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Cyprus Lizards: Patterns of distribution, endemic species habitat suitability modelling and conservation implications

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Abstract. Considering the limited information on the distribution of Cyprus' lizards, especially on endemic and endangered species, herein we explore their spatial patterns, with the aim of addressing this knowledge gap and contributing to informed conservation of the species as they face increasing pressure and threats. We recorded the eleven species present on the island, belonging to five families, of which two are endemic species (i.e. *Laudakia cypriaca*, *Phoenicolacerta troodica*) and four are endemic sub-species (i.e. *Ablepharus budaki budaki*, *Acanthodactylus schreiberi schreiberi*, *Mediodactylus orientalis fitzingeri*, *Ophisops elegans schlueteri*), including one listed as endangered by IUCN. We present new species occurrences and maps for all species, resulting from our extensive systematic survey in 2009. As a novelty, for the lizards and the island, we conducted species distribution modelling (SDM) for five endemic taxa. We used the maximum entropy algorithm (MaxEnt), with a combination of selected environmental predictors and user-defined parameter settings. We provide potential habitat suitability maps and investigate the role of environmental predictors influencing the possible species' distribution. We conclude that temperature, precipitation and vegetation have the most important influence in predicting habitat suitability. We propose five subregions, as a general pattern of differing habitat suitability for lizard species on the island. We discuss the added value and conservation implications of new knowledge and datasets we provide.

Key words: lizards, Cyprus, SDM, MaxEnt, species occurrences, habitat suitability, endemic, conservation.

Introduction

In the past decades, many reptile species have come under severe pressures and threats from factors, such as habitat loss and degradation, climate change and introduction of invasive species (Cox et al., 2022; Farooq et al., 2024), that can negatively affect their distribution. Roll et al. (2017) in analyzing global reptile distribution, highlight the need for integration of reptiles into conservation planning and targeted action plans for their effective protection, especially lizard endemic species. Caetano et al. (2022) stress the underestimated extinction risk of reptile species, as reports assess roughly 20% of the Squamata species are threatened (Cox et al., 2022).

Reptiles, as important components of ecosystems and biodiversity can be used as indicators of environmental health (Farrooq et al., 2024) and as ectotherms to assess the effects of climate change due to global warming (Wilms et al., 2011) in diverse ecosystems. Thus, the need to improve primary knowledge is imperative, to elucidate spatial patterns in distributions, habitat suitability, and composition of various lizard communities in different ecosystems as well as the threats they face, globally (Meiri et al., 2023). Hence, informed conservation decisions can be taken, appropriate management strategies and evidence-based practices can be designed and applied, not limited to: preserve species and their habitats, deal appropriately and effectively with the effects of climate change, habitat loss and fragmentation, land-use changes and the spread of invasive, alien species (Guisan et al., 2013).

Research to elucidate spatial patterns of lizards focused on climatic, topographical and landscape factors (e.g. temperature, precipitation, altitude, vegetation, microhabitat) or their combination (e.g. Alatawi et al., 2020; Sanchooli, 2017). Most of the studies suggest that temperature, as expected, is (directly and/or indirectly) the most important among these factors.

Cyprus, the third largest island (9251 km^2) in the Mediterranean, a hotspot biodiversity area (Myers et al., 2000), lies at the crossroads of three continents, surrounded by the Levant Sea. It's unique geographic position, geological evolution and long-lasting isolation from neighboring land areas, along with the intense Mediterranean climate, have formed a variety of abiotic conditions, resulting in a multitude of different landscapes, a rich biodiversity of species and ecosystems and a relatively high endemism in various taxa (Sparrow & John, 2016). It has an interesting lizard fauna of eleven species from five families i.e. Agamidae: *Laudakia cypriaca* (Daan 1967), Chamaeleonidae: *Chamaeleo chamaeleon* (Linnaeus 1758), Gekkonidae: *Hemidactylus turcicus* (Linnaeus 1758) and *Mediodactylus orientalis* (Stepánek 1937), Lacertidae: *Acanthodactylus schreiberi* (Boulenger 1878), *Ophisops elegans* (Ménétries 1832) and *Phoenicolacerta troodica* (Werner 1936), Scincidae: *Ablepharus budaki* (Göcmen, Kumlutas & Tosunoglu 1996), *Chalcides ocellatus* (Forskål 1775), *Eumeces schneiderii* (Daudin 1802) and *Heremites vittatus* (Olivier 1804) (Kotsakiozi et al., 2024; Uetz et al., 2023). Two are endemic species (i.e. *L. cypriaca*, *P. troodica*), and four are endemic sub-species (i.e. *A. b. budaki*, *A. s. schreiberi*, *M. o. fitzingeri*, *O. e. schlueteri*). As for species protection and conservation, five are included in the related EU Habitat Directive's (92/43/EEC) Annexes for the Natura 2000 (N2K) network while endemic *A. schreiberi* is listed as endangered in the IUCN red list and several others are protected by other biodiversity related conventions (Table S1 Supplementary Material-SM).

Systematic surveys addressing conservation implications on lizard species in Cyprus are limited and habitat/species/area specific (Erotokritou et al., 2024; Michaelides & Kati, 2009). A compilation of species records and biology (Baier et al., 2013; Nikolaou et al., 2014; Zotos et al., 2023) as well as basic knowledge on the ecology (Karameta et al., 2022a), ethology (Savvides et al., 2019), systematics and phylogeography (e.g. Karameta et al., 2022b; Kotsakiozi et al., 2024; Poulakakis et al., 2013,) of some species exists in the literature. However, we identify gaps in knowledge of their distributions and the influence of environmental factors, while recognizing the (relatively) high endemism and the presence of threatened species.

Our objective is to contribute to filling the knowledge gaps, by providing new occurrence maps for all the species and by identifying potentially suitable habitats for five endemic lizard species in Cyprus, for the first time through Species Distribution Modeling (SDM).

In the last two decades, SDM is a favorite approach of investigating the species–environment relation (Soley-Guardia et al., 2024) and it encompasses a set of theories and tools valuable for application in biogeography, ecology, conservation and biology (Franklin, 2023). We used the maximum entropy algorithm (MaxEnt), a machine learning method that utilizes presence-only data and a "background" sample of environments, in the geographical area of interest, to model the potential habitat suitability under the influence of selected explanatory environmental variables (predictors) (Elith et al., 2011; Phillips et al., 2006). We address questions of habitat suitability for each species and discuss the factors influencing it. On this basis and our expert opinion, we discuss the resulting spatial patterns, with reference to protected areas of the N2K network, along with conservation implications. Hence, we aim to guide further targeted field surveys and area prioritizing as a keystone for improved species conservation and protected area management planning.

Materials and methods

Study area

We conducted field surveys in an area extending 5900 km^2 (areas under the effective control of the Republic of Cyprus). The island is characterized by unique geomorphology (Troodos ophiolite mountain range - central-southwest, Pentadaktylos mountain range - north coast, Mesaoria central plain) and intense, temperate Mediterranean climate (Sparrow & John, 2016). We applied a numbered 1 km × 1 km grid on a Cyprus map (scale 1:100000) and selected 100 study areas for field surveys by random numbers. From this selection, we have excluded non accessible areas (e.g. military areas, ports, airports, enclosed private lands, highly dangerous to access sites and densely inhabited urban areas). Finally, we visited 93 areas and made equal search efforts performing four random transects in each study area. Each transect was at least 500 m from the end of the previous transect, in a different orientation and not overlapping. Transects with missing or ambiguous data were disregarded. We recorded species occurrences for training the models only in areas under the effective control of the Republic of Cyprus, while the projections were on the whole island.

Field surveys

We conducted 45 days of field surveys between June and September 2009, which coincide with the breeding period of eight of eleven species and their expected overall peak activity (Baier et al., 2013). We performed a Visual Encounter Survey (VES) along strip transects, 100 m long and 5 m wide (Scott et al., 1994). The same observer walked along each transect once, during morning (8 am – 13 pm) or afternoon hours (4 pm – 7 pm), on sunny days, with minimum cloud cover or wind, documenting each individual. In each transect we assigned one out of four altitude categories (0-499 m, 500-999 m, 1000-1499 m, ≥1500 m up to 1952 m) and one of four vegetation categories based on grouped CORINE land cover level 2 classes (phrygana, maquis, forest, other such as cultivated land/crops/pastures/open spaces). In addition, other abiotic (e.g. atmospheric temperature and relative air humidity at 15 cm above soil) and biotic factors (e.g. characteristic plant species present), were documented at the start of each transect.

Species occurrences and Environmental Predictors Data

We digitized the species occurrence data and processed them, in R software (Vers 4.3.3) (R Core Team, 2024), through the "dismo" package (Hijmans et al., 2023), to produce the occurrence maps for all the species (Fig. S1-S11 SM). For the SDM, we also used QGIS (Vers 3.34.7 LTR) (QGIS.org, 2024) and MaxEnt (Vers 3.4.1) (Phillips et al., 2006).

We excluded repeated occurrences for each species per transect to avoid spatial pseudo replication. For the SDM we canvassed the study area with a 1 km^2 grid and applied spatial filtering to exclude duplicate records in each cell, thus reducing sampling bias due to spatial autocorrelation. All data were set, to a common coordinate reference system (WGS84), cell size (1 km^2) and spatial extent (Cyprus).

Model building and evaluation in MaxEnt

We chose the MaxEnt algorithm, considering it appropriate for our data collection, as it's a reliable, presence-only data approach that can use both continuous and categorical predictor variables and their interactions (Elith et al., 2011; Phillips et al., 2006), has many easily user-defined parameters (Merow et al., 2013), has settings for protection against overfitting of the model (Merow et al., 2013; Radosavljevic & Anderson, 2013) and shows comparatively good predictive performance (Elith et al., 2011; Valavi et al., 2022) even with biased data (Elith et al., 2011), and small sample sizes (Wisz et al., 2008).

Initially, we selected 29 explanatory predicttors (11 climatic, 18 topographic and landscape related) (Table S2 SM), closely related to the biology/ecology of lizards and known habitat preferences of some species under study for the SDM. We redacted environmental predictors considered to exhibit high collinearity using Spearman's correlation coefficient (r_s>0.75) (Table S3 SM), with the "removeCollinearity" function of the "virtualspecies" package (Leroy et al., 2016) in R software (R Core Team, 2024) (Fig. S12 SM). Then, through an iterative SDM approach we redacted more explanatory predictors, we considered not contributing to the models' predictive ability (Jorcin et al., 2019), resulting in a final set (Table 1) of which each species had a unique combination (see column Environmental Predictors, Table 2). To evaluate the environmental predictors' importance in this stepwise procedure and in the final models, we considered the calculated percentage and permutation importance of the predictors (Tables S4-S8 SM), the jackknife tests on gain for the training data, the test data and the AUC (Area Under the Curve) on test data (Fig. S13, S17, S21, S25, S29 SM), and their response curves (Fig. S14, S18, S22, S26, S30 SM).

Table 1. Environmental predictors used in final SDM (a different combination was selected for each species).

Climatic predictors	
Predictor	**Source**
BIO1 = Annual Mean Temperature BIO2 = Mean Diurnal Range (Mean of monthly (max temperature-min temperature) BIO12 = Annual Precipitation	WorldClim (Fick & Hijmans, 2017) (Version 2.1 January 2020 - http://www.worldclim.org/)
Topographic and landscape predictors	
Predictor	**Source**
Mean NDVI for month of March or July Mean_NDVI_03 or Mean_NDVI_07	MODIS Vegetation Index Products - hypertemporal Normalized Difference Vegetation Index (NDVI) - Mean monthly - mean of 15 years – 2000-2014, (https://modis.gsfc.nasa.gov/)
Corine Land Cover 2006 - Code Level 2 - CLC2006	Vegetation index - Corine Land Cover 2006-Copernicus (Code level 2 categories for Cyprus) (https://land.copernicus.eu/paneuropean/corine-land-cover)
Distance from wetlands - wetlands	Distance from water bodies (https://www.cypruswetlands.org/)

Table 2. Model building parameters as selected for the final model in each species.

Endemic species	Number of species occurrences	Data partitioning: training data/test data*	Feature classes and regularization multiplier (RM) **	Environmental predictors
A. budaki	26	60%/40% (16/10)	LQ 2	Mean_NDVI_07, bio01, bio12, wetlands
A. schreiberi	44	75%/25% (33/11)	QT 1	CLC2006 (categorical), bio01, bio02, wetlands
L. cypriaca	53	60%/40% (33/20)	QT 2	Mean_NDVI_03, bio01, bio02, bio12
O. elegans	118	50%/50% (59/59)	QT 1	CLC2006 (categorical), Mean_NDVI_03, bio01, bio02, bio12
P. troodica	92	50%/50% (47/45)	QT 5	CLC2006 (categorical), Mean_NDVI_03, bio01, bio02, bio12

* *In () the number of point occurrences used for training/testing*
** *L – linear, Q – quadratic, T – threshold, RM coefficients 1-5*

We aimed for simple predictive models (*sensu* parsimony principle, mentioned by Phillips et al. (2006)) and to balance each model's complexity and robustness while minimizing overfitting. As best practice, species-specific fine-tuning of model parameters (Morales et al., 2017) can improve the performance of SDMs (Radosavljevic & Anderson, 2014; Shcheglovitova & Anderson, 2013), we performed multiple exploratory models to finally choose a unique combination of parameters for each species.

We fitted models with several combinations of parameters (data partitioning, regularization, feature classes). Since we were comparing single species models of same data and spatial extend, to choose the final model and evaluate the model's credibility and fit, we used three model accuracy metrics and our expert opinion. We relied on AUC values (i.e. AUC on Training data - AUC_{Train}, AUC on Test data - AUC_{Test}) of Receiver Operating Characteristic (ROC) plots a common threshold-independent method (Phillips et al., 2006), along with threshold dependent metrics of the omission rates (OR) for the training and test data on Minimum Training Presence (ORMTP) and 10th percentile Training Presence (OR_{10}) (Radosavljevic & Anderson, 2014) and the AUC_{Diff} (the difference between - AUC_{Train} and - AUC_{Test}) that are reported indicators to potential overfitting (Anderson & Gonzalez, 2011).

Finally, we evaluated the maps of potential habitat suitability for each species, based on the ecology of the species and our expert opinion.

Results

Species occurrences and maps

We recorded 1960 individuals representing all lizard species in Cyprus, during 335 transects. The occurrence maps for all species illustrating new presence areas are illustrated in Fig. S1-S11 SM.

SDM for five endemic species

We provide maps of predicted habitat suitability for each endemic species (Fig. 1). We present the set of AUC evaluation metrics and omission rates for each model in Table 3 and ROC plots (Fig. S15, S19, S23, S27, S31), omission rate plots (Fig. S16, S20, S24, S28, S32) in SM.

***A. budaki*:** precipitation (BIO12) followed by mean daily temperature (BIO01) and average daily temperature range (BIO02), are more important predictors for this species occurrence, followed by vegetation index (Mean_NDVI_07) and distance from wetlands (wetlands). We notice a positive correlation of species occurrence with the increase in vegetation index, while negative with the increase in mean daily temperature and variability and distance from wetlands.

***A. schreiberi*:** mean daily temperature and average daily temperature range, are more important predictors, followed by land cover – vegetation (CLC2006), and distance from wetlands. Species occurrences seem to be positively correlated with specific classes of CLC2006, negatively with the increase of the distance from wetlands and with the increase in mean daily temperature and variability, beyond a certain value.

***L. cypriaca*:** precipitation and mean daily temperature are more important, followed by vegetation index (Mean_NDVI_03) and average daily temperature range. Species occurrences seem to be, beyond a certain value, negatively correlated with the increase of the vegetation index and mean daily temperature variability and negatively with the increase of mean temperature. Interestingly, it appears to be positively related to the increase in precipitation.

***O. elegans*:** precipitation and vegetation index (Mean_NDVI_03) as more important predictors, followed by average daily temperature range and then land cover - vegetation (CLC2006) and mean temperature. We observe a positive correlation of species occurrences with specific classes of CLC2006 and negative with the increase of mean daily temperature and variability. It is initially positively and then negatively correlated with the increase in vegetation index. It appears to be positively related to the increase in precipitation.

***P. troodica*:** the more important predictors are average daily temperature range and mean daily temperature, precipitation, followed by vegetation index (Mean_NDVI_03) and finally land cover - vegetation (CLC2006). Species occurrence seems correlated with specific classes of the CLC2006. It is initially positively and then negatively correlated with the increase of Mean_NDVI_03 and negatively correlated beyond a certain value with the increase of mean daily temperature and variability. It seems to be positively related to the increase in precipitation.

Discussion

Habitat suitability patterns

We deduce that the habitat suitability patterns for endemic lizards in Cyprus, show three prominent features that deserve further attention. Firstly, our species occurrence records are well documented, validated and maps are congruent to the literature so far (Baier et al., 2013; Nicolaou et al., 2014; Zotos et al., 2023). The new occurrences are found mostly in areas south of Troodos massif and some on the higher elevations (>1200 m) as well as in areas of the southeast coast and fewer in the west. The total, raw species occurrence data will be contributing to the expansion of the Cyprus Herp Atlas (Zotos et al., 2023) and are readily available for further use. Spatial patterns of the six species not included in the SDM, namely *C. ocellatus*, *C. chamaeleon*, *E. schneiderii*, *H. turcicus*, *H. vittatus*, *M. orientalis*, need further investigation with more intensive, area - specific systematic research and differentiated methodology for nocturnal and cryptic species.

Secondly, the resulting models seem to predict well the potential suitable habitats for the five endemic lizards, as discussed below. In the model building, we chose the settings with the goal of balancing the models' fit to the data and the models' predictive ability to produce reliable results. All the models had AUCTest values > 0.7 indicating the models' good fit to the testing data (Phillips et al., 2006) and AUCTrain values were > 0.8 (except for *O. elegans* with AUCTrain=0.794 - only marginally noted as good), we note that the discriminative ability of all the models is very good, and they have a good fit to the training data. We conclude that the OR during the training and testing of each of the models have values close to zero for the ORMTP and for OR10 ≤ 0.10, in most models. Thus, considering also the map predictions and our expert opinion, we assess that the models are credible and not prone to overfitting except for a minimal overfitting indicated in the testing data for *A. budaki*, *O. elegans*, *P. troodica*. We suggest that this might be due to a small sample of occurrences for *A. budaki* and the widespread nature of the distribution of *P. troodica* and especially *O. elegans*. Moreover, we assess that the overfitting in our models is minimal due to the very low values of AUCDiff. In addition, we note the rejection of the null hypothesis that our models predict the distribution of the species like random models, as the p-value < 0.05 in all the models (Table 3).

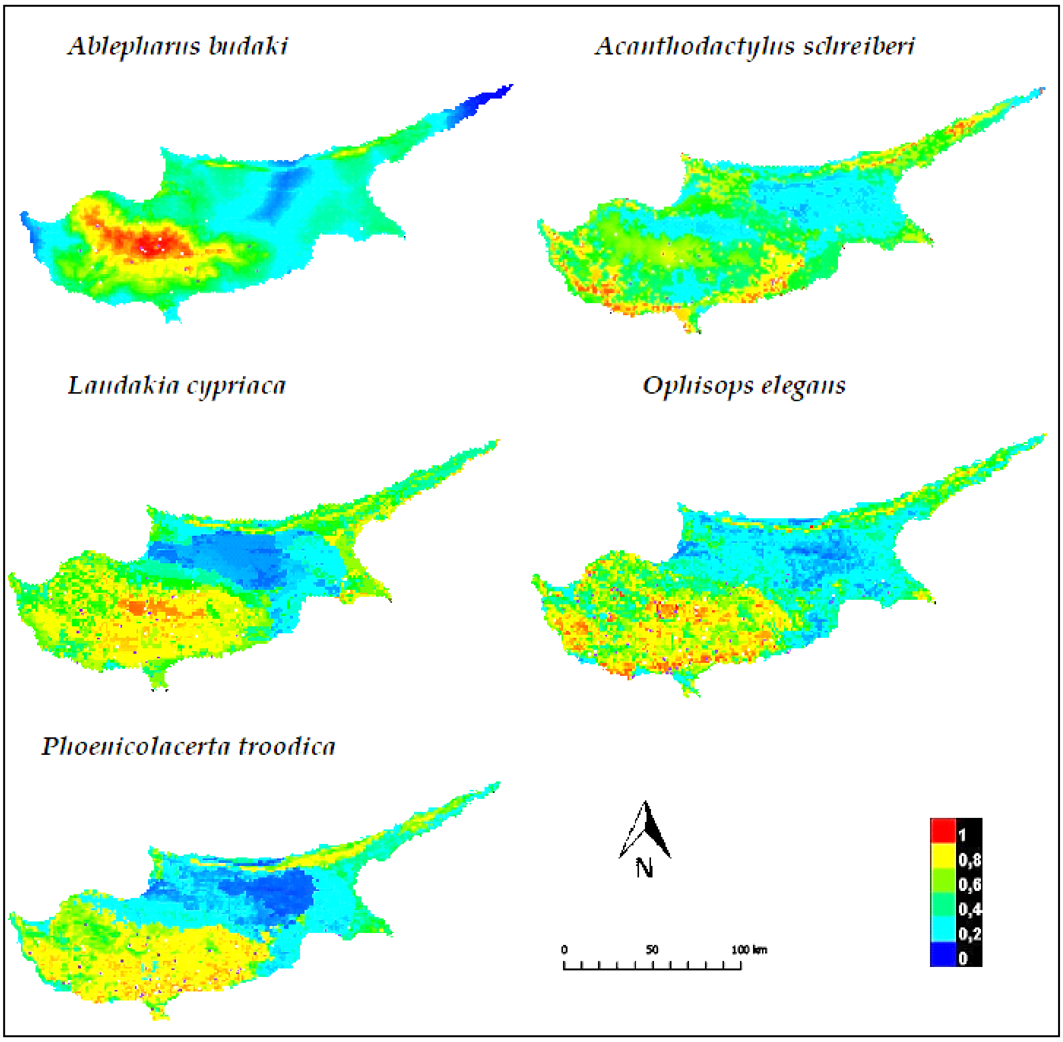

Fig. 1. Species maps for predicted habitat suitability (Predicted habitat suitability ranges from 0 – blue, lowest suitability to 1 – red, highest suitability.

Table 3. Evaluation metrics – AUC and OR.

Endemic species	AUC $_{Train}$	AUC $_{Test}$	AUC $_{Diff}$	Threshold*	Training OR**	Test OR	p-value
A. budaki	0.810	0.772 (s.d.0.071)	0.038	**MTP** **10% TP**	0.000 0.062	0.100 0.100	1.413E-2 8.379E-3
A. schreiberi	0.794	0.740 (s.d.0.062)	0.054	**MTP** **10% TP**	0.000 0.091	0.000 0.091	1.773E-2 1.852E-2
L. cypriaca	0.803	0.793 (s.d.0.034)	0.010	**MTP** **10% TP**	0.000 0.091	0.000 0.100	4.183E-4 3.435E-5
O. elegans	0.808	0.730 (s.d.0.029)	0.078	**MTP** **10% TP**	0.000 0.085	0.034 0.102	1.482E-4 1.457E-5
P. troodica	0.813	0.792 (s.d.0.026)	0.021	**MTP** **10% TP**	0.000 0.085	0.022 0.111	1.72E-6 2.864E-10

**MTP - Minimum Training Presence, 10% TP - 10th percentile Training Presence **OR - Omission Rate*

Thirdly, we conclude the most important predictors in SDM are the mean values and variability in temperature (BIO01 and BIO02), but also the annual precipitation (BIO12). Then follows vegetation land cover through the CORINE vegetation classes but also its health and density through the NDVI indices. In various parts of the world, studies have found similar results to ours, even where the typical environmental characteristics are very different from those in Cyprus. Indicatively, Sillero & Carretero (2013) concluded that temperature was an important predictor for SDM of *Podarcis carbonelli* in the Iberian Peninsula. Javed et al. (2017) in investigating the distribution of *Calodactylodes aureus*, state that temperature variability (i.e. mean daily temperature range BIO02) was one of the best predictors. Jorcin et al. (2019), through an iterative selection of predictors similar to ours, conclude that the distribution of the threatened *Timon lepidus* in France is influenced primarily by climatic variables of precipitation and temperature. Chmelař et al. (2020) report as influential predictors variables of temperature and precipitation along with slope, for the critically endangered *Lacerta viridis* in the Czech Republic. Farquhar et al. (2023) reported temperature seasonality as the main variable predicting the distribution of *Lampropholis delicata* in Australia.

***A. budaki*:** potential suitable habitats for the species are mainly located in areas with wetter conditions (i.e. more precipitation, near wetlands, riparian habitats), lower temperatures and greater vegetation cover in summer (e.g. evergreen vegetation such as coniferous forests and denser maquis vegetation, with dense ground cover and thick leaf litter). Sanchooli (2016) concludes that the distribution patterns of a same genus species, *Ablepharus bivittatus* in Iran, are determined mostly by climatic factors (variables regarding precipitation, temperature and its variability) and habitat slope.

***A. schreiberi*:** is expected to be found in areas with higher temperatures, even more intense thermal variability, from which it seems not to be negatively affected but up to a point. As expected, and previously reported (Baier et al., 2013), more suitable areas for its distribution appear to be coastal areas and lower altitudes, especially areas with sand dunes or sparser vegetation that nonetheless offer sufficient shelter e.g. burrows, based on the effect presented by the CORINE land cover classes and the map of potential habitat suitability. We also expect and report it to be present near rivers (even in the riverbed when there is no water flow), congruent to findings in Michaelides & Kati (2009), or wetlands, most likely due to the presence of suitable substrate and/or abundance of food sources, something we note needs further investigation. Erotokritou et al. (2024) also report that greater abundance of the species is positively related to riparian areas inside N2K network and on lower elevations suggesting maybe effectiveness of conservation actions, something we believe is questionable and needs further investigation to a greater scale to confirm.

***L. cypriaca*:** more suitable habitats for the species are in areas that present a greater range of thermal variation up to a point, however. At the same time, we expect the species to be present in a variety of habitats that do not have a particularly high soil cover – more open spaces, as well as sparse *Pinus* sp. forest, where apparently it can find shelter on/in tree trunks or crevices in rocks where it was often found. The great effect that precipitation seems to have on its distribution needs further investigation, as it is otherwise considered a thermophilic species (Karameta et al., 2022a) that prefers more xeric areas. Possibly this is related to elements of its ecophysiology or food availability. Few studies have been carried out in these areas of the species ecology (e.g. Karameta et al., 2022a).

***O. elegans*:** is expected to occur almost everywhere on the island and in a multitude of habitats, as shown by the effect of the CORINE land cover classes. We assume potential habitat suitability to be determined by temperature and its range of variability; however, it does not seem to be affectted as much by precipitation. The most suitable areas for its distribution appear to be those with moderate soil cover by vegetation, even at the highest altitudes. Oraie et al. (2014) found that most important factors influencing the distribution pattern of *O. elegans* in Iran were variables of precipitation, NDVI and sunshine.

***P. troodica*:** the potential habitat suitability for the species follows a similar pattern to *O. elegans*, but precipitation and the daily temperature variability exhibit a stronger influence on it. We deduce that more humid areas and areas with less thermal variability are more suitable. It is expected to occur in a variety of habitats, but those providing more soil cover by vegetation as denser maquis or even forested areas, or riparian habitats seem to be more suitable.

We conclude that habitat suitability for all species is highest in the south, southwest and northwest of the island, as well as areas of the Troodos Mountain range and some areas on the south-east and north-northeast coasts, while most of the central plain Mesaoria presents with the lowest suitability for all species. We notice that overall, the degree of habitat suitability seems to decrease from west to east, especially for areas with parallel decreasing annual precipitation which has similarly been reported by Sanchooli (2016) for *Ablepharus bivittatus* in the central Iranian plateau.

For these reasons, we propose a basic division of the island into five subregions of differing habitat suitability (Fig. 2), related to the different habitat suitability patterns of the endemic species.

We propose that Subregion 4, which is characterized by greater annual thermal variation, drier conditions, very sparse vegetation, therefore less presence and variety of shelters (leaf litter, fallen tree trunks, dry stones, stones/rocks) but also the absence of suitable habitats in general for lizards, it is the most inhospitable and unsuitable for all species. It's highly unsuitable for species such as *A. budaki* (preference for wetter habitats with dense vegetation/high soil cover and shelters such as dense and thick leaf litter) and *L. cypriaca* (preference for habitats with shelters such as trees and rock formations).

We also suggest that Subregions 1 and 2 are characterized as the most suitable for lizard species, as they present milder conditions of thermal variation, sufficient amounts of precipitation and variety of habitats that also offer a wide range of shelters. Overall, the unique riparian ecosystems (Erotokritou et al., 2024) located in the catchment basins of the large rivers in the southwest (i.e. Xeros, Diarizos, Cha River) and a variety of agro-environments (Zomeni et al., 2018) at Troodos foothills which are located mainly in protected areas of suggested Subregions 1 and 2, offer habitats of potentially high suitability for most of the endemic species. These are followed by Subregion 5 with similar conditions to Subregion 1. In Subregion 3, with altitudes above 1200 m, we indicate that all endemic species/subspecies are expected to occur, but above 1400 m we do not expect to usually encounter A. *schreiberi* and beyond 1700 m we expect to meet the two species with the most frequent occurrence and widespread, i.e. *P. troodica*, *O. elegans*, without excluding the possibility of finding *A. budaki* and even *L. cypriaca*.

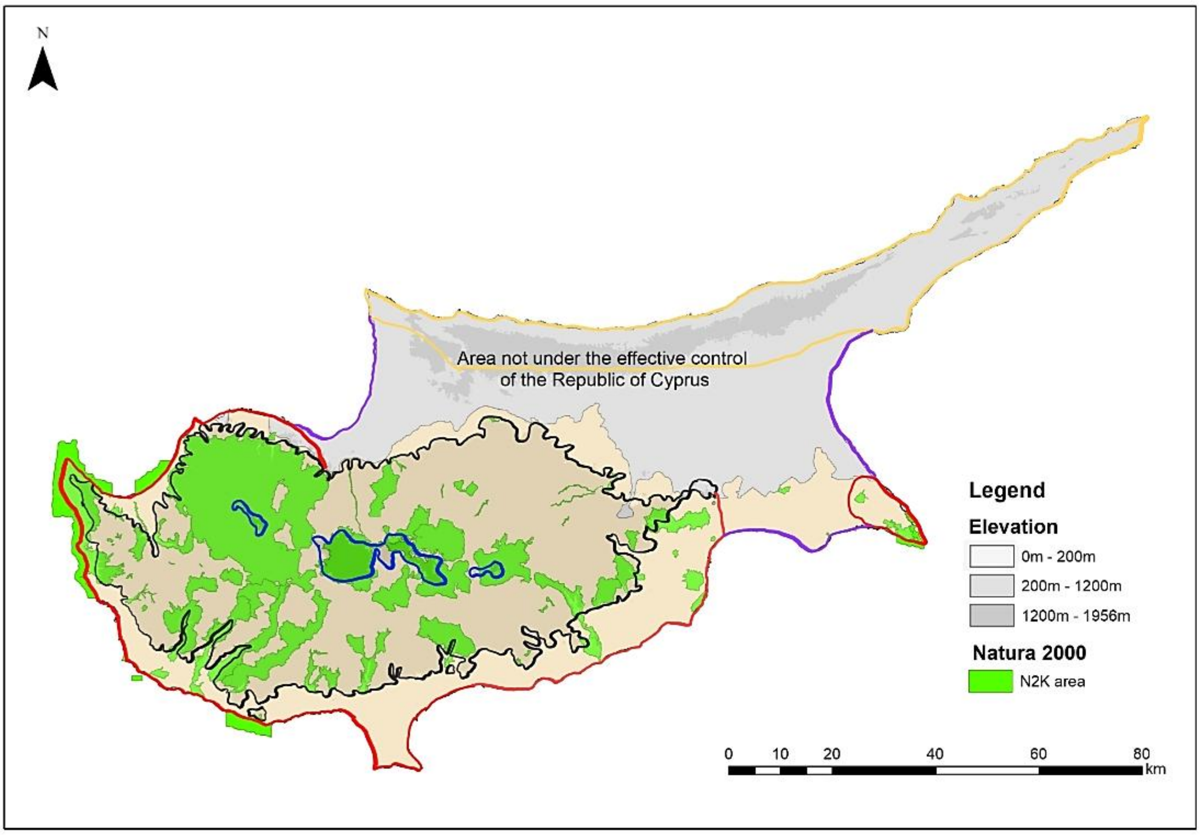

Fig. 2. Map of suggested Subregions (1-5) of differing habitat suitability.

Subregion 1 (red line): Coastal areas up to 200m (south, southwest, west, northwest, southeast - wider area of Cape Greco and wetlands of Lake Paralimni and Lake Oroklini). Characterized by higher average temperature values but a smaller range of variation and great variety of habitats.

Subregion 2 (black line): Areas around the Troodos massif, from 200m to 1200m. Characterized by medium precipitation, temperature and its' range of variation, and a plethora of natural and semi natural habitats (agroenvironments, riparian ecosystems, oak and pine forests, oleo – ceratonion vegetation)

Subregion 3 (blue line): Areas above 1200m with mainly forests (Troodos and Paphos) which are mostly strictly protected areas. Characterized by lower average temperature values, a greater range of variation and high precipitation values and forest vegetation is dominant.

Subregion 4 (purple line): Mesaoria plain and areas on the southeast coast. Characterized (especially the central area of Mesaoria) by greater annual thermal variation, drier conditions, sparse vegetation and less variety of refuges for lizards.

Subregion 5 (yellow line): Karpasia Peninsula (northeast) and north coasts. Characterized by conditions similar to Subregion 1 (though more intense in Pentadaktylos mountain range and Karpasia tip).

Conservation implications

We recognize three aspects of conservation applications that can benefit from our survey and SDM outputs, being: (a) prioritizing areas for targeted surveys and monitoring (Jorcin et al., 2019; Peyton et al., 2022), (b) highlighting protected areas for integrating species occurrences and potential habitat suitability in decisions for concrete management actions (e.g. Chmelař et al., 2020; Lukanov, 2020; Rödder et al., 2016) considering synergies with existing or already planned actions for species (Zotos et al., 2021) or habitats (Christodoulou et al., 2021), (c) suggesting potential investigations (e.g. species distribution and overlap with strictly protected areas) on effectiveness of conservation planning (Carranza et al., 2018).

Knowing the detailed distributions or complementing the occurrence record with SDM (Barends et al., 2020) for endemic lizards and determining which environmental variables are better predictors, is pivotal for establishing conservation priorities in Cyprus. This is more evident in such a diverse environment, isolated and limited in area and resources, where daily temperatures are high and drought is frequent, and apparently more intense recently and even more in the future, in the light of climate change (Vogiatzakis et al., 2016). As Anderson et al. (2022) report, temperate lizard species are more limited in thermoregulating to address heat stress than tropical species. In addition, there is increasing pressure from fires, infrastructure development and overgrazing and habitat loss, degradation and fragmentation are common threats as is desertification in many areas (EIONET 2020; Vogiatzakis et al., 2020). Thus, we can assume that threats and pressures to lizard species in Cyprus, especially the endemics, are on the rise and in need of evaluation.

Limitations and potential optimizations of the study

As explained in the proposed protocol for SDM reporting by Zurrell et al. (2020) and in Soley-Guardia et al. (2024), we acknowledge certain limitations and potential optimizations to our data gathering and processing, model building and evaluation that we suggest considering for future studies. Although in applying our fine-scale systematic sampling (Barends et al., 2020), we tried to minimize the effect of sampling bias, it is unlikely that the predictions will not be affected even slightly. Due to its somewhat cryptic nature the sampling method for *A. budaki* should include hand searching beyond the VES survey to optimize detectability and increase occurrence records and reduce sampling bias. We similarly recommend diversifying the sampling method for extending future SDMs in other cryptic or nocturnal species not modeled herein. We support future use of additional predictors such as qualitative substrate predictors, biotic interactions predictors (e.g. Oraie et al., 2014; Sanchooli, 2016), if they become available to the extent and resolution required to enhance SDM prediction adequately. To increase the credibility of the predictions we suggest evaluating models with non-random and/or spatial partitions of the data (e.g. Valavi et al., 2023).

Conclusions

Despite its small size, Cyprus presents a variety of topographical and bioclimatic conditions, so the occurrence of lizard species is expected to differ from one location to another due to the diversity of resulting habitats. Indeed, we conclude that potentially suitable habitats for endemic lizard species are determined primarily by bioclimatic factors and characteristic patterns extend to suggested subregions. Knowledge emerging from our fine-scale systematic survey, with representative inclusion of different habitats and elevations has filled in occurrence gaps. Also, we believe that our species specific, fine-tuned SDMs along with our expert opinion, give merit to the resulting data in accurately predicting habitat suitability but also to be used, in meaningfully informing conserva-tion decisions and defining priority areas for tar-geted monitoring surveys and concrete manage-ment planning for lizard species in Cyprus, especially the endemics.

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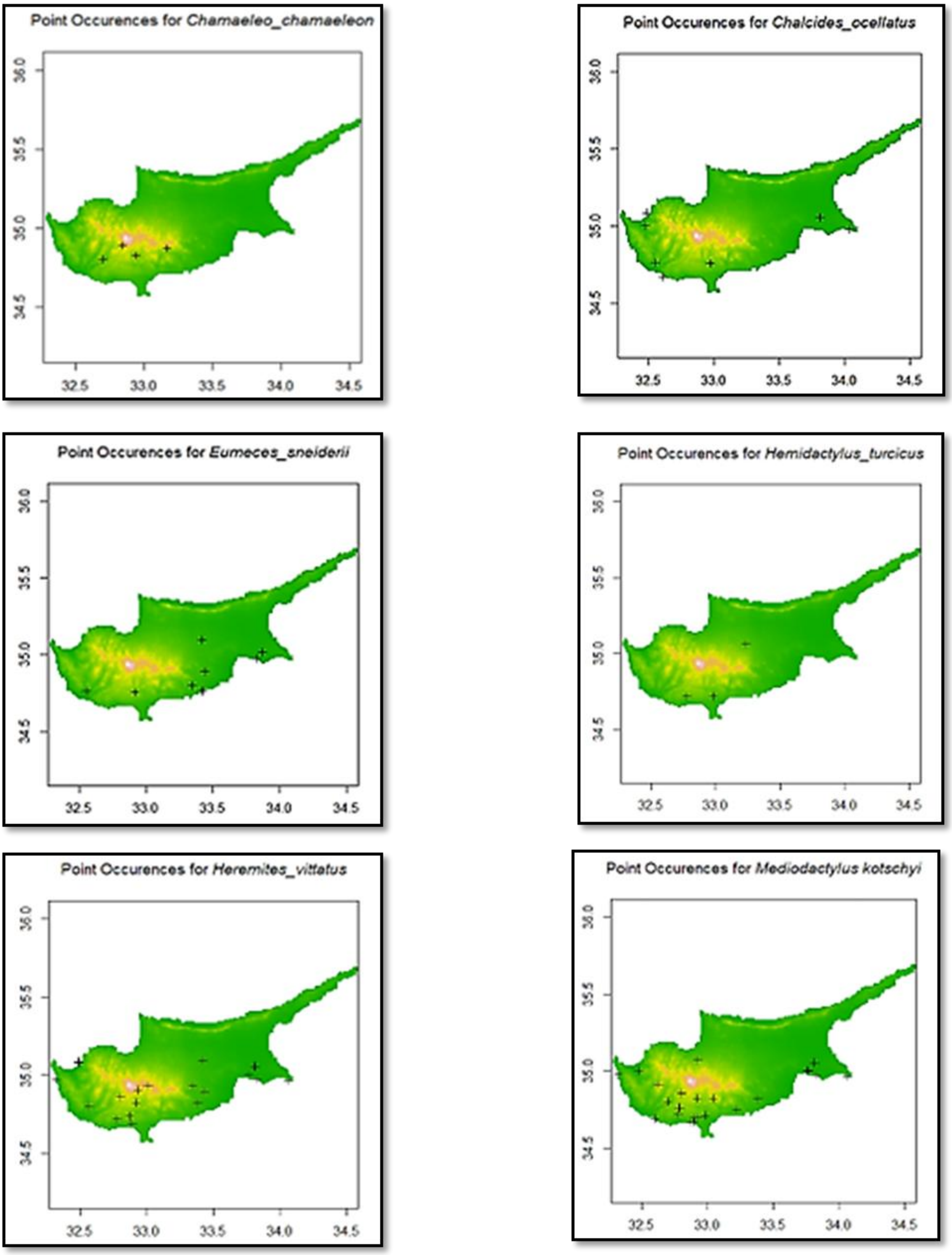
Supplementary material

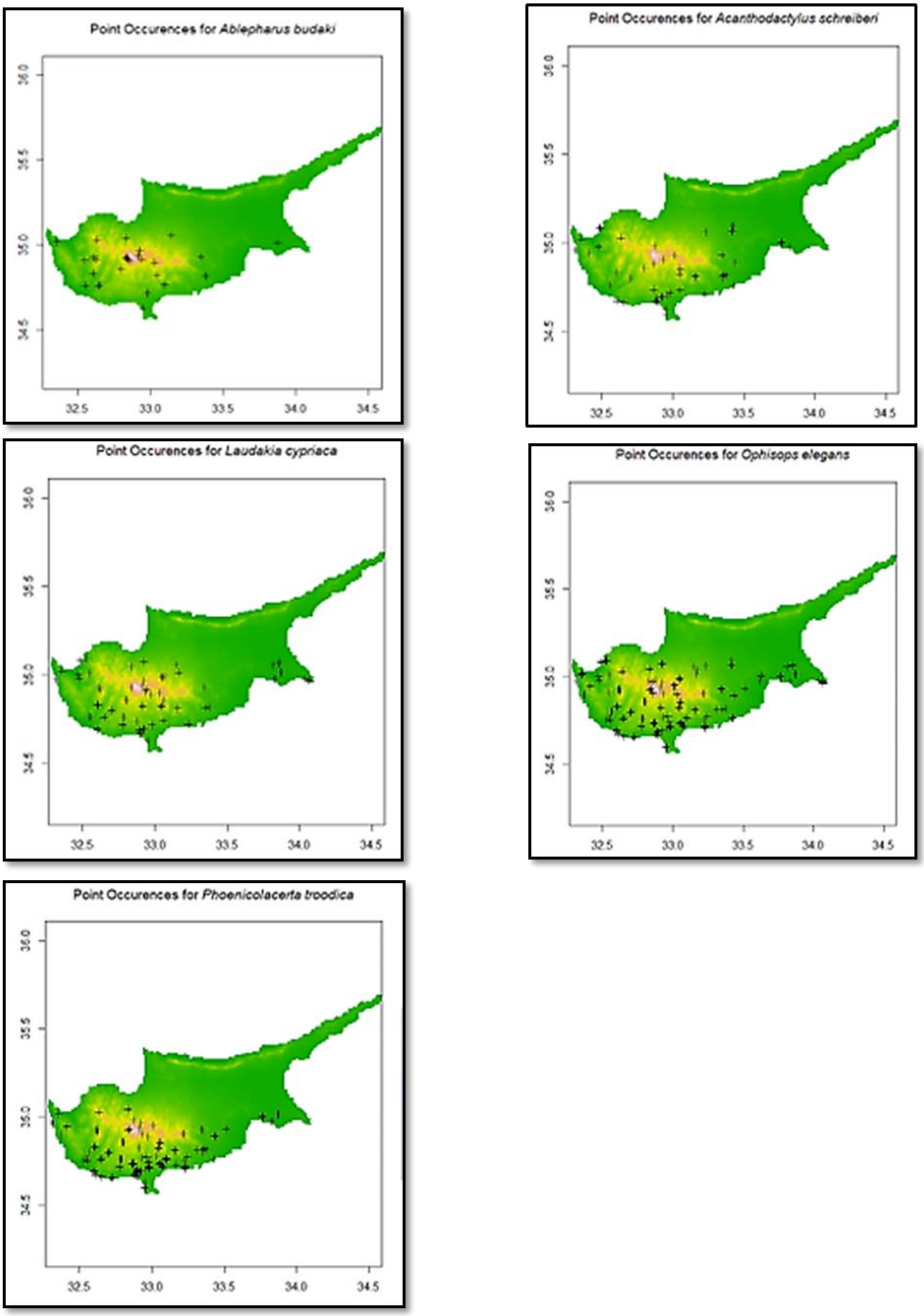
Table S1. Lizard species and their protection/conservation status in Cyprus under National/EU legislation, international conventions and IUCN (COE, 1982; CITES, 1973; EC, 1992; IUCN, 2024; Uetz et al., 2023).

Family	Species	National Law 153(I)/2003 (Annex III) / Habitats Directive 92/43 EC (Annex IV)	Reporting - Article 17 Habitats Directive 92/43 (2013-2018)	Bern Convention (Annex II or III)	CITES Annex II	Red list IUCN
Agamidae	*Laudakia cypriaca****	**-**	**-**	II	-	LC**
Chamaeleonidae	*Chamaeleo chamaeleon*	√	√ **(U1)***	II	√	LC
Gekkonidae	*Hemidactylus turcicus*	**-**	-	III	-	LC
	*Mediodactylus orientalis fitzingeri****	√	√ **(FV)***	II	-	LC
Lacertidae	*Acanthodactylus schreiberi schreiberi****	**-**	-	III	-	**Endangered (EN) - Decreasing****
	*Ophisops elegans schlueteri****	√	√ **(FV)***	II	-	LC
	*Phoenicolacerta troodica****	**-**	-	III	-	LC
Scinkidae	*Ablepharus budaki budaki****	√	√ **(FV)***	II	-	LC
	Chalcides ocellatus	√	√ **(FV)***	II	-	LC
	Eumeces schneideri	-	-	III	-	LC
	Heremites vittatus	-	-	III	-	LC

** ARTICLE 17: U1 - UNFAVOURABLE – INADEQUATE Conservation status, FV – FAVOURABLE Conservation status*
***LC – LEAST CONCERN, EN - ENDANGERED*
****Endemic species/subspecies*



Figures S1-6. Species Occurrences Maps
Chamaeleo chamaeleon, Chalcides ocellatus, Eumeces schneiderii, Heremites vittatus, Hemidactylus turcicus, Mediodactylus orientalis. For these species we preferred not to perform SDM as they had a small occurrence record (n≤20), that might not have produced credible results.



Figures S7-11. Species Occurrences Maps
Ablepharus budaki, Acanthodactylus schreiberi, Ophisops elegans, Laudakia cypriaca, Phoenicolacerta troodica. For these endemic species we performed SDM.

Table S2. Environmental predictors.

Predictor	Source
Climatic predictors	
Predictor	**Source**
1. BIO1 = Annual Mean Temperature 2. BIO2 = Mean Diurnal Range (Mean of monthly (maximum temperature - minimum temperature) 3. BIO5 = Maximum Temperature of Warmest Month 4. BIO6 = Minimum Temperature of Coldest Month 5. BIO10 = Mean Temperature of Warmest Quarter 6. BIO11 = Mean Temperature of Coldest Quarter 7. BIO12 = Annual Precipitation 8. BIO13 = Precipitation of Wettest Month 9. BIO14 = Precipitation of Driest Month 10. BIO16 = Precipitation of Wettest Quarter 11. BIO17 = Precipitation of Driest Quarter	WorldClim (Version 2.1 January 2020 - http://www.worldclim.org/) (Fick & Hijmans, 2017)
Topographic and landscape predictors	
Predictor	**Source**
12-23. Mean NDVI for all 12 months, 1-12 – Mean_NDVI_01-12	MODIS Vegetation Index Products - hypertemporal Normalized Difference Vegetation Index (NDVI) - Mean monthly - mean of 15 years – 2000-2015, (https://modis.gsfc.nasa.gov/)
24. Corine Land Cover 2006 - Code Level 2 - CLC2006	Vegetation index - Corine Land Cover 2006- Copernicus (Code level 2 categories for Cyprus) (https://land.copernicus.eu/paneuropean/corine-land-cover)
25. Forest density – forest_dens	Vegetation Index – Forest density Copernicus (https://land.copernicus.eu/paneuropean/corine-land-cover)
26. Digital Elevation Model (DEM) - dem	DEM - Eratosthenis database
Slopes on terrain - slopes	Slopes - Eratosthenis database
28. Distance from rivers (including smaller streams) – river_dist	Distance from rivers - Eratosthenis database
29. Distance from wetlands - wetlands	Distance from water bodies (https://www.cypruswetlands.org)

Table S3. Collinearity test results.

Highly colinear predictors	Selected predictors
"bio01" "bio06" "bio11" "bio14" "bio17" "dem"	1. "bio01"
"bio02"	2. "bio02"
"bio05" "bio10" "bio12" "bio13" "bio16"	3. "bio12"
"CLC2006"	4. "CLC2006"
"forest_dens"	5. "forest_dens"
"Mean_NDVI_01" "Mean_NDVI_02"	6. "Mean_NDVI_03"
"Mean_NDVI_04", "Mean_NDVI_05" "Mean_NDVI_06", "Mean_NDVI_07" "Mean_NDVI_08", "Mean_NDVI_09" "Mean_NDVI_10", "Mean_NDVI_11" "Mean_NDVI_12"	7. "Mean_NDVI_07"
"Riverdist"	8. "Riverdist"
"slopes"	9. "slopes"
"wetlands"	10. "wetlands"

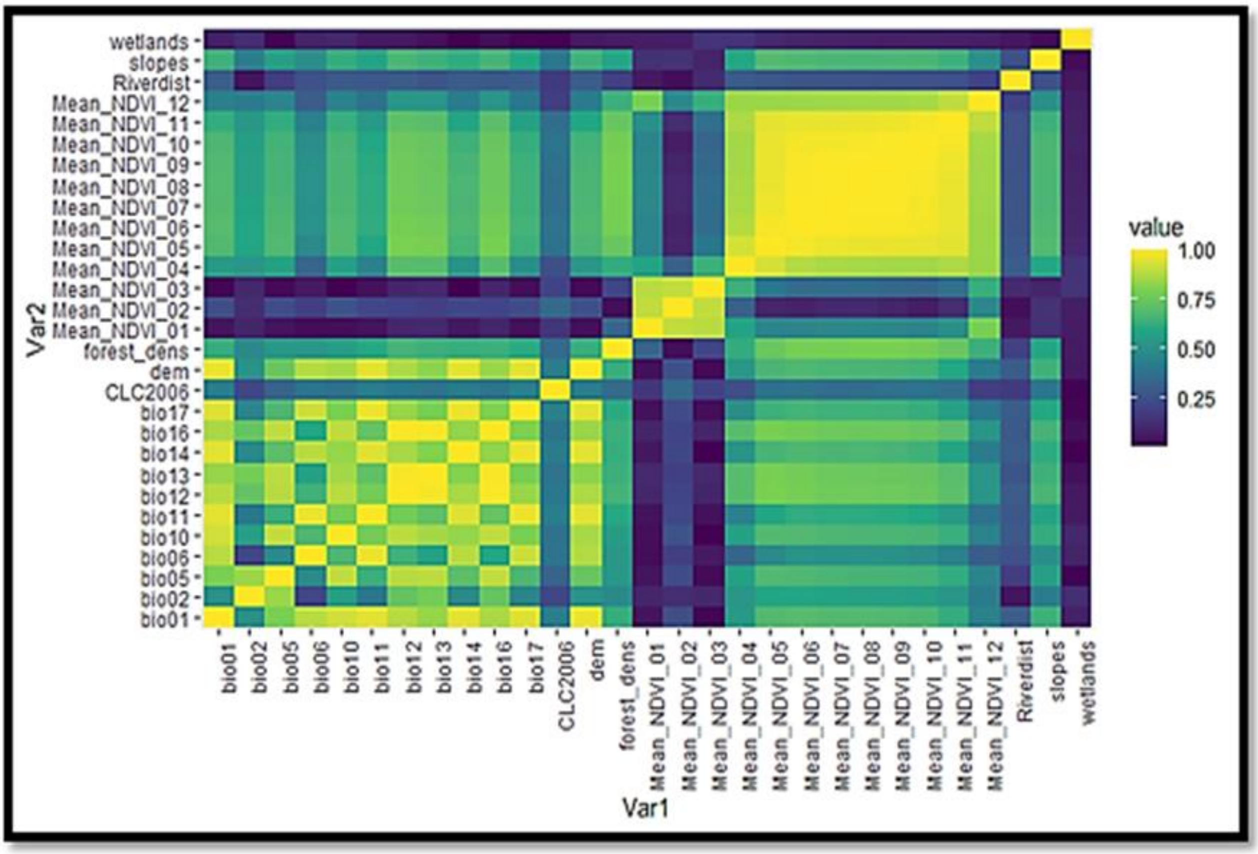


Figure S12. Collinearity test diagram.

Tables S4-S8: Analysis of predictor contribution for each species.

Ablepharus budaki		
Predictor	**Percentage contribution**	**Permutation importance**
Bio12	98.4	88.9
Wetlands	0.9	3.5
Mean_NDVI_07	0.6	1.2
Bio01	0.1	6.3

Acanthodactylus schreiberi		
Predictor	**Percentage contribution**	**Permutation importance**
CLC2006	46.7	23.0
bio01	27.0	46.1
bio02	24.2	30.9
wetlands	2.2	0

Laudakia cypriaca		
Predictor	**Percentage contribution**	**Permutation importance**
bio12	57.1	47.0
bio02	19.1	13.4
Mean_NDVI_03	13.4	14.3
bio01	10.5	25.3

Ophisops elegans		
Predictor	**Percentage contribution**	**Permutation importance**
bio12	45.8	34.3
Mean_NDVI_03	17.4	27.1
bio01	16.6	9.5
bio02	11.5	18.5
CLC2006	8.7	10.5

Phoenicolacerta troodica		
Predictor	**Percentage contribution**	**Permutation importance**
bio02	41.2	55.9
bio01	26.1	16.2
bio12	23.4	13.2
Mean_NDVI_03	8.9	12.0
CLC2006	0.4	2.7

Ablepharus budaki

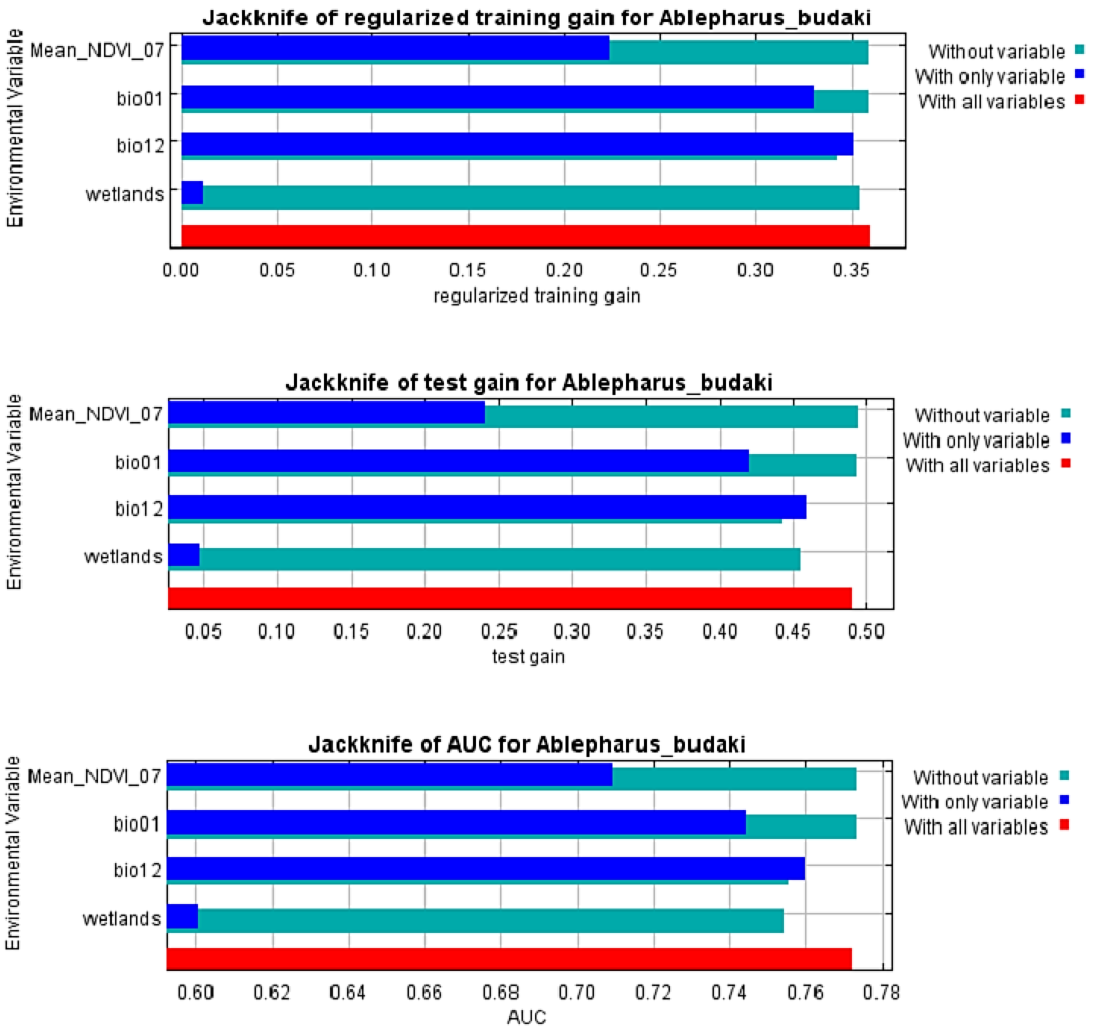


Figure S13. Results of the "Jackknife" process for the predictors.

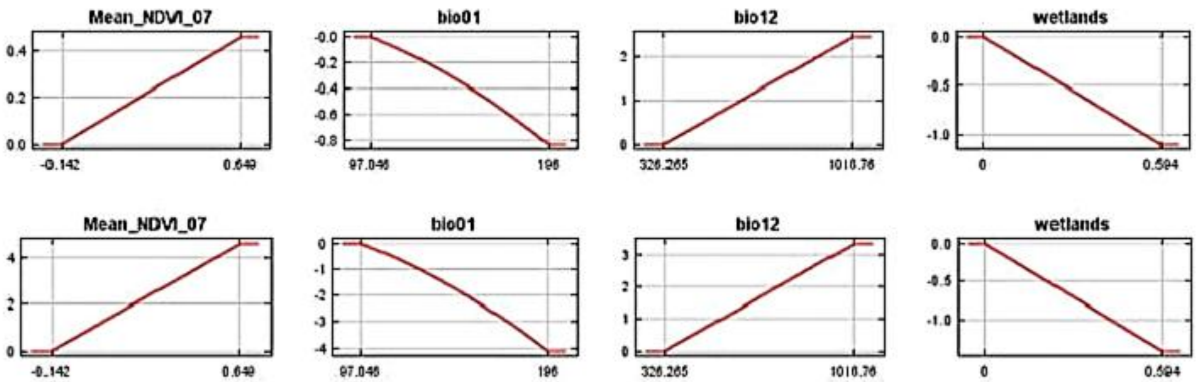


Figure S14. Response curves for predictors (above when all predictors included, below when the predictor is the only one included during model fitting).

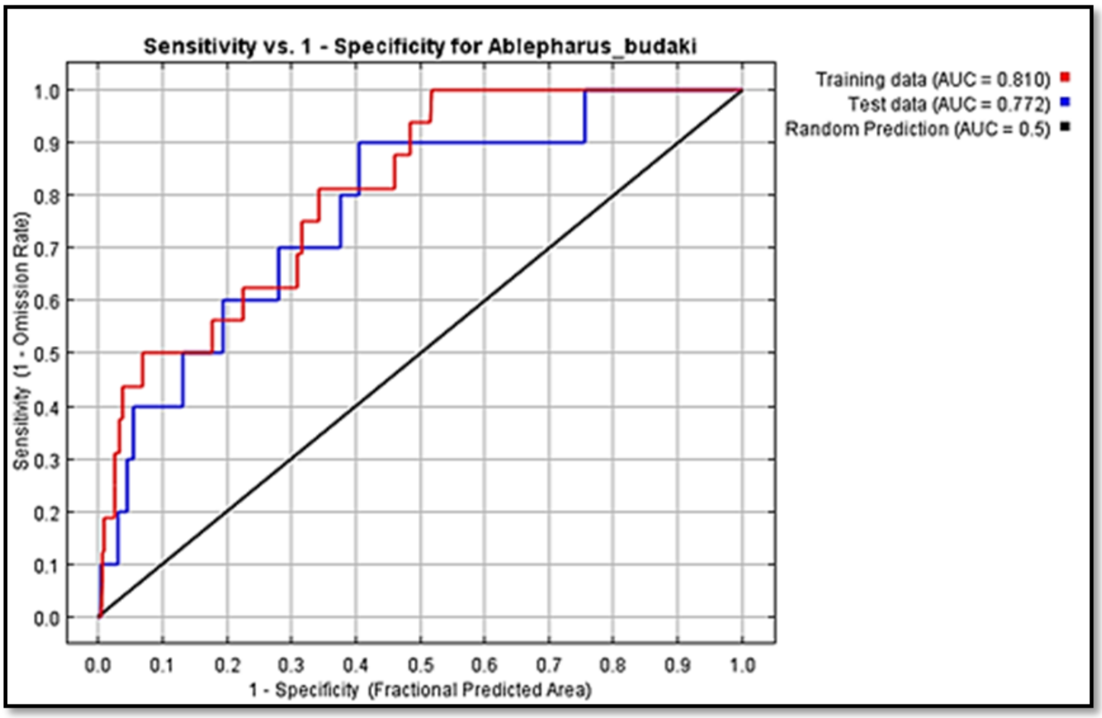


Figure S15. AUC diagram (Sensitivity vs. 1- Specificity).

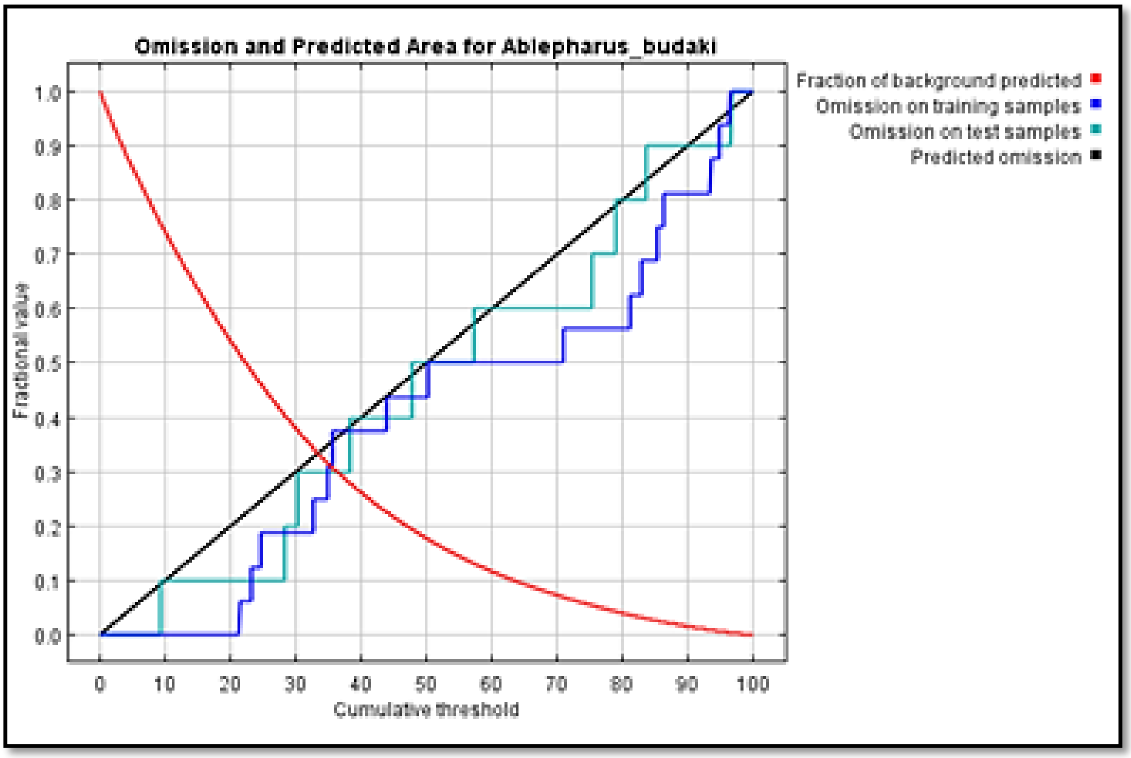


Figure S16. Omission and Predicted area diagram.

Acanthodactylus schreiberi

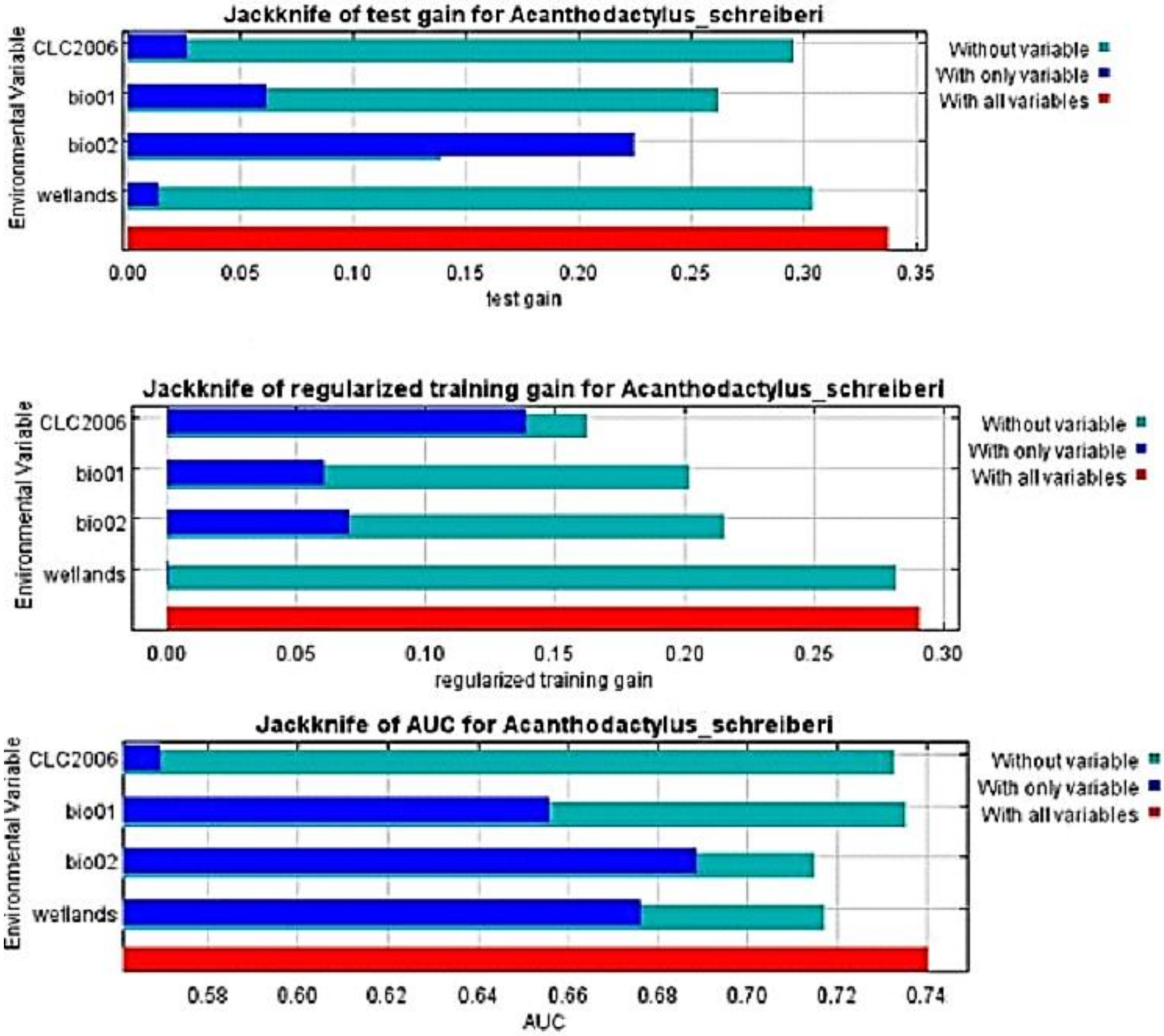


Figure S17. Results of the "Jackknife" process for the predictors.

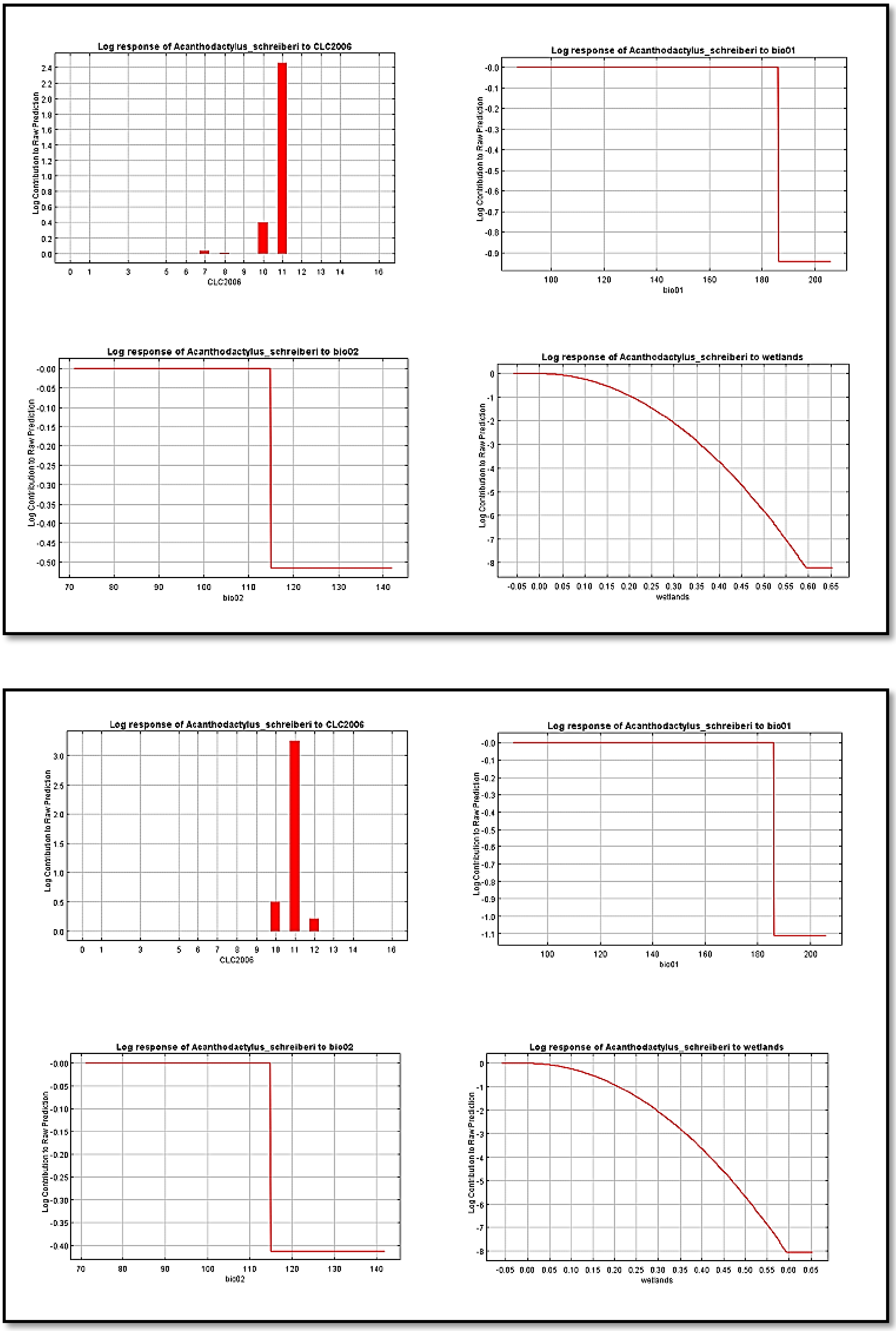


Figure S18(a-b). Response curves for predictors (a- above when all predictors included, b- below when the predictor is the only one included during model fitting).

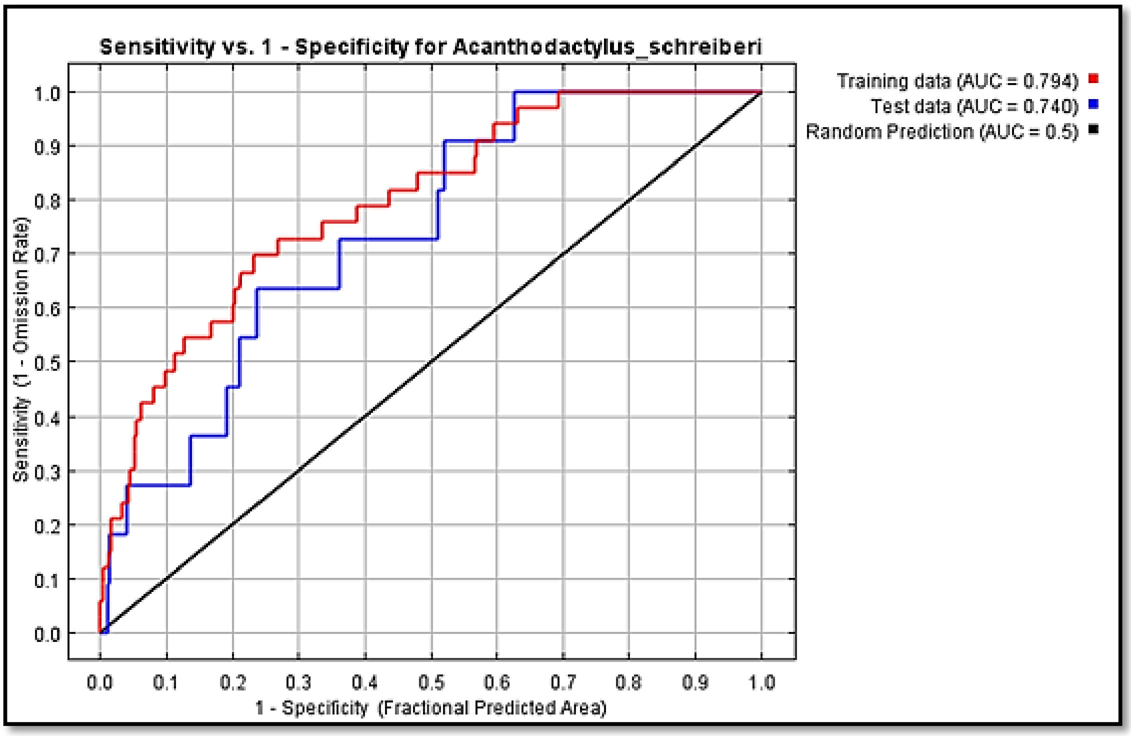


Figure S19. AUC diagram (Sensitivity vs. 1- Specificity).

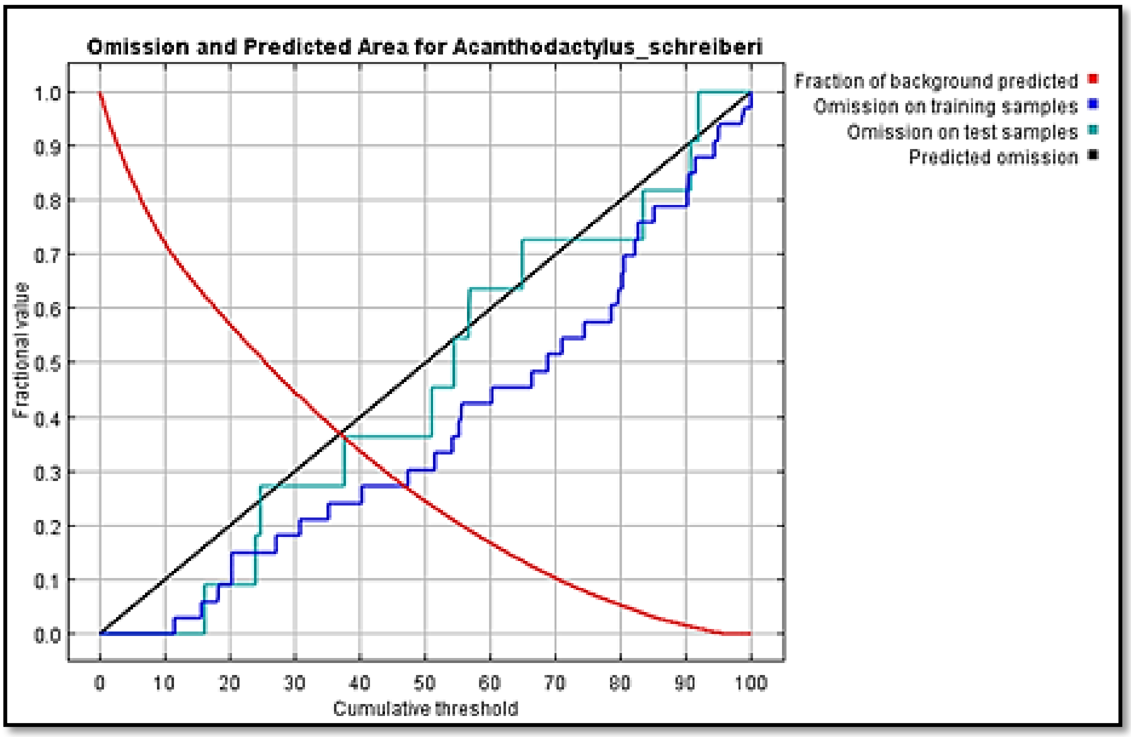


Figure S20. Omission and Predicted area diagram.

Laudakia cypriaca

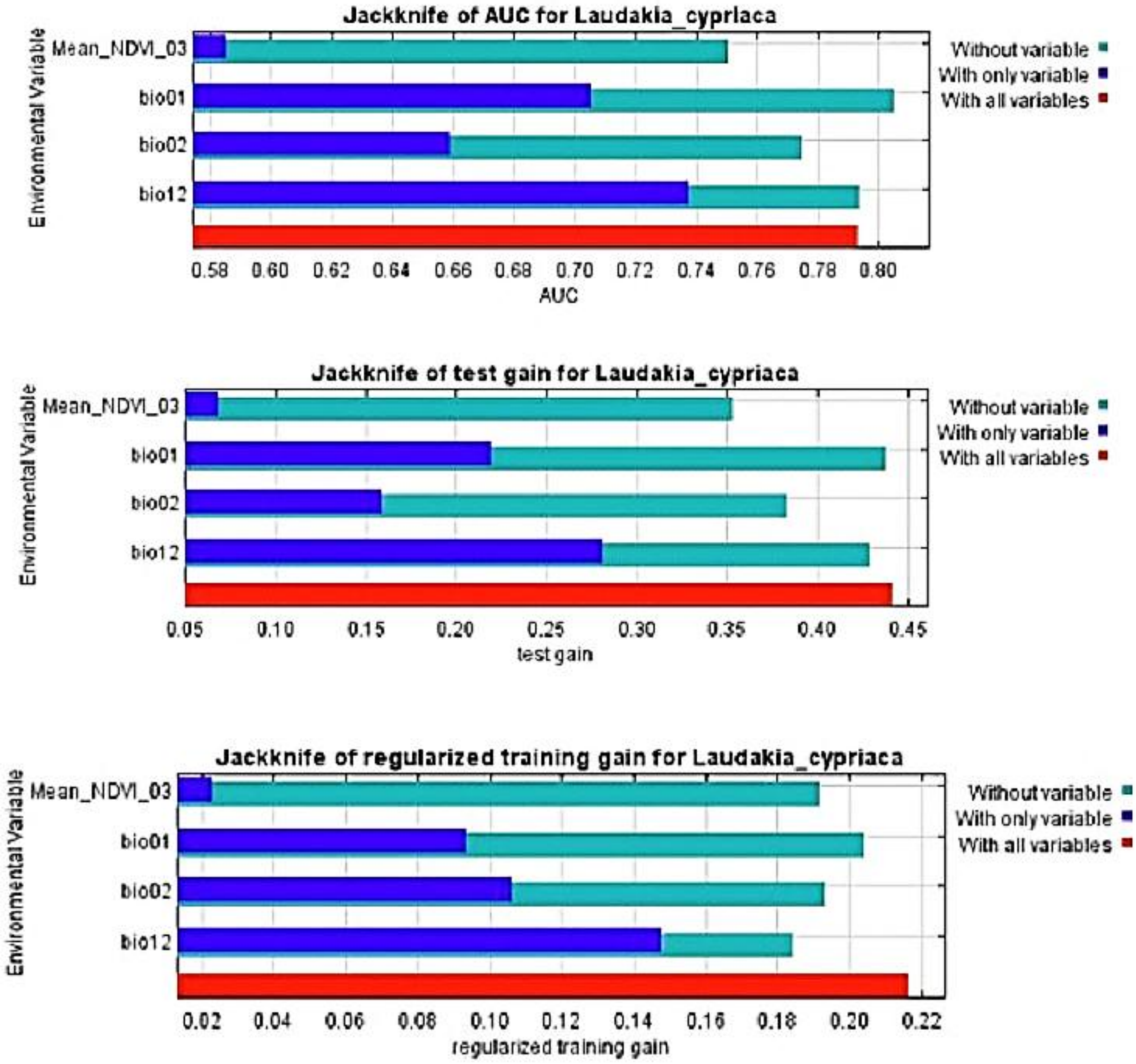


Figure S21. Results of the "Jackknife" process for the predictors.

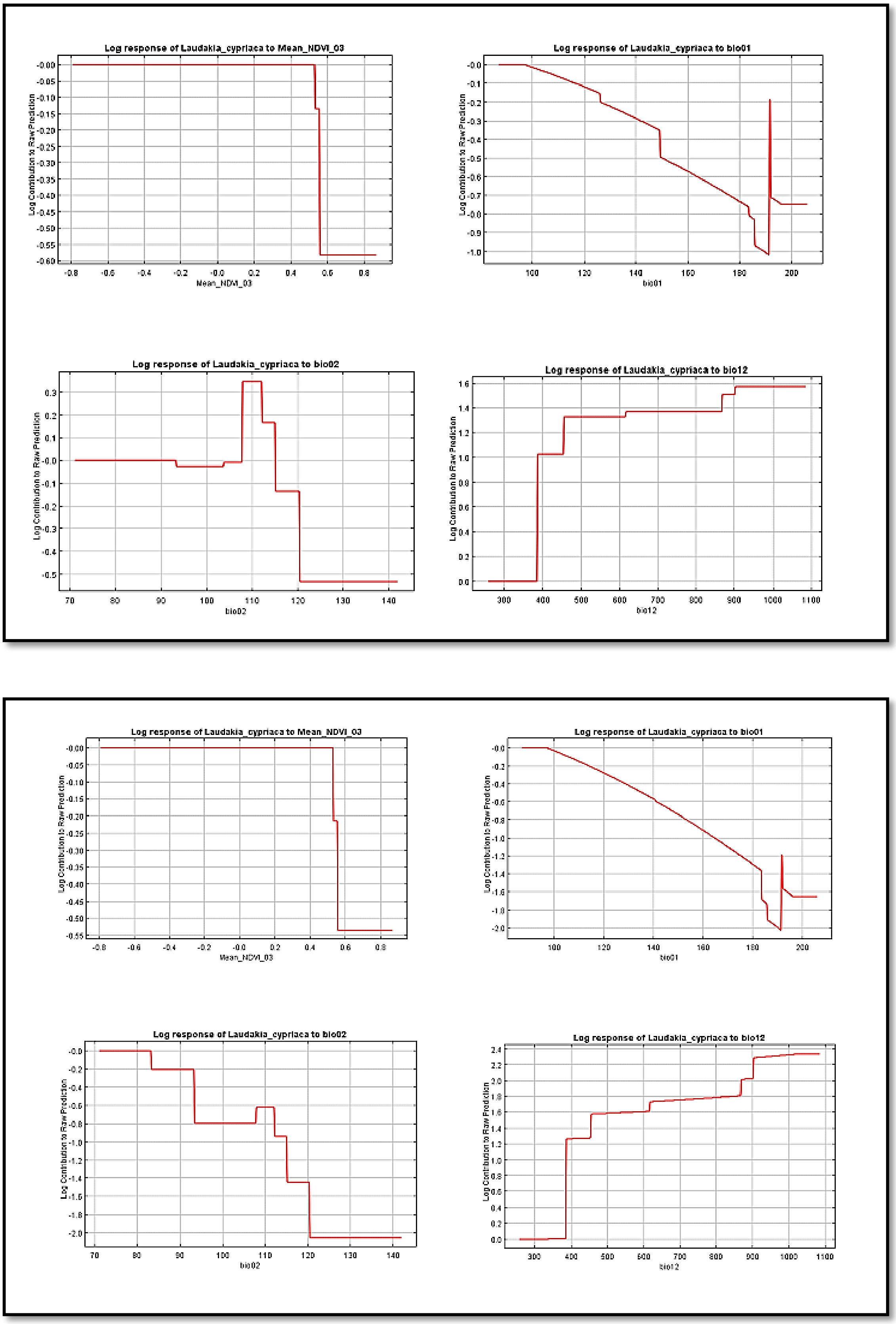
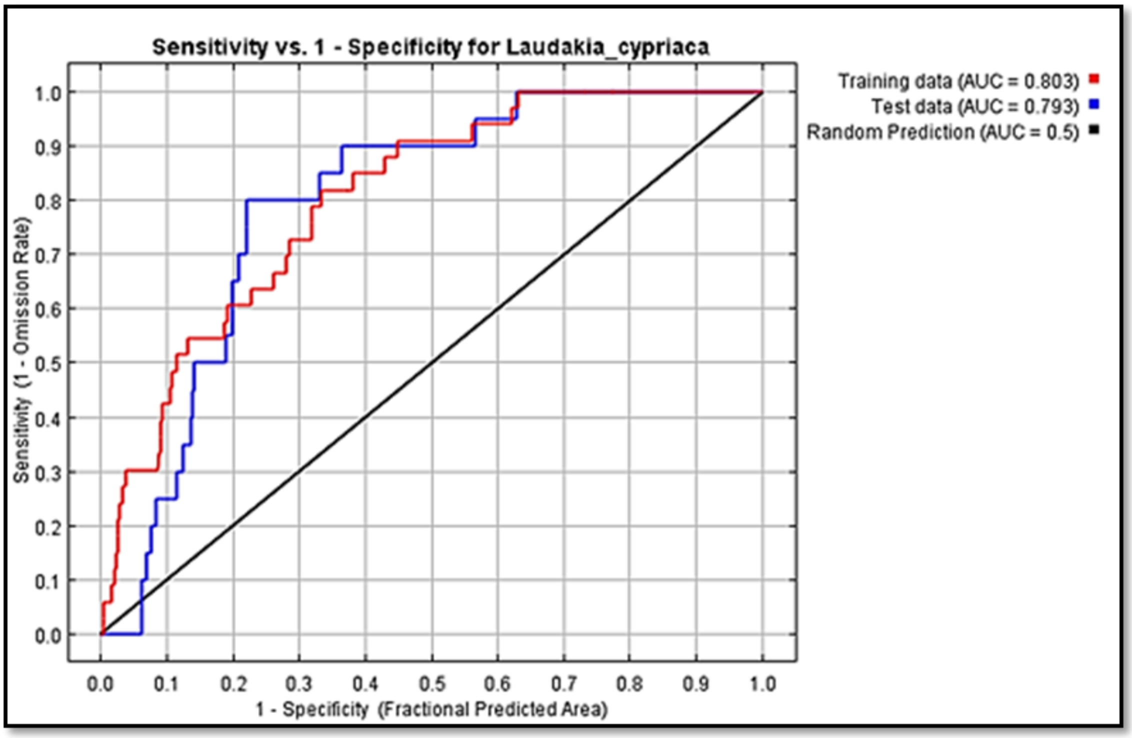


Figure S22(a-b). Response curves for predictors (a- above when all predictors included, b-below when the predictor is the only one included during model fitting).



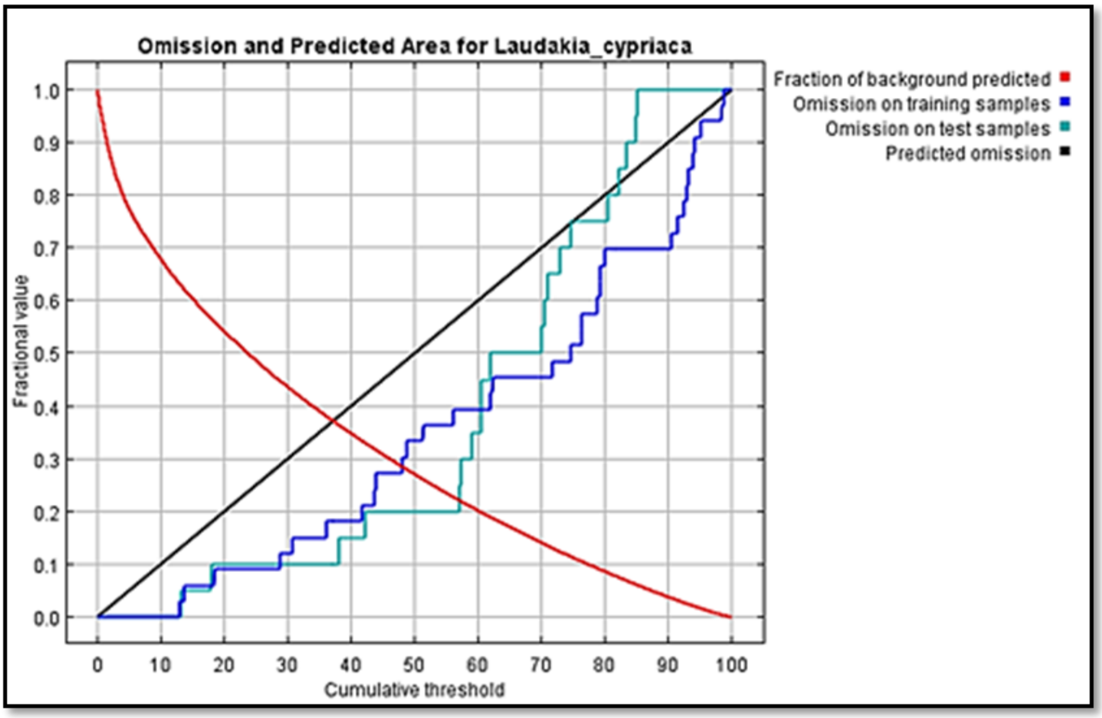


Figure S24. Omission and Predicted area diagram.

Ophisops elegans

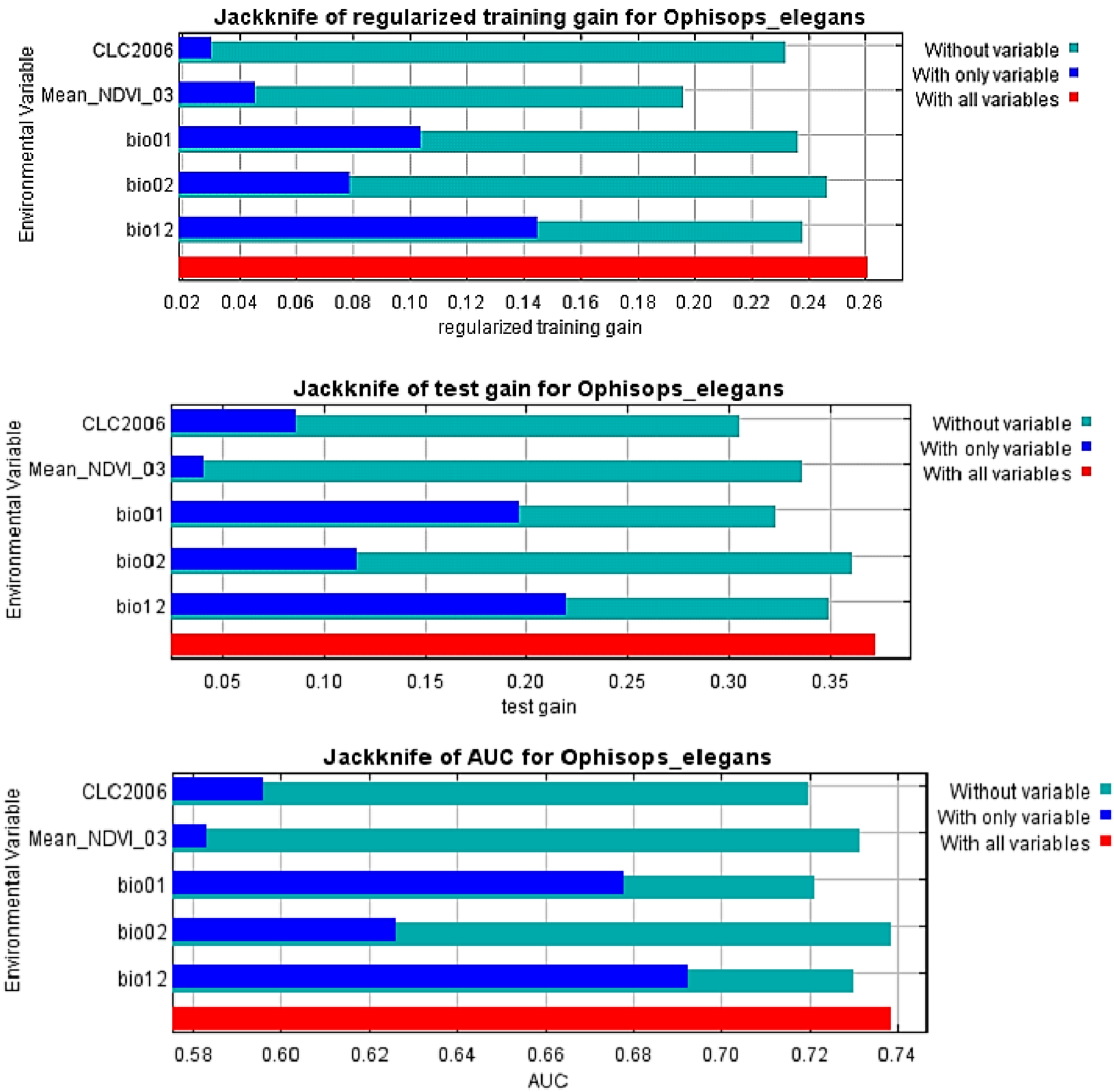
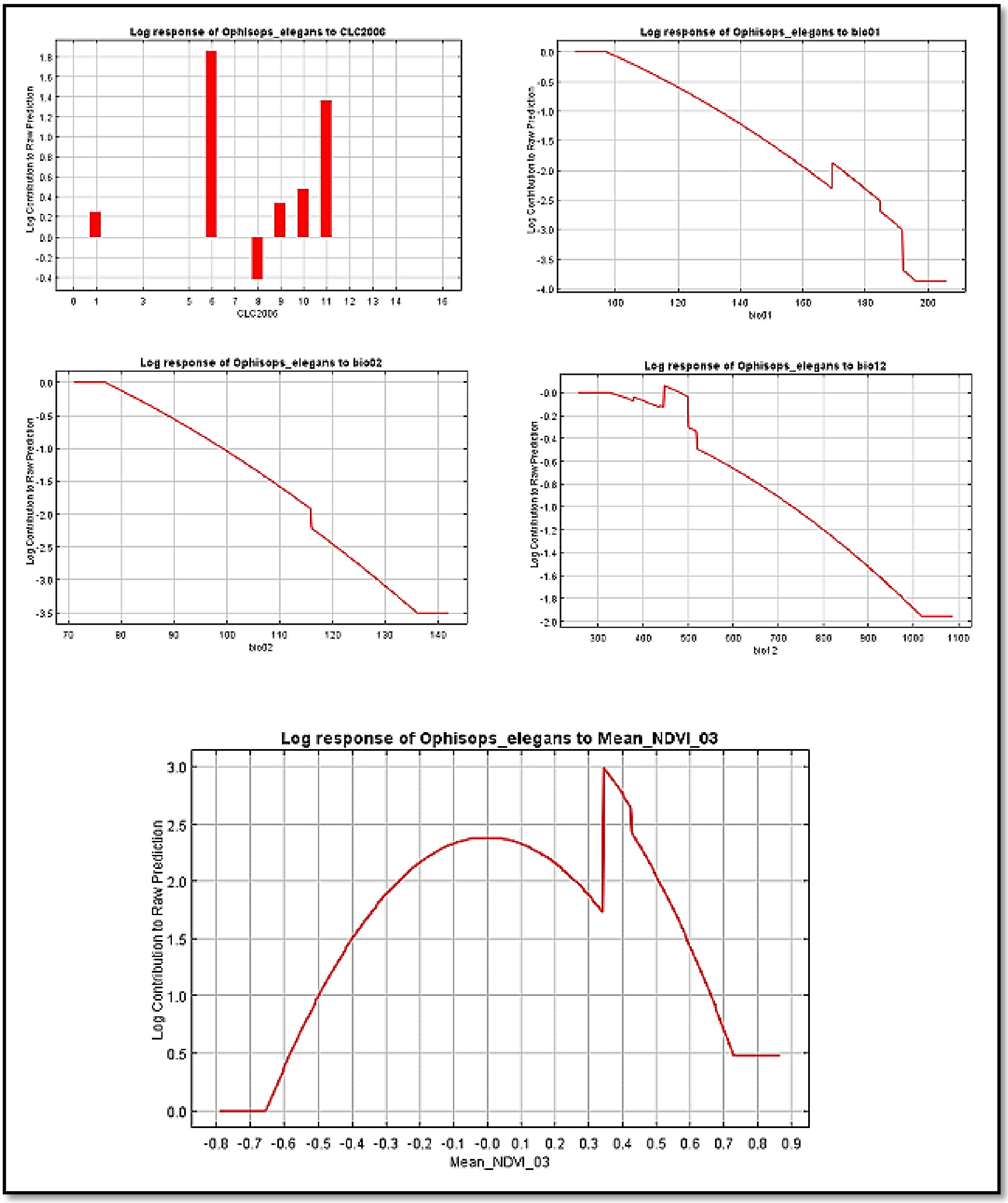


Figure S25. Results of the "Jackknife" process for the predictors.


Log response of Ophisops_elegans to CLC2006
Log Contribution to Raw Prediction
CLC2006
Log response of Ophisops_elegans to bio01
Log Contribution to Raw Prediction
bio01
Log response of Ophisops_elegans to bio02
Log Contribution to Raw Prediction
bio02
Log response of Ophisops_elegans to bio12
Log Contribution to Raw Prediction
bio12
Log response of Ophisops_elegans to Mean_NDVI_03
Log Contribution to Raw Prediction
Mean_NDVI_03

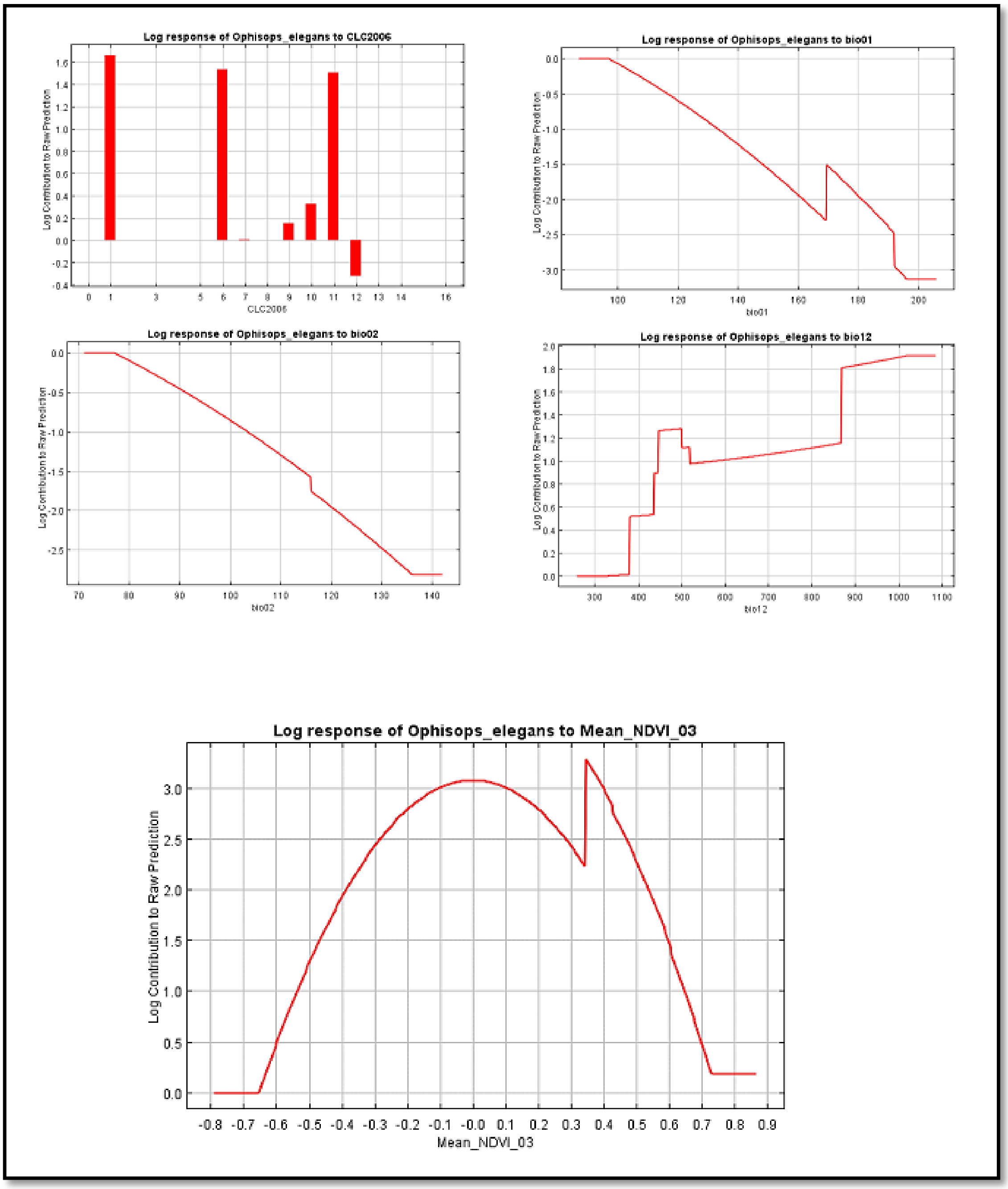


Figure S26(a-b). Response curves for predictors (a-above when all predictors included, b-following when the predictor is the only one included during model fitting.

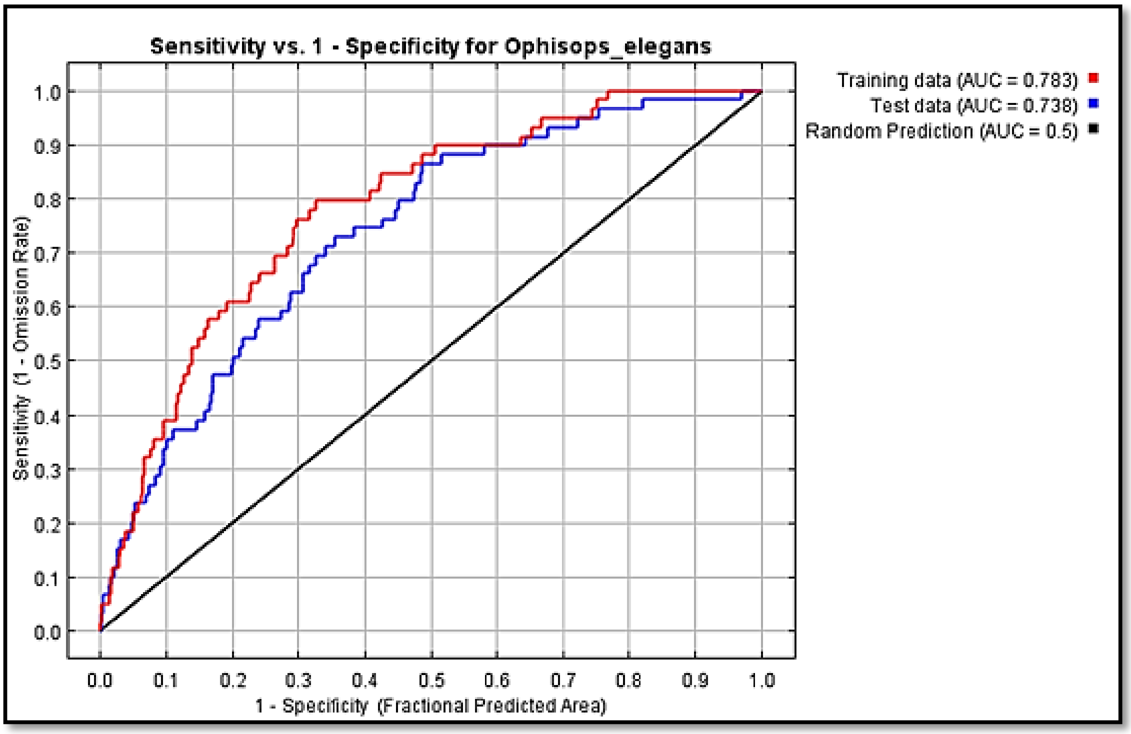


Figure S27. AUC diagram (Sensitivity vs. 1- Specificity).

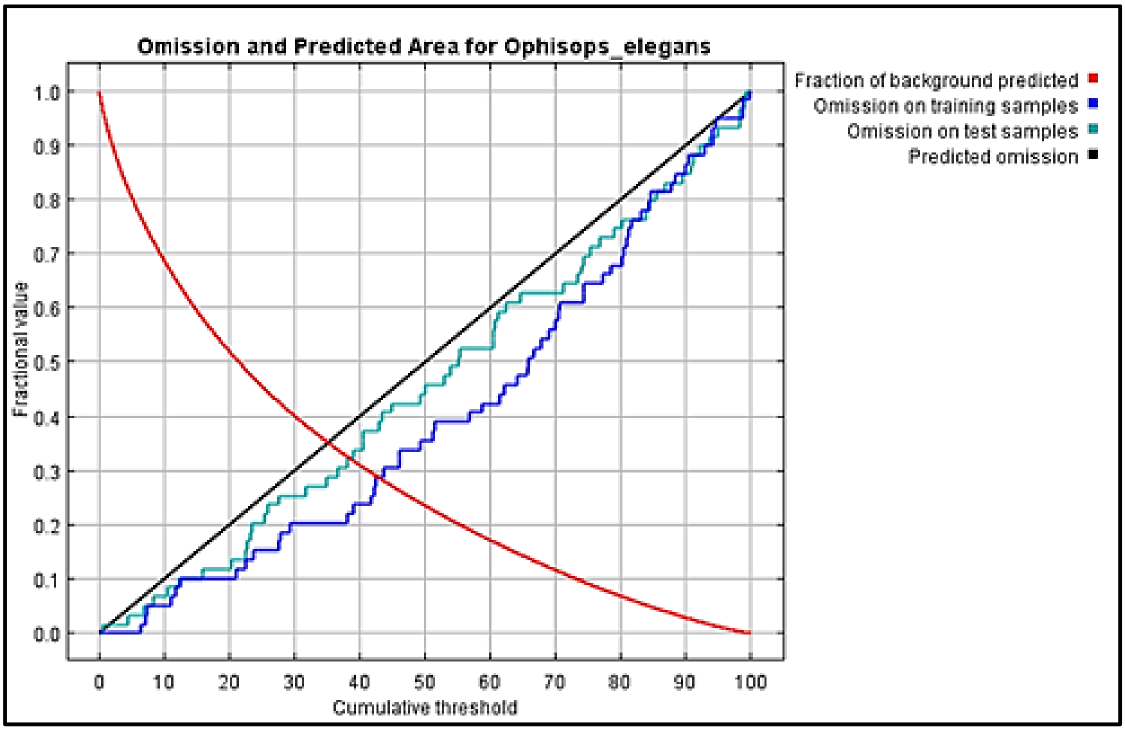


Figure S28. Omission and Predicted area diagram.

Phoenicolacerta troodica

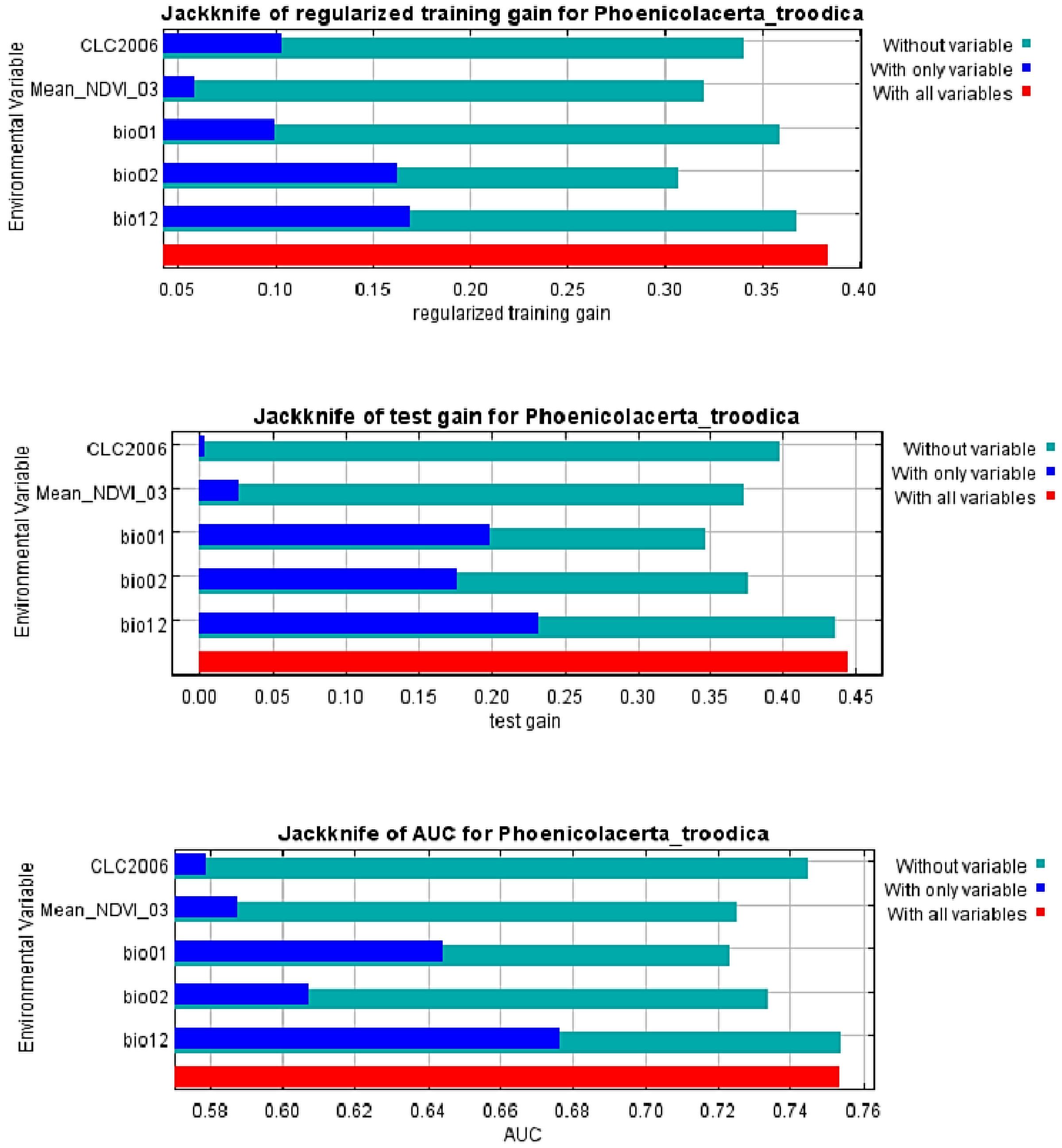
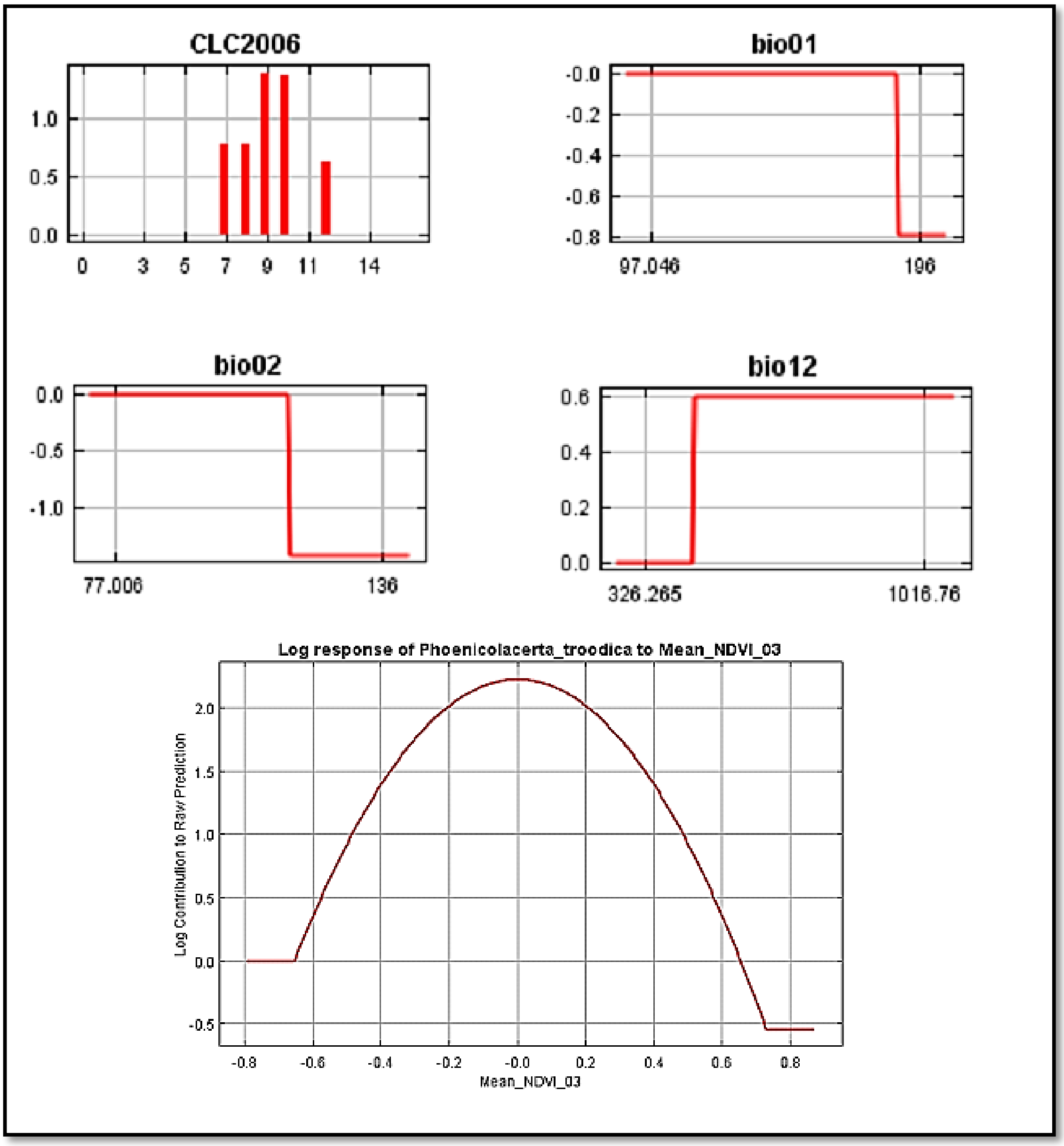


Figure S29. Results of the "Jackknife" process for the predictors.



CLC2006
bio01
bio02
bio12
Log response of Phoenicolacerta_troodica to Mean_NDVI_03
Log Contribution to Raw Prediction
Mean_NDVI_03

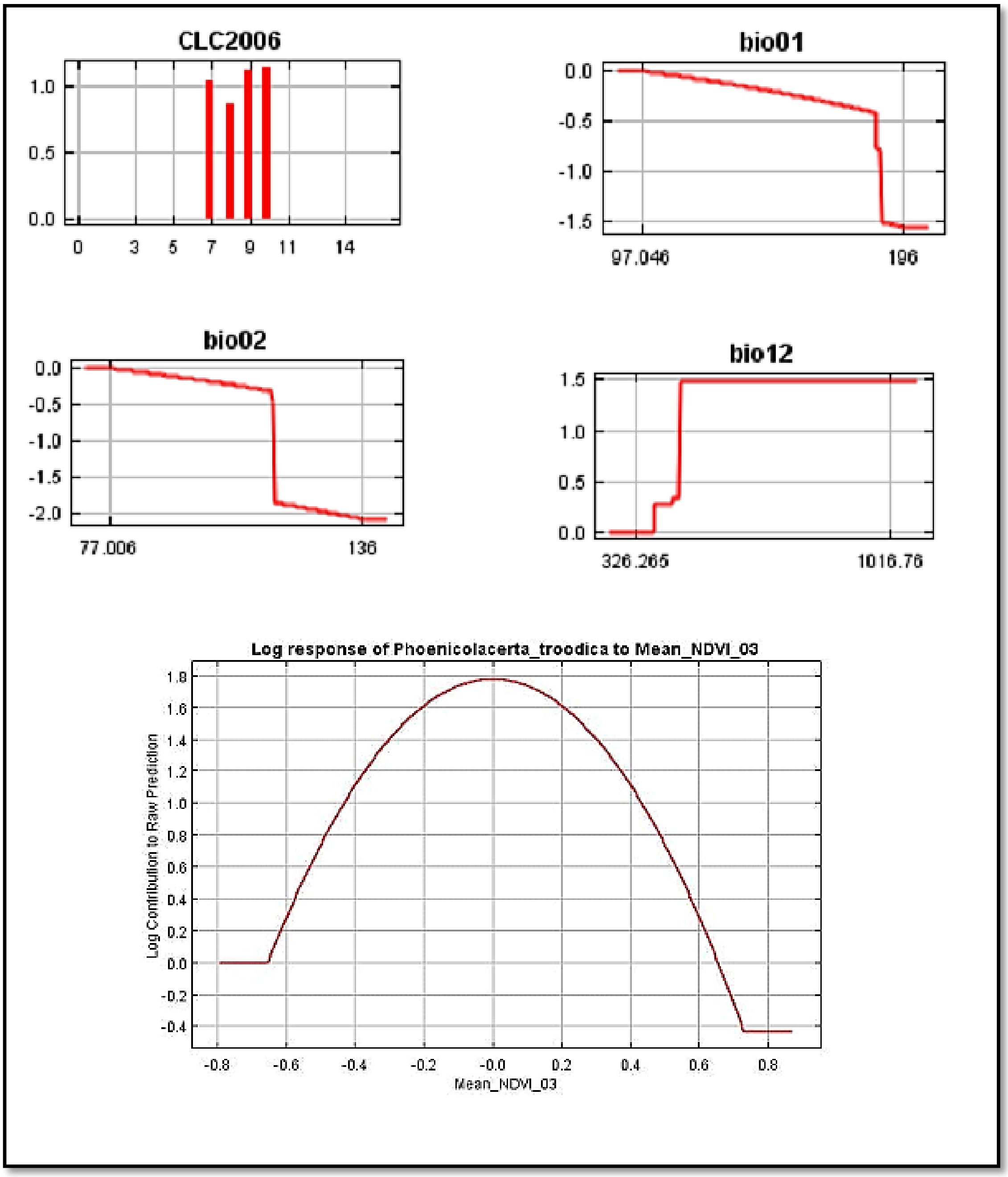


Figure S30(a-b). Response curves for predictors (a-above when all predictors included, b-following when the predictor is the only one included during model fitting).

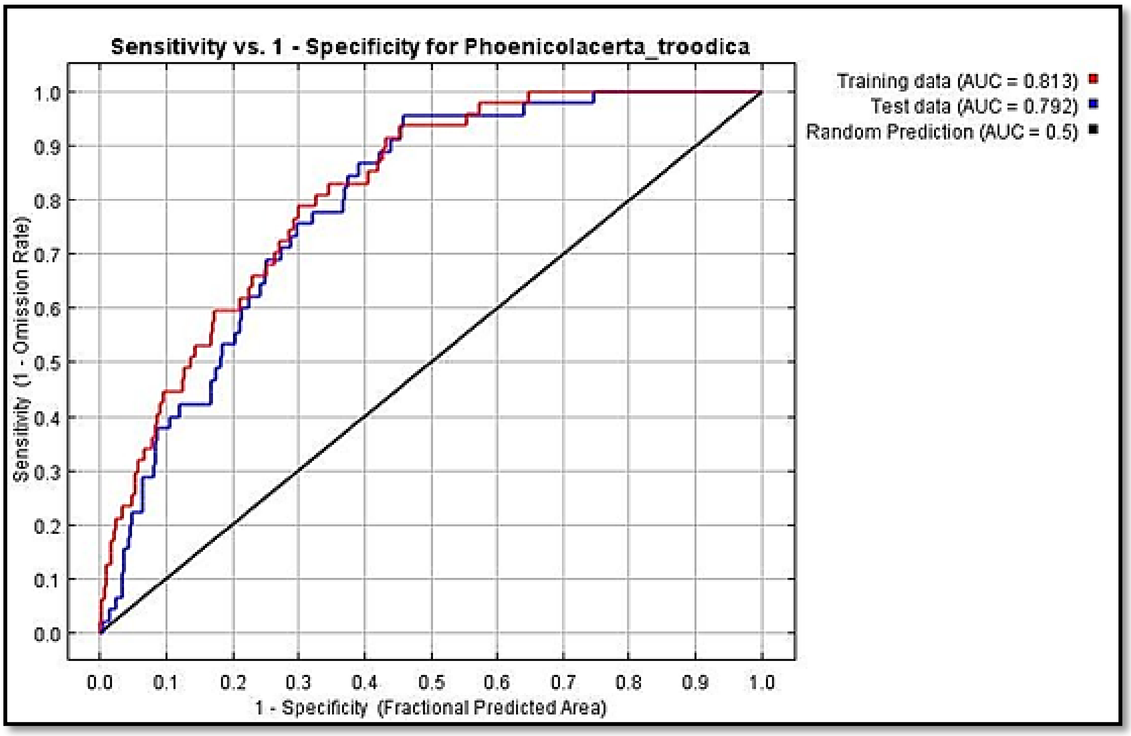


Figure S31. AUC diagram (Sensitivity vs. 1- Specificity).

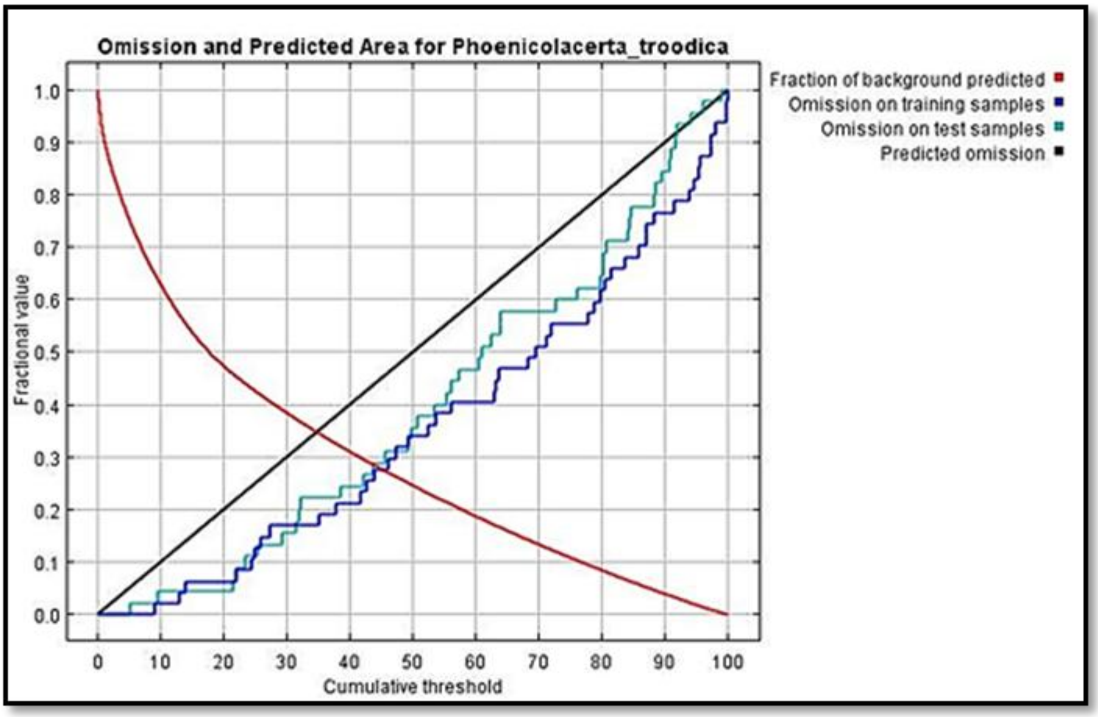


Figure S32. Omission and Predicted area diagram.