. 2007. Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. *Ecography* **30**: 550–560. DOI:10.1111/j.2007.0906-7590.05102.x.
- Phillips S. 2008. Transferability, sample selection bias and background data in presence-only modelling: a response to Peterson *et al.* (2007). *Ecography* **31**: 272–278.
- Phillips S. 2010. A brief tutorial on Maxent. *Lessons in Conservation (LinC)* **3**: 107–135.
- Phillips S, Anderson R, Schapire R. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* **190**: 231–259.
- Phillips S, Dudík M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* **31**: 161–175.
- Polak T, Saltz D. 2011. Reintroduction as an ecosystem restoration technique. *Conservation Biology* **25**: 424–424.
- Richardson DM, Whittaker RJ. 2010. Conservation biogeography—foundations, concepts and challenges. *Diversity and Distributions* **16**: 313–320.
- Starnes L, Starnes W. 1981. Biology of the blackside dace *Phoxinus cumberlandensis*. *American Midland Naturalist* **106**: 360–371.
- Starnes W, Starnes L. 1978. A new cyprinid of the genus *Phoxinus* endemic to the upper Cumberland River drainage. *Copeia* **1978**: 508–516.
- Whittaker RJ, Araújo MB, Paul J, Ladle RJ, Watson JEM, Willis KJ. 2005. Conservation biogeography: assessment and prospect. *Diversity and Distributions* **11**: 3–23.
- Zweig M, Campbell G. 1993. Receiver-operating characteristic (ROC) plots: a fundamental evaluation tool in clinical medicine. *Clinical Chemistry* **39**: 561–577.