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Streamflow regimes and geologic conditions are more important than water temperature when projecting future crayfish distributions

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Abstract

Ongoing changes in climate are expected to alter current species' habitat and potentially result in shifts in species distributions. While climatic conditions are important to a species' ability to persist in an area, for many taxa, other environmental factors, such as geology, land cover, and topography, are also important for providing suitable habitat. Furthermore, aquatic species experience changes in climatic conditions through the effect precipitation and air temperature have on streamflow regimes and water temperature. In this study, species distribution models (SDMs) for ten stream-dwelling crayfish species were generated using a maximum entropy approach across the Mobile River Basin in the southeastern United States. SDMs were developed using model-generated contemporary estimates of streamflow and water temperature as well as geologic, topographic, and land cover data. Future distributions were then projected using global climate model (GCM) projections of streamflow and water temperature. Geology, topography, and streamflow appear to be more important predictors of suitable habitat than water temperature for crayfish species within the Mobile River Basin. Species distributions regulated by limited influences from stream flow and water temperature displayed relatively small changes in projected future habitat distributions based on various GCM scenarios. When shifts in species distributions were projected into the future, these shifts did not appear to follow a northward retreat or expansion, likely due to the limited impact of water temperature on the modeled distributions of suitable habitat for these species. Furthermore, species' habitat distribution responses among future climate scenarios were variable within and among species and did not vary unidirectionally with increased severity of climate change as realized through increased warming patterns.

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1 Introduction

Characterizing the factors that regulate species distributions is a fundamental goal in ecology, biogeography, and conservation (Guisan and Zimmermann 2000; Loiselle et al. 2003; Margules et al. 1994; Sutherland et al. 2013). Accordingly, significant efforts have been made to develop and apply species distribution modeling (SDM) algorithms to delineate areas that constitute suitable habitat for species (Elith et al. 2006; Guisan and Thuiller 2005; Pearson 2010; Phillips et al. 2006). Considering ongoing changes in climate and potential species' responses to these changes (Kharouba and Kerr 2010; Parmesan and Yohe 2003; Walther et al. 2005), SDM techniques have also been used to project alterations in species distributions based on various future climate scenarios (Elith and Leathwick 2009).

While SDM approaches have been applied to freshwater taxa, many of these studies have investigated the response of species to forecasted changes in climate (i.e., precipitation and air temperature) (Comte et al. 2013; Heino et al. 2009; Knouft and Ficklin 2017). This focus on air temperature and precipitation in the absence of other physical environmental characteristics, such as geomorphology and topography (Frissell et al. 1986; Johnson and Gage 1997; Markovic et al. 2012), can potentially result in the perception of climate as being the primary regulator of species distributions. Moreover, while precipitation and air temperature are directly relevant for estimating suitable habitat for terrestrial species, these variables have spatially and temporally varying indirect effects on streamflow and water temperature, which are of primary importance in regulating freshwater species distributions (Al-Chokhachy et al. 2013; Huang and Frimpong 2016; Knouft and Ficklin 2017). Streamflow regimes are critical to the survival, growth, and reproduction of aquatic species, with directional alterations of the streamflow regime shown to impact local biodiversity and cause extirpation of populations (Bain et al. 1988; Bunn and Arthington 2002; Knouft and Chu 2015; Knouft and Ficklin 2017; Poff and Allan 1995; Poff et al. 1997). Water temperature is known to have important effects on various life history traits of aquatic species with species exhibiting specific thermal tolerances (Beitinger et al. 2000; Bennett et al. 2018). Consequently, forecasted changes in water temperature are likely to impact species distributions (Ficke et al. 2007; Rahel and Olden 2008).

Addressing how various environmental conditions can influence estimations of the distribution of future suitable habitat is especially important for freshwater species of conservation concern such as crayfishes, which are among the most threatened taxa in North America (Richman et al. 2015; Taylor et al. 2007). Crayfish function as ecosystem engineers and keystone species through direct modification of the benthos, influences on particulate and sediment dynamics, and their role in the food chain as omnivores and key detritivores (Creed Jr and Reed 2004; Geiger et al. 2005; Momot 1995; Reynolds et al. 2013; Statzner et al. 2000; Statzner et al. 2003). Crayfish commonly exhibit narrow regional endemism (Taylor et al. 2007), which magnifies threats commonly associated with all freshwater aquatic taxa, including alteration of habitat and introduction of nonindigenous organisms (Allan and Flecker 1993; Richman et al. 2015). Nearly half of the 410 crayfish species native to North America have been identified as being at risk, many of which are in the southeastern United States (Taylor et al. 2007).

Considering the dependency of freshwater taxa on streamflow regimes and water temperature and the current threats to native crayfish, characterizing the potential effects of changes in climate on basin hydrology and water temperature is critical to predicting the potential impacts of climate change on these species. Although flow regime and water temperature have been demonstrated to be important factors influencing areas of suitable habitat for some crayfishes

(Hossain et al. 2018; Nolen et al. 2014; Westhoff and Rosenberger 2016), the application of SDM techniques for freshwater invertebrates has generally not incorporated these types of in-stream environmental conditions at a watershed scale (e.g., Capinha et al. 2013; Morehouse et al. 2013). Moreover, geology, land cover, and land slope are important environmental predictors of suitable habitat for crayfishes due to their influence on runoff, physicochemical attributes of the water, in-stream habitat conditions, and substrate characteristics (Dyer et al. 2013; France 1992; Joy and Death 2004; Westhoff et al. 2011). The objective of this study is to use streamflow, water temperature, geologic, topographic, and land cover data to develop SDMs for non-burrowing, stream-dwelling crayfish native to the biologically diverse Mobile River Basin in the southeastern United States. We then use these models in conjunction with estimates of future streamflow and water temperature based on various global climate model (GCM) scenarios to project future distributions of suitable habitat for these taxa.

2 Methods

2.1 Study area

The Mobile River Basin drains approximately 110,000 km² of the southeastern United States, covering the majority of Alabama and extending into Georgia, Mississippi, and Tennessee (Supplementary Fig. 1). Approximately 69% of the basin is covered by forest, with remaining land uses including agriculture (18%), wetlands, streams, and lakes (11%), and urban areas (2%). Elevation ranges from near sea level at the outlet to greater than 900 m above sea level in the Appalachian Mountains located in the northeastern part of the basin. The Mobile Basin is one of the most biodiverse freshwater systems in North America, including numerous endemic species (Lydeard and Mayden 1995).

2.2 SWAT hydrologic modeling

The Soil and Water Assessment Tool (SWAT; Arnold et al. 1998) was used to simulate discharge (m³/s) and water temperature (Ficklin et al. 2012) throughout the Mobile Basin. SWAT is a physically based and distributed hydrologic model initially developed to predict impacts of changes in landscape-management practices on water, sediment, and agricultural yields (Arnold et al. 1998; Neitsch et al. 2005a, b). Recently, SWAT has been used to assess the effects of climate change on hydrologic responses by adjusting precipitation, temperature, and related climatic variables based on future global climate model (GCM) estimates (Chien et al. 2013; Ficklin et al. 2014; Zhang et al. 2016). Spatial heterogeneity is accounted for by partitioning basins into several sub-basins, which are then segregated into hydrologic response units (HRUs) based on unique combinations of environmental conditions (e.g., soil, land cover), which range is size from approximately 1–540 km². Water quantity and quality are estimated for each sub-basin and then routed by streamflow and assigned to outlets within the basin. See Neitsch et al. (2005b) for a more detailed overview of the SWAT model. For this study, a water temperature model coupled within the SWAT model was used to simulate water temperatures throughout the Mobile Basin (Ficklin et al. 2012). This model uses both air temperature and contributing hydrology in each sub-basin to estimate water temperature. The SWAT modeling approach used to estimate contemporary streamflows including input data, calibration, and validation is described in detail in Chien et al. (2013).

Streamflow generated from the SWAT Mobile Basin model was calibrated using SWAT-CUP (Abbaspour et al. 2007) for 82 United States Geological Survey (USGS) streamflow gauges spatially distributed throughout the Mobile Basin. The observed streamflow data were split for calibration and validation, with half of the data used for calibration and the other half for validation. The average Nash-Sutcliffe value, a metric used to quantify predictive power among hydrologic models (Nash and Sutcliffe 1970), for all streamflow gauges was 0.72 with a standard deviation of 0.21 (correlation = 0.89 ± 0.08) for calibration and 0.71 with a standard deviation of 0.19 (correlation = 0.88 ± 0.09) for validation. Water temperature was manually calibrated for seven stream temperature sites, but due to the limited data availability, only calibration was performed. For these seven sites, the average Nash-Sutcliffe value was 0.66 with a mean absolute error of 1.08 °C.

To estimate future streamflows, projections of temperature and precipitation from 14 GCMs for Representative Concentration Pathway 8.5 (RCP 8.5; Supplementary Table 1) were extracted from the Downscaled CMIP5 Climate and Hydrology Projections Archive (http://gdo-dcp.ucllnl.org; Maurer et al. 2014) and integrated into the calibrated and validated SWAT model. RCP 8.5 represents the highest greenhouse gas emissions relative to pre-industrial values for the Coupled Model Intercomparison—Phase 5 GCM (CMIP5; Taylor et al. 2012) ensemble projections. The extracted GCM output was previously downscaled to a 12-km resolution using the daily bias-corrected and constructed analogs approach (BCCA: Maurer et al. 2010).

2.3 Environmental predictor variables

Environmental data consisted of spatially explicit geology, topography, and land cover in addition to the SWAT-generated streamflow and water temperature data sets. These environmental variables are hypothesized to be ecologically relevant in determining suitable habitat for stream-dwelling, non-burrowing crayfish species (Dyer et al. 2013; France 1992; Joy and Death 2004; Nolen et al. 2014; Westhoff et al. 2011; Westhoff and Rosenberger 2016). ArcGIS 10.4.1 was used in data preparation to clip the environmental data with the stream network of the basin. Geologic data for each state was acquired from the USGS (Hardeman et al. 1966; Lawton et al. 1976; Moore 1969; Szabo et al. 1988) as separate shapefiles and converted to raster coverages (spatial resolution of 400 m) of primary rock type across the entire stream network within the Mobile Basin (total of 45 unique rock types). The most prevalent rock types within the stream network included beach sand, shale, sand, and sandstone. The topography of the study area was represented by the slope, which was created by applying the slope tool in ArcGIS to a digital elevation model (DEM) (30 m spatial resolution) of the basin (NED 2000). Land cover data (30 m spatial resolution) for the basin were obtained from the Multi-Resolution Land Characteristic Consortium (Fry et al. 2011). Surrounding land cover around the stream network was determined by using the majority neighborhood focal statistic tool in ArcGIS (neighborhood represented by 2000 m radius about each pixel). Both the slope and land cover raster coverages were simplified to a 400-m resolution for analysis in Maxent.

To use SWAT-derived contemporary hydrologic models for the Mobile Basin in Maxent, three metrics were calculated to summarize streamflow conditions for each sub-basin using monthly averages of daily estimated streamflows including maximum annual streamflow (m^3/s), minimum annual streamflow (m^3/s), and average intra-annual coefficient of variation in streamflow, which quantifies intra-annual streamflow variability. The annual maximum and

minimum metrics were computed as the most extreme (highest and lowest, respectively) average monthly value for each sub-basin within each year, averaged across the years of the study period. Average intra-annual coefficient of variation (CV) in streamflow variability was calculated as:

$$CV = \frac{1}{N} \sum_{i=1}^{N} \left(\frac{STD(Q_m)}{\overline{Q_m}} \right)_i \tag{1}$$

where STD(Qm) and $\overline{Q_m}$ are the standard deviation and average of monthly streamflow in a year, respectively (Chien et al. 2013). These same three metrics were computed identically for the SWAT-derived model of water temperature (°C) using monthly averages in temperature for each sub-basin.

From this set of 14 unique GCM projections of future water temperature and streamflow, we selected the maximum, median, and minimum water warming projections (MAX_{warm}, MED_{warm}, and MIN_{warm}) for the period of 2060–2079 (Supplementary Table 1). To select these sets of future streamflows and water temperatures, we calculated the overall average (across years and sub-basins) of water temperature for this time-period yielding a single mean value for each of the 14 GCM projections of water temperatures. From these values, we selected the maximum, median, and minimum values and selected the corresponding GCM to yield our MAX_{warm}, MED_{warm}, and MIN_{warm} projections of water temperature across the basin. GCMs IPSL-CM5A-LR (Institut Pierre Simon Laplace), GFDL-CM3 (NOAA Geophysical Fluid Dynamics Laboratory), and INM-CM4 (Institute of Numerical Mathematics) produced the MAX_{warm}, MED_{warm}, and MIN_{warm} projections, respectively. Maximum annual, minimum annual, and average annual CV of streamflow and water temperature were computed as above for the future projection period of 2060–2079 for the MAX_{warm}, MED_{warm}, and MIN_{warm} scenarios. These projections of in-stream conditions allowed us to develop models predicting contemporary and future distributions of suitable habitat for each crayfish species across the Mobile Basin. The sub-basin shapefiles of contemporary and future streamflow, as well as water temperature, were then converted into raster coverages (400 m spatial resolution) across the basin and then clipped to the extent of the stream network for use in Maxent. All GIS analyses were carried out using the NAD 1983 UTM Zone 16N projected coordinate system.

2.4 Crayfish distribution data

Only species of crayfish that are not primary or secondary burrowers were included because these taxa generally occupy the stream channel and are subject to variation in flow and water temperature (Hobbs 1981). Distribution data were extracted from a database of all Alabama crayfish vouchered records (Schuster and Taylor, unpublished data). Georeferenced species records from approximately 2600 unique sampling locations in this database are represented by vouchered museum holdings at the Illinois Natural History Survey (INHS), National Museum of Natural History Smithsonian Institution (USNM), and the University of Alabama Decapod Collection (UADC). Species records are represented by vouchered specimens collected by authors CAT and GAS during crayfish-specific field surveys that saved all crayfish species present at the location or from field surveys conducted by other aquatic biologists. Most records not collected by CAT or GAS, particularly those that were obvious range outliers, were visually examined and confirmed by CAT or GAS. All locality data were within the stream sections modeled by SWAT and each species was represented by at least 20

unique sites (Supplementary Fig. 1; Hernandez et al. 2006). Locality data included specimen collections that occurred between 1980 and 2009 to coincide with the time period of the contemporary SWAT hydrologic and water temperature models. The final dataset consisted of ten species from three genera including *Cambarus* (*C. coosae*, *C. halli*, *C. obstipus*, and *C. striatus*), *Faxonius* (*F. erichsonianus*, *F. perfectus*, and *F. validus*), and *Procambarus* (*P. acutus*, *P. spiculifer*, and *P. versutus*). Taxonomy used in this paper follows the recent proposal of Crandall and De Grave (2017). One species, *C. striatus*, will burrow in southern portions of its North American range, but within the majority of the Mobile Basin, the species is most frequently found in flowing streams (Taylor and Schuster, unpublished data). *P. acutus* can also occur in backwaters and swamps; however, like *C. striatus*, *P. acutus* is frequently encountered in lower gradient flowing streams within the Mobile Basin. The total number of locality records across all ten species was 366 and the number of observations per species ranged from 20 to 90 (Supplementary Table 2).

2.5 Species distribution modeling

Distributions of suitable habitat were predicted for all species using Maxent, which has been demonstrated to be a generally accurate and useful method for species distribution modeling based on presence-only data (in comparison to generalized additive models and generalized linear models) (Maxent 3.3.3k; Elith and Leathwick 2009; Phillips and Dudík 2008; Phillips et al. 2006). This approach uses occurrence data and environmental variables across a study region to determine the environmental conditions that constitute a species' abiotic ecological requirements. The resulting SDM is then used to generate probability of occurrence estimates across geographic space (Phillips et al. 2006). We interpret probability of occurrence as a measure of habitat suitability for each species, as unmeasured biotic and abiotic factors may not allow a species to reside in a predicted area despite habitat being otherwise suitable. The environmental variables used in Maxent models for each species included geology (categorical), land cover (categorical), and slope (continuous), as well as maximum annual, minimum annual, and average annual CV of streamflow and water temperature (all continuous). Although some of these environmental variables (e.g., average, maximum, and minimum annual streamflow) co-vary to some degree, Maxent has been demonstrated to be robust to such correlations, and therefore, all variables were retained for analyses (Elith et al. 2011). All crayfish localities occurred only in Alabama; thus, models were developed based on the environmental data along the stream network of the Mobile Basin that fell within Alabama, which represents the majority of the watershed (Supplementary Fig. 1). These models were then projected into the entire basin (including areas in Georgia, Mississippi, and Tennessee). Half of the localities for each species were randomly selected and used for model generation (training data) and the other half were used to validate the models (test data). We set the maximum number of iterations to 100,000 and used the default settings for all other parameters in Maxent (Phillips 2005).

Estimates of the distribution of future suitable habitat for each species were generated using contemporary SDMs projected onto future MAX_{warm}, MED_{warm}, and MIN_{warm} climate projection streamflow and water temperature data as well as contemporary geologic, slope, and land cover data. While geology and slope should be stable physical variables over the projected time period, we also assume landcover will not change. We acknowledge that landcover will likely change over the next 50 years; however, reasonable estimates of future land use changes are not available at the required resolution within the Mobile Basin.

2.6 Model and data analysis

Several measures of SDM quality and variable importance were examined for each species. Model accuracy can be determined by analyzing the area under the receiver operating curve (AUC) value, which ranges from 0.0 to 1.0 (Elith et al. 2006; Phillips et al. 2006). When training and test data are used, an AUC score is calculated for both sets of data. The training data value indicates model fit based on the data used in generating the model, while the test data AUC demonstrates the predictive capabilities of the model (Phillips 2005). An AUC value of 0.5 suggests a model that does not predict better than a random model. While no single AUC score is agreed upon as a threshold for model quality, values greater than 0.5 suggest a better than random prediction (Elith et al. 2006).

The relative contributions of each abiotic variable in determining suitable habitat for each species were also quantified based on permutation importance values, which are determined by taking each variable in turn and altering the values of that variable at training localities. The effects of these permutations are then measured by calculating the corresponding drop in training AUC and normalizing the value to produce a percentage (Phillips 2005). This method is preferable to the percent contribution of variables because it relies on permutation of the final model rather than gains in model fit based on the path in which variables were added during model development (Searcy and Shaffer 2016).

Minimum training presence threshold distributions allow for areas to be considered unsuitable or suitable with a threshold defined as the lowest probability of occurrence at which a species locality was observed. This threshold was used to calculate the length of suitable habitat (linear km) for each species under contemporary and future models across the Mobile Basin (ArcGIS 10.4.1). The length of suitable habitat (measured in linear stream km) was estimated from future distribution projections based on the RCP 8.5 MAX_{warm}, MED_{warm}, and MIN_{warm} climate scenarios. Differences among species and climate projections were assessed by comparing the percent change in habitat availability in future climates relative to contemporary distributions. Amounts of overlap between contemporary and future projections were also quantified. The percent of areas predicted to be suitable based on contemporary estimates projected to remain suitable under future climate scenarios was computed for each species to understand the degree to which distributions of viable habitat were contracting, expanding, or shifting for each species.

3 Results

Training data AUC values were greater than 0.85 for all species (Supplementary Table 2). Testing data AUC values were greater than 0.65, with models for seven of the ten species having AUC values greater than 0.85, suggesting that models were appropriate for estimating the distribution of suitable habitat across the Mobile Basin (Supplementary Table 2). While we recognize that AUC scores greater than 0.65 but less than 0.85 do not suggest relatively high model accuracy, these models are still considered to be better than random (AUC = 0.5) and the environmental variables have some predictive capacity. Therefore, we report results from models developed for all ten species to allow for examination of what degree various environmental factors explain the distributions of suitable habitat for each species.

The quantity of suitable habitat estimated under contemporary climatic conditions was variable among species (Supplementary Table 2). Assessment of SDM variable contributions

indicated that each species' distribution was regulated by a different combination of environmental conditions (Fig. 1). Geology (primary rock type) exhibited the highest permutation importance for six species, suggesting the general influence of this variable in regulating crayfish species distributions in the Mobile Basin. Maximum annual stream flow was the most important predictor variable for two species, and response curves indicated generally negative relationships between maximum flow and probability of suitability among all species (although *P. acutus* exhibited a positive relationship). Slope was the most important variable in estimating suitable habitat for *P. acutus* and *P. spiculifer*, with a negative relationship between probability of presence and slope. None of the water temperature measures were the primary factor regulating suitable habitat for a species. The total importance of streamflow and temperature were highly variable among species, ranging from a total permutation importance of 0–62% and 0–28%, respectively. Average total permutation importance was 26% for the hydrologic metrics and 11% for temperature metrics. Surrounding land cover was marginally important in determining suitable habitat, with permutation importance scores greater than 15% for four species (Fig. 1).

Minimum and maximum annual water temperatures are projected to increase based on SWAT estimates under the MIN_{warm}, MED_{warm}, and MAX_{warm} climate projections from 2060 to 2079, while the average annual CV in temperature is expected to decrease slightly (Fig. S1). Future projections of streamflow discharge are expected to be highest under the MED_{warm} scenario and increase marginally across the MIN_{warm} and MAX_{warm} scenarios relative to contemporary conditions (Fig. S1). Streamflow is also projected to become less variable as evidenced by the decrease in range and mean of average annual CV (Fig. S1).

Amounts and distributions of suitable habitat were predicted to be differentially altered based on the future climate projections, both within and among species (Figs. 2 and 3a; Supplementary Figs. 3–11). *C. coosae*, *F. validus*, and *P. acutus* exhibited changes (increase or decrease) in future distributions of at least 50% in one or more future climate scenarios. *F. erichsonianus*, *F. validus*, and *P. versutus* were the only species which were predicted to respond in a consistent manner across all future warming scenarios (i.e., experienced only expansions or contractions in suitable habitat across the three climate projections). All other species were predicted to experience both expansions and
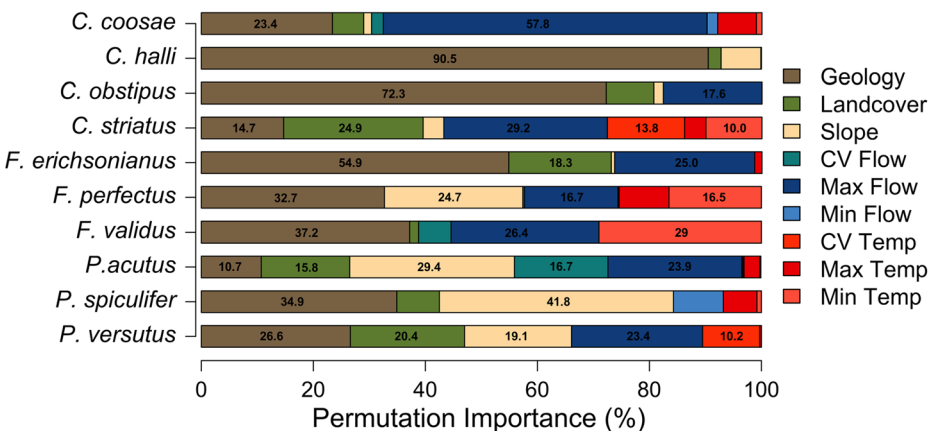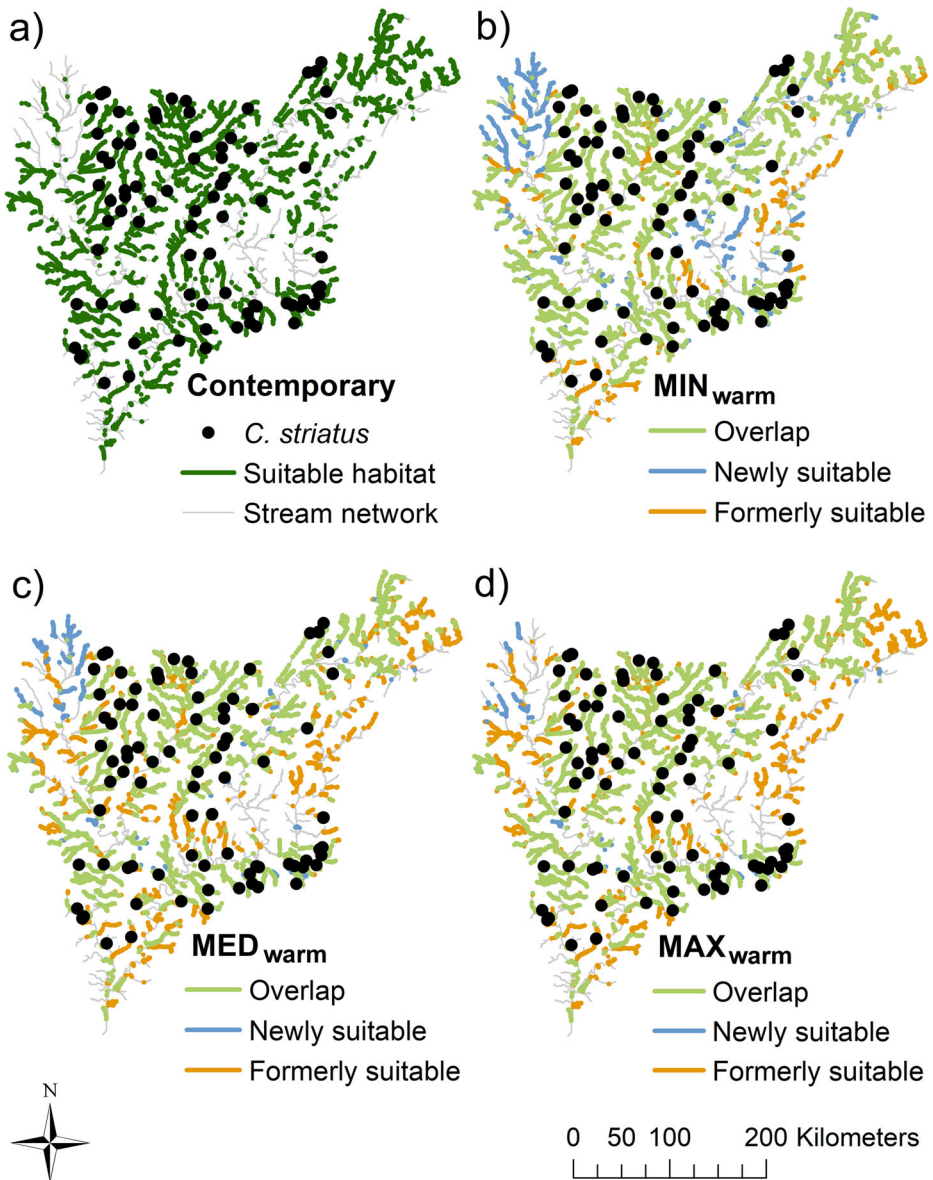

Fig. 1 Contribution of variables [permutation importance (percentage)] in Maxent models for each species

Fig. 2 Distribution of suitable habitat for *C. striatus* under (**a**) contemporary climate conditions and future climate projections (**b**) MIN$_{warm}$, (**c**) MED$_{warm}$, and (**d**) MAX$_{warm}$. Points represent species collection localities of *C. striatus*. **b–d** "Overlap" represents areas predicted to be suitable under contemporary and projected to remain suitable under the warming scenario. "Newly suitable" represents areas that were projected to be suitable in the warming scenario but were not predicted to be suitable in contemporary conditions. "Formerly suitable" corresponds to areas which were predicted as suitable under contemporary climate conditions but not projected to be suitable in the future warming scenario

reductions in suitable habitat depending on the future warming scenario utilized (Fig. 3a). Future projections of suitable habitat overlapped the contemporary distributions by 85% or greater under all three warming scenarios for three of ten species (*C. halli*, *C. obstipus*, and
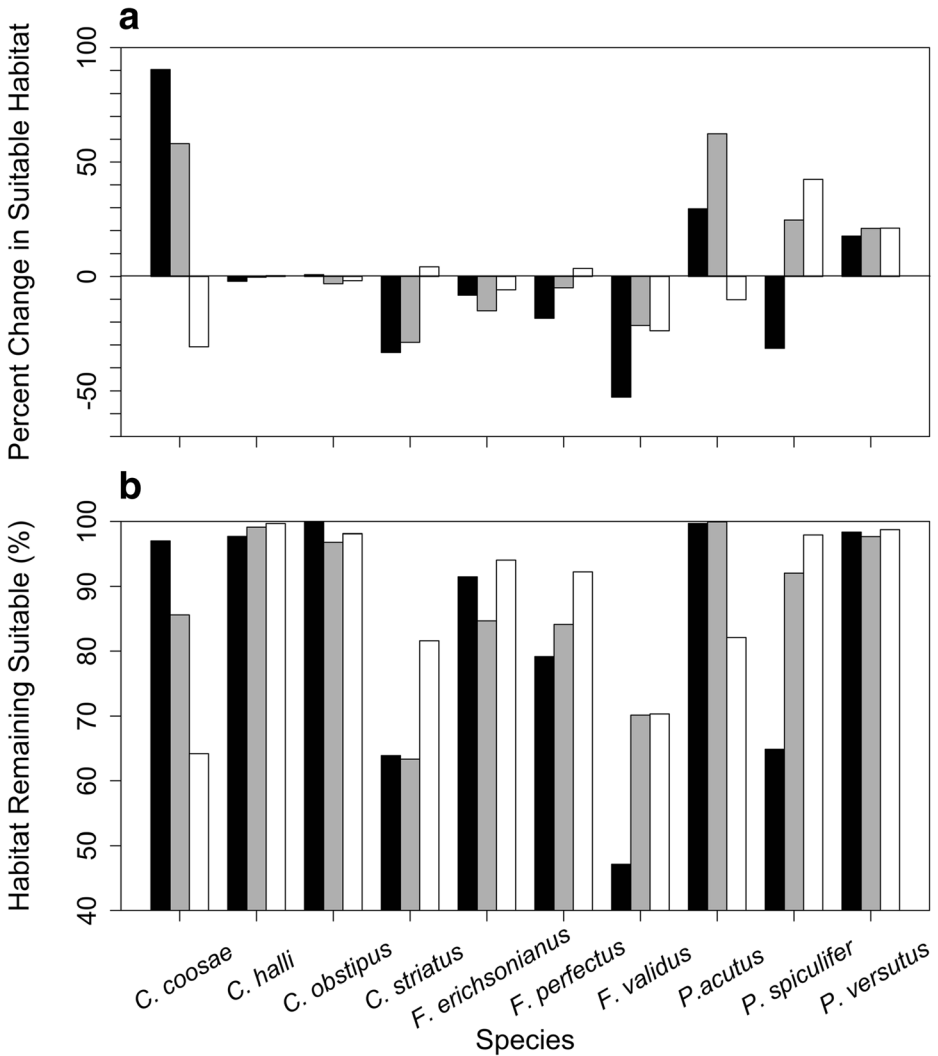
Fig. 3 Crayfish distributional responses to future climate projections. **a** Percent change in amount of suitable habitat predicted under future climate projections. Positive percent changes represent expansions in the distribution of suitable habitat and negative changes represent contractions. **b** Percentage of total original habitat predicted to be suitable under contemporary conditions that is expected to remain suitable for each species under future climate projections. Black, gray and white bars represent the MAX_{warm}, MED_{warm}, and MIN_{warm} future scenarios, respectively

P. versutus). This indicates that the distributions of suitable habitat for most species are projected to shift under future climates away from areas estimated as suitable under contemporary conditions (Fig. 3b). Some species were projected to exhibit dramatic shifts in these distributions, including *F. validus*, which was projected to have less than 50% of its contemporary distribution remaining under at least one future climate projection (Fig. 3b; Supplementary Figs. 3–11).

4 Discussion

The southeastern United States contains some of the highest levels of temperate freshwater biodiversity in the world (Knouft and Page 2011; Taylor 2002). Human transformation of the landscape and ongoing changes in climate have already altered the hydrologic characteristics and water quality of watersheds in this region (Estes et al. 2015; Neupane et al. 2019), with these changes likely contributing to the imperilment of freshwater biodiversity (Freeman et al. 2017; UK: Cambridge Univ. Press et al. 2008; Warren et al. 2000). Projected changes in climate are expected to further exacerbate these habitat impacts, including continued alteration of flow regimes and increasing water temperatures (Neupane et al. 2019; van Vliet et al. 2013). While climate-induced changes in flow and water temperature are expected to continue to alter species distributions and diversity (e.g., Knouft and Ficklin 2017; Wenger et al. 2011), the combined influence of changes in flow and water temperature on freshwater species distributions in the context of other aspects of the physical environment is not well understood.

Species and region-specific ecological and physiological data are generally lacking for most crayfish species (Moore et al. 2013), as a result, the correlative SDM approach integrating museum collection data with environmental data provides the most tractable opportunity to characterize factors regulating crayfish distributions and diversity. The applicability of SDMs is dependent on the ability of the models to discern habitat suitability (Newbold 2010). To develop accurate assessments of habitat suitability, models must incorporate a robust array of environmental predictor variables based on knowledge of the ecology of the study species (Araujo and Guisan 2006; Austin 2002). As such, we were largely able to estimate the contemporary distribution of suitable habitat for crayfish species using an array of physical and hydrologic variables. While geology generally appeared to be the best predictor of species distributions, variables related to streamflow, land cover, and topography also contributed significantly to model performance. However, water temperature does not appear to be particularly influential in regulating the distribution of these species within the Mobile Basin.

Environmental factors not influenced by climate play a critical role in governing the contemporary and future distributions of suitable habitat for crayfish species in the Mobile Basin. For example, geology is the most important predictor of habitat suitability for eight of the ten species in this study. This is likely due to crayfishes' usually strong association with varying benthic substrate/rock size (Stites et al. 2017; Taylor and Schuster 2004; Westhoff and Rabeni 2013). Slope was also important in characterizing suitable habitat for two species (*P. acutus* and *P. spiculifer*), which exhibited a negative relationship between habitat suitability and slope. This is in accordance with previous observations of habitat use in *P. acutus* (Taylor and Schuster 2004) and the observed preference of lower gradient habitats in Alabama populations of *P. spiculifer* (Schuster and Taylor, unpublished data). In addition, both slope and geology were found to be important predictors of crayfish occupancy in the Black River drainage of Arkansas and Missouri by Magoulick et al. (2017). Landcover was also included as a predictor in SDMs for several species and likely reflects a variety of processes (e.g., sedmentation regulation, nutrient runoff). Significant landcover changes have been ongoing in the southeastern United States during the past century, both as conversion to agriculture and urban areas as well as reforestation (Sleeter et al. 2012; Zhao et al. 2013), and these changes will undoubtedly continue. The impact of these changes on in-stream habitat will likely be significant in the coming decades, particularly if precipitation events become more intense (IPCC 2013). Unfortunately, high-resolution landcover change projections are not available for incorporation into our SWAT models, but this issue certainly deserves further attention.

Generally, our results suggest that when species' distributions are primarily governed by environmental factors that are not mediated by climate, projected changes in climate do not appear to greatly alter estimates of future distributions of suitable habitat compared to contemporary distributions.

The lack of species-specific physiological data for crayfishes in this study hinders our ability to comment on the limited influence of temperature on habitat suitability. While hydrology was generally not the most important predictor of suitable habitat, variables related to streamflow did explain a significant amount of variation in species distributions. In particular, maximum annual streamflow appeared to be more important than streamflow variability or minimum annual streamflow, with maximum streamflow generally exhibiting negative relationships with suitability. This result may suggest that non-burrowing crayfishes are limited in their distributions by their ability to remain adhered to the substrate rather than other hydrologic pressures (e.g., low streamflows, seasonal streamflow variability), although more work is needed on this topic. Given that future climate models often project increasing probability of high precipitation events (IPCC 2013), and that our Med$_{warm}$ and Min$_{warm}$ scenarios demonstrate higher maximum annual streamflows, crayfishes may experience greater range contractions due to increases in high flow events. Furthermore, high flow events may also increase in severity as the amount of impervious surface increases during urbanization. Further studies should be aimed at examining the feedbacks between the impacts of climate and land use change on streamflow regimes and how these changes may impact freshwater species distributions.

Future climate projections predict differing flow regimes and water temperatures across the Mobile Basin compared to contemporary conditions. These climate projections resulted in differences among predictions in the amount and distribution of suitable habitat for Mobile Basin crayfishes. Furthermore, directional responses to climate change scenarios were not consistent within species, with the distributions of suitable habitat for most species expected to contract or expand dependent upon the warming scenario used for projections. This finding is noteworthy given most studies demonstrating changes in the distributions of species under climate change are unidirectional relative to increased intensity of climate change (e.g., Bond et al. 2014). However, the variable responses of species among climate scenarios present a challenge for predicting how freshwater species dependent on streamflow will respond in the future. Additionally, projected changes in species distributions did not appear to follow a trend of northward retreat or expansion as predicted for many aquatic species as climate changes (reviewed in Knouft and Ficklin 2017), likely due to the limited influence of water temperature in the SDMs.

While Maxent models (and species distribution models in general) allow for determination of which environmental factors are associated with the distribution of taxa at various spatial scales, they do not provide a mechanistic understanding of why such conditions are important (Kearney and Porter 2009). Given the various impacts that geology can have on in-stream habitat structure and water quality (Meybeck and Helmer 1989), future research should focus on which specific factors regarding geology appear to be critical in governing suitable habitat for these species. For example, the varying porosity and sand content of particular geologic types may be of primary importance to benthic organisms. More experimental work is also needed to determine how increased maximum annual streamflow can render habitat unsuitable for some crayfishes and not others (e.g., Perry et al. 2013). Furthermore, the distribution of suitable habitat is only based on abiotic conditions and does not account for biotic interactions (Elith and Leathwick 2009), which may explain locations within the estimated area of suitable

habitat where a species does not occur (Dormann 2007). Reaches within the basin that constitute suitable habitat may also not be occupied due to inabilities of the species to disperse to these areas (Hein et al. 2011; Huntley et al. 2010); however, the connectedness of the stream network and the wide distribution of some species within the basin suggests this may not be a major constraint.

SDMs developed here suggest that the primary factors impacting distributions of crayfishes, such as geology and topography, are those which are not significantly impacted by human activities. In spite of this, crayfish are known to be experiencing significant population declines in North America (Taylor et al. 2007). While our models suggest that streamflow regimes are important in regulating habitat suitability for these species, this alone does not explain crayfish declines. Other factors that are potentially influencing these declines may include hydrologic modification of rivers by damming and the introduction of invasive species. While these factors are difficult to include in species distribution modeling, future research could benefit from the inclusion of these factors when forecasting changes in the distribution of crayfishes.

While investigation of the potential impacts of climate change on freshwater biodiversity has received considerable attention (Knouft and Ficklin 2017), a limited focus on species in relatively warmer regions has restricted our understanding of the influence of temperature on these taxa. Results from this study suggest that changes in water temperature may not be as important as changes in flow regimes and the conservation of physical habitat for freshwater species persistence in warmer regions in the coming century. This study also demonstrates the importance of selecting a range of relevant environmental variables when developing SDMs to project to potential impacts of climate change on freshwater taxa.

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