Climate change effects on turtles of the genus Kinosternon *(Testudines: Kinosternidae): an assessment of habitat suitability and climate niche conservatism*

Christian Berriozabal-Islas, Aurelio Ramírez-Bautista, Ferdinand Torres-Ángeles, João Fabrício Mota Rodrigues, Rodrigo Macip-Ríos, et al.

ONLINE FIRST

🐴 Springer

Springer

PRIMARY RESEARCH PAPER

Climate change effects on turtles of the genus *Kinosternon* (Testudines: Kinosternidae): an assessment of habitat suitability and climate niche conservatism

Christian Berriozabal-Islas (ORCID) · **Aurelio Ramírez-Bautista** · **Ferdinand Torres-Ángeles** · **João Fabrício Mota Rodrigues** · **Rodrigo Macip-Ríos** · **Pablo Octavio-Aguilar**

Abstract The Chelonian lineage has been exposed to several climate change events along its evolutionary history, but the rapid contemporary change in climate patterns has the potential to erode turtle populations. This study focuses on (1) evaluating the climatically suitable area available for 15 species of mud turtles of the genus *Kinosternon*, and on (2) assessing whether or not these species retain their ancestral climate niche. Occurrence data was collected for these species and, using the Maxent algorithm and WorldClim bioclimatic variables, suitable present and future climatic niche areas were modeled. In addition, we also carried out climatic niche similarity analyses between pairs of species to evaluate whether these conserve their climatic niche. Our models suggest that most species of *Kinosternon* will lose a high proportion of their suitable habitat in the future. Most mud turtle species seem to conserve their climatic niche, suggesting the prevalence of niche conservatism in the group. Our results indicate that several mud turtle species could be at severe risk of disappearing over the next few decades due to the loss of climatically suitable areas and of the conservation of their climatic niches.

Keywords Lagoons · Temperature · Maxent · Microendemic species · American continent

Handling editor: Lee B. Kats

C. Berriozabal-Islas
Programa Educativo de Ingeniería en Biotecnología, Universidad Politécnica de Quintana Roo, Av. Arco Bicentenario M 11, Lote 1119-33, Sm 255, 77500 Cancún, Quintana Roo, Mexico

A. Ramírez-Bautista (✉) · F. Torres-Ángeles · P. Octavio-Aguilar
Centro de Investigaciones Biológicas, Instituto de Ciencias Básicas e Ingeniería, Universidad Autónoma del Estado de Hidalgo, Pachuca, Hidalgo, Mexico
e-mail: ramibautistaa@gmail.com

J. F. Mota Rodrigues
Departamento de Ecologia, Universidade Federal de Goiás, Campus Samambaia 14, CP 131, Goiânia, GO 74001-970, Brazil

R. Macip-Ríos
Escuela Nacional de Estudios Superiores, Unidad Morelia, Universidad Nacional Autónoma de México, Morelia, Michoacán, Mexico

R. Macip-Ríos
Laboratorio Nacional de Síntesis Ecológica y Conservación de Recursos Genéticos, Escuela Nacional de Estudios Superiores Unidad Morelia, Universidad Nacional Autónoma de México, Morelia, Michoacán, Mexico

🍦 Springer

Introduction

The current global climate change is a phenomenon caused largely by the anthropogenic activities, which today is wreaking a considerable effect on the populations of many species, their life cycles, and other biological systems, such as phenology, migratory patterns, biotic interactions, and distribution (Pearson & Dawson, 2003; Stempniewicz et al., 2017). Therefore, climate change is considered one of the most important factors threatening biodiversity and ecosystem function (Thomas et al., 2004; Tanaka et al., 2017). In this context, ectothermic organisms are currently the most threatened by environmental changes, due to the alteration of their thermal niches caused by the greenhouse effect (Sinervo et al., 2010). For example, outbreaks of emerging diseases and infections such as *Batrachochytrium dendrobatidis* Longcore, Pessier & Nichols, 1999 are related to the decline of several populations of amphibian species (Cohen et al., 2019). The link between climate change and these epidemic diseases in amphibians has been attributed to changes in environmental conditions that influence the expansion or contraction of climatic niches (Ron, 2005; Bonetti & Wiens, 2014a, b).

In reptiles, the increase in average environmental temperature causes changes in their spatial distribution, physiological performance, reproductive biology, behavior, and other life-history characteristics (Bickford et al., 2010; Barrows, 2011; Lara-Reséndiz et al., 2019). Since reptiles depend on external heat sources to regulate their body temperature, climate is a key factor influencing their thermal requirements, tolerances, and adaptations in any environment of their distribution (Hertz, 1981; Lara-Reséndiz et al., 2014). For instance, Sinervo et al. (2010) suggested that a continuous increase in temperature could cause a long-term contraction of suitable habitat for lizard species and thus an increase in the risk of local extinction.

This being so, it can be expected that anthropogenic pressures will continue to cause a decrease in freshwater ecosystems, and therefore a negative effect on biodiversity in the coming decades (Davies, 2010; Lukasiewicz et al., 2016). Freshwater turtles are an important component in this aquatic ecosystem (Iverson, 1982; Vogt & Guzmán-Guzmán, 1988). According to Macip-Ríos et al. (2015) and Rhodin et al. (2017), turtles are the most threatened group of reptiles in the world due to climate change-related factors, such as drying up of water bodies and changes in thermal and rain patterns. Furthermore, the movement and home ranges of freshwater turtles are limited because many species are restricted to water bodies with specific abiotic and biotic conditions (Pérez-Pérez et al., 2017; Butler, 2019). For some mud turtles (genus *Kinosternon*) it is documented that species move overland in response to aquatic environment fluctuations, nesting, environmental seasonality, and mating (Cordero et al., 2012). For example, Hall & Steidl (2007) reported that *Kinosternon sonoriense* Le Conte, 1854 can move up to 500 m from one pond to another. Highly aquatic species such *Kinosternon leucostomum* Duméril & Bibron in Duméril & Duméril, 1851 have been reported to be capable of traveling up to 600 meters across land for nesting (Cordero & Swarth, 2010).

Mud turtles (*Kinosternon*) inhabit a wide variety of aquatic environments including streams, lagoons, rivers, seasonal or perennial ponds, irrigation channels, dams, and water tanks in grazing areas throughout its distribution in the Americas (Iverson et al., 2013). Therefore, a number of taxa of this group of turtles have microendemic distributions in several basins across the American continent, and particularly in Mexico; for example, species that are found exclusively in one or two watersheds (Legler & Vogt, 2013; Macip-Ríos et al., 2015). Thus their small distribution and ecological characteristics, such as limited dispersal ability, specialized diet, reduced activity time, and temperature-dependent sex determination (Vogt & Flores-Villela, 1986; Iverson, 1991; Pérez-Pérez et al., 2017), could put the permanence of *Kinosternon* populations at risk at different scales of time and space, since the dynamics of the ecological traits of the genus depend on climate patterns (Sirois et al., 2014). Currently, there are few studies on these aspects of freshwater turtles (Ihlow et al., 2012). One such study evaluates the effect of climate change on five species of the genus *Kinosternon* under different climate change scenarios in North America, using a maximum entropy approach to modeling (Butler et al., 2016). The results of this study showed that areas with suitable climate conditions for *K. baurii* Garman, 1891 and *K. hirtipes* Wagler, 1830 are expected to decrease substantially in the future. In contrast, areas suitable for *K. sonoriense* will remain essentially unchanged, while areas suitable for *K. flavescens*

Agassiz, 1857 and *K. subrubrum* (Bonnaterre, 1789) are expected to increase (Butler et al., 2016).

The historical biogeography of *Kinosternon* turtles also seems to reinforce the influence of climate on the distribution of species. For example, mud turtles have experienced several climate change events throughout their evolutionary history (Cadena et al., 2007), and the fossil record shows that the distribution of this genus has been gradually modified following climate change events over the past several million years (Iverson et al., 2013). However, it is known that current climate change is being dramatically accelerated by anthropic effects (Cleland et al., 2006; Loarie et al., 2009; Hamann et al., 2015). Lavergne et al. (2010) and Wiens et al. (2010) suggest that if a species cannot follow its climatic niche as environmental conditions shift geographically, the species would have to adapt to new environmental conditions or disappear. For example, local extinctions in relatively short periods of time show considerable trends towards climatic niche conservatism (Wiens & Graham, 2005; Sinervo et al., 2018). This is because niches tend to be conserved in the sense that descendant species tend to inhabit geographical areas similar to those inhabited by their immediate ancestors (Wiens et al., 2010; Hu et al., 2016).

Since mud turtles live under a restricted set of climate conditions and evolved conservatively, we characterize the climatic niche of the turtle species within the genus *Kinosternon* (Ihlow et al., 2012; Fagundes et al., 2015). In this study, we hypothesize that the species of the genus *Kinosternon* could lose a large part of their climatic niche during the coming decades, and that species of the genus will show high climate niche conservatism due to their strong dependence on and affinity with the environmental characteristics of the habitats in which they live, in particular microendemic species such as *Kinosternon abaxillare* Baur in Stejneger, 1925, *K. alamosae* Berry & Legler, 1980, *K. chimalhuaca* Berry, Seidel, & Iverson in Rogner, 1996, *K. creaseri* Hartweg, 1934, *K. durangoense* Iverson, 1979, *K. oaxacae* Berry & Iverson, 1980, and *K. stejnegeri* (Hartweg 1938). The aims of this study are to determine the changes in habitat suitability over time using ecological niche models projected under three different climate change scenarios (present, 2050, and 2070), and to evaluate whether species of the genus *Kinosternon* conserve their climatic niches or not, by using an analysis of niche similarity for species occurring throughout the Western Hemisphere (Broennimann et al., 2012; Hu et al., 2016).

Materials and methods

Taxon sampling

The genus *Kinosternon* is composed of about 30 living taxa; 21 species and 9 subspecies (Rhodin et al., 2017; López-Luna et al., 2018). Of this total, we included 15 species in this study, following the taxonomy proposed by Rhodin et al. (2017), which are 50% of the total species. The species *Kinosternon angustipons* Legler, 1965, *K. baurii*, *K. dunni* Schmidt, 1947, *K. hirtipes chapalaense* Iverson, 1981, *K. h. magdalense* Iverson, 1981, *K. h. murrayi* Glass & Hartweg, 1951, *K. h. tarascense* Iverson, 1981, *K. leucostomum postinguinale* Cope, 1887, *K. scorpioides albogulare* Duméril & Bocourt, 1870, *K. s. cruentatum* Duméril & Bibron in Duméril & Duméril 1851, *K. sonoriense longifemorale* Iverson, 1981, *K. steindachneri* Siebenrock, 1906, *K. subrubrum*, *K. s. hippocrepis* Gray, 1856, and *K. vogti* López-Luna et al., 2018 were specifically not included in this analysis because available information is scarce. Occurrence data for 15 species were obtained from three basic sources: (i) geographic records collected in the field over an 11-year period; (ii) online databases, such as Global Biodiversity Information Facility (GBIF, available at www.gbif.org), and HerpNet (http://www.herpnet.org/portal.html); and (iii) from the specialized literature (Iverson, 1992; Berry et al., 1997; Aguirre-León & Aquino-Cruz, 2004; Macip-Ríos et al., 2009; Legler & Vogt, 2013; van Dijk et al., 2014). All data were individually reviewed and records that seemed unreliable for a particular type of information were eliminated from the data base; for example, duplicate records and occurrences far from the known ranges of distribution for each species (Elith et al., 2010). The selected records were georeferenced with the free Google Earth™ program (version 7.0.3.8542) and configured in decimal degrees using the WGS 84 datum converter. Our final database included 5,153 records on 15 different species: *Kinosternon abaxillare* (19 records), *K. acutum* Gray, 1831 (131 records), *K. alamosae* (33 records), *K. stejnegeri* (27 records), *K. chimalhuaca* (72 records), *K. creaseri* (97 records),

K. durangoense (100 records), *K. flavescens* (453 records), *K. herrerai* Stejneger, 1925 (245 records), *K. hirtipes* (701 records), *K. integrum* Le Conte, 1854 (2,067 records), *K. leucostomum* (329 records), *K. oaxacae* (21 records), *K. scorpioides* (Linnaeus, 1766) (760 records), and *K. sonoriense* (98 records) (Fig. 1).

Determination of accessible distribution area

Since bodies of water are very important for the presence of the turtles, we determined accessible areas for each species of turtle from digital layers of watersheds for the American continent at 30 arc-minutes resolution ($\sim$ 1 × 1 km) as a background (Lehner et al., 2006). For each species, we selected only those localities that coincided with a known body of water in accordance with Iverson (1992) and Rhodin et al. (2017).

Climate variables

We downloaded annual means of the meteorological conditions recorded from the periods present and future (2050 and 2070) data of 19 bioclimatic variables available in the WorldClim data base (Hijmans et al., 2005; http://www.worldclim.org/) at 30 arc-minutes spatial resolution ($\sim$ 1 × 1 km). We estimated future projections using the CCSM-GCM model for the present, 2050, and 2070 under two greenhouse concentration scenarios, RCP26 and RCP85, which represent an optimistic (RCP26 = + 2.6 W/m^2) and pessimistic scenario (RCP85 = + 8.5 W/m^2). To identify the variables with the greatest contribution to explaining the spatial-environmental variation for each species, we extracted the values of each variable associated with the occurrence records of each species and used them in a factorial analysis with STATISTICA (ver. 10; StatSoft Inc, 2004). We
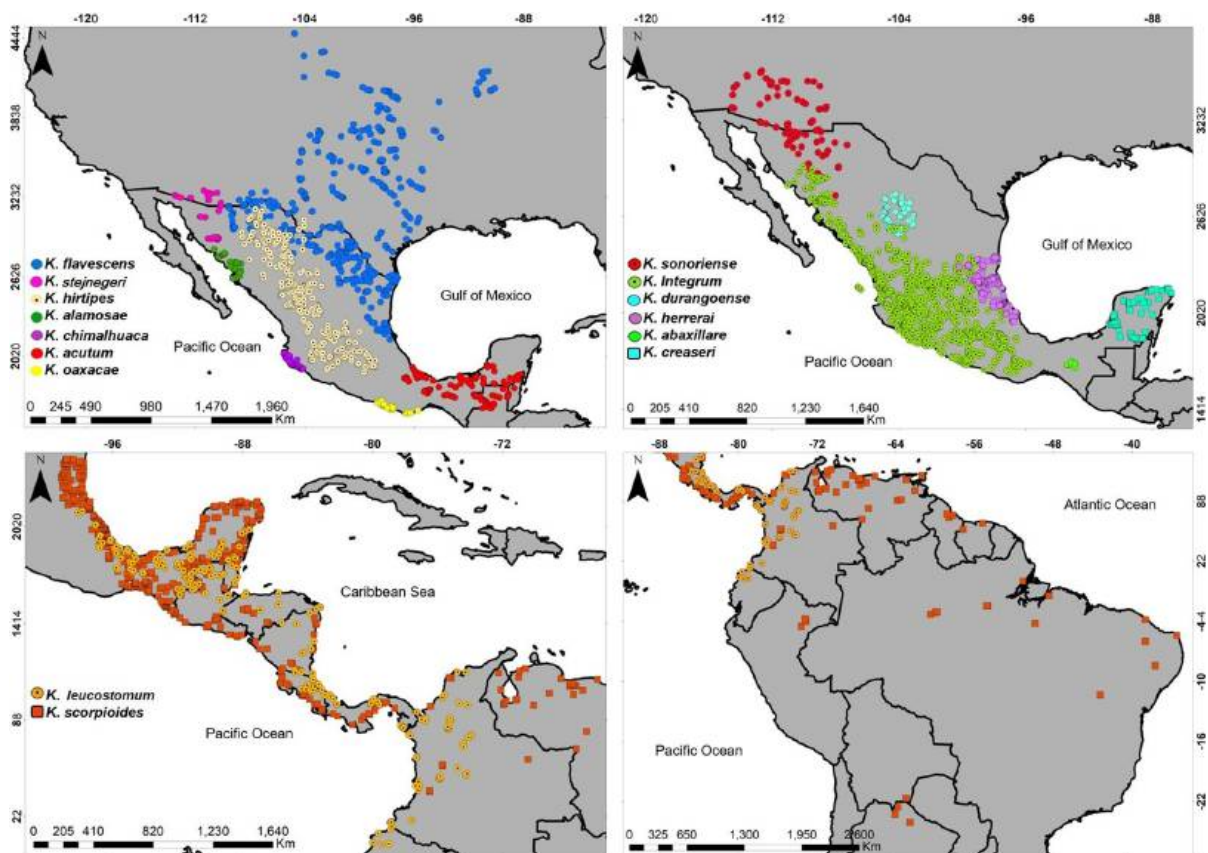

Fig. 1 Records compiled for this study of the turtle species of the genus *Kinosternon* in America

selected the variables with greater explanatory power (inferred from the eigenvalues), while variables with little explanatory power or with high correlations were eliminated. This process avoids multicollinearity among the environmental predictors used. The selected variables were BIO1 = Annual Mean Temperature, BIO2 = Mean Diurnal Range (Mean of monthly (max temp − min temp)), BIO4 = Temperature Seasonality (standard deviation × 100), BIO6 = Min Temperature of Coldest Month, BIO7 = Temperature Annual Range (BIO5 − BIO6), BIO8 = Mean Temperature of Wettest Quarter, BIO9 = Mean Temperature of Driest Quarter, BIO12 = Annual Precipitation, BIO15 = Precipitation Seasonality (Coefficient of Variation).

Climatic niche modeling

We used the maximum entropy modeling method (Phillips et al., 2006) implemented in the MaxEnt program (version 3.3.3; Phillips et al., 2004), which generates habitat suitability maps. The indicator ranges from 0 (low suitability) to 1 (high suitability) (Elith et al., 2011). We generated the models with the default configurations of MaxEnt using the species occurrence and climate data described above. We randomly selected 20% of the data for testing (evaluation of each model) and used the other 80% for training (calibration of the model; Urbina-Cardona & Flores-Villela, 2010). We evaluated the accuracy of the models in MaxEnt (version 3.3.3; Phillips et al., 2004) using the area under the curve (AUC) metric. The models with AUC values between 0.5 and 0.7 were classified as low precision, values between 0.7 and 0.9 were classified as models with good precision, and models with AUC > 0.9 were classified as high precision (Pliscoff & Fuentes-Castillo, 2011).

The probabilistic maps were output in ASCII format; they were imported into the ArcMap GIS 10.3 program (ESRI, 2006) and transformed into binary maps showing areas where the climatic niches are most likely present and absent. These were produced using the criterion of "equal training sensitivity and specificity logistic threshold," which was applied as a cut-off threshold, because it equates errors of commission and of omission in order to balance these two types of errors (Pearson et al., 2007; Ward, 2007). Finally, to assess the impacts of climate change for each species of the genus *Kinosternon*, we

calculated the percentage change between current and future conditions by the formula % change = [(S1 − S0)/S0] × 100%, where S0 is the area with suitable climate conditions for the species according to the reference scenario (current), and S1 is the climatically suitable area for the species under future climate conditions (Gutiérrez & Trejo, 2014).

Climatic niche conservatism

We compared climatic niches among the 15 species of the genus *Kinosternon* according to the analytical framework proposed by Broennimann et al. (2012) using Ecospat (Broennimann et al., 2015) in R (R Core Team, 2014). The environmental variables obtained from the factorial analysis described above were used in these niche comparisons. In this study we used the approach of principal component analysis (PCA-environmental), extracting the first two axes of a PCA, including the 10 bioclimatic variables selected to represent the climatic niche of each species. These axes were represented in an environmental space divided into a 100 × 100-cell grid within the geographical range for each species (Broennimann et al., 2015; Hu et al., 2016). We used the simple kernel density function to calculate the density of the number of occurrences and numbers of each site with particular environmental conditions for each cell within the environmental space (Broennimann et al., 2012).

We measured climatic niche overlap between species pairs in the environmental space using Schoener's D, which ranges from 0 (no overlap) to 1 (total overlap) (Warren et al., 2008). We carried out niche similarity tests according to the methodology proposed by Warren et al. (2008), which is based on 100 randomizations in both directions (A vs. B and B vs. A) in a null model. When the observed overlap value is significant ($P < 0.05$) in a two-way test, the climatic niches of the two species are considered similar, indicating that the climatic niche predicts the climate niche of the other species better than expected by a specific null model.

Results

Ecological niche models

Ecological niche models of the *Kinosternon* species showed high AUC values (> 0.70). The bioclimatic

variables that contributed most to the calibration of the models were BIO8 (Mean Temperature of Wettest Quarter), BIO12 (Annual Precipitation), and BIO15 (Precipitation Seasonality–Coefficient of Variation) (see Table 1).

The ecological niche models showed that most of the species will lose area with conditions suitable for their respective climatic niche under the climate change scenarios considered in this study. The species that will likely lose the most area suitable are *Kinosternon abaxillare*, *K. chimalhuaca*, *K. oaxacae*, *K. scorpioides*, and *K. sonoriense*. The principal reduction occurs in the scenarios with the highest concentrations of greenhouse gases, 2050 RCP85 and 2070 RCP85, while *K. abaxillare* and *K. creaseri* will have significant increases in their distribution area by the year 2050 according to the RCP85 scenario (Table 2, Fig. 2).

Climatic niche similarity (conservatism)

In general, climatic niche similarity values among species of the genus *Kinosternon* were moderately high and significant ($P \leq 0.05$), which suggests high climatic niche conservatism in this genus (Table 3; Fig. 3). Only a few species (with very reduced or microendemic distribution) had low values of niche similarity; *K. abaxillare*, *K. alamosae*,

K. chimalhuaca, *K. durangoense*, and *K. oaxacae* (Table 3, Fig. 3).

Discussion

Based on the variables that contributed the most to the climatic niche models (see Table 1), it is evident that seasonality is particularly important for *Kinosternon* turtles. Our results also indicate that a decline in precipitation and in seasonality is expected under all scenarios. Butler et al. (2016) note that habitat suitability conditions will decline by 81% to 95% in the southeastern United States by 2050. Therefore, we would expect that these species might be vulnerable to climate change, because one of the effects would be an alteration in seasonal patterns where these species occur (Gabriel et al., 2017). It is expected that such environmental modifications will have an impact on some life-history traits, such as activity patterns and reproduction, which could lead to local extinctions (Brown et al., 1997; Ihlow et al., 2012). In addition, it is known that *Kinosternon* turtles have seasonal activity patterns and temperature sex determination, which are also affected by changes in climate patterns (Vogt & Flores-Villela, 1986; Tuma, 2006; Macip-Ríos et al., 2017).

Table 1 Values of area under the curve (AUC) of the models and the five bioclimatic variables that contributed the most to their construction for each species of *Kinosternon*

Species	AUC values	Five most important variables and percent contribution
Kinosternon abaxillare	0.98	BIO15 (53.2%), BIO12 (27.4%), BIO4 (19%), BIO2 (1%), BIO1 (.2%)
Kinosternon acutum	0.77	BIO8 (35%), BIO6 (24%), BIO15 (15%), BIO4 (12%), BIO1 (6%)
Kinosternon alamosae	0.95	BIO9 (47.2%), BIO1 (21.9%), BIO6 (8%), BIO8 (7.3%), BIO15 (6.1%)
Kinosternon stejnegeri	0.95	BIO8 (50%), BIO15 (24%), BIO1 (14%), BIO12 (9%), BIO9 (1.5%)
Kinosternon chimalhuaca	0.91	BIO9 (33.6%), BIO2 (11%), BIO1 (8%), BIO8 (5%), BIO7 (4%)
Kinosternon creaseri	0.78	BIO4 (23%), BIO15 (22%), BIO12 (19%), BIO8 (13%), BIO9 (8%)
Kinosternon durangoense	0.95	BIO9 (28%), BIO2 (24%), BIO4 (19%), BIO7 (13.6%), BIO15 (13.5%)
Kinosternon flavescens	0.85	BIO8 (70.1), BIO4 (7.7%), BIO9 (7.7%), BIO1 (4.6%), BIO12 (4%)
Kinosternon herrerai	0.90	BIO6 (58.9%), BIO12 (10.2%), BIO15 (6.8%), BIO2 (6%), BIO4 (6%)
Kinosternon hirtipes	0.85	BIO15 (42%), BIO4 (14%), BIO9 (11.5%), BIO2 (9%), BIO1 (8.7%)
Kinosternon integrum	0.80	BIO15 (32%), BIO4 (28%), BIO6 (20%), BIO12 (10%), BIO1 (4.8%)
Kinosternon leucostomum	0.80	BIO4 (23.7%), BIO9 (20.5%), BIO12 (19%), BIO7 (11%), BIO15 (7%)
Kinosternon oaxacae	0.94	BIO8 (60%), BIO6 (15.8%), BIO9 (13.8%), BIO4 (8.7%), BIO1 (1.3%)
Kinosternon scorpioides	0.85	BIO4 (23%), BIO8 (30.4%), BIO15 (15.4%), BIO2 (11%), BIO9 (9.2%)
Kinosternon sonoriense	0.85	BIO15 (58.3%), BIO6 (13.9%), BIO2 (7%) BIO8 (4.2%), BIO12 (5%),

Table 2 Geographical area with suitable climate conditions for *Kinosternon* species according to current and future conditions and rate of change in habitat suitability between the present and the future

| Species	Scenario	area (km²)	% change rate current/scenario
Kinosternon abaxillare	Current	4,800.65	
	2050-RCP 2.6	4,360.88	− 9.16
	2050-RCP 8.5	7,885.08	+ 64.25
	2070-RCP 2.6	3,858.58	− 19.62
	2070-RCP 8.5	2,300.77	− 47.90
Kinosternon acutum	Current	100,385.4	− 7.15
	2050-RCP 2.6	93,201.78	
	2050-RCP 8.5	95,867.92	− 4.50
	2070-RCP 2.6	99,881.2	− 0.50
	2070-RCP 8.5	85,901.34	− 14.42
Kinosternon alamosae	Current	21,345.22	
	2050-RCP 2.6	17,400.22	− 18.48
	2050-RCP 8.5	16,333.7	− 23.47
	2070-RCP 2.6	19,513.44	− 8.58
	2070-RCP 8.5	16,205.19	− 24.80
Kinosternon stejnegeri	Current	105,664.83	
	2050-RCP 2.6	101,901.7	− 3.56
	2050-RCP 8.5	106,738.59	+ 1.10
	2070-RCP 2.6	99,567.31	− 5.77
	2070-RCP 8.5	89,304.11	− 15.48
Kinosternon chimalhuaca	Current	2,300.35	
	2050-RCP 2.6	2,860.6	− 1.37
	2050-RCP 8.5	2,211.07	− 23.76
	2070-RCP 2.6	2,388.48	− 17.64
	2070-RCP 8.5	1,150.35	− 60.33
Kinosternon creaseri	Current	50,300.12	
	2050-RCP 2.6	48,080.5	− 4.41
	2050-RCP 8.5	83,367.47	+ 65.74
	2070-RCP 2.6	41,842.19	− 16.81
	2070-RCP 8.5	38,401.3	− 23.65
Kinosternon durangoense	Current	48,201.4	
	2050-RCP 2.6	44,128.13	− 8.45
	2050-RCP 8.5	43,324.38	− 10.11
	2070-RCP 2.6	40,319.11	− 16.35
	2070-RCP 8.5	33,427.18	− 30.65
Kinosternon flavescens	Current	1,231,104.11	
	2050-RCP 2.6	1,022,031.02	− 16.98
	2050-RCP 8.5	1,147,116.68	− 6.82
	2070-RCP 2.6	1,221,241.76	− 0.80
	2070-RCP 8.5	1,013,354.13	− 17.68
Kinosternon herrerai	Current	40,128.48	− 11.72
	2050-RCP 2.6	35,421.92	− 9.32
	2050-RCP 8.5	36,385.29	− 7.51
	2070-RCP 2.6	37, 111.46	− 32.38

Table 2 continued

Species	Scenario	area (km^2)	% change rate current/scenario
	2070-RCP 8.5	27,132.12	
Kinosternon hirtipes	Current	389,669.48	− 10.40
	2050-RCP 2.6	349,113.98	− 9.78
	2050-RCP 8.5	351,549.13	− 18.51
	2070-RCP 2.6	317,519.46	− 22.46
	2070-RCP 8.5	302,120.54	
Kinosternon integrum	Current	489,667.28	− 13.77
	2050-RCP 2.6	422,205.53	− 7.01
	2050-RCP 8.5	455,301.18	− 18.23
	2070-RCP 2.6	400,382.2	− 8.02
	2070-RCP 8.5	450,354.68	
Kinosternon leucostomum	Current	616,365.12	− 9.73
	2050-RCP 2.6	556,385.17	− 45.05
	2050-RCP 8.5	586,462.11	+ 11.84
	2070-RCP 2.6	689,365.19	− 22.51
	2070-RCP 8.5	601,421.1	
Kinosternon oaxacae	Current	3,021.19	+ 3.90
	2050-RCP 2.6	3,139.24	+ 17.87
	2050-RCP 8.5	3,561.12	− 4.87
	2070-RCP 2.6	2,873.95	− 30.50
	2070-RCP 8.5	2,113.12	
Kinosternon scorpioides	Current	1,987,641.98	− 4.38
	2050-RCP 2.6	1,900,539.21	− 31.76
	2050-RCP 8.5	1,356,300.59	− 28.54
	2070-RCP 2.6	1,420,344.77	− 34.15
	2070-RCP 8.5	1,308,678.49	
Kinosternon sonoriense	Current	284,101.28	− 17.59
	2050-RCP 2.6	234,111.31	+ 5.10
	2050-RCP 8.5	298,361.19	− 20.74
	2070-RCP 2.6	225,167.45	− 34.82
	2070-RCP 8.5	185,167.33	

Fossil evidence shows that *Kinosternon* turtles have a Mesoamerican origin dating from the Cretaceous with subsequent radiation to North America (Iverson et al., 2013). However, several studies have documented that the climatic niche of *Kinosternon* species has diminished over time in the evolutionary history of the genus (Rödder et al., 2013, Joyce & Bourque, 2016). Our results show that habitat suitability will continue to decrease considerably for most species, particularly at moderate and high latitudes, where the environment will become drier and highly seasonal (see Table 2). Seager et al. (2007) noted that in the arid

Fig. 2 Habitat suitability area from current and future projected climate models (2050 RCP26, RCP85 and 2070 RCP26, RCP85). Green areas represent the climatic niche projected for the species. **a** *Kinosternon abaxillare*, **b** *K. alamosae*, **c** *K. stejnegeri*, **d** *K. chimalhuaca*, **e** *K. durangoense*, **f** *K. flavescens*, **g** *K. herrerai*, **h** *K. hirtipes*, **i** *K. oaxacae*, **j** *K. sonoriense*, **k** *K. acutum*, **l** *K. creaserie*, **m** *K. integrum*, **n** *K. leucostomum* and **o** *K. scorpioides*

regions of southwestern North America, environmental conditions will be more extreme and will have longer periods of drought.
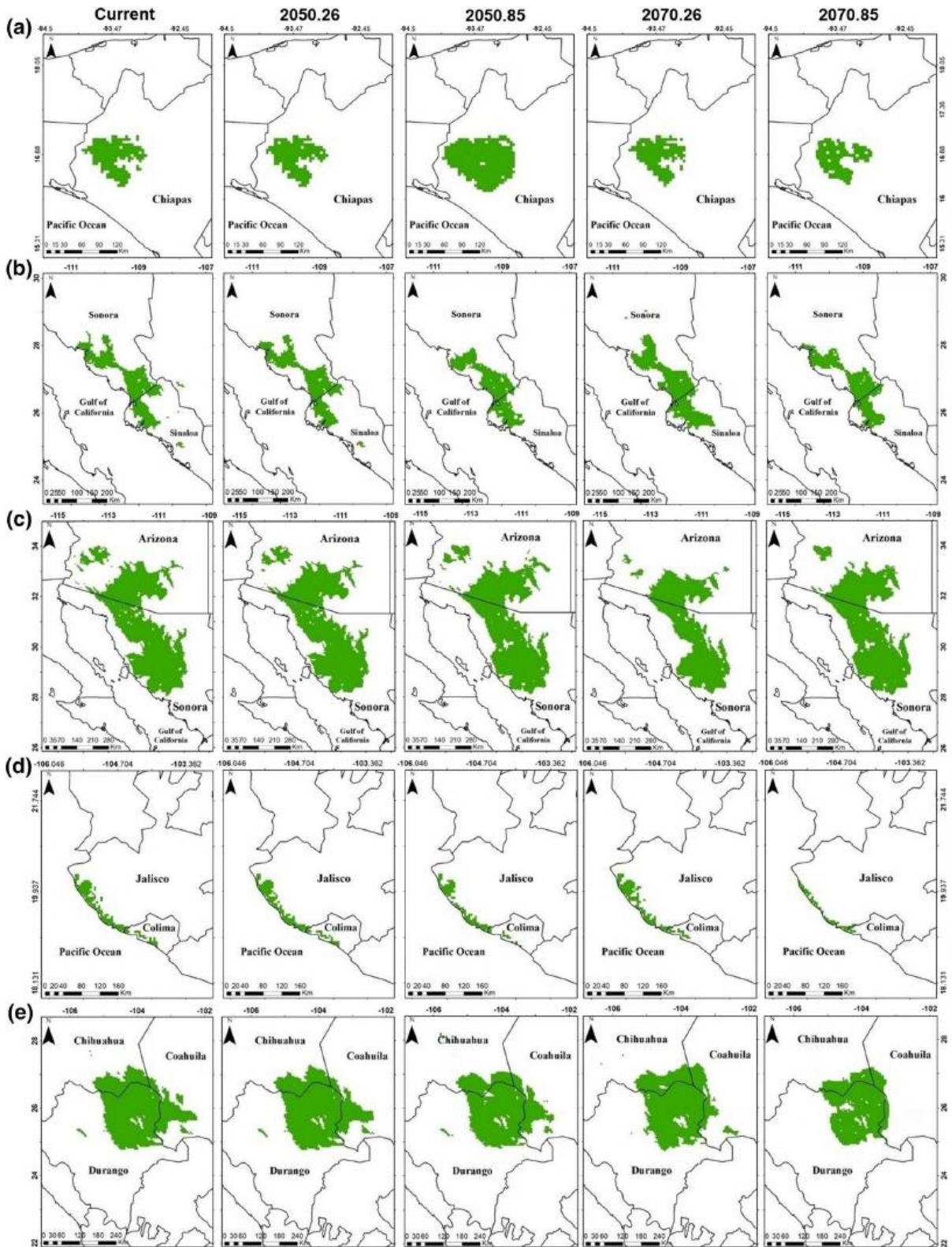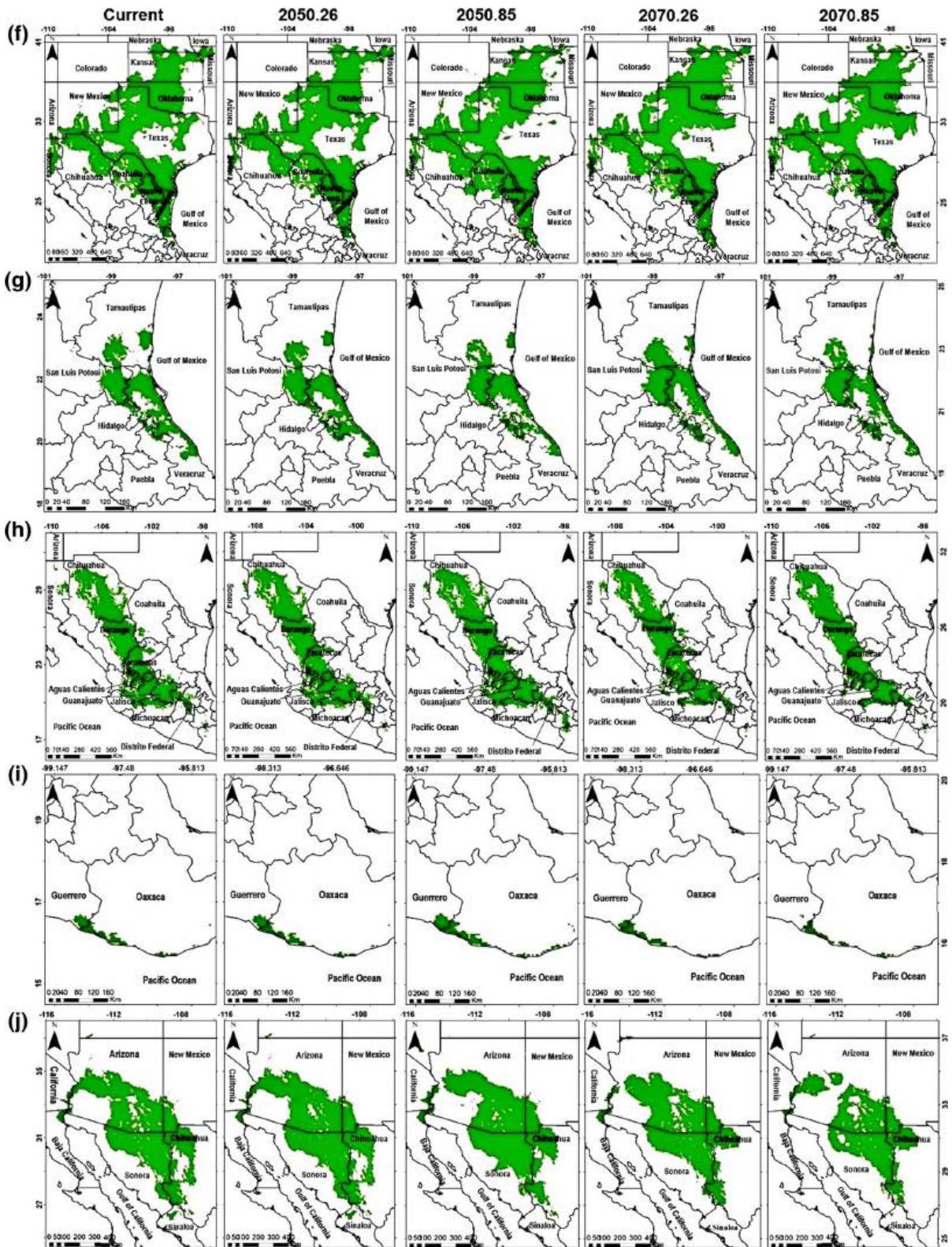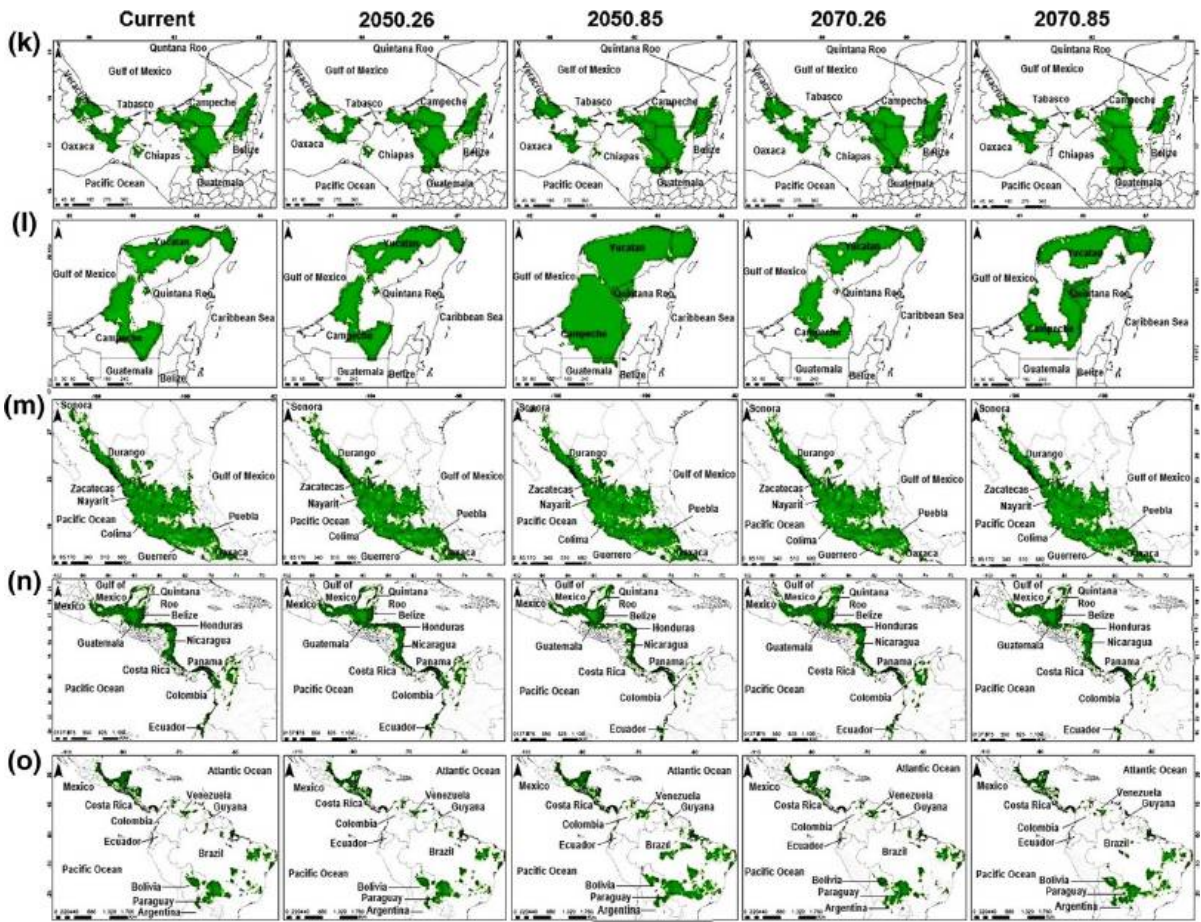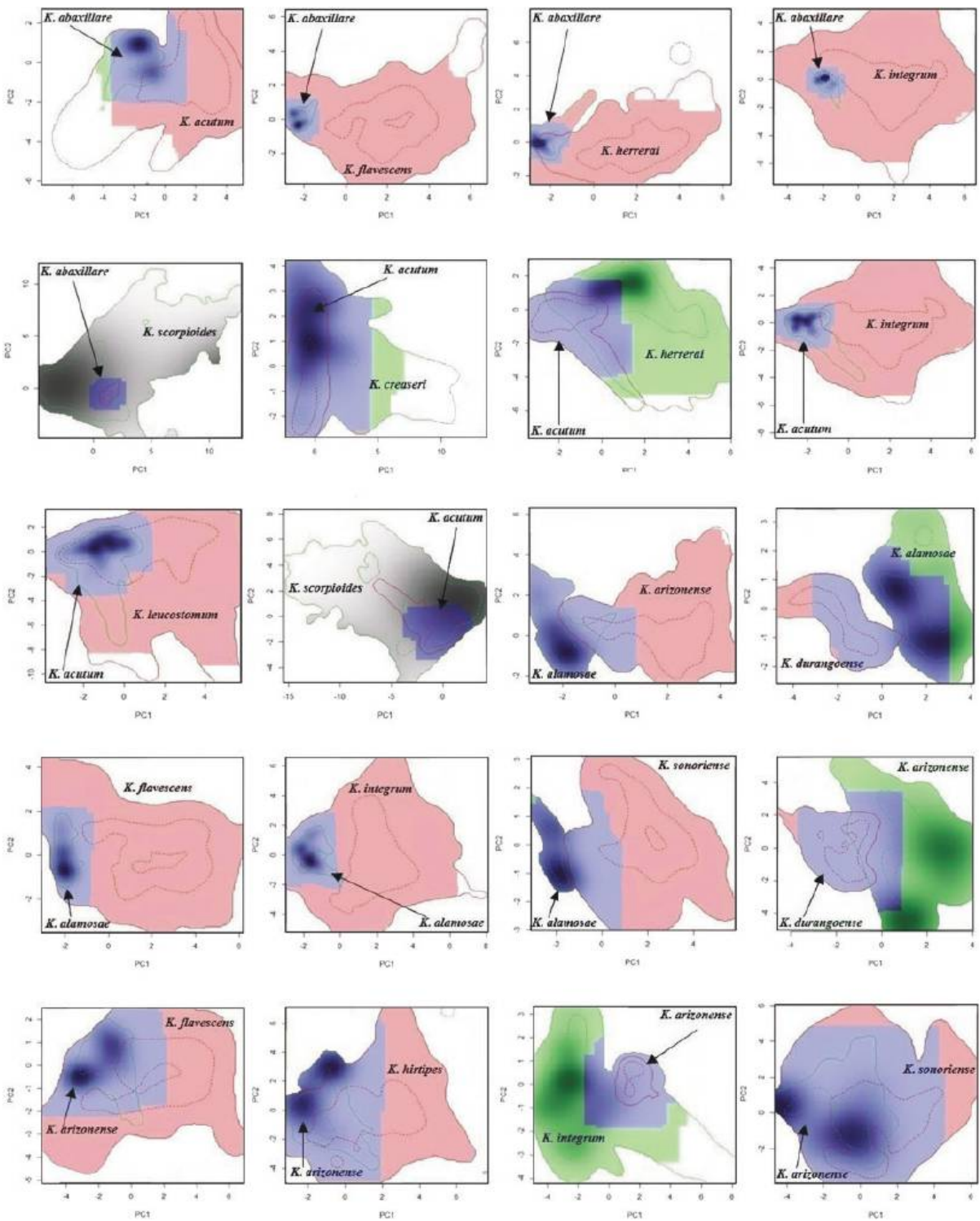
Fig. 2 continued

Fig. 2 continued

The *Kinosternon* turtles are distributed from southern Canada to northern Argentina. Along their distribution, environments can reach lethal temperatures during some months of the year. This being so, they have evolved diverse ecological and physiological adaptations to cope with extreme temperatures and dry conditions (Ultsch, 2006; Pérez-Pérez et al., 2017). However, longer periods of drought and extreme temperatures can go beyond the tolerance rates of their plasticity and are likely to cause decreases in population sizes that could lead to local extinctions (Ligon & Peterson, 2002).

Fig. 3 Pairs of species that showed similar climatic niches in ▶ the environmental space according to principal components analysis (PCA-environmental). The panels represent the niches of species pairs along the first two axes of the PCA. Solid contour lines illustrate the full range (100%) of climate space, and dashed contour lines represent the (50%) available environment (background). Shading shows the density of species occurrences per grid cell. Blue pixels show niche overlap between the two species (conservatism of climate conditions occupied in both species), red pixels and green pixels are the parts of the niche of the species that do not overlap
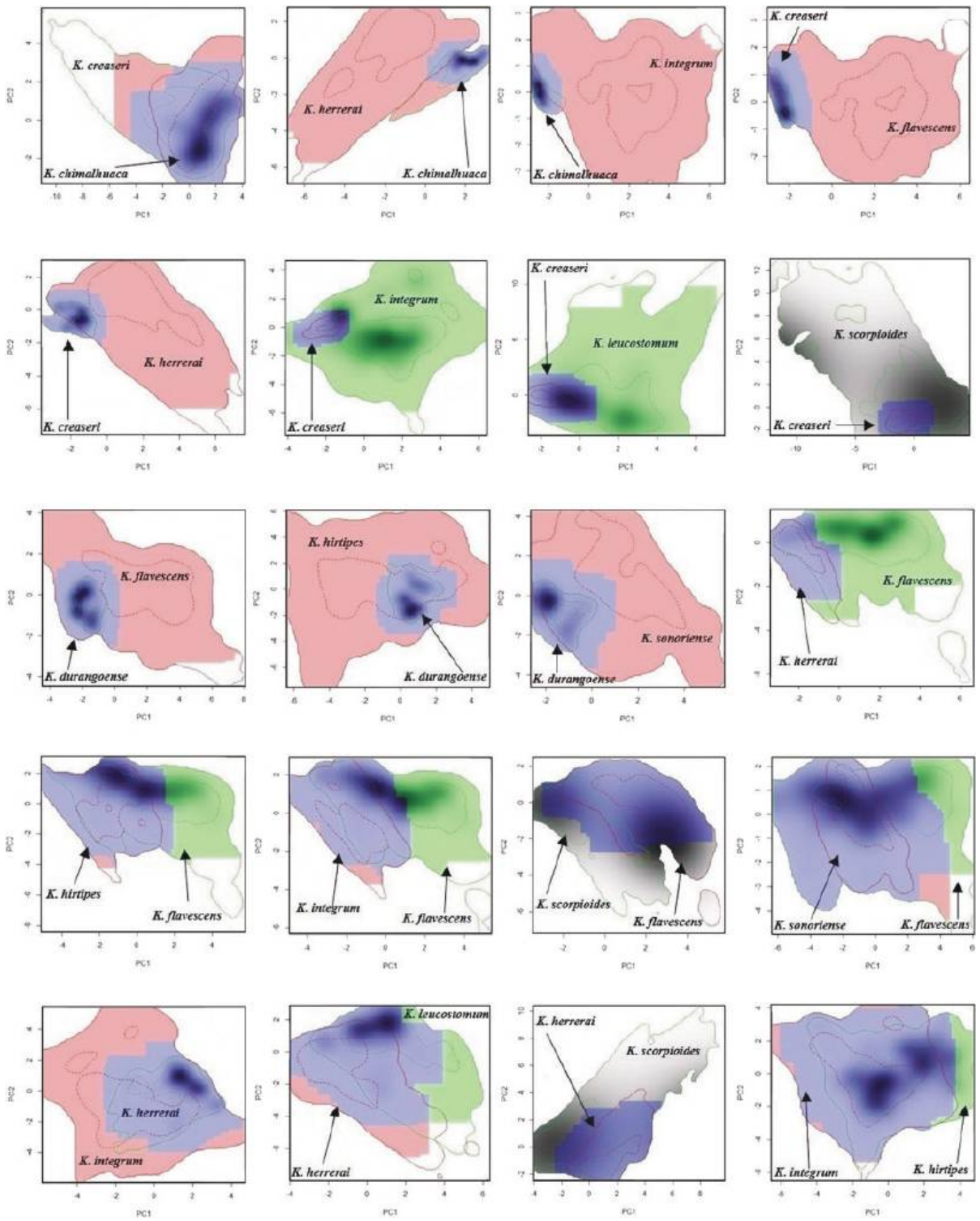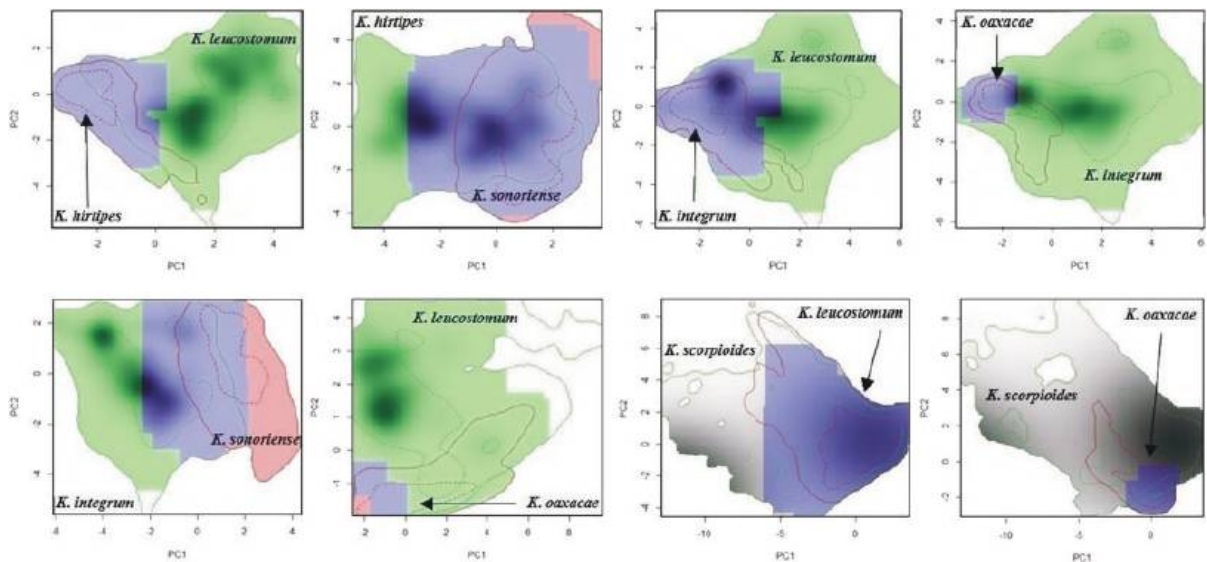
Fig. 3 continued

Fig. 3 continued

Environmental niche models also suggest that climatic niches for *Kinosternon abaxillare*, *K. chimalhuaca*, *K. creaseri*, *K. durangoense*, *K. herrerai*, *K. hirtipes*, *K. oaxacae*, and *K. sonoriense* will decrease considerably during the coming decades (see Table 2). These results are alarming, since several of these taxa are microendemic, occurring only in a very narrow distribution area. For example, the models reveal that by 2050 and 2070, large areas with suitable conditions will be lost from the distribution of *Kinosternon hirtipes*. Therefore, three of its subspecies, *K. h. chapalense* from Lake Chapala and Presa Zapotlán, *K. h. magdalense* from Presa San Juanico, and *K. h. hirtipes* from the Valley of Mexico will be drastically imperiled by the reduction of suitable habitat. Areas with suitable climate conditions for *K. acutum*, *K. alamosae*, *K. flavescens*, *K. integrum*, and *K. stejnegeri* will be less affected. These results coincide in part with those reported by Butler et al. (2016), who state that the habitat suitable for the species *K. hirtipes* will decrease during the coming decades. However, our results differ from theirs for *K. flavescens* and *K. sonoriense*, as Butler et al. (2016) suggest that habitat suitability in these species will increase considerably, but our analysis found expected decreases of 17.68% and 34.82% for these two species respectively.

We found that suitable habitat for four species was projected to expand outside the current geographic ranges. These species are *K. abaxillare*, *K. creaserie*, and to a lesser extent *K. leucostomum* and *K. oaxacae*, and the shift was more obvious in the low-concentration scenario. However, even when the ranges of the species are predicted to increase, these turtles may not be able to expand their ranges in concordance with the shift in suitable habitat (Butler et al., 2016; Waterson et al., 2016). Although turtles of the *Kinosternon* genus have the ability to move for several meters (Hall & Steidl, 2007; Cordero et al., 2012; Pérez-Pérez et al., 2017), anthropic factors such as habitat fragmentation and urbanization are strong barriers that prevent species from establishing themselves in new places with adequate habitat conditions (Semlitsch & Bodie, 2003; Ner & Burke, 2008).

Ihlow et al. (2012) predict that during the coming decades there will be suitable habitat for a great diversity of chelonians in some regions of the planet, while in other places, suitable conditions will be lost. These authors also raise the question of whether turtle species could adjust to the new environmental conditions generated by climate change in the future. Our climatic niche conservatism results suggest that species of the genus *Kinosternon* will not be able to withstand the new environmental conditions generated by climate change, since this lineage of turtles maintains its ancestral niche.

Our results present robust evidence that mud turtles show climatic niche conservatism in both tropical and

Table 3 Climatic niche overlap (D) between species of the genus *Kinosternon* and the significance value (P)

Species	K. acutum	K. alamosae	K. stejnegeri	K. chimalhuaca	K. creaseri	K. durangoense	K. flavescens
K. abaxilare	**D = 0.0788*** **P = 0.009–0.009**	D = 0 P = 1-1	D = 0 P = 1-1	D = 0.0016 **P = 0.9702–0.009**	D = 0 P = 1-1	D = 0 P = 1-1	**D = 0.0514*** **P = 0.0198–0.009**
K. acutum		D = 0 P = 1-1	D = 0 P = 1-1	D = 0.1278 **P = 0.009–0.1584**	**D = 0.2537*** **P = 0.009–0.0277**	D = 0 P = 1-1	D = 0.1608 P = 0.1881–0.009
K. alamosae			**D = 0.0993*** **P = 0.009–0.0178**	D = 0.1278 **P = 0.009–0.5148**	D = 0.1116 P = 0.4257–0.0594	**D = 0.0174*** **P = 0.009–0.0198**	**D = 0.0587*** **P = 0.0495–0.009**
K. stejnegeri				D = 0 P = 1-1	D = 0 P = 1-1	**D = 0.0149*** **P = 0.009–0.0593**	**D = 0.1611*** **P = 0.0198–0.009**
K. chimalhuaca					**D = 0.296*** **P = 0.009–0.0592**	D = 0 P = 1-1	D = 0.0284 **P = 0.009–0.8118**
K. creaseri						D = 0 P = 1-1	**D = 0.0841*** **P = 0.0297–0.009**
K. durangoense							**D = 0.0629*** **P = 0.078–0.009**
K. flavescens							
K. herrerai							
K. hirtipes							
K. integrum							
K. leucostomum							
K. oaxacae							
K. scorpioides							

Species	K. herrerai	K. hirtipes	K. integrum	K. leucostomum	K. oaxacae	K. scorpioides	K. sonoriense
K. abaxilare	**D = 0.0644*** **P = 0.0297–0.05346**	D = 0.0025 P = 0.2079–0.594	**D = 0.0322*** **P = 0.0594–0.009**	D = 0.0289 **P = 0.6237–0.0198**	D = 0 P = 1-1	**D = 0.0035*** **P = 0.0217–0.0198**	D = 0 P = 1-1
K. acutum	**D = 0.2439*** **P = 0.009–0.0592**	D = 0.027 P = 0.4356–0.009	**D = 0.0923*** **P = 0.0593–0.009**	**D = 0.5055*** **P = 0.03069–0.009**	D = 0 P = 1-1	**D = 0.0437*** **P = 0.03168–0.009**	D = 0 P = 1-1
K. alamosae	D = 0 P = 1-1	D = 0.0441 P = 0.891–0.0198	**D = 0.0422*** **P = 0.0267–0.009**	D = 0 P = 1-1	D = 0 P = 1-1	D = 0 P = 1-1	**D = 0.0456*** **P = 0.009–0.0592**
K. stejnegeri	D = 0 P = 1-1	**D = 0.1268*** **P = 0.009–0.0168**	**D = 0.0696*** **P = 0.0495–0.009**	D = 0 P = 1-1	D = 0 P = 1-1	D = 0 P = 1-1	**D = 0.1675*** **P = 0.0465–0.009**
K. chimalhuaca	**D = 0.0262*** **P = 0.0198–0.009**	D = 0.0123 P = 0.5247–0.009	**D = 0.0307*** **P = 0.0495–0.009**	D = 0.0953 P = 0.1485–0.0198	D = 0 P = 1-1	D = 0.0036 P = 0.0891–0.009	D = 0 P = 1-1

Table 3 continued

Species	K. herrerai	K. hirtipes	K. integrum	K. leucostomum	K. oaxacae	K. scorpioides	K. sonoriense
K. creaseri	**D = 0.1115***; **P = 0.009–0.009**	D = 0.0152; P = 0.5445–0.009	**D = 0.0517***; **P = 0.0297–0.009**	**D = 0.0528***; **P = 0.02079–0.009**	D = 0; P = 1–1	**D = 0.0058***; **P = 0.0257–0.009**	D = 0; P = 1–1
K. durangoense	D = 0; P = 1–1	**D = 0.0662***; **P = 0.0316–0.009**	D = 0.0169; P = 0.603–0.009	D = 0; P = 1–1	D = 0; P = 1–1	D = 0; P = 1–1	**D = 0.1638***; **P = 0.0376–0.009**
K. flavescens	**D = 0.2543***; **P = 0.009–0.0594**	**D = 0.2486***; **P = 0.0108–0.0445**	**D = 0.2956***; **P = 0.009–0.0198**	D = 0.1291; P = 0.1188–0.0396	D = 0; P = 1–1	**D = 0.103***; **P = 0.0297–0.0108**	**D = 0.2248***; **P = 0.0396–0.0386**
K. herrerai		D = 0.1631; P = 0.7524–0.6435	**D = 0.3503***; **P = 0.009–0.009**	**D = 0.256***; **P = 0.02574–0.009**	D = 0; P = 1–1	**D = 0.1716***; **P = 0.0326–0.0198**	D = 0; P = 1–1
K. hirtipes			**D = 0.3897***; **P = 0.0198–0.03564**	**D = 0.1033***; **P = 0.0396–0.009**	D = 0.0115; P = 0.6435–0.0297	D = 0.1017; P = 0.0198–0.5445	**D = 0.2799***; **P = 0.0287–0.009**
K. integrum				**D = 0.303***; **P = 0.009–0.0297**	**D = 0.0758***; **P = 0.0593–0.009**	D = 0.0033; P = 0.1188–0.792	**D = 0.0895***; **P = 0.059–0.0118**
K. leucostomum					**D = 0.0009***; **P = 0.0592–0.0297**	**D = 0.1642***; **P = 0.0396–0.009**	D = 0; P = 1–1
K. oaxacae						**D = 0.0535***; **P = 0.0198–0.009**	D = 0; P = 1–1
K. scorpioides							D = 0; P = 1–1

*Species with significant similarity between their climatic niches

Bold values represent significant tests of niche similarity

sub-tropical species from semi-arid zones. It is important to note that *K. hirtipes* and *K. integrum* have climatic niches similar to tropical and semi-arid species, since these species inhabit a great variety of environments along their geographical distribution (Legler & Vogt, 2013); nevertheless, even if this species could occur in sympatry across its distribution, *K. hirtipes* requires perennial aquatic habitats and aestivates only a short period of time (Legler & Vogt, 2013), while *K. integrum* can aestivate for more than 250 days out of water (Aparicio et al., 2018).

Our results are supported by other authors such as Cooper et al. (2011) and Olalla-Tárraga et al. (2011) who found greater niche conservatism in tropical mammals and amphibians than those in temperate regions. Finally, microendemic species, such as *K. abaxillare*, *K. chimalhuaca*, *K. alamosae*, *K. durangoense*, and *K. oaxacae* showed low climate niche similarity with respect to other mud turtles. This pattern may be due to the fact that each of these species have unique local adaptations to a particular environmental niche different from all the other species, as other authors have suggested (Waldron et al., 2006; Bonetti & Wiens, 2014a, b; Maik et al., 2015).

The climatic niche conservatism demonstrated in this study showed a grouping pattern like that reported for the phylogeny of the *Kinosternon* lineage proposed by Iverson et al. (2013). This supports the evidence that species of the genus *Kinosternon* still conserve their ancestral climatic niche. For example, our results also showed that there is climatic niche similarity among *K. acutum*, *K. creaseri*, *K. herrerai*, *K. scorpioide*s, and *K. leucostomum*. These species are also grouped in one of the clades proposed by Iverson et al. (2013), which is composed of species with southern tropical affinity. The species *K. alamosae*, *K. hirtipes*, *K. sonoriense*, *K. durangoense*, *K. integrum*, and *K. stejnegeri* were found within a second larger clade in the phylogeny proposed by Iverson et al. (2013), and also share climatic niche similarity. This latter group includes northern species with an affinity to drier and more seasonal climates.

In conclusion, our climatic niche models and climate niche conservatism results suggest that species of the genus *Kinosternon* could be at severe risk of disappearing over the next few decades due to the loss of climatically suitable areas in their distribution and conservation of their climatic niche. Furthermore, loss and drying up of water bodies could heavily impact mud turtles in the areas they inhabit, which in turn could ultimately impact negatively on human well-being (Chapin et al., 2000).

References

Aguirre-León, G. & O. Aquino-Cruz, 2004. Hábitos alimentarios de *Kinosternon herrerai* Stejneger 1925 (Testudines: Kinosternidae) en el centro de Veracruz, México. Acta Zoológica Mexicana 20: 83–98.

Aparicio, A., I. Enríquez-Mercado, A. Montiel-Ugalde, E. Gaona-Murillo, T. Butterfield & R. Macip-Ríos, 2018. Ecological observations of the Mexican Mud turtle (*Kinosternon integrum*) in the Pátzcuaro Basin, Michoacán, México. Chelonian Conservation and Biology 17: 284–290.

Barrows, C. W., 2011. Sensitivity to climate change for two reptiles at the Mojave-Sonoran Desert interface. Journal of Arid Environments 75: 629–635.

Berry, J. F., M. E. Seidel & J. B. Iverson, 1997. A new species of mud turtle (genus *Kinosternon*) from Jalisco and Colima, Mexico, with notes on its natural History. Chelonian Conservation and Biology 2: 329–337.

Bickford, D., S. D. Howard, D. J. J. Ng & J. A. Sheridan, 2010. Impacts of climate change on the amphibians and reptiles of Southeast Asia. Biodiversity and Conservation 19: 1043–1062.

Bonetti, M. F. & J. J. Wiens, 2014a. Evolution of climatic niche specialization: a phylogenetic analysis in amphibians. Proceedings of the Royal Society B: Biological Sciences. https://doi.org/10.1098/rspb.2013.3229.

Bonetti, M. F. & J. J. Wiens, 2014b. Evolution of climatic niche specialization: a phylogenetic analysis in amphibians. Proceedings of the Royal Society of London B Biological Sciences 281: 20133229.

Broennimann, O., M. C. Fitzpatrick, P. B. Pearman, B. Petitpierre, L. Pellissier, N. G. Yoccoz, W. Thuiller, M. J. Fortin, C. Randin, N. E. Zimmermann, C. H. Graham & A. Guisan, 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. Global Ecology and Biogeography 21: 481–497.

Broennimann, O., B. Petitpierre, C. Randin, R. Engler, V. D. Cola, F. Breiner & Guisan, A, 2015. Ecospat: spatial ecology miscellaneous methods. R package version 1.1. Retrieved from http://CRAN.Rproject.org/package=ecospat

Brown, J. H., T. J. Valone & C. G. Curtin, 1997. Reorganization of an arid ecosystem in response to recent climate change. Proceeding of the National Academy of Sciences of the United States of America 94: 9729–9733.

Butler, C. J., 2019. A review of the effects of climate change on chelonians. Diversity 11: 1–22.

Butler, C. J., B. D. Stanila, J. B. Iverson, P. A. Stone & M. Bryson, 2016. Projected changes in climatic suitability for *Kinosternon* turtles by 2050 and 2070. Ecology and Evolution 6: 7690–7705.

Cadena, E. R., C. M. Jaramillo & M. Paramo, 2007. The first late Pleistocene record of *Kinosternon* (Cryptodira: Kinosternidae) turtles for northern South America, Pubenza Locality, Colombia. South American Journal of Herpetology 2: 201–205.

Chapin III, F. S., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack & S. Díaz, 2000. Consequences of changing biodiversity. Nature 405: 234–242.

Cleland, E. E., N. R. Chiariello, S. R. Loarie, H. A. Mooney & C. B. Field, 2006. Diverse responses of phenology to global changes in a grassland ecosystem. Proceedings of the National Academy of Sciences, USA 103: 13740–13744.

Cohen, J. M., T. A. McMahon, C. Ramsay, E. A. Roznik, E. L. Sauer, S. Bessler, D. J. Civitello, B. K. Delius, N. Halstead, S. A. Knutie, K. H. Nguyen, N. Ortega, B. Sears, M. D. Venesky, S. Young & J. R. Rohr, 2019. Impacts of thermal mismatches on chytrid fungus *Batrachochytrium dendrobatidis* prevalence are moderated by life stage, body size, elevation and latitude. Ecology Letters. https://doi.org/10.1111/ele.13239.

Cooper, N., R. P. Freckleton & W. Jetz, 2011. Phylogenetic conservatism of environmental niches in mammals. Proceedings of the Royal Society B 278: 2384–2391.

Cordero, G. A. & C. W. Swarth, 2010. Notes on the movement and aquatic behaviour of some kinosternid turtles. Acta Zoológica Mexicana 26: 233–235.

Cordero, G. A., R. Reeves & C. W. Swarth, 2012. Long distance aquatic movement and home-range size of an Eastern mud turtle, *Kinosternon subrubrum*, population in the mid-Atlantic region of the United States. Chelonian Conservation and Biology 11: 121–124.

Davies, P. M., 2010. Climate change implications for river restoration in global biodiversity hotspots. Restoration Ecology 18: 261–268.

Elith, J., M. Kearney & S. Phillips, 2010. The art of modelling rangeshifting species. Methods in Ecology and Evolution 1: 330–342.

Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee & C. J. Yates, 2011. A statistical explanation of MaxEnt for ecologists. Diversity and Distributions 17: 43–57.

ESRI, 2006. ArcGIS 10.3. Environmental Systems Research Institute, Redlands.

Fagundes, C. K., R. C. Vogt & P. D. M. Júnior, 2015. Testing the efficiency of protected areas in the Amazon for conserving freshwater turtles. Diversity and Distributions 22: 123–135.

Gabriel, C. J., A. Robock, L. Xia, B. Zambri & B. Kravitz, 2017. The G4Foam experiment: global climate impacts of regional ocean albedo modification. Atmospheric Chemistry and Physics 17: 595–613.

GBIF, 2010. *Kinosternon* spp. http://data.gbif.org/species/; last accessed: 31V.2010.

Gutiérrez, E. & I. Trejo, 2014. Efecto del cambio climático en la distribución potencial de cinco especies arbóreas de bosque templado en México. Revista Mexicana de Biodiversidad 85: 179–188.

Hall, D. H. & R. Steidl, 2007. Movements, activity, and spacing of sonoran mud turtles (*Kinosternon sonoriense*) in interrupted mountain streams. Copeia 2007: 403–412.

Hamann, A., D. Roberts, Q. E. Barber, C. Carroll & S. E. Nielsen, 2015. Velocity of climate change algorithms for guiding conservation and management. Global Change Biology 21: 997–1004.

Hertz, P. E., 1981. Adaptation to altitude in two West Indian anoles (Reptilia: Iguanidae): field thermal biology and physiological ecology. Journal of Zoology 195: 25–37.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones & A. Jarvis, 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965–1978.

Hu, J., O. Broennimann, A. Guisan, B. Wang, Y. Huang & J. Jiang, 2016. Niche conservatism in *Gynandropaa* frogs on the southeastern QinghaiTibetan Plateau. Scientific Reports. https://doi.org/10.1038/srep32624.

Ihlow, F., J. Dambach, J. O. Engler, M. Flecks, T. Hartmann, S. Nekum, H. Rajaei & D. Rödder, 2012. On the brink of extinction? How climate change may affect global chelonian species richness and distribution. Global Change Biology 18: 1520–1530.

Iverson, J. B., 1982. Biomass in turtle populations. A neglected subject. Oecologia 55: 69–79.

Iverson, J. B., 1991. Life history and demography of the yellow mud turtle, *Kinosternon flavescens*. Herpetologica 47: 373–395.

Iverson, J. B., 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Privately Published, Richmond.

Iverson, J. B., L. Minh & C. Ingram, 2013. Molecular phylogenetics of the mud and musk turtle family Kinosternidae. Molecular Phylogenetics and Evolution 69: 929–939.

Joyce, W. G. & J. R. Bourque, 2016. A review of fossil records of turtles of the clade Pan-Kinosternoidea. Bulletin of the Peabody Museum of Natural History 57: 57–95.

Lara-Reséndiz, R. A., A. H. Díaz de la Vega-Pérez, V. H. Jiménez-Arcos, H. Gadsden & F. R. Méndez-De la Cruz, 2014. Thermoregulation in two sympatric populations of lizard: *Sceloporus lineolateralis* and *Sceloporus poinsettii* (Squamata: Phrynosomatidae) in Durango, Mexico. Revista Mexicana de Biodiversidad 85: 875–884.

Lara-Reséndiz, R. A., P. Galina-Tessaro, A. G. Pérez-Delgadillo, J. H. Valdez-Villavicencio & F. R. Méndez-de la Cruz, 2019. Efectos del cambio climático en una especie de lagartija termófila de amplia distribución (*Dipsosaurus dorsalis*): un enfoque ecofisiológico. Revista Mexicana de Biodiversidad 90: 1–11.

Lavergne, S., N. Mouquet, W. Thuiller & O. Ronce, 2010. Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. Annual Review of Ecology and Evolutionary Systematics 41: 321–350.

Legler, J. & R. C. Vogt, 2013. The Turtles of Mexico: Land and Freshwater Forms. University of California Press, California.

Lehner, B., K. Verdin & A. Jarvis, 2006. HydroSHEDS Technical Documentation. World Wildlife Fund US, Washington, DC. Available at http://hydrosheds.cr.usgs.gov

Ligon, D. B. & C. C. Peterson, 2002. Physiological and behavioral variation in estivation among mud turtles (*Kinosternon* spp.). Physiological and Biochemical Zoology 75: 283–293.

Loarie, S. R., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field & D. D. Ackerly, 2009. The velocity of climate change. Nature 462: 1052–1055.

López-Luna, M. A., F. G. Capul-Magaña, A. H. Escobedo-Galván, A. J. González-Hernández, E. Centenero-Alcalá, J. A. Rangel-Mendoza, M. M. Ramírez-Ramírez & E. Cazares-Hernández, 2018. A distinctive new species of mud turtle from Western Mexico. Chelonian Conservation and Biology 17: 2–13.

Lukasiewicz, A., J. Pittock & C. M. Finlayson, 2016. Are we adapting to climate change? A catchment-based adaptation assessment tool for freshwater ecosystems. Climatic Change 138: 641–654.

Macip-Ríos, R., Ma. de L. Arias Cisneros, X. S. Aguilar-Miguel & G. Casas-Andreu, 2009. Population ecology and reproduction of the Mexican turtle (*Kinosternon integrum*) in Tonatico, Estado de México. Western North American Naturalist 69: 501–510

Macip-Ríos, R., R. Ontiveros, S. López-Alcaide & G. Casas-Andreu, 2015. The conservation status of the freshwater and terrestrial turtles of Mexico: a critical review of biodiversity conservation strategies. Revista Mexicana de Biodiversidad 86: 1048–1057.

Macip-Ríos, R., R. N. Ontiveros, A. T. Sánchez-León & G. Casas-Andreu, 2017. Evolution of reproductive effort in mud turtles (Kinosternidae): the role of environmental predictability. Evolutionary Ecology Research 18: 539–554.

Maik, J. M., J. W. Streicher, A. M. Lawing, O. Flores-Villela & M. K. Fujita, 2015. Limitations of climatic data for inferring species boundaries: insights from speckled rattlesnakes. PLoS ONE. https://doi.org/10.1371/journal.pone.0131435.

Ner, S. E. & R. L. Burke, 2008. Direct and indirect effects of urbanization on diamond-backed terrapins of the Hudson River Bight: Distribution and predation in a human-modified estuary. In. Urban Herpetology. (eds). Mitchell, J. C., R. E. J. Brown. & B. Bartholomew. U. Herpetological Conservation, number 3. Society for thc Study of Amphibians and Reptiles

Olalla-Tárraga, M. A., L. McInnes, L. M. Bini, J. A. F. Diniz-Filho, S. A. Fritz, B. A. Hawkins, J. Hortal, C. D. L. Orme, C. Rahbek, M. Á. Rodríguez & A. Purvis, 2011. Climatic niche conservatism and the evolutionary dynamics in species range boundaries: global congruence across mammals and amphibians. Journal of Biogeography 38: 2237–2247.

Pearson, R. G. & T. P. Dawson, 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12: 361–371.

Pearson, R. G., C. J. Raxworthy, M. Nakamura & A. T. Peterson, 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography 34: 102–117.

Pérez-Pérez, A., A. E. López-Moreno, O. Suárez-Rodríguez, J. L. Rheubert & O. Hernández-Gallegos, 2017. How far do adult turtles move? Home range and dispersal of *Kinosternon integrum*. Ecology and Evolution 7: 8220–8231.

Phillips, S. J., M. Dudik & R. E. Schapire, 2004. A maximum entropy approach to species distribution modeling. In Greiner R. & D. Schuurmans (eds), Proceedings of the twenty-first international conference on machine learning New York, NY: Association for Computing Machinery Press: 655–662.

Phillips, S. J., R. P. Anderson & R. E. Schapire, 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190: 231–256.

Pliscoff, P. & T. Fuentes-Castillo, 2011. Modelación de la distribución de especies y ecosistemas en el tiempo y en el espacio: una revisión de las nuevas herramientas y enfoques disponibles. Revista de Geografía Norte Grande 48: 61–79.

R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rhodin, A. G. J., J. B. Iverson, R. Bour, U. Fritz, A. Georges, H. B. Shaffer, & P. P. van Dijk. 2017. Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC. Tortoise and Freshwater Turtle Specialist Group. In Chelonian Research Monographs. (eds). Rhodin, A. G. J., J. B. Iverson, P. P. van Dijk, R. A. Saumure, K. A. Buhlmann, P. C. H. Pritchard & R. A. Mittermeier.

Ron, S. R., 2005. Predicting the distribution of the amphibian pathogen *Batrachochytrium dendrobatidis* in the New World. Biotropica 37: 209–221.

Rödder, D., A. M. Lawing, M. Flecks, F. Ahmadzadeh, J. Dambach, F. Ahmadzadeh, J. Dambach, J. O. Engler, J. C. Habel, T. Hartmann, D. Hörnes, F. Ihlow, K. Schidelko, D. Stiels & P. D. Polly, 2013. Evaluating the significance of paleophylogeographic species distribution models in reconstructing quaternary range-shifts of Nearctic chelonians. PLoS ONE. https://doi.org/10.1371/journal.pone.0072855.

Seager, R., M. Ting, I. Held, Y. Kushnir, J. Lu, G. Vecchi, H. Huang, N. Harnik, A. Leetmaa, N. Lau, C. Li, J. Velez & N. Naik, 2007. Model predictions of an imminent transition to a more arid climate in southwestern North America. Science 316: 1181–1184.

Sinervo, B., F. Méndez-de-la-Cruz, D. B. Miles, B. Heulin, E. Bastiaans, M. Villagrán-Santa Cruz, R. Lara-Resendiz, N. Martínez-Méndez, M. L. Calderón-Espinosa, R. N. Meza-Lázaro, H. Gadsden, L. J. Avila, M. Morando, I. J. De la Riva, P. V. Sepulveda, C. F. Duarte Rocha, N. Ibargüengoytía, C. Aguilar Puntriano, M. Massot, V. Lepetz, T. A. Oksanen, D. G. Chapple, A. M. Bauer, W. R. Branch, J. Clobert & J. W. Sites Jr., 2010. Erosion of lizard diversity by climate change and altered thermal niches. Science 328: 894–899.

Sinervo, B., D. B. Miles, Y. Wu, F. R. Méndez-de la Cruz, S. Kirchhof & Y. Qi, 2018. Climate change, thermal niches,

extinction risk and maternal-effect rescue of toad-headed lizards, *Phrynocephalus*, in thermal extremes of the Arabian Peninsula to the Qinghai–Tibetan Plateau. Integrative Zoology 13: 450–470

Sirois, A. M., J. P. Gibbs, A. L. Whitlock & L. A. Erb, 2014. Effects of habitat alterations on bog turtles (*Glyptemys muhlenbergii*): a comparison of two populations. Journal of Herpetology 48: 455–460.

Semlitsch, R. D. & J. R. Bodie, 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology 17: 1219–1228.

StatSoft, Inc, 2004. Statistica. (data analysis software system), version 10 www.statsoft.com.

Stempniewicz, L., M. Goc, D. Kidawa, J. Urbański, M. Hadwiczak & A. Zwolicki, 2017. Marine birds and mammals foraging in the rapidly deglaciating Arctic fjord: numbers, distribution and habitat preferences. Climatic Change 140: 533–548.

Tanaka, A., K. Takahashi, H. Shiogama, N. Hanasaki, Y. Masaki, A. Ito, H. Noda, Y. Hijioka & S. Emori, 2017. On the scaling of climate impact indicators with global mean temperature increase: a case study of terrestrial ecosystems and water resources. Climatic Change 141: 775–782.

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. Ferreira de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. T. Peterson, O. L. Phillips & S. E. Williams, 2004. Extinction risk from climate change. Nature 427: 145–148.

Tuma, M. W., 2006. Range, habitat use, and seasonal activity of the yellow mud turtle (*Kinosternon flavescens*) in northwestern Illinois: implications for site-specific conservation and management. Chelonian Conservation and Biology 5: 108–120.

Ultsch, G. R., 2006. The ecology of overwintering among turtles: where turtles overwinter and its consequences. Biological Reviews 81: 339–367.

Urbina-Cardona, J. N. & O. Flores-Villela, 2010. Ecological-Niche modeling and prioritization of conservation-Area networks for mexican herpetofauna. Conservation Biology 24: 1031–1041.

van Dijk, P. P., J. B. Iverson, A. G. J. Rhodin, H. B. Shaffer & R. Bour, 2014. Turtles of the world, 7th edition: annotated checklist of taxonomy, synonymy, distribution with maps, and conservation status. Chelonian Research Monographs 5: 329–479.

Vogt, R. C. & O. A. Flores-Villela, 1986. Determinación del sexo en tortugas por la temperatura de incubación de los huevos. Ciencia 37: 21–32.

Vogt, R. C. & S. Guzman-Guzman, 1988. Food partitioning in a neotropical freshwater turtle community. Copeia 1988: 37–47.

Waldron, J. L., S. H. Bennett, S. M. Welch, M. E. Dorcas, J. D. Lanham & W. Kalinowsky, 2006. Habitat specificity and home-range size as attributes of species vulnerability to extinction: a case study using sympatric rattlesnakes. Animal Conservation 9: 414–420.

Ward, D. F., 2007. Modelling the potential geographic distribution of invasive ant species in New Zealand. Biological Invasions 9: 723–735.

Warren, D. L., R. E. Glor & M. Turelli, 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62: 2868–2883.

Waterson, A. M., D. N. Schmidt, P. J. Valdes, P. A. Holroyd, D. B. Nicholson, A. Farnsworth & P. M. Barret, 2016. Modelling the climatic niche of turtles: a deep-time perspective. Proceedings of the Royal Society B 283: 20161408.

Wiens, J. J. & C. H. Graham, 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Review of Ecology, Evolution, and Systematics 36: 519–539.

Wiens, J. J., D. D. Ackerly, A. P. Allen, B. L. Anacker, L. B. Buckley, H. V. Cornell, E. I. Damschen, T. Jonathan Davies, J. A. Grytnes, S. P. Harrison, B. A. Hawkins, R. D. Holt, C. M. McCain & P. R. Stephens, 2010. Niche conservatism as an emerging principle in ecology and conservation biology. Ecology Letters 13: 1310–1324.