



Hydrologic and thermal conditions occupied by a species within a single watershed predict the geographic extent of occurrence of freshwater fishes

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ABSTRACT

Hydrologic regimes and water temperatures are primary predictors of freshwater species occurrence. While these variables have been demonstrated to be important in regulating species diversity at particular locations, whether species occurrences across lotic habitats within a single, relatively small watershed can predict the full geographic extent of a species is unclear. We use river reach estimates of streamflow and water temperature derived from a watershed-scale hydrologic model, coupled with body size measures, to investigate whether the type and variability of thermal and hydrologic habitat used by fish species within the Mobile River Basin (MRB) can predict the overall geographic extent of occurrence (GEO) for these taxa. Locality data for 108 species of fishes within MRB, one of the most ecologically-diverse watersheds in the United States, were intersected with streamflow and water temperature estimates to characterize minimum and maximum streamflow and water temperature conditions and thermal breadth (range of thermal conditions) occupied by each species. Among all species, variation in GEO was associated with variation in thermal breadth and body size. Thermal variables were also important predictors of variation in GEO among Cyprinidae. Flow variables were important predictors of variation in GEO for Centrarchidae, Ictaluridae, and Percidae, and within *Etheostoma* and *Percina*. Results generally indicate that species with large body size, relatively broad thermal tolerances, or preference for relatively high discharge environments tend to exhibit broader distributions across North America, yet these relationships vary among taxonomic groups.

Keywords

Hydrology, thermal breadth, Mobile River Basin, geographic information systems, SWAT

INTRODUCTION

Characterizing the factors regulating species' geographic extent of occurrence (GEO) is a fundamental goal of ecology (Brown & Maurer, 1989). There is a wide range of variability in GEO among taxa, with many species restricted to relatively small geographic extents and others distributed across very large areas (Brown & Maurer, 1989; Gaston, 2000). This variation in GEO has been attributed to a variety of species characteristics, including niche breadth (e.g. Botts, Erasmus, & Alexander, 2013; McCauley, Davis, Werner, & Robeson, 2014; and reviewed in Slatyer, Hirst, & Sexton, 2013), body size (e.g. Pyron, 1999; Goodwin, Dulvy, & Reynolds, 2005), and dispersal abilities (e.g. Lester & Ruttenberg, 2005; Mora & Robertson, 2005), among others. In addition to characterizing environmental conditions regulating species distributions, understanding which factors regulate species' GEO can help refine estimates of changes to distributional extents in response to ongoing environmental change.

Body size and niche breadth are often suggested to influence variation in species' GEO (e.g., Gaston & Blackburn, 1996b; Boucher- Lalonde, Morin, & Currie, 2016). For many taxonomic groups, body size is positively correlated with range size, with several ecological and physiological explanations for this relationship. Possible justifications of these associations include that large-bodied species require larger home ranges (McNab, 1963; Brown & Maurer, 1987), have more successful dispersal capabilities than relatively smaller species (Gaston 1994), and are able to maintain homeostasis over wider ranges of environmental conditions (Gaston, 1990). This positive correlation suggests that smaller bodied species may be at a greater risk of

extirpation (Gaston & Blackburn, 1996a) and understanding additional factors (i.e., niche breadth) that influence the distributions of different taxa can help ensure persistence of small-bodied species across greater geographic extents.

Species occupying relatively broad ranges of environmental conditions (i.e. greater niche breadth) tend to maintain relatively larger population sizes with improved persistence capabilities as these conditions vary (Knouft et al., 2011) and are expected to have a larger GEO due to their ability to tolerate a variety of environmental conditions (Brown, 1984). Hydrologic conditions and water temperature are important determinants of lotic species' environmental niches (e.g. Bain, Finn, & Booke, 1988; Poff & Ward, 1989; Poff et al., 1997) and can ultimately influence their distributions (Knouft & Ficklin, 2017). Because all freshwater fishes are ectothermic, their ranges are constrained by ambient thermal conditions (Brett, 1956; Moyle & Joseph, 2004), and fish living in lotic systems are often adapted to specific hydrologic conditions (Gorman & Karr, 1978). As a result, accurate estimates of streamflow and water temperature, and species occupancies of these environmental conditions, are critical to understanding the distributions of freshwater taxa within watersheds (Poff et al., 1997; Knouft & Ficklin, 2017).

While the importance of these environmental conditions to species persistence within watersheds is well-documented, it is unclear whether the type and breadth of thermal and hydrologic habitat that a species is known to occupy in one part of its range is indicative of the more general ability of a species to persist across broad geographic areas. Additionally, when determining niche breadth over the entire geographic range for a species, it is difficult to

differentiate whether a species with a larger niche breadth can tolerate wider ranges of environmental conditions (i.e., generalist species) or is comprised of many locally adapted populations (Ackerly, 2003). Without understanding the mechanism driving a wider niche breadth for certain taxa, it is difficult to interpret the relationship between niche breadth and geographic extent of occurrence, especially in terms of extirpation risk in the face of local disturbances (Slayter et al., 2013). The primary goal of this study is to determine whether the type and breadth of thermal and hydrologic conditions occupied by species within the Mobile River Basin (MRB), a relatively small watershed with high levels of temperate biodiversity, can predict the GEO for 108 stream fish species across North America. In general, we investigate whether species that occupy a wide range of environmental conditions within a relatively small watershed are likely to have a greater GEO compared to species that occupy a relatively narrow range of environmental conditions. Because body size has been found to be positively correlated with geographic distribution size for many species (e.g. Pyron, 1999; Goodwin et al., 2005), body size is also considered in combination with streamflow and water temperature occupancies for each species.

MATERIALS AND METHODS

Study Area

The MRB is one of the largest watersheds in the United States, encompassing an area over 110,000 km² (Johnson, Kidd, Journey, Zappia, & Atkins, 2002), with a majority of the basin occurring within Alabama (71%) and the remainder reaching into Georgia, Mississippi and Tennessee (Atkins, 2004). The basin has a mean annual discharge of 1,800 m³/s at the outlet (Fig. 1a), and a basin-wide mean annual discharge and water temperature of 80.3 m³/s and 14.3 °C, respectively (Fig. 1b). Over two-thirds of the basin is forested, with agriculture (26%) and urban areas (3%) making up the remaining land use (Johnson et al., 2002). Landforms range from coastal plains near sea level to elevations above 900 m in parts of Georgia (Atkins, 2004). The MRB is one of the most biodiverse temperate rivers in North America, with over 300 freshwater fish species (Benke & Cushing, 2011), 40 of which are endemic to the basin (U.S. Fish and Wildlife Service, 2000). Because of the high levels of fish biodiversity in the MRB, this watershed provides a robust dataset for the study of freshwater fish distributions in North America.

Species locality, hydrologic, and water temperature data

Species occurrence data were obtained from museum records at a variety of institutions (Table S1; accessed through the FishNet 2 Portal, www.fishnet2.com, 2017-02-12) representing collections from 1980 to 2009, which coincides with the period of record for streamflow and water temperature data used in this study. Native GEO estimates for each species were obtained from a previous study conducted by Knouft & Page (2011), in which the area of the GEO of each species was determined using geographic information systems (GIS) distribution maps derived

from Page & Burr (2011). These GEO estimates (km²) encompassed species' native North American ranges and all data were log₁₀-transformed to increase normality. Body size is an important predictor of species distribution sizes in freshwater fishes (Taylor & Gotelli, 1994; Pyron, 1999) and was therefore included as a potential variable in all analyses. Species' maximum total body lengths (cm) were obtained from Page & Burr (2011), log₁₀-transformed, and then used as an estimate of body size (Knouft & Page 2003; Knouft 2004). Species that had at least 20 unique localities that fell within the model-simulated hydrologic data for MRB and were considered non-migratory were included in our study. The final fish occurrence dataset included 16,002 individual records, representing 108 species from nine families (Fig. 1c).

Estimates of streamflow and water temperatures across the MRB for 1980–2009 were derived using the Soil and Water Assessment Tool (SWAT; Arnold, 2012) hydrologic model. SWAT is a basin-scale hydrologic model designed to simulate watershed processes (e.g., streamflow, surface runoff, groundwater flow, evapotranspiration). Surface runoff in the MRB was estimated using the Soil Conservation Service Curve Number method (USDA, 1986). This method assumes any water that does not become surface runoff will enter the soil column where it can be removed by evapotranspiration (ET; Penman-Monteith ET method used for this model), recharge into the deep aquifer, or move laterally in the soil column for streamflow contribution. Groundwater can also contribute to streamflow from shallow and deep aquifers. SWAT uses daily precipitation and minimum and maximum air temperature (obtained from Maurer, Wood, Adam, Lettenmaier, & Nijssen [2002]) to simulate hydrological processes. Relative humidity and

solar radiation inputs were generated using the built-in SWAT stochastic weather generator based on nearby climate stations.

The hydroclimatological water temperature model developed by Ficklin, Luo, Stewart, & Maurer (2012) within SWAT was used to simulate water temperatures. This model uses air temperature and local hydrology (surface runoff, soil water lateral flow, groundwater inflow, and snowmelt generated from SWAT) and streamflow travel time within the basin to estimate water temperature. The Ficklin, Luo, Stewart, & Maurer (2012) water temperature model has been successfully tested in the western United States (Ficklin, Luo, Stewart, & Maurer, 2012), central United States (Ziegler et al., 2016), and eastern United States (Chambers et al., 2017).

To ensure model accuracy, the SWAT MRB model was calibrated and validated for streamflow using the SWAT-Calibration and Uncertainty Program (SWAT-CUP; Abbaspour et al., 2007) with 82 United States Geological Survey (USGS) streamflow gauges within the MRB. For each gauge, the observed streamflow and water temperature data were equally (50:50) split for calibration and validation. The Nash-Sutcliffe model efficiency coefficient (NS; Nash & Sutcliffe, 1970) was used to assess model accuracy for the calibration and validation time periods. The Nash-Sutcliffe model efficiency coefficient is calculated as:

$$NS = 1 - \frac{\sum_{i=1}^n (Y_i^{obs} - Y_i^{sim})^2}{\sum_{i=1}^n (Y_i^{obs} - \bar{Y}^{obs})^2}$$

where Y_i^{obs} is the i th observation for either streamflow or water temperature, Y_i^{sim} is the i th SWAT-simulated value for either streamflow or water temperature, $\overline{Y^{obs}}$ is the mean of the observed streamflow or water temperature, and n is the total number of observations. NS values range from $-\infty$ to 1, where values ≥ 0.5 are deemed “satisfactory” based on the work of Moriasi et al. (2007), where a “satisfactory” rating means the hydrologic model can adequately simulate all aspects of the hydrograph. The mean absolute error (MAE) was also used as a model efficiency metric for water temperature, where a low MAE represents an accurate simulation.

For streamflow, the average NS value (Nash & Sutcliffe, 1970) for the 82 USGS streamflow gauges was 0.72 (standard deviation of 0.21) for calibration and 0.71 (standard deviation of 0.19) for validation. Water temperature was manually calibrated for seven USGS stream temperature sites. The average NS value for these seven sites was 0.61 for calibration with a MAE of 1.19 °C, while the average validation NS and MAE was 0.61 and 1.23 °C, respectively. Model evaluation statistics for streamflow and water temperature were therefore considered “satisfactory”. The calibrated streamflows and water temperatures were used in the GEO analyses.

Estimates of average minimum and maximum annual streamflow (m^3/s) and water temperature ($^{\circ}C$) for each stream reach within the MRB were calculated and converted into grid-based data using monthly averages of each variable at a spatial resolution of 400 m. Streamflow and water temperature data were aligned with all individual species localities using ArcGIS v. 10.4 to determine the minimum and maximum streamflow and water temperature

conditions occupied by each species within the MRB. Thermal breadth was calculated as the range between minimum and maximum water temperatures for each species. Because each species had a minimum flow occurrence close to zero, flow breadth was nearly equal to maximum flow for all species and was not included in further analysis. Minimum and maximum streamflow (F_{min} , F_{max}) and water temperature (T_{min} , T_{max}), and thermal breadth were then used with body size in regression analyses to predict variation in GEO for fishes in the MRB.

Statistical Analyses

We used a model selection approach to determine predictor variables that best explained variation in GEO for 108 fish species (all-species group) and for individual families and genera with greater than seven species in the dataset (Table 1). Using MATLAB v. R2016a to perform multiple linear regression analyses, seven models were tested for each group of species: 1) Body Size model, 2) Flow model: $F_{min} + F_{max}$, 3) Flow model + Body Size model, 4) Temperature model: thermal breadth + $T_{min} + T_{max}$, 5) Temperature model + Body Size model, 6) Temperature model + Flow model, and 7) Temperature model + Flow model + Body Size model. Models were compared using the Akaike Information Criterion for small sample sizes (AICc), and the model with the lowest AICc score was considered the best model for each group (Burnham & Anderson, 2004). Forward stepwise selection was then used to further refine the best model for each group by independently adding variables from the best model and retaining the variable with the lowest AICc score. The remaining variables were independently added again and assessed, and this process continued until the addition of a new variable no longer

resulted in an AICc reduction greater than 2.0 (Burnham & Anderson, 2004). Variables from the second-best model were also included for groups that had a Δ AICc less than 2.0 between the best and second-best model (Table 1).

RESULTS

The best model for each of the ten taxonomic groups produced an average adjusted R^2 of 0.48 (Tables 1 & 2). For the all-species model, Temperature + Body Size was the best model ($R^2 = 0.48$), with thermal breadth as the only temperature variable retained. On average, R^2 values tended to be higher at the family level (0.54) than those at the genus level (0.40). However, there was no clear trend on whether the R^2 would increase or decrease between the taxonomic levels, with *Lepomis* and *Percina* having higher R^2 values and *Etheostoma* and *Notropis* having lower R^2 values than their respective families. Of the four groups of genera, none had the exact same combination of variables included in their best model with those of their respective family's best model (Centrarchidae, Cyprinidae, or Percidae).

Body size was included in seven of the ten best models and was the only predictor variable included for Catostomidae, *Lepomis*, and *Notropis*. Temperature variables were included in the best model for all-species and Cyprinidae, while flow variables were included for Centrarchidae, Ictaluridae, Percidae, *Etheostoma*, and *Percina*. However, no group included both thermal and flow variables in the best model. Across all groups, body size, thermal breadth, and

Fmax exhibited positive relationships with GEO, while GEO decreased with Fmin for Centrarchide and Ictaluridae and increased for *Etheostoma*. Tmax and Tmin were not included in the best model for any group (Table 2).

DISCUSSION

The importance of hydrologic regime and water temperature to the regulation of freshwater species diversity is well-documented (Poff & Ward, 1989; Poff et al. 1997; Knouft & Ficklin, 2017). Yet despite much research on the factors that regulate the geographic distribution of freshwater species (Taylor & Gotelli, 1994; Pyron, 1999; McCauley et al., 2014), no study has investigated whether a species' occupancy of hydrologic and water temperature conditions within a watershed is predictive of that species' GEO. Our results suggest that the thermal and hydrologic conditions a species is known to occupy in one part of its range, while critical to regulating local assemblages, can also be important predictors of GEO for stream fishes in North America. Across all species analyzed, nearly half of the variation in GEO (48%) can be explained by thermal breadth within the MRB and body size. However, the variables selected for each model varied across all families examined, with no two families sharing the same combination of variables.

The Catostomidae model was the only family-level model that did not include any thermal or flow variables. However, variation in Catostomidae GEO can be attributed to body

size. This positive relationship between body size and the GEO was also found by Pyron (1999), who suggested that small-bodied catostomids tended to more specialized and morphologically less primitive resulting in a relatively smaller GEO. The Centrarchidae model did not indicate that body size is a significant predictor of variation in GEO; instead minimum and maximum flow conditions predicted variation in GEO, indicating that habitat generalists in the MRB tend to have greater geographic extents for this family. In contrast, our results indicated that body size is an important predictor of GEO among species of *Lepomis*, a genus within Centrarchidae, which is also consistent with Pyron (1999). The lack of a relationship between body size and GEO at the family level may be due to limited representation of centrarchids in the MRB and the recent identification and splitting of species in the genus *Micropterus* (Page & Burr, 2011). As a result, these relatively larger-bodied species may now have smaller geographic extents than previously thought, diminishing the relationship between body size and GEO for this family.

The Cyprinidae model included thermal breadth and body size, while the *Notropis* model only included body size. The finding that body size is positively correlated with GEO for cyprinids is consistent with previous research conducted by Taylor & Gotelli (1994), which suggested this relationship is impacted by the maintenance and origin of geographic extents for different species. This relationship can be especially troubling for species with small GEOs because smaller-bodied cyprinids and those that occupy relatively smaller habitat breadths have already been found to experience greater occurrences of local extirpation than larger generalist species (Angermeier, 1995). For the Percidae model, variation in GEO was explained by

maximum streamflow and body size, while only maximum streamflow predicted variation in GEO for *Percina*, and maximum and minimum streamflow predicted variation in GEO for *Etheostoma*. The positive relationship between body size and GEO for the Percidae family may be because larger-bodied percids (especially those with larger habitat breadths) may be more likely to occupy previously uncolonized reaches (Shea, Bettoli, Potoka, Saylor, & Shute, 2015). Our findings also indicated that at the family and genus level, percids that can tolerate wider ranges of hydrologic conditions tend to have greater GEOs. Other studies have found that percids occupying a small range of hydrologic environments were more likely to be extirpated than those that tolerate wider ranges (Angermeier, 1995), indicating that species with small GEOs may be at risk of further range contractions. Likewise, Shea et al. (2015) found that extirpation risk increased with high discharge conditions either through the displacement of individuals within a population or disruption of spawning activities. Differences in variables selected for Cyprinidae and Percidae models and those of their respective genera may be a result of niche conservatism at the family level which can create stronger relationships between certain variables and GEO that may not exist at lower taxonomic levels (McNyset, 2009).

While hydrologic and thermal conditions are both important factors regulating the distributions of aquatic species, no model incorporated both types of variables and no two groups of families had the same combination of variables selected. This suggests that individual groups of taxa vary in their sensitivity to different environmental conditions and highlights the influence of phylogenetic constraints on North American fishes (Knouft & Page, 2011). For all groups that

found the best model to include temperature variables, only thermal breadth was retained (excluding T_{min} and T_{max}). This suggests the breadth of thermal habitat occupied is a better predictor of GEO than minimum and maximum thermal tolerances, which could be due to an improved ability to disperse through a wider range of environmental conditions (i.e. generalist species). In contrast, species with a low minimum thermal or high maximum thermal tolerance may have inconsistent dispersal opportunities if they cannot tolerate both high and low thermal conditions (i.e. specialist species), resulting in no clear relationship between these variables and GEO.

The positive correlation between GEO and body size, thermal breadth, and maximum flow suggests that larger-bodied species occupying a wider habitat breadth (i.e., generalist species) in the MRB tend to occupy larger geographic extents across North America compared to the small-bodied specialist species. Of particular note is that the breadth of habitat (i.e., range of thermal and hydrologic tolerances) occupied by species in the MRB is positively correlated with GEO. This suggests that species with relatively small geographic extents may be particularly susceptible to climate-induced changes in streamflow and water temperature due to a more limited range of available thermal and hydrologic habitat at the basin level. This greater sensitivity to changes in climate could hinder their ability to disperse to new areas of suitable thermal and hydrologic habitat (via streams outside of their habitat breadth), resulting in range fragmentation, higher instances of speciation, and an increased chance of local extirpation.

This study determined species' thermal and flow tolerances within a watershed rather than using a controlled laboratory setting. The use of hydrological model output results in a higher uncertainty as compared to using observed data. This uncertainty could stem from input uncertainty (e.g., rainfall, spatial input data), model uncertainty (e.g., simplified representation of hydrologic processes), and/or parameter uncertainty (e.g., uncertain values for model parameters) (Renard et al., 2010). The use of monthly simulations inherently misses the day-to-day streamflow and thermal variability which can also influence habitat range. Additionally, the realized niche of species can be influenced by a host of abiotic and biotic factors (i.e. biotic interactions) which could account for unexplained variation in our models (Slatyer et al., 2013). Regardless, results indicate that data derived from hydrologic models and museum-based distribution data are useful for relating watershed-scale environmental conditions to the extent of freshwater species distributions. Additionally, while non-migratory stream fish are thought to stay within relatively small (<100 m) stream sections (Gerking, 1959; Rodríguez, 2002), many species are considered partial migrators, in which most individuals in a population stay resident and some migrate to other streams (Chapman et al., 2012). However, because minimum and maximum water temperature and streamflow were calculated from monthly averages of each stream reach (1229 within the MRB), it is likely that even partial migrating species would remain within streams with the same hydrologic and thermal averages.

We recognize that by determining habitat breadths within a relatively small watershed that is limited by northern headwaters and the Gulf of Mexico, streamflow and water temperature

tolerances may not be fully realized for some species (Knouft & Anthony, 2016). As a result, these limitations may impact the response of GEO to the full streamflow and water temperature tolerances for species in the MRB, which could account for the lack of relationship between environmental variables in GEO for Catostomidae, *Lepomis*, and *Notropis*. Finally, because studies examining the relationship between niche breadth and GEO typically calculate environmental tolerances across a species entire extent, it is difficult to determine whether a wide habitat breadth is attributed to locally adapted populations or the true ability of a species to tolerate wider ranges of environmental conditions. By determining environmental tolerances within a relatively small watershed, this work can better indicate potential risk of local extirpations for different species in the face of future disturbances.

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TABLES

Table 1. Results from regression analyses including body size, streamflow, and water temperature conditions, and geographic extent of occurrence for freshwater fishes in the Mobile River Basin. Temperature model includes thermal breadth and minimum and maximum water temperature, and flow model includes minimum and maximum streamflow.

	N	Model	R ²	AICc	ΔAICc	w(AIC)
All Species	108	Temperature + Body Size	0.47	218.20	0.00	0.80
		Temperature + Flow + Body Size	0.47	221.22	3.02	0.18
		Flow + Body Size	0.43	225.11	6.91	0.03
		Body Size	0.31	243.14	24.94	0.00
		Temperature	0.28	250.92	32.72	0.00
		Temperature + Flow	0.28	253.07	34.87	0.00
		Flow	0.23	256.38	38.18	0.00
Catostomidae	9	Body Size	0.51	6.56	0.00	0.99
		Flow + Body Size	0.39	17.48	10.91	0.00
		Temperature + Body Size	0.38	29.73	23.17	0.00
		Temperature + Flow	0.12	54.81	48.24	0.00
		Temperature + Flow + Body Size	0.30	122.11	115.55	0.00
		Flow	-	-	-	-
Centrarchidae	15	Flow	0.54	12.11	0.00	0.73
		Flow + Body Size	0.52	15.21	3.10	0.16
		Temperature	0.49	16.23	4.12	0.09
		Temperature + Body Size	0.45	20.61	8.51	0.01
		Body Size	0.01	21.60	9.49	0.01
		Temperature + Flow	0.49	23.65	11.54	0.00
		Temperature + Flow + Body Size	0.45	30.49	18.38	0.00
<i>Lepomis</i> (Centrarchidae)	8	Body Size	0.64	-2.84	0.00	0.99
		Flow	0.20	7.62	10.46	0.01
		Flow + Body Size	0.60	9.72	12.57	0.00
		Temperature	0.54	12.62	15.46	0.00
		Temperature + Body Size	0.91	16.37	19.22	0.00
		Temperature + Flow	0.29	86.59	89.43	0.00
Cyprinidae	35	Temperature + Body Size	0.49	77.47	0.00	0.62
		Flow + Body Size	0.42	79.36	1.89	0.24
		Body Size	0.33	81.24	3.77	0.10
		Temperature + Flow + Body Size	0.46	82.84	5.37	0.04
		Temperature	0.21	88.38	10.91	0.00
		Flow	0.25	89.03	11.55	0.00
		Temperature + Flow	0.24	92.95	15.47	0.00

<i>Notropis</i> (Cyprinidae)	14	Body Size	0.16	37.66	0.00	0.80
		Flow	0.05	41.48	3.82	0.12
		Flow + Body Size	0.15	42.76	5.10	0.06
		Temperature	0.02	46.06	8.40	0.01
		Temperature + Body Size	0.16	47.57	9.91	0.00
		Temperature + Flow	-	-	-	-
		Temperature + Flow + Body Size	-	-	-	-
Ictaluridae	8	Body Size	0.37	19.61	0.00	0.51
		Flow	0.62	19.81	0.19	0.47
		Flow + Body Size	0.67	26.18	6.57	0.02
		Temperature	0.49	31.37	11.75	0.00
		Temperature + Body Size	0.46	48.78	29.16	0.00
		Temperature + Flow	0.37	103.71	84.10	0.00
		Temperature + Flow + Body Size	-	-	-	-
Percidae	33	Flow + Body Size	0.40	72.84	0.00	0.59
		Flow	0.34	74.18	1.34	0.30
		Temperature + Body Size	0.36	77.31	4.47	0.06
		Temperature	0.29	79.12	6.28	0.03
		Temperature + Flow + Body Size	0.38	80.55	7.71	0.01
		Temperature + Flow	0.32	81.36	8.52	0.01
		Body Size	0.07	84.22	11.39	0.00
<i>Etheostoma</i> (Percidae)	17	Flow	0.37	39.46	0.00	0.76
		Flow + Body Size	0.35	42.22	2.77	0.19
		Temperature	0.23	46.22	6.77	0.03
		Body Size	0.01	46.42	6.96	0.02
		Temperature + Body Size	0.21	49.63	10.18	0.01
		Temperature + Flow	0.31	50.84	11.39	0.00
		Temperature + Flow + Body Size	0.26	56.49	17.04	0.00
<i>Percina</i> (Percidae)	13	Flow + Body Size	0.52	35.54	0.00	0.43
		Flow	0.38	35.99	0.45	0.34
		Body Size	0.18	37.34	1.80	0.18
		Temperature	0.39	40.24	4.70	0.04
		Temperature + Body Size	0.44	43.11	7.57	0.01
		Temperature + Flow	0.29	52.22	16.68	0.00
		Temperature + Flow + Body Size	0.40	58.72	23.18	0.00

N indicates number of individuals in model

R² indicates adjusted R² value

AICc is the Akaike's information criterion score for small sample size

'-' indicates negative adjusted R² value

w(AIC) indicates Akaike weights

Table 2. Regression results for the best model for each group predicting variation in geographic range sizes for stream fishes in the Mobile River Basin. A negative ΔAICc score indicates an improved model from the best full model for that group in Table 1, and ‘-’ indicates no changes from the best model for that group from Table 1.

	N	R²	ΔAICc	Coefficient	Estimate	SE	t_{stat}
All Species	108	0.48	-2.16	Intercept	-0.669	0.785	-0.852
				Body Size	1.152	0.180	6.398
				TB	0.212	0.036	5.953
Catostomidae	9	0.51	-	Intercept	3.428	0.813	4.214
				Body Size	1.464	0.479	3.059
Centrarchidae	15	0.54	-	Intercept	5.783	0.282	20.518
				Fmin	-55.879	22.577	-2.475
				Fmax	0.000	0.000	1.920
<i>Lepomis</i> (Centrarchidae)	8	0.64	-	Intercept	4.343	0.525	8.277
				Body Size	1.370	0.375	3.654
Cyprinidae	35	0.50	-5.26	Intercept	-1.992	1.404	-1.418
				Body Size	2.271	0.563	4.035
				TB	0.216	0.061	3.515
<i>Notropis</i> (Cyprinidae)	14	0.16	-	intercept	0.089	2.592	0.034
				Body Size	5.257	2.791	1.883
Ictaluridae	8	0.73	-2.76	Intercept	4.885	0.499	9.785
				Body Size	0.937	0.319	2.936
				Fmin	-22.870	7.530	-3.037
Percidae	33	0.41	-2.13	Intercept	2.899	0.701	4.135
				Body Size	1.576	0.747	2.109
				Fmax	0.001	0.000	4.316
<i>Etheostoma</i> (Percidae)	17	0.37	-	Intercept	4.121	0.295	13.952
				Fmin	2.228	1.524	1.463
				Fmax	0.001	0.000	3.321
<i>Percina</i> (Percidae)	13	0.44	-2.97	Intercept	4.254	0.346	12.279
				Fmax	0.001	0.000	3.200

N indicates number of individuals in model

R² indicates adjusted R² value

AICc is the Akaike's information criterion score for small sample size

SE is standard error

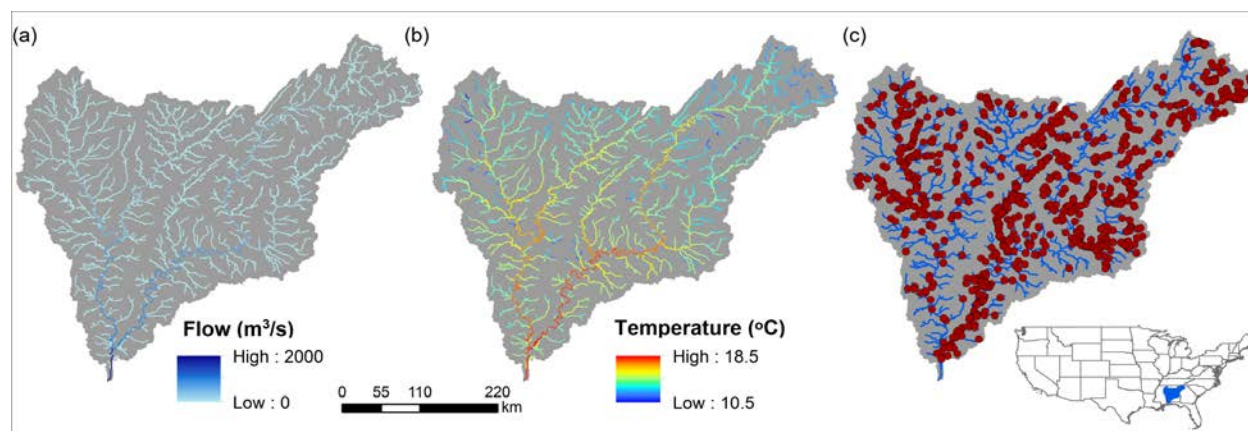


Figure 1

