The influence of coarse-scale environmental features on current and predicted future distributions of narrow-range endemic crayfish populations

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SUMMARY

1. A major limitation to effective management of narrow-range crayfish populations is the paucity of information on the spatial distribution of crayfish species and a general understanding of the interacting environmental variables that drive current and future potential distributional patterns.

2. Maximum Entropy Species Distribution Modeling Software (MaxEnt) was used to predict the current and future potential distributions of four endemic crayfish species in the Ouachita Mountains. Current distributions were modelled using climate, geology, soils, land use, landform and flow variables thought to be important to lotic crayfish. Potential changes in the distribution were forecast by using models trained on current conditions and projecting onto the landscape predicted under climate-change scenarios.

3. The modelled distribution of the four species closely resembled the perceived distribution of each species but also predicted populations in streams and catchments where they had not previously been collected. Soils, elevation and winter precipitation and temperature most strongly related to current distributions and represented 65–87% of the predictive power of the models. Model accuracy was high for all models, and model predictions of new populations were verified through additional field sampling.

4. Current models created using two spatial resolutions (1 and 4.5 km²) showed that fine-resolution data more accurately represented current distributions. For three of the four species, the 1-km² resolution models resulted in more conservative predictions. However, the modelled distributional extent of *Orconectes leptogonopodus* was similar regardless of data resolution. Field validations indicated 1-km² resolution models were more accurate than 4.5-km² resolution models.

5. Future projected (4.5-km² resolution models) model distributions indicated three of the four endemic species would have truncated ranges with low occurrence probabilities under the low-emission scenario, whereas two of four species would be severely restricted in range under moderate–high emissions. Discrepancies in the two emission scenarios probably relate to the exclusion of behavioural adaptations from species-distribution models.

6. These model predictions illustrate possible impacts of climate change on narrow-range endemic crayfish populations. The predictions do not account for biotic interactions, migration, local habitat conditions or species adaptation. However, we identified the constraining landscape features acting on these populations that provide a framework for addressing habitat needs at a fine scale and developing targeted and systematic monitoring programmes.

Keywords: climate change, crayfish, distribution model, endemism, MaxEnt

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Introduction

Potential changes in climate are a major consideration for the future conservation and management of aquatic species. Climate change is expected to affect aquatic systems by altering stream-discharge patterns, increasing water temperatures and increasing the frequency and intensity of droughts and extreme storm events (Poff, 2002; Barnett, Adam & Lettenmaier, 2005; Strzepek *et al.*, 2010). These changes are expected to increase the probability of invasion and the competitive ability of invasive species (Rahel & Olden, 2008), increase local extinctions (Maclean, Wilson & Hassall, 2011) and reduce the distribution of many native species (e.g. Buisson & Grenouillet, 2009; Elith, Kearney & Phillips, 2010; Lyons, 2010). A reduction in suitable environmental conditions is especially problematic for riverine species with limited dispersal capabilities (Woodward *et al.*, 2010) and particularly severe for endemic species whose ranges are already small.

The status of many endemic species, including aquatic invertebrates, is poorly understood (Harding, 2003). Human-induced threats endanger aquatic invertebrates worldwide (e.g. pollutants, Cooper, 1993; habitat loss, Fahrig, 1997; land-use activities, Strayer *et al.*, 2003; non-native species introductions, Richardson & Whittaker, 2010; Wagner & Van Driesche, 2010), and these impacts are likely to be exacerbated by climate change (Muhlfeld *et al.*, 2011). Further, organisms restricted to narrow geographic ranges, either naturally or through anthropogenic alteration, are particularly sensitive to cumulative stresses (Smith & Tirpak, 1989). The importance of conservation efforts for endemic species is recognised (Brooks *et al.*, 2006), but our understanding of the distributional limits of these species and the factors responsible is often inadequate.

Little is known about the vulnerability of crayfish to climate change which is particularly problematic because of their ecological importance to aquatic ecosystems. Crayfish consume significant portions of available detritus, algae and invertebrates (Rabeni, 1992; Momot, 1995) and are prey themselves to hundreds of species at higher trophic levels (DiStefano, 2005), including sportfish (Rabeni, 1992). In some stream systems, the biomass of crayfish exceeds that of all other benthic invertebrates (Rabeni, Gossett & McClendon, 1995).

High rates of secondary production in crayfish occur in habitats that are proportionally small in many streams (e.g. vegetated edges and backwaters) and are some of the first habitats to be affected by reductions in discharge (Brewer, DiStefano & Rabeni, 2009). Loss of habitats associated with high crayfish production may alter the transfer of energy through the trophic web. In regions where drought frequency and temperature are anticipated to increase because of climate change, crayfish species may shift their distributions and have the potential to alter stream-trophic dynamics.

Unfortunately, the distribution of many crayfishes is poorly understood. Climate, geology and latitude are considered major factors affecting the distribution of crayfish (France, 1992), but the majority of studies has only addressed distributions at fine-spatial scales (Nyström, 2002). An alternative to extensive field surveys is to model the distribution of species based on available data and then use the model to underpin monitoring and conservation efforts. Species-distribution models are a popular tool to predict a continuous probability surface from disparate sampled locations of organisms (Elith *et al.*, 2011). Although many modelling approaches are available, Maximum Entropy Species Distribution Modeling Software (MaxEnt; Phillips, Anderson & Schapire, 2006) and Genetic Algorithm Rule-set Production (GARP; Stockwell & Noble, 1992) are the most commonly used, with MaxEnt tending to generate more conservative predictions (Peterson, Papeş & Eaton, 2007). Although this approach has been mostly applied to terrestrial plants (Kumar & Stohlgren, 2009; Menon *et al.*, 2010) and birds (Peterson, Soberón & Sánchez-Cordero, 1999; Young *et al.*, 2009), it is increasingly being used in aquatic ecology (e.g. Domínguez-Domínguez *et al.*, 2006; Chen, Wiley & Mcnyset, 2007).

In this study, we used MaxEnt to predict the distribution of four endemic crayfish species in the Ouachita Mountains of Oklahoma and Arkansas, a region designated as high priority for conserving freshwater biodiversity in the United States (Master *et al.*, 1998). Our objectives were to (i) predict the current distribution of crayfish species using current and historic collection records, (ii) determine the landscape and in-channel factors related to the current distribution of crayfish species and (iii) assess how climate change might influence future distributions of each species. We hypothesised that species whose current distributions related more strongly to temperature and precipitation, or flow variables, would be more susceptible to climate change.

Methods

Distribution models were constructed for four crayfish species endemic to the Ouachita Mountains: *Orconectes leptogonopodus*, *O. menae*, *O. saxatilis* and *Procambarus tenuis*. All are tertiary burrowers, species that burrow under

environmental extremes (e.g. drought) or during repro-duction, and all but *O. leptogonopodus* are listed as species of special concern (Taylor *et al.*, 1996). *Orconectes menae* and *P. tenuis* are classified as vulnerable species, whereas *O. saxatilis* is considered imperiled (Taylor *et al.*, 1996). Very few studies have been conducted on these species, although general descriptions and collection locations have been published. The most extensive crayfish survey in the Ouachita Mountain region occurred in 2004 at 46 sites, primarily in McCurtain County (Bergey, Jones & Fenolio, 2005). *Orconectes menae* was reported from six streams in LeFlore and McCurtain County in Oklahoma (Bergey *et al.*, 2005), and 158 specimens were collected from Polk and Montgomery counties in Arkansas (Williams, 1954). Williams (1954) reported that *O. menae* occurred 'under rocks in clear cold streams'. Robison *et al.* (2009) collected *O. menae* from rocky runs and shallow pool margins of headwater streams, with a few specimens found in larger streams. *Procambarus tenuis* was found at two sites (Pushmataha and LeFlore counties, Oklahoma) in 2002 (Oklahoma Biological Survey, unpubl. data), was rare in collections by S. Jones (unpubl. data) and was not found in surveys by Bergey *et al.* (2005). Robison & McAllister (2008) reported that *P. tenuis* builds simple burrows in clear and cold headwater streams. *Orconectes leptogonopodus* was collected in McCurtain and LeFlore counties of Oklahoma (Bergey *et al.*, 2005). Williams (1954) examined 323 *O. leptogonopodus* specimens from rocky streams (six counties in Arkansas) where it was most often found 'in rapidly flowing water on or near shoals'. *Orconectes saxatilis* is the best studied of the four species and is restricted to seven headwater tributaries of the Kiamichi River (Jones & Bergey, 2007). *Orconectes saxatilis* primarily occupies riffle habitat and builds shallow burrows during summer low-flow conditions (Jones & Bergey, 2007). No other information exists on the ecology of these species.

Study area

The Ouachita Mountains (Fig. 1) are characterised by a mixture of pine, oak and hickory forest, and land-use practices consist primarily of agriculture, logging, ranching and recreation (Woods *et al.*, 2005). The underlying geology in the area is sandstone, shale and metamorphic rock broadly categorised as quartzite (Miser, 1959). Soils primarily comprise silty loam and silty clay (Hlass, Fisher & Turton, 1998), and dominant stream substrates are classified as boulder and cobble (Splinter *et al.*, 2011). Groundwater influence on Ouachita Mountain streams is limited and many dry to a
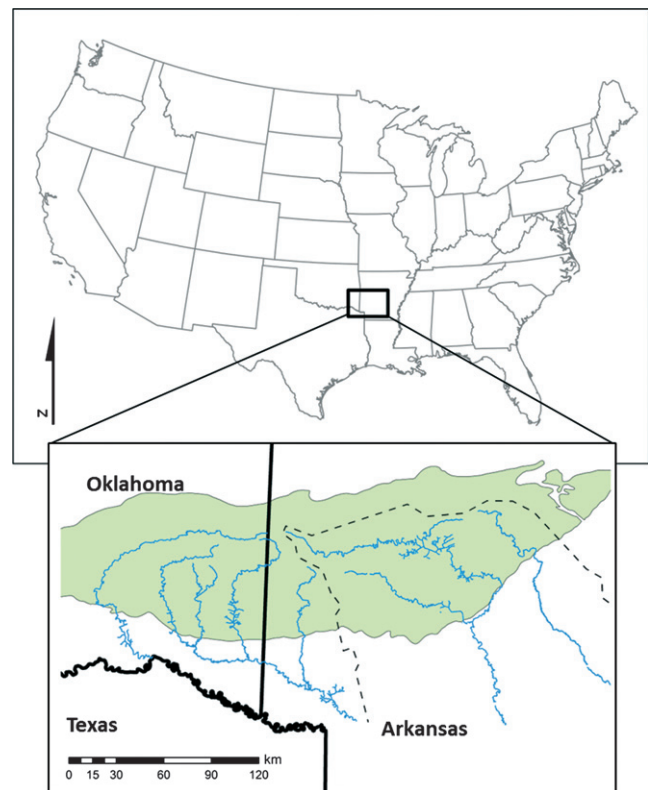

Fig. 1 Location of the Ouachita Mountains (green area) of Oklahoma and Arkansas, U.S.A. Only major rivers are depicted for simplicity (listed from the north-east to south-west): Kiamichi, Little, Ouachita and Saline rivers. The dashed line represents the boundary between the two catchments used to create the river network.

series of isolated pools during the summer (Brown & Matthews, 1995). Streams in the region are generally confined within steep valleys (Splinter *et al.*, 2011) and produce rapid floods during periods of intense rainfall. Streams in this region rarely reach third order (Strahler, 1957) before entering the main channels that exit the Ouachita Mountain region.

Occurrence data

Occurrence data (presence locations) were obtained from three data sources. The Arkansas Game and Fish Commission provided historical data collections (1934–2005), with the majority of data (85%) collected during the mid-1990s. The Oklahoma Biological Survey provided presence data from crayfish surveys conducted from 1992 to 2005, with most data (95%) collected after 2001 (S. Jones, E. Bergey & J. Pigg, unpubl. data). The current study contributed presence data collected via systematic sampling of 17 stream reaches during summer 2011 (J. Dyer, unpubl. data). Combined, we obtained 50 occurrence points to construct species-distribution models for *O. lep-*

togonopodus, 55 for *O. menae*, 17 for *O. saxatilis* and 40 for *P. tenuis*. Because MaxEnt is especially well suited to deal with presence data (Phillips *et al.*, 2006), differences in collection methods were not expected to significantly influence the model outcomes. Descriptions of sampling procedures used for data collected by the Oklahoma Biological Survey, Arkansas Game and Fish Commission and the current study have been summarised in Jones & Bergey (2007), Robison (2001) and DiStefano *et al.* (2003), respectively.

Environmental data

Coarse-scale variables, derived from existing geospatial data, were selected to predict the distributions of the four crayfish species. The importance of many of these variables to the distribution and ecology of aquatic biota was discussed by Brewer *et al.* (2007) and will only be briefly addressed here. We created a river network for the current study using the 1 : 100 000 digital stream network from the national hydrography data set (U.S. Environmental Protection Agency & U.S. Geological Survey, unpubl. data). Two catchments from the Mississippi drainage were merged to form a single extent that included the two major catchments of interest (Little River and Ouachita River; hereafter referred to as river network; Fig. 1). The river network comprised 13 384 individual stream reaches. Landscape-scale climate, geology, soils, land-use and landform data were obtained

from available sources (Table 1). Geology and climate are considered the primary factors that structure the distribution of aquatic biota (Hynes, 1975), including crayfish (France, 1992). Climate variables were chosen to represent seasonal (3 month) trends and annual extremes within the study area (Table 2). Percentages for thirteen lithological classes were based on the digital geology data for Oklahoma (Table 3). The distribution of aquatic biota has been related to soil composition (Brewer *et al.*, 2007; Hopkins & Burr, 2009; Wilson, Roberts & Reid, 2011) and was one of the best predictors describing the distribution of three crayfish species in streams in Missouri, U.S.A. (Westhoff, Rabeni & Sowa, 2011). We derived 31 soil-texture classes for the study area using existing geospatial data (Table 3). Soil classes were based on soil textures and similarities in slope and permeability (US Department of Agriculture, 1951). Sixteen categories of land use were obtained from Homer, Fry & Barnes (2012) and broadly classified areas by dominant vegetation (natural or otherwise), the severity and intensity of land development, type of cropland and wetland type or open water (Table 3). Landform was characterised using a 30-m digital elevation model (Gesch *et al.*, 2009). We created a flow-accumulation layer using ArcGIS 10 (Environmental System Research Institute Inc., Redlands, CA, U.S.A.), with the flow-direction raster provided by NHD Plus (USEPA & USGS, unpubl. data). Stream order was assigned to each stream segment (tributary to tributary) according to Strahler (1957). Data resolution

Table 1 Environmental variables used to create species-distribution models. A season is defined as 3 months of a year. Data sources are free and may be accessed at the web address indicated below. Data resolution associated with each variable is provided

Variable	Source	Resolution
Soil composition (%)	http://soildatamart.nrcs.usda.gov	1 : 250 000
Geology rock type (%)	http://datagateway.nrcs.usda.gov/	1: 100 000
Land-use	http://datagateway.nrcs.usda.gov/	30 m^2
Warmest season temperature (°C)	http://www.worldclim.org/bioclim	1 km^2
Coldest season temperature (°C)	http://www.worldclim.org/bioclim	1 km^2
Wettest season precipitation (mm)	http://www.worldclim.org/bioclim	1 km^2
Driest season precipitation (mm)	http://www.worldclim.org/bioclim	1 km^2
Warmest season precipitation (mm)	http://www.worldclim.org/bioclim	1 km^2
Coldest season precipitation (mm)	http://www.worldclim.org/bioclim	1 km^2
Elevation	http://www.horizon-systems.com/NHDPlus/NHDPlusV1_data.php	30 m^2
Stream order (Strahler)	http://www.horizon-systems.com/NHDPlus/NHDPlusV1_data.php	NA
Flow accumulation	Arc GIS Tools	NA
January temperature (all scenarios 2099)	gisclimatechange.ucar.edu	4.5 km^2
August temperature (all scenarios 2099)	gisclimatechange.ucar.edu	4.5 km^2
January precipitation (all scenarios 2099)	gisclimatechange.ucar.edu	4.5 km^2
August precipitation (all scenarios 2099)	gisclimatechange.ucar.edu	4.5 km^2
July precipitation (all scenarios 2099)	gisclimatechange.ucar.edu	4.5 km^2
March precipitation (all scenarios 2099	gisclimatechange.ucar.edu	4.5 km^2
Stream network	http://www.horizon-systems.com/NHDPlus/NHDPlusV1_data.php	1 : 100.000

NA, not applicable.

Table 2 Mean, range and standard deviation (Stdev) of continuous variables used in fine-resolution (1 km²) current-distribution models

Variable	Ouachita mountain region		Occurrence locations	
	Mean (range)	SD	Mean (range)	SD
Summer temperature (°C)	33 (31–35)	0.38	33 (31–34)	0.49
Winter temperature (°C)	−2 (0 to −4)	0.83	−2 (0 to −4)	0.12
Wet-season precipitation (mm)	402 (348–464)	17.44	418 (377–460)	13.57
Dry-season precipitation (mm)	278 (208–320)	20.24	270 (237–316)	19.68
Summer precipitation (mm)	291 (265–333)	12.71	300 (277–329)	10.38
Winter precipitation (mm)	298 (208–334)	32.17	271 (237–322)	20.71
Elevation (M)	133 (24–548)	89.74	282 (94.2–471)	78.19
Stream order (Stahler)	3 (1–7)	1.40	2.4 (1–6)	1.09
Flow accumulation	21 267 (0–128 000 000)	1186553.00	9246 (0–79 681)	15840.00

Table 3 Variables included in land-use, geology and soil-composition categories

Land use	Geology	Soil composition	
Open water	Limestone	Clay	Loamy sand
Developed – open space	Shale	Clay loam	Rock out crop
Developed – low intensity	Sandstone	Dam	Sandy loam
Developed – medium intensity	Alluvial terrace	Fine sand	Shale loam
Developed – high intensity	Alluvium	Fine sandy loam	Silt
Barren land	Sand	Gravel	Silt clay loam
Deciduous forest	Clay/mud	Gravelly fine sand	Silt loam
Evergreen forest	Novaculite	Gravelly fine sandy loam	Silty clay
Mixed forest	Chert	Gravelly loam	Silty clay loam
Shrub/scrub	Alkalic intrusive rock	Gravelly loamy sand	Stony clay
Grassland/herbaceous	Mixed clastic carbonate	Gravelly silt loam	Stony fine sandy loam
Pasture/hay	Volcanic rock	Gravelly silty clay loam	Stony loam
Cultivated crop land	Conglomerate	Gravely fine sandy loam	Stony silt loam
Woody wetlands		Gravely sandy loam	Udipsammants
Herbacious wetlands		Loam	Udorthents
		Loamy fine sand	

for each environmental variable was chosen by considering: (i) availability of difference resolutions and (ii) how much variation occurred across the study area. Fine-scale resolution (30 m²) was chosen, when available, for layers representing environmental features with high variability across the study area (e.g. elevation), whereas the available low resolution (1 km²) was deemed acceptable for layers representing environmental features with relatively low variability across the region (e.g. precipitation).

Species-distribution modelling

Occurrence data were imported into ArcGIS 10 and overlaid onto the river network. Each occurrence point was assigned geographically to the nearest reach within the network. When multiple occurrence points existed for a single reach, only one point was used to minimise undue influence on the model outcome caused by repeated sampling of the same locations (e.g. bridge access points). We used 50, 55, 17 and 40 occurrence points to construct species-distribution models for *O. leptogonopodus*, *O. menae*, *O. saxatilis* and *P. tenuis*, respectively. Wisz *et al.* (2008) recommended more than 30 occurrence points be used to create a species-distribution model; however, accurate models have been created with as few as five presence locations using MaxEnt (Phillips *et al.*, 2006).

We used a samples-with-data approach in MaxEnt (MaxEnt 3.3.3k; Phillips *et al.*, 2006) to predict the current distribution of each crayfish species. The predicted distribution was projected onto the river network vector data set rather than using the traditional raster output approach (but see Elith, Leathwick & Hastie, 2008). The raster approach divides the study area into a grid where each cell is assigned a single probability-of-occurrence or environmental factor value. Multiple streams can occur within a single grid cell making the raster-based approach more prone to error because a single value is assigned to all streams (Elith *et al.*, 2008). Where individual stream

reaches overlapped multiple raster cells or polygons, data values were assigned based on a weighted (length in each cell) average for continuous environmental data and the longest subsegment in the reach for categorical data. The default settings were used in MaxEnt (Phillips *et al.*, 2006) except for the maximum number of background points. Background points were set to 13 384 to match the number of individual stream reaches. The results from each model were projected spatially using ArcGIS 10.

To predict the potential future distribution of each crayfish species, models trained on current locations and environmental parameters were projected onto conditions expected under climate change (see Phillips & Dudík, 2008). Climate data representing 'future' conditions were obtained from the Community Climate System Model (Table 1), a model based on the fourth assessment report of the International Panel on Climate Change. Future climate data were integrated with the aforementioned contemporary environmental variables (e.g. stream network, geology, soils). Because precipitation and temperature data from the climate-change scenarios were based on a statistically down-scaled model, the climate data were not directly comparable with the data used in our fine-resolution current-distribution models. To compensate, we used the Community Climate System Model 20th-century data (4.5-km^2 resolution; National Center for Atmospheric Research community, unpubl. data) and created a new set of models predicting current distributions. This allowed for appropriate comparison between models because each model used the same set of climate variables (monthly values rather than seasonal averages) and was projected using the same resolutions. We anticipated the models using the 4.5-km^2 resolution data would produce slightly different results than the models created using the finer-resolution data, but we wanted to have models to appropriately compare the relative effects of our climate scenarios.

There were four families of scenarios developed by the International Panel on Climate Change; however, only the greenhouse gas emission predictions (GHG) were of interest in the current study. We were interested in these scenarios because changes in emission rates are predicted to influence precipitation patterns and water availability during already low-flow periods (e.g. drought severity) (Smith & Tirpak, 1989). We used three scenarios: A2, A1B and B1, representing medium–high [19.6–34.5 Giga-tons of Carbon (GtC)], medium–low (13.5–17.9 GtC) and low (2.7–10.4 GtC) GHG emissions, respectively. Each scenario predicts future GHG emission rates based on different combinations of population growth, energy use, land use and technological advances (Pachauri & Reisinger, 2007).

Environmental suitability and model validation

Variable-contribution analyses were used to determine the relative influence of each environmental variable to the model outcome and to identify variables appropriate for the development of response graphs for current models. Relationships established in current coarse-resolution models were held constant in future projections so response graphs and variable contribution were not different under climate-change scenarios. Two sets of statistics, percentage contribution and permutation importance, resulted from variable-contribution analyses in MaxEnt. Percentage contribution is the relative increase in model fit associated with each environmental variable, whereas permutation importance produces an indication of the loss in predictive power associated with the removal of the variable. The former may be more difficult to interpret given correlations among environmental variables included in the model but, without multicolinear variables, allows assessment of which variables had the most influence on the model. MaxEnt produces two types of response graphs that indicate the relative suitability of an environmental variable for a particular species. The appropriate choice of response graph depends on the presence of colinear variables in a model. Extreme colinearity, or multicolinear variables, makes response graphs difficult to interpret unless graphs are developed without the inclusion of colinear variables. We conducted a Pearson's product–moment correlation procedure to identify continuous variables that were multicolinear ($r > 0.65$). Statistical significance ($\alpha < 0.05$) was not used to determine multicolinearity because it simply identified colinear variables rather than extreme cases. We could not statistically determine colinearity between many categorical variables because many (e.g. land use) were based on multiple properties.

Response graphs represent the relative tolerance of each crayfish to a particular environmental feature. Response graphs were developed for variables that cumulatively contributed to at least 70% of the predictive power (indicated by percentage contribution) of the model. Curves were generated to represent responses to continuous data, whereas responses to categorical data were represented by bar charts. Each curve or bar chart was examined to determine the relative suitability of the variable in relation to the presence of the species under current distributions.

We used the cross-validation technique for small data sets recommended by Phillips *et al.* (2006) to check model accuracy. The cross-validation procedure excluded 10% of the occurrence data and then tested the proficiency of

the model to predict the excluded data points. The cross-validation procedure was repeated 10 times for each model, and the mean output was used to determine distribution probabilities and overall model performance. The accuracy of each model was determined using the area under the curve (AUC) statistic generated by receiver operating characteristic (ROC) analysis (Fielding & Bell, 1997). An AUC close to one indicates a very accurate model.

In addition to the cross-validation, model accuracy was verified using quantitative field sampling conducted during summer 2012. Twelve streams in catchments adjacent to the western edge of known crayfish occurrences were randomly selected (Fig. 2). We sampled multiple channel units (a minimum of three riffles, runs and pools) in each selected stream following methods described by DiStefano *et al.* (2003). Briefly, a 1-m^2 quadrat sampler, covered on three sides with 3-mm netting, was firmly placed and sealed on the stream bottom and all crayfish were swept downstream into an attached $1.0 \times 0.5 \times 1.2$ m net. We did not restrict our random selection of streams to those predicted by our models to have a high probability of occurrence, but instead chose streams where species presence had not been previously documented.

Results

Species-distribution modelling

Models (1-km^2 resolution) predicted continuous distributions that extended beyond actual sampled locations (Fig. 2). Low probability of occurrence was predicted in several catchments outside the currently described range of the species. Perhaps more importantly, three of four species were predicted to have a high probability of occurrence in individual streams that had never been sampled (*O. leptogonopodus*) and even in entirely separate catchments (*O. menae* and *P. tenuis*). However, the highest probability of occurrence (>66%) was predicted where known individual species had previously been detected. For each species, excluding *O. saxatilis*, streams west of current sampled locations (particularly in the Glover River drainage) appear to represent the highest chance of finding undetected populations. Our distribution model of *O. saxatilis* indicated only a small chance (<33%) that populations would be located outside previously sampled regions where the species had been encountered.

As expected, there were differences between the current-distribution models created using climate data at two different spatial resolutions (1 and 4.5 km^2; Figs 2 & 3).
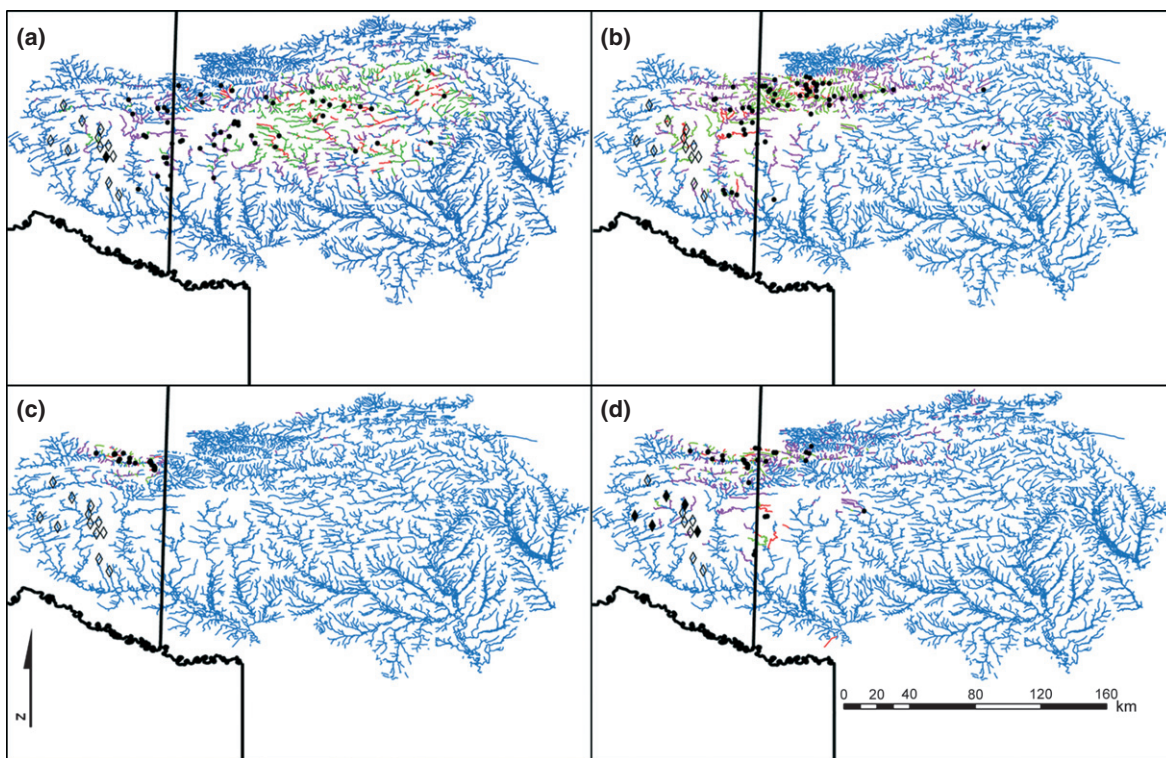

Fig. 2 Current predicted distributions based on 1-km^2 resolution data for (a) *Orconectes leptogonopodus*, (b) *O. menae*, (c) *O. saxatilis* and (d) *Procambarus tenuis*. Probabilities of occurrence are blue <10%; purple 11–32%; green 33–65% and red ≥66%. Occurrence points are indicated by black dots. Locations of field-validation samples are represented by diamonds: solid diamonds indicate sites where species were present while hollow diamonds represent sampled sites without detections.

For three of four species (excluding *O. leptogonopodus*), the 1-km^2 models were more conservative than the models constructed using climate data with 4.5-km^2 resolution. For the most widely distributed species, *O. leptogonopodus*, our coarse-resolution models predicted distributions similar to those predicted using fine-resolution data. The greatest difference in modelling results occurred when predicting the distribution of *O. saxatilis*. The 1-km^2 model predicted moderate–high probabilities of occurrence only at sampled locations and adjacent tributaries, whereas the 4.5-km^2 model predicted a low–moderate probability of occurrence across much of the Ouachita Mountain region. Whereas the models developed for *O. leptogonopodus* were similar in their predictions of distributional extent, the 4.5-km^2 climate data predicted overall lower occurrence probabilities than the 1-km^2 model (Figs 2 & 3).

Comparable distribution changes associated with our climate-change models were observed for several species. Due to discrepancies in environmental data (e.g. resolution), only the 4.5-km^2 resolution current models could be compared with future models. The two emission scenarios depicting moderate–high emissions, A1B and A2, pro-duced similar results for each species (see A1B, Fig. 4). In all climate-change scenarios, *O. leptogonopodus* was predicted to expand its range across most of the study area, with high probabilities of occurrence in the A1B scenario (Fig. 4) and a slightly more conservative prediction for the low-emission scenario (Fig. 5). The predicted distributions of *O. menae* and *O. saxatilis* were greatly reduced under the climate-change scenarios (Figs 4 & 5) compared to the current model (Fig. 3). In the A1B projection (Fig. 4), *P. tenuis* was predicted to have its highest probabilities of occurrence in the western and northern catchments and low probabilities of occurrence in the south-east region of the study area. *Procambarus tenuis* was predicted to have an extremely truncated range in the B1 scenario (Fig. 5) but to experience a dramatic range shift to the western and southern periphery of the Ouachita Mountains under the high-emission scenario (Fig. 4).

Environmental suitability and model validation

Variable-contribution analyses revealed several important patterns in how environmental variables contributed to the species-distribution models. Winter temperature had
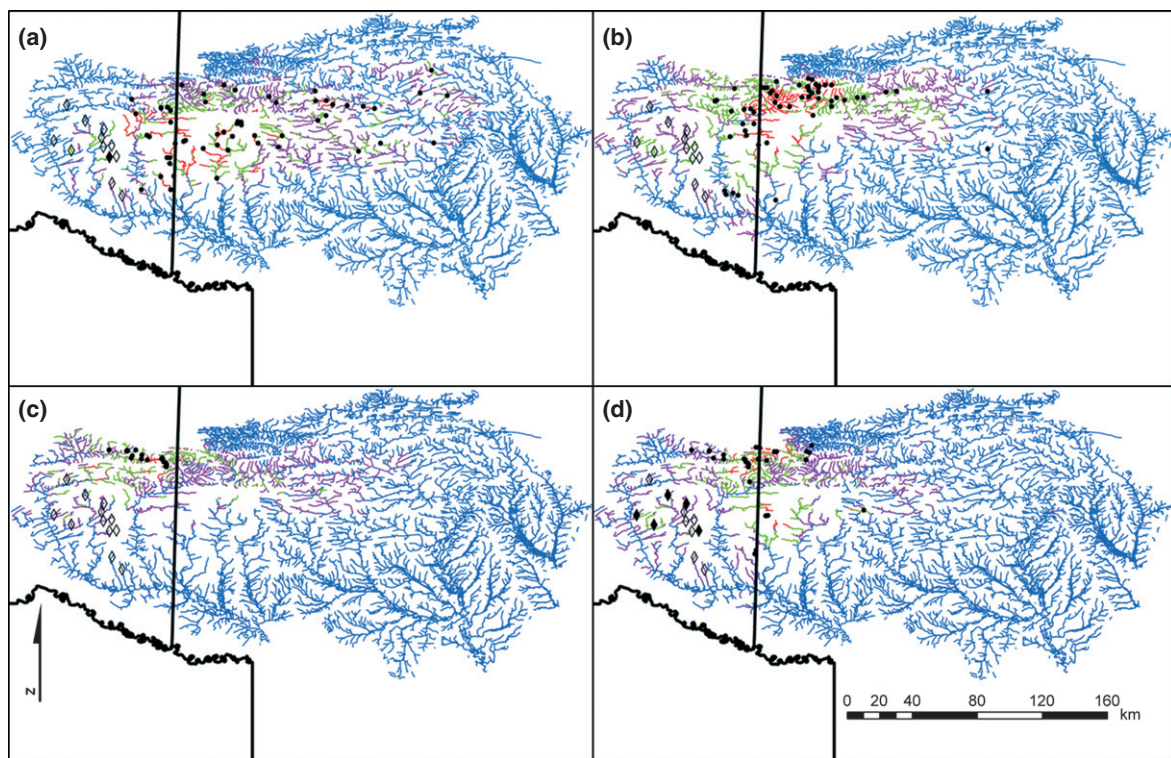

Fig. 3 Current predicted distributions based on 4.5-km^2 resolution data for (a) *Orconectes leptogonopodus*, (b) *O. menae,* (c) *O. saxatilis* and (d) *Procambarus tenuis*. Probabilities of occurrence are blue <10%; purple 11–32%; green 33–65% and red >66%. Occurrence points are indicated by black dots. Locations of field-validation samples are represented by diamonds: solid diamonds indicate sites where species were present while hollow diamonds represent sampled sites without detections.
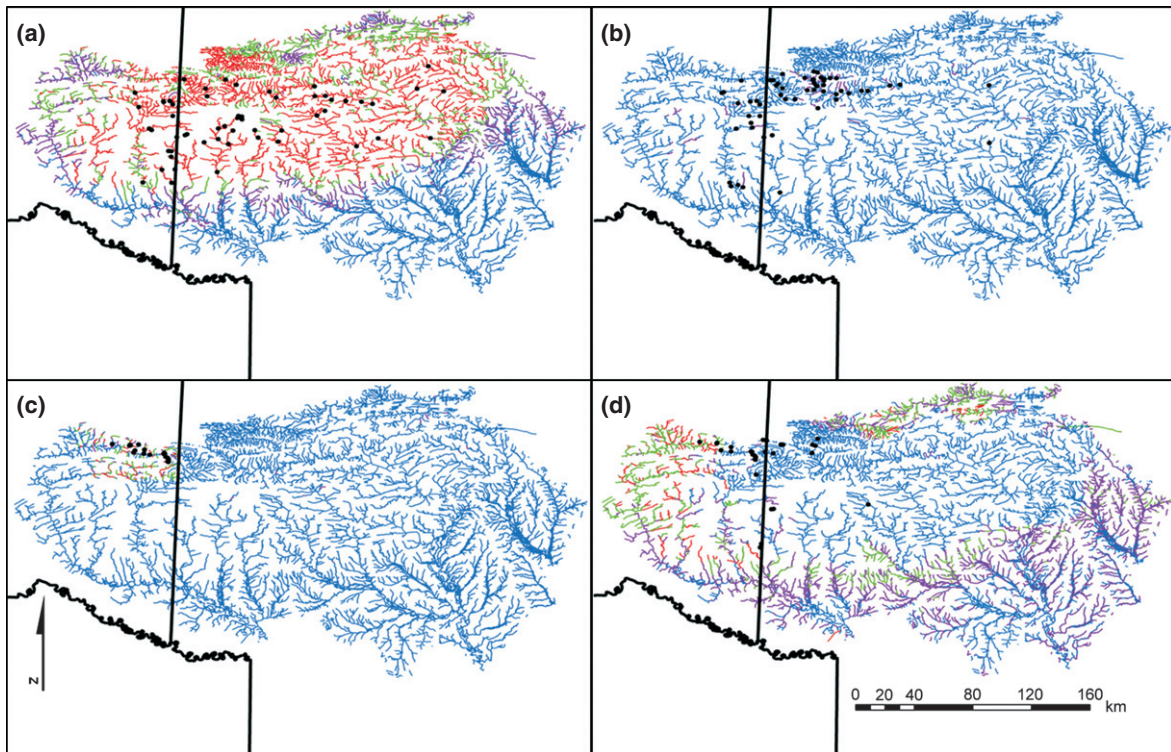
Fig. 4 Future predicted distributions based on a high-emission scenario (A1B). Species distributions are represented by panels: (a) *Orconectes leptogonopodus*, (b) *O. menae*, (c) *O. saxatilis* and (d) *Procambarus tenuis*. Probabilities of occurrence are blue <10%; purple 11–32%; green 33–65% and red >66%. Occurrence points are indicated by black dots.
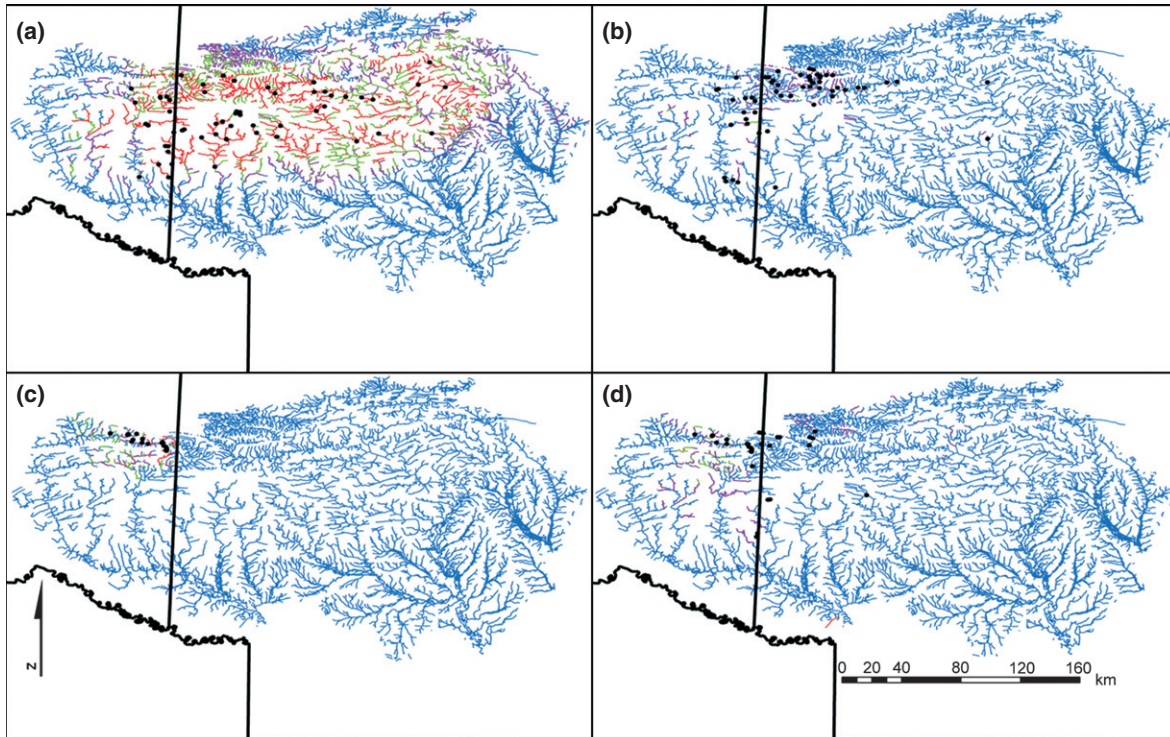

Fig. 5 Future predicted distribution based on a low-emission scenario (B1). Species distributions are indicated in panels: (a) *Orconectes leptogonopodus*, (b) *O. menae*, (c) *O. saxatilis* and (d) *Procambarus tenuis*. Probabilities of occurrence are blue <10%; purple 11–32%; green 33–65% and red >66%. Occurrence points are indicated by black dots.

the highest percentage contribution (>70%) to the model developed for *O. leptogonopodus* (Table 4), whereas soil composition and elevation were the best predictors of distributions for the remaining three species (>55%). Geology was the only additional factor with high explanatory power (>20%) for the distribution of *O. menae*. However, winter precipitation (*O. menae* model) and temperature (*O. saxatilis* model) were factors with high permutation importance based on the final MaxEnt models.

Variable-contribution results of the 4.5 and 1-km^2 resolution models were similar, but indicated some minor differences. Regardless of data resolution, soil and geology were consistently important (represented in the top three variables) for the same species (Tables 4 and 5).

Minor differences in the 4.5 and 1-km^2 resolution models included changes in the order of the variables with low predictive power (Table 5). In addition, temperature, precipitation and land-use variables replaced one another as contributing factors when switching from high- to low-resolution data (e.g. summer precipitation replaced winter temperature in the *O. leptogonopodus* model).

Pearson's product–moment correlations indicated some of the continuous variables used in our models were multicolinear ($r > 0.65$). Elevation was highly correlated with two precipitation variables: winter precipitation ($r = -0.77$) and winter temperature ($r = -0.80$). There were also several correlations among precipitation variables: summer precipitation and wet-season precipitation ($r = 0.66$), summer precipitation and dry-season precipi-

Table 4 Contribution (%) and permutation of importance (importance, %) of environmental variables in 1-km^2 resolution models for four crayfish species: three species of *Orconectes* and one species of *Procambarus*. Contribution is a summation of the regularised gain in all iterations for each variable while permutation importance reflects the effect of randomly permuting the variables on training area under the curve

Variable	*O. leptogonopodus*		*O. menae*		*O. saxatilis*		*P. tenuis*	
	Contribution	Importance	Contribution	Importance	Contribution	Importance	Contribution	Importance
Soil composition	6.9	13.9	20.3	15.0	45.9	2.8	32.9	49.3
Elevation	5.5	15.8	35.4	0.4	16.1	4.1	44.8	17.9
Geology	8.4	0.1	21.1	7.4	0.4	0.2	0.2	0.1
Land-use	0.7	1.2	3.5	2.8	5.0	0.9	8.2	7.3
Stream order (Strahler)	1.6	3.2	2.4	1.9	1.2	0.2	1.0	1.2
Flow accumulation	0.2	0.7	0.8	0.9	2.7	0.5	3.0	4.6
Summer temperature	0.1	0.0	0.4	0.2	0.4	0.2	1.1	6.0
Winter temperature	71.8	52.1	0.4	1.7	17.6	87.0	1.5	5.1
Summer precipitation	0.8	0.5	0.4	5.5	0.0	0.0	0.0	0.0
Winter precipitation	0.0	0.0	9.6	61.0	7.5	0.0	4.2	3.1
Wet-season precipitation	3.4	12.4	0.1	0.3	0.0	0.0	0.7	4.8
Dry-season precipitation	0.6	0.0	5.6	2.8	3.0	4.1	2.4	0.5

Table 5 Contribution (%) and permutation of importance (importance, %) of environmental variables in 4.5-km^2 resolution models for four crayfish species: three species of *Orconectes* and one species of *Procambarus*. Contribution is a summation of the regularised gain in all iterations for each variable while permutation importance reflects the effect of randomly permuting the variables on training area under the curve

Variable	*O. leptogonopodus*		*O. menae*		*O. saxatilis*		*P. tenuis*	
	Contribution	Importance	Contribution	Importance	Contribution	Importance	Contribution	Importance
Soil composition	29.9	16.6	32.3	49.6	25.4	28.1	11.8	19.8
Elevation	15.4	4	47.2	7.8	52.4	14.1	51.7	31.8
Geology	24.4	1.9	2.3	1.8	1.9	6.7	1.6	4.3
Land-use	3.7	2.5	4.7	0.1	2.6	4.0	0.6	3.6
Stream order (Strahler)	0.0	0.0	0.3	1.0	0.6	0.0	0.5	0.5
Flow accumulation	1.0	0.4	0.9	0.9	8.7	8.0	3.5	1.5
Summer temperature	0.9	0.7	1.4	0.6	1.2	10.0	0.0	0.2
Winter temperature	0.1	0.3	0.0	0.0	1.6	22.5	0.0	0.0
Summer precipitation	20.9	65.8	1.4	10.9	0.0	0.0	4.8	7.8
Winter precipitation	2.4	1.4	3.7	3.6	4.2	4.9	22.2	14.4
Wet-season precipitation	0.0	0.1	0.1	0.2	0.1	0.0	0.4	2.9
Dry-season precipitation	1.2	6.3	5.7	21.8	1.2	1.6	2.8	13.3

tation ($r = 0.68$) and winter temperature and winter precipitation ($r = 0.68$).

We created response graphs to demonstrate how occurrence probabilities would change as a single variable of interest was modified. All other variables were removed from each model before response graphs were developed due to use of correlated variables. The response of *O. saxatilis* to winter temperature indicated the species had the highest probability of occurrence between −4 and −3 °C (Fig. 6). The highest occurrence probability for *O. leptogonopodus* was associated with winter temperatures below −4 °C. Elevation response curves for *O. menae* (Fig. 6), *O. saxatilis* and *P. tenuis* indicated high probabilities of occurrence (>66%) at altitudes above 300 m for the two *Orconectes* sp and above 400 m for *P. tenuis*. All four species had high probabilities of occurrence in stoney-sandy loam soils. Additionally, areas with shale, novaculite and sandstone geology contributed significantly to high occurrence probabilities of *O. menae* and *O. leptogonopodus*. Our model predicting the occurrence of *P. tenuis* was the only one to suggest land use was important (Fig. 6). Land-use areas described as opened developed land, forest and pasture were predicted to have the highest probability of *P. tenuis* occurrence.

The cross-validation procedure indicated our models predicted omitted data points much better than would be expected at random. The mean AUC values associated with fine-grain current-distribution models for *O. leptogonopodus*, *O. menae*, *O. saxatilis* and *P. tenuis* were 0.95 (0.03 SD), 0.93 (0.04 SD), 0.98 (0.015 SD) and 0.93 (0.07 SD), respectively. Model performance was similar with coarse-resolution models: mean AUC values were 0.91 (0.05 SD), 0.92 (0.6 SD), 0.97 (0.02 SD) and 0.95 (0.05 SD), respectively.

Quantitative field sampling provided additional validation for our current-distribution models. We detected *O. leptogonopodus* and *P. tenuis* in three streams of the Glover River catchment. *Orconectes leptogonopodus* was found in Middle Carter Creek where we predicted a moderate probability of occurrence using our 4.5-km^2 resolution model (Fig. 3). We did not find *O. leptogonopodus* in tributaries adjacent to Middle Carter Creek where our 4.5-km^2 resolution model indicated extremely low probabilities of occurrence. Three of five locations where *P. tenuis* was found during field sampling were predicted as areas with possible populations via the 1-km^2 resolution model (Fig. 2).
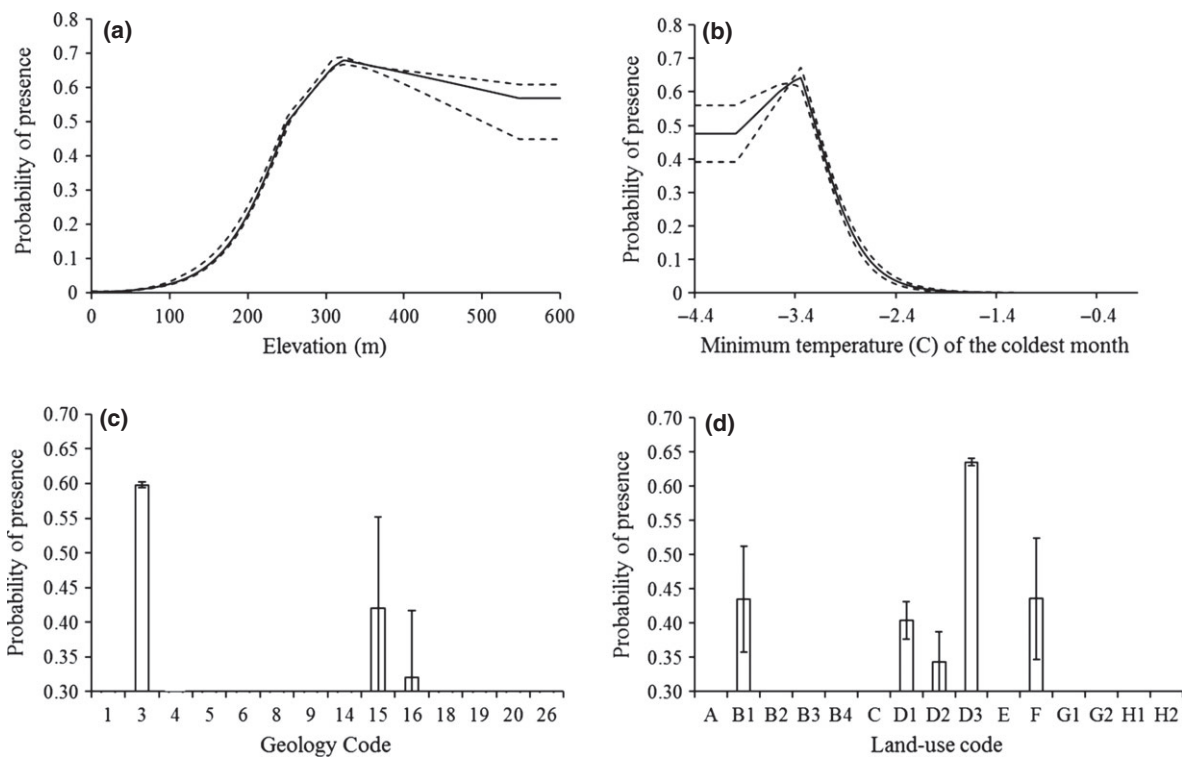

Fig. 6 Response graphs indicating the relationships between: (a) *Orconectes menae* and elevation, (b) *O. saxatilis* and winter temperature, (c) *O. leptogonopodus* and geology and (d) *Procambarus tenuis* and land use. Significant geology classifications include 3 = shale and sandstone, 4 = sandstone and mudstone, 15 = novaculite and 16 = chert. Important land-use variables were B = developed open space; D_1, D_2, D_3 = deciduous, evergreen and mixed forest respectively; F = grassland.

Discussion

Effective crayfish conservation requires knowledge of species distributions. Having a narrow range, in itself, puts some species at risk from potential threats, including invasive species, habitat alteration and poor water quality (Taylor *et al.*, 1996; Lodge *et al.*, 2000; Jones & Bergey, 2007). Changes in distribution may signal a need for conservation action but are difficult to assess for many crayfishes because of poorly known historic distributions (Larson & Olden, 2011). Occurrence patterns from museum records (Schuster, Taylor & Johansen, 2008), gaps in current-distribution data (Horwitz, 1994) and absences in modelled potential distributions may signal range reductions. Combining distribution patterns with habitat and other environmental data, including sympatric species, allows association of particular species with habitat conditions that can be helpful in modelling potential distributions (this study, Feria & Faulkes, 2011), identifying invasion potential (Olden, Vander Zanden & Johnson, 2011) and assessing factors affecting population change (Svobodová *et al.*, 2012).

Species-distribution modelling, as used in the current study, is an excellent technique for identifying populations beyond sampled locations. However, models do not account for mitigating habitat factors, biotic interactions or possible adaptations or behavioural responses that might influence realised distributions. These distributions are often defined using coarse-scale environmental variables (e.g. Brewer *et al.*, 2007; Chen *et al.*, 2007; Westhoff *et al.*, 2011), but numerous factors at finer-spatial scales may ameliorate or exacerbate the realised distribution. For example, land-use changes may create unsuitable habitat at a coarse scale, but stable riparian corridors may mitigate the negative in-channel effects locally (e.g. fish-assemblage response to deforestation; Lorion & Kennedy, 2009). Unintended biotic interactions, on the other hand, may result in distributions that contract more extensively or rapidly than models may predict. For example, we predicted *O. leptogonopodus* to have a high probability of expanding its range under climate-change scenarios while three sympatric species were predicted to undergo a range contraction (excluding *P. tenuis* A1B), but our climate models do not account for the potential of *O. leptogonopodus* to inhabit the niche left vacant by the removal of the other species. Further, correlations between elevation and climate are probably driving the predicted *P. tenuis* range shift in our A1B model, but this takes no account of the species behaviour (e.g. feeding, predator avoidance, movements; Weis, 2010). Species may be able to alter migration patterns in response to climate change (Walther *et al.*, 2002) or adapt to changes phenotypically (Bale *et al.*, 2002; Aitken *et al.*, 2008; Visser, 2008), particularly populations with high genetic diversity (e.g. Aitken *et al.*, 2008). Lack of basic ecological information, including how habitat use at fine-spatial scales constrains or enhances these populations, and an understanding of the competitive or adaptive abilities of these endemic species, makes it difficult to refine our predictions. However, the development of landscape-scale models such as ours provides an excellent foundation to examine the importance of other biotic and abiotic factors.

Landscape-scale environmental factors, such as significant variables in our distribution models, play a major role in the distribution of aquatic organisms because they constrain physicochemical processes at fine-spatial scales (Frissell *et al.*, 1986). Geology and soils within a catchment are known to influence the physicochemical character of the water (Hynes, 1975), run-off patterns and infiltration rates following precipitation events (Beven, 2001; Smakhtin, 2001) and determine morphological characteristics of the streams (Knighton, 1998). Geology relates to the distribution of some crayfish species (e.g. France, 1992; Joy & Death, 2004; Westhoff *et al.*, 2011), but not others (Westhoff, Guyot & DiStefano, 2006). However, few studies have addressed crayfish distributions at coarse resolutions so the dearth of significant findings may simply reflect the lack of studies at this spatial scale. The relatively small distributions of many crayfishes and the lack of fine-resolution geology layers may also be contributing factors. While we did not test the correlation between the categorical variables of soils and geology, soil types are often related to geology (Miller & Donahue, 1990). The relationship between crayfish distribution and soil composition may be due to its suitability for burrowing. Sandy loam is a coarse-grained soil that appears easily excavated by crayfish in this region (J. Dyer, unpubl. data). Constraints placed on these populations may relate to water capacity of the soil (see DiStefano *et al.*, 2009), given that streams in this catchment rise and fall quickly and water availability is scarce during summer and autumn base-flow periods. Different tolerances of these endemic species to soil-water availability rather than instream-water availability may provide insights into species coexistence as well as future distributional changes due to climate patterns.

Elevation was important in determining distributions of three of the crayfish species in this study. Elevation is related to stream gradient, which is associated with several abiotic and biotic factors within streams (Knighton, 1998; Nino, 2002). Generally, we expect higher elevation areas to occur in headwater streams, have coarser substrates, higher water velocities and a high

diversity of aquatic habitats (Rosgen & Silvey, 1996). Headwater streams receive high loads of coarse organic material (Vannote *et al.*, 1980), which is a major food source for many crayfish species (Momot, Gowing & Jones, 1978). Coarse substrates create large interstitial spaces in the streambed that trap coarse organic matter (Parker, 1989) and serve as refuges for crayfish. In addition, headwater streams often have intermittent or temporary flow regimes that create an abundance of shallow-water habitat unsuitable for the persistence of smallmouth bass *Micropterus dolomieu* and other centrarchid predators of crayfish (Schlosser, 1987). *Orconectes menae* and *P. tenuis* are associated with rocky headwater streams (Robison & McAllister, 2008; Robison *et al.*, 2009). Habitat use of *O. saxatilis* has been well studied, with documented use of riffles in headwater tributaries of the Kiamichi River (Jones & Bergey, 2007). These species are known to burrow during dry periods, which is an expected adaptation to harsh flow extremes within this region. Elevation contributed only 5% to the *O. leptogonopodus* model, and it is also the species with the broadest predicted range, indicating it is not restricted to head water streams. Interestingly, these species are sympatric in several streams, suggesting habitat segregation occurs at fine-spatial scales, but their habitat associations are unknown. We suggest future research should address habitat selection at fine scales so that better predictions can be made about species persistence under human-induced landscape change.

Land use was rarely related to species presence, with only *P. tenuis* being related to specific land-use practices. Areas with open pasture (fields managed for forage plants and livestock grazing) and open developed land (areas developed for farming, ranching or logging and lacking urban development) had a moderate probability of species occurrence, but the highest occurrence probability for the species was in mixed forest, the native land cover of the Ouachita Mountains. *Procambarus tenuis* appears to have a patchy distribution and to occur in low densities (Bergey *et al.*, 2005); however, they are not easily detected via traditional sampling techniques, and this may have skewed the relation between occurrence and land-use parameters. This species burrows deeper in the substrate and earlier in the year than sympatric species and often seeks refuge under substrate exceeding 500 mm in diameter (J. Dyer, unpubl. data). The International Union for Conservation of Nature considers the species as data deficient (Crandall, 2010). It is likely that our *P. tenuis* model, in addition to distribution models in general, would be improved by use of more efficient sampling techniques (e.g. quadrat sampler; DiStefano *et al.*, 2003).

Combining species-distribution and global-climate models can help forecast potential range shifts in response to anthropogenic changes to environmental conditions (Hijmans & Graham, 2006; Yates & Bailey, 2010; Klamt, Thompson & Davis, 2011). The species in the current study showed varied responses to the emission scenarios, probably due to interspecific differences in tolerance to precipitation patterns. Although temperatures did increase in all climate-change scenarios, it is unlikely that temperature change alone will exclude crayfish from its current range. Crayfish have thermal optimums for fitness (though usually unknown), but they often inhabit areas outside the most favourable thermal range (Sargent *et al.*, 2011). The changes in precipitation that result from an increase in average temperature are much more likely to have an impact on crayfish distributions. Crayfish occupying headwater streams have evolved to live in areas with natural disturbance; however, climate change may lead to extended drought periods and more intense precipitation events. More intense precipitation would increase streambed scouring, which could flush crayfish downstream and reduce detritus abundance. Precipitation is relatively high and, while fairly uniform across the Ouachita region, is somewhat higher near the headwaters (Negus, Fisher & Marston, 2006). With the exception of *O. leptogonopodus* and *P. tenuis*, other species were predicted to have a very low probability of occurrence under climate-change scenarios. The range expansion of *P. tenuis* in the A1B scenario is probably a result of colinearity between elevation and winter temperature. In the A1B scenario, precipitation amounts in the south-eastern portion of the study area are similar to areas where occurrence probabilities were high in our current model. However, the elevation of the south-eastern region is below 100 m, whereas the species has the highest probability of occurrence where elevations are above 400 m, suggesting these areas will not be suitable for the species unless some adaptation occurs.

Both endemics and freshwater species in general are predicted to be vulnerable to climate change (Sala *et al.*, 2000; Xenopoulos *et al.*, 2005) because of already restricted ranges and limited dispersal opportunities. Our results agree with others (e.g. Daufresne *et al.*, 2003; Chessman, 2009) that response direction to climate change is species specific. Our hypothesis that crayfish species with stronger relations between climate and flow would be more susceptible to climate change is difficult to evaluate because of correlations between elevation, which appears to be most restrictive for three of the species, and some climate variables. However, the models for *O. leptogonopodus* indicate elevation is less important for this species

compared to the others, but winter temperature is very important, and its range actually expands under climate scenarios. Taken together, this evidence suggests elevation placed the largest restrictions on distributional adjustments in response to climate scenarios. The Ouachita Mountain region is predicted to have warmer temperatures, prolonged droughts and more intense precipitation events under global-climate change (Knapp et al., 2008). Adapting to these changes will be difficult for species restricted to headwater streams. Further, these changes are likely to negatively affect tertiary burrowing crayfish during droughts when they tunnel in moist soil to seek refuge from extreme high temperatures and dry conditions (DiStefano et al., 2009).

Use of coarse- or fine-resolution data can have different implications for modelling and ecological understanding (e.g. Wiens, 2002). Used alone, coarse-scale information may not reveal subtle, although important, changes across an environment; however, an abundance of fine-scaled information may overwhelm the capacity of a model (Guisan et al., 2007) or decrease the benefits provided by modelling in terms of reducing field-sampling costs (Stockwell & Peterson, 2002). As a result, ecologists strive to reach a balance between data collection and identifying patterns that vary spatially and temporally. Guisan et al. (2007) evaluated the impacts of varying spatial resolution on model performance and found that while MaxEnt was one of the best techniques when using coarse-resolution data, the models degraded significantly under a 10-fold coarsening of resolution. Further, the authors suggested models with higher predictive power may be necessary to see the effects of scale. Differences in the grain size of climate data had an impact on the predictions of our current-distribution models, with the fine-grain models projecting more conservative distributions than the coarse-resolution models. The 4.5-km^2 resolution models correctly predicted all presence points that we gathered through field validation but it falsely predicted many high-probability areas that we were unable to validate during low-flow sampling. The 1-km^2 models predicted absences much more accurately than the coarse-resolution projection. Furthermore, significant field sampling has been completed targeting capture of *O. saxatilis* (Jones & Bergey, 2007), and our fine-scale model more accurately represented those results than the 4.5-km^2 resolution model. The current study indicates that models of crayfish distributions that have high predictive power may benefit from use of fine-resolution environmental layers (i.e. our field validation indicates these models were more accurate). This study also highlights the importance of field-validation procedures as suggested by Olden, Jackson & Peres-Neto (2002).

The models developed in this study create a framework to examine habitat features that may interact with the coarse-scale factors to influence distributions or population success. For example, in a period of increasing drought, we need to understand how soil composition, water withdrawals and changes in climate patterns interact to determine changes in populations of crayfish. If some species are expected to expand their distributions with a changing climate, how will aquatic communities respond? For example, if *O. leptogonopodus* expands its distribution and other native species ranges contract, will energy flow in these systems remain the same or will higher trophic levels respond differentially to these possible species replacements? Many of these questions require targeted studies that would benefit from a structured and systematic monitoring programme.

Our models have indicated that the distribution of these endemic crayfish populations related primarily to elevation, climate, geology and soils. This information allows us to identify specific areas that are important to conserve endemic crayfish and to prioritise sampling efforts to monitor populations temporally. Our model validation indicated the projected distribution either failed to predict or over predicted actual species locations. While we cannot expect models to be 100% accurate, we can better explain distribution with fine-scale environmental parameters and true absence data. Given the important role crayfish play in ecosystem dynamics and the projected negative effects of climate change, monitoring these populations would increase our understanding of changes in stream function over time. True absence data are rare, but a reasonable approximation could be achieved using targeted sampling that varies temporally and is designed to address specific conservation concerns (e.g. land-use changes, water withdrawals).

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