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Reassessing the Status (Phylogeny, Ecology, Distribution) of Greece's Sole Endemic Mammal *Crocidura zimmermanni* (Eulipotyphla: Soricidae) and Its Relationship to Its Congener *C. gueldenstaedtii* on Crete

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Abstract

Crocidura zimmermanni is the only endemic mammal species of Greece and is classified as Endangered according to IUCN due to its restricted range and probable displacement by its congener *C. gueldenstaedtii*. To investigate the ecology, phylogeny, and distribution of Cretan crocidurines, intensive trapping surveys were conducted and complemented by specimens from the NHMC collections. Here, we present preliminary phylogeny of *C. zimmermanni* based on cyt b, incorporating specimens across the species' geographic range. Additionally, species distribution modeling (SDM) was applied to determine the distribution of the two Cretan shrews and simulate potential range shifts under past and future climate scenarios. SDMs indicated temperature as the primary driver for both *C. zimmermanni* and *C. gueldenstaedtii*'s current distribution in Crete, with negative and positive effects respectively. Future climate projections predicted a reduction in the range of both species, with the severity of contraction increasing under more extreme scenarios. Paleontological evidence and model projections of past and current distribution data seem to concur with the prevalent hypothesis of *C. zimmermanni*'s displacement due to competition with *C. gueldenstaedtii*; however, further research is needed. Finally, new occurrence records for both species shed light on potential contact zones, directing future research regarding the competition between them in Crete.

Keywords: cyt b; climate change; species distribution models; syntopy

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1. Introduction

The genus *Crocidura* is the most speciose mammalian genus and belongs to the order Eulipotyphla, with a wide distribution throughout Eurasia and Africa [1–4]. The Mediterranean island of Crete, Greece, hosts two species of the genus, namely *Crocidura zimmermanni* (Wettstein, 1953) and *Crocidura gueldenstaedtii* (Pallas, 1811) [1,5].

C. zimmermanni represents the sole mammal endemic to Greece and is restricted to the mountain ranges of the island of Crete. It has been assessed as Endangered (EN) by IUCN,

with potential threats being primarily the competition with its congeneric *C. gueldenstaedtii* and climate change [6].

Published knowledge on the species remains very limited.

Crocidura zimmermanni was initially described from the Nida plateau on the Idi massif as a subspecies of the greater white-toothed shrew, *Crocidura russula* [7]. This subspecific status remained valid for over two decades [8,9] and was first questioned in 1973 by Felten et al. [10] based on differences in morphological characters. The elevation of *C. r. zimmermanni* to species level was proposed by Vesmanis & Kahmann [11] based solely on morphological features. This status was later enhanced by karyotypic [12] and limited genetic data based on allele frequencies at allozyme loci [13]. Concurrently, its presence was also confirmed in the Lefka Ori massif in western Crete [13].

The species had been captured at only two localities [7,13] and its presence had been confirmed at nine locations through the analysis of *Tyto alba* pellets, where it occurred at much lower frequencies than *C. gueldenstaedtii* [14]. The latter lack the spatial accuracy necessary to identify the actual habitats of the species, as the hunting range of *Tyto alba* usually has a ~5 km radius [15,16] and can reach up to 20 km [17].

Fossil evidence since the Early Pleistocene suggests that *C. zimmermanni* was previously ubiquitous across Crete, showing minimal morphological differentiation through time [18–20]. Today, however, its range has contracted significantly; it persists solely at high elevations on the Lefka Ori, Idi, and Dikti massifs [1,7,21]. The current distributional pattern is widely attributed to interspecific competition with its congeneric species *C. gueldenstaedtii*. It is hypothesized that this competition resulted in the displacement of *C. zimmermanni* from favorable lowland habitats, effectively restricting the endemic species to suboptimal, high-altitude refugia [5]. As a result, *C. zimmermanni* is considered the sole survivor of Crete's Pleistocene terrestrial mammal fauna. Furthermore, it represents one of only a handful of insular endemic mammals from the Pleistocene that persist within the modern Mediterranean Basin [22]. Its survival is particularly notable given the severe pressure of human disturbance during the Holocene, an epoch that drove many of the region's other insular endemic mammals to extinction [5,23].

In contrast, *C. gueldenstaedtii* occupies a significantly broader geographic range, extending across Europe and the Middle East into western Iran [4]. Within Greece, it is recognized as the most widely distributed and abundant member of the family Soricidae [24]. Its ecological status as a successful generalist likely underpins its ability to occupy the diverse lowland habitats of Crete from which *C. zimmermanni* is now absent. Until recently, the taxonomic status of *C. gueldenstaedtii* remained a subject of significant debate, with the lineage frequently classified as a subspecies within the *C. suaveolens* complex [25,26]. However, recent phylogenetic analyses, utilizing complete mitochondrial genomes, have supported the elevation of this taxon to full species rank [4]. Throughout its range, four subspecies are recognized: *C. g. gueldenstaedtii*, *C. g. cypria*, *C. g. iculisma* and *C. g. mimula* [1].

Crocidura gueldenstaedtii was proposed to have arrived in Crete during the Bronze Age, most probably from Asia Minor, with the earliest archeological evidence dating between circa 2200 and 1550 BCE, during the Minoan period [5,13,27]. Genetic data support this hypothesis, assigning Cretan specimens to *C. gueldenstaedtii* originating from Anatolia and the Middle East [27]. The taxonomic history of the Cretan population of *C. gueldenstaedtii* is marked by significant instability. It was initially described as a distinct species, *Crocidura canae* Miller, 1909, before being downgraded to a subspecies, based on morphological comparisons and variously assigned to *C. russula* [14] or *C. suaveolens* [18]. Subsequent revisions further stripped it of its subspecific status entirely, subsuming it into the broader *C. suaveolens* [13,21] or *C. gueldenstaedtii* [5,11] complexes.

Conversely, the phylogenetic resolution of *C. zimmermanni* remains elusive, as initial molecular studies have relied almost exclusively on a single genetic marker (cytochrome-b, cyt b) from a single specimen [3,28,29] and the primary use of allozymes [13]. This limited sampling has resulted in a poorly defined evolutionary position; the Cretan shrew is variously placed as a sister species to *C. sicula* and *C. canariensis* [28,29], grouped alongside *C. luna* [2], or identified as a sister group to the Afro-European *C. suaveolens* lineage [28]. None of these hypotheses have received robust statistical support, leaving the species' deeper relationships open to debate.

Unlike *C. zimmermanni*, the phylogenetic position of *C. gueldenstaedtii* within the genus is much clearer, since genetic data are substantially more abundant for both mitochondrial and nuclear markers, placing *C. gueldenstaedtii* into the broader *C. suaveolens* species group [4,21,25,26,30–32].

Given the rarity of *C. zimmermanni*'s captures and the limited knowledge of its ecology, species distribution modeling offers a powerful approach for investigating the ecology and distribution of the species [33], as well as for identifying environmentally suitable areas and generating hypotheses regarding the ecological requirements, thereby supporting future survey and conservation efforts [34]. Climate is a driving factor of shrew distribution, as their small size and exceptionally high metabolic rates mean shrews are profoundly susceptible to fluctuations in climatic conditions [35–37]. This sensitivity is twofold: they face immediate physiological constraints regarding thermoregulation and are indirectly impacted by climate-driven shifts in the abundance of their invertebrate prey [36].

Microhabitat features, such as vegetation cover and patch size, are critical for shrews, providing favorable microclimates that buffer against environmental extremes [36]. At a regional scale, while some species show a strong correlation with specific land cover and soil characteristics, others function as habitat generalists, whose distributions are primarily restricted by interspecific competition [38]. Even at a continental scale, the distribution of European shrew species is significantly influenced by these interspecific dynamics [39]. In Europe, the distribution of *C. gueldenstaedtii* is mainly driven by the minimum temperature of the coldest month and temperature seasonality [40].

Integrating these data, the primary aims of this study are threefold:

1. To provide a comprehensive update to presence records, characterize the specific habitat preferences of both crocidurine species of the island of Crete, quantify the extent of their syntopy, and reexamine the validity of morphological characters used to distinguish between them;
2. To advance our knowledge of the species' phylogenetic relationships via the mitochondrial locus of cyt b, reconstructing the first phylogeny of the crocidurine species of Crete; and
3. To employ species distribution modeling (SDM) to define their current bioclimatic envelopes, thereby offering insights into the environmental drivers of their respective ranges, reconstructing past distribution patterns, as well as predicting potential future shifts in response to climate change.

These results will clarify the ecological vulnerabilities of the endemic *C. zimmermanni*, providing a rigorous scientific basis for targeted conservation strategies in a rapidly changing Mediterranean landscape.

2. Materials and Methods

2.1. Samples

Sampling has been conducted from May 2023 to May 2026, using a combination of Sherman and Trip-Trap live traps, targeting the endemic Cretan shrew, for a total of

15,695 trap nights in 33 localities (Supplementary Table S1). Sampling sites were selected based on prior knowledge of species occurrences obtained from the Natural History Museum of Crete–University of Crete (NHMC) collections, as well as older species distribution models (SDMs) based on these occurrences (see Section 2.6). Traps were baited with a commercial snack containing corn, hazelnut, peanut and rapeseed oil. Traps were deployed and baited in the afternoon to encapsulate the peak crepuscular activity. To minimize the risk of mortality from starvation or exposure to extreme weather, traps were inspected at midnight and again shortly after sunrise. For multi-day sampling periods, traps were checked and re-baited daily at noon to ensure consistent attractant potency and trap efficacy. All captured *Crocidura* individuals were euthanized using CO2 and retained as voucher specimens. The samples were preserved in 96% ethanol and were deposited in the NHMC.

As mentioned above, specimens of both species in the NHMC collections (collected from 1989 to 2022) were used in several approaches (morphometrics, DNA analyses, SDMs). In each case, the use of older specimens is clearly mentioned in each corresponding analysis.

2.2. External Morphology

A total of 55 specimens of shrews were examined, for which we had a complete set of measured morphological characters, including 28 individuals of *C. zimmermanni* and 27 individuals of *C. gueldenstaedtii* (see Supplementary Table S2). Samples originated from Crete, both from field work conducted during the present study and from sample collections of the NHMC, with their taxonomic status validated through genetic analysis. All variables were log-transformed prior to statistical analysis.

The morphological characters analyzed were body length (B), tail length (Tail), and hind foot length (HF). Following a non-parametric approach that is suitable for relatively small sample sizes, all ANOVA and ANCOVA comparisons were evaluated for significance using residual randomization procedures with 1000 permutation cycles as implemented in the package 'RRPP' [41] in the R environment. Morphometric variables were log-transformed prior to statistical analyses to better approximate a normal distribution, buffer the effect of trait scale on variable variance and facilitate within- and among-species comparisons [42]. Analysis of variance (ANOVA) was performed using RRPP to assess differences in body length between species as well as among the island's mountain ranges for *C. zimmermanni*. Body length was subsequently included as a covariate in the ANCOVA models to control for potential allometric effects.

Additionally, teeth morphology was qualitatively assessed to examine the usefulness of key characters, specifically the thickness of the cingulum [20], the morphology of the parastyle P4 [18,20], and the relative size of the 2nd and 3rd premolars [18,20].

2.3. DNA Extraction

Tissue samples from 69 shrews, both *C. zimmermanni* and *C. gueldenstaedtii*, from the island of Crete were subjected to DNA extraction from all newly collected specimens, as well as from the collections of the NHMC, with emphasis on the three main mountain ranges of the island, i.e., Lefka Ori, Psiloreitis and Dikti (see Supplementary Table S3). Moreover, five *C. gueldenstaedtii* specimens (four from Syria and one from Rhodes), one *C. cypria* from Cyprus and one *C. leucodon* from Evros (NE Greece) were included in the phylogenetic analyses.

Total genomic DNA was extracted from muscle tissue using a commercially available DNA extraction kit (DNeasy Blood & Tissue Kit-Qiagen, GmbH, 40724 Hilden, Germany) and according to the manufacturer's protocol. For all abovementioned samples, part of the mitochondrial gene cyt b was amplified and sequenced using the primers L14724 and H15149 [1,43]. Double-stranded DNA amplification, consisting of 35 thermal cycles,

was conducted under the following conditions: 1 min of denaturation at 94 °C, 1 min of annealing at 48 °C and 1 min of extension at 72 °C. PCR products were then sequenced on an ABI3730XL automated sequencer, using the PCR primers and the Big-Dye Terminator v.3.1 Cycle Sequencing® reagent package, following the manufacturer's protocol instructions.

Three more *Crocidura* cyt b sequences, which are available in GenBank, were downloaded and incorporated into our dataset (one *C. zimmermanni*, which is the only available sequence of the species in GenBank, and two sequences of *C. russula*, since *C. zimmermanni* was first described as a subspecies of the aforementioned taxon; Supplementary Table S3). To root the phylogeny, four outgroup sequences were selected from the taxa *Suncus etruscus*, *Sorex volnucini* and *Sorex minutus*. Hence, the final dataset consisted of a total of 83 sequences. All newly generated sequences have been deposited in GenBank (accession numbers and details are listed in Supplementary Table S3).

2.4. Alignment & Genetic Distances

Quality control was conducted with CodonCode Aligner v.9.0.1 (CodonCode Corporation®, Centerville, MA, USA), through manual inspection of the nucleotide base signal in the chromatogram of the generated sequences, which also served as an initial aligner. Sequences were then aligned with the MUSCLE algorithm, embedded in MEGA v.10 [44], using the default settings. As cyt b is a coding marker, all obtained sequences were translated into amino acids to check for the presence of premature stop codons.

Genetic divergence was estimated in MEGA, based on pairwise deletion of gaps, using the Tamura-Nei model and including both transitions and transversions. It was performed between all evolutionary lineages produced by the phylogenetic analyses, as well as within the two species of interest.

2.5. Phylogenetic Analyses

The phylogenetic reconstruction was performed using both Maximum Likelihood (ML) and Bayesian Inference (BI) methods. The best DNA substitution models were estimated using PartitionFinder v.2.1.1 [45], under the Bayesian Information Criterion (BIC), with a greedy algorithm and linked branch lengths, and they were subsequently used in the phylogenetic analyses. Since cyt b is a protein-coding gene, partitioning schemes were taken into account for each codon position.

Bayesian Inference (BI) was performed using MrBayes v.3.2.7a [46], with four independent runs and eight sampling chains. The analysis ran for 10^7 generations, with tree sampling every 10^3 generations. The other parameters set for the analysis were as follows: prset applyto = (all), ratepr = variable, unlink statefreq = (all), revmat = (all), shape = (all), pinvar = (all) and tratio = (all). The first 25% of the initial generated trees were discarded as burn-in. The values of average standard deviation of split frequencies (ASDF ≤ 0.01), effective sample sizes of all parameters (ESS > 200) and potential scale reduction factor (PSRF) (=1.0) were checked in Tracer v1.7.2 [47] in order to examine the convergence of the independent runs. Nodes with posterior probabilities > 0.95 were considered statistically strongly supported [48].

Maximum Likelihood analyses were conducted using RAxML-NG v.1.0.3 [49] and the IQ-Tree web server [50], providing the partition scheme identified by PartitionFinder2 for the subsequent selection of the most suitable substitution model. In RAxML, the analysis was performed with 25 starting parsimony trees and 300 bootstrap replicates, while the default settings were employed in the IQ-Tree analysis.

The produced majority-rule consensus tree from BI and the trees from ML analyses were visualized using FigTree v.1.4.2 [51] and edited/refined with CorelDraw [52].

2.6. Species Distribution Modeling

To model the distribution of *C. zimmermanni*, we used 31 presence records from the NHMC collection, including 25 records from specimens gathered between 1989 and 2023 and 6 presence records from the sampling effort of this study (Supplementary Table S4).

To assess the climatic tolerances and niche breadth of *C. gueldenstaedtii*, we modeled its distribution using a global dataset, as the island of Crete does not encompass the full range of bioclimatic conditions that the species inhabits. For Greece, we acquired data from live traps, pitfall traps and pellet analysis from NHMC collections (Supplementary Table S5), supplemented by records from the Global Biodiversity Information Facility (GBIF) (Supplementary Reference List S1), covering the distribution of the species throughout the country. To account for the recent taxonomic elevation of *C. gueldenstaedtii* from the *C. suaveolens* complex [4], we cross-referenced GBIF records with IUCN distribution maps [53], excluding data points that fell outside the species' recognized range. Furthermore, to address regional data deficiencies in the eastern portion of its distribution, we integrated data from the western Balkans [54], Turkey [55], Iran [32] and Syria [56]. As the sampling effort is highly unequal throughout the distribution of the species, we thinned our data to one presence within a radius of 15 km to mitigate sampling bias in our results, using the package "spThin" (ver. 0.2.0) [57], with the final dataset containing 1620 presence localities for *C. gueldenstaedtii*.

To investigate the distribution of *C. zimmermanni*, we used two different environmental datasets with different scales, both covering the extent of Crete (see Section 3.4); the first included land-cover variables and altitude with a 100 m spatial resolution and temporal coverage from 2015 to 2019 (hereafter referred to as land-cover model); the second included climatic variables with a 30 arcsec resolution (hereafter climatic model) to investigate the response of the species to climate change. For *C. gueldenstaedtii*, we developed a climatic model with a 30 arcsec resolution, extending to Europe, North Africa and West Asia to cover the whole extent of the species and areas where dispersal could be possible (see Section 3.4). This model aimed to investigate the climatic preferences of the species and to predict future expansions or constrictions. We refrained from developing a land-cover model for the species, as most presence data have high spatial uncertainty, deriving from pellet analysis or bibliographical sources without accurate coordinates, and thus cannot accurately define the actual land cover that the species occupies.

Current (1979–2013), future (2070–2100) and past climatic variables were obtained from CHELSA [58–60]. For the future, two contrasting Shared Socioeconomic Pathways (SSP1 2.6 and SSP5 8.5) from the MPI-ESM1-HR climate model [61] were selected for species distribution projections under different climate change scenarios. For the past, −40 centennial and −190 centennial were selected, corresponding to the Mid-Holocene and the Last Glacial Maximum respectively. To investigate the past, land-cover data were obtained from Copernicus (https://developers.google.com/earth-engine/datasets/catalog/COPERNICUS_Landcover_100m_Proba-V-C3_Global#bands, accessed on 5 April 2025).

Models created in the past (e.g., [62]) were developed to investigate different model parameters and to inform the aforementioned sampling effort. These models used different combinations of environmental factors as well as alternative algorithms, namely random forest, generalized linear models, artificial neural networks and multivariate regression adaptive splines, implemented using the R package Biomod2 [63]. These previous models used less presence data and were used to inform the sampling effort (see Section 2.1).

For the land-cover model, we used 6 land-cover variables (Bare, Built-Up, Crops, Grass, Shrub, Tree) with continuous values of cover percentage, as well as Altitude and Slope, to explore the species' habitat preferences.

As climatic data are highly relevant in small geographic regions, we chose 5 climatic variables from the 19 bioclimatic variables available that we considered more relevant for the distribution of shrews. Taking into consideration that *C. gueldenstaedtii* is mainly affected by the minimum temperature of the coldest month (Bio6) and the seasonality of climate [40], and it seems to prefer warm and damp environments [13]. We selected mean diurnal range (Bio2), minimum temperature of the coldest month (Bio6), annual precipitation (Bio12), seasonality of precipitation (Bio15) and precipitation of the warmest quarter (Bio18). To avoid collinearity issues, we implemented the Variance Inflation Factor in R with the "usdm" package (ver. 1.1-18 [64]), ensuring that variables did not exceed a VIF value of 5 (Supplementary Table S5).

The R package Biomod2 (version 4.2-6-2) [63] was used to train and evaluate distribution models, as well as to calculate the associated variable importance. The Maxent algorithm was used with 10.000 background points randomly generated. We chose the "filter raster" option to avoid using the same raster value twice by Biomod2 [63], which removed 5 occurrence data points from our climatic model. We used the "tuned" strategy in Biomod2 [63] to select parameters for the Maxent algorithm. To evaluate our models, we used block partitioning to create 4 partitions—3 for training and 1 for evaluation—where we report the mean AUC (Area Under the Receiver Operating Characteristic curve) and TSS (True Skill Statistics) values of all runs. AUC values range from 0 to 1, and TSS values range from −1 to 1. We present the models utilizing the full occurrence dataset, where no evaluation data has been set aside. To assess variable importance, we used 100 permutations per run. Model projection was implemented in ArcGIS pro (ver. 3.5.4) using the minimum maximum stretch type with values of 0 for minimum and 1 for maximum values, consistently for all model projections (Figures 5–7). To reproduce results, see Supplementary Code S1.

3. Results

3.1. Samples

The NHMC collections numbered a total of 56 individuals of *Crocidura zimmermanni*, based on morphological characters from 25 localities. In 5 localities both species were sympatric. 33 individuals were collected through pitfall traps, 22 with Sherman live traps and one individual was found dead.

During the recent sampling effort (see Section 2.1), 21 individuals of *C. zimmermanni* were captured from 6 geographic localities and 14 *C. gueldenstaedtii* from 7 localities, with a capture rate of 13% and 9% per 100 trap nights, respectively. Both species were captured in two localities in syntopy, namely the Nida plateau of the Idi massif and Vasiliki Strata on the Lefka Ori massif. The highest capture rate of *C. zimmermanni* was observed in Romanos, at the Katharo plateau, Dikti massif, with 7 individuals in 1320 trap nights, and in the Omalos plateau at the Lefka Ori massif for *C. gueldenstaedtii*, with 5 individuals in 380 trap nights. Concerning trap efficacy, 8 specimens were caught in Sherman live traps and 27 in Trip-Trap traps. Figure 1 shows known occurrences of the *Crocidura* species of Crete based on specimen records from the NHMC collections and samples collected during the present study (Supplementary Tables S4 and S5) where cases of syntopy/sympatry are highlighted.

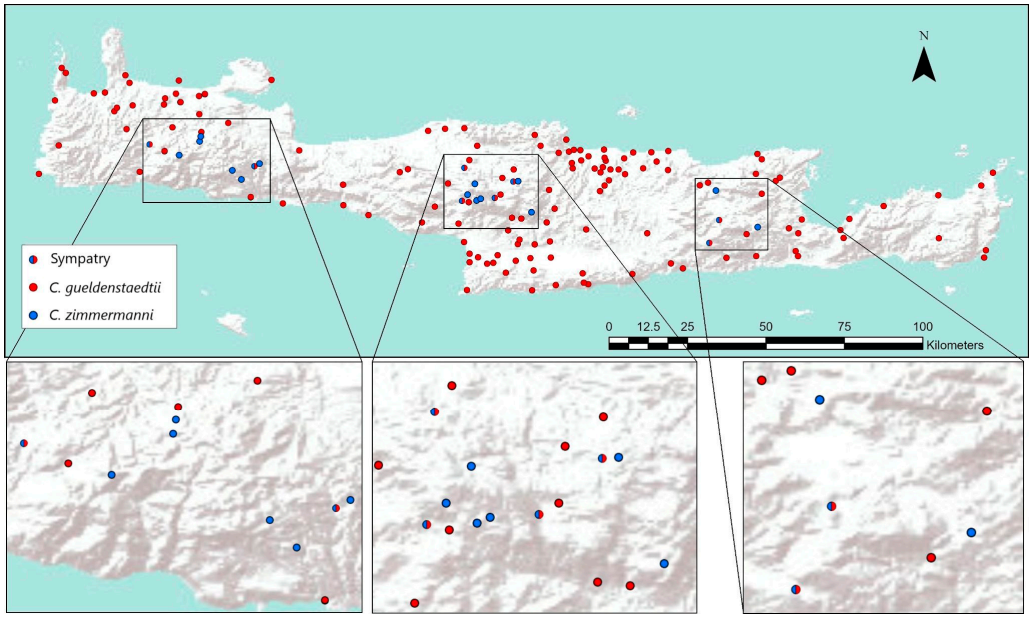


Figure 1. Presence data of *Crocidura* in Crete from the NHMC collection (including old and new sampling efforts). Localities closer than 1 km were grouped into one point.

3.2. Morphology

Measurements in the form of mean values and ranges of each character for the two focal species are presented on Table 1 (for individual measurements, see Supplementary Table S2).

Table 1. Measurements of external characters. Mean values (mm) in bold. Minimum and maximum values in parentheses.

Species	Hind Foot	Body Length	Tail Length
C. gueldenstaedtii (n = 27)	**12** (11–13)	**68** (58–79)	**44** (38–53)
C. zimmermanni (n = 28)	**12.8** (11–15)	**70.9** (60–86)	**37.8** (33–42)

The comparative analysis of the two species revealed significant morphological differentiation. Analysis of variance (ANOVA) showed no statistically significant difference in body length between species ($R^2 = 0.050$, $F = 2.79$, $p = 0.109$), suggesting that body length was not strongly confounded with species identity. Body length was therefore included as a covariate in subsequent analyses to control for its effect when testing the effect of species.

Results of the ANCOVA showed that hind foot length was significantly influenced by both species ($p = 0.001$) and body length ($R^2 = 0.109$, $F = 9.06$, $p = 0.004$), indicating an allometric component. In contrast, tail length was not significantly associated with body length ($p = 0.632$), but remained strongly differentiated between species ($p = 0.001$) (Figure 2). No significant interaction between species and body length was detected for either trait (HF: $p = 0.398$; T: $p = 0.960$), indicating similar allometric relationships across species.

The multivariate analysis (MANOVA) confirmed the findings of the ANCOVA. The overall effect of species was highly significant ($F = 51.24$, $p = 0.001$, $R^2 = 0.484$), indicating that the two species differ significantly in their overall morphological profile (Figure 3). Body length also had a significant multivariate effect ($F = 3.39$, $p = 0.036$, $R^2 = 0.032$), suggesting that part of the variation in the combined morphological traits is associated with body size. However, the Species × Body Length interaction was not significant ($F = 0.28$, $p = 0.770$, $R^2 = 0.003$), indicating no evidence for species-specific multivariate allometric slopes. Overall, these results suggest that the two species are morphologically differentiated

in hind foot and tail length, while the relationship between body length and the combined morphological traits is broadly similar across species.

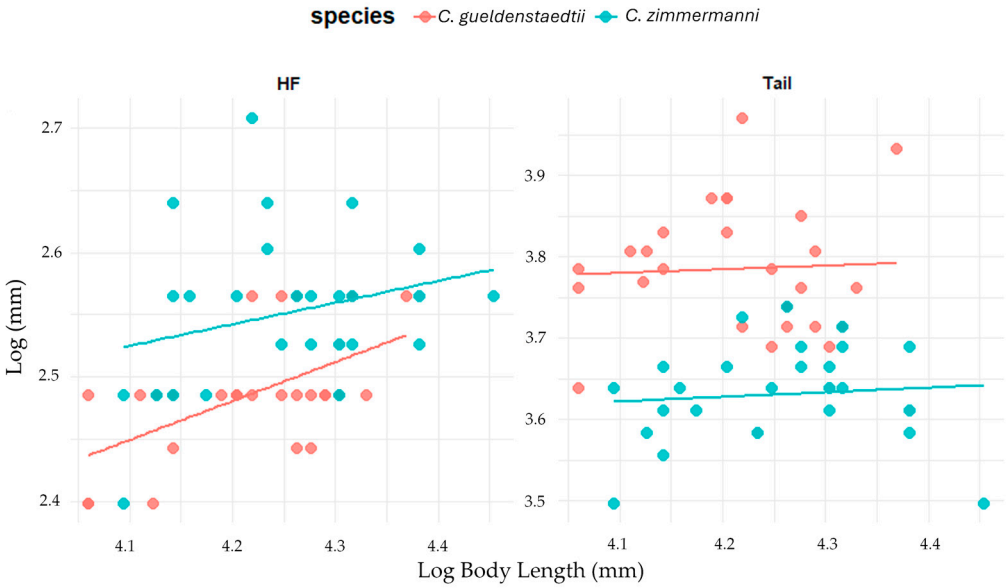


Figure 2. Relationships between log-transformed body length and morphological traits (HF and Tail) in *C. gueldenstaedtii* and *C. zimmermanni*. Points represent individual specimen measurements, and lines indicate species-specific linear regressions. Hind foot length increases with body size in both species, whereas tail length shows a weak association with body size but clear differentiation between species.

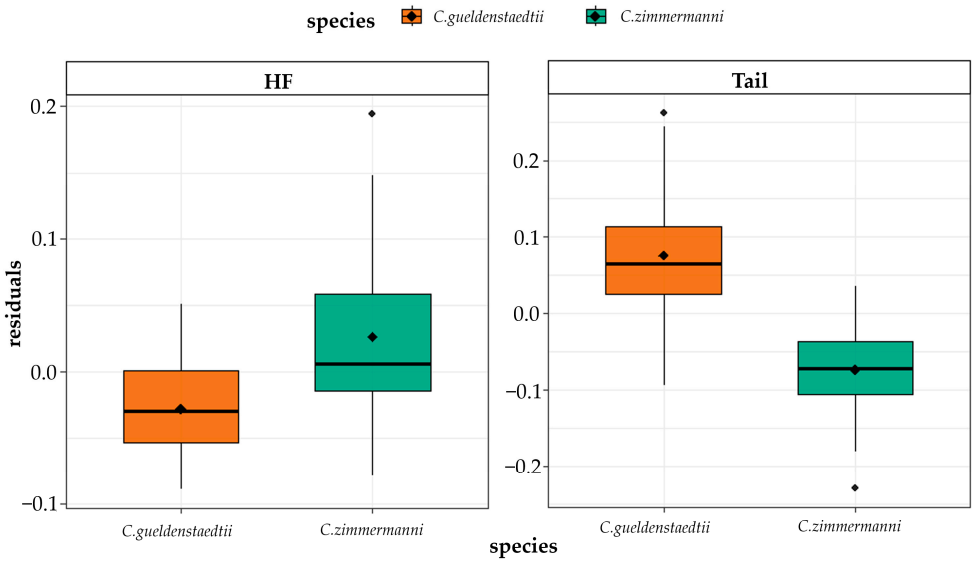


Figure 3. Residual variation in morphological traits after controlling for body length.

The intraspecific analysis of *C. zimmermanni* across the three mountain regions revealed no statistically significant morphological differentiation. Body length did not differ significantly among Dikti, Idi, and Lefka Ori ($R^2 = 0.015$, $F = 0.19$, $p = 0.838$), and pairwise comparisons also showed no significant differences between mountain regions.

Similarly, no significant differences were detected among mountain regions for hind foot length or tail length. Hind foot length was not significantly affected by mountain region ($R^2 = 0.101$, $F = 1.46$, $p = 0.262$), and tail length also showed no significant mountain effect ($R^2 = 0.085$, $F = 1.12$, $p = 0.336$). These results indicate that the examined populations of

C. zimmermanni from Dikti, Idi, and Lefka Ori do not differ significantly in the measured morphological traits.

Regarding the qualitative examination of tooth characters, we examined 33 *C. zimmermanni* and 36 *C. gueldenstaedtii* specimens confirmed molecularly (Supplementary Table S3). In all *C. zimmermanni* specimens, the 2nd and 3rd upper unicuspid teeth were longer than the parastyle of P4, with thick cingula; the 3rd distinctly larger than the 2nd, while all *C. gueldenstaedtii* had similarly sized 2nd and 3rd unicuspids that did not surpass the parastyle P4, with thinner cingula. The morphology of the parastyle of P4 (rounded in *C. zimmermanni*) could not be safely assessed, as the rounding of the specific tooth element could be attributed to wear.

3.3. Phylogenetics

The multiple sequence alignment of cyt b fragments had a length of 430 bp, with 103 (24%) variable sites, 89 (20.7%) of which were parsimony informative [131 (30.5%) and 113 (26.3%) respectively, when outgroups were included].

The best-fit nucleotide substitution models for each analysis are shown in Table 2.

Table 2. Best-fit substitution models for each codon position of the amplified cyt b fragment for all three phylogenetic analyses applied in this study.

DNA Fragment	BI	RAxML-NG	IQ-Tree
cytb_pos1	K80 + I	GTR + FC + G4m + B	TNe + I
cytb_pos2	F81	GTR + FC + G4m + B	F81 + F
cytb_pos3	HKY + I	GTR + FC + G4m + B	TPM2 + F

All three phylogenetic analyses produced trees with the same topology, with lnL values of −1559.28 for MrBayes, −1429.223 for RAxML-NG and −1439.930 for IQ-Tree. In the BI analysis, all Markov Chain Monte Carlo (MCMC) diagnostics showed convergence and stability (ASDF = 0.0039, all PSRF values = 1, ESS well over 200 for all parameters).

All species of the genus *Crocidura* used in the phylogenetic analyses were well distinguished, with high to full support. Concerning the interspecific phylogenetic relationships, all nodes were highly supported (posterior probability, pp > 0.95) in BI. However, in ML analyses, the corresponding phylogenetic relationships remained unresolved. The monophyly of the genus (pp = 1, bs = 100) and the sister group relationship of *C. gueldenstaedtii* with *C. cypria* (pp = 1, bs = 78 & 88) were the only relationships supported by both phylogenetic analyses (Figure 4). No intraspecific genetic structure was detected among the populations of the focal species on the island of Crete. Concerning *C. gueldenstaedtii*, the observed divergence was shallow, with even samples from Rhodes and Syria exhibiting no differentiation from those originating from Crete.

The genetic distances between all species used in this dataset are presented in Table 3. Within the genus *Crocidura*, the highest distance was observed between *C. gueldenstaedtii* and *C. russula* (19.2%), while the lowest was between *C. gueldenstaedtii* and *C. cypria* (6.3%). Notably, the divergence between *C. gueldenstaedtii* and *C. zimmermanni* reaches 15%. Conversely, intraspecific variation within both *C. gueldenstaedtii* and *C. zimmermanni* was negligible. Mean pairwise genetic divergence was effectively zero, with maximum differentiation reaching only 0.07% and 0.11% respectively.

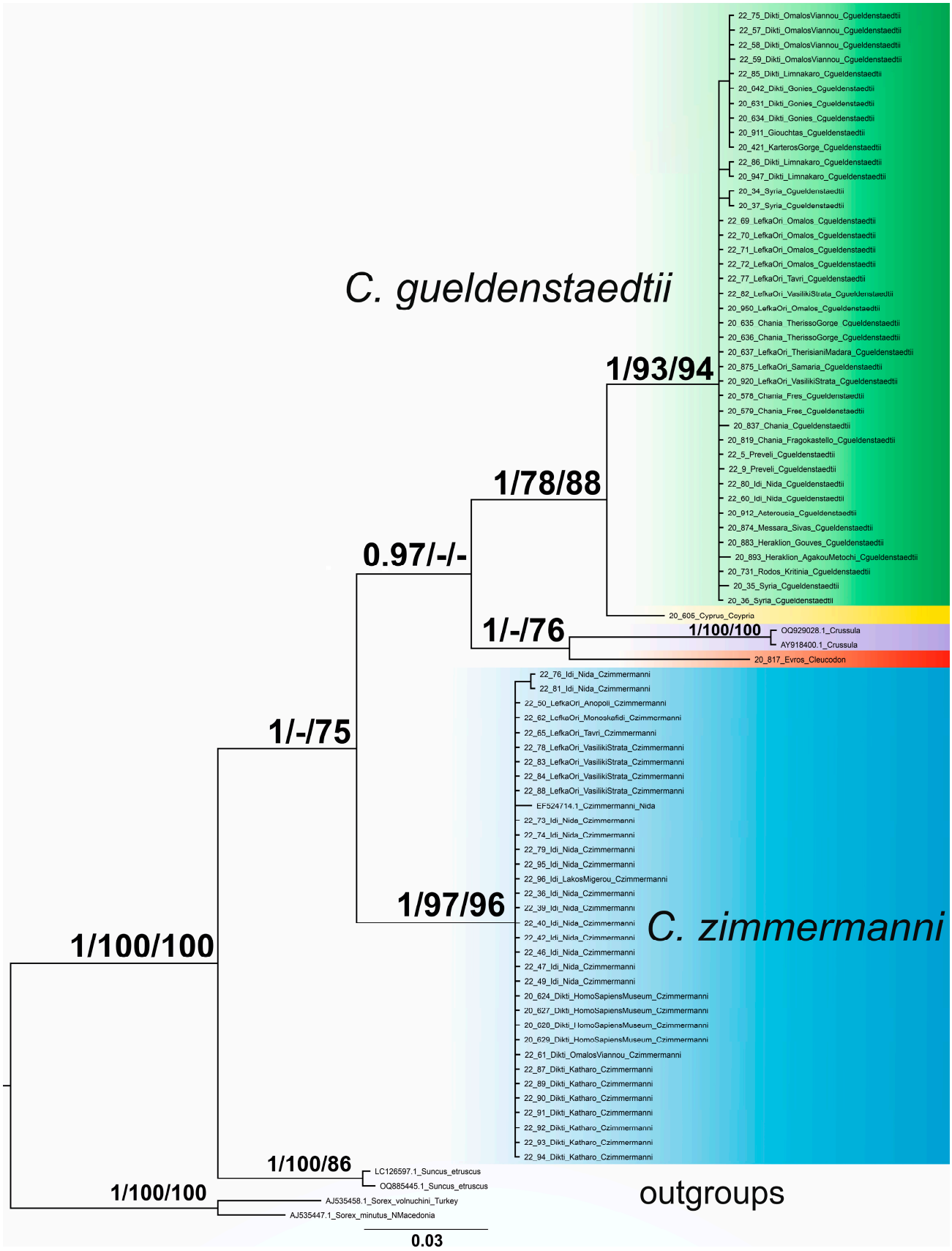


Figure 4. Phylogenetic tree based on the cyt b mitochondrial fragments (BI & ML topology). Bayesian posterior probabilities (PP) and maximum likelihood bootstrap support values (BS) are represented above the nodes as follows: PP/BS(RAxML)/BS(IQ-Tree). Only posterior probabilities greater than

0.95 and bootstrap values higher than 75% (ML) are displayed. Yellow, purple and red colors indicate *C. cypria*, *C. russula* and *C. leucodon* populations, respectively.

Table 3. Pairwise genetic distances (%) among species included in the dataset based on mitochondrial cyt b sequences, calculated under the Tamura-Nei model. The highest and lowest values in interspecific sequence divergence within the genus *Crocidura* are highlighted. Diagonal values (shown in red) correspond to the mean intraspecific pairwise genetic distances.

Species	1	2	3	4	5	6	7
1. *Sorex volnuchini*	-						
2. *Sorex minutus*	5.9	-					
3. *Suncus etruscus*	20.7	20.0	0				
4. *C. russula*	21.6	21.3	21.9	0			
5. *C. zimmermanni*	21.1	20.1	13.9	17.3	0		
6. *C. gueldenstaedtii*	18.8	22.2	16.5	**19.2**	15.0	0	
7. *C. cypria*	21.3	23.2	18.2	15.8	15.5	**6.3**	-
8. *C. leucodon*	21.1	22.0	20.2	13.9	17.1	16.2	12.6

3.4. Species Distribution Modeling

The land cover model for *C. zimmermanni* (Figure 5) had a very high evaluation, yielding an AUC of 0.943 and a TSS of 0.669 (Supplementary Table S7). The most important variable was altitude (Supplementary Figure S1), with a positive impact on distribution (Supplementary Figure S2). Similarly, the climatic model (Figure 6) achieved high evaluation scores (AUC = 0.935 and TSS = 0.712). In this model, the minimum temperature of the coldest month (Bio6) was the most important variable (Supplementary Figure S3), showing a negative correlation with the species distribution (Supplementary Figure S4), while precipitation and seasonality had no effect. Collectively, these models confirm that suitable habitats for *C. zimmermanni* are restricted to high-altitude, cold-temperature environments.

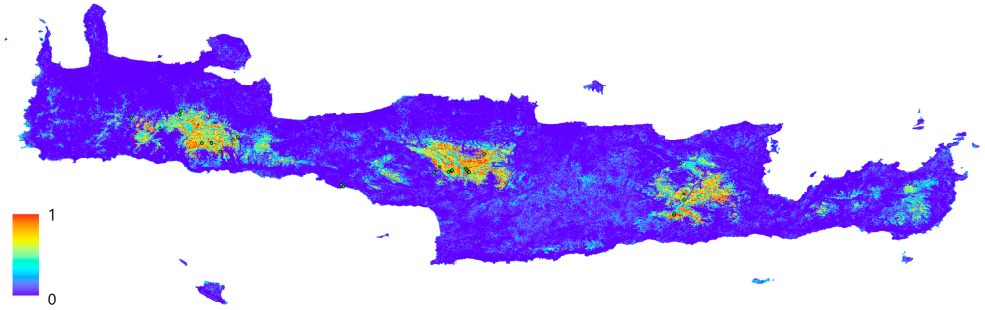


Figure 5. Land-cover model for *C. zimmermanni*. The color ramp denotes the probability of presence, with warm colors representing high probability.

The climatic model for *C. gueldenstaedtii* (Figure 7) yielded an acceptable evaluation (AUC = 0.76, TSS = 0.32). The minimum temperature of the coldest month (Bio6) emerged as the primary predictor (Supplementary Figure S5), supplemented by significant contributions from annual precipitation (Bio12) and precipitation of the warmest quarter (Bio18). In contrast to the endemic *C. zimmermanni*, temperature had a positive correlation with the probability of occurrence for *C. gueldenstaedtii*, while minimal values of precipitation-related variables (Bio12, Bio18) indicated absence (Supplementary Figure S6).

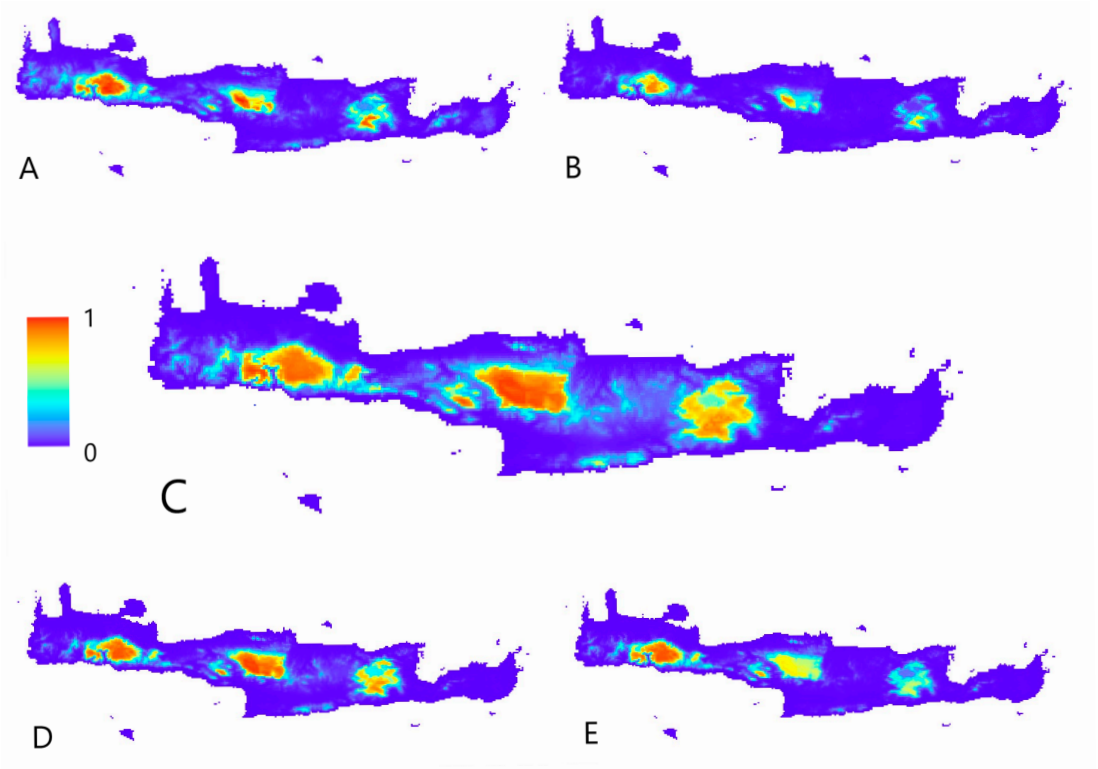


Figure 6. Climatic model projections for *C. zimmermanni* depicting the probability of suitable habitats. (**A**) Past: Last Glacial Maximum; (**B**) past: Mid-Holocene; (**C**) current; (**D**) future: SSP1-2.6 2070-2100; (**E**) future: SSP5-8.5 2070-2100. The color ramp denotes the probability of presence, with warm colors representing high probability.

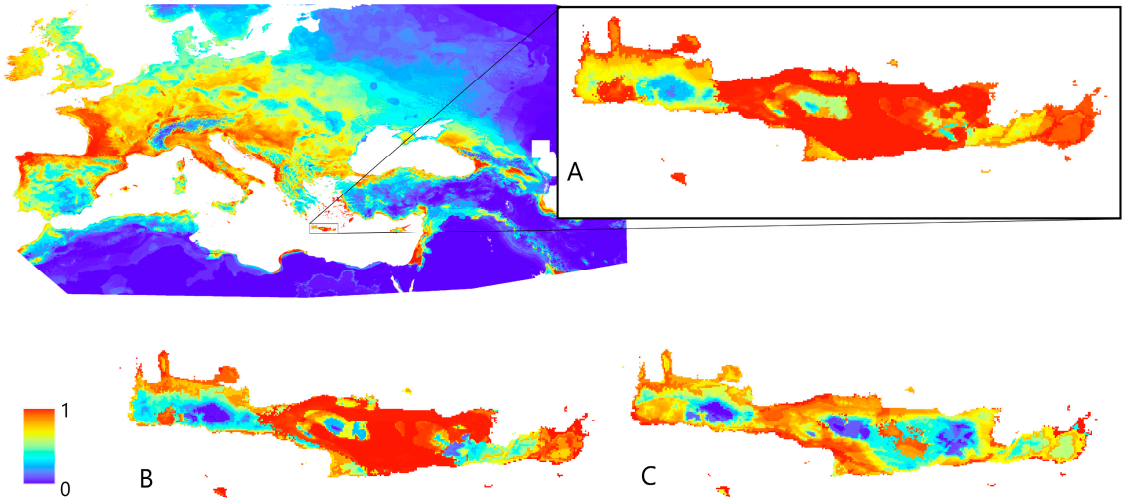


Figure 7. *C. gueldenstaedtii* climatic model projections depicting the probability of suitable habitats. (**A**) Current; (**B**) future: SSP1-2.6 2070-2100; (**C**) future: SSP5-8.5 2070-2100. The color ramp denotes the probability of presence, with warm colors representing high probability.

4. Discussion

Published records of captured specimens of *C. zimmermanni* until now have been confined to two localities, one on the Idi massif [7] and another on the Lefka Ori massif [13]. Data from *Tyto alba* pellet analysis showed that the species has a wider distribution and is present in localities close to the third mountain range of Crete, i.e., Dikti the massif [14]. Here, we present 30 new localities where a total of 80 specimens of *C. zimmermanni* have

been captured either through live traps or pitfall traps (Supplementary Table S4). The highest recorded altitude for this species is in Lochria (Idi massif) at 1950 m a.s.l. This is 500 m higher than the Nida plateau, which represents both the type locality of the holotype and the highest previously published record. The lowest altitude at which the species was found was 650 m a.s.l. at Kouroutes on the southern slopes of Ida Mountain. The species is potentially found at lower altitudes, but the current sampling effort was confined to higher altitudes, and no significant investigation has been conducted into all the lowland habitats that could potentially host the species, especially considering the low capture rate of the species. In contrast, *C. gueldenstaedtii* inhabits locations from sea level up to 1400 m a.s.l.

It is widely accepted that the present distribution of *C. zimmermanni* is mostly shaped by the antagonistic pressure from *C. gueldenstaedtii* [1,5,21]. Yet, syntopy has been reported since the discovery of the species on the Nida plateau [7]. In fact, this caused confusion regarding to the validity of the sample labels [65], but it was later confirmed as a case of syntopy by Vogel et al. [13]. Based on our data, both species co-occurred in the records from the year 2008 and were found to be syntopic again during the period 2023–2025, with *C. zimmermanni* found at a higher abundance. According to our data, syntopy was recorded in three additional cases (Vasiliki Strata- Lefka Ori massif, Zominthos, and Kouroutes at Idi massif), where specimens of both species were found at the same trapping sites without any observable differences in microhabitats. Notably, in Kouroutes, the species were captured in the same pitfall trap, indicating that both species utilize the same space. These habitats are all rocky shrublands with various degrees of inclination, and the altitude does not exceed 1400 m a.s.l. Cases of sympatry were observed in 4 localities (Omalos Viannou, Tavri plateau, Limnakaro plateau, Zominthos). In the cases of Tavri plateau and Limnakaro, previous sampling expeditions had found only specimens of *C. zimmermanni*, while during the present study's sampling effort, we only found *C. gueldenstaedtii* specimens, which might indicate a replacement of *C. zimmermanni*, but can also be attributed to chance. In flat wet grasslands forming the center of plateaus with minimal rock cover and low shrub cover, *C. gueldenstaedtii* was dominant, while *C. zimmermanni* was absent, as in the cases of Omalos in the Lefka Ori massif and Omalos Viannou in the Dikti massif. In the latter case, *C. zimmermanni* was found on the slopes defining the margins of the plateau, where the cover of shrubs and rocks was denser. In contrast, *C. zimmermanni* was present in rocky habitats with high inclination and very sparse vegetation, as in Rouvas and Ai Giorgis Ethelontis, Idi massif, where *C. gueldenstaedtii* was absent. Patch composition of the various microhabitats most likely allows the presence of the two species in syntopy [36,66,67]. However, the notes mentioned are based on limited data, as the capture rate varied and cannot support the claim of species absences in any case. Further investigation is needed to clarify the actual habitat preference.

Our species distribution models indicate that sympatry is widespread across the three mountain ranges, with *C. gueldenstaedtii* being absent only at the highest altitudes. It is worth noting that the species was found in four new localities accurately predicted by older models (see Sections 2.1 and 2.6). Additionally, these localities included the one with the highest capture rate (i.e., the Romanos locality at Katharo plateau, Dikti massif). Altitude and temperature were the most significant variables, consistent with the results of the preliminary models, regardless of the algorithm implemented, the variables selected or the number of presence records used. In our land-cover model, altitude emerged as the most significant predictor for *C. zimmermanni*. However, elevation is highly correlated with climatic variables, particularly in restricted island geographies like Crete, where latitudinal variation is minimal. While these results suggest that climate is a primary driver of distribution, the coarse scale of our models may overlook the importance of microclimatic buffering [36]. Given the small size and restricted home ranges of shrews [68], it is highly

likely that individuals exploit favorable microhabitat patches [36,66,67] at a grain much finer than currently captured by standard environmental layers. Therefore, the perceived importance of altitude may mask fine-scale habitat requirements that facilitate persistence in seemingly marginal areas. As mentioned, climate—and specifically temperature—is fundamental in shaping shrew distribution [35–37]. Some species (e.g., *Sorex araneus*, *Neomys fodiens*) have developed adaptations, like Dehnel's phenomenon, in order to persist during winter in colder climates, where they undergo a reduction in body and brain size to decrease their metabolic needs [69,70]. In contrast, *C. gueldenstaedtii* exhibits a predictable metabolic response to cold stress, increasing its metabolic rate as ambient temperatures decline. Notably, this thermoregulatory strategy appears consistent across the species' range, with no significant physiological divergence observed between insular and continental populations [71].

The morphometry of *C. zimmermanni* was represented by 10 individuals in the literature [11,14]. Our measurements show that *C. zimmermanni* can reach a body length of up to 86 mm, whereas the longest specimen previously reported measured 78 mm. We also found a greater overlap in hind foot length between the two species than previously reported, with *C. gueldenstaedtii* reaching up to 13 mm and *C. zimmermanni* measuring as little as 11 mm. Yet, most specimens conform to previously reported measurements [14]. Tail length was one of the first characters that differentiated the two species [7], albeit based on a small number of specimens. Our results agree with the aforementioned studies, while no differentiation is observed in individuals from different mountain ranges. The combination of hind foot length and relative tail size is adequate to identify mature individuals.

Concerning teeth morphology, the relative size difference of the 2nd and 3rd premolars in the maxilla—where the latter is greater than the former in *C. zimmermanni*, and both are of the same size in *C. gueldenstaedtii* [18]—was a very reliable character as it was unaffected by tooth wear and visible to the naked eye. The thickness of the cingulum [20] was also evidently greater in *C. zimmermanni* compared to *C. gueldenstaedtii* when observed under a stereoscope. The morphology of the parastyle P4 [18,20] did not offer reliable discrimination, as both species displayed pointy and/or rounded teeth.

A musky odor is a noted character of *C. gueldenstaedtii* since it was first described [72]. Moreover, the genus is associated with strong odors, as they are commonly referred to as musk shrews. During fieldwork and handling, *C. gueldenstaedtii* indeed had this characteristic odor, contrary to *C. zimmermanni*, which had no noticeable smell.

For two decades following its discovery, research on *C. zimmermanni* relied almost exclusively on morphological characterization [5,10,11,18] and foundational cytogenetic analyses [12,13,21]. Molecular data remain remarkably sparse, with most conclusions relying on the analysis of a single individual examined across a series of studies [2,3,28,29]. This reliance on a single specimen represents a significant gap in our understanding of the species' genetic diversity and evolutionary history.

This is the first phylogenetic study on the Cretan endemic shrew *C. zimmermanni*. In total, 33 new sequences of a fragment of cyt b are now available, covering the entire distributional range of the species across the three highest mountain ranges of the island of Crete. These three populations are considered isolated. The most widely accepted hypothesis explaining their current distribution is that *C. gueldenstaedtii* outcompeted *C. zimmermanni* in the lowlands of the island during historic times, resulting in the restriction of *C. zimmermanni* to high-altitude habitats [5,6,21].

The phylogenetic analyses support the monophyly of the genus *Crocidura*, with *C. zimmermanni* being the sister group to a clade that contains all the other species of the genus used in this study (*C. gueldenstaedtii*, *C. cypria*, *C. leucodon* and *C. russula*). The basal phylogenetic position of *C. zimmermanni*, even though not supported by all analyses,

contradicts previously published phylogenetic trees [2,3,29] where either *C. leucodon* or *C. russula* are placed in more external nodes than *C. zimmermanni*. However, it is important to note that all prior reconstructions of the *Crocidura* phylogeny, including *C. zimmermanni*, remained largely unresolved, characterized by low branch support and unstable branching patterns. Even though the current study incorporates samples from the whole distributional range of *C. zimmermanni*, it is restricted to a sole 430-bp mitochondrial fragment. Thus, this phylogenetic reconstruction should be accounted as a preliminary contribution to understanding relationships among the Cretan samples, rather than as having resolved deeper relationships within *Crocidura* in Crete. Further work, with the use of Next Generation Sequencing (NGS) data, is under preparation.

The genetic distance between *C. zimmermanni* and *C. gueldenstaedtii* reaches 15%, revealing high differentiation in cyt b. This divergence is even higher between *C. zimmermanni* and the other crocidurine taxa (Table 3), which is similar to that reported by [28]. It is interesting that the divergence between *C. zimmermanni* and *C. gueldenstaedtii* is lower than that among the latter and *C. leucodon* or *C. russula*, even though they seem closely related in the phylogenetic tree.

Moreover, the phylogenetic trees did not show any phylogenetic structure within the focal species (*C. zimmermanni* and *C. gueldenstaedtii*). In *C. gueldenstaedtii*, even the specimens from Syria were fully nested within the Cretan lineage. This supports the hypothesis that *C. gueldenstaedtii* colonized Crete, probably through human-aided dispersal, from the Middle East [26]. The only relationship that was fully supported was between *C. gueldenstaedtii* and its sister taxon, *C. cypria*. This result, unsurprisingly, coincides with the results of İbis et al. [4] on the whole mitogenomes of several taxa of the genus, including the aforementioned ones, which cluster these two as the closest relatives. The pairwise distance between *C. gueldenstaedtii* and *C. cypria* is 6.3%, the lowest among the taxa used in this study, while the intra-specific variation in *C. gueldenstaedtii* is negligible (0.07%). In Dubey et al. [26], the comparison between specimens of *C. gueldenstaedtii* and *C. cypria* showed greater differentiation (7.7%). This may be attributed to the fact that their dataset for *C. gueldenstaedtii* included, except for individuals from Crete, specimens covering a much wider geographic range throughout Europe and Asia, since the intra-clade divergence was also higher (0.6%) compared to this dataset.

SDM past projections (Mid-Holocene, Last Glacial Maximum) show that there were fewer habitats available for *C. zimmermanni*, according to its current climatic preferences. As the species is known to have inhabited the island since the Middle Pleistocene and has been reported from a few localities at low altitudes as late as the Bronze Age [5,12,27], climate alone cannot explain its past distribution. This is evident as our models failed to recognize any habitats in lower altitudes, especially along the coastline, where fossils of the species have been found [18]. Fossil records lack precise chronological estimates, and thus we cannot project our models at a specific time period. However, the fossil record indicates that *C. zimmermanni*'s present restriction to the highlands was not the case in the past. Consequently, we assume the current distribution of *C. zimmermanni* is probably due to competition with *C. gueldenstaedtii*, which was introduced in Crete during the Minoan Era [5,12,27]. Interaction between shrew species affects their distribution even at coarse scales and changes across climatic gradients [39]. In the case studied here, the introduced species outcompeted *C. zimmermanni* in the favorable lowland habitats, but failed to do so at the limits of *C. zimmermanni's* distribution in the highlands, where it had already, albeit marginally, adapted. Our models, not designed to process paleontological evidence, translate the present situation as a preference for lowland, warmer habitats for *C. gueldenstaedtii* versus highland cooler ones for *C. zimmermanni* respectively. Yet, the hypothesis of displacement due to competition requires further research to be confirmed

and to understand the underlying mechanisms that may have led to the current distribution of *C. zimmermanni*.

An alternative hypothesis would be that *C. zimmermanni* was forced to adapt to the cooler highlands due to competition with the newcomer. However, the main assumption of this hypothesis, i.e., a very rapid (since the Bronze Age) adaptation to cool highlands, makes it very unlikely to have occurred. This leaves us with the previous assumption of a formerly large (including highlands) distribution of *C. zimmermanni*, which has been restricted by its congeneric competitor. This hypothesis allows for cases of syntopy, as observed in a similar situation between *C. gueldenstaedtii* and *C. russula*, attributed to microhabitat conditions [36].

On the other hand, we should not neglect the potential impact of the human-mediated introduction of small carnivores (e.g., marten, weasel) during the same period on the island of Crete, as Crete did not host Carnivora at previous times, with the exception of *Lutragale cretensis* (an extinct otter species) [19,72,73]. This could also potentially have impacted the distribution of the species, as *C. zimmermanni* may lack anti-predatory adaptations, like the absence of a strong "musky" scent, mentioned previously, which may have increased the palatability of *C. zimmermanni* to mammalian predators in contrast to other shrews [74–77].

The future projections are alarming, as they predict constraints for both species, either due to increased temperatures for *C. zimmermanni* or due to decreased precipitation in the case of *C. gueldenstaedtii*. In a hopeful scenario, where competition is the limiting factor for *C. zimmermanni* and climate is just a proxy for this relationship, the decline of *C. gueldenstaedtii* may lead to an expansion of the endemic species distribution. However, if there is a reduction in the distribution of both species, many habitats will lose an important invertebrate regulator, leading to more vulnerable ecosystems.

5. Conclusions

Shrews represent one of the most elusive mammalian groups to study in the wild [78]. Although barn owl (*Tyto alba*) pellet analysis is one of the most effective methods for studying shrews' distribution [79], this approach is subject to bias; in the case of *C. zimmermanni*, the owl's absence at high altitudes precludes its use as a reliable monitoring tool. Consequently, alternative methods of sampling need to be implemented. While pitfall trapping is the most efficient way to collect *C. zimmermanni* to date, its lethal nature is undesirable for a threatened endemic. Alternatively, live trapping offers a non-lethal way, with negligible mortality (through regular checking of the traps), though low capture rate remains a significant challenge. To overcome these limitations, a multi-modal approach incorporating indirect sampling—such as bioacoustics and environmental DNA (eDNA)—is essential for a comprehensive ecological assessment.

Further work is needed in order to unravel the true phylogenetic position of *C. zimmermanni* within the genus. *Crocidura* is the most speciose genus among all mammalian groups, with a very wide distributional range [1,4]. This fact makes it very hard to ensure the use of representatives from all nominal taxa within the genus to resolve their phylogenetic relationships. A wider collaboration between institutions from all geographical zones of their range, as well as the use of data from Next Generation Sequencing (NGS) techniques, would promote the accomplishment of such an endeavor.

The SDMs adequately define the current distribution of both *Crocidura* species in Crete, based on temperature, with opposite effects for the two species. This seems to agree with the prevalent hypothesis that *C. zimmermanni* is being displaced by *C. gueldenstaedtii* in warmer and more favorable conditions; however, further research is required.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/d18110694/s1: Reference S1: Complete list of dataset citations for the Global Biodiversity Information Facility. Table S1: Sampling effort during the 2023–2026. Table S2: Measurements of length of hind foot (HF), body and tail for *Crocidura* from Crete. Table S3: List of species that were sequenced and used in this study, their geographic location, deposit codes of the collection in the Natural History Museum of Crete (NHMC) and accession numbers of cyt b sequences. Table S4: *Crocidura zimmermanni* samples from the collection of Natural History Museum of Crete (NHMC). Table S5: Localities and sampling method of *C. gueldenstaedtii* samples in the NHMC collection used for SDM. Table S6: VIF values and minimum and maximum correlation coefficients for the environmental datasets used for SDM. Table S7: Model evaluations. Figure S1: Variable importance for the land cover model of the distribution of *C. zimmermanni*. Figure S2: Response curves for the land cover model of *C. zimmermanni*'s distribution. Figure S3: Variable importance for the climatic model of *C. zimmermanni*'s distribution. Figure S4: Response curves for the climatic model of *C. zimmermanni*'s distribution. Figure S6: Variable importance for the climatic model of *C. gueldenstaedtii*'s distribution. Figure S7: Response curves for the climatic model of *C. gueldenstaedtii*'s distribution. Code S1: Script used in Species Distribution Modeling.

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Institutional Review Board Statement: The research has been conducted in accordance with Presidential Degree 67/81 of the Greek legislature and approved by the Research Ethics Committee of the University of Crete (protocol code 161/15.12.2023).

Data Availability Statement: The sequencing reads are available from the Sequence Read Archive (SRA) under the BioProject accession numbers listed in Supplementary Table S3. All other data are available as Supplementary Material appended to this manuscript.

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Conflicts of Interest: The authors declare no conflicts of interest.

Abbreviations

The following abbreviations are used in this manuscript:

AUC	Area Under the ROC (Receiver Operating Characteristic) Curve
NHMC	Natural History Museum of Crete
PCR	Polymerase Chain Reaction
SDM	Species Distribution Modeling
TSS	True Skill Statistics

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