Received: 20 August 2021 | Revised: 8 March 2022 | Accepted: 13 March 2022

DOI: 10.1002/aqc.3816

RESEARCH ARTICLE

WILEY

Geospatial assessment of freshwater invasive species to inform turtle conservation and management

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Funding information
U.S. Fish and Wildlife Service, Grant/Award Number: F18AF01162

Abstract

1. Identifying the ecological factors that determine the spread of invasive species is key to adequately managing endangered species in freshwater ecosystems. Invasive species are a main threat to turtles, which are targets of major conservation efforts worldwide.
2. In freshwater ecosystems of the south-western USA, invasive bullfrog (*Lithobates catesbeianus*) and crayfish species (*Faxonius virilis* and *Procambarus clarkii*) represent a major risk to the desert mud turtle (*Kinosternon sonoriense sonoriense*), state-listed as a Species of Greatest Conservation Need in Arizona. As a species in the early stages of population decline, the desert mud turtle is a top candidate for the development of management plans to decrease extinction risk.
3. An invasion risk assessment tool was built from available occurrence data for *K. s. sonoriense* and the invasive bullfrog and crayfish species in Arizona using 5,886 de-duplicated records from public databases and reports from the Arizona Game and Fish Department. The occurrence density of *K. s. sonoriense* was calculated state-wide to define populations in which the level of invasion by bullfrog and crayfish was assessed. The environmental factors associated with the abundance of invasive species in populations of *K. s. sonoriense* were then analysed.
4. A higher prevalence of crayfish and bullfrog was detected in turtle populations located in perennial streams. Invasive abundance was significantly higher in turtle populations at higher elevation and closer to the main river trunk for both invasive taxa. Higher bullfrog abundance was detected near human settlements, whereas crayfish were more abundant further from human settlements.
5. These results will inform which populations of *K. s. sonoriense* require intensive surveying and control of invasive species to maintain the health of native desert mud turtle populations. This study provides valuable information regarding the environmental conditions associated with the abundance of invasive species threatening turtle populations, helping to develop science-based management of freshwater ecosystems.

KEYWORDS

bullfrog, crayfish, *Faxonius virilis*, *Kinosternon sonoriense*, *Lithobates catesbeianus*, *Procambarus clarkii*

1 | INTRODUCTION

Invasive species pose a major threat to aquatic biodiversity (Gurevitch & Padilla, 2004; Didham et al., 2005) and freshwater ecosystems are vulnerable to invasion, especially in arid climates (Davis, Kerezsy & Nicol, 2017). Invasive species can have minor to major effects that can drive native species to extinction, including modifying the physical or chemical freshwater conditions and altering trophic dynamics (Carpenter, Stanley & Vander Zanden, 2011). Furthermore, invasive species can have additive effects on native freshwater species through predation, competition or disease transmission (Rahel & Olden, 2008; Gallardo et al., 2016). The first step towards the conservation and management of freshwater species is to develop tools to identify, manage and eradicate invasive species with the aim of improving native species preservation and recovering native ecosystem health and services (Prior et al., 2018). Different ecological factors such as climate, geography, hydrology, biological interactions and human disturbance can determine invasion dynamics at different spatiotemporal scales (Milbau et al., 2009). Thus, understanding the interactions and ecological characteristics that affect invasion is critical for developing science-based management of invasive species.

Nearly one-half of the world's turtles are listed as threatened by IUCN criteria and they are therefore a target of major conservation efforts worldwide (Stanford et al., 2020). Multiple factors are driving chelonian population declines including climate change, habitat loss, illegal trade for meat and the pet industry, impacts of invasive species and synergistic interactions among these threats. Turtles are long lived and reach high densities, and their decline and loss can be especially damaging in freshwater ecosystems where they provide ecosystem functions such as nutrient cycling, soil bioturbation and water quality regulation (Lovich et al., 2018; Santori et al., 2020). Invasive species can adversely affect native turtle populations by competition, predation and habitat modification, and by acting as disease vectors (e.g. *Mycoplasma*, ranavirus, herpesvirus; Stanford et al., 2020). Therefore, one major strategy to manage turtles against the impacts of invasive species is to identify and characterize invasive species impacts on native freshwater turtle populations.

In the freshwater systems of the arid south-western USA, the native Sonora mud turtle (*Kinosternon sonoriense*) is widely distributed in ponds, rivers and streams. This is one of the most arid-dwelling species in the genus *Kinosternon* (Hensley et al., 2010; Iverson, Le & Ingram, 2013; Butler et al., 2016). Two subspecies have been described: *K. s. sonoriense* (desert mud turtle) and *K. s. longifemorale* (Sonoyta mud turtle), with the latter listed as Endangered under the US Federal Endangered Species Act and Critically Endangered by the International Union for Conservation of Nature (IUCN; Rosen & Stone, 2017); it occurs in only five locations across the USA–Mexico border. The *K. s. sonoriense* subspecies is categorized as a Species of Greatest Conservation Need in the Arizona State Wildlife Action Plan (Arizona Game and Fish Department, 2012) and Near Threatened by the IUCN (van Dijk, 2011). Therefore, *K. s. sonoriense* is a top candidate for the development of management plans to decrease its extinction risk, as intervention and effective management at this stage could stabilize populations of the desert mud turtle before their conservation status deteriorates to that of its sister subspecies (Stone, Congdon & Smith, 2014).

In Arizona, *K. s. sonoriense* (hereafter, desert mud turtle) is adversely affected by invasive species, particularly by two species of crayfish (*Faxonius virilis* and *Procambarus clarkii*) and the American bullfrog (*Lithobates catesbeianus*), which originated from eastern North America and are widely distributed in freshwater ecosystems across the south-western USA (Rosen & Schwalbe, 1995; Carpenter, 2005; Hensley et al., 2010). These three species are highly successful generalists that have invaded freshwater systems globally and exert adverse impacts on native biota by altering ecosystem dynamics and trophic interactions (Adams & Pearl, 2007; Ficetola, Thuiller & Miaud, 2007; Gherardi, 2007; Gherardi et al., 2011). In addition to indirect bottom-up effects, all three of these invasive species prey upon hatchling mud turtles and decrease population recruitment (Akins & Jones, 2010; Hensley et al., 2010). Bullfrogs can also carry and may transmit diseases that affect turtles, such as ranaviruses (Winzeler et al., 2015; Chinchar & Duffus, 2019).

Several factors are expected to determine the distribution and abundance of these invasive species across the arid south west. Elevation can limit dispersal and is correlated with environmental variables such as temperature, topography and stream order (Dyer et al., 2013; Peterson et al., 2013). For freshwater species living in desert ecosystems, the proximity and persistence of main water sources may also be relevant for invasive abundance (Peterson et al., 2013; Nolen et al., 2014). In addition, the distance to human disturbance sources (such as roads or human settlements) may be associated with higher propagule pressure and therefore be a good predictor of the presence and abundance of invasive species (Capinha, Brotons & Anastácio, 2013; Anderson, 2019; Mouser, Mollenhauer & Brewer, 2019). These individual factors may affect invasive species distributions and densities both directly and interactively.

Removal of invasive crayfish and bullfrogs has proved difficult, time consuming, and expensive. Thus, the development of risk assessment tools is necessary to identify the invasion prevalence of these species across the range of the desert mud turtle in order to prioritize areas in which to target management efforts. This risk assessment tool can also be used to design studies to understand the ecological impacts of different invasion levels on turtle populations, and in particular to design studies that will reveal the source localities for the invasions to mitigate against future invasions (e.g. using genetic data). This study used 86 years of data from four different sources that consisted of 5,886 de-duplicated and georeferenced GPS locality records. These data were aggregated to build a risk assessment tool for freshwater invasive species focusing on native desert mud turtle populations in Arizona. The main objectives were to characterize the invasion level of bullfrogs and crayfish throughout the distribution of desert mud turtle populations, and to determine which of the tested environmental variables explain the abundance of invasive species in order to guide and improve management strategies.

2 | METHODS

2.1 | Occurrence and environmental data acquisition and curation

For *K. s. sonoriense* and the invasive bullfrog (*L. catesbeianus*) and crayfish species (*F. virilis*, *P. clarkii*), occurrence records since 1935 were obtained from 376 Arizona Game and Fish Department reports, the public citizen science databases iNaturalist and iMapInvasives and Arizona State University collections (Table 1). Citizen science databases, such as iNaturalist or iMapInvasives, help improve geographical modelling and the detection of invasive species, and other studies have proved the utility of these tools to define management strategies (Maynard-Bean et al., 2020; Werenkraut, Baudino & Roy, 2020). To avoid pseudoreplication by counting records from different times in the same location, data points were de-duplicated, leaving only one record per locality. The original/de-duplicated datasets had 2,091/1,354 occurrences for mud turtle, 5,170/1,537 for bullfrog, and 6,563/2,995 for crayfish (Table 1, Figure 1a).

Occurrence data were plotted with the geographic information system software ArcGIS v10.6 (Esri Inc., 2018; Figure 1a) using the WGS84 coordinate system. The digital elevation model from the WorldClim database (Fick & Hijmans, 2017) and a rivers and streams layer for Arizona (Arizona State Land Department, 1993) were included. The Arizona road network (US Census Bureau, 2019) and the Arizona city point layer (AZGeo Data Hub, 2020) were added as proxies for human disturbance. Water flow accumulation was calculated in ArcGIS v10.6 using the elevation layer. For this, the 'Fill' tool was used to fill missing pixel data in the elevation raster, then 'Flow direction' was used to estimate the water flow direction through the landscape given elevation, and finally the 'Flow accumulation' tool was used to calculate the amount of flow accumulated in each cell of the final raster. For each occurrence point of the three taxa, the corresponding elevation, the distance to the nearest human settlement, the distance to the nearest road, the distance to the closest main river trunk, flow accumulation and the stream persistence (i.e. perennial or intermittent) of the closest stream were measured (Figure 2).

2.2 | Invasion risk assessment of turtle populations

Two approaches were used to assess the invasion risk. First, desert mud turtle populations were defined using the kernel density function in ArcGIS and convex polygons were generated around areas that had a turtle density higher than 0.005 occurrences km^{-2}. The abundance of invasive species was then counted within these areas. Second, a 5 km buffer was generated from each occurrence point of *K. s. sonoriense*, and the abundance of bullfrog and crayfish occurrences was calculated as the sum of occurrences within that 5 km area. Both crayfish species were analysed together, because they are ecologically similar and affect turtle populations in similar ways (Twardochleb, Olden & Larson, 2013).

2.3 | Variables associated with invasive species abundance in turtle populations

Generalized linear models (GLMs) were used to assess which environmental variables (elevation, human disturbance, distance to rivers and stream persistence) at turtle occurrence points were associated with the abundance of bullfrog or crayfish records within 5 km of those occurrences. To evaluate which proxy of human disturbance was a better predictor of invasive species abundance, distance to the nearest road and distance to the nearest city or town were analysed in separate models. The response variable was the number of invasive records in a specific turtle locality, and data were therefore analysed with a Poisson point processes model (Warton & Shepherd, 2010). When analysing ecological count data, it is likely that models violate assumptions of over-dispersion (i.e. model residuals have an excess of variability; Richards, 2008; Campbell, 2021). Therefore, over-dispersion was tested with the 'dispersiontest' function from the 'AER' package (Zeileis & Kleiber, 2008) in the R software 3.6.3 (R Core Team, 2020). As data were over-dispersed, a log link function for a quasi-Poisson probability distribution in the response variables was used. The analyses were run both with and without interaction terms to evaluate whether nonlinear additive effects between variables provided more explanatory power to the models. As the relationships detected between invasive species abundance and elevation and

TABLE 1 Description of the data sources used in this study and the number of raw and filtered occurrences per source

			Number of filtered occurrences (number of raw occurrences)		
Data Source	Reference	Time period	Desert mud turtle	Bullfrog	Crayfish
iNaturalist	Ueda (2021)	2001–2020	198 (281)	290 (309)	115 (119)
iMap Invasives	NatureServe (2021)	1981–2015	NA	NA	530 (1,742)
ASU Collections	Arizona State University Biocollections (2020)	1935–2020	221 (578)	NA	NA
AZGFD reports	376 reports + departmental database	1935–2020	935 (1,232)	1,247 (4,861)	2,350 (4,702)
Total:			1,354 (2,091)	1,327 (5,170)	2,995 (6,563)

Abbreviations: ASU, Arizona State University; AZGFD, Arizona Game and Fish Department.

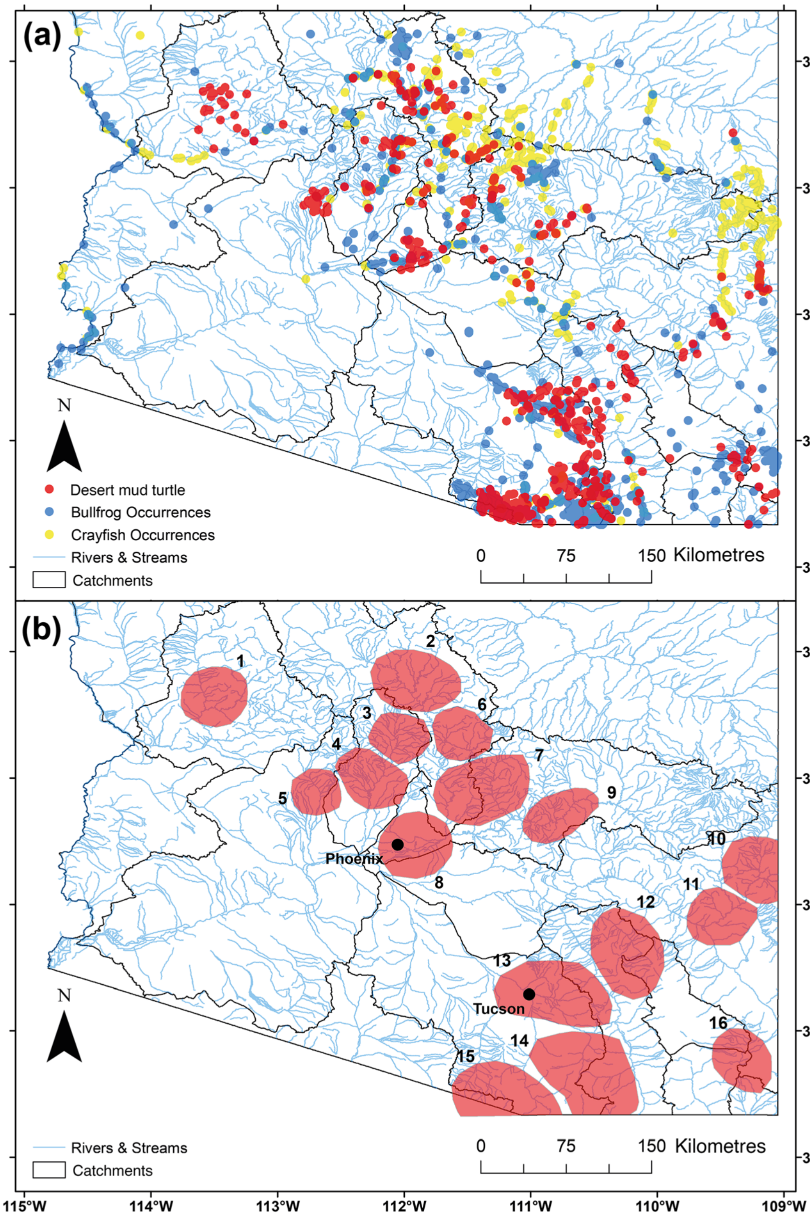

FIGURE 1 (a) Occurrence data for the three focal taxa in Arizona: *Kinosternon sonoriense sonoriense* (red), *Lithobates catesbeianus* (blue) and crayfish (*Faxonius virilis* and *Procambarus clarkii*, yellow). (b) Desert mud turtle populations defined by a kernel density > 0.005 turtle occurrences km^{-2}

distance to the main river were not independent from flow accumulation, the association between flow accumulation and abundance of invasive records, within 5 km from turtle occurrences, was also tested with a GLM using a quasi-Poisson probability distribution. Models were compared and evaluated by leave-one-out cross validation (LOOCV), and the prediction error was calculated with the 'boot' package (Canty, 2002). The best model for each response variable was selected by the lowest LOOCV error score. In order to evaluate a possible temporal trend in which relationships between variables may have changed over time, the data were separated into two subsets corresponding to invasive records before 1999 (210 and 146 records for bullfrog and crayfish respectively) and from 1999 to 2019 (1,327 and 2,849 records for bullfrog and crayfish respectively), and analyses were additionally run for each temporal dataset separately. All statistical analyses were performed in R.

3 | RESULTS

Based on species occurrences and the environmental covariate data from the whole de-duplicated dataset, the average (and range) elevations were 1,165 (343–1,912) masl for *K. s. sonoriense*, 1,249 (29–2,560) masl for bullfrog, and 1,659 (47–2,770) masl for crayfish. The average distance to the nearest road was 10.27 (0–38.21) km for *K. s. sonoriense*, 8.85 (0–62.25) km for bullfrog and 9.25 (0–39.58) km for crayfish. The average distance to the nearest city was 7.96 (0.044–24.82) km for *K. s. sonoriense*, 6.31 (0.02–38.2) km for bullfrog and 11.18 (0–60.72) km for crayfish. The average distance to the main river was 10.08 (0–33.01) km for *K. s. sonoriense*, 10.52 (0–45.58) km for bullfrog and 8.53 (0–37.27) km for crayfish. The occurrence count regarding stream persistence for *K. s. sonoriense* was 639 in intermittent and 301 in perennial streams, for bullfrog it was

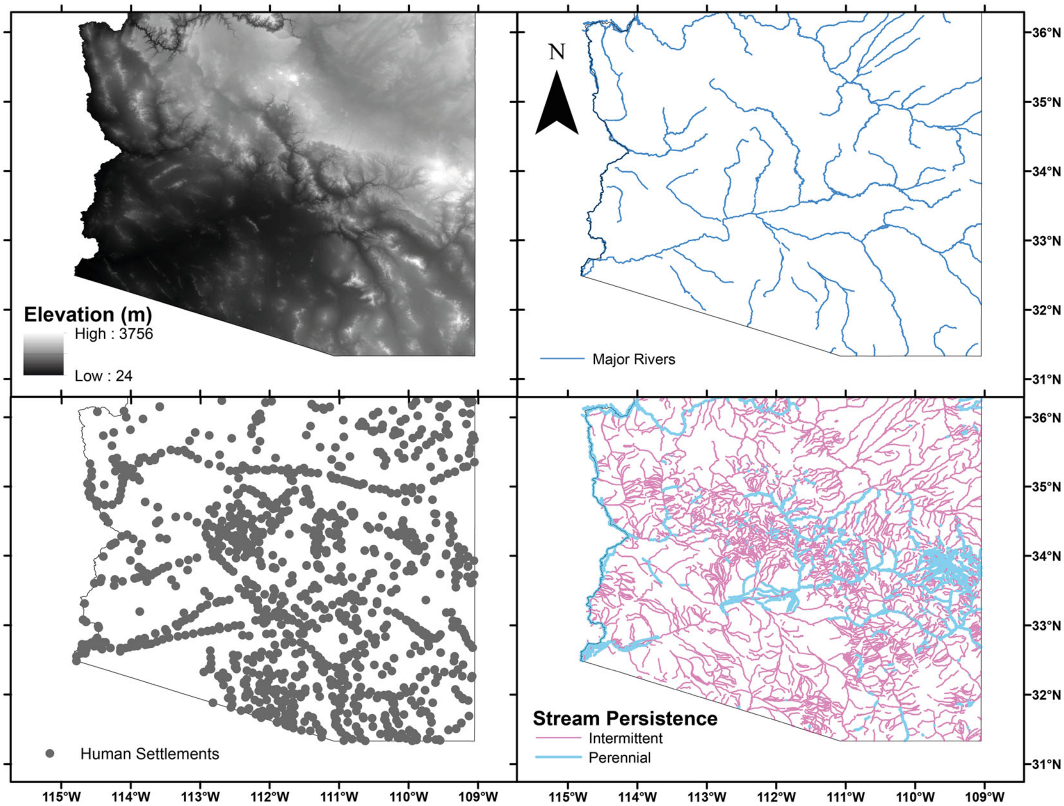

FIGURE 2 Environmental variables used in the study to determine factors associated with the abundance of bullfrogs and crayfish. Variables are: (a) elevation, (b) distance to the main river trunk, (c) distance to the nearest human settlement and (d) stream persistence (intermittent or perennial)

1,137 in intermittent and 400 in perennial streams and for crayfish 635 in intermittent and 2,360 in perennial streams.

The kernel density defined 16 mud turtle populations (Figure 1b), and in those populations the bullfrog abundance ranged from 0 to 332 occurrences and crayfish occurrence count ranged from 0 to 517. There were high invasion levels for both taxa in the central-northern part of the mud turtle's distribution (in the Phoenix metropolitan area; populations 2, 3, 6 and 7; Figure 3) and in the south-eastern part of Arizona (near the city of Tucson; populations 13–15; Figure 3); there were three uninvaded or low-invaded mud turtle populations (i.e. fewer than six observations of invasive species; populations 1, 5 and 12; Figure 3). Within 5 km from turtle records, the mean bullfrog abundance was 27.96 (range 0–101) and the mean crayfish abundance was 15.17 (range 0–371).

The best model for bullfrog abundance within 5 km from turtle occurrences included elevation, distance to the main river, distance to the nearest city and river persistence (LOOCV error = 16.99; see Tables S1–S3 for the other models). The GLM detected a significant positive relationship with elevation (Figure 4a) and with river persistence (perennial > intermittent; Figure 5c), and a significant negative relationship with distance to the nearest city (Figure 4c) and distance to the main river (Figure 5a). The best model for crayfish abundance within 5 km from turtle records also included elevation, distance to the main river, distance to the nearest city and river persistence (LOOCV error = 25.59; see Tables S1–S3 for the other models). A significant positive relationship was detected with elevation (Figure 4b), distance to the nearest city (Figure 4d) and river persistence (perennial > intermittent; Figure 5d) and a significant negative relationship with distance to the main river (Figure 5b). When testing for a relationship between invasive abundance and flow accumulation, a significant negative relationship was detected for bullfrogs and no significant relationship was detected for crayfish (Figure S1), which suggests no downstream accumulation of invasive species. Models separating the dataset by time intervals produced equivalent results to those including the full dataset, except that crayfish abundance records before 1999 only had a significant negative relationship with distance to the nearest city (Table S4). This could be due to a lower number of observations and reduced statistical power.

3.1 | Caveats and data limitations

There are caveats and limitations regarding the data and analyses performed in this study. The models used occurrence data of presences detected for the species and true absences were *not* included, which means the results may be affected by sampling effort where more frequented areas have higher abundances. However,

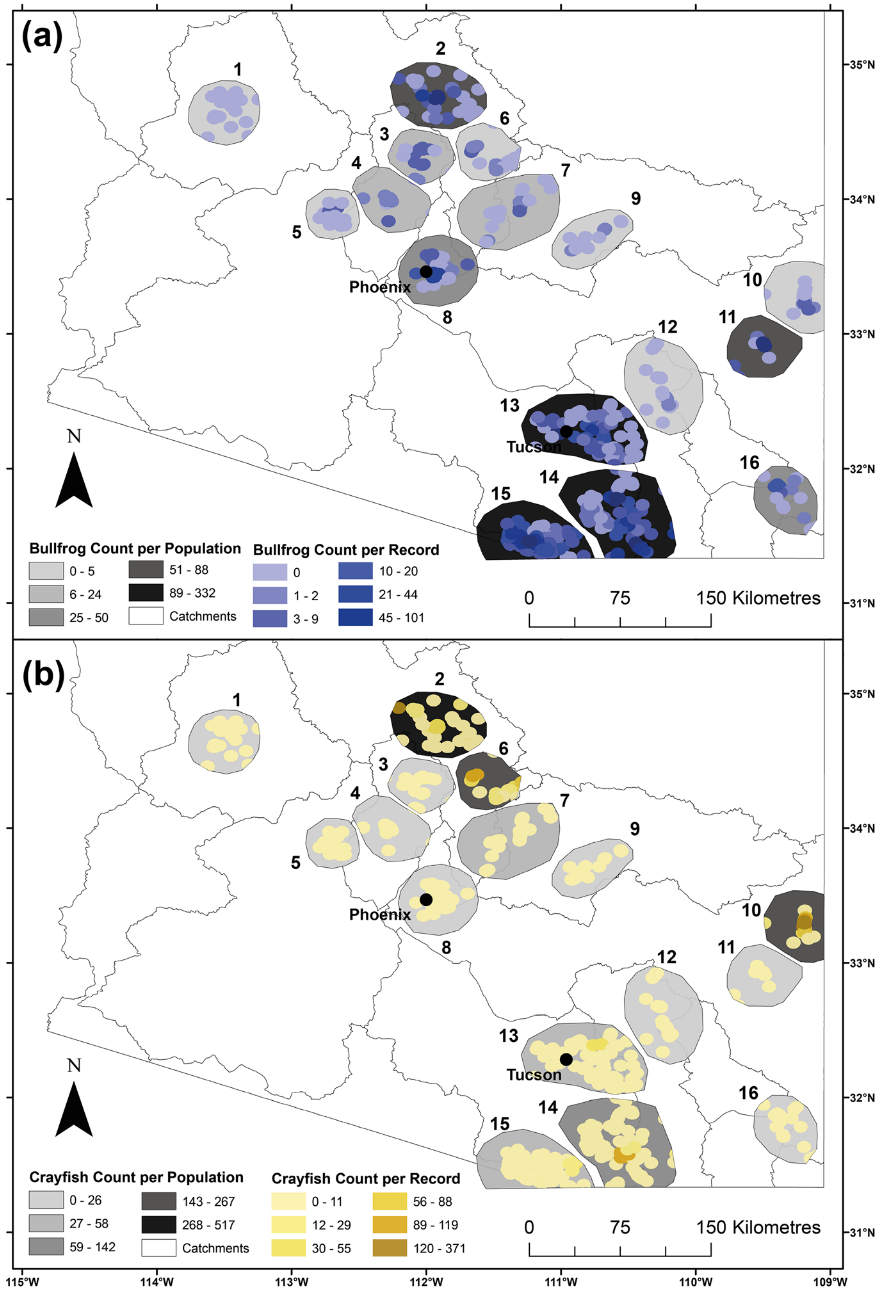

FIGURE 3 Bullfrog and crayfish abundances. Numbered polygons represent populations of *Kinosternon s. sonoriense* defined in Figure 1b. Number of occurrences within 5 km from turtle records are shown for (a) bullfrogs and (b) crayfish in colour (blue, yellow), where darker colours represent higher abundance at that site. Polygons of mud turtle populations are shaded in grey according to the aggregate number of occurrences within that population, where darker grey represents higher numbers of bullfrogs and crayfish in panels a and b, respectively

point process models are recommended to analyse presence-only data (Warton & Shepherd, 2010; Renner et al., 2015), especially as they provide clarity about which variable is being modelled (in this case the number of presence records). Although true absence data were not available, the presence data should represent a true and cumulative biological signal (from 1935 to 2021).

Analysing the dataset by time intervals showed that results were generally consistent; however, a change in the relationship between crayfish abundance and distance to cities may correspond to a possible temporal effect. Alternatively, this could be the result of differences in the number of observations between the datasets, or differences in sampling effort or sampling locations over time. In addition, the original sampling or detection methods across taxa might differ, which could bias the detection in each field observation. Nevertheless, these are inherent limitations of the data, but these observations are perhaps the most common resources that agencies have for developing effective management strategies and are therefore of utmost importance. Despite these limitations, the models provided good statistical power and reveal how ecological variables are associated with the abundance of invasive species in turtle populations. The LOOCV error estimates were high and R^2 values were relatively low, suggesting that the models may be overfitted (Table 2) despite de-duplicating the dataset. This may simply be another limitation of the data, and could be improved by incorporating sample effort and true absences into future studies.

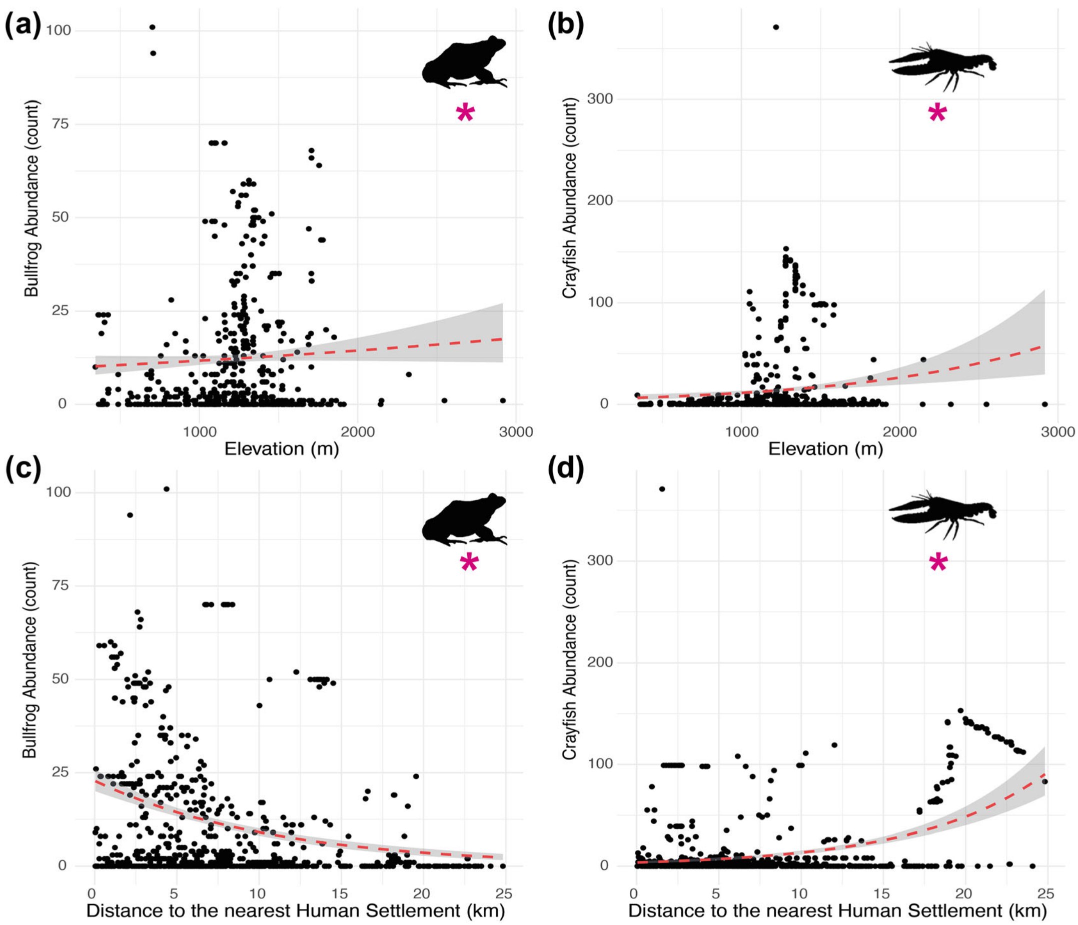

FIGURE 4 Relationship between bullfrog and crayfish abundance within 5 km of *Kinosternon s. sonoriense* occurrences and elevation (a, b) and their distances to nearest human settlement (c, d), respectively. The red dotted line represents the quasi-Poisson regression. The asterisk represents significant relationships

4 | DISCUSSION

Science-based management of invasive species is a powerful approach to focus conservation efforts on the areas of most need in order to improve the status of vulnerable populations. In this study, 5,886 de-duplicated locality records were compiled from state and public databases and the invasion level of invasive bullfrog and crayfish species was assessed within populations of the desert mud turtle, a Species of Greatest Conservation Need in Arizona. Associations of invasive abundance and four environmental variables were also assessed. The models showed good explanatory power but lower predictive power, suggesting that the models may be somewhat overfitted, which is a limitation of this data type (see Section 3). The results showed that both invasive taxa were more abundant in persistent streams, near the main trunk of a river than in tributaries, and at higher elevations, although these last two variables are correlated ($R = 0.492$; $P < 0.001$). Bullfrogs and crayfish showed opposite patterns regarding distance to human settlements: bullfrogs were more abundant in turtle populations near human settlements and crayfish were more abundant in turtle populations further from cities or towns. From the data it is unclear whether crayfish preferentially colonize more distant streams or whether they are outcompeted or have poor survival in more frequented areas.

Crayfish and bullfrog invasion were more prevalent in turtle populations situated near permanent (perennial) streams, which is consistent with studies reporting that these invasive species require persistent water bodies to sustain stable populations (Cruz & Rebelo, 2007; Peterson et al., 2013). Although bullfrog abundance was significantly higher within turtle populations in permanent streams, the total number of bullfrog records (in and out of turtle populations) was higher in intermittent streams (1,137 vs 400). The association of crayfish with perennial streams was much stronger than for bullfrogs. This pattern is not surprising as crayfish are more water-dependent for dispersal, which limits their dispersal only to areas of the drainage networks that have perennially flowing branches, or via human transfers (e.g. to use as bait). In contrast, bullfrogs are less water dependent than crayfish for dispersal (Gherardi, Barbaresi & Salvi, 2000; Smith & Green, 2005), allowing them to colonize new intermittent streams once they begin flowing again, which may explain the higher median bullfrog occurrence in intermittent streams. Bullfrogs can use temporary water bodies, but they require permanent water for reproduction (Gahl, Calhoun & Graves, 2009), so

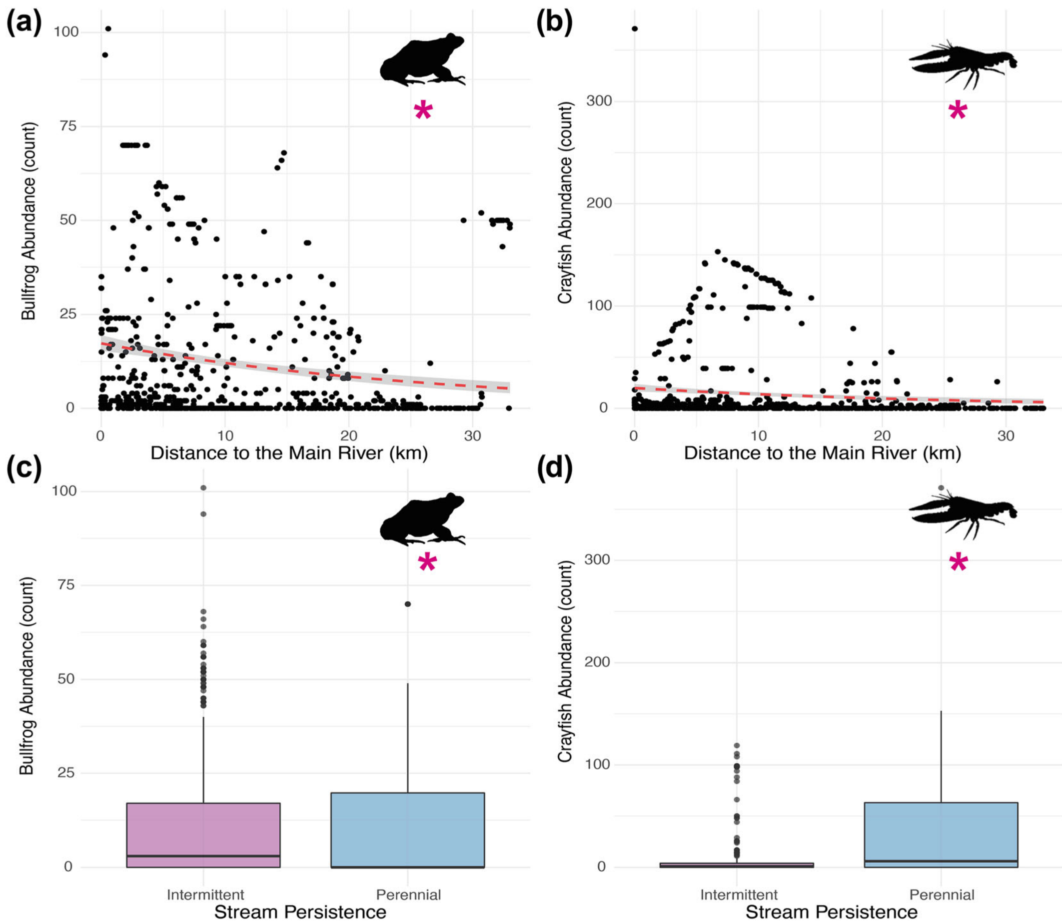

FIGURE 5 Relationship between bullfrog and crayfish abundance within 5 km of *Kinosternon s. sonoriense* occurrences, and distance to the main river trunk (a, b) and in relation to stream persistence (c, d). The red dotted line in panels a and b represents the quasi-Poisson regression. The asterisk represents significant relationships

TABLE 2 Generalized linear models used to test the relationship between environmental variables and bullfrog and crayfish abundances within 5 km of *Kinosternon s. sonoriense* occurrences. Distance to the nearest human settlement was used as a proxy of human disturbance, and models do not include interaction. These models had the lowest LOOCV error (see Tables S1–S3 for alternative models)

	Bullfrog		Crayfish	
Variable	Estimate	*p*	Estimate	*p*
Elevation	0.0013	<0.001	0.0018	<0.001
Distance to human settlement	−0.10	<0.001	0.072	<0.001
Distance to river	−0,046	<0.001	−0.061	<0.001
Stream persistence	0.44	<0.001	1.50	<0.001
R^2	0.19		0.43	
LOOCV error	16.99		25.59	

Abbreviation: LOOCV, Leave-one-out cross validation.

intermittent streams are unlikely to be used over periods of long drought in Arizona.

Crayfish and bullfrogs were more abundant closer to main river channels, probably reflecting ecological differences. This could also be an artefact of their point of invasion or introduction being in larger channels; however, detailed information about the sources of introduction is not currently available for Arizona. Although the downstream spread of invasive species has been described previously (Light, 2003; Bubb, Thom & Lucas, 2004; Kerby et al., 2005; Sepúlveda et al., 2015), this is unlikely to explain the results because flow accumulation was not a significant predictor of invasive abundance (Figure S2). This result suggests that further work should test whether these trunks are the main locations where the species are artificially introduced into the waterways. It may also be that flow accumulation patterns are different or less relevant in arid environments where many streams flow intermittently.

A significant relationship was detected for elevation, with both crayfish and bullfrogs more abundant at higher elevations. Nori et al. (2011) found that the high elevations of the Andes Mountains in north-western Argentina limited bullfrog invasion, and elevation appears also to limit crayfish dispersal or persistence (Light, 2003; Cruz & Rebelo, 2007). However, other studies have found higher probability of occurrence of some crayfish species at higher elevations (> 400 m; Dyer et al., 2013; Mouser, Mollenhauer & Brewer, 2019). In this study, higher abundance of bullfrogs and crayfish were detected at higher elevations (even above 1,000 masl), which might be explained by an indirect association of higher elevations with suitable conditions for these species, such as other climatic, physicochemical or biological parameters (e.g. temperature; Seiler & Turner, 2004; Ficetola, Thuiller & Miaud, 2007; Adams & Marks, 2016).

Considering proxies for human disturbance, models using distance to the nearest city instead of distance to roads had higher predictive power (Table 2, Table S1). Furthermore, areas near cities also presented higher abundance of invasive species (Figure 3). Proximity to cities may be a better descriptor of human disturbance and it is possible that areas closer to cities might put higher propagule pressure on invasive species (Hamer & McDonnell, 2008). A negative relationship was reported for bullfrog abundance, where higher abundances occurred closer to cities, consistent with expectations. Other studies have also reported higher invasive abundance in more disturbed environments (Riley et al., 2005; Ficetola, Thuiller & Miaud, 2007; Sepúlveda et al., 2015; Sepulveda, 2018). In contrast, crayfish abundance was significantly positively correlated with distance from cities, where lower abundances were recorded closer to cities. However, a significant negative relationship was detected between distance from cities and crayfish abundance for early records of crayfish (before 1999; Table S4). This change in the relationship may correspond to a temporal effect of crayfish dispersing and establishing to other locations further from cities or human settlements, or the result of different sampling efforts over time.

The association of invasive abundance with distance to the main river, elevation and distance to cities may be driven primarily by the source(s) of invasion, which is a primary determinant for invasive bullfrog and crayfish presence (Cruz & Rebelo, 2007; Sepúlveda et al., 2015), and may be generating a stronger signal than the effect of the ecological variables measured. Exactly where invasive individuals were introduced into these drainage networks is not known, so these models can be used in future research to study introductions and invasion dynamics in these locations.

The model of invasion level developed here can be used as a risk assessment tool for turtle conservation. The results presented here have direct implications for invasive species management in four ways. First, managers could use this model to define turtle populations most affected by invasive species and prioritize management actions. Such a prioritization tool is valuable considering limited financial and personnel resources. Second, the model can be used to detect uninvaded populations and allow managers to focus efforts on monitoring bullfrog and/or crayfish spread to prevent invasion, or to catch propagules in early stages of invasion when eradication has a higher chance of success. Third, identification of populations with limited invasion provides an ecosystem baseline against which the health of populations in other areas can be compared. This is important for assessing the conservation status of the species. Fourth, the delineation of turtle populations based on invasion level, from high and low invasive pressures, can be used to study the demographic and health consequences to turtles in these co-existing areas and improve monitoring programmes. As eradication of the invaders may be cost-prohibitive, studying invasion intensity can identify density thresholds where turtles can maintain healthy, self-sustaining populations in the presence of invasives, allowing a management strategy of control at a given density of invasion instead of the goal of full eradication. Sampling genetic information from the invasive populations could reveal source–sink dynamics and help determine where these invasive species are being introduced to the system and whether these invasions are continuing or are historical. The ecological knowledge generated in this study is essential for managing these invasive species (Adams & Pearl, 2007; Gherardi et al., 2011). Control efforts could be prioritized on locations matching the environmental features associated with higher abundance of invasive species (persistent streams, closer to the main river, near human settlements and in high elevation) and that have not yet been colonized, and therefore prevent further spread of these species.

Other studies have used geospatial data to assess threats to turtle populations. Santori et al. (2018) used community science data to assess the mortality of the eastern long-necked turtle, *Chelodina longicollis*, associated with roads. Nicholson et al. (2020) used museum data to assess the effects of roads and invasive bullfrogs on western pond turtle populations. Ryberg et al. (2017) integrated habitat modelling with data on land use change to assess the conservation status of the western chicken turtle (*Deirochelys reticularia miaria*). Here, this study developed a risk assessment tool for a species of conservation concern, the desert mud turtle, to inform management practices to maintain native turtle populations in the face of invasive threats. Removal of these non-native species has been achieved in small water bodies; the catch–depletion method using different catching techniques (e.g. hand, spear, net) has been useful in removing bullfrogs (Louette, Devisscher & Adriaens, 2013; Kamoroff et al., 2020), whereas pond draining, the use of biocides and electric shock treatments are alternatives to remove crayfish (Holdich, Gydemo & Rogers, 2017; Peay et al., 2019). The information provided by this risk assessment tool, combined with successful removal methods, could help to improve the health of turtles inhabiting the waterways of the American Southwest.

ACKNOWLEDGEMENTS

This project was funded by the Arizona Game and Fish Department from U.S. Fish and Wildlife Service (USFWS) grant F18AF01162. RAD was supported by the doctoral scholarship 72200094 (ANID, Chile) and the College of Liberal Arts and Sciences at Arizona State University. The authors thank Jeff Sorensen for providing crayfish records from the Arizona Game and Fish Department's Invertebrate Wildlife Program, and Tom R. Jones for valuable comments on the manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Bullfrog and crayfish occurrence records in Arizona are available in an Arizona State University Dataverse: 10.48349/ASU/PMLVXF.

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How to cite this article: Araya-Donoso, R., Orton, J.P., Ryan, M.J., Jones, C.A., Kusumi, K. & Dolby, G.A. (2022). Geospatial assessment of freshwater invasive species to inform turtle conservation and management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 1–12. https://doi.org/10.1002/aqc.3816