The invasive Ringed Crayfish: understanding occurrence patterns in the southwest Ozark Highlands

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ABSTRACT

Invasive species are one of the largest drivers of declining biodiversity in stream ecosystems worldwide; however, factors explaining successful invasions are poorly understood. Ringed Crayfish *Orconectes neglectus* is non-native in many areas and its success as an invader has been hypothesized to be due to biotic factors (i.e., competition), but this has never been confirmed. However, I hypothesized persistence of Ringed Crayfish may instead be due to abiotic factors. Therefore, my objective was to identify environmental factors related to the relative abundance of the Ringed Crayfish in streams of the southwest Ozark Highlands where it is native. Crayfish were collected from 14 streams using tow-barge electrofishing and kick-seining. I used multiple linear regression to examine the relationship between landscape factors (e.g., geology, percent agriculture, soil texture, distance to impoundment, catchment size, stream segment drainage, water temperature) and the relative abundance of Ringed Crayfish within its native range. My results indicated that shale lithology and possibly warm water temperatures are negatively related to relative abundance of Ringed Crayfish. This research aids managers in understanding what abiotic conditions may foster or inhibit the successful invasion of Ringed Crayfish outside their native range.

INTRODUCTION

Biodiversity supports proper ecosystem functioning and in turn promotes ecosystem services. Biodiversity is a measure of the number of different kinds of living organisms considered at all levels of organization: genetic, species, and higher taxonomic-level variation. Diversity benefits proper ecosystem functioning in several ways including nutrient cycling, stability, and productivity (Cardinale 2012). Diverse ecosystems cycle more nutrients more efficiently than less specious systems and are buffered from drastic changes because they contain keystone species (Cardinale 2012). Properly functioning ecosystems provide many ecosystem services such as food and water provision, disease resistance, nutrient and waste management, climate regulation, and recreational services (Corvalán et al. 2005). Several factors threaten the diversity of stream ecosystems including land-use changes, the spread of invasive species, and climate change (Sala 2000).

Crayfish, a keystone species, are vulnerable to many of these threats (Dyer et al. 2013). A keystone species plays a crucial role in the functioning of an ecosystem that is disproportionate to their relative abundance (Paine 1966). Crayfish act as both predator and prey within a system and are a major processor of organic matter (Momot 1995). For example, crayfish are an important prey species and can comprise > 60% of the caloric intake of adult Smallmouth Bass *Micropterus dolomieu* (Rabeni 1992). In addition to being consumed, crayfish may also compete with fish for food (e.g., Rainbow Trout *Oncorhynchus mykiss*; Momot 1995). Crayfish also consume detritus and plant material, which makes them an important processor of carbon in stream ecosystems (Momot 1995). The importance of crayfish to ecosystem functioning is particularly important in areas of the world where crayfish diversity is high.

North America has high crayfish diversity, but many species have narrow ranges, increasing their extinction risk. Over 70% (363 of 500) of all crayfish species occur in North America (Taylor 2007). Within North America, two species are presumed to be extinct, 66 are endangered, 52 are threatened, and 54 are classified as vulnerable (Taylor 2007). Almost half of the crayfish species in North America only occur within one state's political boundaries (Taylor 2007). Smaller populations of animals naturally have higher risks of extinction (Pimm 1988) and this includes many crayfishes. Increased extinction risk, coupled with anthropogenic threats (e.g., habitat alteration, introduced species; Jones and Bergey 2007), poses a significant problem for the persistence and conservation of these species.

Climate change, habitat loss, and invasive species are major threats to crayfish diversity. Dyer et al. (2013) suggested that climate change could affect species differently with range expansion for some species and range contractions for others. Contreras-Balderas and Lonzano-Vilano (1996) documented the extinction of undescribed crayfish species in Mexico due to habitat loss attributed to human water use. Climate change and habitat loss are significant threats to crayfish persistence in the United States, but interactions with invasive species are as considered the greatest threat (Lodge 2000). For example, the invasive Rusty Crayfish *Orconectes rusticus* negatively affects fish, benthic algae, aquatic macrophytes, and aquatic invertebrates in the United States by reducing their abundance (Olden et al. 2006).

Introductions of non-native crayfish have been documented throughout North America (e.g., Rusty Crayfish, Viral Crayfish *Orconectes virilis*, Red Swamp Crayfish *Procambarus clarkii*; Larson and Olden 2011), but our understanding of the mechanisms related to successful invasions is lacking. Although successful invasions are rare (Williamson and Fitter 1996a), when they do occur, the consequences on native species can be disastrous as observed with the invasion of the Rusty Crayfish. At the most basic level, for a species to successfully invade a new habitat it must be transported from one area to another, become established (i.e., reproduce) in the novel habitat, and then spread to other regions (Kolar and Lodge 2001). Successful invaders share common characteristics including widespread distributions (Williamson and Fitter 1996b), and a wide range of physiological tolerances (Marchetti 2004). Successful invasions typically involve multiple introduction events with numerous individuals released during each event (Kolar and Lodge 2001). Understanding what makes a species a successful invader and how successful invasions occur provides a means to predict future invasions or range expansions, and may provide options for population control.

The Ringed Crayfish *Orconectes neglectus* is an example of a crayfish experiencing a range expansion through accidental introductions. The Ringed Crayfish is native to most of Nebraska, northeast Colorado, north and southeast Kansas, northeast Oklahoma, northwest Arkansas, and southwest Missouri (Schainost 2011). The species has invaded other areas and is thought to be displacing native crayfish (Bouchard 1977; Larson and Magoulick 2009). Ringed Crayfish have been recorded in the Eleven Point River drainage of Missouri and threatens the Coldwater Crayfish *Orconectes eupunctus* (Larson and Magoulick 2009). It has also become established in the Rogue River of Oregon where it puts the Klamath Signal Crayfish *Pacifastacus leniusculus klamathensis* at risk (Bouchard 1977). The Ringed Crayfish shares some of the characteristics of other successful invaders: broad distribution and a broad physiological tolerance as shown by being found in many different ecosystems (Pflieger 1996; Schainost 2011). However, the exact mechanism that allows it to outcompete native species is unknown.

Biotic factors (e.g., competition, predator avoidance capabilities, and growth rate) are hypothesized to be a primary mechanism of successful invasions by the Ringed Crayfish; however, the role of abiotic factors (e.g., habitat alterations) is unknown. Rabalais and Magoulick (2006) found that the reintroduced Coldwater Crayfish, originally thought to be displaced by the Ringed Crayfish, could survive and grow in their former range. These findings suggest that displacement of the Coldwater Crayfish was a result of biotic rather than abiotic factors. However, neither juvenile competition nor adult competition explained displacement of Coldwater Crayfish by Ringed Crayfish (Rabalais and Magoulick 2006; Larson and Magoulick 2009). An alternative hypothesis is that certain abiotic factors might facilitate success of Ringed Crayfish. Therefore, the objective of my study was to identify environmental factors related to the relative abundance of Ringed Crayfish. Results from this study will help managers predict the likely success or failure of this species if introduced under similar conditions as found in our study area.

METHODS

Study Area

From July to October 2014-2015, crayfish were collected from 17 sites in 14 streams of the Ozark Highlands of northeast Oklahoma and southwest Missouri (Figure 1). The Ozark Highlands ecoregion is characterized by cherty-limestone lithology, which results in a karst topography (Woods et al. 2005). Spring-fed streams are common, which contributes to the high species diversity of the region (Woods et al. 2005). Oak-hickory and oak-hickory-pine forest is the natural vegetation in the region, but many of the low topography areas have been converted to pastureland (Woods et al. 2005).

Crayfish Data

Crayfish were collected using both electrofishing and kick-seining methods. We electrofished with a tow-barge electrofisher (Infinity Box, Midwest Lake Management, Polo, Missouri). Electrofishing settings were pulsed direct current (DC), 60 Hz, and a 25% duty cycle. Voltage was adjusted to achieve a target power (W) that maintained a consistent electric field regardless of ambient water conductivity as described by Miranda (2009). Electrofishing effort was not standardized across the sites and areas < 0.2-m (the electrofisher was too large to move into those areas) or > 1.3-m deep (over wader depth) were not sampled. In addition, one riffle at each site was kick-seined twice if the majority of the substrate was small enough (< 200 mm). All crayfish were humanely euthanized and preserved in formalin. GPS coordinates of crayfish-sampling locations (reaches) were recorded to provide a spatial reference for calculating environmental attributes.

Crayfish were brought to the lab for measurements and identification. I identified each crayfish to species and measured carapace length using Vernier calipers (1.0 mm). Age-0 crayfish (carapace length < 21mm) were determined using length-frequency histograms and excluded from the analysis because habitat use can differ between juveniles and adults (Gore and Bryant 1990). I chose to use relative abundance for the analysis rather than density because sampling effort was not consistent among samples and relative abundance would provide a more accurate representation of the Ringed Crayfish population at each site.

Environmental Data

Environmental variables hypothesized to explain the distribution of crayfish species were obtained from a variety of spatial data sources and imported into ArcMAP (10.2.1, ESRI, Red Lands, California; Table 1). GPS coordinates were imported to ArcMAP and converted to a vector layer to provide a spatial reference for each site. Each site was assessed using the stream segment (one tributary to the next) encompassing the site.

I quantified percent land use that was agricultural and distance to impoundment to better understand the influences of humans on the distribution of Ringed Crayfish. Alterations to stream ecosystems can have a significant influence on the occupying species. For example, stream species have evolved to live in certain flow regimes, which are altered by both impoundments and agriculture (Poff et al. 1997). I chose to use percent agriculture for the land-use component of my model because Westhoff et al. (2011) found agriculture to be the most important anthropogenic factor related to distribution of several species of crayfish. To determine percent agriculture around each site, a 500-m buffer was formed around the stream segment that contained the sampling location. The land-use data set was converted to a binary raster (1 = agriculture, 0 = non agriculture). The clip tool was used to determine percent agriculture inside the 500-m buffer. A 500-m buffer was chosen to analyze percent agriculture because local land use can have more of an effect on stream taxa distributions than broader-scale catchment variables (Stanfield and Kilgour 2012). Distance to impoundment (km) was determined by measuring manually from the study site along the stream to the nearest downstream impoundment.

I included variables that represented both geology and soil because of their critical role in explaining the distribution of aquatic taxa, including crayfishes (Westhoff et al. 2011; Nolen et al. 2014). Geology is important to aquatic taxa because it influences the abiotic characteristics of the stream and therefore the stream community (Neff and Jackson 2012). Soil texture is important to the distribution of fishes (Brewer et al. 2007) and crayfishes (Westhoff et al. 2011; Dyer et al. 2013). In order to maintain consistency, geology and soil were obtained using the same methods used to obtain percent agriculture. Geology of the stream segment was defined as the dominant lithology inside the buffer and soil was defined as the dominant soil texture class inside the buffer.

Because my focus was the relationship between landscape variables and Ringed Crayfish occurrence, instream habitat was not assessed with the exception of relative thermal differences among the sites. Temperature is an important variable that influences the distribution of aquatic taxa (Allan and Castillo 2007), including crayfish (Usio et al. 2006); therefore, I chose water temperature as one of my variables. I classified water temperature at each site as either warm (>21°C) or cool (≤21°C) based on a natural break in the instream measurements. Water temperature (0.1°C) was measured at the furthest downstream point of each site at a similar time of day under summer conditions (June-August) using a conductivity pen (Myron L Company, Carlsbad, California; Model PT1).

Catchment size and stream segment drainage area were included in my variable set because they can be linked to stream size and flow conditions (Hansen 2001). Stream size can be important to the diversity of aquatic species because species composition changes as you move from the headwaters to the mouth of stream ecosystems (Allan and Castillo 2007). Discharge conditions influence the distribution of stream species because they have evolved to live under specific flow regimes that influence the abiotic characteristics of the stream (Bunn and Arthington 2002). To obtain the variables for analysis, catchment size and the stream segment drainage were joined to the stream segment of interest using ArcMAP.

Data Analysis

I fit a linear regression model to examine relationships between landscape variables and the relative abundance of Ringed Crayfish. Multiple linear regression was chosen because I hypothesized that the relative abundance of Ringed Crayfish could not be adequately explained by a single variable. Linear regression works by describing the relationship between an explanatory variable (x-axis) and the response variable (y-axis). Multiple linear regression works with the same basic principles as linear regression, but can handle more than one explanatory variable. I assessed significance at $\alpha \leq 0.10$. My dataset contained a mix of continuous and categorical explanatory variables. An important assumption of multiple regression is that the explanatory variables are orthogonal (i.e., free of extreme correlations). I used the Pearson product-moment correlation coefficient and considered multicollineaity where $r \geq |0.28|$ (Graham 2003). Graham (2003) determined this level of collinearity affected parameter estimates in multiple regression scenarios. Soil texture was removed from the analysis due to lack of variation among study sites (15 sites were silt loam and two were sandy loam). I treated geology and water temperature (both categorical) as dummy variables. Dummy variables make the use of categorical variables in linear regression possible by assigning the variable a one or zero to indicate presence or absence of the variable. Alluvium was the reference variable for geology and cool was the reference variable for water temperature. I natural-log transformed distance to impoundment, catchment size, and stream segment drainage to improve linearity. All analyses were performed using R (version 3.2.2, R Core Development Team, 2014).

Diagnostic plots of residuals revealed evidence of heteroscedasticity and non-normality. Consequently, I arcsine square root transformed relative abundance. Arcsine square root is a common transformation for proportions when using linear models (Gotelli and Ellison 2004). After performing the transformation of relative abundance, diagnostic plots of residuals suggested reasonably equal variance and normality.

RESULTS

The relative abundance of Ringed Crayfish and environmental characteristics were variable among study sites. Values are reported as mean ± SD unless otherwise noted. The total number of Ringed Crayfish collected was 1,009 individuals (59.35, ±64.12), which were used to calculate relative abundance (0.78, ±0.27). Distance to impoundment ranged from 0.45 to 85.08 km (23.15, ±26.05 km) and percent agriculture ranged from 0 to 79.34% (44.09, ±19.01 %). Catchment size ranged from 0.13 to 38.00 km^2 (261.99, ±197.15 km^2) and stream segment drainage ranged from 53.48 to 779.91 km^2 (8.75, ±11.83 km^2). I classified the temperature regime of 10 streams as warmwater and seven as coolwater. The distribution of dominant lithology across the sites was alluvium (*n* = 2), chert (*n* = 6), limestone (*n* = 4), and shale (*n* = 5).

No evidence of multicollinearity among continuous variables was detected ($r \geq |0.28|$); however, my initial model suggested overfitting and influential points. There was evidence of overdispersion (standard error exceeded the parameter estimates) for catchment size and stream segment drainage. Since neither of these variables were contributing to the model (i.e., parameter estimates were extremely low), I removed them from further analysis. Cook's distance indicated two data points with values > 0.5. To avoid deleting observations, I removed percent agriculture from the analysis to eliminate influential points because it was not contributing to the model. After removing percent agriculture, Cook's distance still indicated one data point with a value > 0.5 (Evansville Creek). This influential point was presumably due to Evansville Creek being the second furthest site from an impoundment and having the lowest relative abundance of Ringed Crayfish. I choose to remove Evansville Creek from the analysis and found all remaining data points had Cook's distance values < 0.5.

Geology, water temperature, and distance to impoundment were used in the final model explaining the relative abundance of Ringed Crayfish (adjusted R^2 = 0.52, $F_{5,10}$ = 4.25, P = 0.02; Table 2). Although all three variables were used in the model, only geology with a dominant lithology of shale was significant in explaining the relative abundance of Ringed Crayfish (t_{10} = 0.12, P = 0.03; Figure 2). Streams with dominant lithology of shale, chert, or limestone were negatively associated with relative abundance of Ringed Crayfish. Streams that I classified as warmwater were negatively associated with the relative abundance of Ringed Crayfish when compared to those classified as coolwater (Figure 3).

DISCUSSION

I found lower abundances of Ringed Crayfish in areas where the dominate lithology was shale. Geology is an important factor to consider when determining the distribution of aquatic taxa, especially crayfishes (Westhoff et al. 2011; Nolen et al. 2014). For example, the Saint Francis River Crayfish *Orconectes quadruncus* was associated with igneous geology whereas Big Creek Crayfish *Orconectes peruncus* was associated with limestone and dolomite geology (Westhoff et al. 2011). Geology is important to distributions of aquatic taxa because it structures both the physical and chemical properties of the stream such as discharge, conductivity, temperature, dissolved oxygen, soil, and pH (Neff and Jackson 2012).

Substrate stability is one possible reason why shale lithology was negatively related to the abundance of Ringed Crayfish. Shale lithology may be related to streambed stability because shale has a platy shape, which makes it susceptible to being moved downstream (Magalhaes and Chau 1983). Several aquatic taxa may be affected by streambed instability. For example, insect diversity decreases when substrate stability decreases (Cobb et al. 1992), suggesting that substrate stability plays a role in insect diversity. Less stable substrate may also negatively affects mussels because less stable substrate is likely to crush mussels or send them downstream during periods of high flow (Morales et al. 2006; Allen and Vaughn 2010). There has been little work done to assess the influences of substrate stability on crayfish; however, stream bank stability (Parkyn and Collier 2004) and certain substrate sizes (Dyer et al. 2015) provides refuges for crayfish during floods, droughts, and other harsh conditions. The negative relationship between shale and relative abundance may suggest that Ringed Crayfish prefer more stable substrate or substrates more readily used to construct burrows.

Shale lithology may be important to Ringed Crayfish distribution because of its relationship to pH. Catchment geology is the most significant determinant of stream chemistry (Cushing and Allan 2001). For example, Nolen et al. (2014) found that *Orconectes marchandi* was positively associated with dolomite geology, which suggests they prefer water with a neutral pH. Shale is largely composed of silica (Bluth 1994) and silica can cause streams to have higher pH levels (Hem 1985). Crayfish often depend on neutral or higher pH because lower pH limits the amount of calcium in water. Crayfish need calcium to produce their exoskeleton (Reynolds 2002). The negative relationship between shale and relative abundance may suggest that Ringed Crayfish prefer neutral pH.

Water temperature is also important to the distribution and abundance of aquatic taxa, including crayfishes. Some crayfish species better tolerate variation in water temperature. For example, Nolen et al. (2014) found that water temperature was not important as a predictor of occurrence for two species of crayfish: Coldwater Crayfish and Hubb's Crayfish *Orconectes hubbsi*. Alternatively, temperature was the most important predictor of the invasive Signal Crayfish *Pacifastacus leniusculus* with highest abundances where water temperatures exceeded 18°C and no crayfish occurred where water temperatures were less than 14.5°C (Usio et al.

2005). Although not statistically significant, trends in my data suggest a negative relationship may exist between streams classified as warmwater and relative abundance of Ringed Crayfish, with preferences likely for cooler temperatures (Figure 3). Ringed Crayfish have been invading cooler streams located in Oregon and New York (Bouchard 1977; Daniels et al. 2001), which also suggests that they may prefer cooler streams. Growth of crayfish is regulated by water temperature and species adapted to cooler waters usually demonstrate slower growth, longer life spans, and overall larger size (Reynolds 2002). Having a larger overall size may allow Ringed Crayfish to outcompete other species (Gherardi 2002).

Calculating geology and temperature as continuous variables, rather than categorical variables, may provide additional insight to Ringed Crayfish tolerances. Treating geology as a continuous variable would allow quantification of what percentage of certain geology types are contributing to distribution of Ringed Crayfish. I could then build a broken-line regression model to determine if multiple lines could be fit to the data, thereby suggesting a threshold response to lithology. Other stream organisms (e.g., Smallmouth Bass, Brewer et al. 2007) show threshold responses to different geology types. Another way I could have improved my results would be to assess possible interactions between temperature and geology. Possible collinearity may prevent temperature from being statistically significant, even if ecologically important.

Sampling across the entire distribution of Ringed Crayfish may also have improved my results by allowing me to determine if these relationships are only observed at the southern extent of the species range or throughout their distribution. Ringed Crayfish are a wide-ranging species (Schainost 2011), which suggests they may have wide physiological tolerances. Their broad distribution may have allowed different environmental preferences to develop at different extents of their range because of interactions between landscape and local habitat conditions

(Brewer et al. 2007). Further, range contractions are most common at the edges of a species range, likely because the abiotic conditions become less suitable (Sexton et al. 2009). This suggests that, although using data across the entire distribution would be useful, my study captures conditions that may be marginal habitat for Ringed Crayfish. Therefore, these data are helpful for examining conditions that could be considered marginal habitat for the species and thus, help to identify conditions where the species may not persist.

The results of my study provide evidence that some environmental factors, such as geology and perhaps water temperature, may facilitate or inhibit invasion success by Ringed Crayfish. It appears that shale lithology and warmer water temperatures may inhibit expansion by Ringed Crayfish. Developing a framework such as that used by Dyer et al. (2013) to predict the distribution of crayfish would be beneficial to understanding these patterns. My results could be used to establish a monitoring protocol to assess expansion within the southern extent of this species' range. Further laboratory studies showing the relationships between substrate stability, burrowing, temperature and crayfish survival would be useful to understanding the mechanisms that explain the observed trends. Ultimately, it is an understanding of the mechanisms that explain my observations that will be most instructive to developing methods to prevent invasion of this species. Preventing the spread of introductions will help to maintain the native diversity of regions.

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FIGURES AND TABLES

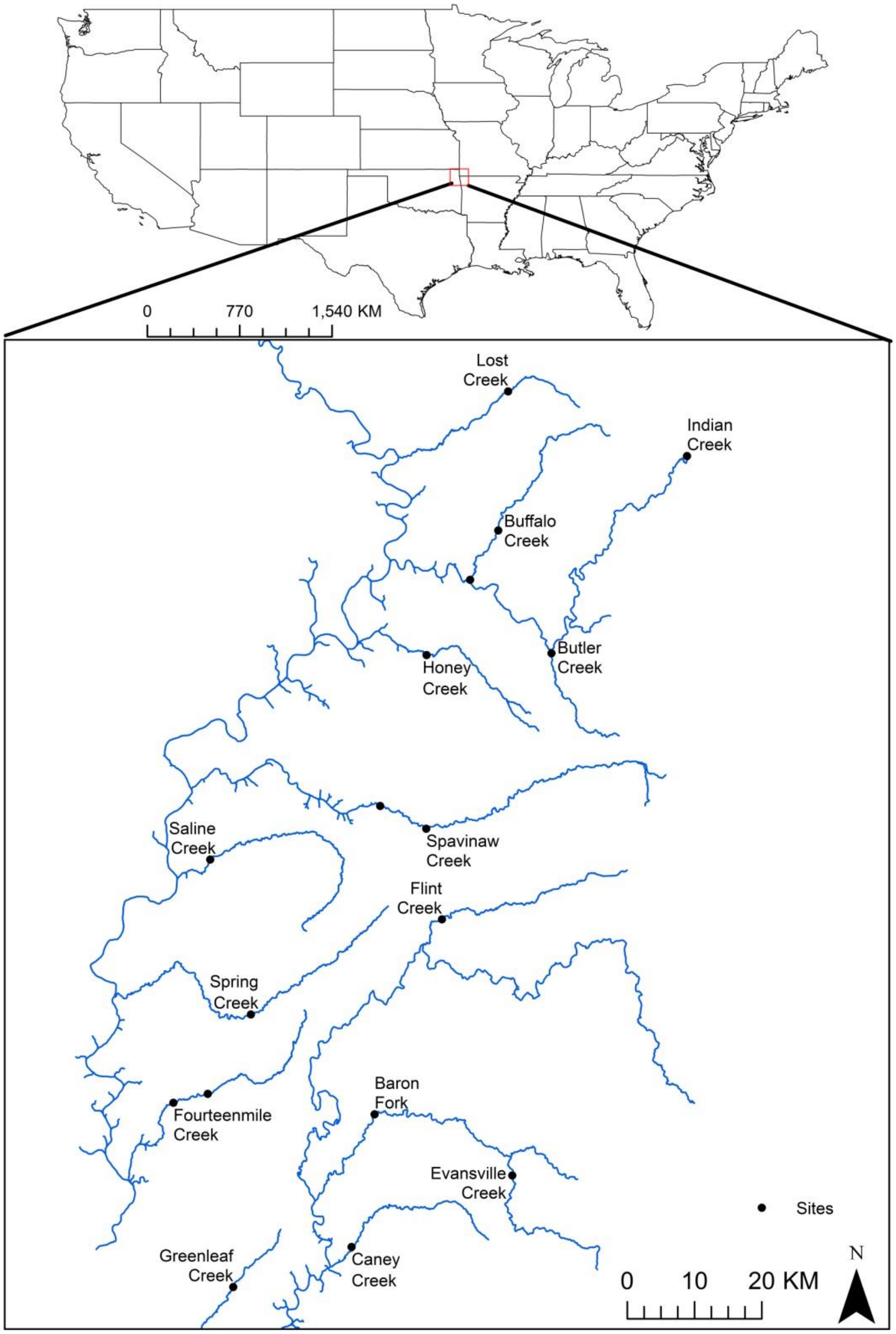

Figure 1: Map of the study area showing the location of each study site within the Ozark Highlands of northeast Oklahoma and southwest Missouri, USA.

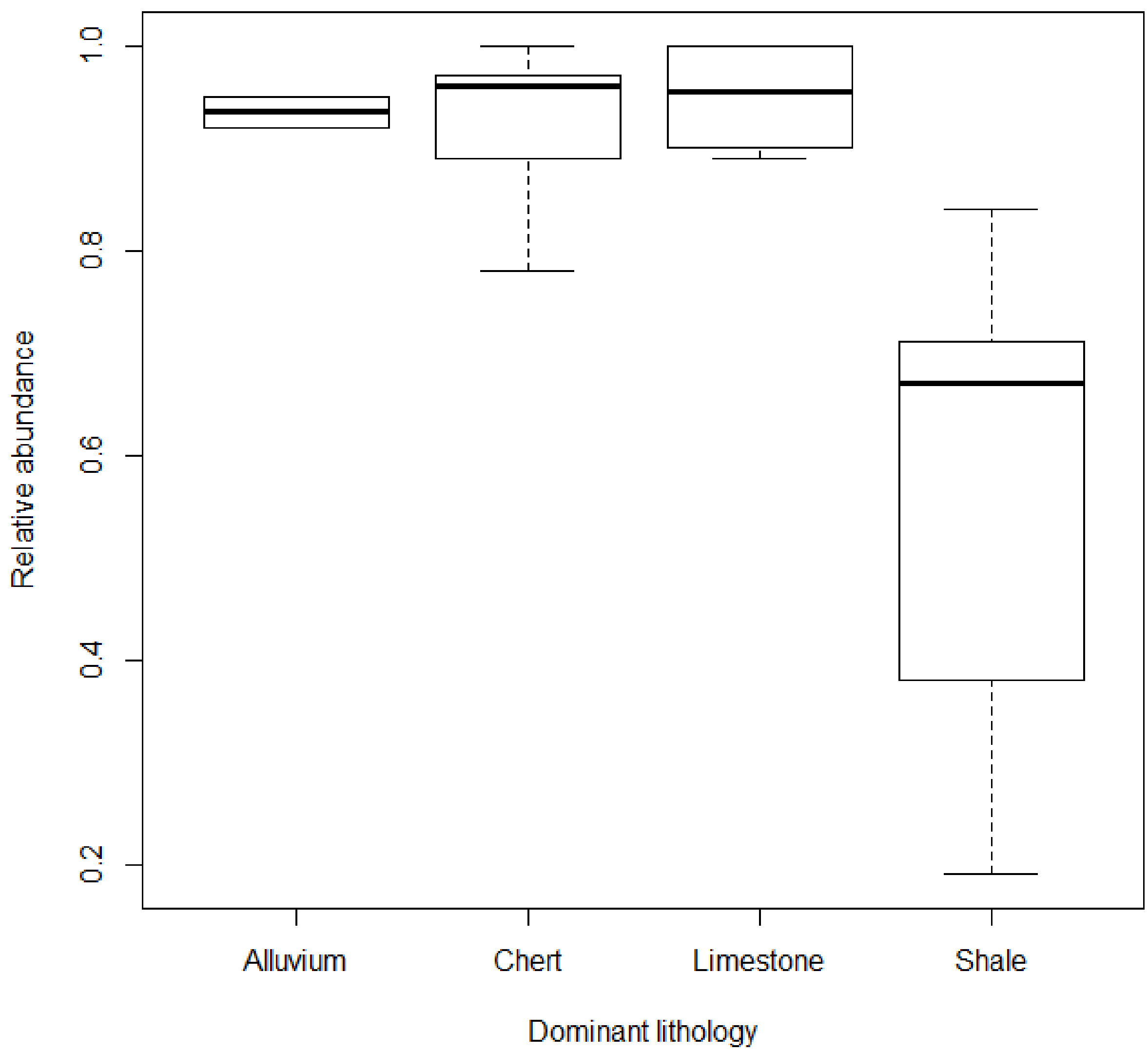

Figure 2: The relationship between the dominant lithology at each site and the relative abundance of Ringed Crayfish. Shale lithology was negatively associated with relative abundance of Ringed Crayfish (t_{10} = 0.12, P = 0.03).

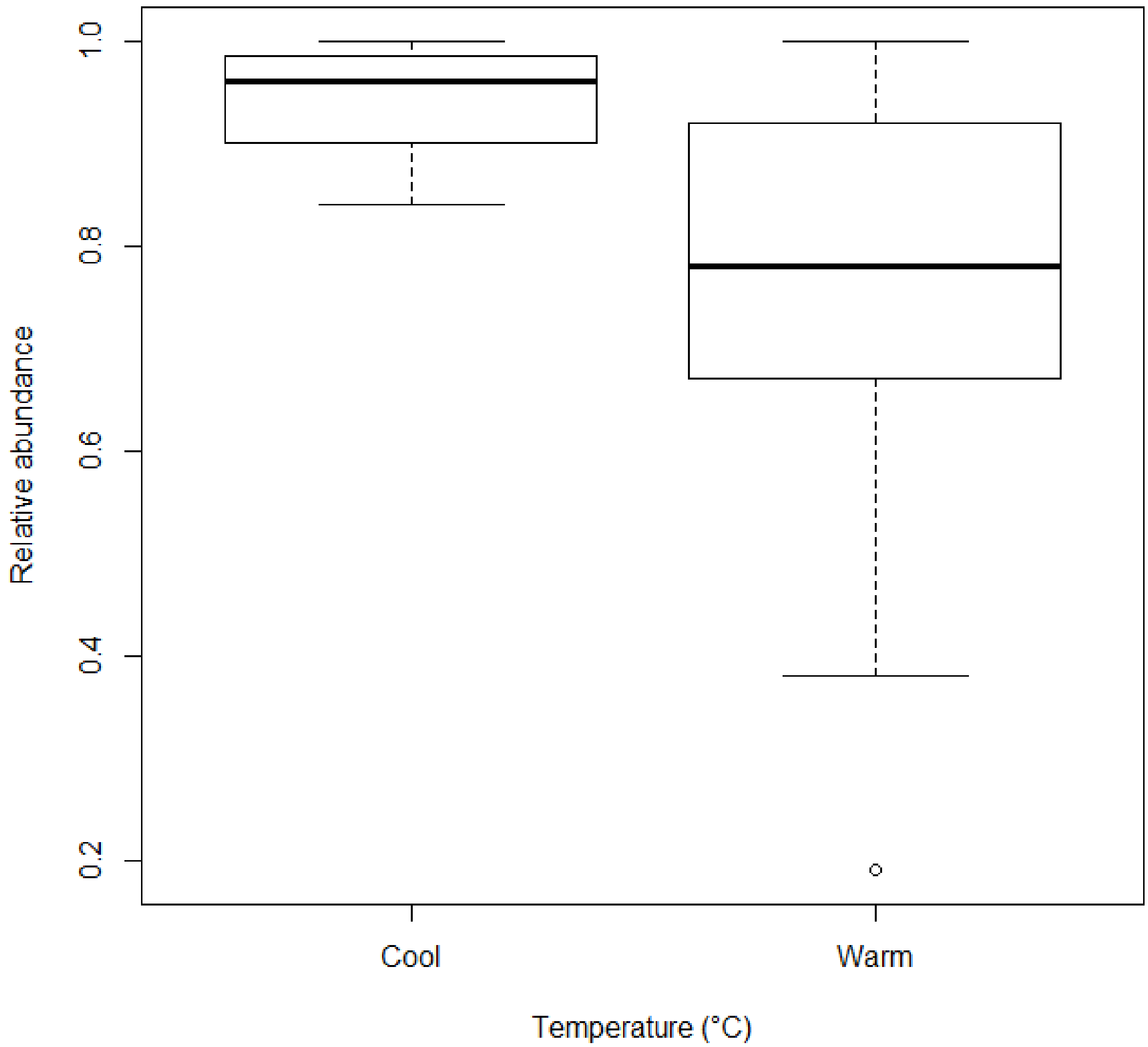

Figure 3: The relationship between temperature classification (warmwater >21°C, coolwater 21≤°C) of each site in the Ozark Highlands ecoregion and the relative abundance of Ringed Crayfish.

Table 1: Environmental data used to model the relationship between landscape variables and the occurrence of the Ringed Crayfish. The study was completed in the Ozark Highlands of Oklahoma and Missouri, USA.

Habitat variable	**Description**	**Source**
Geology	The dominant lithology within a 500-m buffer of each site	USGS (2005)
Soil texture	The dominant soil texture within a 500-m buffer of each site	Miller and White (1998)
Percent agriculture	The percentage of land use that was agricultural within a 500-m buffer of each site	USDA, NRCS (2011)
Distance to impoundment	Distance (km) from site to nearest downstream impoundment	USEPA, USGS (2012)
Catchment size	The cumulative size of the catchment (km^2)	USEPA, USGS (2012)
Stream segment drainage	Area draining directly to the stream segment (km^2)	USEPA, USGS (2012)
Water temperature	Stream temperature classified as warm (>21ºC) or cool (≤21ºC)	Recorded at site

Table 2: Results of a multiple linear regression model relating landscape variables to the relative abundance of Ringed Crayfish among 16 sites, located in the Ozark Highlands of northeast Oklahoma and southwest Missouri, USA.

Parameter	**Estimate**	**Standard error**	**t statistic**	**P-value**
Intercept	1.52	0.23	6.75	0.00
Distance to impoundment	-0.01	0.05	-0.25	0.81
Water temperature	-0.18	0.13	-1.38	0.20
Chert lithology	-0.10	0.20	-0.51	0.63
Limestone lithology	-0.02	0.22	-0.10	0.92
Shale lithology	-0.49	0.19	-2.61	0.03