Late Pleistocene to Holocene distributional stasis in scorpions along the Baja California peninsula

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Received 5 July 2013; revised 5 October 2013; accepted for publication 5 October 2013

The biota of the Baja California peninsula (BCP) assembled in response to a complex history of Neogene tectonics and Quaternary climates. We constructed species distribution models (SDMs) for 13 scorpion species from the BCP to compare current suitable habitat with that at the latest glacial maximum about 21 000 years ago. Using these SDMs, we modelled climatic suitability in relation to latitude along the BCP. Our SDMs suggested that most BCP scorpion distributions have remained remarkably conserved across the latest glacial to interglacial climatic transformation. Three areas of climatic suitability coincide remarkably well with genetic discontinuities in other co-distributed taxa along the BCP, indicating that long-term persistence of zones of abrupt climatic transition offer a viable alternative, or synergistic enhancement, to hypotheses of trans-peninsular seaways as drivers of peninsular divergences. © 2014 The Linnean Society of London, Biological Journal of the Linnean Society, 2014, 111, 450–461.


INTRODUCTION

Quaternary climate change has profoundly influenced the associations of species, communities, ecosystems and biotas. Cooler climates during the last glacial maximum (LGM, c. 21 000 years ago) followed by the period of warming (albeit not a simple linear warming trend) from the LGM until the present represents an episode of climatic transition that can be deciphered for understanding how species and biotas might respond to current and future climatic warming. Molecular genetics (e.g. Klicka & Zink, 1997; Avise, 2000) and palaeontology (e.g. Betancourt, Van Devender & Martin, 1990; Macfadden, 2006) have provided keen insights into the evolutionary responses of species to climate change during this period of time. Species distribution modelling (SDM), also referred to as ecological niche modelling (see Saupe et al., 2012), is emerging as an additional tool for assessing potential species responses to changing climate. By using climate data to derive SDMs, and then projecting these models onto climatic simulations of the LGM ('hindcasting'), investigators seek to reconstruct the impact of Quaternary climate change on the distributional responses of species. One outcome might be the emergence of common response patterns within and among co-distributed species, providing a tool for predicting the future assembly and disassembly of regional biotas.

The Baja California peninsula (BCP) of Mexico is the second longest terrestrial peninsula in the world, and possesses a diverse array of desert and tropical dry forest environments. Originally, the BCP (Fig. 1) was thought to have a dispersal-dominated biotic history (Savage, 1960), with desert species leaving and re-entering the peninsula in concert with glacial–interglacial climatic cycles. Later advances in our understanding of plate tectonics, however, facilitated complex vicariant hypotheses that better explained
the distribution of biodiversity along the BCP (e.g. Hess, 1962; Murphy, 1983; Grismer, 1994). Starting with seafloor spreading, rifting and volcanic origination of islands that coalesced into the modern peninsula during the mid-Miocene (e.g. Lonsdale, 1989; Spencer & Normark, 1989; Stock & Hodges, 1989), geological activity is now widely held to have heavily influenced the diversification, distribution and composition of the BCP biota (Carreño & Helenes, 2002).

Recent studies have revealed a number of spatially congruent genealogical breaks across the BCP (Upton & Murphy, 1997; Riddle et al., 2000; Murphy & Aguirre-Léon, 2002; Crews & Hedin, 2006; Lindell, Méndez-de la Cruz & Murphy, 2008; Bryson et al., 2012). The spatial congruence of molecular breaks across these disparate taxonomic groups prompted the hypothesis that vicariant events driven by the formation of trans-peninsular seaways could have isolated populations that subsequently reunited at

Figure 1. Map of the Baja California peninsula with major geographical regions delineated and hypothesized trans-peninsular breaks shown: A, mid-peninsular break; B, Loreto break; C, La Paz break.
contact zones following a period of evolutionary divergence (Lindell, Méndez-de la Cruz & Murphy, 2005, 2008). Others have suggested that genetic discontinuities can be explained by abrupt habitat transitions created by latitudinal gradients in climatic patterns, as an alternative to trans-peninsular seaway vicariance (Grimal, 2002; further discussed by Riddle & Hafner, 2006). A third possibility is that abrupt habitat transitions operated synergistically with trans-peninsular seaways to reinforce long-term isolation of populations (Riddle & Hafner, 2006).

To examine the potential impact that historical climate change has had on biodiversity along the BCP, we modelled the current and past distributions of 13 scorpion species representing four families (Caraboctonidae, Chactidae, Scorpionidae, Vaejovidae) distributed along the peninsula. Scorpions are particularly diverse and well documented on the BCP and occupy an array of habitat types (Williams, 1980; Due & Polis, 1986). Quaternary climate fluctuations, such as the period between now and the LGM, have driven profound distributional shifts in many desert species (e.g. Jezkova et al., 2009; Olah-Hemmings et al., 2010; Wilson & Pitts, 2012; Graham et al., 2013a, 2013b). Based on these studies, we predicted similar dynamic shifts in the reconstructed distributions of scorpions along the BCP as desert habitats contracted and expanded. The absence of large shifts in suitable habitat between the LGM and the present day would support an alternative hypothesis of stability in climatically mediated distributions.

### MATERIAL AND METHODS

#### SCORPION OCCURRENCE DATA

Occurrence records for 13 species of scorpions from the BCP (Table 1) were obtained from museum records (California Academy of Sciences and San Diego Natural History Museum), private collections and from the literature (Stahnke, 1968, 1969; Williams, 1970a, 1970b, 1970c, 1971, 1974, 1980; Williams & Lee, 1975; Siom, 1991). Although over 60 species of scorpion are found on the BCP (Williams, 1980), these 13 species were selected because of their relatively wide distributions across...
one or more of the northern, central, southern and Cape regions of the BCP. Although common along the BCP, we did not include Centruroides exilicauda in this study because genetic data suggest that it might represent a complex of cryptic species (Gantenbein, Fet & Barker, 2001). We used Google Earth (http://earth.google.com) to estimate latitude and longitude (Appendix S1) for specimens lacking GPS coordinates using standard georeferencing techniques (Chapman & Wieczorek, 2006). We used only records with maximum error distances under 5 km to match the resolution of the climatic layers. We adhere to the taxonomic nomenclature proposed by Soleglad & Fet (2006). We used only records with the program Maxent v.3.1.0 (Phillips, Dudik & Schapire, 2004) to develop SDMs for the 13 scorpion species. The Maxent algorithm has been shown to perform well in a comprehensive assessment of modelling approaches (Elith et al., 2006), and it uses presence-only species occurrence records and environmental data in the form of GIS layers to approximate environmental requirements for a species by finding the distribution that maximized entropy, subject to constraints imposed by the occurrence records. In other words, the values of the environmental (in this case climatic) variables act as constraints on the unknown distribution, forcing the mean and variance of the output SDMs to approximate that of the occurrence data values.

Current (0 kya) and LGM SDMs were developed for each of the 13 scorpion species using the logistic regression output of Maxent. For 0 kya climatic conditions, models were reconstructed using 19 global bioclimatic layers (temperature and precipitation information) downloaded from the WorldClim database (Hijmans et al., 2005) at a resolution of 2.5 min. Current models were projected onto two general circulation models simulated for the LGM at approximately 21 kya, the Community Climate System Model (CCSM; Otto-Bliesner et al., 2006) and the Model for Interdisciplinary Research on Climate (MIROC v.3.2; Hasumi & Emori, 2004). Since there can be slight variation in SDMs depending on which occurrence record is used to seed each run, we created six current models and projected them on three CCSM and three MIROC models for each species. SDMs were then concatenated and averaged in ArcMap v.9.2 (ESRI, Inc.) to form consensus models for each species under 0 kya and LGM climates, thus capturing some of the intrinsic variation between model runs.

We used random seeding and default settings (regularization = 1; convergence threshold = 0.00001, iterations = 500) in Maxent, with the exception of an additional 0 kya run for each species used for model evaluation where the random test percentage was set to 25%. To visually depict models, we used the average lowest training presence (LTP) threshold (average among models) for each species (with 100% of the data used for training) so that nearly all areas predicted by SDMs would have logistic probability values greater than that of the occurrence record with the smallest value. For better visualization of our models, we averaged the LTP and the highest presence value for each species and imposed this value as an additional threshold. This latter threshold was used only to better visually represent SDMs and was not used in area or centroid calculations (see below). Models were validated using the Receiver Operating Characteristic for its area under the curve (AUC) value.

Our methodology outlined above and SDMs in general are built on a number of assumptions discussed elsewhere (e.g. Nogués-Bravo, 2009) but that warrant mentioning again. When projecting present-day models to past climatic landscapes such as the LGM, a depiction of suitable areas at the LGM is obtained for a species that matches habitat preferences in the present-day (Peterson & Nyári, 2008). Accordingly, this method assumes niche stability within the species being analysed (Nogués-Bravo, 2009). The absence of fossil data for scorpions across the BCP prevents us from directly testing this assumption of niche stability. Whereas many studies have found that species niches have been stable since the LGM (e.g. Martinez-Meyer, Peterson & Hargrove, 2004; Martinez-Meyer & Peterson, 2006), a growing number of recent studies have found contrasting evidence that suggests niche stability may vary (Elith, Kearney & Phillips, 2010), even over relatively short time scales (Ahmadzadeh et al., 2013). Given the evolutionary antiquity of scorpions (derived from amphibious ancestors over 400 Mya) and long history of several species in south-western North America (Bryson et al., 2013; Bryson, Savary & Prendini, 2013), we make the critical assumption that ecological niches of the 13 species in the BCP have been conserved over the past 21 kya, but acknowledge that our results and discussion are built up from the foundation of this untested and potentially erroneous assumption.

**Area and Centroid Calculations**

To qualitatively compare SDMs between species, the total size (km²) as well as the latitude and longitude of centroid position (the estimated centre of each of SDM) were calculated for each scorpion SDM in ArcMap. Area was calculated by converting Maxent...
output ascii files to rasters consisting of integers and then transforming the rasters to polygons using the LTP. All grid cells with values greater than the LTP were included in the polygons, for which their individual areas were calculated and summed for each species. Centroids were calculated by converting each grid cell above the LTP threshold to a point (using the raster to point function in ArcToolbox) and averaging the latitude and longitude of each point for each species. Distances between centroids were calculated using the Haversine Formula, which incorporates curvature of the earth by giving great-circle distances between two points on a sphere. Small to no shifts in suitable habitat from the LGM to the present among the scorpions suggest stability in the distributions of those species. All spatial analyses were conducted using the Albers Equal Area Conic map projection.

RESULTS

MODEL PERFORMANCE

We compiled 736 total occurrence records (Table 1). Current SDMs projected to CCSM and MIROC climate layers yielded different reconstructions for the LGM. MIROC layers produced SDMs that depicted more dramatic geographical range shifts compared with CCSM layers, but often to the degree that there was no or little suitable habitat anywhere across the BCP during the LGM. This has been observed in other studies (e.g. Habel et al., 2010; Olah-Hemmings et al., 2010; McGuire & Davis, 2013) and may be related to sensitivity of the models to differences in the modelled climate of the LGM based on sea ice levels (MIROC simulates warmer and wetter conditions compared with CCSM; Otto-Bliesner et al., 2006). We therefore chose to use only the CCSM SDMs and excluded MIROC models from subsequent analyses (however, MIROC models are provided in Appendix S2). Current SDMs had high predictive success rates and performed significantly better than random in Receiver Operating Characteristic analyses, with AUC scores for testing data greater than 0.95 (Table 1).

GENERAL DISTRIBUTIONAL PATTERNS

ALONG THE BCP

Current SDMs for the 13 species on the BCP fell primarily into four regional categories: (1) northern peninsular (extending into coastal California and the Mojave Desert), (2) mid-peninsular, (3) southern peninsular and (4) the Cape Region (summarized in Fig. 2; shown fully in Appendices S2–S5). Based on the models, the northern peninsular group consisted of three species with relatively large ranges that extended from the mid-peninsula well into portions of central California and southern Nevada. This group displayed the least congruence among suitable regions; high climatic suitability in the north decreased southward at approximately 30.5°N, 25°N and 26°N in Anuroctonus pococchi, Hoffmannius puritanus and Kochius hirsuticauda, respectively (Appendix S7). At the mid-peninsula, climatic suitability within all three species quickly peaked at about 24°N, but then began to drop off at different locations between 29°N and 30°N (Appendix S8). The SDMs for the third group, comprising four species with relatively small ranges in the southern peninsula between Bahia Concepción and Cabo San Lucas, depicted a nearly linear relationship between climatic suitability and latitude, with high climatic suitability found within each species at the southern tip of the peninsula that then steadily declined to the north until it reached a sharp decrease at 26°N for each species (Appendix S9). Models suggested that the four species in the Cape Region group had the smallest ranges (all <23,000 km²) and that each showed a nearly linear decline in climatic suitability starting at the southern tip of the Cape to between 24°N and 25°N (Appendix S10). Comparing trends among all SDMs revealed three areas along the BCP where climatic suitability tended to quickly shift with latitude: approximately at 24°N, 26°N and 30°N.

The predicted habitat for all but one of the 13 species was remarkably stable across the BCP since the LGM. The general trend in the distributions of these species was high climatic suitability along a north–south axis of the peninsula flanked by transitional areas of less than 1° latitude where suitability quickly decreased from high to low (summarized in Fig. 3; shown fully in Appendices S6–S9). The predicted habitat of Kochius bruneus was the only deviation of this pattern. For this species, habitat at the LGM exhibited a change in centroid Figure 2. Species distribution models based on current and last glacial maximum (LGM) conditions for representative scorpion species distributed throughout the northern (Hoffmannius puritanus), middle (Hadrurus concolorous), southern (Hoffmannius vittatus) and Cape (Bioculus caboensis) regions of the Baja California peninsula. The CCSM (our preferred model) and MIROC LGM models are shown for comparison. Shading represents probability of occurrence, with darkest shading representing suitable habitat. Black dots indicate occurrence records used in the modelling and white stars indicate model area centroids. Species distribution models constructed for the remaining nine scorpion species from the Baja California peninsula are presented in Appendices S3–S6.
position of 260.6 km and a change in area of 85 479.2 km² (Appendix S4). The change in centroid position of the other BCP species (Fig. 4) ranged from 5.04 to 260.6 km (mean = 85.89 km), and change in area ranged from −104 606.4 to 85 479.16 km² (mean = −16 251.98 km²).

**DISCUSSION**

**PLEISTOCENE DISTRIBUTIONAL STASIS**

Our results suggest that the suitable habitat for scorpion species in the BCP has remained remarkably stable since the Late Pleistocene. This finding is in
stark contrast to dramatic distributional shifts since the Late Pleistocene inferred for arid-adapted taxa elsewhere in western North America, including heteromyid rodents (Jezkova et al., 2009), rattle-snakes and gnatcatchers (Waltari et al., 2007), phrynosomatid lizards (T. Jezkova, unpubl. data) and invertebrates (Wilson & Pitts, 2012) including scorpions (Graham et al., 2013a, 2013b). This discrepancy has several potential explanations. First, the proximity of the BCP to ocean currents may have influenced this pattern of distributional stasis in scorpions in the BCP. Oceans are well known to buffer coastal climates (Rahmstorf, 2002), effectively acting as large sources and sinks for latent heat. Stewart & Lister (2001) hypothesize that proximity to the relatively temperate conditions of oceans could have allowed for persistence of coastal coniferous forest refugia in northern Europe during the Late Pleistocene. In a similar fashion, the BCP, flanked by the Pacific Ocean to the west and the Sea of Cortés to the east, could also be predisposed to such a coastal effect. The SDMs of Anuroctonus pococki, a widely distributed species across the northern BCP and into coastal California, suggest that this species' suitable habitat remained remarkably stable from the LGM onward (Appendix S2), lending additional support to the ocean-buffering hypothesis. Distributions of mid-latitude species (c. 40–20°N), if flanked by considerable bodies of water, might therefore be somewhat resistant to the often severe range shifts and contractions associated with glacial cycles.

The discrepancy between relatively stable distributions of scorpions in the BCP compared with arid-adapted taxa in western North America might also be explained by the more southern latitude of the BCP. The impacts of Pleistocene climatic fluctuations on species distributions are generally thought to be stronger as the distance from the equator increases (Hewitt, 2004). SDMs for species in the south-western USA and mainland Mexico at approximately the same latitudes as the BCP often fail to predict dramatic distributional shifts since the Late Pleistocene (e.g. Peterson, Martinez-Meyer & González-Salazar, 2004; McGuire et al., 2007; Oláh-Hemmings et al., 2010), or at least do not show the significant loss of habitat in the north and massive shifts of suitable habitat to the south as observed in arid-adapted taxa at more northern latitudes (e.g. T. Jezkova, unpubl. data; Waltari et al., 2007; Jezkova et al., 2009; Wilson & Pitts, 2012; Graham et al., 2013a). These former studies provide support for a latitudinal distance-from-the-equator explanation for distributional stasis in scorpions in the BCP as an alternative to an ocean-buffering hypothesis. In fact, the combination of both factors may explain our observed pattern of stable habitat for scorpion species in the BCP since the Late Pleistocene. However, the ocean-buffering and distance-from-equator hypotheses are both in conflict with fossil data from early Holocene packrat middens, which suggest that vegetation assembles on the BCP have in fact not been resilient to range shifts (Rhode, 2002).

**SCORPION SDMs AND BIOGEOGRAPHICAL HISTORY IN THE BCP**

Emerging genetic information from species along the BCP indicate that the biogeographical history of the region is complex (Riddle & Hafner, 2006). Numerous trans-peninsular genetic discontinuities have been explained by phenomena such as ephemeral trans-peninsular seaways (Minch & Leslie, 1991; Upton & Murphy, 1997; Riddle et al., 2000a, b; Murphy & Aguirre-Léon, 2002; Mulcahy & Macey, 2009), abrupt ecological and climatic changes (Grismer, 2002), and unusual dispersal events (Wood, Fisher & Reeder, 2008). Our scorpion SDMs add another piece to the puzzling biotic history of the BCP.

Perhaps the most interesting of the genetic divergences across the BCP, especially in light of our scorpion SDMs, are three trans-peninsular breaks outlined and described by Lindell et al. (2005): the mid-peninsular break, the Loreto break and the Isthmus of La Paz break (Fig. 1). Divergences in these areas have been substantially debated, with the mid-peninsular break being the most provocative, and differing degrees of genetic divergence in these areas.
have complicated molecular dating estimates (Leaché, Crews & Hickerson, 2007). Most authors, however, posit multiple or reoccurring seaways to explain the variety of genetic divergences in these regions and the corresponding array of estimated divergence dates (Lindell et al., 2005; Crews & Hedin, 2006; Leaché et al., 2007; Hafner & Riddle, 2011). Although speculated early in discussions of biotic diversification in the region (Grismer, 2002), relatively little consideration has been given to the hypothesis that vicariance of terrestrial lineages could be due to climatic constraints, either alone or synergistically with seaways.

Twelve of our 13 scorpion SDMs show sharp transitions in habitat suitability almost precisely across the three trans-peninsular breaks, providing some of the first evidence that long-term climatic stability may have produced patterns of divergence between species. On the Isthmus of La Paz, for example, scorpion SDMs reveal two potential sister species relationships, perhaps associated with the Isthmus of La Paz break: *Kochius punctipalpi* and *Hadrurus hirsutus* in the Cape Region (Appendix S5), and *Kochius bruneus* and *Hadrurus concolorous* (Appendix S3) found north of the Cape. The SDMs of each of these species display a sharp decrease in climatic suitability in the area of the La Paz break. Similar trends are apparent in SDMs of other scorpion species in the vicinity of the mid-peninsular and Loreto breaks (Appendices S6–S8). If patterns of climatic and habitat stability across this admittedly relatively short time slice from the LGM to present were expanded to a considerably deeper timeframe, then we find it conceivable that genetic discontinuities could have arisen in association with localized adaptation to differential climate regimes. Such a pattern, however, would be contradictory to the conclusions of Lindell, Ngo & Murphy (2006), who stated that climate-induced habitat fragmentation could not adequately explain mid-peninsular genetic breaks.

Although our SDMs suggest that vicariance across the BCP could be due to climatic constraints, it seems difficult to reconcile accumulation of congruent genetic breaks across multiple taxa (including marine fishes, Riginos, 2005) with a variety of ecological traits and presumably niche requirements without still invoking additional concerted events such as the previously mentioned trans-peninsular seaways. Nonetheless, hypotheses like that of the Vizcaino Seaway, for which little geological evidence exists (Lindell et al., 2006; but see Helenes & Carreño, 1999; Carreño & Helenes, 2002; and Ledesma-Vázquez, 2002), might be due for reappraisal, and the possibility that climate was largely responsible for the complex phylogeographical patterns along the BCP should be given more consideration.

ACKNOWLEDGEMENTS

We thank S. C. Williams, V. F. Lee and C. E. Griswold for granting loans from the California Academy of Sciences. We are grateful to J. R. Jaeger for providing assistance with collecting and transporting specimens; T. Jezkova for support with distribution modelling; L. Hancock for georeferencing assistance; M. A. Wall for kindly allowing access to the scorpions at the San Diego Natural History Museum; M. E. Soleglad for scorpion occurrence records; and E. E. Saupe, M. E. Eckstut and T. Jezkova for helpful reviews of earlier versions of the manuscript. We thank three anonymous reviewers for their important comments.

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Appendix S1. Coordinates (in decimal degrees) used to generate species distribution models.

Appendix S2. Maxent models created using data from the Model for Interdisciplinary Research on Climate (MIROC).

Appendix S3. Species distribution models created with Maxent for three scorpion species distributed in southern California, USA, and northern Baja California, Mexico: (A, B) Anuroctonus pococki, (C, D) Hoffmannius puritanus and (E, F) Kochius hirsuticauda. Maps A, C and E are present predictions, with black dots indicating occurrences used in the modelling; maps B, D and F are Maxent predictions at the LGM. White stars indicate model area centroids and shading represents probability of occurrence, with darkest shading being most suitable and lightest shading representing unsuitable habitat (see Methods for modelling details).

Appendix S4. Species distribution models created with Maxent for three scorpion species distributed along the central portion of the BCP, Mexico: (A, B) Hadrurus concolorous, (C, D) Hadrurus pinteri, (E, F) Kochius bruneus. Maps A, C and E are present predictions, with black dots indicating occurrences used in the modelling; maps B, D and F are Maxent predictions at the LGM. White stars indicate model area centroids and shading represents probability of occurrence, with darkest shading being most suitable and lightest shading representing unsuitable habitat (see Methods for modelling details).

Appendix S5. Species distribution models created with Maxent for scorpion species distributed along the southern portion of Baja California, Mexico: (A, B) Bioculus comonadae, (C, D) Hoffmannius diazi, (E, F) Hoffmannius vittatus, (G, H) Nullibrotheas allenii. Maps A, C, E and G are present predictions, with black dots indicating occurrences used in the modelling; maps B, D, F and H are Maxent predictions at the LGM. White stars indicate model area centroids and shading represents probability of occurrence, with darkest shading being most suitable and lightest shading representing unsuitable habitat (see Methods for modelling details).

Appendix S6. Species distribution models created with Maxent for three scorpion species endemic to the Baja California Cape Region, Mexico: (A, B) Bioculus caboensis, (C, D) Hadrurus hirsutus, (E, F) Kochius punctipalpi. Maps A, C and E are present predictions, with black dots indicating occurrences used in the modelling; maps B, D and F are Maxent predictions at the LGM. White stars indicate model area centroids and shading represents probability of occurrence, with darkest shading being most suitable and lightest shading representing unsuitable habitat (see Methods for modelling details).

Appendix S7. Correlation between latitude (x axis) and habitat suitability (y axis) for three scorpion species occurring in northern Baja California. Grey diamonds represent individual grid cells from Maxent species distribution models, and the black line is a moving average trendline based on the average of every 200 grid cells.

Appendix S8. Correlation between latitude (x axis) and habitat suitability (y axis) for three scorpion species occurring in middle of the BCP. Grey diamonds represent individual grid cells from Maxent species distribution models, and the black line is a moving average trendline based on the average of every 200 grid cells.

Appendix S9. Correlation between latitude (x axis) and habitat suitability (y axis) for three scorpion species occurring in southern Baja California. Grey diamonds represent individual grid cells from Maxent species distribution models, and the black line is a moving average trendline based on the average of every 200 grid cells.

Appendix S10. Correlation between latitude (x axis) and habitat suitability (y axis) for three scorpion species endemic to the Baja California Cape Region. Grey diamonds represent individual grid cells from Maxent species distribution models, and the black line is a moving average trendline based on the average of every 200 grid cells.

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