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Habitat associations and distributions of two endemic crayfishes, *Cambarus* (*Erebicambarus*) *maculatus* Hobbs & Pflieger, 1988 and *Faxonius* (*Billecambarus*) *harrisonii* (Faxon, 1884) (Decapoda: Astacoidea: Cambaridae), in the Meramec River drainage, Missouri, USA

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ABSTRACT

Understanding the habitat associations and distributions of rare species is important to inform management and policy decisions. *Cambarus* (*Erebicambarus*) *maculatus* Hobbs & Pflieger, 1988, the freckled crayfish, and *Faxonius* (*Billecambarus*) *harrisonii* (Faxon, 1884), the belted crayfish, are two of Missouri's endemic crayfish species. Both species are listed as Vulnerable (S3) on Missouri's Species and Communities of Conservation Concern Checklist due to their limited range within the Meramec River drainage (MRD) and the impact of anthropogenic activities therein. Their distributional overlap offers an opportunity for multi-species research to address gaps in information required for conservation. We sampled 140 sites throughout the MRD during the summers of 2017 and 2018 for crayfishes and associated habitat variables, which we related to crayfish presence in an occupancy modeling framework. We found that *C. maculatus* occupancy was associated with larger stream size, boulder substrate, dolomite lithology, aquatic vegetation beds, dissolved oxygen, and pool mesohabitat. *Faxonius harrisonii* occupancy increased with boulder substrate, aquatic vegetation beds, the presence of *C. maculatus*, and decreased in third-order streams. We also expanded the known range for both species within the MRD. Range estimates (watershed area) for *C. maculatus* and *F. harrisonii* were 4,347 km^2 and 3,690 km^2, respectively. This study demonstrates the importance of targeted rather than opportunistic sampling for species distribution.

Key Words: conservation, detection probability, habitat specialists, occupancy modeling, range, vulnerable species

INTRODUCTION

Crayfishes are one of the most globally threatened, and the third most imperiled, freshwater taxa in the US (Wilcove & Master, 2005; Taylor *et al.*, 2007; Richman *et al.*, 2015). Of the approximately 400 species within the US and Canada, 48% are listed as Endangered, Threatened, or Vulnerable (Taylor *et al.*, 2007). Many species are particularly vulnerable to habitat alterations due to their small range (Taylor *et al.*, 2007; Richman *et al.*, 2015). Approximately 45% of crayfishes in the US are distributed within a single state's political boundary, some within a single river drainage (Taylor *et al.*, 2007). Within these limited ranges, their distributions can be clustered and therefore vulnerable to localized

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disturbances. Information is unfortunately limited for many native crayfishes. Habitat studies have been conducted for only 10% of North America's described species (Westhoff *et al.*, 2006). Poor understanding of habitat associations and current distributions hampers conservation planning and policy decisions intended to protect aquatic diversity (Abell, 2002; Westhoff *et al.*, 2006).

Extirpation of crayfishes poses serious consequences to the function of aquatic ecosystem where they occur. Crayfishes convert basal resources (e.g., detritus) into biomass, which is then available to higher trophic levels (Huryn & Wallace, 1987; Rabeni, 1992; Usio, 2000). Crayfishes in North American headwater streams often constitute > 50% of the invertebrate biomass (Huryn & Wallace, 1987; Haggerty *et al.*, 2002) and are prey for over 200 aquatic, terrestrial, and avian species (DiStefano, 2005). Stream sport fish, such as the largemouth bass (*Micropterus salmoides* Lacepède, 1802), rock bass (*Ambloplites rupestris* Rafinesque, 1817), and smallmouth bass (*M. dolomieu* Lacepède, 1802) feed primarily on crayfishes, which may account for over 60% of the diet of these fishes (Probst *et al.*, 1984; Olson & Young, 2003; Wheeler & Allen, 2003; Roell & DiStefano, 2010). In addition to a considerable influence on the biologic community (Creed, 1994; Momot, 1995), crayfishes affect habitat structure itself through their burrowing behaviors or alteration of vegetative cover (Creed, 1994; Matsuzaki *et al.*, 2009; Willis-Jones *et al.*, 2016). Due to their collective role in aquatic food webs and as ecosystem engineers, crayfishes are considered keystone or dominant species in freshwater ecosystems (Creed, 1994; Momot, 1995; Willis-Jones *et al.*, 2016).

The freckled crayfish, *Cambarus* (*Erebicambarus*) *maculatus* (Hobbs & Pflieger, 1988) and the belted crayfish, *Faxonius* (*Billecambarus*) *harrisonii* (Faxon, 1884) are both endemic to the Meramec River drainage (MRD) in eastern Missouri, USA. *Faxonius harrisonii* was also introduced in the adjacent St. Francis River drainage, but is not widespread in the system (Westhoff, 2011; DiStefano *et al.*, 2015). *Cambarus maculatus* and *F. harrisonii* have among the smallest ranges of all crayfishes in the US and Canada (Pflieger, 1996; Taylor *et al.*, 2007), increasing their vulnerability to human activities (Taylor *et al.*, 2007; Richman *et al.*, 2015). Both species are currently categorized as Vulnerable (S3) on Missouri's Species and Communities of Conservation Concern Checklist (Missouri Department of Conservation, 2019). NatureServe lists *C. maculatus* as Apparently Secure (G4; Cordeiro *et al.*, 2010) and *F. harrisonii* as Vulnerable (G3; Cordeiro *et al.*, 2009). Conservation status for these species is largely based from opportunistic sampling events and sampling performed in the 1970s to 1980s by Pflieger (1996). Recent observations indicate that both species have declined in a considerable portion of their range due to lead-zinc mining activities (Allert *et al.*, 2013) and may be impacted by agricultural practices as well as the expanding metropolitan area of St. Louis within their drainage (Blanc, 1999; DiStefano *et al.*, 2016b). Observations of *C. maculatus* suggest they are habitat specialists and have traits of a K-strategist relative to other crayfish species (DiStefano *et al.*, 2016b), further increasing their vulnerability to environmental change. Some research suggests upgrading the conservation status for *C. maculatus* to improve protection (Crandall, 1998; Larson & Olden, 2010). Despite these concerns, very little research has been devoted to habitat associations or distribution of either species.

The first proposed strategic plan for conserving the diverse and highly endemic crayfish fauna of the US specifically highlights the need for research to document species' habitat and distributions (Taylor *et al.*, 2019). Understanding habitat associations allows managers to protect habitat important to the persistence of a species (Abell, 2002; Westhoff *et al.*, 2006). Occupancy modeling is an effective way to assess the habitat associations of a species, while accounting for error in detection, which is especially likely to occur for rare or cryptic species (MacKenzie *et al.*, 2006). Further, knowledge of a species distribution is necessary to inform policy decisions regarding its conservation (Westhoff *et al.*, 2006; Taylor *et al.*, 2019). Many state and federal agencies use the size and characteristics of a species range as a factor in determining whether a species warrants special management or protection (IUCN Standards and Petitions Subcommittee, 2014; United States Fish and Wildlife Service, 2016). Baseline distribution data allow managers to monitor changes in distribution or range size to indicate changes in the conservation status of the species. Our study therefore had two primary objectives: 1) to evaluate the habitat associations of *C. maculatus* and *F. harrisonii* through occupancy modeling, and 2) to determine and update the distribution and range of these species within the MRD. Our goal is to provide managers with the information necessary to inform future management and conservation regarding these species of conservation concern.

METHODS

Sampling area

The MRD covers an area of 10,265 km^2 within the northeast corner of the Ozark Highland Ecoregion (hereafter "Ozarks") of the US. The Ozarks are characterized by high biological diversity and endemism, with over 160 species of plants and animals found nowhere else in the world (United States Geological Survey, 2009). The Ozarks is remarkable for its rich crayfish fauna of 25 species, with 16 endemic to the region (Pflieger, 1996; Abell *et al.*, 2000). The region contains many springs and caves due to its underlining limestone and dolomite lithologies and associated karst topography (Pflieger, 1996). Mean annual rainfall in the Ozarks is typically between 104–125 cm (Woods *et al.*, 2005). The MRD land cover consists of 66% forested, 23% agriculture, 8% urban/developed, and 3% grassland/wetland (United States Geological Survey, 2014). The MRD is composed of three river sub-drainages: Big, Bourbeuse, and Meramec rivers (Fig. 1). Both the Big and the Bourbeuse rivers flow into the lower Meramec River, which then feeds into the Mississippi River just south of St. Louis, MO. Streams within the Meramec and Big rivers sub-drainages are typical Ozark streams, with coarse chert bottoms surrounded by large gravel bars and forested lands, steeper gradients, and relatively clear water under baseflow conditions. Streams in the Bourbeuse River sub-drainage are more characteristic of Ozark-prairie border streams, with silty and sandy substrate, low gradients, and increased agriculture within their floodplain (Blanc, 1999). The Big River basin drains a large portion of the Old Lead Belt, which was historically one of the largest producers of lead-zinc in the world (Missouri Department of Natural Resources, 2010). Although mining largely ceased in the 1970s, contamination from mine tailings continues to adversely affect aquatic fauna in the Big River sub-drainage (Besser *et al.*, 2007; Missouri Department of Natural Resources, 2010; Allert *et al.*, 2013).

Study timing

Crayfish sampling occurred for two field seasons from June-August 2017 and 2018. The first season (2017) focused on evaluating the habitat associations of *C. maculatus* and *F. harrisonii* through occupancy modeling (objective 1), whereas the second season (2018) focused on determining the distribution and range of the two species (objective 2). Habitat variables were measured during the first field season to facilitate the occupancy modeling. Collection of habitat variables and occupancy modeling did not occur for sites sampled during the second field season to allocate more time for sampling additional sites for distributional purposes. Because the two field seasons had different objectives, we performed different protocols for stream segment selection and crayfish sampling for each.

Stream segment and site selection for objective 1

Due to the rarity of both target species, we limited our stream segment selection (defined by Frissell *et al.*, 1986) for the first field

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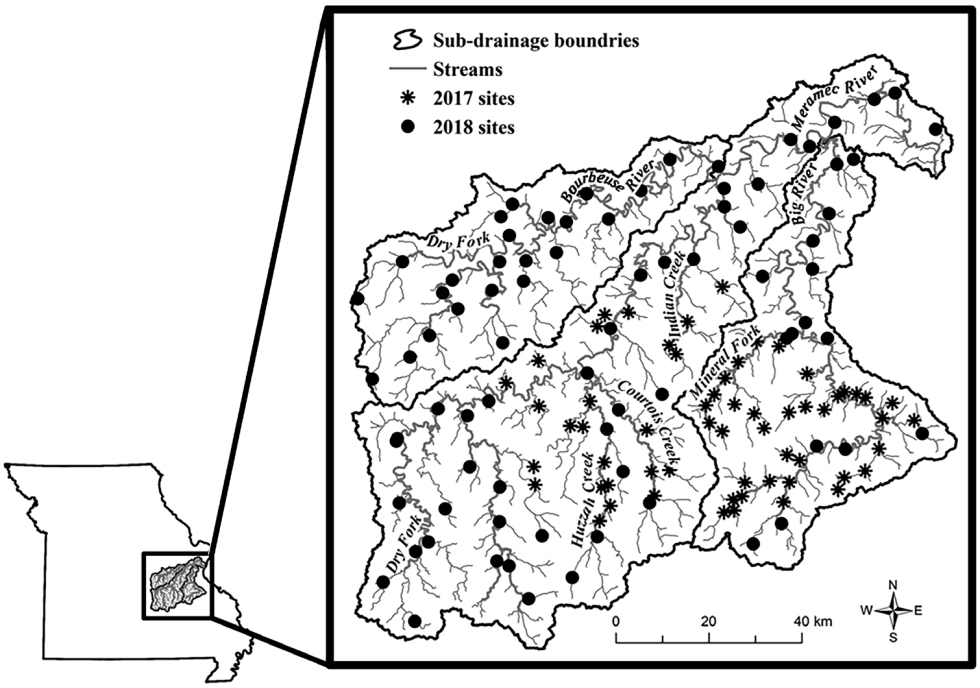

Figure 1. Meramec River drainage, Missouri with 2017 and 2018 sample sites. Black lines represent river sub-drainage boundaries between the Bourbeuse River (upper left), Meramec River (middle), and Big River sub-drainages (right).

season to an area containing the majority of previous collections (i.e., within their known range prior to this study). Stream segments were therefore selected within the Big and Meramec rivers sub-drainages and not the Bourbeuse River sub-drainage, which contained few prior collections. We narrowed the scope of our first field season to this area to obtain a ratio of occupied to unoccupied sites favorable for occupancy modeling (20–80% occupied; MacKenzie *et al.*, 2006) intended to provide insight to habitat associations within its range. We selected segments from the Big and Meramec river sub-drainages that were stream orders 2–4 (Strahler, 1957), with a minimum length of 200 m, and containing a road access point to ensure the segments were wadable, accessible, and contained flowing water. Segments were chosen through a random stratified sampling method to provide a relatively equal number of sites for each stream order. Segments were at least one river kilometer apart to reduce clumping, and bolster independence of sites.

Site locations within eligible stream segments were chosen by randomly assigning each segment a proportion between 0 and 1 (i.e., 0.1, 0.2, …0.9). This proportion was multiplied by the segment length to identify the distance downstream from the upstream boundary of the segment as the upstream boundary of the sampling site. A site consisted of a reach of stream within a stream segment containing a riffle, run, and pool mesohabitat unit sequence (although not necessarily in that order). We differentiated between riffle, run, and pool mesohabitat units according to descriptions by DiStefano *et al.* (2003). Each mesohabitat unit had a minimum longitudinal length of 17 m. If the minimum distance was not met, we extended our site downstream to the next riffle, run, and pool sequence (site then encompassed more than one mesohabitat sequence). In total, 60 sites were sampled in the first field season, with 36 in the Big River sub-drainage and 24 in the Meramec River sub-drainage (Fig. 1). Detection or non-detection of the target species was recorded for each site to evaluate occupancy probability.

Stream segment and site selection for objective 2

Sampling in 2018 supplemented detection/non-detection data from 2017 to provide an updated description of the distributions and ranges of the species (objective 2), focusing on areas of the MRD without reliable records of their presence. We sampled in 29 of the MRD's 12-digit hydrological units (HUC12s; United States Geological Survey [no date]) in 2017. For 2018, we randomly selected one stream segment in each of the remaining 71 hydrological units to ensure each HUC12 of the drainage contained at least one representative. We again selected only stream segments with a minimum length of 200 m and containing a road access point; however, we enlarged our sampling extent to include stream orders of 2–7, given results in the first season that *C. maculatus* was associated with larger streams. In addition to these randomly selected 71 segments, we sampled an extra nine segments to determine crayfish presence within observed gaps in their distributions. Sites in 2018 again included a riffle, run, and pool sequence. The location of the site within a segment was not randomly located as in 2017 sampling, but directed towards habitats with large substrate and aquatic vegetation ("best" habitat based on 2017 occupancy model results) to maximize detection probability. We sampled 80 total sites in the second field season, with 40 in the Meramec River, 15 in the Big River, and 25 in the previously unsampled Bourbeuse River sub-drainage (Fig. 1).

Crayfish sampling for objective 1

Crayfish sampling progressed from the downstream boundary of each site towards the upper boundary. The repeat sampling necessary for occupancy modeling was completed through three spatially replicated surveys in each of the three types of mesohabitat units. Replicated surveys were performed spatially rather than temporally to allot more effort towards sampling different sites within the MRD. A survey for riffle and run habitat consisted of an area 5 m long spanning the river longitudinally. Within this 5 m area, three 1 m^2 kick-seine subsamples were spaced 1 m apart longitudinally and randomly placed in one of nine crosswise proportions of the stream's wetted width. The subsamples were performed using a kick-seine method described by Engelbert *et al.* (2016). After three kick-seine subsamples were made, an additional 5 min visual timed-search ensued in each 5 m section of stream. The 5 min timed-search consisted of two surveyors using viewing

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buckets or snorkels and catching crayfishes by hand. The timed-search helped ensure crayfish presence had not gone undetected due to the random placement of the kick-seine subsamples.

We devised an altered protocol for sampling in pool habitats to accommodate greater water depth and lower velocities, which render kick-seining ineffective. Pool mesohabitats, including backwater areas, were sampled with a larger 3 m long × 1.5 m high, 3 mm mesh drag seine. Three 10 min timed-search samples using the drag seine were taken from the pool mesohabitat. Timed-search samples were directed towards the lateral, shallower pool margins and habitats with large substrate, root wads, and aquatic vegetation. Each timed-search sample took place within a 30 m longitudinal section of the pool mesohabitat. An additional visual 5 min timed-search was completed after the initial 10 min timed-search with the drag seine. This 5 min timed-search included two surveyors using viewing buckets or snorkels to target large substrate and deep pool habitat not effectively sampled with the seine within the same 30 m long area that encompassed the 10 min timed-search. In total for each site, six surveys (18 kick-seine subsamples plus three 5 min visual timed-searches) were completed in the riffle and run mesohabitats, and three surveys (three 10 min timed-searches with the drag seine, followed by three 5 min visual timed-searches) in the pool mesohabitat. Detection or non-detection was documented for each of the nine surveys to assess detection probability of the target species. In addition to the collection of the target species, densities and presence of non-target crayfish species were also recorded. All surveyors were trained in crayfish sampling procedures and identification prior to sampling to reduce observer error.

Crayfish sampling for objective 2

For the second field season, crayfish sampling was similar to the first season for stream orders 2–4. The larger stream orders (5–7) required a different approach because these streams were often not wadable. For stream orders 5–7, we performed four 15-min visual timed-searches with one sample in the riffle and run mesohabitat and three in the pool mesohabitat. Each survey was contained within a maximum longitudinal area of 50 m. The visual timed-searches consisted of two surveyors each scanning a lateral half of the river with snorkeling gear or viewing buckets to collect crayfishes by hand or with small dip nets. After each 15 min survey in the pool mesohabitat, a 10 min timed-search was made in the pool margins with the drag seine. We focused 2018 efforts on pool habitat because the majority of our 2017 target species collections occurred in pool mesohabitats.

Collection of detection and habitat variables

We recorded the mesohabitat unit type (riffle, run, or pool) and the survey method (riffle/run survey or pool survey) for each crayfish survey. Collection of all other *in situ* (local scale) habitat and detection variables ensued after crayfish sampling was completed within a site. Local-scale habitat and detection variables were measured in nine transects that spanned the stream laterally in the area where each crayfish survey occurred. Habitat variables were computed by averaging (for continuous data) or counting (for discrete data) all measurements/observations taken within a site, while detection variables were analyzed per transect. Instream habitat evaluations followed a protocol similar to that of Fitzpatrick *et al.* (1998), Bain & Stevenson (1999), Kaufmann *et al.* (1999), and Dodd *et al.* (2008). At five proportional locations along each transect, water depth and current velocity were measured using a wading rod and Hach FH950® (Hach, Loveland, CO, USA) handheld flow meter. Dominant surficial substrate size, substrate embeddedness, and presence of filamentous algae were recorded via visual survey of the streambed within a 10 cm radius of the wading rod. The diameter of the surficial substrate was classified by the modified Wentworth Scale (Bovee & Milhous, 1978; Bain *et al.*, 1985; Bain, 1999). Substrate embeddedness was described as the percent to which larger substrate particles were enclosed by finer-sized particles (Fitzpatrick *et al.*, 1998). The presence of aquatic vegetation beds and boulders (> 256 mm diameter) were recorded if present within 1 m upstream or downstream of the transect line. Bank vegetation cover was evaluated in a similar fashion, extending the 2 m wide transect onto the surrounding bank. Bank vegetation cover was visually assessed as the percent coverage of herbaceous or woody plants within the 2 m wide belt extending from the streams wetted edge to 10 m up the bank (Dodd *et al.*, 2008). Discharge was calculated for each site by measuring water depth and velocity at 10 proportions of the stream's wetted width (Dodd *et al.*, 2008), typically within the run mesohabitat where the streambed was a uniform U shape. Water quality variables, such as dissolved oxygen, conductivity, and pH were measured once at the upper end of each site using a YSI Professional Plus® (YSI Inc., Yellow Springs, OH, USA). Sediment lead concentrations were obtained from Pavlowsky *et al.* (2010).

Landscape-scale variables were collected using ArcGIS® 10.4.1 software by Esri.ArcGIS® with map layers provided by Missouri Spatial Data Information Service (http://www.msdis.missouri.edu/data/mapdata/index.html), United States Department of Agriculture (https://datagateway.nrcs.usda.gov/), and the United States Geological Survey (2005, 2014). Variables analyzed using ArcGIS software included watershed area, stream order, land cover type, and dolomite lithology. Local catchments were created for each site using the "watershed tool" to analyze watershed area, land cover type, and dolomite lithology. Percent land cover was computed for agriculture (pasture and row crop), impervious/developed, and forested land uses. Additional details about the analysis and collection of habitat data are provided by Chilton (2019).

Data analysis for occupancy modeling

Occupancy modeling was performed with habitat and crayfish presence data from a single season (2017). All variables that were considered in the occupancy modeling were initially selected because similar studies of other crayfish species indicated these variables were important to crayfish occupancy or detection (Table 1). Analyses were performed to identify strongly correlated variables (absolute value of Pearson's correlation coefficient (r) > 0.60; Evans, 1996; Supplementary material Table S1). If two or more variables were correlated, then the more general or easier to obtain variable (e.g., stream order) was kept, and the more specific variable (e.g., mean wetted width) was excluded to reduce redundancy within the models. Variables that were homogeneous across sites were also excluded from the occupancy models. These filters provided a convenient and unbiased way to reduce the number of variables included in the occupancy models to help prevent overfitting. The occupancy models included two detection variables and 12 habitat variables for *C. maculatus*, and three detection variables and 11 habitat variables for *F. harrisonii*. All continuous or discrete variables were scaled by subtracting the mean and dividing by the standard deviation. Stream order, presence of the other target crayfish species, mesohabitat unit, and survey method were treated as categorical variables and were not scaled. Stream order and mesohabitat unit included multiple categories, and one category was selected to be the reference to which changes in occupancy would be compared. For example, second-order streams were considered the reference, and coefficient estimates for third- and fourth-order streams were interpreted as the change in occupancy from a second-order stream to a third- or fourth-order stream.

A chi-square test for homogeneity of naïve occupancy rates (occupancy probability not informed by detection) indicated *C. maculatus* presence was not proportionally similar between riffle, run, and pool mesohabitat units ($\chi^2 = 15.58$, $P < 0.01$).

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Table 1. List of all detection and habitat variables collected in the study with their range of measured values for 2017 sampling sites, units of measurement, and reference to previous studies indicating these variables were potentially important to detection or occupancy of crayfishes. Not all variables were used in the occupancy models. [1]Variable included in the occupancy modeling; [2]variable excluded from the occupancy modeling due to strong correlation ($|r| > 0.60$) with another variable; [3]variable excluded from the occupancy modeling due to homogeneity (low variability) across sites.

Variable	Range (min–max)	Unit of measurement	Reference
Detection variables			
Survey method [1]	0–1	Riffle/run survey (coded as 0) or pool survey method (coded as 1)	Engelbert *et al.*, 2016
Current velocity [1]	–0.0–1.1	Meters per second	Magoulick *et al.*, 2017
Water depth [2]	1–140	Centimeters	Magoulick *et al.*, 2017
Filamentous algae [1]	0–5	Number of benthic surveys containing algae per transect	Smith *et al.*, 1996
Habitat variables			
Dissolved oxygen [1]	38–129	% saturation	Haddaway *et al.*, 2015
Conductivity [1]	51–957	Microsiemens per centimeter	Magoulick *et al.*, 2017
pH [3]	7.1–8.7	0–14 scale	Haddaway *et al.*, 2015
Stream order [1]	2–4	Strahler stream order (categorical variable with 2nd order as reference)	Nolen *et al.*, 2014
Stream wetted width [2]	1–39	Meters	Westhoff *et al.*, 2006
Stream discharge [2]	0.0–1.7	Cubic meters per second	Nolen *et al.*, 2014
Watershed area [2]	4.9–341	Square kilometers	Mouser *et al.*, 2018
Boulders [1]	0–9	Number of transects containing boulder substrate (substrate diameter > 256 mm)	DiStefano *et al.*, 2016b; Stites *et al.*, 2017
Substrate size [2]	1–6	Modified Wentworth scale (coded 1–6; fine–coarse)	Westhoff *et al.*, 2006
Embeddedness [1]	0–87.5	% coverage of largest substrate by finer particles	DiStefano *et al.*, 2008
Aquatic vegetation beds [1]	0–7	Number of transects containing beds of aquatic vegetation	Flinders & Magoulick, 2007
Bank vegetation cover [1]	10–90	% of bank covered by herbaceous or woody vegetation	Naura & Robinson, 1998
Presence of other target crayfish species [1]	0–1	Coded 0 for absent or 1 for present	Garvey *et al.*, 1994; Blank & Figler, 1996
Density of non-target species [1]	0–31.7	Average crayfishes per square meter subsample	Garvey *et al.*, 1994; Blank & Figler, 1996
Dolomite [1]	24–100	% contributing area that contains dolomite as its primary surficial lithology	Nolen *et al.*, 2014; Magoulick *et al.*, 2017
Agriculture land use [1]	0–56	% contributing area of local catchment	Frisch *et al.*, 2016
Impervious/developed land use [2]	0.6–36	% contributing area of local catchment	Dyer *et al.*, 2013; Frisch *et al.*, 2016
Forested land use [2]	35–98	% contributing area of local catchment	Magoulick *et al.*, 2017
Lead concentration [3]	0–1	Sediment Pb concentration > 128 ppm (probable effects concentration; 0 = No, 1 = Yes)	MacDonald *et al.*, 2000; Allert *et al.*, 2013
Mesohabitat unit [1]	0–3	Riffle, run, or pool (categorical with riffle as reference; coded 0–3)	Flinders & Magoulick, 2007

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Naïve occupancy rates revealed *C. maculatus* was far more likely to inhabit pools than other mesohabitat units (Fig. 2). Preliminary model results indicated the significant difference in naïve occupancy rates was due to a change in occupancy rate and not detection probability between the three mesohabitat units. We therefore redefined a site for the *C. maculatus* occupancy model to a mesohabitat unit scale to maintain consistent occupancy probability between our surveys, which is an important assumption of the occupancy modeling framework. Each mesohabitat unit was considered its own site, with three spatially replicated surveys for a total of 180 sites to be used in the *C. maculatus* occupancy model. To account for lack of independence among adjacent mesohabitat units within the same stream segment, we included the previous site numbering (1–60) in the model as a random effect. The chi-square test was not significant for naïve occupancy rates between the three mesohabitat units for *F. harrisonii* ($\chi^2 = 2.43$, $P = 0.30$), however, rates were significantly different between the two sub-drainages (Big and Meramec river; $\chi^2 = 14.95$, $P < 0.01$). We therefore treated sub-drainage as a random effect in the *F. harrisonii* occupancy model to account for the apparent difference in occupancy probability between the two sub-drainages. The occupancy rates were similar between the Meramec River and Big River sub-drainage for *C. maculatus* ($\chi^2 < 0.01$, $P = 1.00$), therefore we did not include sub-drainage as a random effect in the *C. maculatus* model. Yates continuity correction (Yates, 1934) was used in the chi-square test for comparing naïve occupancy rates between the two sub-drainages.

We conducted the occupancy modeling using a Bayesian hierarchical approach performed in the statistical program R (R Core Team, 2017) with the jagsUI package (Kellner, 2017) using code developed by Kéry & Schaub (2012). We specified vague normal priors with a variance of 200 for all habitat and detection parameters. To obtain a large effective sample size (n eff) for each estimate, we performed the modeling with 3 Markov chains, 2 million iterations, a thin-rate of 5, and 400,000 burn-ins. This yielded a net of 960,000 samples from the posterior. The models would converge with less iterations, but more iterations yielded estimates that were more consistent and with larger effective sample sizes. We used a single model containing all selected detection and occupancy predictors for each crayfish species, rather than performing model selection (similar to Hobbs *et al.*, 2012). This technique allowed us to compare relative importance of different habitat variables to occupancy of the target species. We tested the single model for lack of fit by calculating a Bayesian *P*-value and variance inflation factor ($\hat{c}$ statistic). The Bayesian *P*-value is defined as the probability that the simulated data are more extreme than the observed data, and values close to zero or one indicate lack of fit (Gelman *et al.*, 2004; Hobbs *et al.*, 2012). Overdispersion occurs when important parameters are missing from the model or parameters are not independent, and is indicated when the $\hat{c}$ statistic exceeds one (Burnham & Anderson, 2002; Kéry & Schaub, 2012). Bayesian *P*-value and $\hat{c}$ values were close to 0.5 and 1, respectively, so we concluded that the fit of our models was reasonable for the comparison of parameter coefficient estimates. No interactions between parameters were investigated in this study due to the potential to over-parameterize the models. We assessed relative importance of the parameter by comparing standardized coefficient estimates and their associated 90% credible intervals. A parameter was considered significant to occupancy or detection of the crayfish species when its 90% credible interval did not overlap zero.

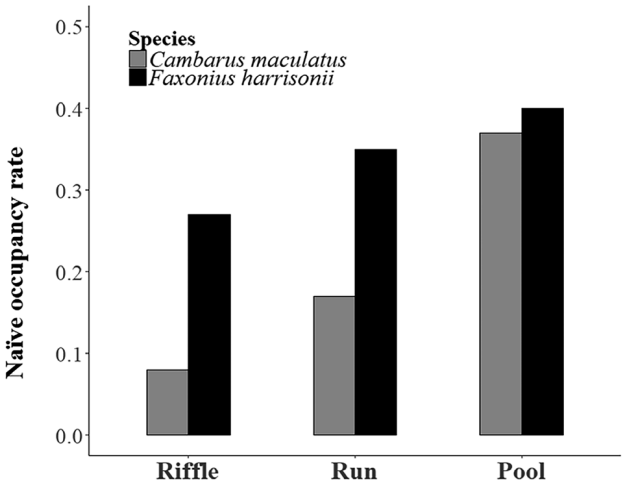

Figure 2. Naïve occupancy rates for *Cambarus maculatus* and *Faxonius harrisonii* within different mesohabitat units during 2017 sampling in the Meramec River drainage, Missouri.

Analyzing distribution & range

Universal Transverse Mercator (UTM) coordinates were recorded at the upper and lower boundary of each site. The upper boundary coordinates were mapped with ArcGIS® 10.4.1 software to illustrate capture locations of the target crayfish species. The crayfish detection/non-detection information from our sampling in 2017–2018 was combined with recent data collected by the Missouri Department of Conservation (MDC) from 2012–2017 to depict the current distribution of the crayfishes within the MRD. Alternatively, data collected prior to 2012 (1977–2011; Missouri Department of Conservation, 2017) were considered historical data. These data were not all collected with an extensive sampling protocol, but rather contain largely detection data from various opportunistic sampling events. An estimate of range was created by mapping all HUC12s that contained at least one location where crayfish were detected. We used this technique to compare the range sizes (watershed area) between our target species using historical and current data.

RESULTS

Occupancy & detection probability

Naïve occupancy rates for *C. maculatus* and *F. harrisonii* were 0.47 and 0.45, respectively, in the first season of crayfish sampling within their formerly known range, and 0.30 and 0.33 in the second season, which occurred throughout the MRD. *Cambarus maculatus* was found in higher-order streams in 2017, and *F. harrisonii* was more prevalent in the Big River sub-drainage (Table 2). In 2018, both species occupied mainstem reaches of stream orders 5–7 more often than smaller tributaries of orders 2–4. *Faxonius harrisonii* was again more common in the Big River sub-drainage than in other sub-drainages, with 73% of sites in the Big River sub-drainage containing *F. harrisonii*. The Bourbeuse River sub-drainage contained the lowest naïve occupancy rate, where *C. maculatus* and *F. harrisonii* were collected at only 16% and 20% of sites, respectively. *Faxonius harrisonii* was more locally abundant than *C. maculatus*. In total, 585 individual *F. harrisonii* were captured compared to 270 *C. maculatus*. Crayfish densities (crayfish per 1 m^2) within all kick-seine subsamples were 0.06 for *F. harrisonii* and 0.01 for *C. maculatus* (see Supplementary material Table S2 for estimates of crayfish density).

Predicted mean estimates of occupancy probability (Ψ) from the models were 0.26 for *C. maculatus* and 0.51 for *F. harrisonii*. Note that the definition of a site was different for the two species (mesohabitat unit for *C. maculatus*, and riffle-run-pool sequence for *F. harrisonii*). Predicted detection probability (P) for a survey was 0.46 for *C. maculatus* and 0.43 for *F. harrisonii*. The only factor that affected crayfish detection (90% credible interval non-overlapping zero) was the survey method used to collect *F. harrisonii* (Table 3),

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Table 2. A comparison of naïve occupancy rates for *Cambarus maculatus* and *Faxonius harrisonii* in different stream orders and sub-drainages of the Meramec River drainage, Missouri for 2017 and 2018 field seasons. The table also includes the total number of sites sampled for different stream orders and sub-drainages in 2017 and 2018.

	2017			**2018**		
	C. maculatus	*F. harrisonii*	no. of *sites*	*C. maculatus*	*F. harrisonii*	no. of *sites*
Second-order	0.15	0.40	20	0.11	0.17	18
Third-order	0.50	0.32	22	0.10	0.14	21
Fourth-order	0.78	0.67	18	0.08	0.08	12
Fifth-order	N/A	N/A	0	0.53	0.47	15
Sixth-order	N/A	N/A	0	0.80	0.80	5
Seventh-order	N/A	N/A	0	0.78	0.89	9
Big	0.47	0.67	36	0.40	0.73	15
Meramec	0.46	0.13	24	0.35	0.25	40
Bourbeuse	N/A	N/A	0	0.16	0.20	25
All sites	**0.47**	**0.45**	**60**	**0.30**	**0.33**	**80**

with a positive relationship between *F. harrisonii* detection probability and timed-search surveys in pool mesohabitat.

Habitat associations

For *C. maculatus*, fourth-order streams, boulders, dolomite, aquatic vegetation beds, dissolved oxygen, and pool mesohabitat were positive predictors of occupancy (Table 3, Fig. 3A). Fourth-order streams had the largest coefficient estimate and therefore the strongest relationship to crayfish presence. There was also a strong relationship between *C. maculatus* occupancy and the number of transects containing boulders. The occupancy model portrayed a weaker relationship for aquatic vegetation beds, pool mesohabitat, and dissolved oxygen, with 90% credible intervals nearly overlapping zero.

Faxonius harrisonii occupancy was negatively associated with third-order streams and positively associated with boulders, aquatic vegetation beds, and the presence of *C. maculatus* (Table 3, Fig. 3B). The presence of *C. maculatus* had the largest coefficient estimate in the model; however, the relationship was less certain with wider ranging 90% credible intervals. There was once again a strong association between number of transects containing boulders and crayfish presence, but less pronounced than in the *C. maculatus* model. Sub-drainage (treated as a random effect) also had a substantial influence on *F. harrisonii* occupancy. *Faxonius harrisonii* had a negative relationship with the Meramec River sub-drainage and a positive relationship to the Big River sub-drainage (Table 3).

Distribution & range of crayfishes in the MRD

In total, 140 sites were sampled for crayfish presence throughout the MRD (Fig. 1). The Meramec River sub-drainage covered the largest watershed area and therefore contained the most sites (64), followed by the Big (51) and the Bourbeuse (25) sub-drainages. Our sampling detected *C. maculatus* and *F. harrisonii* within 34 and 37 stream segments, respectively, where they had not been previously detected (Fig. 4). *Cambarus maculatus* was undetected within one segment in the Bourbeuse River sub-drainage, and *F. harrisonii* was undetected at four segments within the Big River sub-drainage where they were historically present. New areas of the MRD with *C. maculatus* detections included headwaters of the Meramec River and the lower reaches of all three sub-drainages. New collections of *F. harrisonii* were from the lower Bourbeuse River and throughout the mainstem of the Meramec River. Historically (1979–2011), the majority of *F. harrisonii* collections occurred in the Big River sub-drainage with only a few isolated occurrences in the Bourbeuse River and Meramec River sub-drainages. Current data (2012–2018; Fig. 4B, D) revealed crayfish distributions are more connected between the three sub-drainages than previous data indicated (Fig. 4A, C). Similar to the distribution maps, the range maps, represented as HUC 12 watershed area, illustrated a larger known range throughout the MRD for both species (Fig. 4). The estimated range size using historical collection data (1977–2011) of *C. maculatus* was 2,156 km^2 compared to their current range (2012–2018) of 4,347 km^2. The known range of *F. harrisonii* also increased from a historical range of 1,536 km^2 to a current range of 3,690 km^2. The target species were sympatric within 31 sites, and 3,523 km^2 of their current ranges overlapped.

DISCUSSION

Occupancy models predicted moderate levels of occupancy and detection probability for both species. Occupancy probabilities were estimated from an area of the MRD containing the majority of previous collections of the species (Big and Meramec river sub-drainages), and therefore, were likely greater than probabilities outside of this area (Bourbeuse River sub-drainage). Naïve occupancy rates for *F. harrisonii*, differed substantially among the three sub-drainages. This species was commonly collected within the Big River sub-drainage but rarely found within the Meramec River or Bourbeuse River sub-drainages. Pool surveys were crucial to the collection of both species. The target species were often observed within bluff pools, which typically contained greater water depths and larger substrate. The aggressive behavior and slow maneuverability of *C. maculatus* facilitated their collection by hand after dislodging boulder substrate. *Faxonius harrisonii* was more agile and most effectively sampled with the drag seine in pool surveys. Rice *et al.* (2020) also noted the importance of sampling pool mesohabitat, which is often unrepresented in lotic crayfish surveys. We recommend future sampling for these species include pool surveys, since this was related to both occupancy and detection probability. In contrast to Magoulick *et al.* (2017), we did not find a significant relationship between current velocity and detection probability. Current velocity is likely to be important in larger streams (stream orders 5–7), which were not included in 2017 sampling. Other detection variables not investigated in our models are likely to influence detection of the target species. We were unable to assess water turbidity, which would likely affect visual timed-searches.

Occupancy of both species was related to stream size, presence of boulder substrate, and aquatic vegetation, indicating habitat restoration or improvement projects might benefit *C. maculatus* and *F. harrisonii* simultaneously. *Cambarus maculatus* was found more often in higher-order streams (4–7), favoring mainstem areas of

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Table 3. Results from *Cambarus maculatus* and *Faxonius harrisonii* occupancy models. The table includes mean coefficient estimate (β_i) values, standard deviations (SD), and 90% credible intervals (CI) for each parameter. Credible intervals that do not overlap zero (significant) are bolded.

	***C. maculatus* model**			***F. harrisonii* model**		
Parameter	**Estimate**	**SD**	**90% CI**	**Estimate**	**SD**	**90% CI**
Occupancy parameters						
Mean constant term (β_0)	–26.08	5.16	**(–34.81, –17.86)**	–0.73	6.33	(–11.13, 9.68)
Constant term (β_0) for Meramec	N/A	N/A	N/A	–16.88	6.42	**(–28.07, –7.03)**
Constant term (β_0) for Big	N/A	N/A	N/A	14.90	6.95	**(2.30, 25.89)**
Third-order stream	6.43	4.48	(–1.10, 13.62)	–10.59	5.25	**(–19.50, –2.12)**
Fourth-order stream	26.43	6.35	**(16.47, 37.28)**	–1.13	11.15	(–17.18, 19.53)
Boulders	12.85	3.33	**(7.81, 18.70)**	7.36	3.81	**(1.98, 14.35)**
Dolomite	7.41	2.95	**(2.92, 12.54)**	2.16	4.77	(–5.94, 9.57)
Agriculture	–2.93	2.32	(–6.87, 0.73)	0.93	4.86	(–5.26, 11.28)
Aquatic vegetation beds	4.78	2.87	**(0.38, 9.69)**	7.94	4.59	**(0.40, 15.64)**
Embeddedness	1.68	2.34	(–1.81, 5.76)	11.91	6.54	(–0.69, 21.18)
Bank vegetation cover	1.41	2.08	(–1.87, 4.93)	–3.86	3.36	(–9.43, 1.31)
Dissolved oxygen	4.17	2.62	**(0.12, 8.67)**	–5.42	4.44	(–12.64, 2.12)
Conductivity	0.34	2.13	(–3.28, 3.66)	–1.59	2.62	(–6.24, 2.27)
Non-target density	1.90	2.03	(–1.40, 5.26)	–7.24	6.36	(–15.52, 7.03)
F. harrisonii presence	0.08	3.77	(–6.20, 6.14)	N/A	N/A	N/A
C. maculatus presence	N/A	N/A	N/A	13.86	7.64	**(0.71, 26.45)**
Run mesohabitat unit	–1.32	4.10	(–8.37, 4.95)	N/A	N/A	N/A
Pool mesohabitat unit	6.59	3.93	**(0.53, 13.26)**	N/A	N/A	N/A
Detection parameters						
Constant term (β_0)	–0.17	0.23	(–0.55, 0.19)	–0.65	0.17	**(–0.93, –0.37)**
Filamentous algae	–0.34	0.21	(–0.68, 0.00)	0.14	0.16	(–0.12, 0.41)
Current velocity	–0.25	0.24	(–0.63, 0.14)	–0.17	0.17	(–0.46, 0.10)
Survey method	N/A	N/A	N/A	1.08	0.30	**(0.59, 1.58)**
Detection and occupancy probability						
Occupancy probability (Ψ)	0.26	0.02	**(0.23, 0.30)**	0.51	0.02	**(0.47, 0.55)**
Detection probability (p)	0.46	0.05	**(0.37, 0.55)**	0.43	0.03	**(0.38, 0.49)**

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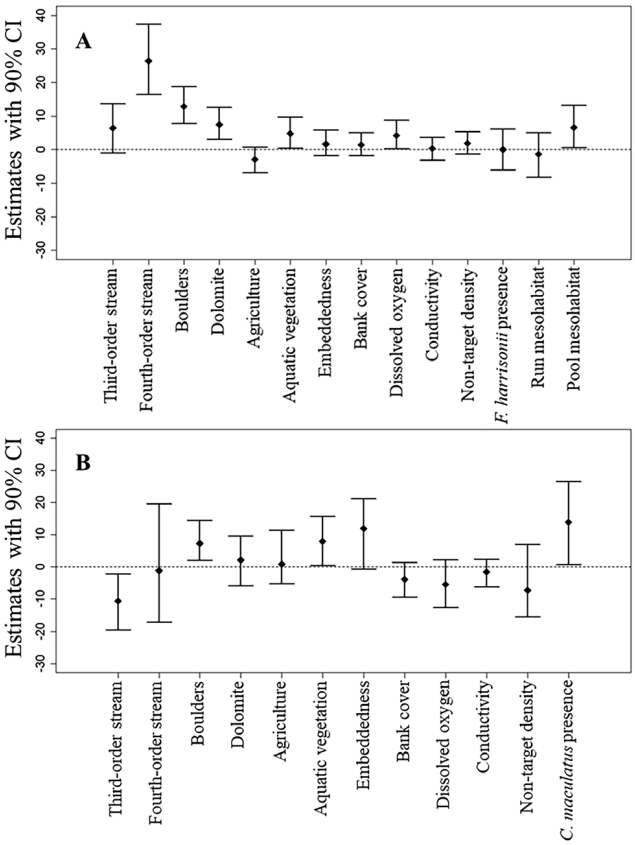

Figure 3. Mean coefficient estimates (β_i) and their associated 90% credible intervals (CI) for habitat parameters analyzed in the *Cambarus maculatus* occupancy model (**A**) and *Faxonius harrisonii* occupancy model (**B**).

the drainage over smaller tributaries. Nolen *et al.* (2014) observed a similar relationship between larger stream orders and presence of *C. hubbsi* (Creaser, 1931) and *F. eupunctus* (Williams, 1952) in the Black River drainage, and Rice *et al.* (2020) detected *F. eupunctus* in only fourth-order and larger streams in the Eleven Point River drainage. *Faxonius harrisonii* generally followed the same pattern; however, the occupancy model indicated a negative association with third-order streams. *Faxonius harrisonii* was not observed in second- or third-order streams within the Meramec River sub-drainage, but was often found within smaller tributaries of the Big River sub-drainage. Further investigations would be needed to identify the underlining mechanism for the absence of *F. harrisonii* within third-order streams, especially within the Meramec River sub-drainage. A different metric of stream size (e.g., watershed area, discharge, or mean wetted width) might have revealed more about this relationship. A study by Mouser *et al.* (2018) found watershed area was an important predictor of occurrence for *Faxonius* species in the Ozarks.

The results of the occupancy models confirmed DiStefano *et al.* (2016b), who noted *C. maculatus* favored large substrate. Boulder (> 256 mm diameter) was the dominant substrate type in 6% of benthic habitat surveys, yet 94% of *C. maculatus* and 82% of *F. harrisonii* captures occurred in surveys containing at least one boulder. Although both species were associated with boulder substrate, we observed *C. maculatus* most often underneath very large boulders, whereas *F. harrisonii* was frequently located in large cobble to small boulder sized substrate. The two species may be partitioning their use of substrate sizes, facilitating sympatry within sites. This observation may be worthy of further investigation with a finer assessment of substrate size. Westhoff *et al.* (2006), Flinders & Magoulick (2007), and DiStefano *et al.* (2008) also observed an association between large substrate and crayfish presence in Ozark streams. Siltation of reaches containing large substrate is a potential threat to these species, as it clogs interstitial spaces around large substrate (DiStefano *et al.*, 2008). Surprisingly, embeddedness of substrate, bank vegetation cover, and agriculture land use were not significant predictors for either species. We hypothesize these variables were not significant because our sampling extent in 2017 did not include the Bourbeuse River sub-drainage, which contains a greater composition of agriculture land use and fine sediment than the Big and Meramec rivers sub-drainages. Despite uncertainty, some evidence suggests agriculture land use does impact presence of *C. maculatus*. The majority (91%) of posterior samples for agriculture land use in the *C. maculatus* occupancy model were negative, indicating a potential negative association with *C. maculatus* presence. Increased agriculture land use within the Bourbeuse River sub-drainage relative to the other sub-drainages, may explain the observed lower naïve occupancy rates within the sub-drainage during 2018 sampling; however, this hypothesis would require further testing. Aquatic vegetation beds were weakly (90% credible intervals nearly overlapping zero) associated to presence of both species. Aquatic vegetation beds, often consisted of *Justicia* spp. (water willow), appeared to provide quality habitat for crayfishes, especially when accompanied by large substrate. Aquatic vegetation offers a potential refuge and source of food for some juvenile Ozark crayfishes (DiStefano *et al.*, 2003; Flinders & Magoulick, 2007).

Cambarus maculatus was also associated with dolomite lithology. Nolen *et al.* (2014) and Magoulick *et al.* (2017) noted dolomite lithology as a significant predictor of Ozark crayfish species and discussed the potential importance of surficial lithology to water quality variables such as conductivity and pH. *Cambarus maculatus* occupancy was also positively associated with higher levels of dissolved oxygen. Our assessment of dissolved oxygen included only one measurement within each site, which can be influenced by time of day and water temperature. We recommend the collection of recurring dissolved oxygen measurements over time within sites to gain a better understanding of this relationship. Because interspecific competition of crayfish species is well documented (Garvey *et al.*, 1994; Blank & Figler, 1996; Pearl *et al.*, 2013), the positive association between *F. harrisonii* and *C. maculatus* presence was unexpected. Pflieger (1996) also noted an association of occurrence between *F. harrisonii* and *C. maculatus*. Westhoff & Rabeni (2013) similarly observed little evidence of competitive exclusion between *F. quadruncus* (Creaser, 1933) and *F. hylas* (Faxon, 1890) within sympatric locations in the St. Francis River drainage of Missouri. The association between the target species is probably because they both inhabit similar habitat types rather than a mutualistic relationship between them.

Other habitat variables not evaluated in our occupancy models are probably important to crayfish presence and may require investigation. Allert *et al.* (2013) revealed decreased crayfish survival and densities with increased heavy metals concentration within mining impacted areas of the Big River sub-drainage. It is likely that metal concentrations influence crayfish presence, but our study design was not intended to assess this relationship. We also did not have adequate sample sizes to investigate possible ontogenetic shifts in habitat use, which generalizes our model to the species level, but may fail to identify factors important to individual life stages. This is worthy of further investigation, as DiStefano *et al.* (2003) reported ontogenetic shifts in macrohabitat use of juvenile and adult Ozark crayfishes. We also caution against the use of our occupancy model as a predictive model outside of the range of our sampling extent. Our sampling extent included data collection during the summer months of June-August in daylight hours. It is unknown whether the target species occupy different habitat seasonally or nocturnally.

Our efforts increased the known range for both crayfish species, most likely due to limited sampling of the MRD in previous

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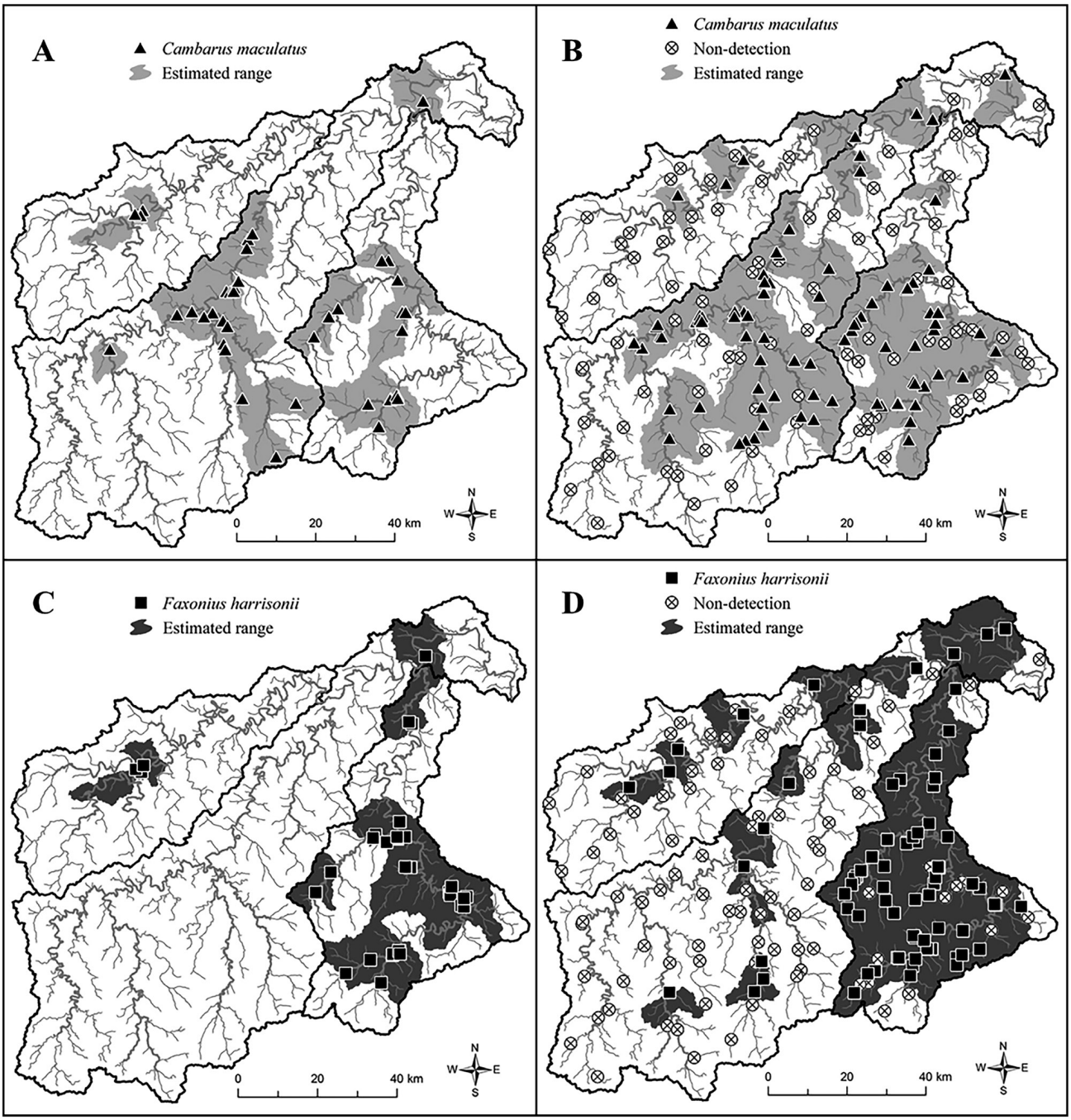

Figure 4. Distribution and range maps for *Cambarus maculatus* from 1977–2011 (**A**) and 2012–2018 (**B**), and for *Faxonius harrisonii* from 1979–2011 (**C**) and 2012–2018 (**D**) in the Meramac River drainage, Missouri.

years, rather than range expansion. Estimates of species range and distribution are likely underestimated, since we did not account for error in detection and were unable to sample all streams within the drainage. *Cambarus maculatus* was observed to be more locally rare, but had a larger estimated range by 657 km^2 than *F. harrisonii*. Almost all (95%) of the current range of *F. harrisonii* overlapped with that of *C. maculatus*, indicating conservation efforts and future monitoring can occur concurrently for both species. Our study revealed a more extensive and connected distribution for these species among the sub-drainages than formerly known. Interconnection of different crayfish populations within the MRD is likely important for the continued survival of the species by allowing genetic flow and recolonization of extirpated reaches. Prior to our study, *F. harrisonii* was believed to exist almost exclusively in the Big River sub-drainage (Pflieger, 1996), and populations of *C. maculatus* in the sub-drainages appeared isolated from one another (Missouri Department of Conservation, 2017). Conservation efforts for these two species might have overlooked the Bourbeuse River sub-drainage entirely, if extensive sampling had not revealed several new occupied locations within the sub-drainage, thus demonstrating the importance of targeted rather than opportunistic sampling for species distribution. Studies by Kilian *et al.* (2010), Taylor *et al.* (2011), and Egly & Larson (2018) also resulted in amendments to range estimates, further highlighting the importance of targeted crayfish sampling.

Our study revealed two crayfishes that were previously unknown to occur in the MRD; *Creaserinus fodiens* (Cottle, 1863) (digger crayfish) and *Procambarus acutus* (Girard, 1852) (white river

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crawfish). *Procambarus acutus* was captured at two sites in the upper Meramec River sub-drainage; *C. fodiens* was found at several sites within the middle portion of the Bourbeuse River sub-drainage. *Creaserinus fodiens* is listed as a Species of Conservation Concern in Missouri (Missouri Department of Conservation, 2019). It is native to some adjacent river systems and could potentially have been overlooked in historical sampling in the Bourbeuse River sub-drainage, especially since it is a primary burrowing crayfish that can be difficult to capture (Pflieger, 1996). *Procambarus acutus* is invasive to several locations outside of its native range of the Mississippi lowlands (DiStefano *et al.*, 2015). It was commonly sold as fish bait in Missouri prior to 2013 (DiStefano *et al.*, 2009; 2016a) and could have been spread to the upper Meramec River sub-drainage through bait bucket introductions (DiStefano *et al.*, 2015).

Despite the increase in the known range of both species within the MRD, their range remains comparatively small, and the species remain vulnerable to extirpation. The MRD is impacted by habitat alterations due to the growing metropolitan area of St. Louis, historical lead-zinc mining, and agriculture practices (Blanc, 1999; Allert *et al.*, 2013; DiStefano *et al.*, 2016b). We therefore recommend monitoring of *C. maculatus* and *F. harrisonii* to periodically reassess their conservation status designation.

The overlapping ranges of our study crayfishes provided a rare opportunity for a combined study with complementary information to inform assessment of both their ecology and overall status for conservation purposes. Due to the imperilment of aquatic species (Ricciardi & Rasmussen, 1999; Dudgeon *et al.*, 2006), agencies such as the U.S. Fish and Wildlife Service have an increased number of candidate species to evaluate for potential protection. Our study indicates species with overlapping ranges provide an opportunity for agencies to engage in multi-species status assessments, thereby gaining valuable information in a cost-effective manner.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Crustacean Biology* online.

S1 Table. Pearson's correlation coefficient (r) matrix for habitat variables collected during 2017 field season.

S2 Table. Crayfish density within kick-seine subsamples during the 2017 and 2018 sampling seasons.

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