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Riverscape correlates for distribution of threatened spotfin chub *Erimonax monachus* in the Tennessee River Basin, USA

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ABSTRACT: Globally, aquatic biodiversity is imperiled at an increasing rate, especially in diversity hotspots such as the southeastern USA. The spotfin chub *Erimonax monachus* is a federally threatened minnow with a disjunct distribution resulting from numerous impoundments on the Tennessee River and its tributaries in the heart of the southeastern USA. Recovery actions required to remove federal protection for *E. monachus* are dependent on the establishment of additional populations within the historical range of the species, but little is known regarding macroscale habitat requirements that could guide conservation planning. We analyzed local- and network-scale watershed attributes to develop an ecological niche model (ENM) for *E. monachus* useful for directing conservation actions at sampled and unsampled sites across the Tennessee River Basin. We found *E. monachus* occurred most often in larger streams with large upstream catchment areas and minimal alteration to forested uplands, but all of these sites were in close proximity to high densities of downstream dams due to populations being restricted to large-stream habitat upstream of reservoirs. The ENM showed the highest probability of *E. monachus* occurrence among catchment locations with known extant populations; however, additional historical and previously unoccupied catchments showed potential for successful (re)introductions, provided that fine-scale habitats are appropriate. Our framework can be used to identify potential survey and (re)introduction sites for *E. monachus* as well as other rare riverine fishes and represents a method for identifying areas of high priority for conserving aquatic biodiversity.

KEY WORDS: Ecological niche model · Species restoration · Landscape alteration · Biodiversity preservation

1. INTRODUCTION

Globally, biodiversity diminished over the last century in both terrestrial and aquatic realms as human domination of ecosystems increased (Vitousek et al. 1997). Aquatic fauna such as freshwater mussels, fishes, aquatic invertebrates, crayfishes, and amphibians are disproportionally at risk of imperilment compared with terrestrial organisms (Richter et al. 1997, Dudgeon et al. 2006). Multiple anthropogenic factors contribute to aquatic habitat alteration and, consequently, the abundances and distributions of fauna occupying aquatic environments. These factors include habitat degradation, water pollution, over-exploitation, introduction of non-indigenous and invasive species, and impoundment and flow modification of river systems (Miller 1972, Cole & Landers 1995, Dudgeon et al. 2006). Slowing or halting bio-

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diversity loss requires greater understanding of interactions among the multiple threats that influence organism distributions and abundances (Strayer & Dudgeon 2010).

Stream fishes represent a well-studied but widely declining group of freshwater organisms (Closs et al. 2016). Threats to stream fish diversity are similar to other aquatic organisms, but riverine landscape alterations that cause increased sedimentation and population fragmentation are among the most widespread threats (Angermeier 1995, Warren et al. 2000, Sutherland et al. 2002). Improper or inadequate erosion control techniques have substantially increased sedimentation to streams and rivers, effectively altering local habitat templates and flow regimes that molded evolutionary adaptations of stream fishes (Lytle & Poff 2004). Impoundment of rivers has isolated many endemic riverine fishes while completely decimating others reliant on continuously flowing systems for migratory spawning (Liermann et al. 2012, Perkin et al. 2015a). Only 42 rivers with unimpounded longitudinal lengths greater than 200 km remain in the conterminous USA, and less than 2% of all streams are of adequate quality to be federally protected as wild and scenic (Benke 1990). Dams and impoundments are of special concern because they directly block fish passage throughout a river network, limiting fish habitat ranges and disconnecting gene flow between meta-populations (Gido et al. 2016). In addition, impoundments disrupt ecological processes, in particular the natural discharge and thermal regime of rivers (Petts 1986, Poff et al. 1997). This is concerning because riverine fish depend on relatively natural discharge and thermal regimes to trigger spawning and sustain recruitment and survival; thus, dams can hinder the presence and timing of fish reproduction (Craven et al. 2010, Olden & Naiman 2010, Perkin et al. 2016). Addressing declines in stream fish diversity will in part require understanding how existing or future dams influence the distribution and abundance of species (Olden 2016). Specifically, limited understanding of life history, habitat connectivity, and flow regime requirements of fishes are identified as research areas critical for improving fish diversity conservation (Cooke et al. 2012).

The southeastern USA has the highest diversity of freshwater fishes, the largest number of endemic species, and the largest number of imperiled fishes in North America (Warren & Burr 1994, Warren et al. 2000). In fact, the southeastern USA is ranked among global hotspots for fish biodiversity (Abell et al. 2008). The Tennessee River Basin is one of the most diverse drainage basins in the USA, harboring approximately 250 species and subspecies (Starnes & Etnier 1986). Fishes in the families Cyprinidae (minnows) and Percidae (darters) are the 2 most diverse groups in the Tennessee River Basin and are proportionally the most imperiled species (Warren & Burr 1994). Conserving these diverse groups requires understanding the appropriate spatial scales for implementing conservation initiatives (Fausch et al. 2002, Kanno et al. 2012a), and Etnier (1997) identified medium-sized rivers as preferred habitats for many imperiled fishes in the region. Consequently, species requiring medium-sized streams can be used as sentinels to enhance our understanding of fish diversity decline (Wenger 2008). Because of the high level of diversity and relatively intact nature of the Tennessee Basin fauna, a portion of the Tennessee River was recently designated as a native fish conservation area (NFCA) (Williams et al. 2011). This designation points to the potential for the existence of other unidentified high-quality habitats in the basin that could be used to promote conservation of declining or imperiled fishes.

The spotfin chub *Erimonax monachus* is endemic to the Tennessee River and is associated with medium-sized rivers in disjunct populations throughout the basin (Etnier & Starnes 1991). *E. monachus* is a small-bodied cyprinid that was historically extant over a wide range covering 5 states: Alabama, Georgia, North Carolina, Tennessee, and Virginia. The species was historically distributed across 4 physiographic provinces and 12 tributary systems of the Tennessee River (Jenkins & Burkhead 1984). However, populations are fragmented by various anthropogenic barriers and are now localized to only 4 tributary systems: (1) the Little Tennessee River, North Carolina; (2) the Buffalo and (3) Emory rivers, Tennessee; and (4) the north and middle forks of the Holston River in Tennessee and Virginia (Jenkins & Burkhead 1984). The US Fish and Wildlife Service (USFWS) now recognizes *E. monachus* as a threatened species under the Endangered Species Act (Federal Register 1977), and extirpations are attributed primarily to fragmentation, habitat degradation, and hydrologic alteration (Jenkins & Burkhead 1984). However, this species has been reintroduced in several catchments with historical records and introduced in additional catchments within the Tennessee River Basin (P. Rakes, Conservation Fisheries, pers. comm.) as part of recovery efforts. *E. monachus* is a fractional crevice spawner characterized by females depositing eggs in gaps among large substrates several times from May through mid-August

(Jenkins & Burkhead 1984). It is hypothesized that fragmented access to appropriate spawning habitat is a leading factor contributing to local extirpations (Etnier & Starnes 1993). However, each extant population appears to use fine-scale habitats according to availability, though silt-laden substrates are typically avoided (Jenkins & Burkhead 1984, Kanno et al. 2012b). Based on the apparent plasticity of fine-scale habitat associations, broader-scale habitats might be appropriate for describing and predicting the distribution of the species.

The purpose of our study was to analyze catchment characteristics across *E. monachus*'s historical range within the Tennessee River Basin to identify factors influencing current distribution. The primary objective of the *E. monachus* recovery plan is to restore viable populations to a significant portion of their historical range so they no longer require federal protection under the Endangered Species Act (USFWS 1983). Specifically, the recovery plan calls for the protection and preservation of naturally extant populations and determination of the feasibility of reestablishing populations throughout their historical range. Thus, we sought to develop an ecological niche model (ENM; Peterson & Soberón 2012) that describes the spatial locations of high-priority habitats, both currently occupied and potentially occupied. Once developed, an ENM could be used to guide management decisions regarding the protection of extant populations and to identify segments with suitable habitat for additional reintroductions to fulfill recovery objectives for the species. We hypothesized that *E. monachus* extirpations would be correlated with habitat fragmentation, especially due to large impoundments that limit suitable habitat across the Tennessee River Basin. Because large impoundments are likely to be permanent structures on riverscapes for the foreseeable future, identifying potential reintroduction sites at previously unsampled areas represents a much-needed research endeavor for guiding progress towards conservation goals (Olden 2016).

2. MATERIALS AND METHODS

2.1. Study area

The Tennessee River is the largest tributary to the Ohio River, comprising ~20% of the Ohio River Basin and containing >90% of fish species found throughout the basin (White et al. 2005). The Tennessee River Basin (~105 000 km^2) traverses 7 states: Alabama, Georgia, Kentucky, Mississippi, North Carolina, Tennessee, and Virginia (Fig. 1A). The headwaters begin in the mountains of southwestern Virginia, western North Carolina, and northern Georgia. Major tributaries include the Clinch, Powell, Holston, French Broad, Little Tennessee, Hiwassee, Emory, Elk, Buffalo, and Duck rivers. The con-

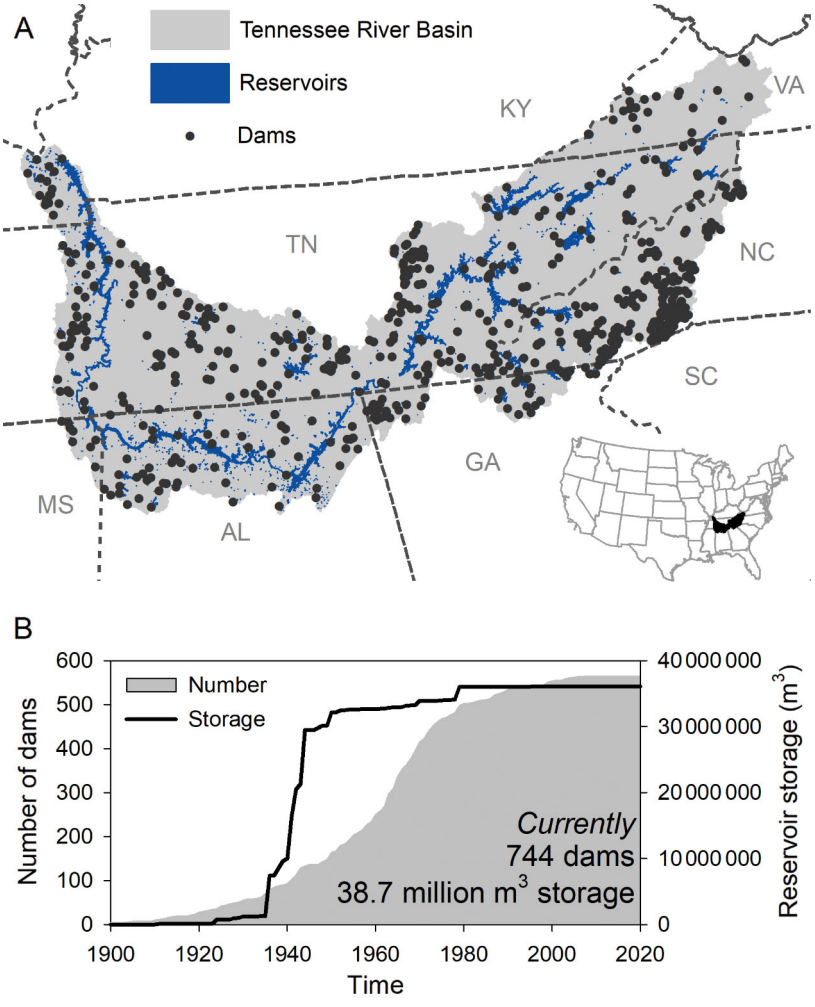

Fig. 1. (A) Tennessee River Basin in the southeastern USA illustrating extensive habitat fragmentation by dams and reservoirs. (B) Timing of dam construction increased most between 1950 and 1980 for dams that have date data, and the 744 current dams create reservoirs with a combined storage capacity >38.7 m m^{-3} of water. Dams without dates were excluded from the timeline of accumulation

fluence of the Holston and French Broad rivers forms the Tennessee River proper, which flows ~1050 km to its confluence with the Ohio River (White et al. 2005). Although the Tennessee River Basin is large and speciose, habitat fragmentation and hydrologic alteration have negatively affected aquatic species diversity (Neves & Angermeier 1990).

Hydrologic alteration of the Tennessee River and its tributaries began in the early 1900s for navigation, flood control, and hydroelectric power (Toplovich 2017, https://www.tva.gov/About-TVA/Our-History). Hales Bar Dam was constructed on the Tennessee River near Chattanooga, TN, between 1905 and 1913. Wilson Dam on the lower Tennessee River was finished in 1924. By the early 1930s, several other impoundments were constructed in headwater systems, including on the Cheoah, Ocoee, Toccoa, and Watauga rivers. Creation of the Tennessee Valley Authority (TVA) in 1933 resulted in rapid production of hydroelectric and navigational dams along the Tennessee River and its tributaries (Fig. 1B). Tellico Dam was completed in 1979 and was the last major reservoir created within the Tennessee River Basin. Today, the TVA operates 9 locks and dams on the main stem of the Tennessee River and 23 dams on its tributaries. Other utility companies operate hydroelectric dams on several tributaries, and 744 total dams with a collective storage capacity of 38 736 126 m^3 are documented in the National Anthropogenic Barrier Dataset (Ostroff et al. 2013). Additionally, navigation canals have been constructed between the Tennessee and Tombigbee rivers and between the Tennessee and Cumberland rivers. Consequently, the Tennessee River basin is a highly altered and regulated system of reservoirs connected by intermittent free-flowing riverine segments (Neves & Angermeier 1990).

Very few subcatchments within the Tennessee River Basin remain unimpounded. The Buffalo, Emory, and Sequatchie rivers are the only systems that flow unimpeded to the Tennessee River. Upper portions of the Clinch, French Broad, Holston, and Powell rivers also have substantial free-flowing segments but are impounded prior to their confluences with the Tennessee River. Several rivers, such as the Little Tennessee River, have small overflow impoundments in their upper reaches but retain large segments of free-flowing water between impoundments. Identifying large, intact catchments to promote long-term viability of native fish populations is a major goal of NFCAs (Williams et al. 2011). The Little Tennessee River was recently designated as an NFCA by the North Carolina Wildlife Federation to enhance collaboration among multiple agencies and organizations to provide sustainable catchment management practices and protect native fish, including *Erimonax monachus*. Several other catchments, including those harboring extant populations of *E. monachus*, meet the criteria for designation as NFCAs.

2.2. Landscape data

We conducted spatial analyses to relate landscape characteristics to the distribution of *E. monachus*. Geospatial data included 52 parameters describing natural stream gradients, stream network connectivity, catchment land use and land cover, terrestrial and aquatic landscape alterations, and habitat disturbance indices for the entire Tennessee River Basin (Table 1). These data were obtained from the US Geological Survey National Hydrography Dataset (NHD) Version 2 Plus described by McKay et al. (2012) and extension attributes developed for habitat disturbances (Esselman et al. 2011) and stream network connectivity (Cooper & Infante 2017). We compiled land use and land cover data, landscape alteration densities, and habitat disturbance data at 2 spatial extents, local catchments and network catchments. These data were originally collected and analyzed from 2005 to 2015, which corresponds to the fish occurrence data for our analyses. Local catchments were defined as the area of land draining directly into an interconfluence stream segment (i.e. length of stream between 2 confluences), whereas network catchments included all upstream areas across multiple local catchments (see illustrations in Perkin et al. 2019). All geospatial data were linked to NHD streamlines in ArcMap 10.4.1 GIS (ESRI 2015).

2.3. Fish occurrence data

We confined the spatial extent of our investigation to the historical and contemporary distribution of *E. monachus* (Table 2). Extirpated populations were determined from historical records (Jenkins & Burkhead 1984, Etnier & Starnes 1993), and the current distribution as well as catchments where *E. monachus* have been successfully (re)introduced were provided by Conservation Fisheries (P. Rakes & J. R. Shute unpubl. data). Abrams Creek represents the sole unsuccessful reintroduction to date and was included in analyses based on the species' historical

Table 1. Predictor variables used to model distribution of *Erimonax monachus*. Note: In their calculation of metrics, Cooper & Infante (2017) defined main stems as streams of similar or larger streams compared with the focal stream segment

Variable	Description and units
Natural stream gradient	
N_AREASQKM	Catchment area of total upstream network (km^2)[a]
L_AREASQKM	Local catchment area (km^2)[c]
StreamOrder	Stream order (Strahler 1957)[b]
RunOffVC	Estimated runoff for stream segment (mm)[b]
SLOPE	Stream channel slope ($m\ m^{-1}$)[b]
TempVC	Average annual air temperature (°C × 100)[b]
MINELEVSMO	Minimum elevation of stream segment (cm)[b]
Network connectivity	
DMD	Density of downstream mainstem dams (no. 100 km^{-1})[c]
DM2D	Distance to downstream mainstem dam (km)[c]
DMO	Percent of open (i.e. free of dams) downstream main stem
SMST	Segment mainstream length (km)[c]
STOT	Total segment network length between 2 dams (km)[c]
TMD	Total mainstem dam density (no. 100 km^{-1})[c]
TM2D	Total mainstem distance between upstream and downstream dams (km)[c]
TMO	Total percent of open mainstem habitat (%)[c]
UDOR	Percent of estimated annual discharge stored in upstream reservoirs (%)[c]
UMD	Upstream mainstem dam density per mainstem length (no. 100 km^{-1})[c]
UM2D	Distance to upstream mainstem dam (km)[c]
UMO	Percent of open upstream main stem (%)[c]
UNDC	Upstream dam density (no. km^{-2})[c]
UNDR	Upstream network dam density per stream network length (no. 100 km^{-1})[c]
USC	Total upstream reservoir storage per stream network catchment area (hectare-meters km^{-2})[c]
USR	Total upstream reservoir storage volume per stream network length (hectare-meters 100 km^{-1})[c]
Land cover and land use	
L_ or N_CROPS	Percent crop land use in local or network catchment (%)[a]
L_ or N_PASTURE	Percent pasture land use in local or network catchment (%)[a]
L_ or N_URBANL	Percent low-intensity urban land use in local or network catchment (%)[a]
L_ or N_URBANM	Percent medium-intensity urban land use in local or network catchment (%)[a]
L_ or N_URBANH	Percent high-intensity urban land use in local or network catchment (%)[a]
Landscape alteration density	
L_ or N_CERC_DENS	Density of Superfund National Priorities List sites within local or network catchment
L_ or N_DAMS_DENS	Density of dams in local or network catchment (no. km^{-2})[a]
L_ or N_MINES_DENS	Density of mines in local or network catchment (no. km^{-2})[a]
L_ or N_NPDES_DENS	Density of National Pollutant Discharge Elimination System sites in local or network catchment (no. km^{-2})[a]
L_ or N_POP_DENS	Human population density in local or network catchment (people km^{-2})[a]
L_ or N_ROAD_DENS	Density of roads in local or network catchment (crossings km^{-2})[a]
L_ or N_ROAD_L_DENS	Density of road length in local or network catchment (km km^{-2})[a]
L_ or N_TRI_DENS	Density of toxic release inventory sites (TRI) in local or network catchment (no. km^{-2})[a]
Habitat disturbance index	
CumDistIndx	Averaged anthropogenic disturbance index (1 = highest risk of habitat degradation; 5 = lowest risk of habitat degradation)[a]
NDistIndx	Habitat disturbance index for upstream network (1 = highest risk of habitat degradation; 5 = lowest risk of habitat degradation)[a]
LDistIndx	Habitat disturbance index for local catchment (1 = highest risk of habitat degradation; 5 = lowest risk of habitat degradation)[a]

[a]Esselman et al. (2011); [b]McKay et al. (2012); [c]Cooper & Infante (2017)

distribution. We also included additional locations where the species is permitted for introductions based on Federal Register regulations (Federal Register 2002, 2005, 2007). Within this geographic area (Fig. 2A), we developed a presence–absence dataset for *E. monachus* using survey collections conducted by the TVA (J. Simmons, TVA, unpubl. data). Extant *E. monachus* and whitetail shiner *Cyprinella galactura* occurrences were documented by the TVA during Index of Biotic Integrity surveys between 1986

Table 2. Variables influencing *Erimonax monachus* distribution for major catchments with extant, extirpated, reintroduced, and introduced *E. monachus* populations throughout the Tennessee River Basin, and catchments permitted for future introductions. agr: agricultural; dev: developed; (–) not present

ID	River system	Status	State	Total drainage area (km^2)	Stream order	Altered land use (agr/dev) (%)
1	Buffalo River	Extant	Tennessee	1991.4	4	19.5/4.1
2	Shoal Creek	Reintroduced	Alabama, Tennessee	1284.9	5	31.1/7.5
3	Little Bear Creek	Extirpated	Alabama	184.8	–	24.6/6.7
4	Chickamauga Creek	Extirpated	Georgia, Tennessee	1205.0	–	21.1/25.3
5	Whites Creek	Extirpated	Tennessee	369.4	–	7.4/7.5
6	Emory River	Extant	Tennessee	2248.3	3, 4, 5, 6	10.6/10.3
7	Tellico River	Introduced	North Carolina, Tennessee	546.9	4	7.7/3.2
8	Citico Creek	Extirpated	Tennessee	184.8	–	0.3/1.8
9	Cheoah River	Introduced	North Carolina	557.8	4	1.4/3.8
10	Abrams Creek	Extirpated/ unsuccessful reintroduction	Tennessee	225.7	–	3.7/1.7
11	Little Tennessee River	Extant	North Carolina	1154.7	5	17.8/22.8
12	Tuckasegee River	Extirpated	North Carolina	1769.1	–	2.7/5.8
13	French Broad River	Extirpated	North Carolina	4866.6	–	25.2/27.1
14	Lower French Broad River	Permitted	Tennessee	520.4	7	33.1/12.5
15	Lower Holston River	Permitted	Tennessee	903.3	6	32.4/14.3
16	Powell River	Extirpated	Tennessee, Virginia	1994.5	–	11.1/10.1
17	Clinch River	Extirpated	Tennessee, Virginia	3842.5	–	19.6/8.0
18	North Fork Holston River	Extant	Tennessee, Virginia	2488.3	2, 3, 4, 6	23.5/4.3
19	Middle Fork Holston River	Extant	Tennessee, Virginia	625.5	4	40.1/9.0
20	South Fork Holston River	Extirpated	Tennessee, Virginia	1194.6	–	25.2/27.1

and 2017 (Fig. 2B). Locations where *E. monachus* were collected by the TVA were listed as occupied. We assumed the collections detecting *C. galactura* but not *E. monachus* represented sufficient sampling effort to conclude the absence of *E. monachus* because both species have a high degree of co-occurrence, use similar habitats, and are known to hybridize (Burkhead & Bauer 1983, Etnier & Starnes 1993, Jenkins & Burkhead 1993). Some locations designated as absent could have *E. monachus* present due to their rarity; however, most sites were sampled multiple times between 1986 and 2017 without detection. Therefore, we can reasonably assume they do not occupy absent sites for the purpose of this study. Additionally, most sites were systematically sampled across the species' distribution in the last 10 yr corresponding with contemporary landscape data. This dataset included 237 unique sampling locations, including 36 where *E. monachus* was present and 201 where *E. monachus* was considered absent (i.e. only *C. galactura* was collected).

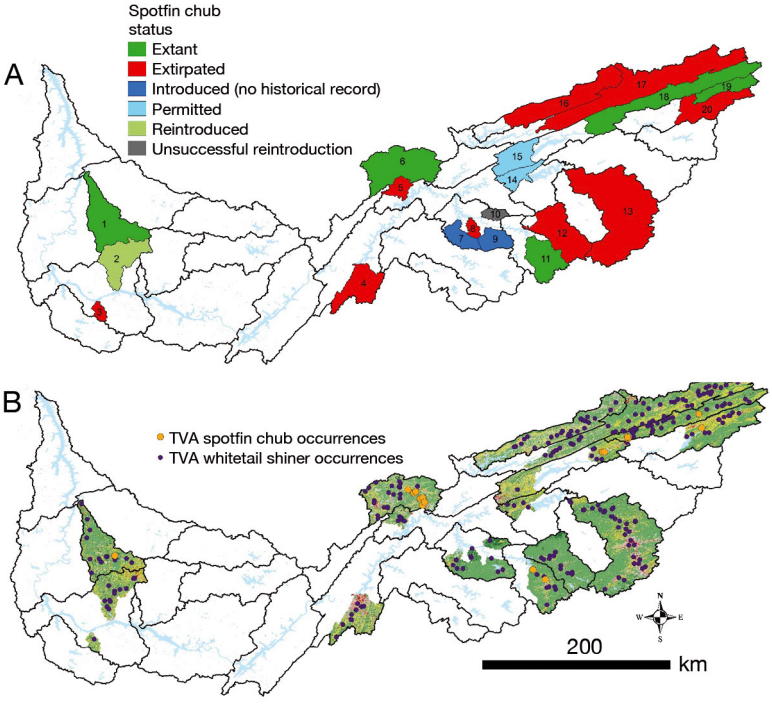

Fig. 2. (A) Status of *Erimonax monachus* in subcatchments of the Tennessee River Basin throughout their historical distribution. (B) *E. monachus* and *Cyprinella galactura* observations from Tennessee Valley Authority (TVA) sampling from 1986 to 2017 overlaying current land use patterns. Green land use signifies forested areas, yellow indicates agricultural land use, and red represents development

2.4. Statistical analysis

We identified stream segments from the NHD that overlapped spatially with the 237 sampling locations using GPS coordinates from the TVA collections. We joined *E. monachus* presence–absence data with the 52 landscape metrics and fit a random forest (RF) classification model to describe *E. monachus* occurrence (Cutler et al. 2007). For the RF model, *E. monachus* occurrence (1 = present; 0 = absent) was the response variable, and the landscape metrics (Table 1) were the predictor variables. We fit the model using the randomForest function from the randomForest package in R, including 2000 trees with 3 variables tried at each split (Liaw & Wiener 2002). We determined the number of variables tried at each split using the tuneRF function from the randomForest package and addressed class imbalance using the synthetic minority over-sampling technique (SMOTE) method described by Chawla et al. (2002) with the SMOTE function from the DMwR package (Torgo 2010) in R. The resampling with SMOTE improved the imbalanced data (0 = 201 observations; 1 = 36 observations) so that 72 observations of each class were created. We assessed model fit to the training data using metrics described by Evans & Cushman (2009), including out-of-bag (OOB) error rate, sensitivity (i.e. proportion of observed positives correctly predicted), specificity (i.e. proportion of observed absences correctly predicted), and Kappa ([observed accuracy − expected accuracy]/[1 − expected accuracy]; range 0–1). We also tested model significance following the methods of Murphy et al. (2010). We then used 5-fold cross-validation using the rf.crossValidation function from the rfUtilities package (Evans & Murphy 2018) to assess mean sensitivity, specificity, and Kappa across 5 subsets of the data following the methods described by Evans et al. (2011). Finally, we assessed model sensitivity, specificity, and Kappa when the trained model was used to predict occurrence of *E. monachus* from an independent dataset collected by Russ (2006). Russ (2006) conducted surveys for *E. monachus* at 57 sites distributed across the Emory River Basin and documented presence or absence of the species at each site (see additional details in Kanno et al. 2012b). We used the confusionMatrix function from the caret package (Kuhn et al. 2019) to assess accuracy (and bootstrapped 95% CIs), sensitivity, specificity, and Kappa of the model when applied to the independent dataset.

We assessed relative variable importance in the model using the rf.partial.prob function from the rfUtilities package and created partial dependence plots (PDPs) with overlaid LOWESS regression lines using the methods described by Baruch-Mordo et al. (2013). Variable importance was measured using the metric mean decrease in Gini, which measures the decrease in classification accuracy as variables are excluded from trees. The largest mean decrease in Gini represents the most important variable; thus, the ranking according to Gini, rather than the Gini score itself, gives insight into variable importance. PDPs illustrate the effect of a single predictor variable across its range of observed values while holding all others at their mean (Friedman 2001). We scaled the *y*-axis of PDPs to the probability of *E. monachus* occurrence using the rf.partial.prob function, which gives both the typical splined PDP plus an overlaid LOWESS regression line with 95% CIs (Evans et al. 2011). All analyses were conducted in R version 3.5.2 (R Core Team 2018).

2.5. Ecological niche projections

We used our ENM to predict the probability of occurrence of *E. monachus* for all stream segments within the historical and contemporary range of the species. This approach is useful for evaluating habitats at previously unsampled sites and across broad spatial extents. We used the predict function from the randomForest package to fit model predictions for the probability of occurrence (0–1) to stream segment data across all subcatchments shown in Fig. 2. We first mapped predicted occurrences within the Emory River Basin to illustrate agreement between our ENM and observations by Russ (2006). We then developed predictions for all stream segments within the historical or introduced range of *E. monachus* in the Tennessee River Basin.

3. RESULTS

Our ENM suggested *Erimonax monachus* distribution is influenced by landscape-level characteristics and alterations. Model performance assessment from the training dataset included a low error rate (OOB error rate = 4.17%), 93% of observed positives correctly predicted (sensitivity = 0.93), 96% of observed absences correctly predicted (specificity = 0.96), and Kappa = 0.88, and the model explained a significant level of variation in occurrence ($p < 0.0001$). Five-fold cross-validation results showed mean sensitivity was 0.75, mean specificity was 1.00, and mean Kappa was

Table 3. Ecological niche model performance based on sensitivity, specificity, and Kappa from training data, 5-fold cross-validation, and testing on a dataset (i.e. Russ 2006) not included in model training

Performance metric	Training data	Five-fold cross-validation	Russ (2006)
Sensitivity	0.93	0.75	0.92
Specificity	0.96	1.00	0.88
Kappa	0.88	0.87	0.71

0.87 (Table 3). When tested on the independent dataset collected by Russ (2006), the ENM sensitivity was 0.92, specificity was 0.88, and Kappa was 0.71. Model accuracy when tested against data from Russ (2006) was 89.1% (95% CI = 77.8–95.9%). The 6 most important variables were catchment area, percent of the local catchment covered by pasture land use, road length density in the network catchment, minimum stream channel elevation, stream order, and stream runoff. Among land use and landscape alteration metrics, data compiled at the network catchment scale tended to be more important than the same metrics compiled at the local network catchment scale, pasture land use being the exception (Fig. 3).

PDPs illustrated *E. monachus* responses to the 6 most important landscape metrics (Fig. 4). Probability of occurrence was highest among stream segments with intermediate-sized (2000–3000 km^2) upstream network catchments but fell precipitously in smaller streams (Fig. 4A). Probability of occurrence declined in a linear pattern as the percent of the local catchment covered by pasture land use increased from 0 to 40%, and occurrence remained low when >40% of local catchments were covered by pasture land use (Fig. 4B). Probability of occurrence was highest at lower densities of road lengths (0.3–0.5 km km^{-2}) in the network catchment (Fig. 4C). Probability of occurrence was also greatest at intermediate minimum stream channel elevations (20 000–25 000 cm) but declined as elevation increased (Fig. 4D). Stream order was treated as a factor in the analysis, and partial dependence for stream order showed the highest probability of occurrence among stream orders 5 and 6 (Fig. 4E). Probability of occurrence was highest for streams with intermediate levels of modeled runoff (900–1000 mm) but declined as runoff increased to 1200 or declined to 400 (Fig. 4F).

PDPs for the 12 next most important variables showed the probability of *E. monachus* occurrence was greatest among least disturbed streams of intermediate size (Fig. 5). Probability of occurrence was

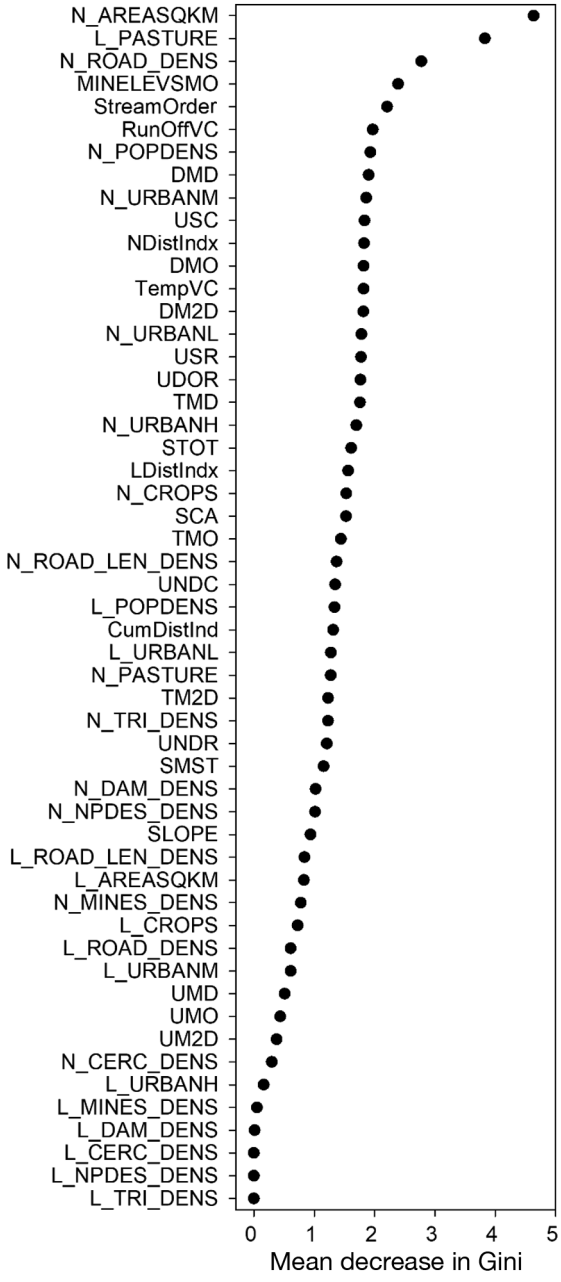

Fig. 3. Variable importance plot of the best-fitting random forest model determining *Erimonax monachus* occurrence throughout their current distribution

highest among stream segments with low human population density (<40 people km^{-2}) in the network catchment (Fig. 5A), intermediate densities (0.35–0.40 dams 100 km^{-2}) of downstream mainstem dams (Fig. 5B), intermediate percent medium-intensity urban land use (0.4–0.5%) in the network catchment (Fig. 5C), and minimum (<6 ha m^{-1} km^{-2}) upstream reservoir storage per stream network catchment area (Fig. 5D). Probability of occurrence was greatest

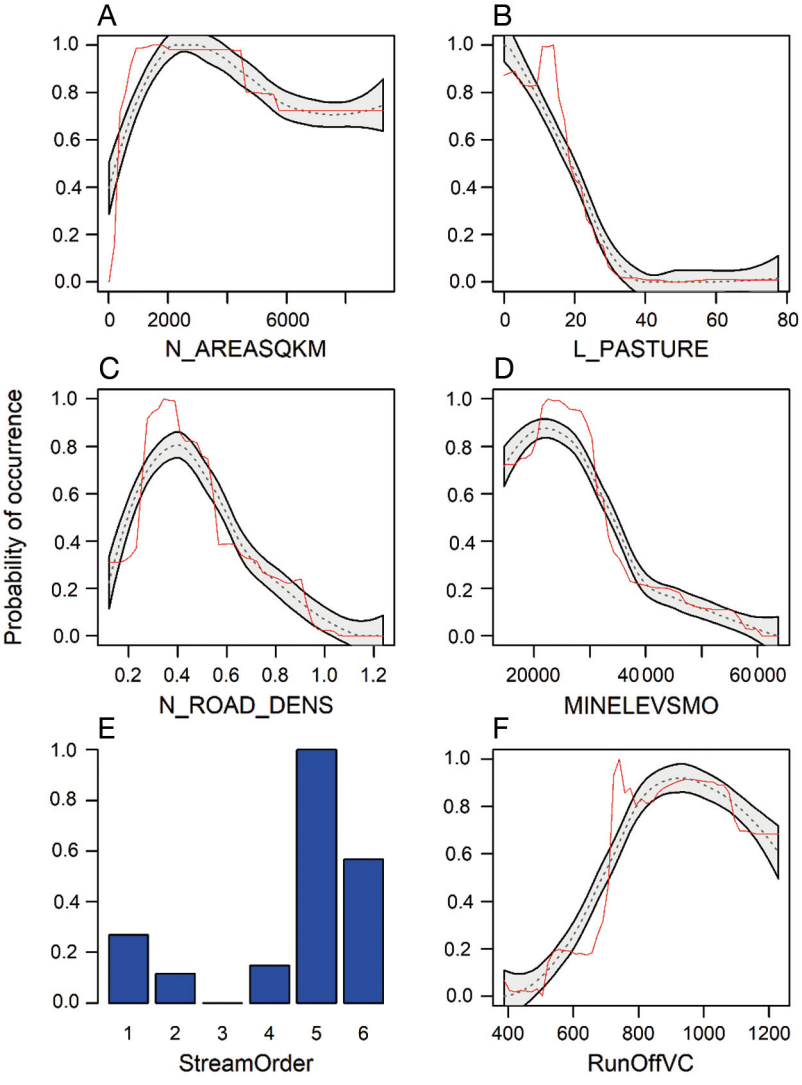

Fig. 4. Partial dependence plots (red lines), overlaid with LOWESS regression curves (black dashed lines) and 95% CIs (solid black lines, gray filled areas) of the 6 most important variables included in the ecological niche model fit to *Erimonax monachus* occurrence. See Table 1 for variable descriptions, scales, and units

among stream segments with minimal risk of habitat degradation (Fig. 5E), smaller percentages (3–4%) of downstream mainstem streams free of dams (Fig. 5F), higher (1350–1400°C × 100) annual air temperatures (Fig. 5G), and shorter distances (50–100 km) to downstream mainstem dams (Fig. 5H). Probability of occurrence was highest among stream segments with lower percentages (4–6%) of low-intensity urban land use in network catchments (Fig. 5I), minimal (<750 hectare-meters^{-1} 100 km^{-1}) total upstream reservoir storage volume per stream network length (Fig. 5J), no annual discharge stored in upstream reservoirs (Fig. 5K), and lower (0.25–0.35 dams 100 km^{-1}) total mainstem dam density (Fig. 5L).

Projections from the ENM showed strong agreement with the independent test dataset and highlighted current and potential conservation priorities for *E. monachus*. In the Emory River Basin, probability of occurrence was highest (0.75–1.00) in the lower Emory River where Russ (2006) documented occurrence of the species (Fig. 6). The ENM predicted low probability of occurrence among smaller and higher-elevation streams in the Emory River Basin, the same locations where Russ (2006) did not report occurrence of the species despite widespread search efforts. Across the Tennessee River Basin, *E. monachus* probability of occurrence was predicted to be >0.75 at locations where the species is known to persist, including portions of the Emory, Buffalo, Little Tennessee, North Fork Holston, and Middle Fork Holston rivers (Fig. 7). The ENM also highlighted areas of potential occurrence based on riverscape conditions, including limited portions of the lower Powell River and lower Whites Creek. Elsewhere in the Tennessee River Basin, the ENM predicted large areas of intermediate probabilities of occurrence (0.50–0.74) among stream segments where reintroductions have occurred, including Shoal Creek, the Tellico River, and lower Abrams Creek. The ENM did not predict probability of occurrence >0.50 for any segment in the Cheoah River, a location where the species is known to persist as the result of introductions. Predictions from the ENM showed intermediate probability of occurrence (0.50–0.74) for sections of the lower Holston and lower French Broad rivers, 2 locations permitted for reintroduction attempts.

4. DISCUSSION

The Tennessee River Basin was altered extensively after 1900, resulting in 744 known dams with >38.7 million m^3 of combined storage capacity. Much of the natural channel in the Tennessee River and its major tributaries is inundated by large reservoirs or chan-

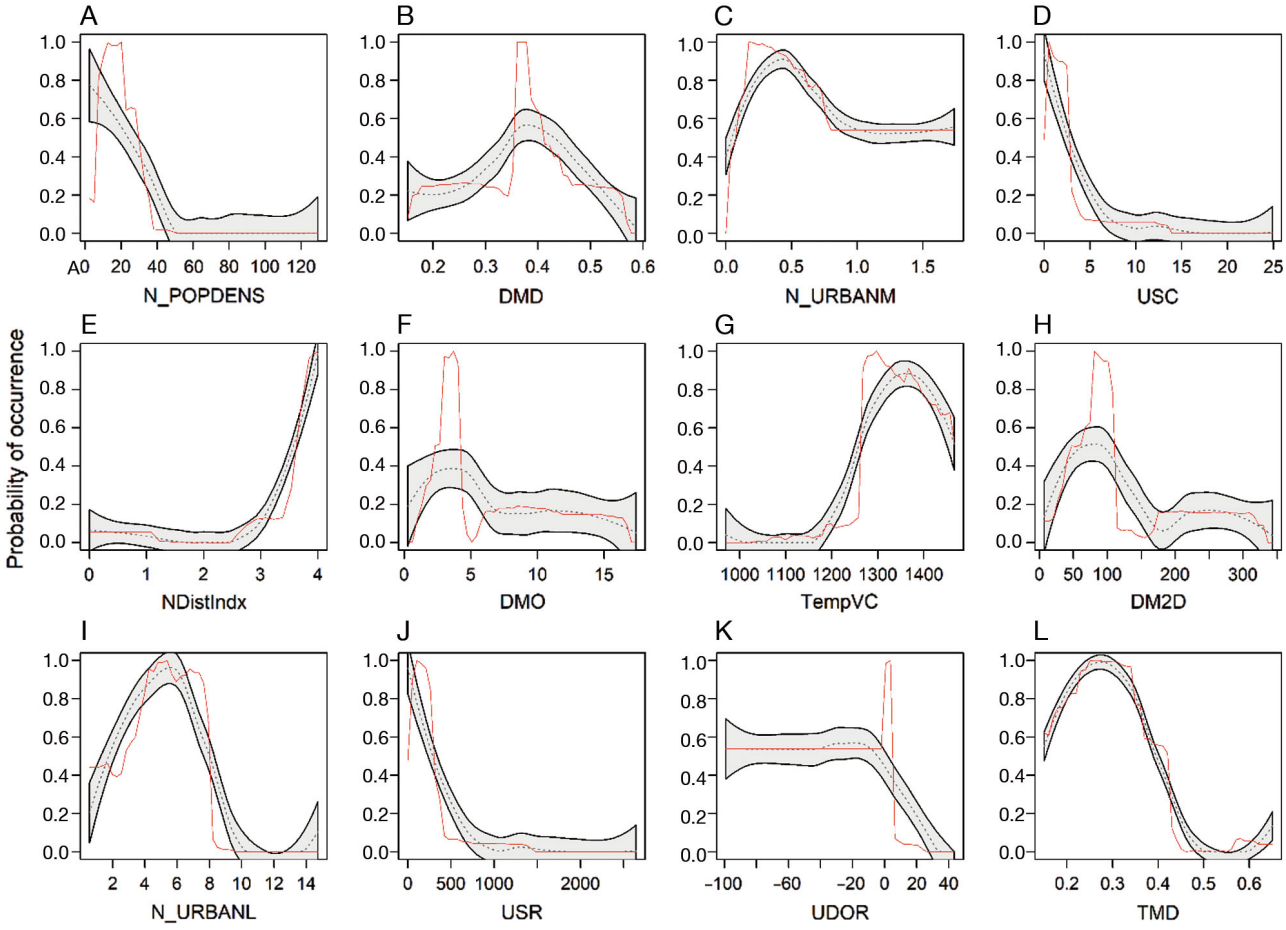

Fig. 5. Partial dependence plots (red lines), overlaid with LOWESS regression curves (black dashed lines) and 95% CIs (solid black lines, gray filled areas) of the 12 intermediate-importance variables included in the ecological niche model fit to *Erimonax monachus* occurrence. See Table 1 for variable descriptions, scales, and units

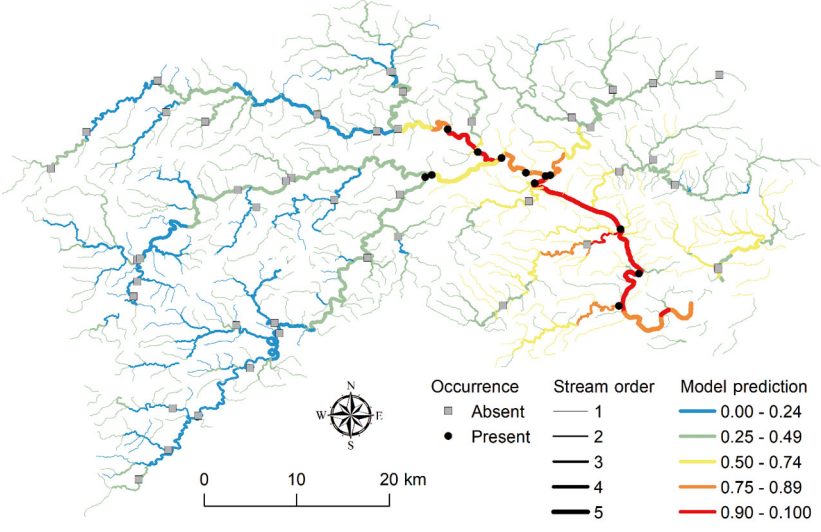

Fig. 6. Emory River basin, Tennessee, USA, illustrating validation of the ecological niche model (ENM) developed for *Erimonax monachus*. Stream lines are colored according to the probability of occurrence from the ENM and are sized according to stream order. Points from Russ (2006) show the presence (black circles) or absence (gray boxes) of *E. monachus* at 57 sampling sites

nelized, resulting in profound effects on the aquatic fauna (Neves & Angermeier 1990, Etnier & Starnes 1991, Knight et al. 2012). Many fish species have thrived because of the altered hydrography and river morphology, whereas others have been extirpated from the basin (McManamay et al. 2013). Other species that require medium-sized streams, such as *Erimonax monachus*, have persisted in localized and highly fragmented populations (Etnier 1997). We found modeled *E. monachus* occurrences were greatest in streams with network catchment drainage areas 300 to 1000 km^2, stream order 5 or 6, and elevations 1000 to 3500 cm. These remnants of medium-sized streams are isolated by reservoirs that are likely impassable by *E. monachus*, and the

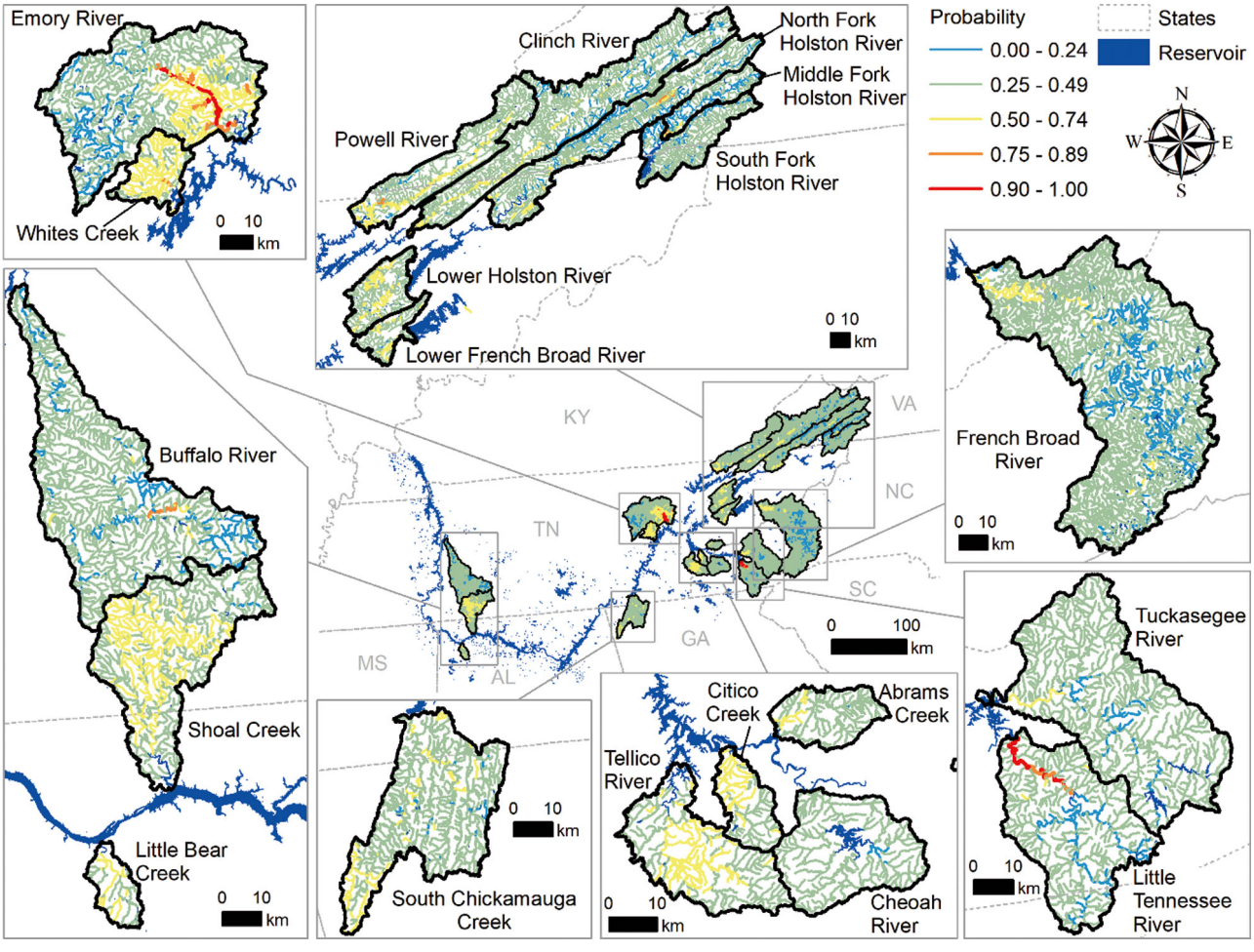

Fig. 7. Probability of *Erimonax monachus* occurrence throughout the historical distribution of the species based on landscape-level suitability identified by ecological niche modelling

species is relegated to isolated patches of habitat that are differentially affected by human alterations to landscapes (Jenkins & Burkhead 1984). Conservation of the species requires maintenance of existing occupied habitats and identifying where habitats appropriate for reintroductions might exist (USFWS 1983).

We found that stream network connectivity metrics, both natural and altered, were a strong predictor of *E. monachus* occurrence. The current distribution of the species now exists in the largest remaining streams on the margins of large reservoirs, including stream segments within 100 river km of downstream dams (DM2D < 100 km), where <4 % of downstream mainstem river habitat is free of dams (DMO < 4 %), and where the density of downstream dams is high (DMD > 0.35 dam km^{-1}). We suspect that these connectivity patterns are not reflective of *E. monachus* dependence on reservoirs but rather that habitats historically used by the species are now inundated under reservoirs and populations are relegated to the remaining large stream habitats persisting upstream of reservoirs. The entire historical distribution of the species is unknown, but the current disjunct distribution does provide anecdotal evidence of a much larger historical distribution (Etnier & Starnes 1993). Although individuals did not likely traverse the entire length of the Tennessee River within a single lifetime, it is possible that individuals moved between adjacent catchments to interbreed and maintain genetic diversity and connectivity. Such dispersal opportunities are now thwarted by large dams and impoundments, meaning that smaller and isolated populations must contend with environmental fluctuations without the benefit of metapopulation dynamics (e.g. Roberts et al. 2013). A result is the strong potential for rare disturbance events, either natural or anthropogenic, to cause localized extirpations in a manner consistent with the ecological

ratcheting hypothesis (ERH). The ERH posits that disturbances with temporal extents that exceed the generation time of affected species and result in population extirpation are reinforced by habitat fragmentation that prevents recolonization once the disturbance subsides (Perkin et al. 2015b). Fragmentation through impoundment and altered hydrologic regimes has played a role in the current distribution of *E. monachus* (Jenkins & Burkhead 1984). However, fragmented populations persisted for over 60 yr in some isolated reaches but not in other reaches with similar habitat connectivity. If historical extirpations were due to acute stressors or chronic perturbations that are now alleviated, these systems may represent potential reintroduction sites necessary to fulfill the objectives of the recovery plan (USFWS 1983). For this reason, it is critical to consider interactions among multiple forms of habitat alteration and how they might jointly influence distribution.

We found evidence that human alterations to landscapes beyond connectivity affect the distribution of *E. monachus*. Changes to land use are among the primary causes for native species loss, especially in the historically forested southeastern USA (Warren et al. 2000). Agricultural land uses in particular are problematic because they alter sediment deposition regimes and contribute to loss of habitat through siltation in streams (Allan et al. 1997, Burcher et al. 2007). Previous works at fine spatial scales documented silt substrate avoidance by *E. monachus* (Kanno et al. 2012b), and we found that broad-scale distributions were negatively influenced by the same agricultural land uses that contribute to siltation. In particular, we found that *E. monachus* occurrence was greatest among stream segments with <10% pasture land use and <0.1% cultivated crop land use in the upstream network catchment and <20% pasture land use in the upstream local catchment. Furthermore, other land use alterations that promote altered runoff and sediment regimes were influential, evident through the higher occurrence of *E. monachus* in segments with <0.60 road km^{-2} in the upstream network catchment. These anthropogenic alterations each represent composites of the habitat disturbance index developed by Esselman et al. (2011), and we found that *E. monachus* occurrence was greatest among stream habitats with low habitat disturbance in the upstream network catchment (NDistIndx > 3.75). Unfortunately, land uses such as pasture and crop that are most likely to result in degraded water and habitat quality tend to occur in lower elevations and around larger rivers, the same habitats naturally used by *E. monachus*. Evidence from previous works suggests historical land uses likely influence the contemporary distribution of *E. monachus*, though additional historical land use data are necessary to understand how (Harding et al. 1998). The inescapable influence of 'the ghosts of riverscapes past' was likely a contributor to the incongruence between predictions and observations of *E. monachus* in our model (Perkin et al. 2013, 2015b, 2019).

Furthermore, our study did not include direct measures of water quality that likely influence distribution of *E. monachus* (e.g. Hitt et al. 2016), nor did we address the encroachment of an invasive species (Ridgway & Bettoli 2017). Future research should address the influences of these parameters as broad-scale datasets become available.

Our framework is useful for conservation planning within fragmented and human-affected riverscapes. The ENM we developed highlighted known habitat hotspots for *E. monachus*, including the Emory River and the Little Tennessee River. However, our model also highlighted appropriate habitats where successful reintroductions have occurred, including Shoal Creek and the Tellico River. Three additional catchments, Whites Creek, the Tuckasegee River, and the French Broad River, were identified as having a high probability of harboring *E. monachus* if reintroductions were to occur. These systems should be surveyed for the best in-stream habitat to maximize the success of any future reintroductions (Kanno et al. 2012b). This point is particularly relevant because failed reintroductions are costly from the perspective of funds, effort, and the demise of individuals placed into insufficient habitats. For example, Gibbs (2009) showed that reintroduction of *E. monachus* into lower Abrams Creek was unsuccessful despite high-quality habitats and extensive stocking efforts (Shute et al. 2005). In our ENM, the probability of occurrence for *E. monachus* in lower Abrams Creek was 0.30 to 0.49, suggesting a low probability of successful reintroduction. Therefore, factors other than coarse-scale habitat alone influence the success of reintroductions, as recently discussed by Malone et al. (2018). Additionally, historical records from smaller catchments (<300 km^2), such as Abrams, Citico, and Little Bear creeks, may represent temporary use by the species or individuals uncharacteristically present when sampling occurred (e.g. migrants to sink habitats). As a second example, our model predicted low probability of occurrence (0.30–0.49) for *E. monachus* in the Cheoah River, a location where a reintroduced population has persisted for at least 8 yr (S. Fraley pers. comm.). Thus, we suggest that ENM is only one aspect of reintroduction planning

that should take place, a point recently made by Malone et al. (2018). Local conditions and in-stream characteristics are known to influence the occurrence of *E. monachus* but have only been extensively studied in 2 of the 5 extant populations (Kanno et al. 2012b). Our model provides some insight into other locations that might be more thoroughly investigated to assess (re)introduction potential.

Our analytical framework is applicable to other rare species, especially those with unknown or patchy historical distributions. Availability of broad-scale sampling datasets is increasing (Troia & McManamay 2017), which allows for exploratory analyses of species distributions such as those presented herein (Huang & Frimpong 2015). Knowledge of landscape-level drivers of current fish distributions can be used to identify additional sites where sampling could be targeted or reintroductions proposed. Of particular interest to natural resource managers is the incorporation of scale in conservation planning (Wellemeyer et al. 2019). We used habitat alteration metrics measured at 2 scales, local catchment and network catchment, and found landscape alterations measured at the network catchment scale correlated more strongly with *E. monachus* distribution. In these instances where network catchment scale alterations are most influential, broad-scale conservation initiatives such as NFCAs can be established. Our work supports recent calls for catchment-level management practices, including maintaining riparian buffers and restoring connectivity, to sustain suitable habitat and provide long-term population viability for rare and sensitive species (Gido et al. 2016, Wipfli & Richardson 2016).

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