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A species distribution model for the endemic Cyprus whip snake (*Hierophis cypriensis*) is consistent with a transient period of isolated evolution in the Troodos Range

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The Cyprus whip snake (*Hierophis cypriensis* Schätti, 1985) is endemic to Cyprus and occurs in forested regions of the Troodos Range in the central part of the island, but surprisingly, has not been reported from such areas in the Kyrenia Range of northern Cyprus. Here, we provide the first comprehensive GPS-based assessment of the distribution of this endangered snake in Cyprus. We use species distribution modelling to demonstrate that areas with suitable habitat for the Cyprus whip snake are largely limited to the Troodos Range. The Kyrenia Range contains only a few grid cells of medium habitat suitability according to the environmental parameters assessed. The Mesaoria Plain, which lies between the two mountain ranges, likely functions as an ecological barrier with unsuitable habitat conditions. Consistent with this pattern of distribution, we hypothesise that this species was restricted to the Troodos Range during the early phases of speciation. Adaptation to environmental conditions in the Troodos Range may have prevented subsequent range extension to other ecological niches when the rest of the island emerged.

Key words: adaptation, Colubridae, dispersal, distribution, Kyrenia Range, model, speciation

INTRODUCTION

Cyprus, an oceanic island in the eastern Mediterranean Sea, has a diverse set of amphibians and reptiles, but the origin, composition, and evolution of this island fauna have traditionally been difficult to explain (Böhme & Wiedl 1994; Baier et al., 2013; Poulakakis et al., 2013). A major challenge for zoogeographical studies is the complex geological composition and history of the island. Cyprus originated from two independent islets that united to form the modern island, where they gave rise to two mountain ranges, the Troodos and Kyrenia Ranges (McCallum & Robertson, 1990; Robertson & Xenophontos, 1993, 1997). This "two-island origin" of Cyprus may have shaped the distribution of the modern herpetofauna on the island, but detailed analyses are not available (Göçmen et al., 2009; Baier et al., 2013).

Aside from several endemic subspecies, the island boasts three endemic species: the recently described Cyprus Water Frog (*Pelophylax cypriensis*) (Plötner et al., 2012), the Troodos Lizard (*Phoenicolacerta troodica*), and the Cyprus whip snake (*Hierophis cypriensis*). While the Cyprus Water Frog and the Troodos Lizard are widely distributed across the island, the Cyprus whip snake has only been reported from forested areas in the Troodos Range in the central part of the island (Baier et al., 2013). Remarkably, other regions of the island, notably the Kyrenia Range in the northern part, also support forested areas roughly similar to those in the Troodos Range. Missing records may simply reflect sampling gaps that will be resolved by further studies. Several Cyprus reptile species are rarely observed or occur at very few localities, and the herpetological exploration of the island is not well advanced compared to other European countries. However, since quantitative characterisations of the ecological niche of the Cyprus whip snake are not available, it remains unclear whether its predicted distribution could exceed its known occurrence.

Here, we provide the first GPS-based account of the extant distribution of the Cyprus whip snake. This snake is threatened by habitat degradation and direct persecution (Baier et al., 2013), and is classified as Endangered in the IUCN Red List of Threatened Species (IUCN, 2013). We then use species distribution modeling with an ensemble forecast approach to determine the potential distribution of the Cyprus whip snake based on a comprehensive set of remote sensing variables. We finally provide a hypothetical model for the evolutionary history of the Cyprus whip snake in Cyprus that is consistent with the species distribution model.

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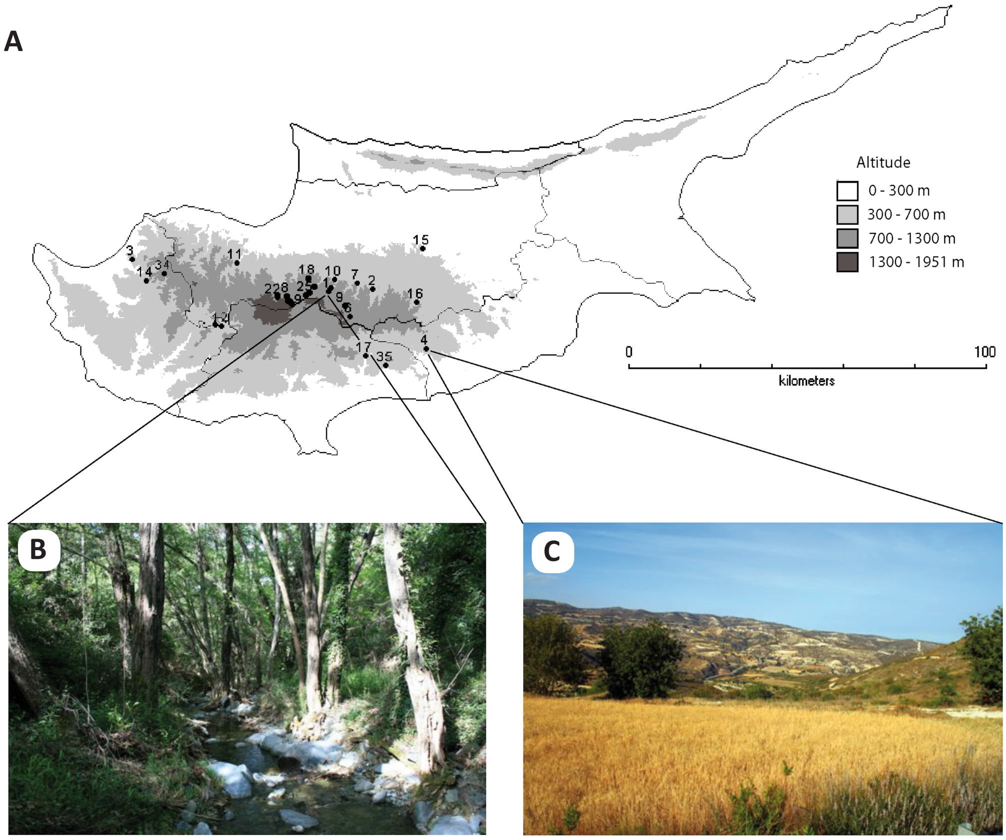

Fig. 1. Distribution and habitat diversity of the Cyprus whip snake. (A) Distribution of the Cyprus whip snake based on records reported in this study. (B) Typical habitat of the Cyprus whip snake at the site of record #1, Lagoudera stream, district Nicosia, April 2008. (C) Unusual habitat of the Cyprus whip snake at the site of record #4, road from Lageia to Choirokoitia, district Larnaca, May 2008.

MATERIALS AND METHODS

The first two authors collected distribution records of the Cyprus whip snake with hand-held GPS devices through live observation or road kills in the Troodos Range. One of the authors (FB) also screened suitable habitats in the Kyrenia Range in 2008. We also included localities of Baier et al., (2013) that had been recorded with GPS devices, but excluded records based only on descriptive geo-referencing. Geographic coordinates of all 35 locality records were available with a precision of ~0.0001° (=~10 m). All records were deposited in the Herpetological Repository of Cyprus (http://www.herprepository.org) under accession numbers 409, 428, 433, 513, 525, and 1302–1331.

We first took a conservative approach to model the distribution of the Cyprus whip snake with a minimal set of variables. For this we used the program MaxEnt v.3.3.3e (Phillips et al., 2006), which uses presence-only distribution data to create species distribution models (SDMs) based on the maximum entropy principle applied to a set of environmental variables. Through repeated rounds of machine learning with training points, an initially maximized ("maximum" entropy) probability distribution is subject to constraints from environmental predictors or features derived thereof. The resulting modified probability distribution is projected onto geographical space and describes habitat quality by assigning a Maxent value (ranging from 0 to 1 applying the logistic output) to each grid cell in the geographical layer (Phillips et al., 2006). The quality of the distribution model can be evaluated by AUC (Area Under Curve) scores, which refer to the discriminatory power of the model to distinguish training from background points and range from 0.5 (random prediction) to 1.0 (perfect prediction). We compiled climate data from the WorldClim database (Hijmans et al., 2005), vegetation data from the Global Land Cover 2000 database (Global Land Cover 2000 database, 2003), and data about actual evapotranspiration from the Global Soil Water Balance Geospatial Database (Trabucco & Zomer, 2010). The Cyprus whip snake has previously been found in forested areas with moderate climate across low to high altitudes (Baier et al., 2013). To capture the characteristics of this habitat in the best possible way, we first selected a set of variables that appear most important for the Cyprus whip snake. Using an inter-variable correlation threshold of r^2<0.75, we then chose six environmental variables that underlie the Maxent species distribution model: Bio10 (Mean Temperature of Warmest Quarter), Bio11 (Mean Temperature of Coldest Quarter), Bio16 (Precipitation of Wettest Quarter), Bio17 (Precipitation of Warmest Quarter), coverage (vegetation) and actual evapotranspiration. All tiles used to assemble the layers had a resolution of 30 arc-second (~1 km^2), and were assembled in DIVA-GIS v.7.5.0 (Hijmans et al., 2012a).

In a second approach, we computed an ensemble species distribution model based on a variety of different

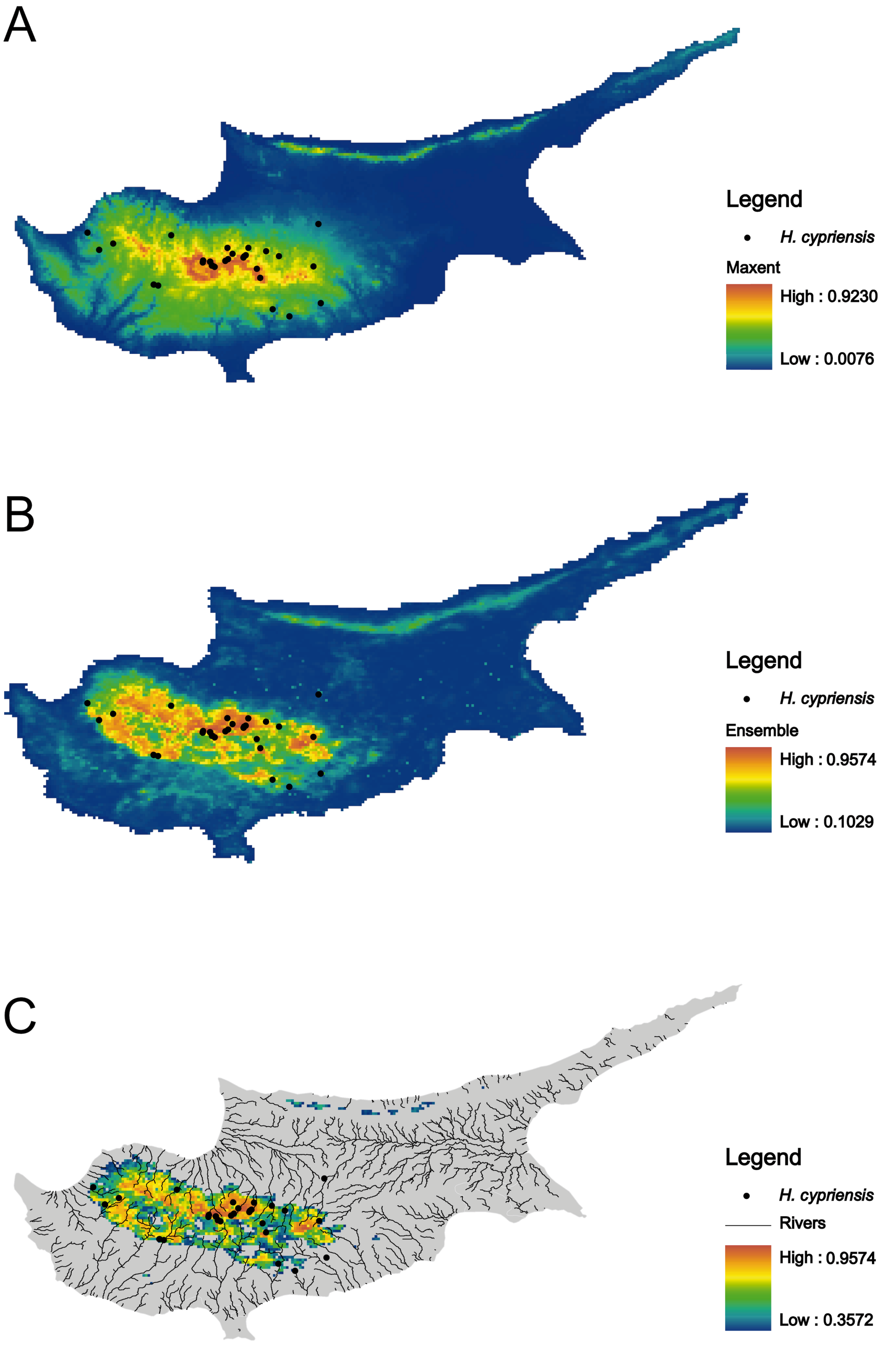

Fig. 2. Species Distribution Models for the Cyprus whip snake. (A, B, C) Species distribution model #1, species distribution model #2, and reclassified species distribution model #2 for the Cyprus whip snake, respectively. Records reported in this study are indicated as black dots; heat map colour coding indicates Maxent/Ensemble values ranging from 0 to 1 (low to high habitat suitability). In (C) black lines represent watercourses.

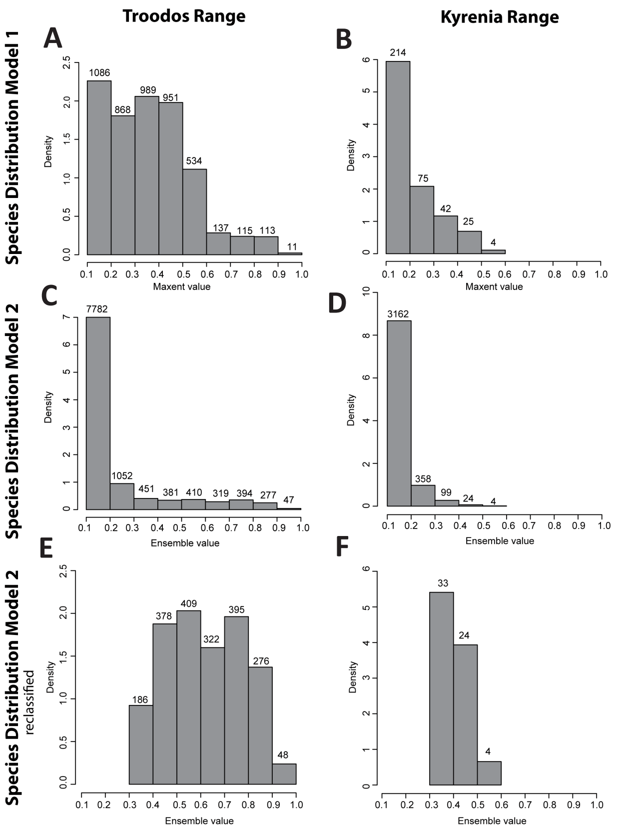

Fig. 3. Quantification of predicted habitat suitability for the Cyprus whip snake in the Troodos and Kyrenia Ranges. (A, B) Distribution of Maxent values in the Troodos and Kyrenia Ranges, respectively, according to distribution model 1 (see Fig. 2A). (C, D) Distribution of Ensemble values in the Troodos and Kyrenia Ranges, respectively, according to distribution model 2 (see Fig. 2B). (E, F) Distribution of Ensemble values in the Troodos and Kyrenia Ranges, respectively, according to the reclassified distribution model 2 (See Fig. 2C). Numbers above bars represent the number of grid cells (=square kilometres) with a Maxent/Ensemble value in the respective range.

algorithms and remote sensing variables, which were derived from a set of pre-processed variables originating from MODIS sensors of two NASA satellites with a spatial resolution of 30 arc sec and a temporal resolution of 8-days in MOD11A2 and 16-days in MCD43B4 (Mu et al., 2007; Scharlemann et al., 2008). These data sets are available from the EDENext project (http://www.edenext.eu) and comprise monthly averages of the enhanced vegetation index (EVI), the normalised vegetation index (NDVI), day and night time land surface temperatures as well as a middle infra-red. The latter reflects the water content within vegetation. All data sets reflect monthly averages of original scans collected between 2001 and 2005. Using the *dismo* and *raster* packages for Cran R (Hijmans et al., 2012b; Hijmans & van Etten, 2012), we computed a new derived set of variables describing annual seasonal variation such as annual averages and minimum and maximum scores per month. As study area we defined the island of Cyprus and assessed multi-colinearity by computing pairwise coefficients of determination based on Spearman rank correlations. Out of the comprehensive set of predictors we selected a subset of eleven variables with r^2<0.75 (minimum middle infrared score of three consecutive months [ED1503_bio11]; minimum monthly middle infrared score [ED1503_bio6]; mean temperature of warmest quarter [ED150708_bio10]; mean temperature of coldest quarter [ED150708_bio11]; isothermality [ED150708_bio3]; temperature annual range [ED150708_bio7]; minimum NDVI score of three consecutive months [ED1514_bio11]; NDVI annual range [ED1514_bio7]; annual mean of EVI[ED1515_bio1]; maximum EVI score of three consecutive months [ED1515_bio10]; minimum EVI score of three consecutive months [ED1515_bio11]). Ensemble species distribution models were computed with the *biomod2* package v.2.1.15 (Thuiller et al., 2013) for Cran R. The following seven algorithms were used: 'Artificial Neuronal Networks' (ANN), 'Generalised Additive Models' (GAM), 'Generalised Boosting Models' (GBM), 'Generalised Linear Models' (GLM), 'Multivariate Adaptive Regression Splines' (MARS), 'Surface Range Envelopes' (SRE) and 'Maxent'. Species records were randomly split into subsets of 80% used for model training and 20% for model evaluation with five iterations per algorithm and three different sets of 1000 randomly selected pseudo-absence records. We evaluated model performance with AUC, 'Cohen's Kappa' and the 'True Skill Statistic' (TSS) (Allouche et al., 2006). Subsequently, a weighted ensemble was computed based on all SDMs with ROC>0.7. As a presence/absence threshold, we computed an optimised cut-off score based on the overall AUC score.

To compare the predicted habitat quality of the Kyrenia Range and the Troodos Range, we retrieved Maxent/Ensemble values for all 1 km^2 grid cells north and south of a cut-off line at 35.23°N. We then removed missing data points and Maxent/Ensemble values that were smaller than 0.10, because we reasoned that values below this threshold indicate habitats that are clearly not suitable for the Cyprus whip snake. With this methodology, all remaining Maxent/Ensemble values refer to the areas of the Troodos and Kyrenia ranges.

RESULTS

Distribution of the Cyprus whip snake

The distribution of the Cyprus whip snake based on the records reported in this study is shown in Fig. 1A. Records are distributed across the entire extent of the Troodos Range, with a few records from the southeastern and northeastern foothills (records #4 and #15, Fig. 1A). Habitats in the core of the distribution range (Fig. 1B) appear different from habitats in these peripheral areas (Fig. 1C). Many records seem to be concentrated along stream valleys (see Fig. 2C). The altitude of records ranges from 270–1156 m, with most records around 700–800 m.

Species Distribution Models

Our initial distribution model (Fig. 2A) had an AUC value of 0.895, and gave high Maxent values for most known localities of occurrence. However, four records in the foothills of the Troodos Range (#3, 4, 15, 35 in Fig. 1A) had low Maxent values (0.10–0.23). An analysis of variable contribution revealed that mean precipitation of the driest quarter provided by far the largest contribution to the model (59.9%), while actual evapotranspiration (26.9%), mean temperature of the coldest quarter (6.3%), mean temperature of the warmest quarter (6.1%), and all other variables contributed considerably less.

The Ensemble model (Fig. 2B) had high scores in all three evaluation metrics (Kappa=0.70, TSS=0.826, AUC=0.963). In the SDMs with AUC>0.7, ED1514_bio11 had the highest contribution (51.3%), followed by ED1503_bio6 (26.4%), ED150708_bio7 (23.1%), ED1514_bio7 (20.3%), ED150708_bio3 (14.0%), ED1515_bio1 (13.6%), ED1515_bio10 (13.4%), ED1503_bio11 (12.4%), ED150708_bio10 (11.0%), ED150708_bio11 (10.4%) and ED1515_bio11 (9.3%). Note that variable contribution in biomod2 is estimated based on a permutation approach and reflects relative rankings. Therefore, the total sum is not necessarily equal to 100%.

Since model 2 more accurately represented the range of known distribution records, we proceeded to generate a reclassified version of this model (Fig. 2C). For this purpose, the smallest Ensemble value at a known site of occurrence is chosen as a cut-off value. Values below this cut-off are discarded; all other values are reclassified according to this new range of Ensemble values.

Potential Occurrence Outside the Known Distribution Range

According to both models, the Mesaoria Plain does not provide suitable conditions for the Cyprus whip snake, with Maxent/Ensemble values being 0 or close to 0 across most of the plain. The Kyrenia Range was the only area outside the Troodos Range with values greater than our cut-off of 0.1. We therefore proceeded to quantify and compare the predicted species distribution in the Troodos Range and the Kyrenia Range (Fig. 3).

In both distribution models, Maxent/Ensemble values in the Troodos Range cover the entire range from 0.1–1, reflecting a spatial continuum of predicted habitat quality (Fig. 3A and 3C, respectively). Both models indicate that the Kyrenia Range provides considerably less suitable habitat conditions for the Cyprus whip snake than the Troodos Range. The largest Maxent/Ensemble value inside the Kyrenia Range is 0.535 according to both models, but the distribution of values indicates that most grid cells in the Kyrenia Range exhibit much lower probabilities (Fig. 3B and 3D, respectively). According to the reclassified model 2, the Troodos Range has a much higher fraction of grid cells with Ensemble values equal or greater to the smallest Ensemble value at a known record (Fig. 3E and 3F, respectively), indicating a larger area with suitable habitat quality for the Cyprus whip snake in the Troodos Range.

DISCUSSION

Our species distribution models indicate that suitable habitats for the Cyprus whip snake are largely limited to the Troodos Range in the central part of the island. The Kyrenia Range does mostly not present suitable habitat conditions according to the environmental variables assessed. The models also indicate that the Mesaoria Plain is a strong ecological barrier for the Cyprus whip snake. Together, these data suggest that the Cyprus whip snake is narrowly adapted to environmental conditions in the Troodos Range. If populations exist at all in the Kyrenia Range, they are likely limited to local occurrence and potentially not viable.

The Cyprus whip snake was introduced to science as a new species only in 1985, and consequently not much is known about its distribution and ecological niche (Schätti 1985; Baier et al., 2013). In accordance with previous observations, occurrence of the snake within the Troodos Range is primarily predicted in forested areas with cooler, more humid microclimates at altitudes of 400–800 m. From qualitative records, the Cyprus whip snake has previously been reported to occur from sea level to 1900 m (Baier et al., 2013), but these records have yet to be confirmed with GPS technology. Within this macrohabitat, predicted habitat quality is often maximised close to watercourses, and most of our records were made indeed along streams (see Fig. 2C). While snakes in Cyprus often occur close to water bodies due to the arid climate of the island (Baier et al., 2013), this highlights that the Cyprus whip snake in particular may favour streams as part of its microhabitat. The absence of streams from the core areas of the Kyrenia Range (see Fig. 2C) may explain why habitats in the Kyrenia Range are mostly unsuitable for the Cyprus whip snake.

How can this restricted distribution pattern be historically rationalised? One hypothesis is that the Cyprus whip snake was once distributed over the entire island, but that population size and number somehow severely decreased in all areas of the island except for the Troodos Range. Although early human settlers probably harvested much of the forest in the Mesaoria plain (Meiggs, 1982), we are unaware of historic evidence for environmental changes or other factors that selectively affected the Kyrenia Range more drastically than the Troodos Range. In addition, according to this line of reasoning one could still imagine that patches of suitable habitat and isolated viable populations remained in the Kyrenia Range, which is not consistent with our species distribution models and our knowledge of the distribution of the Cyprus whip snake. Still, if only patchy suitable habitats and low population density existed in the Kyrenia Range from the beginning, deforestation or other drastic environmental changes may have completely wiped out these populations.

A different hypothesis rationalises the restricted distribution of the Cyprus whip snake with a period of transient isolated evolution that led to narrow ecological adaptation to the Troodos Range and prevented subsequent range extension across the island. According to this hypothesis and consistent with our results, species distribution modelling should not predict suitable habitat quality elsewhere on the island if the environmental differences between the Troodos Range and the rest of the island persisted since the time of isolated evolution. When could this transient isolated evolution have happened? Phylogenetic analyses position the

Cyprus whip snake next to *Hierophis gemonensis* on the Balkan Peninsula and *Hierophis viridiflavus* in the West Mediterranean region, which together form the sister clade of *Hierophis spinalis* in the eastern Palaearctic (Schätti & Monsch, 2004, Utiger & Schätti, 2004). Although detailed phylogeographic analyses are not yet available, the considerable morphological divergence of the Cyprus whip snake from these congeneric relatives supports the theory of its isolation in Cyprus since the Messinian Salinity Crisis (MSC, 5.59–5.33 mya) (Utiger & Schätti, 2004). During the MSC, the Mediterranean Sea was completely desiccated, and terrestrial immigration over the sea floor was probably possible (Hadjisterkotis et al., 2000; Poulakakis et al., 2013). The Troodos Range emerged above sea level possibly approximately 22 mya, while the Kyrenia Range only emerged during the late Pliocene to early Quaternary (approximately 2–4 mya) (McCallum & Robertson, 1990; Robertson & Xenophontos, 1993). Separated by a shallow sea strait, these structures evolved independently for a further period of time, and were united to become a single island only during the early Quaternary (<2.6 mya) (Robertson & Xenophontos, 1997; McCallum & Robertson, 1990). Ancestors of the Cyprus whip snake that arrived during the MSC thus likely settled on the “proto-island” that gave rise to the Troodos Range, because the Kyrenia Range had not yet risen above sea level at that time (McCallum & Robertson, 1990). Speciation during the time between the MSC and the rise of the Kyrenia Range could have led to close adaptation to conditions in the Troodos Range. As a result, even if individuals spread across the island after the rise of the Kyrenia Range and the creation of modern Cyprus, viable populations may have only survived in the Troodos Range because of unsuitable habitat conditions elsewhere. This hypothesis also advocates the presence of other species that are endemic to Cyprus and only occur in the Troodos Range. Indeed, several such species exist, e.g., the carabid beetles *Trechus cyprinus* (Franz, 1987), *Trechus olympicus* (Piochard de la Brûlerie, 1876), *Tachys cyprius* (Coulon, 2004) and *Bembidion cyprium* (De Monte, 1949, Austin et al., 2008).

At present, the implications of the two-island origin of Cyprus for the biogeography of the island are not well understood. More studies are thus needed that determine the phylogeographic age of the endemic species of Cyprus and provide information on environmental conditions in the past. Overall, the Troodos Range may be unique in Cyprus in “nurturing” species that are not only endemic to Cyprus, but also “endemic to Troodos”.

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