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# Biogeographic Inferences on the Evolutionary History of the King Cobra (*Ophiophagus hannah*, Cantor 1836) Species Complex

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King cobra (*Ophiophagus hannah*) is a snake widely distributed through southeastern tropical Asia, but in two separate subpopulations: one located in the Western Ghats (western Indian Peninsula) and the other much more extensive, ranging between the southern slopes of the Himalayas, Assam, Indochina to southeastern China. Similarly, it also appears in numerous tropical archipelagos such as Indonesia, the Philippines, and the Andaman Islands, but surprisingly it is absent from other large islands like Sri Lanka and Taiwan. In this study, we evaluated how climate could be shaping the distribution of this snake and estimated the future distribution of the species utilizing ecological niche modelling. To evaluate the effect of paleoclimatic conditions on the genetic structure of this species we performed Bayesian phylogenetic analysis under a molecular clock using mitochondrial DNA. Our analyses indicated that the current distribution of *O. hannah* is strongly influenced by the availability of humid climate conditions. King cobras have a long evolutionary history reflected in the appearance of four main mitochondrial lineages before the Pliocene (the Western Ghats, southeastern mainland Asia, Luzon, and Indonesia), congruently with paleoclimatic models that indicated the availability of suitable conditions for this species in these refugia during the glacial cycles. Climate history could explain the absence of *O. hannah* in Sri Lanka and Taiwan due to the absence of suitable climatic corridors when these islands were connected to the mainland (20,000 years ago). Future projections (2050–2070) did not suggest significant range shifts in the region, even considering the worst global warming scenarios.

**Key words:** Paleobiogeography, *Ophiophagus hannah*, Niche modelling, Climate change, Evolutionary history.

## BACKGROUND

The king cobra (*Ophiophagus hannah*) is an iconic reptile because it is the largest venomous snake in the world, reaching a maximum length of 5.5 m (Charlton 2018). These snakes are widely distributed throughout southeastern tropical Asia, from east Pakistan to Bali, reaching northwards the southern foothills of the Himalayas and southern coastal China (Fig. 1, Charlton 2018), along with an elevational range from sea level up to 2303 m (Dolia 2018). The species mainly lives in primary tropical forests and scrubland, but it is adaptable, also penetrating more disturbed habitats like cultivated fields and suburban environments (Lim et al. 2011; Shankar et al. 2013; Marshall et al. 2018).

Despite being widely distributed, this species shows an enigmatic distributional pattern, because is present in several tropical archipelagos but absent in

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others, which harbour apparently suitable climatic conditions, such as Sri Lanka and Taiwan. This is surprising due to the proximity of these islands to the mainland and the presence of this snake in some more remote archipelagos like the Philippines or the Andaman Islands.

Similarly, other biogeographic aspects of this species are poorly understood. For example, whether the species has a mainland origin and then spread to the Indo-Pacific archipelagos or vice versa, or the effect that glacial cycles may have had on genetic differentiation (Kundu et al. 2020). The effect of the glaciations could be twofold, on the one hand facilitating the dispersal towards the Indo-Pacific archipelagos using newly formed land bridges (Sharma et al. 2018), but also reducing the interconnectivity among subpopulations in the mainland, caused by a possible collapse on the extension of wet forests (Wurster et al. 2010). These fluctuations could have left a footprint on the phylogenetic structure of this species. In this sense the species can be split into four lineages remarkably distinct at the morphological and genetic level (Shankar et al. 2021), thus supporting that *O. hannah* is a species complex.

King cobras are currently threatened and classified as vulnerable with a tendency towards a decreasing species range (Stuart et al. 2012). The rapid growth of the human population in the region reduces the habitat of *Ophiophagus hannah* displacing this trophic specialist to lower quality habitats and putting this snake in close contact with humans, thus increasing the mortality induced by humans, such as road mortality and poaching (Zhou and Jiang 2004; Marshal et al. 2018; Healey et al. 2020).

Another factor that can threaten their populations could be global warming, due to the reductions in forest area and prey availability. Thus, the assessment of the potential range shifts of this endangered species in the next decades can be useful for developing of future conservation strategies (Guisan et al. 2013).

We aimed to analyse the past and future changes in the geographic range of the king cobra concerning its current distribution, defining which environmental conditions determine the species occurrence. Specifically, we addressed whether the climatic changes combined with the eustatic changes during the last glacial maximum episode led to changes in their geographic range to the previous interglacial period and whether they could have shaped the species' genetic structure. In addition, we tested for congruence between niche stability during the last glacial-interglacial cycles, middle Pleistocene and Pliocene, and intraspecific genetic structure. Finally, we evaluated the possible variability in the geographic range caused by global warming and evaluated its implications for the conservation of the species.

## MATERIALS AND METHODS

### Ecological niche modelling

First, we collected 493 records based on literature sources to model the climatic niche of *Ophiophagus hannah* (Table S1, Fig. 1). The niche models were built based on 19 bioclimatic variables provided by the WorldClim 2 database (Fick and Hijmans 2017). We assessed present, past, and future niche suitability by mapping statistical models under current (historical) conditions (Hijmans et al. 2005), one entire glacial-interglacial cycle, mid-Holocene (6000 years), last glacial maximum (LGM, 20000 years), and Last Interglacial (LIG, 135000 years), and Chibanian age (Middle Pleistocene, 787000 years) and Piacenzian age (Late Pliocene, 3.3 million years) (Otto-Bliesner et al. 2006; Dolan et al. 2015; Brown et al. 2018). To evaluate the effect of the expected climate change, we used the Community Climate System Model (CCSM 4) and two climate scenarios: the Representative Concentration Pathway (RCP) 4.5 (intermediate scenario) and 8.5 (worst-case scenario) for 2050 and 2070 (Gent et al. 2011).

The niche models were performed after selecting a subset of variables for their low correlation and high explanatory capacity, based on the variance inflation factor (VIF) (Stine 1995). To do this, we generated 500 random points (background) in a maximum distance of 200 km from the points of occurrence and we described the environmental conditions in these localities (Phillips and Elith 2013). These data were used to estimate the VIF through a logistic regression model, comparing the occurrence data with the background (Phillips and Elith 2013). For the subsequent niche models, we retained those variables showing a VIF < 10 (Salmerón-Gómez et al. 2016). Monthly maximum and minimum temperatures (2–7 bioclimatic variables) were not included as they were not available in the paleoclimatic simulations (Brown et al. 2018). This minimum subset was generated to avoid including highly correlated variables and reduce the chances to build an overfitted model (Peterson and Nakazawa 2008). Spatial thinning was used to reduce autocorrelation bias from clustered occurrence data (Aiello-Lammens et al. 2015), removing those occurrence records within a specified distance of 5 km and generating a new subset of 304 records. These calculations were carried out in the R statistical programming environment, using the packages dismo (Hijmans et al. 2021) and spThin (Aiello-Lammens et al. 2015).

To visualize niche suitability in south-eastern Asia, we used the maximum entropy algorithm (Maxent, Phillips et al. 2006), because it is suitable for datasets based only on occurrences (Elith et al. 2006). To do this, we assessed several combinations of candidate models built with different features (L: linear, Q: quadratic, P: product, T: threshold, and H: hinge) and regularization multipliers (rm; 0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0) by selecting the optimal model using the Akaike criterion adjusted for finite samples AICc (Muscarella et al. 2014). The final Maxent model was built after running 30 replicates with 75% of the locations allocated to training, using the combination of settings optimal for this dataset (Muscarella et al. 2014). The model performance was determined using the area under the receiver operator curve (AUC). In general, suitable models have to exceed a threshold of AUC greater than 0.75 (Pearce and Ferrier 2000). We also evaluated the performance of the calibration model using threshold-dependent metrics. The threshold was defined as the 10th percentile of the presence value. The localities of absence were restricted as those outside the range of distribution of the species, based on the IUCN ESRI shapefile (IUCN 2022). This approach allowed us to evaluate the model adequacy, but assuming that the 10% data may suffer from errors, which is particularly appropriate if they come from databases where the accuracy may vary among observers or over time (Raes et al. 2009). This threshold was used to reclassify the model and estimate its accuracy (with 95 confidence intervals) (Whytock et al. 2021). The models were built using all the records for the species, and each genetic clade separately, to assess whether there is interclade divergence in their environmental responses. The effect of the sample size on the performance of these models was estimated by evaluating the stability of the predictions in several models built with 5,10, 25, 50 and 75% random samples of the occurrences, with threshold-dependent statistics (Hernandez et al. 2006).

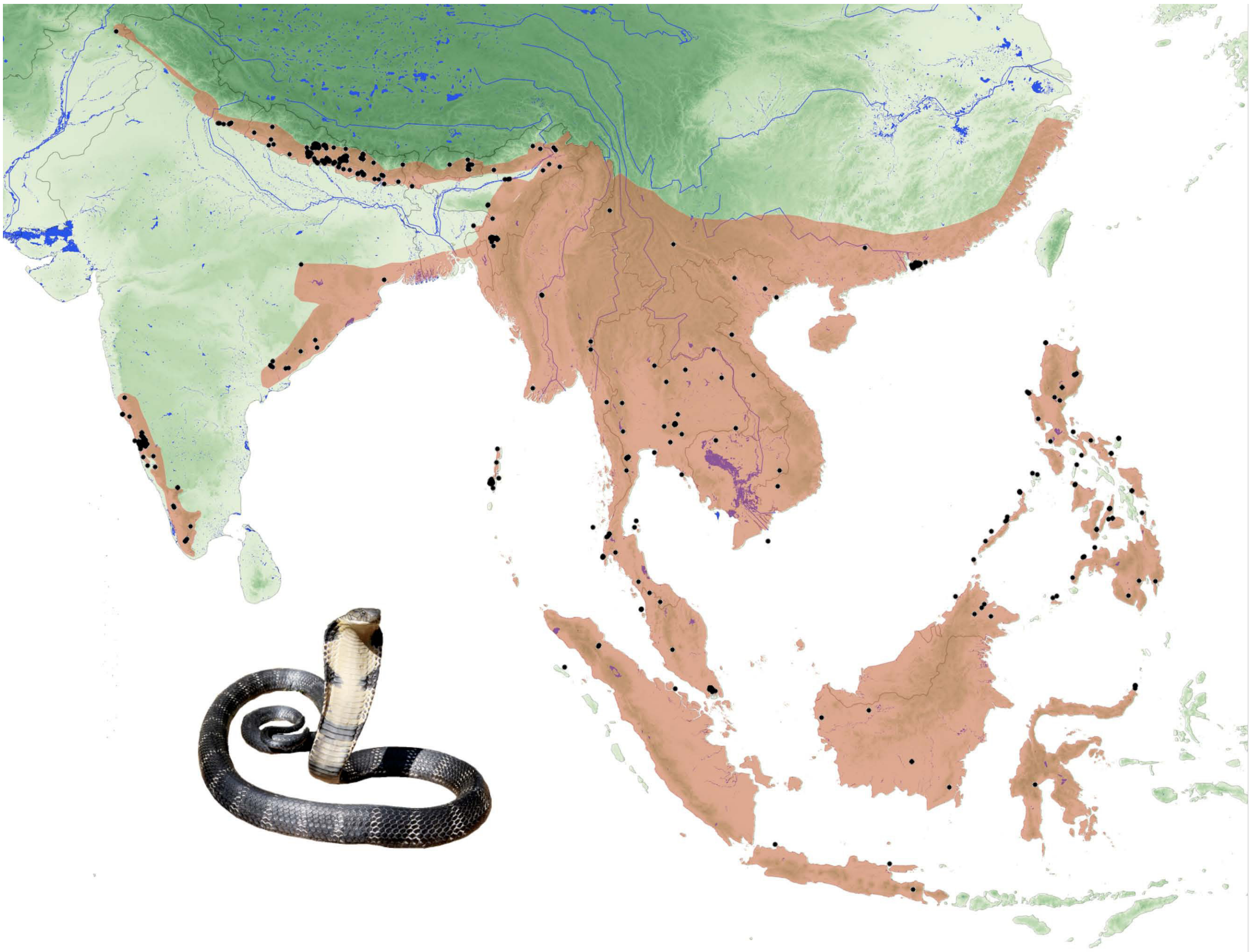

**Fig. 1.** Geographic distribution of the king cobra (*Ophiophagus hannah*). Black dots are the presence localities used for biogeographic analysis.

The set of ecological niche models were generated using MaxEnt 3.4.3 (Phillips et al. 2017) using the ENMval (Muscarella et al. 2014) routines in R and accuracy was estimated using the caret package (Kuhn 2021).

We estimated the potential distribution of *O. hannah* under changing past and future conditions by projecting current species climate relationships to these scenarios (Svenning et al. 2008). The resulting past and current projections were summed to build maps of climate stability, ranging from 0 to 6 (*i.e.*, conditions suitable during the six periods). To do this, the projections were first transformed into fuzzified rasters, assigning values between 0 and 1 and dividing the two groups at a midpoint (0.5). Those regions with high stability values can be considered potential refugia (Devitt et al. 2013). The Maxent projections were processed with Quantum-GIS 3.16.0 (Quantum GIS Development Team 2021).

## Ecological niche divergence

Niche divergence among the genetic clades of *O. hannah* was evaluated using the blob rangebreak test since it provides more reliable results than other ecological similarity tests (Glor and Warren 2011). This test evaluates the environmental overlap comparing the values of two similarity metrics (Schoener's D and Hellinger distance I; Hellinger 1909; Schoener 1968) with those generated by pseudoreplicate data (Warren et al. 2014). Both metrics range from 0 to 1, with 0 indicating no niche overlap and 1 indicating identical niches. The blob rangebreak test determines whether the climate of the regions occupied by two species are more different than expected by chance. This test was constructed using a binomial generalized linear model and replicated 1000 times to assess their statistical significance (Warren and Dinnage 2021). These analyses were carried out using the ENMTools package (Warren and Dinnage 2021) in R.

## Phylogenetic analysis

Mitochondrial DNA sequences of the Cytochrome *b* (645 nuc) and ND4 (595 nuc) genes comprising forty-five *O. hannah* and nine elapid snakes outgroups were gathered from GenBank (Table S2) and aligned using Bioedit 7.2. (Hall 1999). We used Bayesian inference as implemented in BEAST 2.6.2. (Bouckaert et al. 2014) to estimate phylogenetic relationships among populations of *O. hannah* and to determine the time of divergence among them. Bayesian analyses were performed by running three MCMC chains of $10^8$ iterations, sampling them each $10^4$ times using a starting tree generated by a Yule model and HKY + gamma model of DNA evolution. A relaxed molecular log normal clock was implemented using tree calibration points under log-normal distribution. The oldest fossil record of crown elapids (McCartney et al. 2014), dated at 24.9 Mya as a mean divergence and the early caenophidian snake (37.2 Mya, Head et al. 2005) as a maximum, was used to adjust a log-normal distribution with prior mean (3.18) and SD (0.27). The split between Hydrophiinae and the other Australian elapids dated at a minimum age of 16 Mya (Scanlon et al. 2003) and maximum age of 26 Mya (lack of fossil record in Australia, Travouillon et al. 2006) were chosen to set a log-normal distribution with prior mean (2.72) and SD (0.33). The third point of the calibration was the divergence between *Naja* and *Hemachatus* cobras using a mean of 18 Mya based on the occurrence of *Naja romani* (Szyndlar and Rage 1990) and as maximum age of 32 Mya, according to the record of undescribed Oligocene elapids (Rage 1988) to select prior values of the mean (2.85) and SD (0.31) of the log-normal distribution. Runs were checked for convergence and effective sampling size (ESS) using Tracer 1.7 (Rambaut et al. 2018). After pooling the posterior sample of trees, we discarded the 50% to compute the maximum credibility tree used in the analysis.

# RESULTS

Bayesian phylogenetic analysis achieved satisfactory convergence in the three runs and ESS were in all the cases considerably larger than 200. The maximum credibility tree evidenced the monophyly of *O. hannah* and revealed the existence of four geographically structured main clades supported by high posterior probabilities (Fig. 2). One clade occupies the Luzon island in the northern Philippines and another is distributed along the Indonesian Archipelago, the island of Mindoro in the central Philippines and Malaysia (Indomalayan clade). The relationships between these two clades and with the others are not well supported. In contrast, the other two clades grouped with strong support. Thus, one clade is endemic of the Indian Western Ghats and the other is widely distributed along the north and east India, Nepal, Andaman Islands, and Indochina (Indochinese clade) with the only exception of Malaysia. Molecular clock analysis dated the minimum divergence between the four main clades of king cobra at 5.0–3.5 Mya (lower value of the 95% interval of confidence), clearly predating Pleistocene times.

A total of six variables were selected for their low reciprocal correlation: mean temperature of warmest quarter (VIF = 3.379), mean temperature of coldest quarter (VIF = 6.497), annual precipitation (VIF = 3.296), precipitation seasonality (VIF = 6.985), precipitation of driest quarter (VIF = 5.745), and precipitation of warmest quarter (VIF = 1.975). The best Maxent model based on AICc was generated with LQHPT features and rm = 2. This model showed good overall performance (mean AUC = 0.881 ± 0.009 SD, after 30 replicates). For the threshold of the 10th percentile of the presence values, the model showed a high accuracy (0.909, 95% CI = 0.888–0.927), *i.e.*, the model adequately discriminated presences from absences, although it had a percentage of error. Model predictions were stable for variations in sample size of 5% accuracy = 0.846 (95% CI = 0.546,0.981), 10% accuracy = 0.960 (95% CI = 0.797,0.999), 25%, accuracy = 0.944 (95% CI = 0.864,0.985), 50% accuracy = 0.870 (95% CI = 0.802,0.921) , 75% accuracy = 0.885 (95% CI = 0.833,0.926).

On average, and for the full set of records, the annual precipitation showed permutation importance of 40.8%, mean temperature of the coldest quarter of 20.7%, seasonal precipitation of 13.3%, mean temperature of the warmest quarter of 13.3%, precipitation of warmest quarter of 8.2%, and precipitation of driest quarter of 3.6%. For the Indochinese clade, the AUC was 0.904 and the variables with higher permutation importance were precipitation of driest quarter (49.3%) and annual precipitation (35.9%). For the Indomalayan clade, the AUC was 0.917 and the variables with higher permutation importance were mean temperature of coldest quarter (92.9%) and precipitation of driest quarter (3.9%). For the Luzon clade, the AUC was 0.865 and the variables with higher permutation importance were precipitation of driest quarter (53.4%) and mean temperature of coldest quarter (33.3%). For the Western Ghats clade, the AUC was 0.978 and the variables with higher permutation importance were precipitation of driest quarter (52.7%)

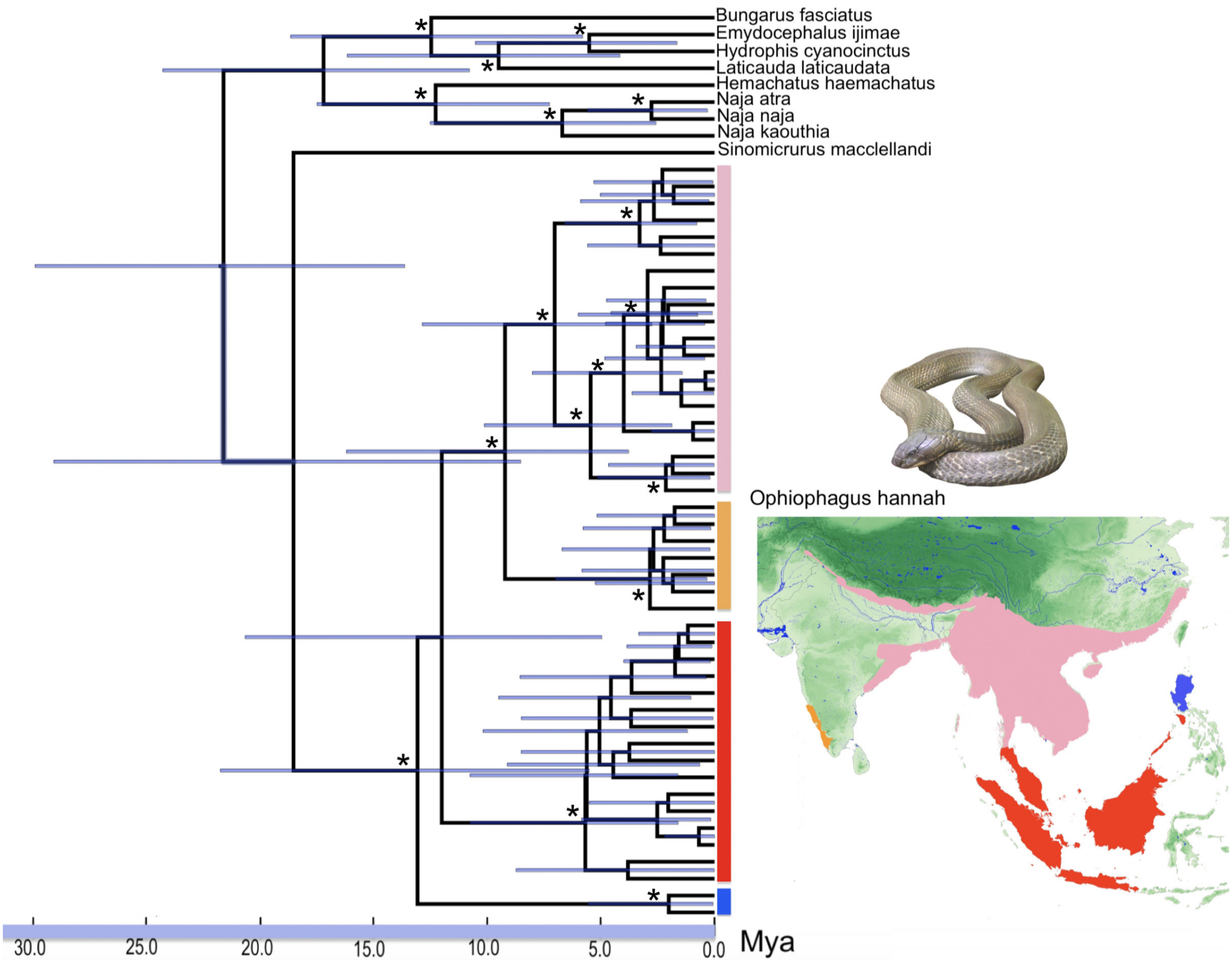

**Fig. 2.** Bayesian phylogeny of *Ophiophagus hannah* based on mitochondrial concatenated sequences depicting the main four clades. Nodes marked with asterisks are supported by posterior probabilities equal or larger than 0.9.

and annual precipitation (42.2%).

The results of the Maxent projections indicated that the estimated distribution of the species in Southeast Asia has been relatively stable in the last 3.3 Ma (Fig. 3). The models showed greater terrestrial connectivity between the islands of the Indonesian archipelago during the LGM, which together with moderately suitable conditions could have favoured the snake dispersion eastwards.

The predicted current distribution indicated that large parts of central India and the colder mountain and inland climates in the Himalayas and central China are potential barriers for the species. However, the model predicts the occurrence of *Ophiophagus hannah* with high probability in Sri Lanka, Taiwan and Eastern Indonesian islands, where the species is currently absent. The stability map reveals that the existence of two disconnected refugia in southwestern Asia and the southwestern region of the Indian subcontinent (Fig. 4), predicting high genetic diversity across the subpopulations of *O. Hannah*. Future projections 2050–2070 suggest small niche contractions (*e.g.*, in Borneo; Fig. 5), but without losing any of the refugia.

Niche overlap values from niche models under current conditions are low to high (Table 1). The results of the blob rangebreak test were not significantly different from the null distribution, *i.e.*, the environmental characteristics did not significantly differ among the regions occupied by each clade, except when comparing the Indochina with Malaysia-Indonesia and Western Ghats niche models (Table 1). Overall the results of the blob rangebreak test indicated that the environmental niche has been conserved in some lineages but not in all.

## DISCUSSION

In this study, we provided the first analysis of the biogeography of the King Cobra from an evolutionary perspective, based on projections of the species' fundamental niche in a series of paleoclimatic simulations, spanning up to the late Pliocene (3.3 Mya). The models showed good performance and were relatively robust to variations in sample size (as expected in models generated by Maxent; Wisz et al. 2008), although they had a small margin of error derived from databases built from heterogeneous sources (Raes et al. 2009).

Current conditions niche models indicated that the distribution of this snake is determined, regardless of the clade, by the amount of rainfall. This species inhabits regions with very high amounts of rainfall, which exceeds 1500 mm $y^{-1}$ in most or all of its distribution range (Kriticos et al. 2012). It is possible that these environmental requirements could be related to the trophic specialization of this snake. Tropical wet areas hold the highest species richness of snakes (Terribile et al. 2009), containing very species-rich assemblages where interspecific competition is reduced by trophic

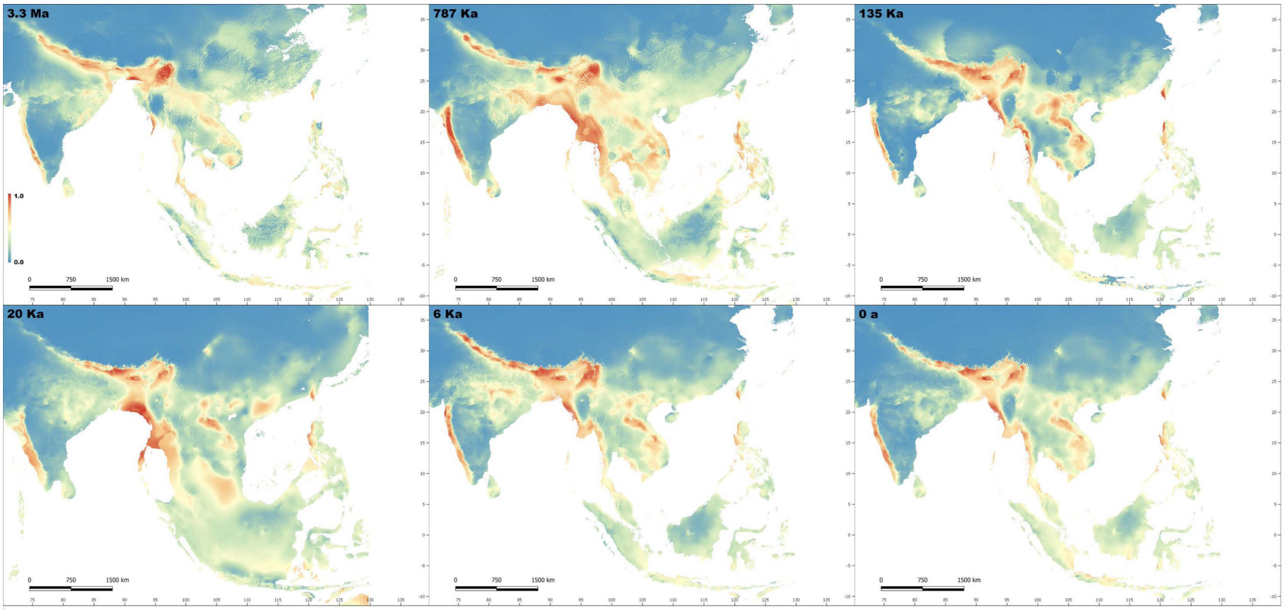

**Fig. 3.** Ecological niche models built with Maxent based on WorldClim 2 variables, showing a sequence of paleo-climatic projections, mid Holocene (6 Ka), last glacial maximum (LGM, 20 Ka), and Last Interglacial (LIG, 135 Ka), and Chibanian age (Middle Pleistocene, 787 Ka) and Piacenzian age (Late Pliocene, 3.3 Ma) and under present conditions: ka, thousand years ago, ma million years ago.

partitioning (Andreone and Luiselli 2009; Sampaio et al. 2018). Ophiophagy is a trophic specialization developed by king cobras and other very large tropical snakes that, given their large size, can feed even on other snakes, including reticulated pythons (O'Shea 2018; Guedes 2021). Thus, we suggest that the use of very humid habitats for this species could be related to greater availability of snake prey.

These relatively strict environmental requirements could have influenced the genetic structure and morphologic differentiation of *Ophiophagus hannah*, giving place to (Shankar et al. 2021). In this sense, the blob rangebreak test indicated an abrupt environmental gradient and moderate-low ecological overlap between the Indochinese, Western Ghats and Indo-Malayan clades, suggesting parapatric speciation. This separation could be promoted by climate barriers, particularly depending on the longer periods of seasonal drought typical of transition between the monsoon and steppe climate of the central and southern parts of the Indian Peninsula (Kriticos et al. 2012). In the case of the transition between Malaysia and Indochina, the separation between clades also coincides with a sudden change in rainfall regimes, in this case between a highly seasonal monsoon to warm rainforest, with rainfall more regularly distributed throughout the year (Kriticos et al. 2012).

Projections based on paleoclimatic simulations allow us to detect several long-term refugia that would explain the preservation of ancient genetic differentiation among subpopulations. Our genetic analyses revealed that the divergence among the four main clades occurred before the Pleistocene and is similar to that found in other elapids and particularly in cobras (genus *Naja*; Kazemi et al. 2020). Therefore, this genetic structuring must have persisted throughout the glacial oscillations. The projections showed a high probability of available refugia throughout the Pleistocene-Holocene oscillations for the Western Ghats and Indo-Chinese and less consistently for the Indonesian lineage. The models also corroborated the existence of suitable paleoclimatic conditions on the island of Luzon (Philippines), where there is an endemic lineage that may deserve species status, as it lacks

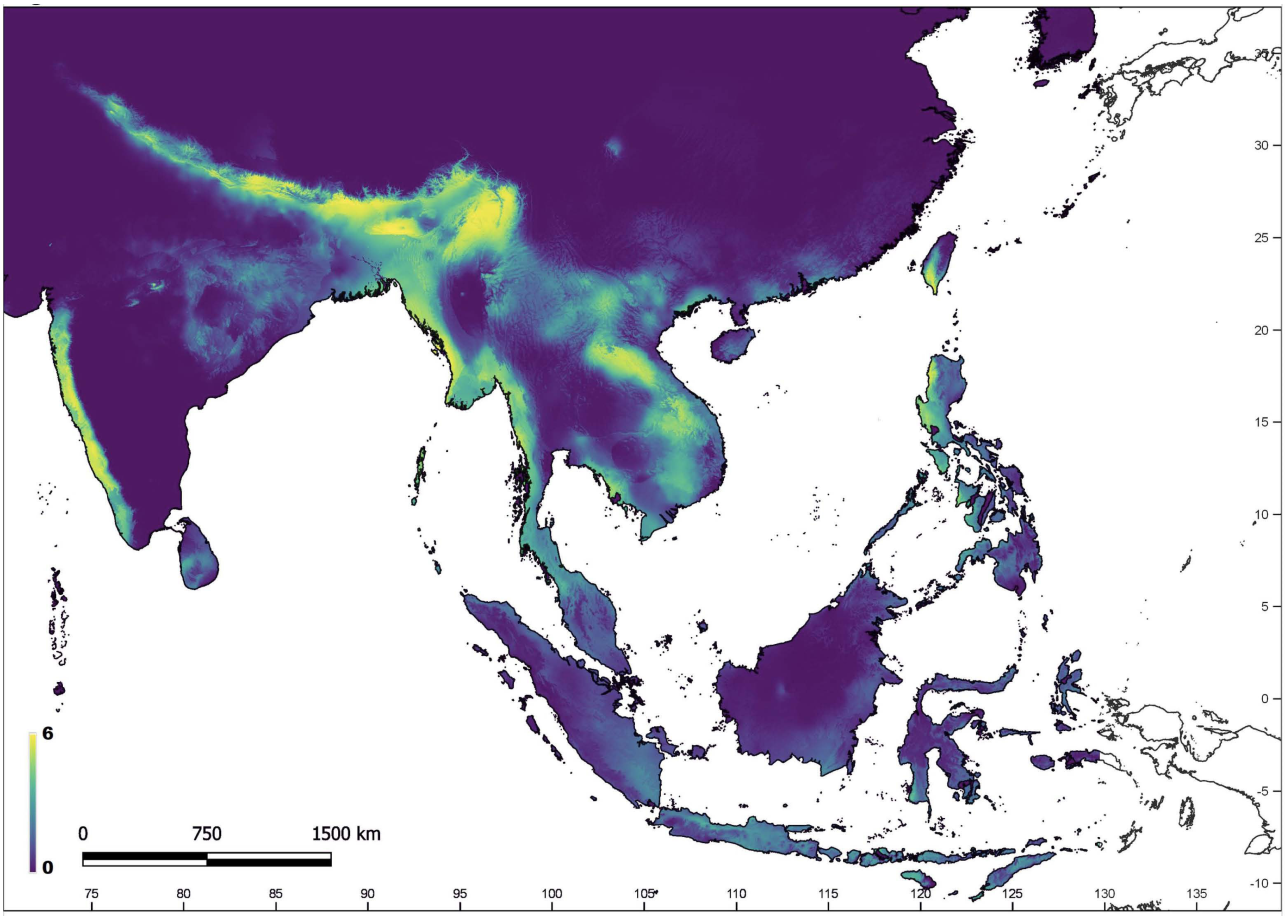

**Fig. 4.** Model of the niche stability along the paleo-climatic sequence. The region in yellow indicates greater temporal stability and putative refugia for each clade of *O. hannah*.

nuclear introgression (Shankar et al. 2021).

Interestingly, other subpopulations of King cobra in this archipelago (Mindanao) belong to the Indo-Malayan lineage. This fact, together with the lower probability of available refugia on other islands except for Luzon, suggests that the origin of these Philippine subpopulations could be attributable to comparatively recent colonization from Indonesia. Evidence from oxygen isotopic composition showed several events of regression of the sea level since early Pleistocene (up to -120 m; Chappell and Shackleton 1986; Prentice and Denton 1988; Voris 2000) allowing terrestrial dispersal from mainland Asia to Indonesia and across short marine distances to central and southern Philippines (Heaney et al. 2005). However, the split between the Luzon and the other lineages predates the Pleistocene, suggesting that older transmarine colonization is the origin of this lineage. Greater connectivity among the large Indonesian islands and favourable climatic conditions possibly favoured the eastward expansion

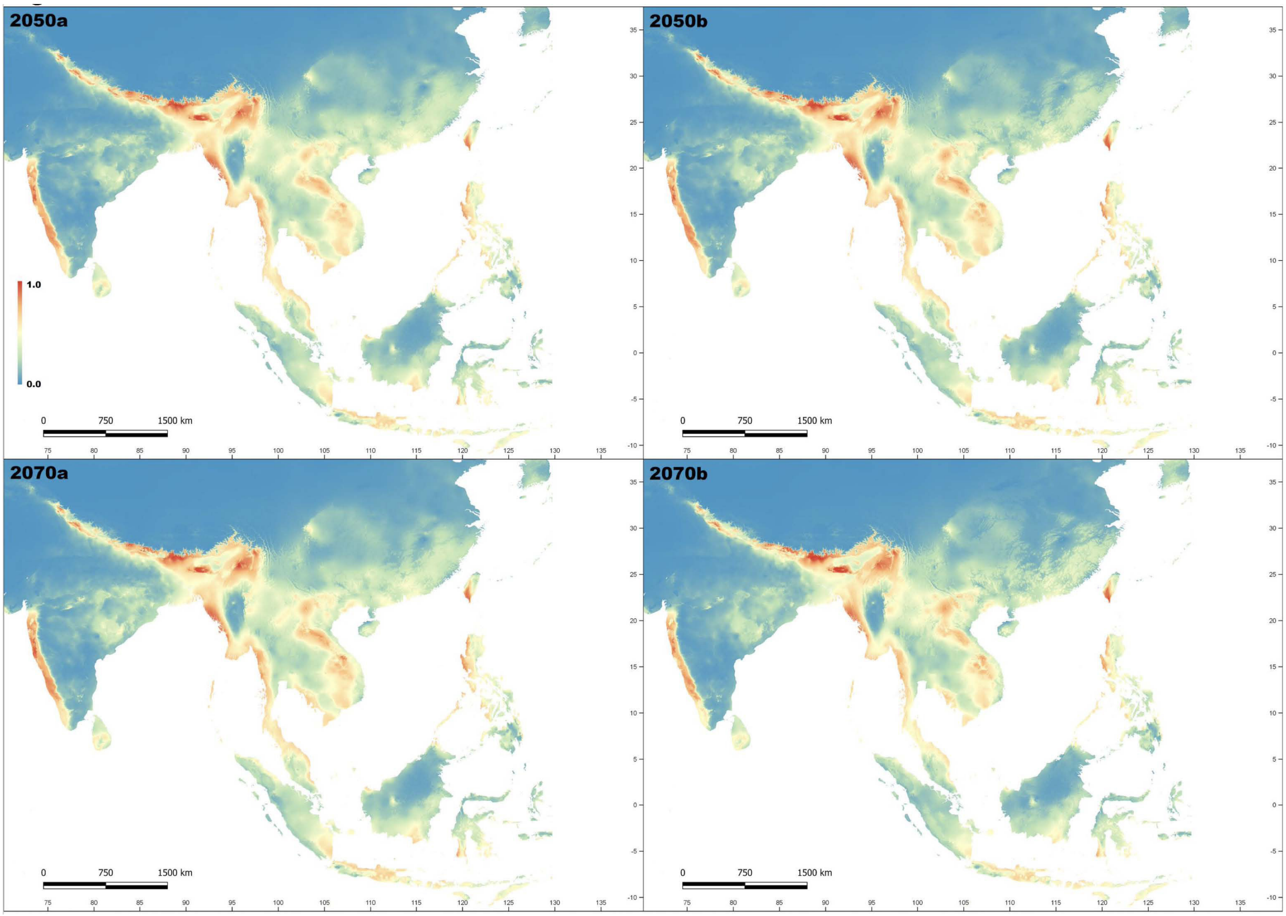

**Fig. 5.** Ecological niche models built with Maxent based on WorldClim 2 variables, evaluating the effect of expected climate change under different scenarios. a) RCP4.5 (intermediate scenario); b) RCP8.5 (worst-case scenario).

**Table 1.** Climate similarity among the regions occupied by the four clades of *Ophiophagus hannah*, estimated with the blob rangebreak tests. Significant differences at alpha = 0.05 are marked with an asterisk. First value is the D Schoener's index and the second the I, Hellinger distance. In both metrics values close to 1 indicate higher similarity

| | Indochinese | Indo-Malayan | Luzon | Western Ghats |
|---|---|---|---|---|
| Indochinese | 1/1 | | | |
| Indo-Malayan | 0.156*/0.319* | 1/1 | | |
| Luzon | 0.339/0.594 | 0.648/0.852 | 1/1 | |
| Western Ghats | 0.203*/0.424* | 0.274/0.502 | 0.372/0.595 | 1/1 |

of the Indo-Malayan clade during the LGM, although without surpassing Weber's line.

Paleoclimatic models also allowed us to answer other questions about the biogeographic history of *O. hannah*. Taiwan shares 78% of its snake fauna with southern China (Uetz and Hošek 2020–2015), suggesting extensive species exchanges between both regions. In this sense, recent phylogenetic studies showed that the Chinese cobra (*Naja atra*) was able to spread to Taiwan during the late Pleistocene (Lin et al. 2014). However, in the case of *O. hannah*, our models indicated that the conditions were not optimal for its presence in southern China during the LGM when the land bridges connecting Taiwan were available. Similarly, Sri Lanka comprises a rich snake fauna, with numerous widespread species also shared with mainland India, for example, *Naja naja*, *Bungarus caeruleus*, *Ahaetulla nasuta*, *Ptyas mucosus*, and *Python molurus* (Pyron et al. 2013). These exchanges could have been favoured by the formation of intermittent land bridges throughout the Pleistocene (Chauhan 2008). However, the passage of *O. hannah* from its refugia in the Western Ghats and Assam/western Bengal to Sri Lanka has never been favoured by the presence of suitable climatic corridors. In contrast, habitat suitability for colonization of Andaman Islands has been higher for the past 787,000 years, especially during the LMG when a land bridge connected these islands to the mainland.

The requirements of hyper-humid environments make it challenging for species to persist in the face of global warming, as has been postulated for other humid tropical species (Alford et al. 2007). Few studies have assessed the putative effects of climate warming on snake distributions, but they agree that suitable habitats are decreasing (*e.g.*, Lourenço-de-Morales et al. 2019; Miszei et al. 2021). Our projections did not suggest that this may also be the scenario for the King cobra, although predictions on the risk of extinction based only on climatic variables could be biased in snakes (Cabrielli et al. 2014). This may be also the case of a highly specialized predator like *O. hannah*, which depends on the high availability of other species of snakes that in turn could be adversely affected by environmental stress (Reading et al. 2010).

## CONCLUSIONS

Molecular phylogenetics combined with climate niche analysis gives a well-supported explanation of the evolutionary history of *Ophiophagus hannah* from a paleoclimatic and genetic perspective and provide evidence that the species' range and genetic structuring may make it resilient to the challenges of climatic change.

### List of abbreviations

DNA, LGM, LIG, RCP, CCSM 4, VIF, L, Q, P, T, H, rm, AICc, AUC, ESS, Ka, Ma.

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**Authors' contributions:** Both authors contributed equally to the manuscript.

**Competing interests:** FA and DE declare that they have no conflict of interest.

**Availability of data and materials:** We agree to include supplementary data in order to get accessible to other researchers the data used in our analysis.

**Consent for publication:** Not applicable.

**Ethics approval consent to participate:** Not applicable.

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## Suplementary materials

**Table S1.** Data on king cobra occurences. (download)

**Table S2.** GeneBank sequences. (download)