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What bit the Ancient Egyptians? Niche modelling to identify the snakes described in the Brooklyn medical papyrus

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What bit the Ancient Egyptians? Niche modelling to identify the snakes described in the Brooklyn medical papyrus

Abstract

The Brooklyn Papyrus is a medical treatise from Ancient Egypt (~660-330 BCE) focusing on snakebite. Herpetologists have proposed identifications for many of the animals it describes, but some remain uncertain partly because the species no longer live in Egypt. This paper uses niche modelling to predict the palaeodistributions of ten of these snake species, to test some proposed identifications. Occurrence records and environmental variables were used to generate maximum entropy models for each species in the present day and the mid-Holocene (~4,000 BCE). Our models performed very well, generating AUC scores ≥0.867 and successfully predicting species' current ranges. Nine species' predicted palaeodistributions included areas within Ancient Egypt, and four (*Bitis arietans*, *Dolichophis jugularis*, *Macrovipera lebetina* and *Daboia mauritanica*) were within modern Egypt. *Daboia palaestinae* was also predicted to occupy a patch of suitable habitat inside modern Egypt, but separate from the species' core range. The tenth species, *Causus rhombeatus*, would have been present in kingdoms that were the Ancient Egyptians' regular trading partners. We therefore conclude that all ten species modelled in this study could have bitten Ancient Egyptian people. Our study demonstrates the usefulness of niche modelling in informing debates about the species ancient cultures may have interacted with.

Keywords

Ancient Egypt; snakes; Brooklyn Papyrus; MaxENT; niche modelling; palaeodistributions

Word count: 5,992

Introduction

The Brooklyn Papyrus is thought to be the handbook of the Priests of Serquet who treated snakebite victims in Ancient Egypt (Golding, 2020). It dates to ~660-330 BCE (Aufrère, 2012; Golding, 2020), but is thought to be a copy of an older original (Golding, 2020), and was donated to the Brooklyn Museum in the mid-1900s by the family of the American journalist and Egyptologist Charles Edwin Wilbour (Brooklyn Museum, 2021). In 38 registries, the Brooklyn Papyrus describes 37 snakes, though the first 13 descriptions have been lost, and one chameleon. It details the effects of bites from each of the described snakes, recommends treatments and assesses chances of survival (Sauneron, 1966).

The first translation of the Brooklyn Papyrus was completed by French Egyptologist Serge Sauneron in 1966-1970 and posthumously published by the French Institute of Oriental Archaeology in Cairo (Sauneron, 1989). Sauneron's intensive study of the papyrus included description and interpretation, as well as efforts to piece fragments back together and make damaged sections legible (Sauneron, 1968). Once as much of the papyrus as possible had been reassembled, Sauneron also attempted to identify the snakes it described. He proposed 'probable' or 'possible' species identifications for just over half of descriptions, and got a further 20% as far as family level (Sauneron, 1989).

Sauneron was not the only scientist interested in the Brooklyn Papyrus snakes. Since the mid-1990s, Nunn (1996, writing in collaboration with D.A. Warrell), Leitz (1997), Brix (2011) and Aufrère (2012) have all revisited the descriptions and offered interpretations. Finally, Golding (2020) offered identifications for all the snakes based on another new exploration. These five authors' works identify different proportions of the snakes listed in the Papyrus and their identifications overlap but often disagree (see Table 1).

The visible disagreements over the identity of the described snakes probably have several causes. In some cases, the ancient descriptions may be too vague. Similarly, there may not be a one-to-one match between a 'type' of snake recognised by the Brooklyn Papyrus and modern species (which some authors have suggested might imply that some described snakes are actually male and female, adult and juvenile, or colour morphs of what we would recognise as a single species today). Further differences may result from the fact that modern authors have used different methodologies and evidence-bases (Andreozzi, 2020; Golding, 2020) and taxonomies have changed (e.g. Wüster and Broadley, 2003; Carranza et al., 2006). They might even reflect changing views of the likelihood of encountering specific contending species in Ancient Egypt. The number of snakes listed in the Brooklyn Papyrus as possessing dangerous bites significantly exceeds the number of venomous snakes in present-day Egypt. Modern Egypt has eight front-fanged species (five vipers and three elapids; Uetz et al., 2021) that are capable of significant envenoming, and a small number of opisthoglyphous species, such as *Malpolon* spp., *Psammophis* spp. And *Hemorrhois* spp., that occasionally cause minor envenoming (Weinstein et al., 2011). This mismatch suggests that the Brooklyn Papyrus descriptions are not all of species we would expect to see in modern Egypt or its environs. Some encounters with non-Egyptian species may have occurred within Ancient Egypt, which had wider borders (Figure 1), but, as already noted by Sauneron (1989, p. 149), there is also the intriguing possibility that some species have undergone considerable distributional changes. Perhaps some species not presently found within even the ancient borders of Egypt might have occurred there in the early to mid-Holocene and persisted into historical times, before going locally extinct as a result of climate change, anthropogenic habitat change, or both.

Climate shifts in Holocene Egypt

The landscape of Egypt has changed drastically in the Holocene. In the early Holocene at ~8,500 BCE, monsoon rains transformed the previously dry Egyptian Sahara into a grassland and the Nile Valley into a damp wetland with ample precipitation (Butzer, 1976; Kuper and Kröpelin, 2006; Hamdan et al., 2020a-b; Zaky, et al., 2020). Pollen samples suggest extensive open vegetation, together with helophyte and herbaceous plants typical of a moister environment than we see today (Zaky et al., 2020), and faunal remains corroborate this interpretation. Early Holocene Egypt had ostriches, elephants and giraffes (Gautier, 1993), and recent discoveries of amphibians and softshell turtles (*Cyclanorbis senegalensis*) all point to a mixed savannah-wetland habitat (Baha El Din, 2006).

In the mid-Holocene (about 5,300 BCE), this moist environment began to disappear as the rains shifted south, leaving just a few ecological oases for wetland species (Butzer, 1995; Kuper and Kröpelin, 2006). Forest and woodland habitats came to occupy most of Ethiopia and the parallel coasts of the Red Sea (see Figure 2), while grasslands became ubiquitous across the Sudan and Arabia (Golding, 2020). The vast desert we know from modern times, however, would have been restricted to inland Egypt (ibid.). As this drying of north-eastern Africa continued, the moist climatic and vegetational zones retreated further and further south, taking with them the Afro-tropical species previously found in Egypt. The effects of these significant climatic changes and particularly the mid-Holocene aridification are likely to have been particularly significant for ectotherms like snakes (Brito et al., 2011; Barlow et al., 2013; Martínez-Freiría, et al., 2015, 2017). These range shifts, coupled with the possibility of relictual populations in mesic enclaves, might explain why the authors of the Brooklyn Papyrus recorded a herpetofauna in Ancient Egypt that may have differed significantly from that seen in the present.

In this paper, we will use species distribution modelling to explore the possibility that a number of snake species not currently found within the boundaries of either present-day or Ancient Egypt might have occurred there in historical times and have formed the basis for some of the snake descriptions in the Brooklyn Papyrus. We will also investigate the possibility that environmental change has reshaped the Egyptian herpetofauna since the mid-Holocene, such that few if any of the species encountered by ancient Egyptians during the time of the Brooklyn Papyrus would be known to those living there today. We anticipate that many of the snakes described in the Brooklyn Papyrus are hard to identify because they now live only in the Levant, the Maghreb and/or the Afro-tropical zone, and may not have been considered by previous authors interpreting the papyrus.

Materials and Methods

Species Distribution Models (SDMs) are built using occurrence data and maps of environmental variables (Elith and Leathwick, 2009). They have been used with success in multiple recent studies on African and Levantine snakes (e.g. Kalboussi and Achour, 2018; Zacarias and Loyola, 2019; Yousefi, et al., 2020), though the species chosen represent only a fraction of their living diversity. SDMs can provide useful information about the ecological tolerances and preferences of a species, and can be used to project potential distributions of suitable habitat at specified points in the past or future. Maximum entropy modelling, the most common form, can also cope with small samples of presence-only data, and can be run using open-access software and datasets (Phillips and Dudik, 2008). Here we used maximum entropy methods via MaxEnt 3.4.4 (Phillips et al., 2004).

Study area and species

The Ancient Egyptian empire lasted for nearly 3,000 years, roughly 3,000-332 BCE (Van De Mieroop, 2021). Its borders were in flux throughout (Smith, 1961; Shaw, 2000). Although the Brooklyn Papyrus itself dates to the Late Period of Ancient Egypt, around 660-330 BCE (Aufrère, 2012; Golding, 2020), it is believed to be a copy of an older document of uncertain date. The Brooklyn Papyrus may bear some resemblance to the older Edwin Smith Papyrus, which may date to 1550-1600 BCE (Golding, 2020), but even acknowledging this similarity does not help us pinpoint the precise time of writing and thereby estimate where Egypt's borders then lay. Instead, we have used the borders as they were during the New Kingdom (~1,500-1,000 BCE; Shaw, 2000), which represent the widest extent of the territories held by Ancient Egypt (Figure 1).

To select species, we compiled the proposed identifications in Table 1 and picked out those that presently do not live within Egypt but could plausibly have lived in north-eastern Africa in the Holocene or late Pleistocene based on their ecological requirementsre. Our criteria of inclusion were: (i) past proposal as species mentioned in the papyrus by other authors (Table 1); (ii) ecological plausibility, i.e., species occurring in open savanna or scrub formations rather than forest species; (iii) biogeographic plausibility, excluding previously suggested species restricted to southern Africa; (iv) easy identifiability by a competent naturalist, excluding species complexes of difficult-to-distinguish species; and (v) species not previously proposed, but that satisfy criteria (ii) – (iv) by occupying open formations in northeastern Africa within reasonable proximity of the Ancient Egyptian kingdoms. Initial distribution information to guide the choice of focal species was sourced from Geniez (2018), Sindaco et al. (2013), Spawls et al. (2023), Spawls & Branch (2020) and Trape (2023). See Supplemental Information 1 & 2 for a listing and detailed discussion of all included species. From the resulting list we selected ten focal species, including taxa from several different biogeographic regions. Our study therefore includes several Afro-tropical species (*Naja nigricollis*, *Dendroaspis polylepis*, *Bitis arietans*, *Causus resimus*, *Causus rhombeatus* and *Dispholidus typus*) that could have followed a northward expansion of savannah into Ancient Egypt during the Pleistocene/early Holocene, and some from the Maghreb and/or Levant which could conceivably have expanded their ranges east or south, most likely along the Mediterranean coast, into the focal area during times of more mesic climates. The Levantine species selected were *Daboia palaestinae*, *Macrovipera lebetina* and *Dolichophis jugularis*, while *Daboia mauritanica* is Maghrebi.

Data collection

Occurrence data for each species was compiled from online databases (GBIF, 2020; iNaturalist, 2020; VertNet, 2020) and the published literature (see Supplemental Information 1). We included names of recently subsumed taxa where relevant. These datasets were checked against species' known distributions in Google Earth Pro (2020) using maps from

Spawls and Branch (2020) for African species and the IUCN (2020) Red List for Levantine ones. Points outside a species' known range were removed. For *Macrovipera lebetina* we included occurrences for the subspecies *M. lebetina transmediterranea*, whose status is debated (Spawls and Branch, 2020), because preliminary test models including and excluding this subspecies produced nearly identical outcomes.

High-resolution (30 arc-second) maps of nineteen bioclimate variables were downloaded from the WorldClim database (Fick and Hijmans, 2017) for the present day and the mid-Holocene (~4,000 BCE). The mid-Holocene datasets came from three different General Circulation Models (GCMs), namely the CCSM4, MIROC-ESM and MPI-ESM-P models. Three GCMs were used to ensure we could explore a range of projected palaeodistributions for each species, as different models' bioclimate maps do vary.

In addition to climate, we considered it important to explore the impact of ecoregions in the SDMs for these snakes, as the distribution of some snake species may be restricted by the availability of suitable vegetation cover as much as climate (Spawls and Branch, 2020), which could reduce the predictive power of climate-only models. This is especially important as ecoregion maps are not available for the mid-Holocene, so including vegetation in our predictive models would involve assuming present-day ecoregions were similar enough to warrant inclusion (which we considered dubious). We therefore tested the impact (if any) of excluding ecoregions from our predictive models of current distributions by generating and comparing models including and excluding this variable, before proceeding to create and interpret models of ancient distributions based solely on bioclimate variables. For this, we downloaded the WWF's Terrestrial Ecoregions of the World dataset (Olson et al., 2001).

Data processing

Occurrence datasets were spatially rarefied in ArcGIS 10.7.1 (ESRI, 2020) using the SDM Toolbox 2.0 (Brown et al., 2017) and a minimum distance of 1km. This reduced clustering and ensured we did not violate MaxEnt's assumption of roughly random sampling across the species' range (Phillips et al., 2004, 2009; Anderson and Gonzalez Jr., 2011; Boria et al., 2014). The minimum distance for rarefication is usually derived from the target species' home range size, but the elusive and under-represented nature of snakes (Todd and Nowakowski, 2020) made this impractical. We noticed afterwards that our African species' occurrence datasets remained biased towards South Africa, presumably as a result of encounter and/or recording bias. To rectify this, we extracted the South African points and re-rarefied them using a minimum distance of 10km. Our final sample sizes ranged from 68 (*Daboia mauritanica*) to 1277 (*Bitis arietans*; see Supplemental Information 1).

Environmental variables were also processed in ArcGIS 10.7.1 (ESRI, 2020). We identified a 'study region' that included the full current ranges of each species plus a 'buffer' (Boria et al., 2014) chosen so we could project suitable habitat expansion and contraction in the region of interest. This buffer zone could have been defined as simply an additional five or ten degrees of space in each direction (north, south, east and west), but in this instance it was simpler to define it geographically. We therefore chose to include the Afro-tropical, Maghrebi and Levantine regions alongside Ancient Egypt, and modelled each species' suitable habitat in a region that included all of Africa as well as the Levant as far north as southern Europe and as far West as at least the western edge of the Arabian peninsula.

Maps were cut to size using the 'Clip' tool. SDMs that use spatially autocorrelated environmental layers risk bias and lowered accuracy (Hill and Winder, 2019), so we used the SDM Toolbox 2.0 to identify highly correlated pairs or sets of bioclimate variables with correlation coefficients >0.8, and selected an independent subset to retain. While we initially hoped to include overarching variables like mean annual temperature and rainfall within this subset, these each turned out to be highly correlated with multiple other more specific variables that were independent of each other. We therefore removed these summary variables in order to retain more of the others which were more likely to act as limiters on snake species' distributions (for instance, we retained temperature and rainfall extremes, and multiple measures of seasonal or daily variability). We also removed variables containing derivative data instead of those they were derived from, for instance removing isothermality in order to retain mean diurnal temperature range, so as to try to keep those variables that seemed most likely to be ecologically significant to our target taxa.

The final models included eleven bioclimate variables, six relating to temperature (mean diurnal range, maximum temperature of the warmest month, minimum temperature of the coldest month, temperature annual range, mean temperature of the wettest quarter and mean temperature of the driest quarter) and five to rainfall (precipitation of the wettest month, precipitation of the driest month, precipitation seasonality, precipitation of the warmest quarter and precipitation of the coldest quarter).

Species distribution modelling

MaxEnt 3.4.4 (Philips et al., 2004) was first used to build present-day SDMs and check the significance (if any) of vegetation to our target species' ecology. We used fourfold cross-validation with 1,500 maximum iterations to ensure all data was used to its fullest extent, and allowed MaxEnt to use random background points from across the study area (Africa and the Levant) for all species to optimise the use of our presence-only occurrence data (Elith et al., 2011). We assessed model performance using the Area Under the Receiver Operating Curve (AUC) score, with values >0.8 considered good, >0.9 excellent and >0.99 potentially indicating overfitting (Fielding and Bell, 1997). Present-day models' accuracy was also confirmed by visual checks and superimposition of the species' known ranges in ArcGIS.

Two initial models were run first, one using bioclimate and ecoregions and the other just bioclimate variables. *Causus resimus* was the only species where the model including ecoregions was better able to predict the species' known distribution than the climate-only model. For *Daboia mauritanica* and *Daboia palaestinae*, ecoregions made a large percentage contribution (52.5% and 28.8% respectively) but the climate-only model still outperformed the ecoregion-and-climate version in predictive accuracy. Having thereby established that climate-only models were the better predictors of present-day distributions for nine of ten of our species, we are confident that climate-only models are also able to accurately predict mid-Holocene distributions in the absence of available ecoregion models (see above).

Predictive models were run using current occurrences and bioclimate variables as training data and palaeoclimate maps as projection layers. Model outputs were imported back into ArcGIS for exploration. We chose not to select an arbitrary suitability threshold by which to distinguish putatively suitable and unsuitable habitats and generate a range area (after Pearson et al., 2004, 2007), and instead treated all areas as scoring above 0 in our model as suitable for the target species. Our reasoning for this is that most of our species are undersampled, which implies that cutting out areas that are predicted to be suitable but marginal, for instance, would further reduce an already restricted dataset. In addition, as we had already subjected all our datasets to rigorous quality control, we had no reason to believe these areas were not suitable enough to be occupied, albeit perhaps at low densities. Maps of the net change in habitat suitability between the mid-Holocene and the present were then created using the 'Raster Calculator' tool and the MaxEnt output maps of habitat suitability in the present day and as an average of the three mid-Holocene projections.

Results

Our SDMs showed good to excellent performance with AUC scores ≥0.867 for all species. One model, for *Daboia palaestinae*, had an AUC score of 0.992, which might indicate some overfitting, but as it is built with the best data currently available we report the results anyway. All ten species' present-day models relied upon a mix of temperature and precipitation variables (see Supplemental Information 3), suggesting that their distributions would have been responsive to climatic changes in early-mid Holocene Egypt. The present-day models also accurately predicted the known distributions of all species except *Causus resimus* (see Supplemental Information 4). For *C. resimus*, our model predicted a substantial, unbroken area of high habitat suitability stretching across all sub-Saharan Africa as far south as Northern Namibia, which is much larger than the species' actual (known) distribution. The documented range of *C. resimus* is instead split into three and restricted to central Africa, with one population found on the coasts of Kenya and Somalia, a second in western Angola and southern Congo, and the third and largest across a strip extending from Nigeria to Ethiopia and down into Uganda, Tanzania and the DRC around Lake Victoria (Luiselli et al., 2021). Our model thus substantially overpredicted the known range of *C. resimus*.

Nine of our ten species were predicted areas of suitable habitat within the boundaries of the Ancient Egyptian empire during the mid-Holocene (Figures 3-4), and five (*Bitis arietans*, *Daboia mauritanica*, *Daboia palaestinae*, *Dolichophis jugularis* and *Macrovipera lebetina*) within modern Egypt. For the purposes of the summaries that follow, and as shown in Figure 2 (above), Ancient Egypt includes all of modern Egypt, the eastern edge of Libya, roughly the northern half of what is now Sudan, the Sinai Peninsula, the whole of Israel, Palestine and Lebanon, the north-west corner of Saudi Arabia, the western edges of Jordan and Syria and a small part of southern Turkey, where it meets the Syrian border.

Afro-tropical species

For *Bitis arietans* our models predicted a wide and continuous band of suitable habitat in ancient Egypt (Figure 3a). It would have been able to occupy what is now the southeastern corner of Egypt and northeast Sudan, with this area forming the northernmost portion of the species' mid-Holocene potential range. This block of suitable habitat is, moreover, continuous with others to the south and scores quite highly on suitability according to our model, suggesting that *B. arietans* would have been an important entry in the Brooklyn Papyrus. Today, *B. arietans* is the most common highly venomous snake in sub-Saharan

Africa, and our models suggest that its palaeodistribution would have extended further north than its current range (Figure 5a), placing ancient Egyptians at risk from its bite.

Habitat suitabilities for *Causus resimus* in ancient Egypt were not as high as for *B. arietans* (Figure 3b), but the species might have been present in what is now northern Sudan. This area is continuous with suitable habitats further south in Eritrea and Somalia, though not with the most suitable habitats in the mid-Holocene, which are in a separate block to the west. In fact, as Figure 5b shows, it is only in the very eastern coastal parts of ancient Egypt that habitat suitabilities were higher in the mid-Holocene than in the present. It is harder to say, therefore, that *C. resimus* would definitely have been featured in the Brooklyn Papyrus, but it could have been of interest to the compilers.

For *Causus rhombeatus*, suitable habitat in the mid-Holocene seems to have been limited to northern Eritrea just south of the Ancient Egyptian empire (Figure 3c). This species is therefore perhaps less likely to feature in the Brooklyn Papyrus. Like *C. resimus*, however, its bite is painful enough to be of potential medical relevance, and while the northernmost extent of *C. rhombeatus*' range looks to have been further south in the mid-Holocene than today (Figure 5c), it would still have occupied areas traversed by ancient Egyptian travellers.

The *Dendroaspis polylepis* model (Figure 3d) predicted a substantial block of suitable habitat north of the species' current range in the mid-Holocene (compare Figure 5d). This formed a band of suitable habitat which extended from Chad through central Sudan to the coast, and northwards into the southeasternmost corner of Ancient Egypt in the mid-Holocene. The northernmost parts were, moreover, quite highly suitable and connected to highly suitable habitats further south in Ethiopia, which makes it quite likely that this species was present at the time. This species is, moreover, a large and highly venomous species that would draw the attention of local people and medical professionals alike.

Our SDM for *Dispholidus typus* also suggested that the south-easternmost corner of ancient Egypt would have been suitable for this species, though more marginal than the region further south which is the species' current core habitat (Figure 3e and 5e). These areas might not have been consistently connected to areas further south in the mid-Holocene, however, which might make for a lower density occupation of this range. That said, *D. typus* is another large and highly venomous snake, easily able to kill a human. Being able to recognise it and treat its bite would have been a high priority.

Predictions of suitable habitat for *Naja nigricollis* (Figure 3f), the last of our chosen Afro-tropical taxa, extend considerably further north in the mid-Holocene than in the present day (see also Figure 5f). This band of habitat is moderately to highly suitable and continuous, implying that this species would very likely have occupied it. Once again, *Naja nigricollis* being present in ancient Egypt may have had significant impacts on the local population as its venom can be painful or even lethal. *N. nigricollis* is also capable of spitting its venom, which might have helped distinguish the effects of its venom from those of other snakes and made it more distinctive to those writing the Brooklyn Papyrus descriptions. This short summary thus suggests that all six of our chosen Afro-tropical snake species could have been encountered by the ancient Egyptians, with *Bitis arietans*, *Dendroaspis polylepis* and *Naja nigricollis* likely to have been more prominent in the local herpetofauna than the others. They are all, however, potentially of medical interest.

Levantine species

Daboia palaestinae is currently found in the Levant, but during the mid-Holocene would also have occurred in the northern part of ancient Egypt including the Sinai Peninsula (Figure 4a). This zone of suitable habitat extended from northeastern Libya in the west all across modern Egypt, but the suitability scores are low in the middle and higher at either end. The high suitability habitat within modern Egypt thus might have been occupied, but the snake would have had to cross lower suitability areas to do so. Ancient Egyptians would, however, still probably have encountered this species in northeastern Libya and/or the Sinai.

For *Dolichopis jugularis* there would have been suitable habitats available in the Sinai peninsula, northern Egypt (including the Nile delta) and the northern parts of Saudi Arabia during mid-Holocene (Figure 4b and 6b), though some of these patches may have been separated from the species' more northerly core range by less suitable conditions in the Levant. There is, however, a continuous zone across the northern coast of the Sinai Peninsula that would likely have brought this species into ancient Egypt. This discontinuous distribution of suitable habitat, coupled with the fact that *D. jugularis* is functionally non-venomous, might make it seem a less likely candidate for inclusion in the Brooklyn Papyrus. It is, however, a large snake which displays distinctive defensive behaviour which might make a bite a memorable and traumatic experience even if it were unlikely to be a fatal one.

Macrovipera lebetina, like *Daboia palaestinae*, was predicted a substantial, continuous zone of highly suitable habitat extending along the north coast of Egypt and into

Libya (Figure 4c). This coastline was much more suitable in the mid-Holocene than it is today (Figure 6c), which would explain the species' absence from modern Egypt. All three of our Levantine species, therefore, seem strong candidates for inclusion in the Brooklyn Papyrus descriptions of ancient Egyptian herpetofauna, with *M. lebetina* and *Daboia palaestinae* potentially encountered more often than *Dolichophis jugularis*, but the latter also displaying distinctive defensive behaviours that would make it very visible to locals.

Maghrebi species

Our final study species was *Daboia mauritanica*, currently found in the Maghreb. *D. mauritanica* was predicted to have some suitable habitat within ancient Egypt, this time along the western part of the northern coastline, from Libya into the middle of modern Egypt (Figure 4d). The eastern part of this range is in fact also suitable today (compare Figure 6d), but is not thought to be occupied, perhaps because the intervening stretch was much more suitable in the mid-Holocene than today. Overall, habitat suitability scores for *D. mauritanica* in the mid-Holocene are lower than for the Levantine taxa, and this zone of suitable habitat may have been separated from the rest of the species' range even then. The fact that it too could have been encountered by the ancient Egyptians does, however, suggest that species currently confined to either the Levant or the Maghreb may once have encountered one another.

Discussion

Ecology, environmental change and range shifts in Ancient Egyptian snakes

Nine of the ten species we selected were predicted to have lived in Ancient Egypt, even though today they are either Afro-tropical, Levantine or Maghrebi. Five (*Bitis arietans, Daboia mauritanica, Dolichophis jugularis, Macrovipera lebetina* and *Daboia palaestinae*) may have lived within modern Egypt in the mid-Holocene, though *D. palaestinae* would have had to cross low-suitability intervening regions to get there. The three Levantine species all seem quite likely to have occupied parts of the north coast of ancient Egypt, as the models predicted continuous zones of highly suitable habitat extending across the whole country. The Maghrebi species *Daboia mauritanica* is perhaps somewhat less likely to occupy the same coastline, but would have found suitable habitats there. Among the Afro-tropical species, *Bitis arietans, Dendroaspis polylepis* and *Naja nigricollis* seem somewhat more likely to occur in the southeastern corner of ancient Egypt than *Causus resimus* and *Dispholidus typus*, whose suitable habitats are either less continuous or lower-scoring.

Of these five species, *Bitis arietans* is the only one currently living in the Afro-tropical zone. Our finding for *B. arietans* corroborates Biton and Bailon (2021)'s suggestion based on Late Pleistocene *Bitis* remains in Israel that Afro-tropical snakes could have experienced repeated substantial range shifts in the Pleistocene-Holocene period. The modelling of other Afro-tropical taxa also showed northwards range shifts in the mid-Holocene, but with two different patterns. *Causus rhombeatus*, *Dendroaspis polylepis* and *Dispholidus typus* (Figures 3c-e) are predicted to have expanded north along the eastern and Red Sea coasts, like *Bitis arietans* (Figure 3a), but less far. The latter two would have reached southern Ancient Egypt but not the modern border, while *Causus rhombeatus* reached southern Sudan. *Naja nigricollis* and *Causus resimus*, however, were predicted to have undergone inland northerly range expansions in our mid-Holocene models (Figures 3f and 3b). They would have been found in parts of Ancient Egypt that are now northern and northwestern Sudan.

All three Levantine species were predicted to have mid-Holocene ranges that included parts of modern Egypt's Mediterranean coast (Figure 4a-c). *Macrovipera lebetina* may have occupied the whole Mediterranean coastline, while *Dolichophis jugularis* and *Daboia palaestinae* would have found only the eastern sections habitable. Both these species' hold on this coast would have been more tenuous than *Macrovipera lebetina*'s, with *D. palaestinae* having to cross a significant area of less suitable habitat in the Sinai peninsula. For *Dolichophis jugularis*, suitable areas of the eastern Mediterranean coasts were continuous with other good habitats, but their overall suitability scores were relatively low. Our results for preliminary models with and without the subspecies *Macrovipera lebetina transmediterranea*, moreover, found no differences in predictive power. Given that we then projected suitable conditions for this species in Ancient Egpyt, our findings fit with Jiménez Robles & del Mármol Marín (2012)'s suggestion that this subspecies has only recently become separated from the main population.

Finally, *Daboia mauritanica*, the only Maghrebi species we included, was also predicted to range along Egypt's Mediterranean coast in the mid-Holocene (Figure 4d), though this time starting from the west and extending approximately as far as the modern city Mersa Matruh. Our mid-Holocene models for *D. mauritanica* match those of Martínez-Freiría, et al. (2017) fairly well where our study areas overlapped, but ours predicted less suitable habitat in Tunisia and inland Morocco, and more along the northern Libyan and Egyptian coasts. We note that Martínez-Freiría, et al. (2017) used a more complex set of environmental variables and a different modelling method to us, as well as a study area that did not extend as far east.

Only *Causus rhombeatus*, our last Afro-tropical species, was not predicted to range into Ancient Egypt in the mid-Holocene (Figure 3c). To assume that a species must occur within a country's boundaries to encounter that country's citizens, however, would be an oversight. Ancient Egyptians would have travelled regularly for trade, to gather resources and to make war. Trade routes between Egypt and Syria-Palestine, Arabia, Assyria, Nubia, Libya, Sheba (modern Yemen) and Punt are all well-documented (Redford, 1997; Shaw, 2000). The precise location of Punt is uncertain, but it was probably somewhere in modern Eritrea, Ethiopia and/or Somalia (Shaw, 2000), well within the predicted mid-Holocene ranges of all our Afro-tropical species including *Causus rhombeatus*. Evidence suggests that trade expeditions went by both land and sea, and a round-trip from Memphis to Nubia would take ~7 months (Redford, 1997), plenty of time for merchants and envoys to grow familiar with dangerous snakes. Ancient Egyptian trade with the Kingdom of Sheba might also have meant further contact with *Bitis arietans* in the isolated, extralimital population that lived and lives in Yemen and coastal Saudi Arabia (Figure 3a).

Using SDMs to corroborate interpretations of ancient texts

To our knowledge, this study is the first of its kind and SDMs have not yet been trialled as a means of corroborating species identifications from an ancient text like the Brooklyn Papyrus. Our findings strongly support the idea that the snakes described in the Papyrus will not all be found among the modern Egyptian herpetofauna, but will include species that today we might class as Afro-tropical, Levantine or even Maghrebi. Our models themselves cannot resolve the extensive disagreements as to which specific description corresponds to which modern species. It is worth noting, however, that all six of the authors listed in Table 1 (Sauneron, 1989; Leitz, 1997; Brix, 2011; Aufrère, 2012; and Golding, 2020) proposed one or more of the non-native candidate species that we modelled.

Sauneron (1989) and Golding (2020), for instance, identified snake 25 as *Naja nigricollis*, though Brix (2011) thought this might have been snake 16 and Aufrère (2012) snake 17. Our models confirm that this species is likely to have lived in Ancient Egypt. Snake 30 was twice putatively identified as *Causus resimus* (Brix, 2011; Golding, 2020), while snake 27 was twice identified as *Bitis arietans* (Nunn, 1996; Golding, 2020), although snake 27 has also been matched twice to *Echis coloratus* and *Bitis arietans* might also be snake 33 (Brix, 2011). Both these species, however, were also probably native to the area at the time and have significant bites, so are plausible identifications. We also modelled species that had *not* previously been proposed as identifications for Brooklyn Papyrus snakes, including *Causus rhombeatus*, *Dispholidus typus*, *Daboia mauritanica* and *Dendroaspis polylepis*. The fact that our models suggest three of these taxa also lived in Ancient Egypt strongly implies that an evaluation of other non-native taxa might identify additional equally plausible contenders, especially if Maghrebi snakes are included alongside Levantine and Afro-tropical ones.

Limitations and future work

We were unable to test all proposed non-native identifications for Brooklyn Papyrus snakes, let alone all those one might propose taking our findings into account. Future work could usefully build on our findings to look further afield, perhaps systematically, to assist in the (re)interpretation of this text. It would also be useful to generate models for more time-points in the ~6,000 years since the mid-Holocene, to facilitate more nuanced reconstructions of how the snake community of this region may have changed through time. Although the continuous climatic data needed to build such models are not yet freely available online, filling in this temporal gap would facilitate a more nuanced understanding of ancient Egyptians' interactions with snakes and help zooarchaeologists understand the knock-on effects of ongoing anthropogenic and environmental changes on the regional herpetofauna. The question of whether regional extinctions of snakes since the mid-Holocene have formed an 'ecological cascade' or were each individually determined by changes in local conditions could alternatively be addressed by exploring in more detail the potential interactions between species identified using SDMs, but this would entail a different approach focused on characterising their respective niches rather than projecting them geographically.

Data limitations may also affect efforts to model other taxa listed in Table 1, or from the three large regions that might now house snakes relevant to egyptologists. Overall, however, the single most significant limitation of our work was that we only explored the climatic niches of our study species, excluding not just Olson et al. (2001)'s ecoregion map but also other potentially relevant variables like vegetation, altitude, groundwater tables and anthropogenic impacts, largely due to their non-availability for Holocene reconstruction. Only *Causus resimus*' SDM was noticeably affected by our excluding ecoregions data, but the resulting present-day distribution based solely on climate was considerably larger than that mapped by Spawls and Branch (2020), which suggests this taxon is distributed in five large populations and some smaller ones. The discrepancy between the predicted and realised niches of *C. resimus* may indicate a reliance on specific habitat structure(s) that we have not yet identified or that some ecoregions or other landscape features are acting as constraints on this species' dispersal, which SDMs do not specifically evaluate.

Most snakes are thought to be highly climate-dependent (Brito et al., 2011; Barlow et al., 2013; Martínez-Freiría, et al., 2015, 2017), but other factors are presumably also important. Our present-day models, for instance, suggested that our African and Levantine species are sensitive to water levels (see Supplemental Information 2). Three precipitation variables (precipitation of the warmest quarter, the wettest month and the coldest quarter) were each regularly among the top three contributing variables to our species' SDMs, with most species recording a high percentage contribution from at least two of these. Precipitation, of course, is not the only source of water in the Nile valley, which has formed a north-south riverine corridor since the Oligocene (Fielding et al., 2018), and species dependent on mesic habitats might have persisted on the floodplain longer than climate-only models suggest, perhaps aided or hampered by early irrigation systems and agricultural expansion (Butzer, 1976; Shaw, 2000), before eventually being driven to local extinction by millennia of agriculture, habitat changes and direct human persecution. Being able to incorporate accurate maps of floodplain extents, groundwater tables, human influences and habitat structures in the present-day and the mid-Holocene would no doubt significantly improvement model accuracy and power. We also note the extreme dearth of herpetological collections from the Sudanese portion of the Nile Valley between Wadi Halfa and Khartoum, and suggest that renewed survey efforts there could potentially reveal relict populations of Afrotropical species not currently known from the area.

Conclusion

This paper reports the first use of niche modelling to test proposed identifications for Brooklyn Papyrus snakes and explore how Holocene environmental changes have shaped northeastern Africa's snake diversity. Our results suggest that all ten of our selected species could have been encountered by patients of the Priests of Serquet (nine within Ancient Egypt and one in neighbouring kingdoms) and that the Ancient Egyptian herpetofauna could have included species that are now restricted to the Afro-tropics, the Levant or even the Maghreb. Although our models (like most SDMs) could be improved with more evenly distributed occurrence points and the addition of potentially pertinent environmental variables, they represent a solid foundation for future work on the Brooklyn Papyrus and broader questions of ancient archaeozoology, and illustrate the potential of the approach in informing the identification of animals mentioned in ancient texts.

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Declaration of Interest Statement

The authors have no competing interests to declare.

Supplemental Information and Data Availability

Numbered pieces of supplemental information are provided separately. An accompanying dataset for this paper on the OSF (Open Science Framework) website, which will be made publicly available when the paper is published. This view only link will work in the meantime: https://osf.io/desnm/?view_only=8dfc40ea41964829863745c55dbc2d0f

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Tables

Table 1: proposed identifications for the snakes described in the Brooklyn Papyrus according to six different authors' evaluations, with updated taxonomy. Registry numbers 1 -13 have been lost. Binomials in blue denote species that do not live within modern Egypt (IUCN, 2020; Spawls and Branch, 2020).

Registry number of snake	**Identity according to Sauneron (1989)**	**Identity according to Nunn (1996)**	**Identity according to Leitz (1997)**	**Identity according to Brix (2011)**	**Identity according to Aufrère (2012)**	**Identity according to Golding (2020)**
14	Possibly large elapid	*Naja pallida* (part) (now *N. nubiae*)	-	*Naja haje*	Viperidae	Probably *Naja nubiae*, perhaps *N. pallida*
15	Large elapid	Possibly *Coluber* (now *Platyceps*) *rhodorhachis*, *Malpolon moilensis*	*Naja haje*	*Naja pallida* (part) (now *N. nubiae*)	Elapidae	*Naja pallida*
16	*Walterinnesia aegyptia*	*Walterinnesia aegyptia*, *Atractaspis microlepidota* (now *A. engaddensis* or *A. phillipsi*)	*Walterinnesia aegyptia*	*Naja nigricollis*	*Walterinnesia aegyptia*	Most likely *Walterinnesia aegyptia*, possibly *Atractaspis microlepidota* (now *A. engaddensis* or *A. phillipsi*)
17	Possibly "*Zamenis*" sp. – likely one of what is now *Platyceps*, *Hemorrhois* or *Spalerosophis* sp.	-	*Naja mossambica pallida*, now *Naja nubiae*	*Naja mossambica*	*Naja nigricollis*	*Naja haje*
18	Probably *Pseudocerastes persicus* (part), now *P. fieldi*.	*Pseudocerastes persicus* (part, now *P. fieldi*), *Cerastes cerastes* (hornless)	*Vipera ammodytes* male	*Pseudocerastes persicus*, now *P. fieldi*	*Pseudocerastes persicus fieldi* (now *P. fieldi*)	*Cerastes gasperettii*, possibly *Cerastes cerastes* (hornless)
19	Conceivably *Leptotyphlops cairi* , now *Myriopholis cairi*)	-	*Echis pyramidum*	*Echis pyramidum*	-	*Atractaspis engaddensis*
20	*Echis coloratus*	*Eryx jaculus*	*Psammophis schokari*, *Psammophis sibilans*	*Chamaeotortus aulicus* (now *Dipsadoboa aulica*)	*Psammophis aegyptius*, Elapidae	*Echis pyramidum*

21	*Natrix* sp.	*Psammophis* or *Philothamnus*	*Natrix tessellata*	*Atheris hispida*	*Natrix tessellata*, *Platyceps florulentus*	*Atheris hispida*
22	*Vipera persica fieldi*, now *Pseudocerastes fieldi*	Disagrees with Sauneron, but offers no ID	*Vipera ammodytes* female	*Cerastes vipera*	Viperidae	*Pseudocerastes persicus fieldi*, now *P. fieldi*.
23	*Telescopus obtusus*	*Cerastes* (pale variant)	*Telescopus fallax hoogstraali*, now *T. hoogstraali*	*Macrovipera deserti* (now *Daboia mauritanica*)	Elapidae	*Echis coloratus*
24	Elapidae	-	*Telescopus dhara*	*Macrovipera lebetina*	Elapidae	*Macrovipera lebetina*
25	*Naja nigricollis* (part) – now *Naja nubiae*	-	*Malpolon monspessulanus* (part), now *M. insignitus*	*Malpolon monspessulanus* (part), now *M. insignitus*	*Malpolon monspessulanus* (part), now *M. insignitus*	*Naja nigricollis*
26	Unidentified viper (p. 155), *Echis carinatus* (part), now *E. pyramidum* (p. 164)	*Echis pyramidum*	*Vipera* (now *Daboia*) *palaestinae*	*Atheris nitschei*	Viperidae	*Echis pyramidum* (with distinctive head marking)
27	*Echis carinatus* (part), now *E. pyramidum* (p. 155-156) or *Bitis* (p. 165)	*Bitis arietans*	*Echis coloratus*	*Echis coloratus*	-	*Bitis arietans*
28	*Cerastes cerastes*	*Cerastes cerastes*	*Cerastes cerastes*	*Cerastes cerastes*	*Cerastes cerastes*	*Cerastes cerastes*, *Cerastes gasperettii* (horned)
29	*Cerastes vipera*	*Cerastes vipera* or immature, hornless *Cerastes cerastes*	*Cerastes vipera*	*Vipera latastei*	-	*Cerastes vipera*
30	Unidentified viper (p. 155), *Echis carinatus* (part), now *E. pyramidum* (p. 164)	-	Unknown but not *Echis*	*Causus resimus*	Viperidae	*Causus resimus*
31	Unidentified viper	-	*Platyceps rhodorachis*	*Psammophis tanganicus*	*Echis coloratus*	*Cerastes vipera* of the coastal region
32	*Naja haje*	Disagrees with Sauneron but offers no ID	*Malpolon moilensis*	*Malpolon moilensis*	-	Probably *Naja nubiae*, possibly *Naja pallida*
33	*Echis carinatus* (part), now *E. pyramidum*	*Echis* sp.	*Pseudocerastes persicus fieldi*, now *P. fieldi*	*Bitis arietans*	Elapidae	*Pseudocerastes persicus fieldi*, now *P. fieldi*

34	Possibly *Malpolon moilensis*	-	-	*Telescopus tripolitanus*	-	Possibly *Malpolon moilensis*
35	Unknown elapid	*Walterinnesia aegyptia*, *Atractaspis microlepidota*	-	-	-	*Pseudocerastes persicus fieldi* (dark variant), now *P. fieldi*
36	*Psammophis sibilans*	Possibly *Echis pyramidum*	*Eryx jaculus*	*Coluber* (now *Dolichophis*) *jugularis*	*Psammophis sibilans*	*Psammophis schokari*
37	*Psammophis schokari*	-	Possibly *Hemorrhois nummifer*	*Psammophis biseriatus*	Colubridae	*Psammophis sibilans*

Figures

Figure 1:

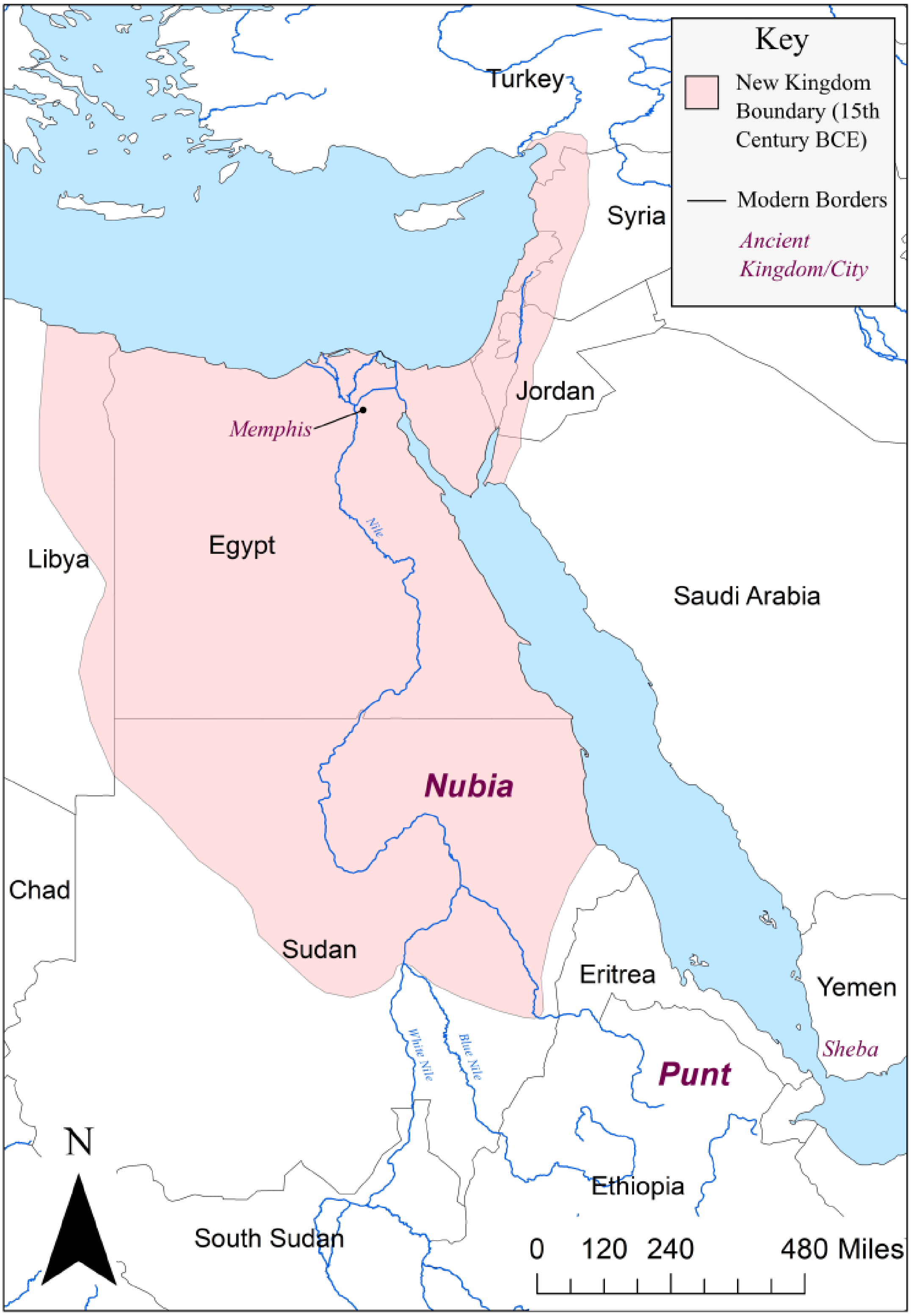
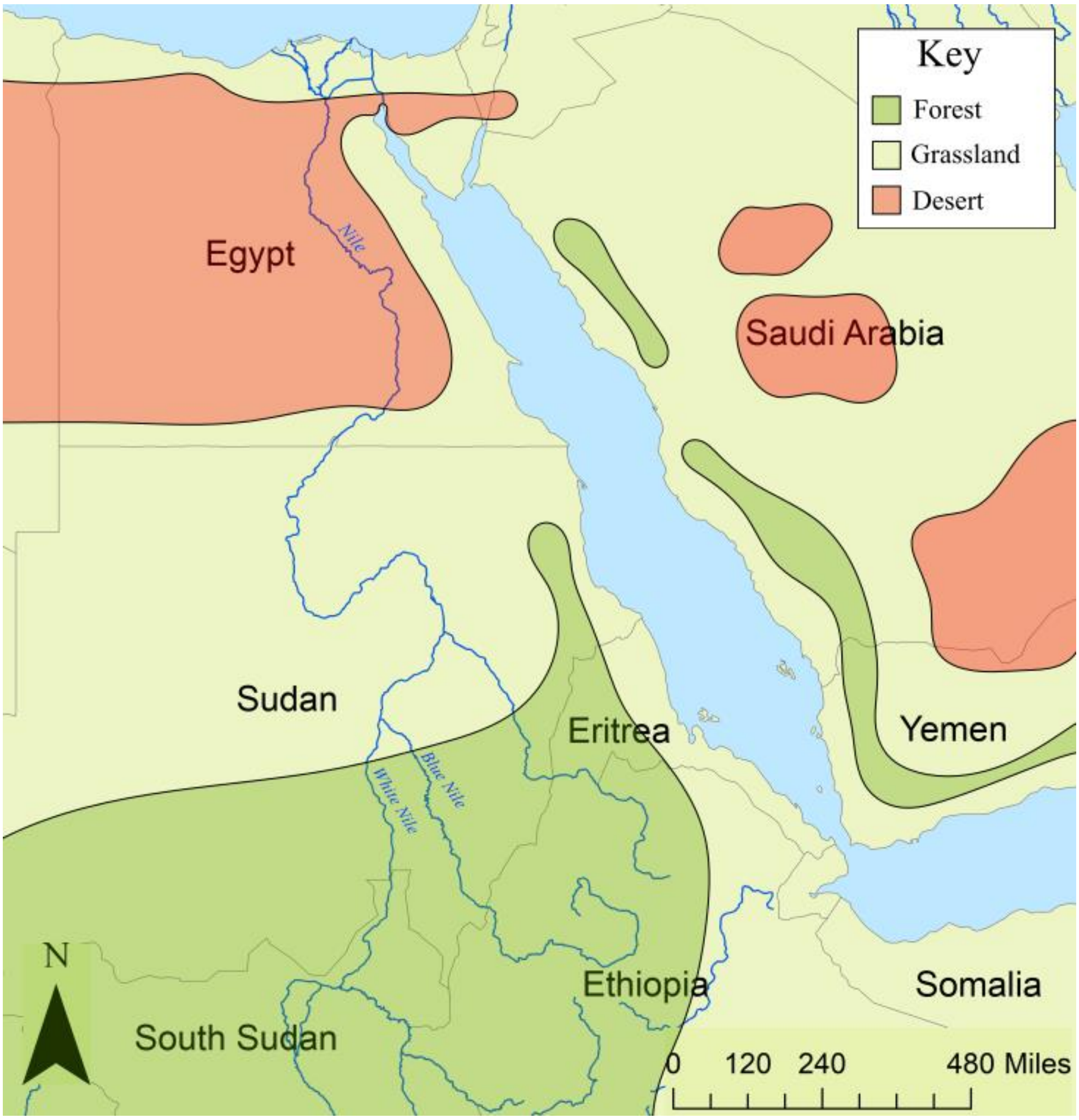


Figure 2: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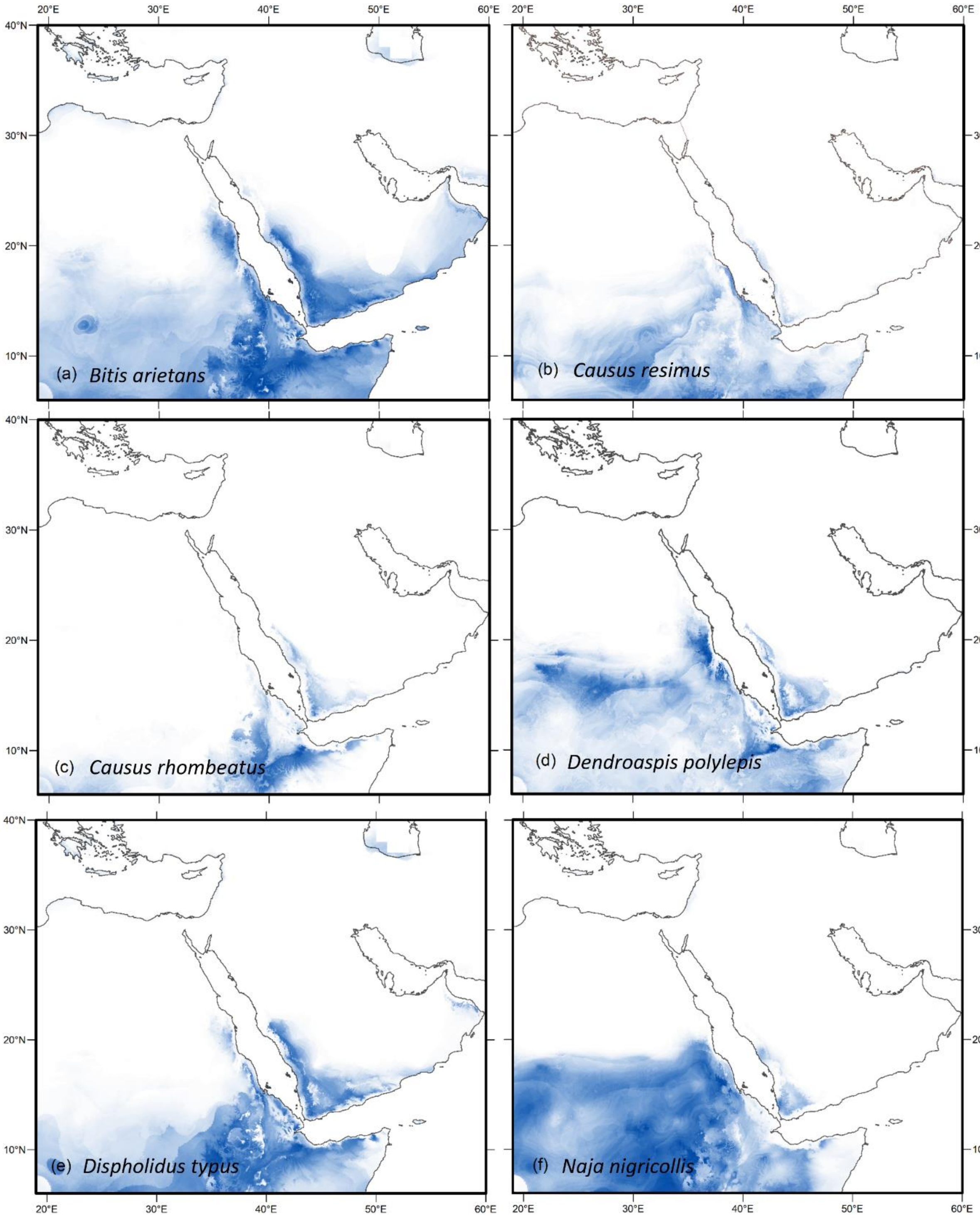
Forest
Grassland
Desert
Egypt
Nile
Saudi Arabia
Sudan
Eritrea
Yemen
Blue Nile
White Nile
Ethiopia
Somalia
South Sudan
N
0
120
240
480 Miles

Figure 3: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30°E
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60°E
40°N
30°N
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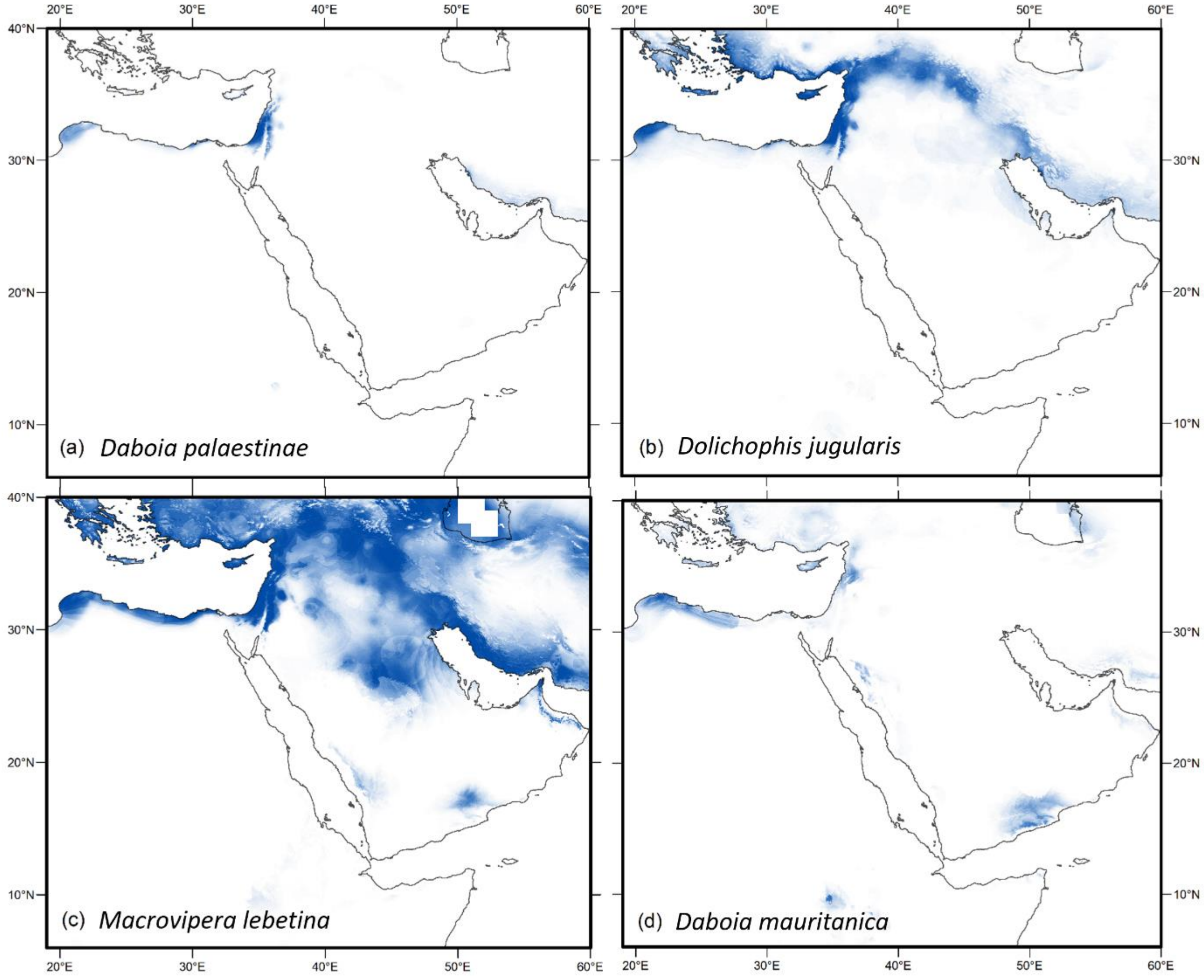
10°N
(a) Bitis arietans
(b) Causus resimus
(c) Causus rhombeatus
(d) Dendroaspis polylepis
(e) Dispholidus typus
(f) Naja nigricollis

Figure 4: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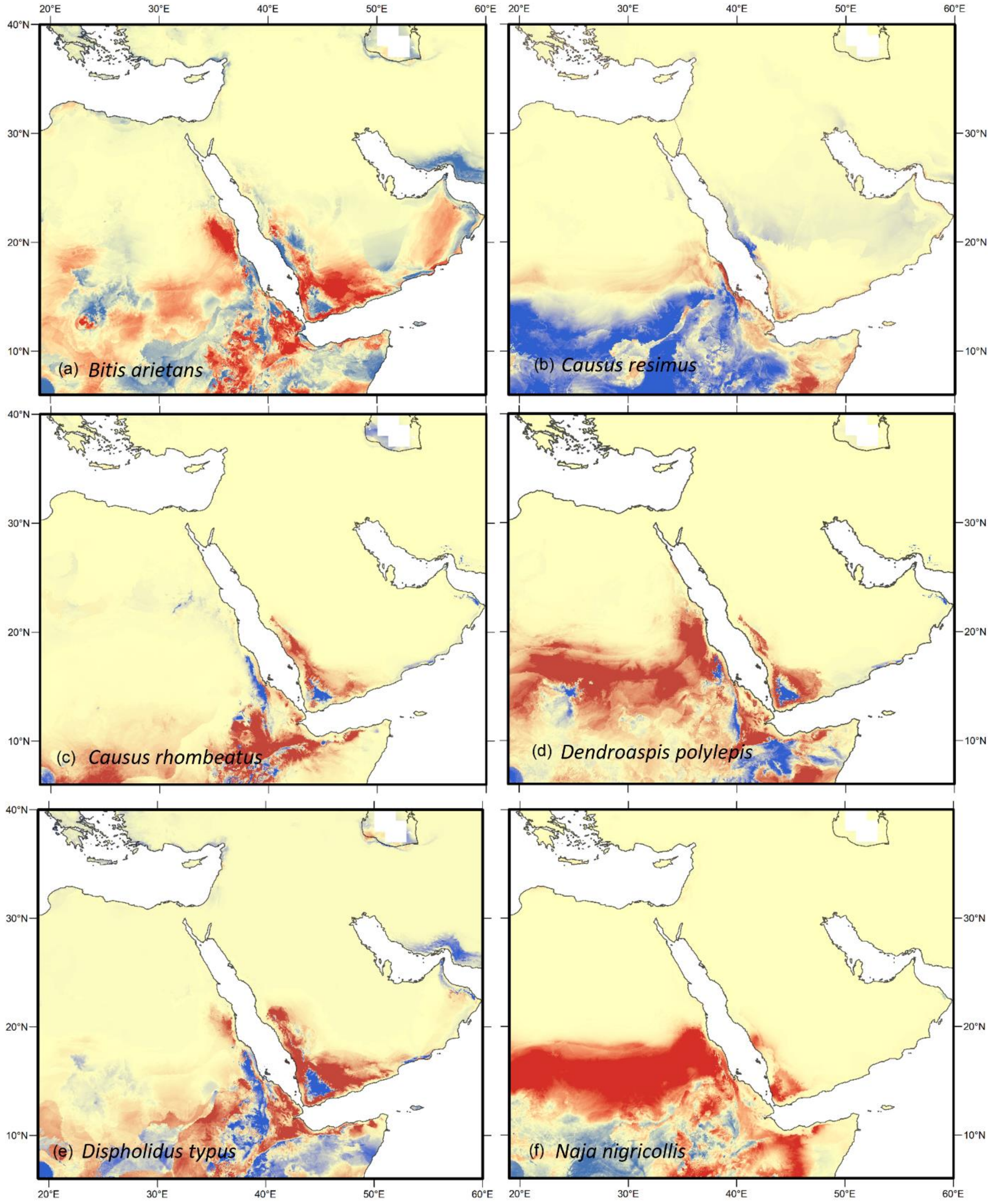
(a) *Daboia palaestinae*
(b) *Dolichophis jugularis*
(c) *Macrovipera lebetina*
(d) *Daboia mauritanica*

Figure 5: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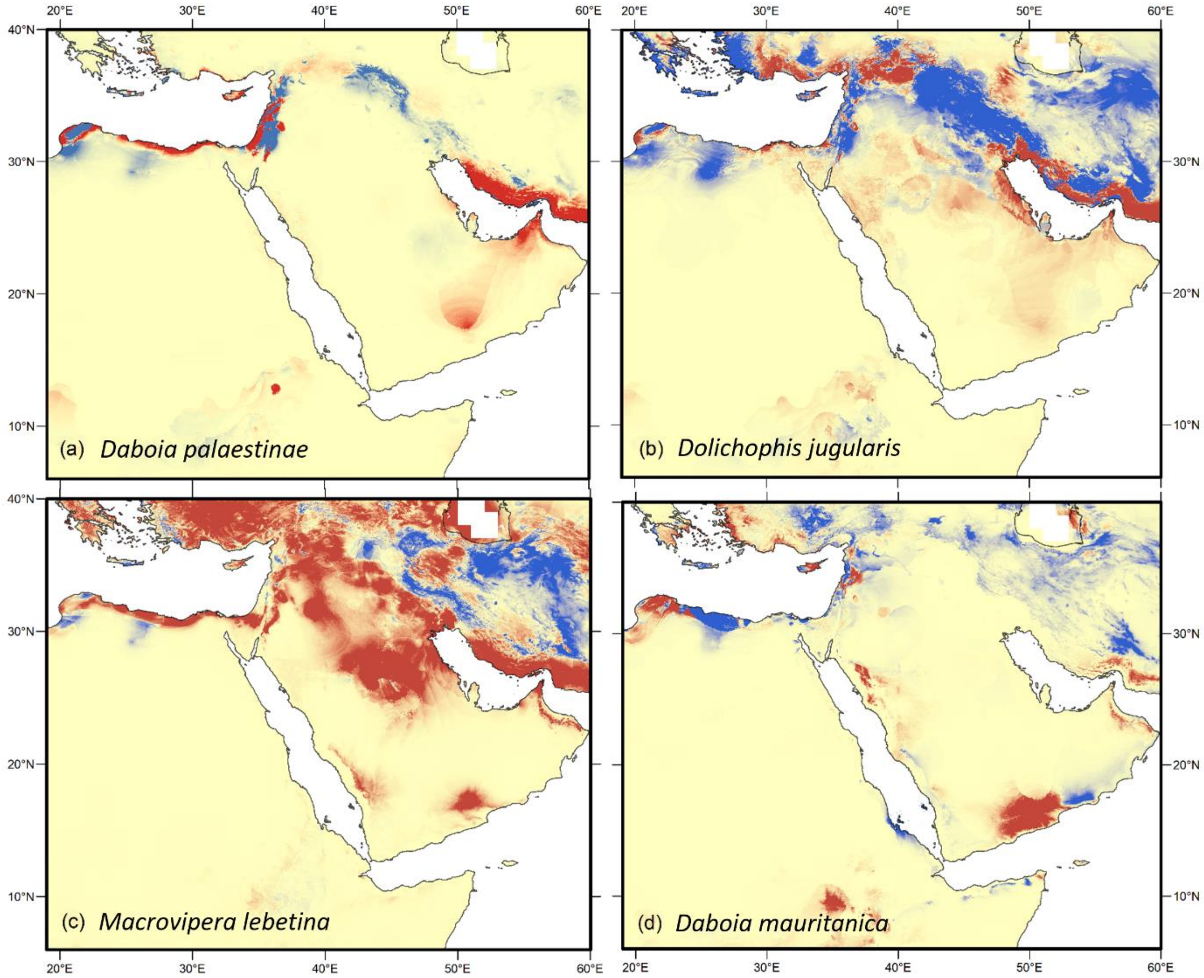
(a) *Bitis arietans*
(b) *Causus resimus*
(c) *Causus rhombeatus*
(d) *Dendroaspis polylepis*
(e) *Dispholidus typus*
(f) *Naja nigricollis*

Figure 6: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20°N
10°N
(a) *Daboia palaestinae*
(b) *Dolichophis jugularis*
(c) *Macrovipera lebetina*
(d) *Daboia mauritanica*

Figure Captions

Figure 1: The approximate boundaries of Ancient and modern Egypt based on Redford (1997), Shaw (2000) and Nacu (2011).

Figure 2: Vegetation patterns at approximately 5,000 BCE, in the mid-Holocene. Digitised and derived from Golding (2020).

Figure 3: Average predicted habitat suitability in the mid-Holocene for Afro-tropical species (a) *Bitis arietans*, (b) *Causus resimus*, (c) *Causus rhombeatus*, (d) *Dendrospis polylepis*, (e) *Dispholidus typus* and (f) *Naja nigricollis*. Calculated by taking the mean value for each grid cell from model outputs using three different General Circulation Models, namely CCSM4, MIROC-ESM and MPI-ESM-P and displayed such that white = 0 (unsuitable) and dark blue = 1 (the most suitable habitat).

Figure 4: Average predicted habitat suitability in the mid-Holocene for Levantine species (a) *Daboia palaestinae*, (b) *Dolichophis jugularis* and (c) *Macrovipera lebetina* and Maghrebi species (d) *Daboia mauritanica*. Calculations and colour scheme as for Figure 3

Figure 5: Differences in predicted habitat suitability between the mid-Holocene and present-day for Afro-tropical species (a) *Bitis arietans*, (b) *Causus resimus*, (c) *Causus rhombeatus*, (d) *Dendrospis polylepis*, (e) *Dispholidus typus* and (f) *Naja nigricollis*. Calculated by subtracting habitat suitability in the present from average habitat suitability in the mid-Holocene, such that yellow = no change, dark red = habitats that were much more suitable in the mid-Holocene than today and dark blue = habitats much less suitable in the mid-Holocene than today.

Figure 6: Differences in predicted habitat suitability between the mid-Holocene and present-day for Levantine species (a) *Daboia palaestinae*, (b) *Dolichophis jugularis* and (c) *Macrovipera lebetina* and Maghrebi species (d) *Daboia mauritanica*. Calculations and colour scheme as for Figure 5.