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Do fishes enjoy the view? A MaxEnt assessment of fish habitat suitability within scenic rivers

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ABSTRACT

Scenic rivers programs are a potential tool to conserve freshwater habitat but few studies have attempted to characterize fish habitat within scenic rivers. Using the Virginia Scenic Rivers Program as a case study, we built species distribution models for a representative set of Virginia freshwater fishes and tested whether model-predicted habitat suitability values for scenic rivers are consistently higher than the range-wide average values. We began by selecting 33 fish species that were broadly representative of the complete functional trait space comprised by Virginia's freshwater ichthyofauna. This subset included 11 state-listed imperiled species. Next, we built maximum entropy species distribution models for each of the 33 fishes and used the models to predict habitat suitability throughout each species' range. Habitat suitability within state-listed scenic rivers was then summarized and compared with the complete, state-wide distribution of habitat suitability for each species. For 21 of 33 species, model-predicted habitat suitability was significantly higher in currently listed Virginia scenic rivers than in the state-wide distribution; of these 21 species, 5 were imperiled taxa. Furthermore, habitat suitability within scenic rivers is predicted to exceed the range-wide average by a significant margin for 25 species, including eight imperiled species, if all pending scenic listing petitions are approved. We conclude that scenic rivers provide important conservation benefits to Virginia's freshwater fishes. We also note that our flexible, model-based process can be applied in other rivers and used to inform other types of freshwater conservation programs that seek to identify and protect the highest quality habitats.

1. Introduction

Habitat degradation has long been recognized as a key threat to biological diversity (Fahrig, 2003; MEA, 2005; Newbold et al., 2015) and is a topic of particular concern in freshwater ecosystems. Effects of habitat degradation tend to be exacerbated in freshwater because freshwater biodiversity is, on a per-unit-area basis, much higher than in marine or terrestrial ecosystems (Dudgeon et al., 2006). Serial discontinuities, such as dams and impoundments, create extensive fragmentation within river landscapes (Nilsson et al., 2005). Human demand for freshwater is also increasing at a pace that often exceeds supply (Postel and Richter, 2003). This imbalance is particularly acute in regions where climate change has created more arid conditions (Palmer et al., 2008). In the worst-case scenario, habitat loss may approach 100% as a river is drawn down to zero flow (Wong et al., 2007).

Fortunately, some successful and widely implemented strategies to monitor and protect freshwater biodiversity have emerged. Regional to national-scale biological assessment programs are notable examples. These programs use fish and/or invertebrate samples to gauge the overall health of freshwater ecosystems and can be used to develop explicit regulatory criteria (Davis and Simon, 1995; Wright et al., 2000). Environmental flow programs are also good examples of concerted efforts to protect freshwater biodiversity. Environmental flows are managed flow regimes that seek to balance the needs of natural ecosystems with human uses (Arthington et al., 2006). As the database on environmental flows research has grown, so too has their application in regulatory frameworks (MacDonnell, 2009; Arthington et al., 2018).

One strategy to protect aquatic habitat that has received little

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attention in the conservation literature, but is gaining traction in the U.S., is scenic river designation. A U.S. national scenic rivers program was launched in 1968 with passage of the Wild and Scenic Rivers Act. This new conservation program sought to ensure that rivers possessing "outstandingly remarkable scenic, recreational, geologic, fish and wildlife, historic, cultural, or other similar values, shall be preserved in free-flowing condition" (IWSRCC, 2019). Three classes of rivers are now recognized under the Wild and Scenic Rivers Act: wild, scenic, and recreational. Each class entails unique listing criteria and regulatory provisions (IWSRCC, 1999), but all are rooted in the normative determination that river landscapes with strong aesthetic qualities are valuable resources and worthy of protection. As of 2019, the National Wild and Scenic Rivers System has grown from an initial population of 27 rivers to encompass >21,000 total km of river habitat, representing 209 river systems distributed throughout 41 states and the Commonwealth of Puerto Rico (IWSRCC, 2019).

State-level scenic rivers programs that mimic key components of the National System have also been established in 31 states (Palmer, 2017). For example, the Virginia Scenic Rivers Program (VSRP) and the National System both restrict activities that alter natural flow regimes within listed rivers, including the construction of hydropower and river navigation facilities (IWSRCC, 1999; Strickler et al., 2018). Another feature that is common to scenic rivers programs is the public process used to prepare and evaluate listing petitions. Because new scenic river designations may affect personal property rights and commercial activities, a dual process of public feedback and government review is essential. Robust knowledge of the benefits that scenic rivers provide may, in turn, be a key factor in maintaining or bolstering support for scenic rivers programs (Acreman et al., 2020).

Evidence of the economic benefits that scenic rivers provide was recently summarized by Bowker and Bergstrom (2017). A survey of the National Wild and Scenic Rivers System estimated that the average net economic benefit (in 2016 U.S.D.) of a listed river in the National System is \$99 visitor^{-1} day^{-1}, with a maximum benefit of \$501 visitor^{-1} day^{-1} (estimated for the Middle Fork Salmon River, Idaho). These economic benefits have been linked to specific human activities (e.g., Moore and Siderelis, 2003; Keith et al., 2008; Bowker et al., 2014), providing public support for scenic rivers programs. Unfortunately, comparable information on the benefits of scenic river listing (or of aesthetic quality in general; see Gobster et al., 2007; Tribot et al., 2018) for instream biota or ecosystem health is not readily available.

Numerous studies of aquatic biota have been conducted in U.S. scenic rivers, but without demonstrating an effect of scenic listing per se. For example, McRae and Diana (2005) documented links between instream habitat and densities of juvenile brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*) in the Au Sable River, Michigan; Heard et al. (2012) examined fishes within the Big Bend reach of the Rio Grande, Texas, associating spatial and temporal changes in fish assemblage structure with flood events; and the matrix models of Rogosch et al. (2019) predicted that climate induced changes in flow regime will favor growth of nonnative over native fishes in the Verde River, Arizona. These studies provide information on the ecology of resident biota and on management strategies to protect them. Knowledge of fish-flow relationships in the Verde River may, for instance, be useful in scheduling dam releases. However, proof that scenic river listing itself has a measurable effect on instream biota logically requires one of two lines of evidence: (i) before-and-after data demonstrating a post-listing change; or (ii) statistical contrasts showing that environmental conditions within scenic rivers are distinct from conditions within a comparable sample of rivers that are not legally recognized as scenic.

An efficient tool to prepare the later type of evidence – statistical comparisons of scenic and non-scenic rivers – is species distribution modeling. Species distribution models are built by first detecting associations between species' occurrences and local environmental conditions, then using statistical functions, such as the logistic or *s*-shaped function, to characterize those associations. Once a distribution model has been constructed for a species of interest, it can be used to predict habitat suitability or the probability of presence at every locality within a modeled landscape (Elith and Leathwick, 2009). In an assessment of scenic river benefits, a species distribution model could predict habitat suitability for every river segment within a complete river basin. Model predictions could then be used to determine whether listed rivers provide high quality habitat relative to non-listed rivers. Alternatively, model predictions could be combined for multiple species and used to identify optimal configurations of scenic river listings that would provide the highest quality habitat to the greatest number of species.

Here, we demonstrate a novel, model-based process to estimate habitat quality for native fishes throughout entire river basins, then to test for differences in habitat quality between designated scenic and non-designated rivers. As an empirical context, we focus on the VSRP. Created in 1970, the mission of the VSRP is to "identify, designate and help protect rivers and streams that possess outstanding scenic, recreational, historic and natural characteristics of statewide significance." The VSRP was ideal for our study because it is thoroughly documented (www.dcr.virginia.gov/recreational-planning/srmain), the number and extent of listed rivers (1094 river km distributed among 33 currently listed rivers, with 66 additional rivers under consideration for listing) is sufficient to perform robust comparisons with non-listed rivers, and the locations of all listed rivers are readily accessible in a digital, georeferenced format.

We begin by compiling georeferenced data on stream and river network topology, fish species occurrences, and a suite of local environmental variables (i.e., model predictors or covariates) throughout Virginia and adjacent parts of Maryland, West Virginia, and North Carolina (see 2.1 Study area). Next, we build maximum entropy (MaxEnt) species distribution models (Phillips et al., 2006; Phillips et al., 2019) for a representative subset of 33 Virginia native fishes and use the models to estimate habitat suitability throughout the study area. We then subset habitat suitability estimates within listed VSRP river segments and compare them to the complete distribution of habitat suitability throughout each species' range across the study area. This approach addresses a fundamental question: Is habitat suitability within scenic rivers consistently higher than in other parts of a given species' range? It also allows us to pose this question at two scales: for individual species and as an aggregate measure across all modeled species.

2. Material and methods

2.1. Study area

Our study focused on the three major, east-flowing river systems of Virginia: the Potomac River; the combined James, York, and Rappahannock Rivers; and the combined Roanoke and Chowan Rivers (Fig. 1A). The James/York/Rappahannock Rivers and Roanoke/Chowan Rivers were treated as combined systems because the numbers of fish occurrence records within the relatively small York, Rappahannock and Chowan Rivers were not sufficient for direct modeling comparisons with the larger Potomac, James, and Roanoke Rivers, but we did not wish to exclude these smaller rivers from this study. We included the complete spatial extent of each river system in modeling analyses, rather than truncating the Potomac and Roanoke/Chowan River basins at the Virginia state line, to ensure that the species distribution models were representative of all habitats available within a given basin. To model habitat suitability for a given species, it is first necessary to define the complete distribution of habitats that the species can potentially gain access to; failure to do so can bias the covariate response functions and outputs of species distribution models (Elith et al., 2011; Yates et al., 2018). However, it was not necessary to account for habitat in rivers to the north or south of the three study basins, even for species with much broader distributions (e.g., largemouth bass, *Micropterus salmoides*), because movement between major river basins is largely precluded by the Atlantic Ocean. In effect, we treated each of the resident fish species

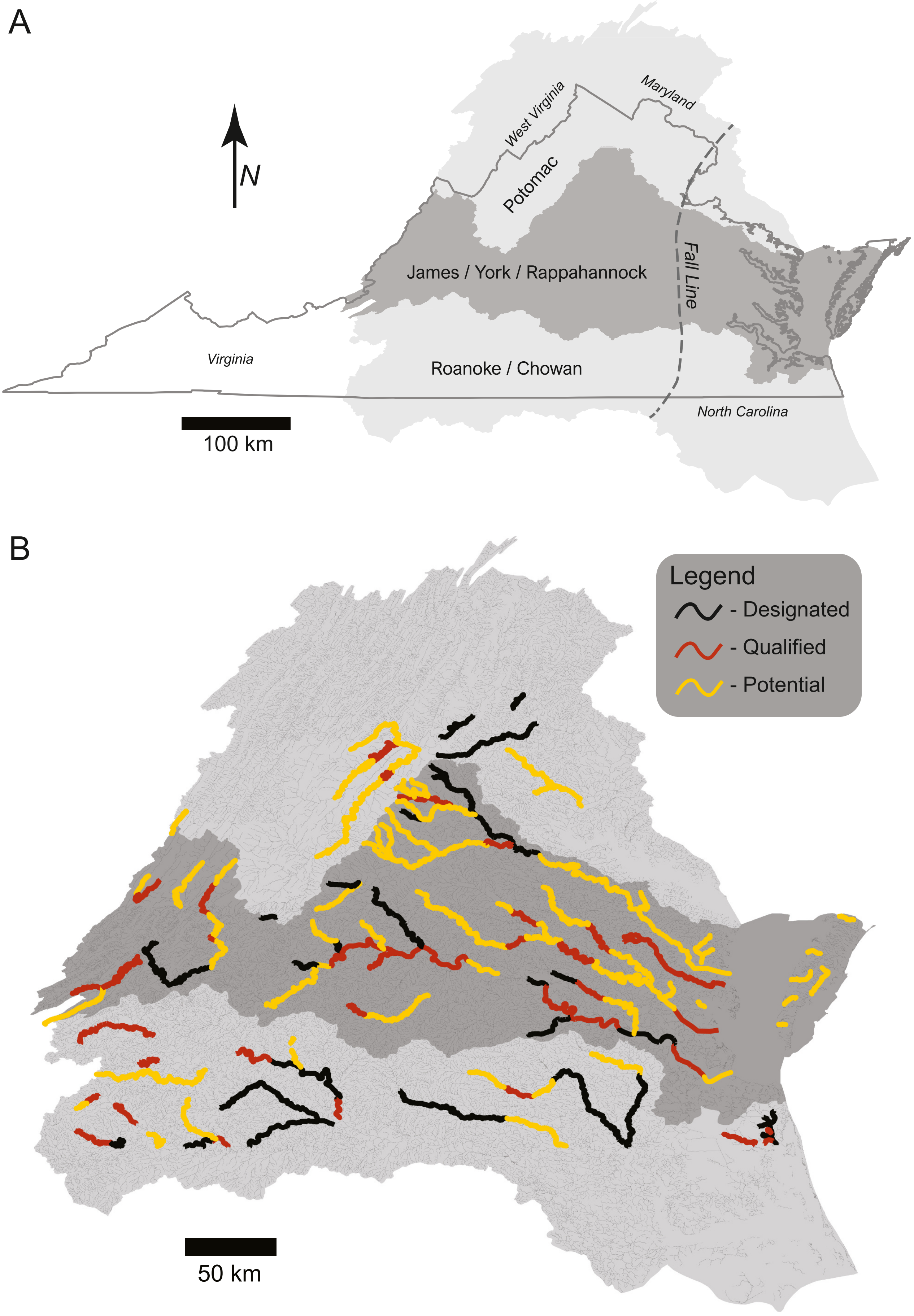

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Fig. 1. Maps of the east-flowing, Atlantic Slope rivers included in this study. (A) Three major river systems are recognized: the Potomac River; the combined James, York, and Rappahannock Rivers; and the combined Roanoke and Chowan Rivers. The Fall Line is also shown, separating the Coastal Plain from the Piedmont and Appalachian ranges. (B) Closeup of the complete 1:000,000 scale NHDplusV2 river network, superimposed on the boundaries of the three major river systems. Stream and river segments that are currently included in the VSRP (Designated), selected but awaiting approval by the Virginia State Legislature (Qualified), or recommended and awaiting further evaluation (Potential) are shown as black, red, and yellow segments, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

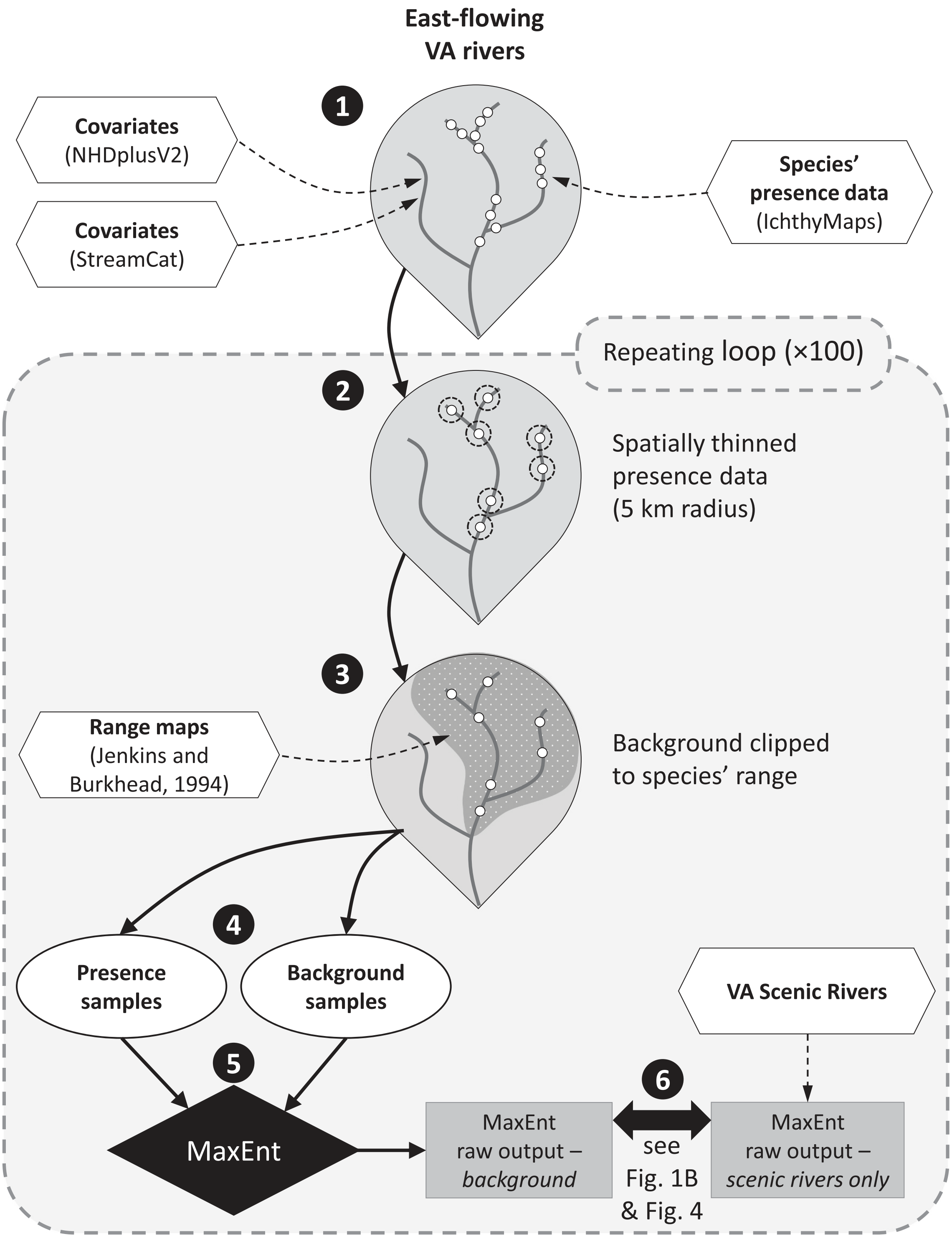

Fig. 2. Diagram of the workflow used to model habitat suitability for each of the 33 representative fish species. Workflow steps include: (1) superimposing environmental data from the NHDplusV2 attribute tables and the StreamCat database, as well as IchthyMaps fish presence records, on the NHDplusV2 digital river network; (2) thinning species' presence records to minimize spatial sampling bias; (3) clipping the background for each species to its known primary range; (4) creating a random background sample, then importing the thinned species' presence records and covariate data into MaxEnt; (5) building MaxEnt models of habitat suitability; and (6) comparing predicted habitat suitability at scenic river sites with habitat suitability throughout the entire background. Steps 2–6 are contained within a loop; 100 iterations were performed for each species to ensure the modeling results were robust to the random subsampling procedures used in steps 2 and 4.

within the three major river basins as an ecologically and evolutionarily distinct unit that did not have access to other river basins. Following this logic, we excluded rivers in the southwest corner of Virginia (the New, Holston, Clinch, and Powell Rivers), each of which flows west and is part of the larger Ohio or Tennessee River. Including them in our analyses would have required the addition of a large volume of fish occurrence and covariate data from beyond the state of Virginia.

2.2. River network and environmental covariate data

We used the 1:100,000 scale, Version 2 National Hydrography Dataset Plus (NHDplusV2; McKay et al., 2015) to represent streams and rivers (all flowing waters, ranging from small streams to large rivers, are hereafter referenced as rivers) throughout the three river systems, including each of the rivers currently (as of November 2019) featured in the VSRP (Fig. 1B). All environmental covariates and fish presence records were spatially cross-referenced to the river network with the unique identifier, or COMID, assigned to each of the NHDplusV2 river segments (step 1 in Fig. 2). In the fish habitat models, the individual, linear river segments were treated as independent spatial units, analogous to the use of individual cells in grid-based models.

Environmental covariates were obtained from the NHDplusV2 attribute tables (McKay et al., 2015) and the Stream-Catchment dataset (StreamCat; Hill et al., 2016). StreamCat is a collection of >500 environmental variables that have been spatially cross-referenced to the NHDplusV2 river network using the unique COMID values. From the NHDplusV2 attribute tables and StreamCat, 50 variables were selected for use as potential covariates in fish habitat models. They included a mix of channel morphology, hydrology, geology, agricultural activity, land use, anthropogenic disturbance, and climate variables that are known to influence fish habitat and assemblage structure (e.g., Richards et al., 1996; Angermeier and Winston, 1999; Allan, 2004; Torgersen et al., 2006; McGarvey et al., 2018) and should therefore be important to freshwater fishes. Strongly skewed variables were natural log (ln) transformed to increase normality. All 50 covariates are listed and defined in Appendix A.

2.3. Representative fish data

Fish occurrence records were downloaded from the IchthyMaps database (Frimpong et al., 2016). IchthyMaps is a compilation of historical (1950–1990 collection dates) fish samples, cross-referenced to discrete river reaches within the NHDplusV2 network by COMID (Fig. 2, step 1). We queried all IchthyMaps fish occurrences within the three study river systems, resulting in a master list of 32,879 individual presence records distributed among 202 species. IchthyMaps records were compiled from multiple sources, without systematic information on original field sampling effort (Frimpong et al., 2016), and were therefore treated as presence-only records in this study.

From the list of 202 fishes within the three rivers, we sought to identify a subset that was broadly representative of the collective ichthyofauna of the three river systems (Fig. 1A). To do so, we focused on two specific criteria: functional trait diversity and imperilment status. In this way, we were able to simultaneously address the *coarse* filter and *fine* filter conservation goals of the Virginia Department of Conservation and Recreation (hereafter Department) (Wilson and Tuberville, 2003). Including a broad range of functional traits ensured that much of the ecological diversity represented by the Virginia freshwater ichthyofauna would be represented in our study, consistent with a coarse filter conservation strategy. By contrast, including a select group of imperiled species allowed us to focus directly on their individual needs, consistent with a fine filter conservation strategy.

We began by compiling data on 13 functional traits from primary and secondary literature sources. These traits included measures of species' body size, longevity, feeding behavior, physical habitat use, water column position, egg deposition strategy, parental care, spawning season, and migratory behavior (see Woods and McGarvey, 2018). Our functional traits analysis was similar to the process of Angermeier (1995) but featured a slightly expanded list of traits and did not focus exclusively on imperiled species' traits. From the list of 202 species present within the study system, complete or nearly complete trait records were obtained for 179 species. Second, trait data were combined and coded (dummy coding used for categorical variables) in a species × trait matrix. From the species × trait matrix, which included continuous, integer, and categorical variables, Gower dissimilarities (Gower, 1971) were calculated among all species pairs. Third, principal coordinates analysis was used to build two-dimensional ordinations of functional trait space for the 179 fish species. We retained the first three principal coordinate axes, representing gradients in body size and fecundity, reproductive behavior and parental care, and instream physical habitat, respectively (Fig. 3). The FD package in R (Laliberté et al., 2014) was used to calculate Gower dissimilarities and perform functional trait analyses. A subset of imperiled fishes was queried from the designated list of Species of Greatest Conservation Need (SGCN) in the Virginia Wildlife Action Plan (VDGIF, 2015). Finally, we used the functional trait ordination plots to identify subsets of species that collectively spanned the breadth of the first three principal coordinate axes, while representing non-SGCN and SGCN species in a 3:1 ratio. This process resulted in a final list of 33 fishes, including 11 SGCN taxa (Table 1).

2.4. Modeling fish habitat suitability

For each of the 33 representative fish species, habitat modeling was performed within a 5-step loop: (i) perform spatial thinning of the species' presence records (Fig. 2, step 2); (ii) delineate the species' range within the three river systems (Fig. 2, step 3) and use all river segments within the range as the MaxEnt *background* (Fig. 2, step 4; see next section for background definition); (iii) test different combinations of model covariates to determine which are the most effective predictors of the species' presence (Fig. 2, step 5); and (iv) use the final model to predict habitat suitability for every river segment within the complete background (Fig. 2, step 6). Each step is described in detail below. The loop was repeated ×100 for each species to ensure that the modeling results were not sensitive to the outcome of a single iteration of the spatial thinning or background sampling process (see below). Final habitat suitability predictions were then calculated for each species as the mean averages among the 100 looping iterations, hereafter referred to as *ensemble* predictions.

2.4.1. Preparation of species presence and background data

Spatial clustering of the original sample locations (i.e., multiple occurrence points in relatively close spatial proximity) was observed for many species (see original species' distribution maps in Jenkins and Burkhead, 1994). Spatial thinning of the species' presence records was therefore used to minimize sampling bias prior to building fish habitat models (Merow et al., 2013; Kiedrzyński et al., 2017). For each of the 33 representative fish species, a 5 km radial buffer was plotted around the centroid of every presence location. Presence records were then thinned by locating spatially proximal records with intersecting buffers and randomly removing neighbors until none of the remaining buffers overlapped (Fig. 2, step 2). The buffer radius was chosen to minimize the possibility that proximal records could represent a single individual that was sampled on separate occasions. A 5 km buffer was deemed sufficient because longitudinal movements by stream and river fishes are generally limited to distances <5 km (e.g., Gerking, 1959; Rodríguez, 2002; Breen et al., 2009). Spatial thinning was conducted with the spThin package in R (Aiello-Lammens et al., 2015).

An appropriate background was then specified for each fish species. In a MaxEnt model, the background is the collection of habitat units (individual river segments in this context) that a species can potentially occur at; it serves as a null distribution to assess the influence of model covariates at sites of known presence, relative to all available sites or

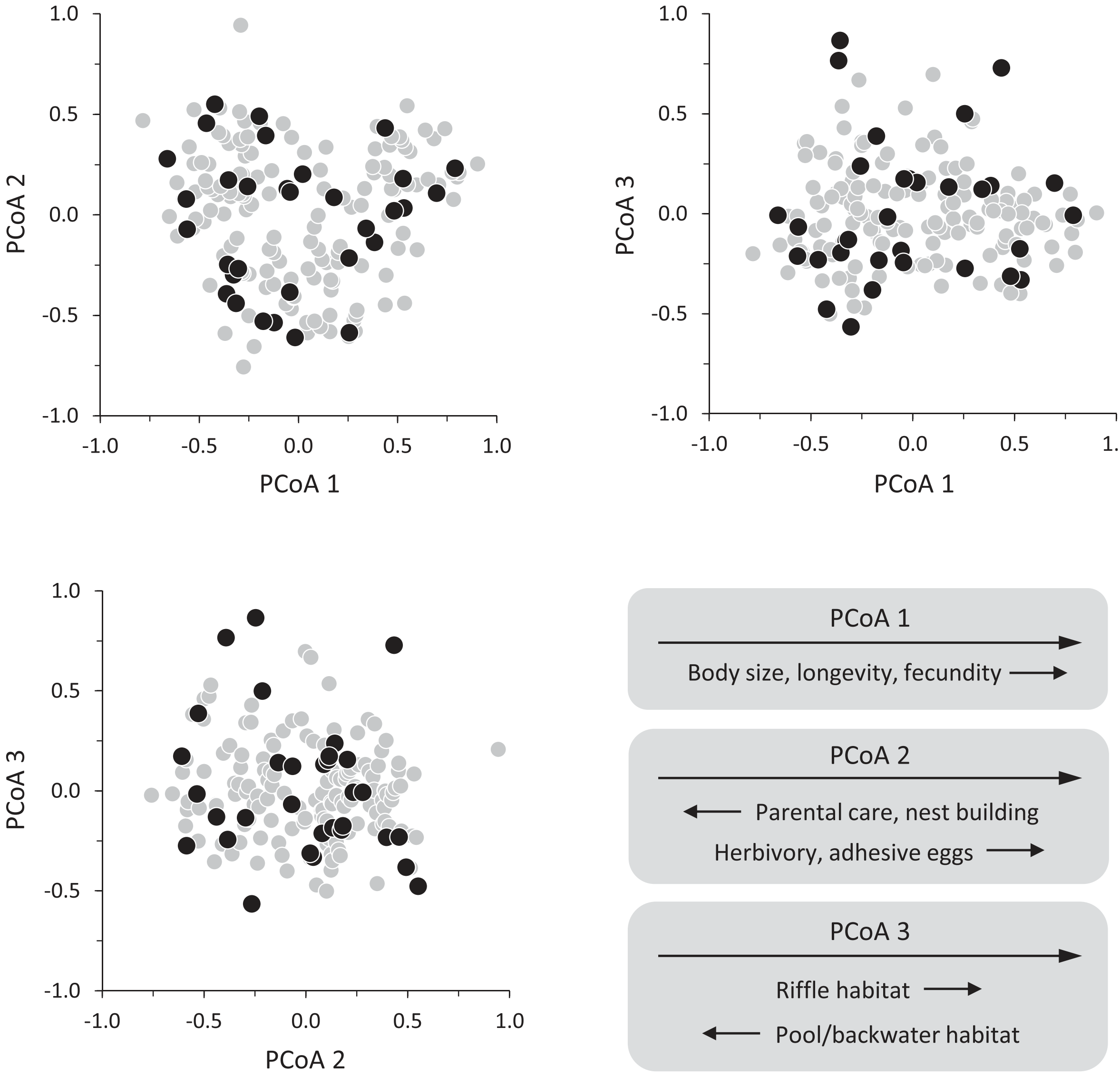

Fig. 3. Ordination biplots showing the first three principal coordinate (PCoA) axes from the fish functional trait analysis. Each point represents one of the 179 fish species included in the functional trait analysis. The 33 species modeled in this study are shown as black points and the remaining species are shown as grey points. Associations between key functional traits and each of the three PCoA axes are shown at lower right, with the direction of the association (positive or negative, relative to the axis direction) illustrated by left- or right-facing arrows. Notably, the black points encompass most of the two-dimensional space shown in each biplot. Hence, the 33 selected species are broadly representative of the complete functional trait space for Virginia freshwater fishes.

habitats (Elith et al., 2011). Over- or under-estimating the extent of the background can misrepresent the range of local environmental conditions that are accessible to a species, thereby creating model bias (Phillips et al., 2009; Yates et al., 2018). We used species' historical range maps from Jenkins and Burkhead (1994) to delineate the range of each of the 33 fish species within the three river systems. Specifically, we determined whether a given species occurred in each of the three major river systems and whether it was constrained to rivers above or below the Fall Line, where the low-gradient Coastal Plain meets the upland Piedmont (Fig. 1A). NHDplusV2 river segments within the range were then used as the species' background (Fig. 2, step 3).

2.4.2. *Building MaxEnt habitat suitability models*

MaxEnt was chosen for this study because it can accommodate variable numbers of species presence records and has outperformed other presence-only modeling algorithms in direct comparisons (Hernandez et al., 2006; Aguirre-Gutiérrez et al., 2013). For each of the 33 modeled species, we randomly sampled 20% of the background river segments, rather than using the MaxEnt default background sample size of 10,000 units. This was prudent because the total background sizes were highly variable among species, ranging from 13,506 to 67,781 river segments. Next, the background samples were combined with the spatially thinned presence records (Fig. 2, step 4) and an iterative process of comparing models that included different combinations of covariates was used to refine the MaxEnt model for each species (Fig. 2, step 5). Multiple combinations of covariates were evaluated using MaxEnt permutation importance tables (Searcy and Shaffer, 2016) and jackknife plots to identify effective predictors of species' presence. Pearson correlation (r) matrices were also used to identify and remove highly correlated covariates; $|r| > 0.70$ was used as a threshold to screen collinear predictors (Brun et al., 2020).

All habitat suitability models were created with the MaxEnt Java software version 3.4.4 (Phillips et al., 2019) and all data were prepared in *species with data* format (i.e., tabular rather than grid data). MaxEnt models were limited to relatively simple hinge features to avoid model overfitting (Elith et al., 2011). The default regularization setting was

Table 1

MaxEnt model summaries for the 33 modeled fish species. Species are group by families, listed in phylogenetic order. State-listed 'Species of Greatest Conservation Need' are indicated by asterisks (*). Sample sizes (N) are shown for the complete set of Ichthymaps records within the three study river basins and for the mean number of samples (in parentheses) remaining after spatial thinning. Range values reflect species' distributions within combinations of the three study rivers ('P' = Potomac River; 'JYR' = James/York/Rappahannock Rivers; 'RC' = Roanoke/Chowan Rivers; or 'All'), with longitudinal distributions shown in parentheses ('Above' = above the Fall Line; 'Below' = below the Fall Line; or 'All'). Model covariates are the final covariates used in each species' model (covariate labels are defined in Appendix A). Mean regularized training gain ('RTG' column) and mean MaxEnt area under the curve ('$\text{AUC}_{\text{pseudo}}$' column) values from the 100 model testing iterations are shown with standard deviations (±1 s.d., in parentheses) for each species.

Family	Species	N	Range	Model covariates	RTG	$\text{AUC}_{\text{pseudo}}$
Lepisosteidae	*Lepisosteus osseus*	59 (47)	JYR + RC (Below)	OmCat + Slope + PopDen2010Cat + Tmax8110Cat + FertCat + PctAg2006Slp10Cat + RunoffCat + StreamOrder + KffactCat + PctImp2001Cat	0.999 (0.147)	0.886 (0.018)
Anguillidae	*Anguilla rostrata**	576 (298)	All (All)	MSST_2008 + PctCrop2001Cat + ArbolateSum + PctImp2001Cat + PctMxFst2001Cat + PctWdWet2001Cat + OmCat + Fe2O3Cat + NH4_2008Cat	0.615 (0.047)	0.813 (0.011)
Clupeidae	*Dorosoma cepedianum*	66 (52)	JYR + RC (All)	Slope + ArbolateSum + CaOCat + ElevCat + PctMxFst2001Cat + OmCat + PctConif2001Cat + Pestic97Cat + Na2OCat	1.241 (0.059)	0.923 (0.006)
Cyprinidae	*Luxilus albeolus*	213 (92)	RC (Above)	ArbolateSum + RunoffCat + PctUrban2001Cat + K2OCat + PctMxFst2001Cat + Tmean8110Cat + OmCat + NO3_2008Cat + PermCat + PctHay2001Cat	0.486 (0.040)	0.813 (0.009)
	Lythrurus ardens	409 (172)	JYR + RC (Above)	ArbolateSum + PctGrs2001Cat + PctMxFst2001Cat + PctConif2001Cat + Tmax8110Cat + InorgNWetDep_2008Cat + PctImp2001Cat + PctAg2006Slp10Cat + OmCat + Precip8110Cat	0.560 (0.034)	0.815 (0.007)
	*Margariscus margarita**	40 (26)	P (Above)	CaOCat + PctHay2001Cat + PctConif2001Cat + PctCrop2001Cat + WtDepCat + Slope + RunoffCat + Tmax8110Cat + RckDepCat	1.400 (0.098)	0.942 (0.008)
	Nocomis leptocephalus	1022 (295)	JYR + RC (Above)	ArbolateSum + PctMxFst2001Cat + PctConif2001Cat + PctDecid2001Cat + PctImp2001Cat + SCat + PctWdWet2001Cat + PctAg2006Slp10Cat + PctCrop2001Cat + PctHay2001Cat	0.440 (0.031)	0.777 (0.009)
	Nocomis raneyi	170 (85)	JYR + RC (Above)	NO3_2008Cat + SandCat + Tmax8110Cat + PctConif2001Cat + ArbolateSum + PctMxFst2001Cat + BFICat + RunoffCat + PctGrs2001Cat	0.802 (0.057)	0.871 (0.007)
	*Notropis altipinnis**	93 (47)	RC (Above)	BFICat + PctCrop2001Cat + MSST_2008 + RunoffCat + PctWdWet2001Cat + PctConif2001Cat + PctUrban2001Cat + StreamOrder + PctMxFst2001Cat + SandCat	1.302 (0.087)	0.924 (0.007)
	Notropis amoenus	314 (182)	All (All)	ArbolateSum + MSST_2008 + PctImp2001Cat + BFICat + PctDecid2001Cat + WtDepCat + PctCrop2001Cat + HydrlCondCat + RunoffCat + PctWdWet2001Cat	0.726 (0.036)	0.839 (0.006)
	*Notropis chalybaeus**	42 (30)	JYR + RC (Below)	PctMxFst2001Cat + ArbolateSum + WtDepCat + PctConif2001Cat + Fe2O3Cat + OmCat + PctImp2001Cat + Slope + PctDecid2001Cat + CBNFCat	1.443 (0.153)	0.951 (0.008)
	Notropis hudsonius	368 (210)	All (All)	ArbolateSum + PctImp2001Cat + MWST_2008 + Fe2O3Cat + PctAg2006Slp10Cat + PctConif2001Cat + ManureCat + KffactCat	0.592 (0.048)	0.802 (0.013)
	Pimephales notatus	335 (155)	P + JYR (Above)	ArbolateSum + Tmax8110Cat + WtDepCat + PctUrban2001Cat + PctConif2001Cat + PctDecid2001Cat + PctAg2006Slp10Cat + PctMxFst2001Cat + OmCat + HydrlCondCat	0.727 (0.045)	0.844 (0.008)
Catostomidae	*Erimyzon sucetta**	51 (31)	RC (Below)	KffactCat + PctConif2001Cat + ManureCat + PctUrban2001Cat + StreamOrder + NH4_2008Cat + Slope + OmCat + FertCat + K2OCat	1.714 (0.078)	0.974 (0.004)
	*Hypentelium roanokense**	304 (78)	RC (Above)	PctAg2006Slp10Cat + BFICat + ArbolateSum + PctUrban2001Cat + ElevCat + HydrlCondCat + PctGrs2001Cat + PctDecid2001Cat + Slope + Al2O3Cat	0.709 (0.064)	0.860 (0.011)
	*Moxostoma collapsum**	94 (57)	RC (Above)	ArbolateSum + RckDepCat + PctWdWet2001Cat + RunoffCat + RdDensCat + Pestic97Cat + SCat + PctCrop2001Cat + Slope + WtDepCat	0.842 (0.084)	0.870 (0.012)
	Moxostoma erythrurum	191 (96)	All (Above)	ArbolateSum + PctAg2006Slp10Cat + PctHay2001Cat + HydrlCondCat + Precip8110Cat + Al2O3Cat + RckDepCat + ElevCat + ClayCat + PctGrs2001Cat	0.746 (0.061)	0.853 (0.009)
	Thoburnia rhothoeca	481 (126)	JYR + RC (Above)	Tmean8110Cat + ArbolateSum + PctMxFst2001Cat + FertCat + RckDepCat + PctConif2001Cat + ManureCat + RunoffCat + PctAg2006Slp10Cat + PctCrop2001Cat	0.906 (0.040)	0.872 (0.007)
Ictaluridae	*Ameiurus nebulosus*	219 (163)	All (All)	MSST_2008 + ArbolateSum + PctImp2001Cat + Precip8110Cat + PctHay2001Cat + WtDepCat + PopDen2010Cat + CBNFCat + NO3_2008Cat	0.666 (0.024)	0.831 (0.004)
	*Noturus gyrinus**	152 (93)	All (Below)	MSST_2008 + Al2O3Cat + PctGrs2001Cat + FertCat + KffactCat + PctWdWet2001Cat + PctImp2001Cat	0.941 (0.066)	0.873 (0.008)
Esocidae	*Esox niger*	401 (214)	JYR + RC (All)	PctCrop2001Cat + WtDepCat + ArbolateSum + MSST_2008 + PctGrs2001Cat + PctHay2001Cat + PctWdWet2001Cat + PctConif2001Cat + PctAg2006Slp10Cat + KffactCat	0.501 (0.025)	0.788 (0.006)
Salmonidae	*Salvelinus fontinalis**	240 (97)	All (Above)	Tmax8110Cat + ArbolateSum + PctConif2001Cat + ElevCat + PctWdWet2001Cat + CaOCat + PctMxFst2001Cat + HUDen2010Cat + MWST_2008	1.480 (0.057)	0.927 (0.005)
Aphredoderidae	*Aphredoderus sayanus*	292 (147)	JYR + RC (All)	ElevCat + NH4_2008Cat + PctWdWet2001Cat + ArbolateSum + RckDepCat + PctGrs2001Cat + PctUrban2001Cat + PctCrop2001Cat + PctConif2001Cat	0.774 (0.034)	0.857 (0.005)
Cottidae	*Cottus caeruleomentum*	487 (161)	All (Above)	Tmax8110Cat + ArbolateSum + PctWdWet2001Cat + PctDecid2001Cat + Slope + HydrlCondCat + PctUrban2001Cat + PctConif2001Cat + BFICat + PctMxFst2001Cat	1.225 (0.055)	0.904 (0.006)
	Cottus girardi	150 (82)	P (Above)	Slope + ArbolateSum + PctMxFst2001Cat + CaOCat + ElevCat + RckDepCat + SCat + PctCrop2001Cat	0.717 (0.047)	0.852 (0.008)
Centrarchidae	*Acantharchus pomotis**	156 (93)	JYR + RC (Below)	BFICat + PctUrban2001Cat + PctHay2001Cat + ArbolateSum + PctConif2001Cat + CaOCat + CBNFCat + Tmin8110Cat + Pestic97Cat + SN_2008Cat	0.884 (0.057)	0.885 (0.008)
	Enneacanthus gloriosus	205 (108)	JYR + RC (Below)	ArbolateSum + PctCrop2001Cat + PctWdWet2001Cat + PctDecid2001Cat + KffactCat + CaOCat + PctUrban2001Cat + PctAg2006Slp10Cat + ClayCat + PctHay2001Cat	0.605 (0.047)	0.829 (0.010)
	Lepomis auritus	614 (330)	All (All)	ArbolateSum + MSST_2008 + NO3_2008Cat + PctUrban2001Cat + PctCrop2001Cat + PctConif2001Cat + KffactCat + PctAg2006Slp10Cat	0.725 (0.030)	0.830 (0.005)
	Micropterus salmoides	413 (255)	All (All)	ArbolateSum + MSST_2008 + PctConif2001Cat + PctImp2001Cat + PctCrop2001Cat + NH4_2008Cat + KffactCat + PctGrs2001Cat	0.593 (0.029)	0.810 (0.006)
Percidae			RC (Below)			

(*continued on next page*)

Table 1 (*continued*)

Family	Species	N	Range	Model covariates	RTG	AUC$_{pseudo}$
	Etheostoma fusiforme	123 (60)		MSST_2008 + PctConif2001Cat + PctGrs2001Cat + PctImp2001Cat + Al2O3Cat + RckDepCat + PctCrop2001Cat + ElevCat + PctDecid2001Cat + HUDen2010Cat	0.786 (0.060)	0.872 (0.012)
	Etheostoma olmstedi	490 (239)	All (All)	NH4_2008Cat + PctUrban2001Cat + MSST_2008 + PctCrop2001Cat + ArbolateSum + PctWdWet2001Cat + NO3_2008Cat + PctDecid2001Cat + PctConif2001Cat	0.690 (0.028)	0.840 (0.005)
	Etheostoma vitreum	341 (160)	JYR + RC (All)	StreamOrder + PctAg2006Slp10Cat + PctGrs2001Cat + RunoffCat + NH4_2008Cat + PctConif2001Cat + ManureCat	0.713 (0.041)	0.830 (0.007)
	*Percina rex**	54 (26)	RC (Above)	StreamOrder + InorgNWetDep_2008Cat + RunoffCat + PctConif2001Cat + PctCrop2001Cat + PctImp2001Cat + MWST_2008 + Na2OCat + BFICat + PctMxFst2001Cat	1.366 (0.132)	0.950 (0.007)

used in all model runs while the maximum numbers of background points and model iterations were arbitrarily increased to 50,000 and 5000, respectively, to accommodate the large size of the background (67,781 total river segments). Importantly, the MaxEnt raw output was used for all models, rather than cumulative, logistic, or cloglog output. Raw output was ideal because it provides a direct measure of habitat suitability without invoking assumptions regarding species' prevalence or detection probability (Elith et al., 2011; Merow et al., 2013). Once completed, the final models were used to predict habitat suitability as the MaxEnt raw output (i.e., ensemble average of the 100 looping iterations) at every river segment within a species' range. All MaxEnt raw output values were ln-transformed to reduce the strong right-skew (for the 33 modeled fishes, mean skewness = +6.768; mean kurtosis = +175.674) and to rescale the very small values (overall range = $2.710e^{-9}$–$2.262e^{-2}$) that are typical of MaxEnt raw output.

Two metrics of model performance were used to assess the habitat suitability models: the MaxEnt regularized training gain (RTG) and the MaxEnt area under the curve (AUC) statistic. RTG measures the distance between a multivariate distribution of model covariates sampled randomly from the background and a second distribution from sites of known species' presence (Elith et al., 2011). Larger RTG values reflect increasingly specialized or narrow habitat requirements, relative to the background. Base-*e* exponentiation of the RTG also provides an intuitive (relative to unitless RTG values) odds ratio comparing habitat suitability at known presence sites with a random sample of background sites. The MaxEnt AUC was calculated for all model training and model validation results from the ensemble results, then used to evaluate discriminatory capability for each of the final models. We hereafter refer to the MaxEnt AUC statistic as AUC$_{pseudo}$ because MaxEnt compares known presence sites with random background sites, rather than known absence sites. Large AUC$_{pseudo}$ values therefore indicate that predicted habitat suitability is consistently higher at presence sites than at random background sites (Merow et al., 2013).

2.5. *Scenic rivers assessment*

VSRP river segments were downloaded as a shapefile from the Department (www.dcr.virginia.gov/recreational-planning/vop-gis-data). The scenic rivers shapefile was aligned with the NHDplusV2 river network and used to query river segments that are currently (as of November 2019) recognized by VSRP. Three classes of rivers are included in the VSRP data. *Designated* segments have previously been reviewed and authorized by the Virginia General Assembly (State Legislature) for inclusion in the VSRP. *Qualified* segments have been evaluated by Department staff and recommended for VSRP listing by local stakeholders but have not been approved by the General Assembly. *Potential* segments have been nominated for listing and undergone preliminary review but are awaiting further consideration by Department staff, local stakeholders and the General Assembly. Together, these three classes of VSRP segments create a nested or cumulative sequence in the number and spatial extent of VSRP rivers: currently Designated segments are the least extensive, combined Designated + Qualified segments are more extensive, and combined Designated + Qualified + Potential segments are the most extensive (Fig. 1B). This cumulative sequence was used to address "what if" questions regarding the potential benefits of adding new river segments to the VSRP, for individual species as well as for species combinations. Note that unlike the three classes of rivers within the National Wild and Scenic Rivers System (see Section 1. Introduction), the three classes of VSRP river segments do not entail different listing standards or regulatory requirements; they refer only to rivers at different stages of the state listing and approval process.

Fish habitat suitability (ln MaxEnt raw output) within VSRP streams and rivers was then assessed with two methods (Fig. 2, step 6). First, for each of the 33 fish species, kernel densities were used to estimate probability density functions for the complete background and for each of the three cumulative classes of VSRP segments (Designated-only, Designated + Qualified, and Designated + Qualified + Potential). Density functions for the three cumulative VARSP classes were plotted and superimposed on the background density function for each species. Then the areas of overlap between the background and the three classes

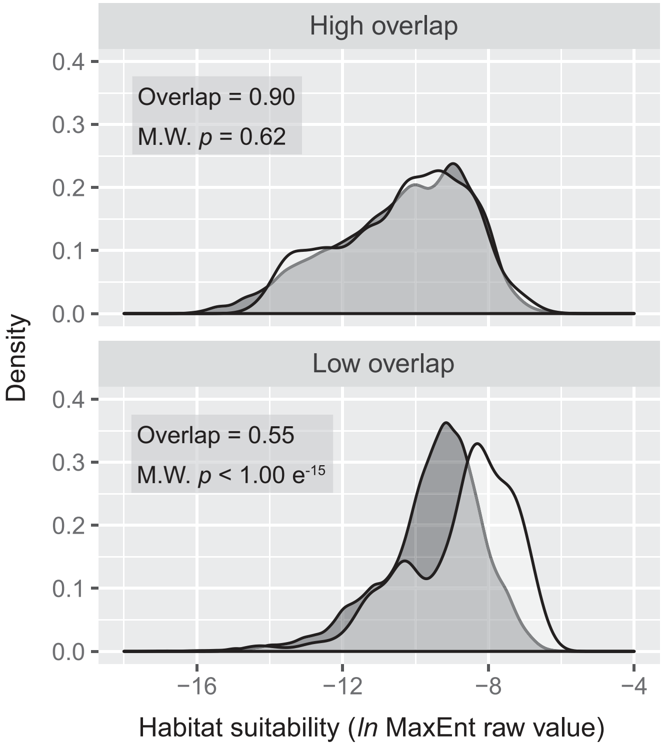

Fig. 4. Kernel density plots demonstrating overlap between river segments within the VSRP and throughout a hypothetical species' range (i.e., complete background). High and low levels of overlap are illustrated in the upper and lower panels, respectively. In each plot, MaxEnt predicted habitat suitability is shown on the *x*-axis, the background distribution is shown in dark grey, and the Scenic distribution is shown in light grey. Inset values show the area of overlap between VSRP and background distributions, as well as *p*-values from 2-sided Mann-Whitney *U* tests.

of VSRP segments were calculated. Overlap values ranged from 0 to 1, with larger values reflecting more extensive overlap among density functions. Examples of density plots with high and low levels of overlap are shown for two hypothetical species in Fig. 4. We interpreted a high degree of overlap as evidence that the VSRP segments, which were subset from the complete background, do not collectively represent more suitable habitats than the complete population of background segments. Alternatively, a low degree of overlap was interpreted as evidence that VSRP segments tend to selectively incorporate the most (or least) suitable habitats within a species' background.

Second, Mann-Whitney *U* tests were used to compare ranked habitat suitability (ln MaxEnt raw output) between the background and the three cumulative classes of VSRP segments. Specifically, we tested the null hypothesis that VSRP segments are, on average, neither more nor less suitable habitats than the background segments. Because we did not a priori assume that average habitat suitability would be higher or lower in the VSRP segments, we used 2-sided tests.

Finally, we used ordinary least squares regression to assess whether certain functional trait expressions were more or less likely to be represented within the scenic rivers. Regression models were built comparing species' functional traits, as represented by the first three principal coordinate axes from the functional trait analysis, against the area of overlap among scenic rivers and each species' background. Nine separate models were built, allowing us to compare each of the three principal coordinate axes with each of the three nested classes of VSRP segments. In these models, the 33 representative fish species were used as replicate observations; each species represented a single value on each of the three principal coordinates (i.e., functional trait axes) and a single area of overlap value for each class of VSRP segments.

Complete R code to reproduce the MaxEnt models and to compare the VSRP segments with the background for each species are provided with all raw fish and covariate data in the Supplementary Data.

3. Results

3.1. Habitat suitability models

Each of the final models included 7–10 covariates. Among the model covariates, indices of channel size and morphology were most frequently used. Thirty of 33 models included either Strahler stream order (*StreamOrder*) or the cumulative length of all upstream river segments (*ArbolateSum*, which is strongly, positively correlated with basin area), while nine models included channel slope (*Slope*; see Table 1). Indices of agricultural activity (e.g., % crop cover, *PctCrop2001Cat*, 16 models; % agriculture on steep slopes, *PctAg2006Slp10Cat*, 12 models) and of urbanization (e.g., % urban cover, *PctUrban2001Cat*, 11 models; % impervious cover, *PctImp2001Cat*, 12 models) were also consistent, useful predictors of fish habitat. Other covariates that were frequently used in fish habitat models included indices of forested landcover (e.g., % mixed forest cover, *PctMxFst2001Cat*, 14 models; % coniferous forest cover, *PctConif2001Cat*, 22 models), hydrology (e.g., base flow index, *BFICat*, 7 models; water table depth, *WtDeptCat*, 7 models), and climate (e.g., maximum annual air temperature, *Tmax8110Cat*, 7 models).

Mean RTG (ensemble average of 100 iterations for each species) ranged from 0.440 to 1.714, with a grand mean and standard deviation of 0.876 and 0.326, respectively (Table 1). Thus, the mean odds ratio (e^{RTG}) comparing habitat suitability among sites of known presence and random background sites was always $\geq$1.380 and on average, was 2.067. Mean $\text{AUC}_{\text{pseudo}}$ values ranged from 0.777 to 0.974 (grand mean = 0.864; 1 s.d. = 0.050). Complete diagnostics from each of the final models, including the full MaxEnt reports, are provided in the Supplementary data.

3.2. Habitat within scenic rivers

Overlap in the habitat suitability density functions (ln MaxEnt raw

Table 2

Overlap in habitat suitability (ln MaxEnt raw outputs; see Fig. 4) between species' backgrounds and the three cumulative classes of VSRP segments (‘D’ = Designated; ‘D + Q’ = Designated + Qualified; ‘D + Q + P’ = Designated + Qualified + Potential). Smaller overlap values reflect scenic rivers that are increasingly distinct from the background. Significant differences between background and VSRP segments were inferred from Mann-Whitney tests (i.e., mean *p*-values among the 100 model testing iterations) and are indicated by parenthetic labels next to overlap values: ns = $p > 0.01$; a = $p \leq 0.01$; b = $p \leq 0.001$; c = $p \leq 0.0001$. Positive and negative signs next to significance labels shown whether average habitat suitability in the VSRP segments is higher (+) or lower (−) than in background segments. Species are grouped by families, listed in phylogenetic order. State-listed ‘Species of Greatest Conservation Need’ indicated by asterisks (*).

Family	Species	D	D + Q	D + Q + P
Lepisosteidae	*Lepisosteus osseus*	0.623 (ns)	0.704 (a +)	0.734 (ns)
Anguillidae	*Anguilla rostrata**	0.516 (c +)	0.506 (c +)	0.505 (c +)
Clupeidae	*Dorosoma cepedianum*	0.395 (c +)	0.345 (c +)	0.339 (c +)
Cyprinidae	*Luxilus albeolus*	0.543 (a +)	0.530 (b +)	0.482 (c +)
	Lythrurus ardens	0.534 (c +)	0.534 (c +)	0.527 (c +)
	*Margariscus margarita**	0.577 (c +)	0.566 (c +)	0.722 (c +)
	Nocomis leptocephalus	0.662 (a +)	0.682 (a +)	0.656 (c +)
	Nocomis raneyi	0.425 (c +)	0.352 (c +)	0.349 (c +)
	*Notropis altipinnis**	0.596 (a +)	0.649 (ns)	0.632 (a +)
	Notropis amoenus	0.383 (c +)	0.441 (c +)	0.463 (c +)
	*Notropis chalybaeus**	0.688 (ns)	0.803 (ns)	0.846 (ns)
	Notropis hudsonius	0.282 (c +)	0.294 (c +)	0.305 (c +)
	Pimephales notatus	0.584 (c +)	0.620 (c +)	0.604 (c +)
Catostomidae	*Erimyzon sucetta**	0.735 (ns)	0.752 (ns)	0.705 (b +)
	*Hypentelium roanokense**	0.685 (ns)	0.755 (ns)	0.777 (ns)
	*Moxostoma collapsum**	0.314 (c +)	0.321 (c +)	0.348 (c +)
	Moxostoma erythrurum	0.529 (c +)	0.493 (c +)	0.537 (c +)
	Thoburnia rhothoeca	0.718 (ns)	0.710 (c +)	0.664 (c +)
Ictaluridae	*Ameiurus nebulosus*	0.503 (c +)	0.479 (c +)	0.469 (c +)
	*Noturus gyrinus**	0.633 (b +)	0.687 (c +)	0.759 (a +)
Esocidae	*Esox niger*	0.697 (c +)	0.654 (c +)	0.646 (c +)
Salmonidae	*Salvelinus fontinalis**	0.848 (ns)	0.852 (ns)	0.842 (c +)
Aphredoderidae	*Aphredoderus sayanus*	0.755 (a +)	0.779 (a +)	0.779 (b +)
Cottidae	*Cottus caeruleomentum*	0.858 (ns)	0.884 (ns)	0.845 (ns)
	Cottus girardi	0.662 (ns)	0.676 (ns)	0.653 (ns)
Centrarchidae	*Acantharchus pomotis**	0.730 (ns)	0.708 (c −)	0.697 (c −)
	Enneacanthus gloriosus	0.708 (ns)	0.778 (ns)	0.808 (ns)
	Lepomis auritus	0.393 (c +)	0.396 (c +)	0.396 (c +)
	Micropterus salmoides	0.354 (c +)	0.336 (c +)	0.348 (c +)
Percidae	*Etheostoma fusiforme*	0.750 (ns)	0.776 (ns)	0.784 (ns)
	Etheostoma olmstedi	0.640 (c +)	0.637 (c +)	0.641 (c +)
	Etheostoma vitreum	0.569 (c +)	0.611 (c +)	0.615 (c +)
	*Percina rex**	0.765 (ns)	0.699 (ns)	0.574 (c +)

output) for background and currently Designated scenic river segments was highly variable (Table 2). Overlap ranged from 0.282 to 0.858 (mean = 0.596; 1 s.d. = 0.149) and was lowest for spottail shiner (*Notropis hudsonius*) and notchlip redhorse (*Moxostoma collapsum*). Hence, we predict these two species currently receive the greatest protective benefit (of the 33 representative fishes) from the VSRP; density functions for Designated segments were the most distinct from their respective background density functions for these species, suggesting that Designated rivers already include many of the best habitats within the study region. Greatest overlap was observed for brook trout and Blue Ridge sculpin (*Cottus caeruleomentum*), suggesting these species currently receive the least protective benefit from the VSRP.

Changes in overlap that were predicted to occur with additional VSRP listings were also variable. Relative to the currently Designated segments, overlap generally decreased with the addition of Qualified and of Qualified + Potential segments for nine species and increased for 12 species (Table 2). Changes in overlap were mixed for the remaining 12 species; for instance, overlap decreased with the addition of Qualified segments for golden redhorse (*Moxostoma erythrurum*) but increased with the addition of Qualified + Potential segments. Kernel density plots are provided with overlap statistics and maps of predicted habitat suitability for all species and for each of the three VSRP class comparisons in Appendix B.

Mann-Whitney tests indicated that habitat suitability is significantly higher in currently Designated segments than within the complete population of background segments for 21 of the 33 representative fish species (Table 2). Of these 21 fishes, five were SGCN taxa. When Qualified segments were added to the cumulative population of VSRP segments, predicted habitat suitability in scenic rivers was significantly higher than in background segments for 22 species, including four SGCN fishes. This number increased to 25 species, including eight SGCN taxa, when Potential segments were added to the cumulative VSRP population. For one species, the mud sunfish (*Acantharchus pomotis*), the addition of Qualified and Potential segments resulted in cumulative populations of VSRP segments that had significantly lower habitat suitability values than the background segments (Table 2).

No significant associations were detected between species' functional traits and the area of overlap among background and scenic river segments. Among all regression models (i.e., 1st, 2nd or 3rd principal coordinate axis predicting area of overlap for Designated, Designated + Qualified, or Designated + Qualified + Potential rivers), the largest coefficient of determination was 0.03 and the smallest *p*-value was 0.17 (Appendix C). Thus, we found no evidence to indicate that some fish functional traits are more likely than others to occur within scenic rivers.

4. Discussion

Our results suggest that the VSRP does, in fact, incorporate high quality fish habitat. To better understand these results and their conservation implications, we address three questions: (i) What factors explain why predicted habitat suitability is high for many fishes in VSRP rivers?; (ii) What implications do the modeling results have for coarse scale and fine scale conservation efforts in Virginia?; and (iii) What broader relevance might this study have for other freshwater habitat conservation programs?

4.1. Why is fish habitat suitability high in VSRP rivers?

MaxEnt diagnostics showed that for most species, predicted habitat suitability is most closely and consistently associated with river size. Among all model covariates, *StreamOrder* and the *ArbolateSum* (summed length of upstream river segments), both of which increase with river size, were the two most common and influential predictors of habitat suitability (Table 1). For both covariates, the MaxEnt response curves consistently demonstrated one of two associations with habitat suitability: a continuous positive association, indicating that habitat suitability is highest in the largest rivers (Fig. 5A), or a modal, convex-up association, indicating that habitat suitability peaks in rivers of intermediate size (Fig. 5B).

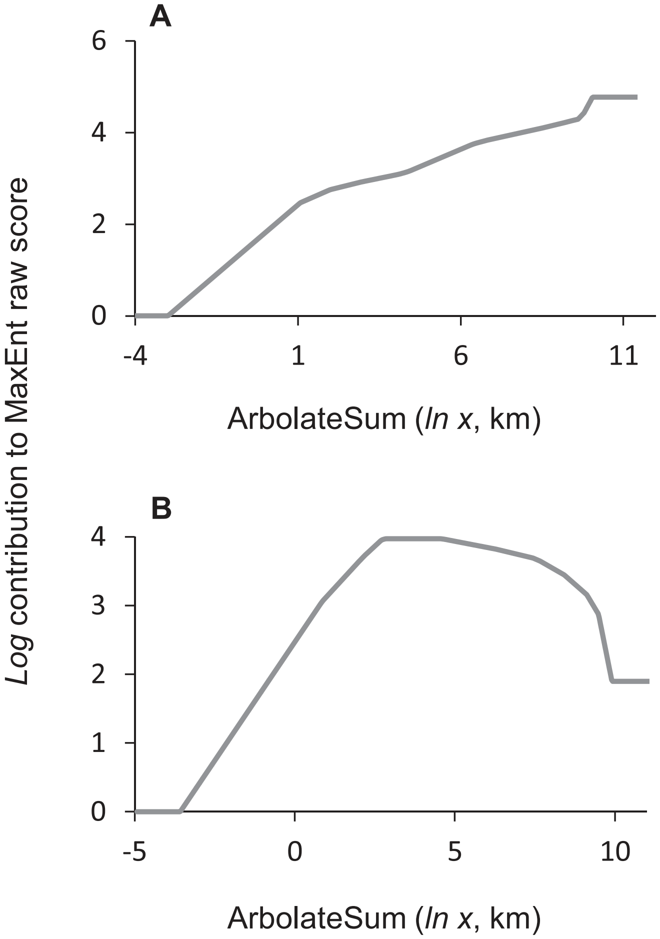

Fig. 5. MaxEnt response curves demonstrating the effect of *ArbolateSum* (summed length of upstream river segments) on model-predicted fish habitat suitability. Panel A illustrates a strong positive association between *ArbolateSum* and habitat suitability for golden redhorse (*Moxostoma erythrurum*). Panel B shows a unimodal association for bluehead chub (*Nocomis leptocephalus*). Complete galleries of the MaxEnt response curves are provided for all species and model covariates in species' individual results folders, in the Supplementary Data (DOI: https://doi.org/10.6084/m9.figshare.11678391).

Predicting that maximum habitat suitability will occur in midsize to large rivers is consistent with empirical studies of large river ecology. Large rivers are characterized by greater hydrologic and thermal stability than smaller systems, due to the buffering effect of large water volume (Johnson et al., 1995). Lateral connections with floodplain habitats also create a more diverse selection of aquatic habitats than in smaller, upstream reaches with constrained channels. Floodplain connections in turn provide nursery habitat for juvenile fishes and an abundance of terrestrial food subsidies (Galat and Zweimüller, 2001; Schiemer et al., 2001). These large river conditions facilitate high densities of fishes with diverse diets (Dettmers et al., 2001). In turn, fish richness often peaks in large, downstream river reaches (e.g., McGarvey and Ward, 2008; McGarvey, 2011; Hitt and Roberts, 2012). It is therefore logical to expect that for many fish species, habitat suitability will be highest in large rivers.

A strong link between river size and fish habitat suitability also provides a simple explanation for the VSRP results. Habitat suitability is high in VSRP segments, relative to background segments, because midsize to large rivers are favored by the VSRP. Comparisons between

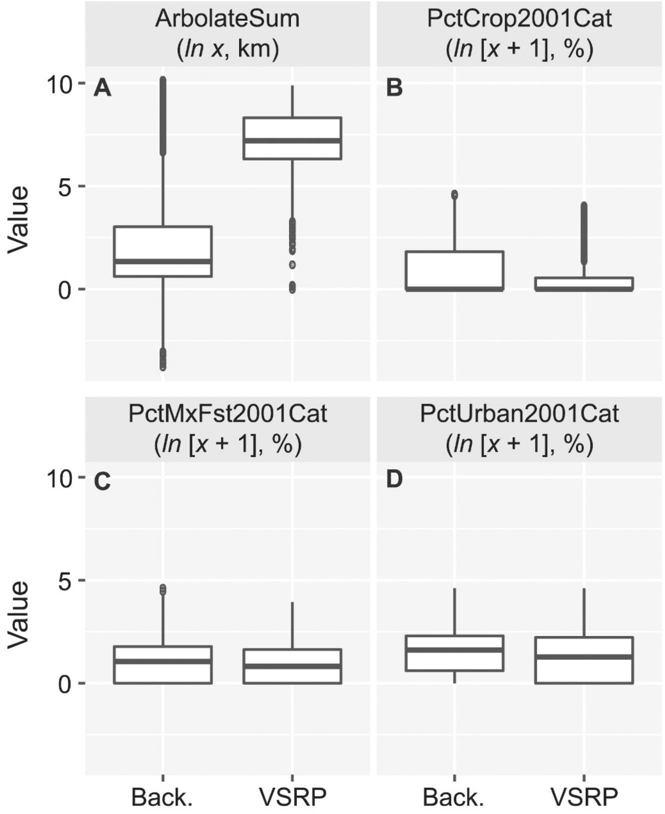

Fig. 6. Boxplots comparing distributions of exemplar covariates for the complete background (Back.) and currently Designated segments within the Virginia Scenic Rivers Program (VSRP). The four covariates represent river size (ArbolateSum; panel A), agricultural influences (PctCrop2001Cat; panel B), forest cover (PctMxFst2001Cat; panel C), and urban influences (PctUrban2001Cat; panel D). For each plot, the background includes all river segments within the three study basins; the data are not specific to the background of an individual species. Horizontal boxplot lines depict the 25th, 50th, and 75th percentiles, whiskers depict 5th and 95th percentiles, and points depict outliers. All plots utilize a common scale on the *y*-axis, with data transformations and units shown in parentheses next to the covariate labels. Complete covariate definitions are provided in Appendix A.

currently Designated VSRP segments and the complete population of background segments (i.e., all stream and river segments within the three study basins) support this hypothesis. For instance, boxplots of ArbolateSum values show that river segments within the VSRP are, on average, much larger than background segments (Fig. 6A). However, differences between VSRP and background river segments are not evident for indicators of agriculture (Fig. 6B), forest cover (Fig. 6C), and urbanization (Fig. 6D). Taken together, the MaxEnt response curves (Fig. 5) and VSRP vs. background comparisons (Fig. 6) suggest that an affinity for midsize to large rivers, shared by many fish species and the VSRP selection process, provides a parsimonious explanation for high habitat suitability within VSRP rivers.

4.2. Coarse vs. fine conservation filters

In the guiding document *Virginia's Precious Heritage*, the Department explains its use of fine and coarse conservation filters: “The more widely understood…‘fine filter’ approach…is to focus on protecting individual rare species. Another approach, which is considered the ‘coarse filter’, is to protect…natural community types. By protecting natural communities…most of the state's flora and fauna will be protected” (Wilson and Tuberville, 2003, p. 1-1). The aggregate results presented here for the 33 modeled species are consistent with a coarse filter conservation strategy. Our functional trait analysis was designed to ensure that all body sizes, fecundity levels, reproductive behaviors, parental care strategies, and instream habitat types were represented by the collective modeling results (see Fig. 3). The results should therefore be applicable to most of the freshwater fishes within the east-flowing rivers of Virginia. In this way, we have established a broad, coarse filter strategy to estimate the fraction of the total ichthyofauna that is expected to benefit from VSRP protective measures.

For 21 of 33 modeled species, predicted habitat suitability was significantly higher in currently Designated VSRP segments than elsewhere within the respective range (Table 2). Thus, we submit that many of the best available habitats for ~64% of the native fishes that were represented in the function trait analysis ($n = 179$) will tend to occur within the VSRP network. Furthermore, with approval of pending listing petitions for Qualified and Potential segments, we predict that VSRP protection will be extended to four additional species, bringing the total margin to 76% of all native fishes. This recognition begs an important question: What particular benefits are these fishes likely to experience when inhabiting VSRP rivers?

To our knowledge, data to measure specific ecological benefits that VSRP rivers provide to resident biota do not yet exist. Nevertheless, we anticipate that one major benefit will be the protection of instream flows. The Virginia Scenic Rivers Act specifies that artificial structures, including but not limited to dams, may not impede natural flows or fish movements within a Designated scenic river without explicit approval by the Virginia General Assembly (Virginia Code, 2021). This regulation provides a nexus for implementing environmental flows within scenic rivers and therefore has tremendous conservation potential. When applied to fish, environmental flows often focus on links between species' life histories and different dimensions of the hydrograph (Poff et al., 1997; Bunn and Arthington, 2002; Mims and Olden, 2011). For example, rapid increases in discharge serve as migratory cues for coho salmon (*Oncorhynchus kisutch*; Naiman et al., 2002) and spawning cues for Colorado pikeminnow (*Ptychocheilus lucius*; Nesler et al., 1988). Environmental flows are central to river management efforts around the world (Sood et al., 2017; Tickner et al., 2020) and have recently been studied in the Potomac River Basin (Buchanan et al., 2013; Hitt et al., 2020). As climate change and anthropogenic demand alter the hydrology of Virginia rivers (Neff et al., 2000; Schulte et al., 2016), interest in environmental flows is likely to increase (e.g., Kleiner et al., 2020; Rapp et al., 2020) and the VSRP should be positioned to play a key role. In the best-case scenario, a comprehensive environmental flows plan for the VSRP river network could be developed, ensuring that a majority (64–76%) of Virginia's native fishes have access to essential habitat.

The modeling results can also benefit fine scale conservation of SGCN taxa. In a simple application, maps of predicted habitat suitability can be used to prioritize future VSRP listings. For instance, we predict the SGCN fishes brook trout and Roanoke logperch (*Percina rex*) would both experience a significant increase in habitat suitability within VSRP segments if all Qualified and Potential segments were simultaneously added to the VSRP (Table 2). But if new VSRP listings were limited to one or several rivers, the MaxEnt results could provide a means of ranking candidate rivers. Brook Trout conservation may benefit most by adding Back Creek (James River Basin; mean ln MaxEnt raw = −6.656) or sections of the Jackson River (James River Basin; mean ln MaxEnt raw = −6.233), where water temperatures are cooler and channel gradients are steeper, to the VSRP. Alternatively, to protect the Roanoke Logperch, we suggest that the Pigg River (Roanoke River Basin; mean *ln* MaxEnt raw = −7.147) should be the top VSRP listing priority (see also Rosenberger, 2002; Lahey and Angermeier, 2007).

Another fine scale application is an explicit focus on river connectivity. For example, the American eel (*Anguilla rostrata*) is a catadromous, SGCN fish that historically occupied upstream river reaches in each of the three study basins (Jenkins and Burkhead, 1994). Widespread population declines throughout the North American range have resulted from habitat degradation, migration barriers, entrainment in hydroelectric turbines, and overfishing (Haro et al., 2000). Now, efforts to restore American eel populations are under way, including major dam removal and fish passage projects. The 2004 removal of Embry Dam on the Rappahannock River is a telling case study. Dam removal restored access to hundreds of kilometers of upstream habitat and within six years, significant increases in American eel abundance were observed in headwater streams (Hitt et al., 2012). The success of this restoration project is consistent with the model predictions for American eel: abundant, highly suitable habitat was predicted upstream of Embry Dam (located at the Fall Line; see *A. rostrata* map in Appendix B). Highly suitable habitat was also predicted throughout the Roanoke River Basin, where multiple large dams (e.g., John H. Kerr, Niagara, and Leesville Dams) have truncated the range of the American eel. In this context, model predictions could be used to prioritize installation of fish passage facilities or outright dam removal projects that would provide access to the greatest amount of highly suitable habitat. To facilitate these types of habitat selection decisions for any of the 33 modeled species, we provide a table of all predicted habitat suitability values, indexed by COMID, in Appendix D.

4.3. A transferable process to predict habitat suitability within freshwater ecosystems

We believe that our modeling results can immediately enhance VSRP planning. But we also emphasize that the modeling process used here (see Fig. 2) is fully transferable to other river systems. The requisite fish occurrence records (Frimpong et al., 2016), river network data (McKay et al., 2015) and covariate data (Hill et al., 2016) are freely available, as is the MaxEnt modeling software (Phillips et al., 2019) and the R code used to build each of our 33 fish models (Supplementary Data). By modifying and repurposing the R code, others can build comparable habitat models for fishes that occur in the study rivers but were not included in the present analyses. Furthermore, because the IchthyMaps, NHDplusV2, and StreamCat data encompass the contiguous U.S., our modeling process can immediately be adapted for use in many other U.S. rivers.

Transferability of the modeling process should be particularly high for eastern U.S. rivers, many of which share comparable physical habitat and fish species' lists with the present study rivers. For instance, we queried four of the most commonly selected and influential covariates in the 33 fish models – *ArbolateSum*, *Slope*, *PctCrop2001Cat*, and *PctMxFst2001Cat* – from three adjacent river basins to the north (Susquehanna, Delaware, and Hudson Rivers) and south (Pee Dee, Cape Fear, and the combined Neuse/Pamlico Rivers). When basin-wide distributions of the four covariates were compared among these six additional rivers and the three river systems included in the present study, we observed extensive overlap (Appendix E). This overlap indicates that river morphology and land use in adjacent river basins will often reflect conditions observed within our study rivers. Many of the fishes included in this study also have native ranges that extend far to the north and/or south of the study rivers. For example, the American eel and largemouth bass are native to all major rivers along the eastern U.S. and to much of the Mississippi Basin, while the range of the brook trout extends from the Mid-Atlantic to the northeastern U.S. and Canada (Jenkins and Burkhead, 1994).

Moreover, digital information on river networks and the fishes that inhabit them are increasingly accessible in other regions. For example, digital river network data are available at the global scale though HydroSHEDS (river network topology; Lehner et al., 2008) and HydroATLAS (river reach covariates; Linke et al., 2019; see also Domisch et al., 2015). Fish species' occurrence records (e.g., Buisson et al., 2008; BeSlagic et al., 2013) and trait characteristics (e.g., Brosse et al., 2021; Froese and Pauly, 2021) have also been compiled in digital repositories and traditional publications. By combining these alternative data resources with the modeling procedure demonstrated here, it will be possible to model fish habitat suitability in new regions and to integrate the results in other conservation applications. This last point is important because scenic rivers are just one of the strategies currently being used to protect freshwater habitat (Acreman et al., 2020; Arthington, 2021). Other freshwater conservation strategies exist, such as Special Areas of Concern in the U.K. (Cowx et al., 2009), and many of these could benefit from broad-scale estimates of habitat suitability.

Data statement

Supplementary Data for this article can be found online at Figshare (DOI: https://doi.org/10.6084/m9.figshare.11678391). Complete instructions to work with the data and re-run the species distribution models are provided in the ReadMe.txt file.

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CRediT authorship contribution statement

Daniel J. McGarvey: Conceptualization, Methodology, Validation, Writing – original draft, Supervision. **Alexander L. Brown:** Formal analysis, Investigation, Writing – review & editing. **Elsa B. Chen:** Formal analysis, Investigation, Writing – review & editing. **Catherine B. Viverette:** Formal analysis, Investigation, Writing – review & editing. **Philip A. Tuley:** Formal analysis, Investigation, Writing – review & editing. **Olivia C. Latham:** Formal analysis, Investigation, Writing – review & editing. **Phillip M. Gibbs:** Formal analysis, Investigation, Writing – review & editing. **Allyson E. Richins:** Formal analysis, Investigation, Writing – review & editing. **Michelle C. Deadwyler:** Formal analysis, Investigation, Writing – review & editing. **Baron Lin:** Formal analysis, Investigation, Writing – review & editing. **Erik A. Kaseloo:** Formal analysis, Investigation, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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