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Spatial turnover and bioregional structure of reptile assemblages across Türkiye

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SUMMARY

Türkiye represents one of the most important biogeographic transition areas in the Mediterranean Basin, linking Mediterranean, Euro-Siberian, and Irano-Turanian biotas. Owing to its complex topography, climatic heterogeneity, and geological history, the country harbors exceptionally diverse reptile assemblages. However, large-scale quantitative analyses of reptile community structure across Türkiye remain limited. In this study, I used cleaned occurrence records obtained from the Global Biodiversity Information Facility (GBIF) to investigate spatial patterns of reptile assemblages across Türkiye using a grid-based macroecological framework. A total of 6609 occurrence records representing 139 reptile taxa (138 named species and one genus-level unit) were analyzed within 50 × 50 km grid cells. Of the 151 species included in the harmonized union of the two most recent national checklists, 131 (86.8%) were represented in the dataset. Species richness analyses, beta diversity decomposition, non-metric multidimensional scaling (NMDS), and hierarchical clustering approaches were used to evaluate assemblage differentiation and identify major reptile bioregions. Reptile species richness exhibited strong spatial heterogeneity across Türkiye, with highest richness values concentrated primarily along Mediterranean coastal regions and parts of southeastern Anatolia. Total beta diversity among assemblages was high (mean βSOR = 0.878), with species turnover accounting for approximately 85.9% of total beta diversity, whereas nestedness contributed only 14.1%. Null-model analyses confirmed that observed turnover values exceeded random expectations (SES = 14.61, $p < 0.001$), indicating that reptile assemblages across Türkiye are primarily structured by deterministic processes of spatial species replacement rather than stochastic assembly or ordered species loss. Ordination and clustering analyses additionally revealed distinct assemblage regions broadly corresponding to Mediterranean coastal systems, central Anatolian steppes, eastern Anatolian highlands, and Black Sea-associated regions. Overall, the findings demonstrate that reptile assemblages across Türkiye exhibit pronounced compositional turnover and strong spatial structuring associated with major environmental and biogeographic gradients. This study additionally highlights the utility of GBIF-based macroecological approaches for investigating large-scale biodiversity patterns and provides a quantitative framework for future biogeographic and conservation studies in the region.

INTRODUCTION

Anatolia represents one of the most important biogeographic transition zones within the Western Palearctic, linking the Mediterranean, Euro-Siberian, and Irano-Turanian biotic regions. Owing to its complex topography, climatic heterogeneity, and geological history, the region harbors exceptionally high biodiversity and endemism across multiple taxonomic groups (Bilgin 2011, Ambarlı et al. 2016). The Anatolian Peninsula is situated at the intersection of three global biodiversity hotspots the Mediterranean Basin, the Caucasus, and the Irano-Anatolian hotspot creating strong environmental gradients and pronounced faunal turnover across relatively short geographic distances.

Reptiles constitute one of the most biogeographically informative vertebrate groups in Anatolia due to their strong climatic sensitivity, limited dispersal capacities, and high levels of regional endemism. Previous studies have highlighted the complex zoogeographic structure of Anatolian reptile assemblages and emphasized the role of Anatolia as a diversification center and contact zone between Asian and European faunas (Sindaco et al. 2000, Ficetola et al. 2018, Yaşar et al. 2021). Comprehensive checklists and faunistic syntheses have repeatedly demonstrated the unusually high species richness and endemism rate of Turkish herpetofauna (Kurnaz 2020, Yaşar et al. 2021), and recent molecular and morphological revisions have continued to reveal cryptic diversity within the region, including the description of new species (Kurnaz and Şahin 2021b, Arribas et al. 2022, Kurnaz et al. 2022) and previously unrecognized phylogeographic structuring (Kornilios et al. 2012, Jablonski et al. 2019). In particular, the Anatolian Diagonal and associated mountain systems have long been considered major barriers and transition zones shaping species distributions and phylogeographic structure throughout the peninsula.

Despite the recognized biogeographic importance of Anatolia, large-scale quantitative analyses of reptile assemblage structure across the entire peninsula remain relatively limited. Most previous studies have focused on local faunas, species inventories, phylogeographic patterns, or taxonomic revisions rather than spatial turnover and community-level bioregionalization. Where quantitative spatial approaches have been adopted, they have predominantly relied on species-level ecological niche modeling (e.g. Kurnaz and Şahin 2021a, Kurnaz and Hosseinian Yousefkhani 2021, Şahin et al. 2021, 2022) rather than community-level analyses of multi-species assemblage structure. However, recent advances in macroecology and the increasing availability of biodiversity databases such as the Global Biodiversity Information Facility (GBIF) now permit comprehensive analyses of assemblage composition and beta diversity at broad spatial scales.

Beta diversity decomposition provides an effective framework for evaluating the processes underlying assemblage differentiation. In particular, separating total beta diversity into turnover and nestedness components enables the distinction between species replacement among regions and simple richness gradients resulting from species loss (Baselga 2010). Turnover-dominated systems generally indicate strong environmental filtering, historical isolation, or biogeographic barriers, whereas nestedness-dominated systems reflect ordered species loss across environmental gradients. Therefore, beta diversity decomposition can provide valuable insights into the spatial organization of Anatolian reptile assemblages and the role of Anatolia as a major transition zone between adjacent biogeographic regions.

In this study, I used GBIF occurrence records to investigate spatial patterns of reptile assemblages across Anatolia using a grid-based macroecological framework. Specifically, I aimed to: (i) quantify spatial patterns of reptile species richness, (ii) evaluate the relative contributions of turnover and nestedness to overall beta diversity, and (iii) identify major reptile bioregions across Anatolia using clustering and ordination approaches. I hypothesized that reptile assemblages across Anatolia would exhibit high compositional turnover reflecting the peninsula's role as a complex biogeographic transition zone linking Mediterranean, Euro-Siberian, and Irano-Turanian biotas.

MATERIALS AND METHODS

Study area

The study area covers the whole of Türkiye (ca. 783,600 km²; 36–42° N, 26–45° E), including both the Anatolian and the Thracian peninsulas. Relief is extreme: elevation rises from sea level to 5137 m at Mount Ağrı, and two major chains the Pontic

Mountains along the Black Sea and the Taurus Mountains along the Mediterranean run parallel to the coasts and enclose the Central Anatolian Plateau, which lies mostly between 800 and 1200 m. The two chains converge in eastern Anatolia and are connected to the Taurus system by the Anatolian Diagonal, a NE–SW oriented montane corridor repeatedly identified as a major biogeographic boundary (Davis 1971, Çiplak 2003). This configuration generates steep climatic gradients over short distances. The Aegean and Mediterranean coasts have a Mediterranean climate with hot, dry summers and mild, wet winters (mean annual precipitation ca. 600–1000 mm); the eastern Black Sea coast is humid temperate, lacks a marked dry season and locally exceeds 2000 mm of annual precipitation; the Central Anatolian Plateau is semi-arid and continental (ca. 300–400 mm), with pronounced summer drought and severe winter frost; eastern Anatolia experiences a cold continental montane climate with prolonged snow cover; and south-eastern Anatolia grades into the hot, semi-arid Mesopotamian lowlands. Accordingly, the country encompasses three phytogeographical regions Euro-Siberian, Mediterranean and Irano-Turanian (Davis 1971, Zohary 1973) and vegetation ranging from Mediterranean maquis and sclerophyllous woodland through Colchic humid forest to continental steppe, alpine meadow and semi-desert. This combination of pronounced habitat heterogeneity and strong environmental gradients makes Türkiye a particularly suitable system for analyses of large-scale assemblage turnover.

Occurrence data

Reptile occurrence records were obtained from the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/). Records belonging to the orders Squamata and Testudines were downloaded through the rgbif interface to the GBIF API (Chamberlain et al. 2025). Only records from Türkiye containing geographic coordinates were retained for analyses.

The downloaded occurrence dataset included records derived from multiple observation types, including human observations, preserved specimens, material citations, and museum collections. Records lacking species-level identification or geographic coordinates were excluded from subsequent analyses.

Data cleaning and quality control

Spatial and taxonomic cleaning procedures were applied to reduce potential biases associated with public biodiversity databases. Duplicate occurrences sharing identical coordinates and species identity were removed.

Potentially problematic coordinates were identified using the CoordinateCleaner package (Zizka et al. 2019). The cleaning workflow included tests for:

- equal latitude and longitude values,
- country centroids,
- country capitals,
- biodiversity institutions,
- GBIF headquarters,
- sea coordinates, and
- zero coordinates.

In addition to the geographical filters listed above, the positional precision of the records was considered explicitly. No maximum value for coordinateUncertaintyInMeters was imposed a priori, for two reasons. First, this field is not populated for a large proportion of the Turkish records, and particularly not for the older museum material that provides the only coverage of several poorly surveyed regions; a strict threshold would therefore have removed data non-randomly with respect to space and would have accentuated precisely the geographical bias that the present analyses seek to control. Second, all analyses were conducted at a resolution of 50 × 50 km, at which positional errors of the order of a few kilometers rarely alter the assignment of an occurrence to a grid cell. Spatial validity was accordingly ensured through the CoordinateCleaner tests listed above, which target the systematic georeferencing errors country centroids, institutional coordinates, capitals and sea coordinates that displace records by distances comparable to or greater than the grid resolution.

Taxonomic names were standardized in two steps. Names were first matched against the GBIF Backbone Taxonomy during download and were subsequently revised manually against the two most recent checklists of the Turkish herpetofauna, Kurnaz (2020) and Yaşar et al. (2021), which were adopted as the taxonomic reference framework of this study. Analyses were conducted at species rank: subspecific names were collapsed to the corresponding species, and records identified only to genus or to a higher rank were discarded, with a single exception. A set of *Testudo* (Linnaeus, 1758)

records that could not be assigned with confidence to either *T. graeca* (Linnaeus, 1758) or *T. hermanni* (Gmelin, 1789) was retained as one genus-level operational taxonomic unit (*Testudo* sp.), since discarding it would have removed occurrences of a genus that is otherwise well represented across the country. The analyzed dataset therefore comprises 139 operational taxa: 138 named species and this single genus-level unit. Orthographic variants and generic reassignments referring to the same taxon were merged (e.g. *Iranolacerta brandti*/*brandtii* (De Filippi, 1863), *Ablepharus*/*Asymblepharus bivittatus* (Ménétries, 1832), *Letheobia episcopa*/*episcopus* (Franzen and Wallach, 2002*)*, *Eirenis coronella* (Schlegel, 1837))/*coronelloides* (Jan, 1862*)*, *Walterinnesia aegyptia*/*morgani* (Lataste, 1887), *Darevskia praticola* (Eversmann, 1834)/*pontica* (Lantz & Cyrén, 1918)). The same treatment was applied to *Ophiomorus punctatissimus* (Bibron & Bory De St. Vincent, 1833): the Turkish populations were referred to that species until *O. kardesi* (Kornilios, Kumlutaş, Lymberakis and Ilgaz, 2018) was described from them (Kornilios et al. 2018), so records carrying the older name were relabelled and pooled with those already identified as *O. kardesi*. Where the GBIF backbone applies a species concept that differs from that of the national checklists (e.g. *Lacerta trilineata* (Bedriaga, 1886) vs. *L. diplochondrodes* (Wettstein, 1952), *Anguis fragilis* (Linnaeus, 1758) vs. *A. colchica* (Nordmann, 1840), *Timon princeps* (Blanford, 1874) vs. *T. kurdistanicus* (Suchow, 1936), *Asaccus elisae* (Werner, 1896) vs. *A. barani* (Torki, Ahmadzadeh, Ilgaz, Avci & Kumlutas, 2011), *Eirenis persicus* (Anderson, 1872) vs. *E. occidentalis* (Rajabizadeh, Nagy, Adriaens, Avci, Masroor, Schmidtler, Nazarov, Esmaeili & Christiaens, 2015)), the records could not be reassigned without re-examination of the underlying material and were therefore retained as separate operational taxonomic units and flagged in Supplementary Table S1. Taxonomic screening reduced the raw name list from 150 nominal taxa to the 139 units analyzed here: ten names were removed and one further name (*Ophiomorus punctatissimus*, Bibron & Bory De St. Vincent, 1833) was merged into an accepted species, as described above. The ten removals concern names whose species is not part of the Turkish reptile fauna (*Boaedon mendesi* (Ceríaco, Arellano, Jadin, Marques, Parrinha & Hallermann, 2021), *Darevskia saxicola* (Eversmann, 1834), *Eremias velox* (Pallas, 1771), *Hierophis gemonensis* (Laurenti, 1768), *Pelodiscus sinensis* (Wiegmann, 1835), *Phrynocephalus helioscopus* (Pallas, 1771), *P. persicus* (De Filippi, 1863), *Podarcis erhardii* (Bedriaga, 1882), *Vipera dinniki* (Nikolsky, 1913)) or whose Turkish records are currently referred to another species (*Malpolon monspessulanus* (Hermann, 1804) to *M. insignitus* (Geoffroy Saint-Hilaire, 1827)); together they accounted for 25 of the species-by-cell records of the raw matrix, and they are itemized in Supplementary Table S1. Three of these names *Boaedon mendesi* (Ceríaco, Arellano, Jadin, Marques, Parrinha & Hallermann, 2021), an Afrotropical lamprophiid, *Pelodiscus sinensis* (Wiegmann, 1835), an East Asian softshell turtle, and *Vipera dinniki* (Nikolsky, 1913), a Caucasian viper corresponds to evident misidentifications or georeferencing errors rather than to contested taxonomy. The two established alien species, *Trachemys scripta* (Thunberg in Schoepff, 1792) and *Podarcis siculus* (Rafinesque-Schmaltz, 1810), were retained in the analyses, since both maintain reproducing populations in the country and form part of the reptile assemblages as currently constituted.

After cleaning procedures, the final dataset consisted of 6609 unique reptile occurrence records.

Spatial framework

Occurrence records were converted to spatial features using the sf package (Pebesma 2018). To allow metric spatial analyses, all geometries were projected to the WGS84 / UTM Zone 36N coordinate reference system (EPSG:32636).

A regular grid system covering Anatolia was generated using 50 × 50 km grid cells. Grid construction and spatial intersection procedures were performed using functions implemented in the sf package. The grid comprised 384 cells intersecting the terrestrial territory of the country, of which 309 (80.5%) contained at least one cleaned occurrence record. Grid cells lacking occurrence records were retained for richness mapping but excluded from community-level analyses.

Occurrence records were spatially assigned to grid cells using spatial intersection procedures. A species-by-site presence–absence matrix was subsequently constructed, where rows represented grid cells and columns represented reptile taxa.

Species richness analyses

Species richness was calculated as the total number of reptile species occurring within each grid cell. Richness maps were generated using the ggplot2 package (Wickham 2016) together with color scales from the *viridis* package (Garnier et al. 2024).

Beta diversity decomposition

Total beta diversity and its turnover and nestedness components were quantified using the betapart package (Baselga and Orme 2012). Pairwise Sørensen dissimilarity was partitioned into:

- total beta diversity (βSOR),
- turnover component (βSIM), and
- nestedness-resultant component (βSNE).

This framework allows differentiation between assemblage variation resulting from species replacement and variation caused by ordered species loss.

Community ordination and bioregionalization

Community compositional gradients were evaluated using non-metric multidimensional scaling (NMDS) implemented in the vegan package (Oksanen et al. 2024). Ordinations were performed using Jaccard dissimilarity based on presence–absence data.

To reduce the influence of poorly sampled cells, grid cells with fewer than five occurrence records were excluded from ordination and clustering analyses.

Hierarchical clustering analyses were conducted using Ward's minimum variance method (ward.D2) based on Jaccard dissimilarity matrices. Clustering results were used to identify major reptile bioregions across Anatolia.

Null model analysis

To evaluate whether observed reptile assemblage turnover differed from random expectations, null-model analyses were performed using randomized community matrices generated with the vegan package (Oksanen et al. 2024). A fixed–fixed randomization algorithm was applied using the permatfull function, preserving both species occurrence frequencies and site richness values during matrix randomization.

A total of 999 randomized presence–absence matrices were generated from the observed community matrix. For each randomized matrix, Sørensen beta diversity was partitioned into turnover (βSIM), nestedness (βSNE), and total beta diversity (βSOR) components using the betapart package (Baselga and Orme 2012). Mean turnover values obtained from randomized assemblages were compared with observed turnover values.

Standardized effect sizes (SES) were calculated as:

$$SES = (Observed - Mean\_Null) / SD\_Null$$

where Observed represents the observed mean turnover value, Mean_Null represents the mean turnover obtained from randomized matrices, and SD_Null corresponds to the standard deviation of null distributions. One-tailed probabilities were calculated to evaluate whether observed turnover exceeded null expectations.

Sampling completeness and bias assessment

Because GBIF-derived occurrence datasets are known to exhibit substantial spatial and taxonomic biases (Meyer et al. 2016), several complementary approaches were used to assess the potential influence of uneven sampling effort on the inferred biogeographic patterns. First, sampling effort was quantified for each grid cell as the total number of cleaned occurrence records, and the spatial distribution of sampling intensity was visualized across the study area to identify under-sampled regions. Second, asymptotic species richness was estimated for the dataset as a whole using the Chao2 incidence-based estimator implemented in the iNEXT package (Hsieh et al. 2016), and sample coverage was computed as a complementary measure of the completeness of the incidence data; both quantities were obtained from the final 139-taxon incidence matrix. The two measures are not equivalent: sample coverage estimates the proportion of the total incidence of the assemblage that is accounted for by the taxa already detected, whereas the ratio of observed to asymptotic richness estimates the proportion of the estimated regional species pool that the recorded taxa represent.

Third, a threshold sensitivity analysis was performed by repeating the beta diversity decomposition and ordination analyses at three minimum sampling thresholds per grid cell ($n \geq 5$, $n \geq 10$, and $n \geq 20$ records). This procedure tested whether the dominance of turnover over nestedness and the overall bioregionalization structure remained

qualitatively consistent when only better-sampled cells were retained. Finally, the relationship between species richness per grid cell and the corresponding number of occurrence records was examined using Spearman rank correlation to evaluate the extent to which observed richness patterns might be driven by uneven sampling effort. Finally, the taxonomic completeness of the dataset was evaluated by comparing the species list recovered from the cleaned occurrence data with the two most recent national checklists (Kurnaz 2020, Yaşar et al. 2021). Species listed in either checklist but not represented in the dataset were identified, and their likely causes of absence (range restriction, detectability, or unresolved taxonomy) were examined; the full comparison is given in Supplementary Table S1.

Statistical environment

All analyses were performed in R version 4.4.2 (R Core Team 2024).

RESULTS

Occurrence dataset and spatial coverage

After data cleaning and quality-control procedures, a total of 6609 unique reptile occurrence records were retained for analyses. The final dataset represented 139 reptile taxa, 138 identified to species rank and one genus-level unit (*Testudo* sp.), subspecific names having been collapsed to the corresponding species (see Materials and Methods) distributed across 309 occupied 50 × 50 km grid cells, that is 80.5% of the 384 cells covering the country.

Spatial coverage of occurrence records was heterogeneous across the study area. Sampling density was generally higher along the Mediterranean coast, western Anatolia, and portions of the Black Sea region, whereas relatively lower sampling intensity was observed in parts of eastern and central Anatolia.

Taxonomic coverage of the dataset

The 138 named species recovered from the cleaned dataset were compared with the two most recent checklists of Turkish reptiles (Kurnaz 2020: 145 species; Yaşar et al. 2021: 141 species), the harmonized union of which comprises 151 species. Of these, 131 species (86.8%) were represented by at least one cleaned occurrence record (87.6% of the list of Kurnaz 2020 and 90.1% of that of Yaşar et al. 2021), and 123 species were common to all three sources (Supplementary Table S1). Occupancy was strongly right-skewed across the 139 analyzed taxa, ranging from a single grid cell (21 taxa) to 222 cells (*Testudo graeca*, Linnaeus, 1758), with a median of 8 and a mean of 19.0 occupied cells; 61 taxa were recorded in five or fewer cells, and the analyzed matrix contains 2639 species-by-cell records.

Twenty species listed in at least one checklist were not represented in the dataset, and these fall into two clearly distinct groups. The first comprises species that enter Türkiye only at the extreme margin of their global ranges and are known from a small number of localities in south-eastern Anatolia and the Levantine border zone: *Eublepharis angramainyu* (Anderson and Leviton, 1966), *Stenodactylus grandiceps* (Haas, 1952), *Mesalina microlepis* (Angel, 1936), *Varanus griseus* (Daudin, 1803), *Heremites septemtaeniatus* (Reuss, 1834), *Platyceps ventromaculatus* (Gray, 1834), *P. rhodorachis* (Jan, 1863), *Rhynchocalamus melanocephalus* (Jan, 1862), *R. satunini* (Nikolsky, 1899), *Daboia palaestinae* (Werner, 1938), *Elaphe dione* (Pallas, 1773)) and *Eirenis aurolineatus* (Venzmer, 1919)). Most of these taxa are nocturnal, fossorial or otherwise secretive, and their Turkish records derive largely from museum material that has not yet been mobilised to GBIF. The second group comprises recently described, recently resurrected or taxonomically contentious taxa whose Turkish occurrences are still filed under a parental name in the GBIF backbone: *Anatololacerta budaki* (Eiselt and Schmidtler, 1986), *Darevskia adjarica* (Darevsky and Eiselt, 1980), *D. dryada* (Darevsky and Eiselt, 1980), *D. mixta* (Méhely, 1909), *Vipera barani* (Böhme and Joger, 1983), *V. olguni* (Tunıyev, Avcı, Tunıyev, Agasıan, and Agasıan 2012), *V. pontica* (Billing, Nilson and Sattler, 1990) and *V. renardi* (Christoph, 1861). Conversely, seven of the 138 named species in the dataset are not accepted in either checklist: *Anguis fragilis* (Linnaeus, 1758), *Asaccus elisae* (Werner, 1896), *Eirenis persicus* (Anderson, 1872), *Lacerta trilineata* (Bedriaga, 1886), *Timon princeps* (Blanford, 1874), *Platyceps karelini* (Brandt, 1838) and *Darevskia josefschmidtleri* (Arribas, Candan, Kornilios, Ayaz, Kumlutaş, Gül, Yilmaz, Caynak & Ilgaz, 2022), all of which represent alternative or superseded species concepts for taxa that are themselves present in the dataset and none of which therefore adds a species to the fauna.

Spatial patterns of species richness

Reptile species richness exhibited strong spatial heterogeneity across Anatolia (Fig. 1). Species richness per grid cell ranged from 1 to 31 species, with a mean richness of 6.2 species per grid.

The highest richness values were primarily concentrated along the Mediterranean coastal belt and southwestern Anatolia. Additional richness concentrations were observed in southeastern Anatolia and portions of the eastern Black Sea region. In contrast, lower richness values generally characterized central Anatolian steppe regions and parts of eastern Anatolia.

Overall, richness patterns suggested strong environmental and biogeographic gradients across the Anatolian Peninsula.

Beta diversity decomposition

Total beta diversity among reptile assemblages across Anatolia was high (mean βSOR = 0.878), indicating substantial compositional differentiation among grid cells.

Beta diversity decomposition revealed that assemblage variation was overwhelmingly dominated by species turnover rather than nestedness (Fig. 2). The turnover component accounted for approximately 85.9% of total beta diversity (mean βSIM = 0.754), whereas the nestedness component represented only 14.1% of total beta diversity (mean βSNE = 0.124).

The distribution of pairwise turnover values showed consistently high compositional replacement among many grid-cell pairs (Fig. 2). These results indicate that reptile assemblages across Anatolia are primarily structured by spatial species replacement rather than ordered species loss. Applying the decomposition to the assemblage as a whole rather than to pairs of grid cells returned the same picture: βSOR = 0.8413, of which turnover accounted for βSIM = 0.6795 (80.8% of total beta diversity) and the nestedness-resultant component for βSNE = 0.1618 (19.2%). The pairwise and multiple-site decompositions therefore agree in identifying species replacement as the dominant component of assemblage differentiation across Anatolia.

Community ordination

Non-metric multidimensional scaling (NMDS) analyses revealed substantial compositional differentiation among reptile assemblages across Anatolia (Fig. 3). After excluding poorly sampled grid cells, the NMDS solution produced a stress value of 0.213. Although this value approaches the upper limit of interpretability for two-dimensional ordinations (Clarke 1993), the recovered configuration was considered informative for visualizing broad compositional gradients but should be interpreted with caution; clustering and bioregionalization analyses were used as the primary basis for spatial delineation.

Ordination patterns suggested the presence of multiple assemblage gradients across Anatolia, particularly between Mediterranean coastal assemblages, central Anatolian steppe assemblages, and eastern montane assemblages.

Bioregionalization

Hierarchical clustering analyses identified distinct spatial structuring of reptile assemblages across Anatolia (Figs. 4 and 5). Depending on the selected clustering threshold, between four and six major assemblage regions were consistently recovered.

The resulting bioregionalization patterns broadly corresponded to major Anatolian biogeographic divisions. Mediterranean coastal assemblages formed a relatively cohesive southern region, whereas central Anatolian assemblages showed differentiation consistent with steppe ecosystems. Eastern Anatolia and portions of the Black Sea region also exhibited distinct assemblage compositions.

Several transition zones were observed between major assemblage regions, particularly along central-eastern Anatolia and montane systems associated with the Anatolian Diagonal. These transition areas were characterized by rapid turnover in reptile species composition among neighboring grid cells.

Overall, the observed bioregionalization patterns strongly support the role of Anatolia as a major biogeographic transition zone linking Mediterranean, Euro-Siberian, and Irano-Turanian biotas.

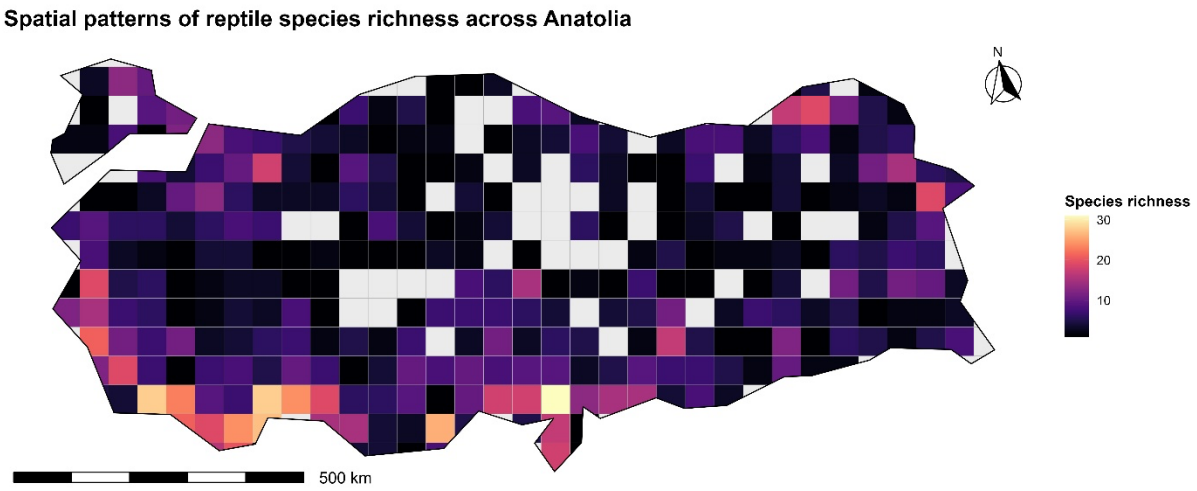

Figure 1. Spatial patterns of reptile species richness across Anatolia. Species richness was calculated within 50 × 50 km grid cells using cleaned GBIF occurrence records for reptile taxa (Squamata and Testudines). Warmer colors indicate higher species richness, whereas grey cells represent grid cells without available occurrence records.

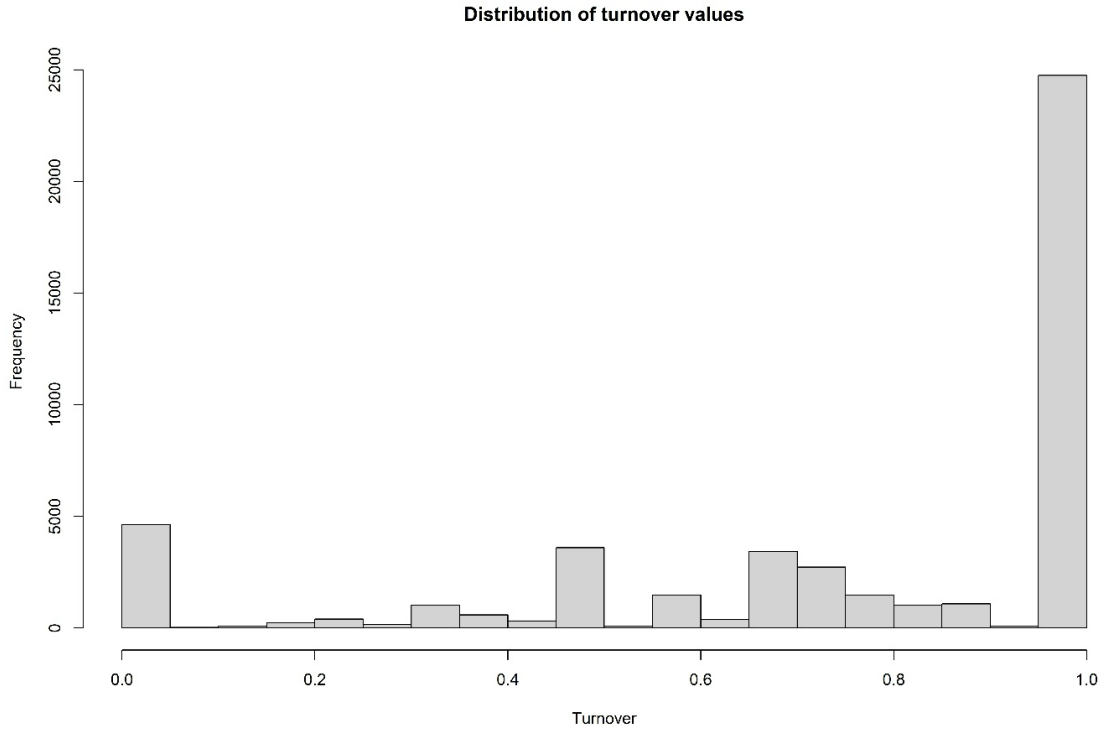

Figure 2. Distribution of pairwise turnover values among reptile assemblages across Anatolia. Turnover values were calculated using the turnover component (βSIM) of Sørensen beta diversity decomposition. The predominance of high turnover values indicates strong compositional replacement among Anatolian reptile assemblages.

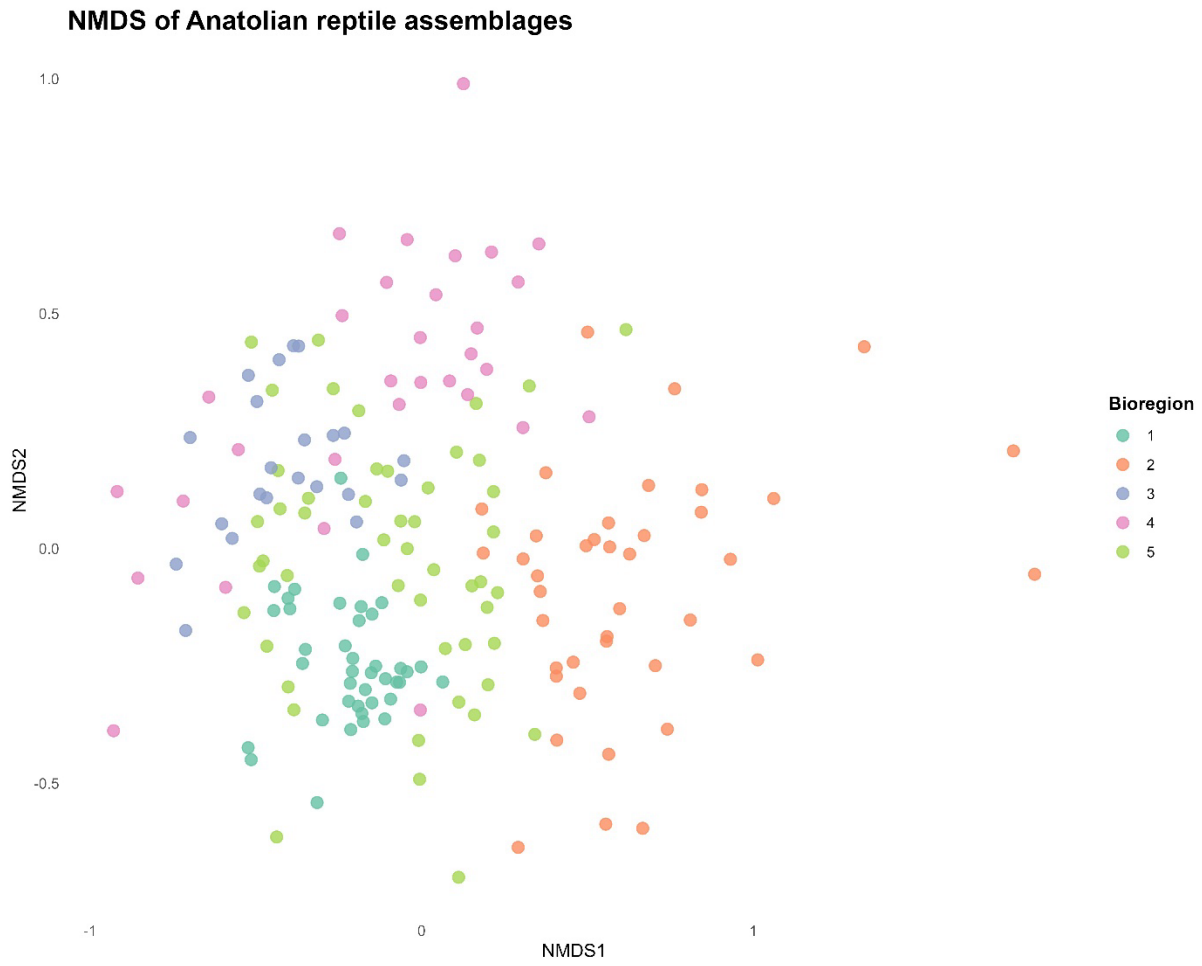

Figure 3. Non-metric multidimensional scaling (NMDS) ordination of reptile assemblages across Anatolia. Ordination was based on Jaccard dissimilarity calculated from species presence–absence data. Each point represents a 50 × 50 km grid cell. The NMDS analysis revealed substantial compositional differentiation among assemblages across Anatolia.

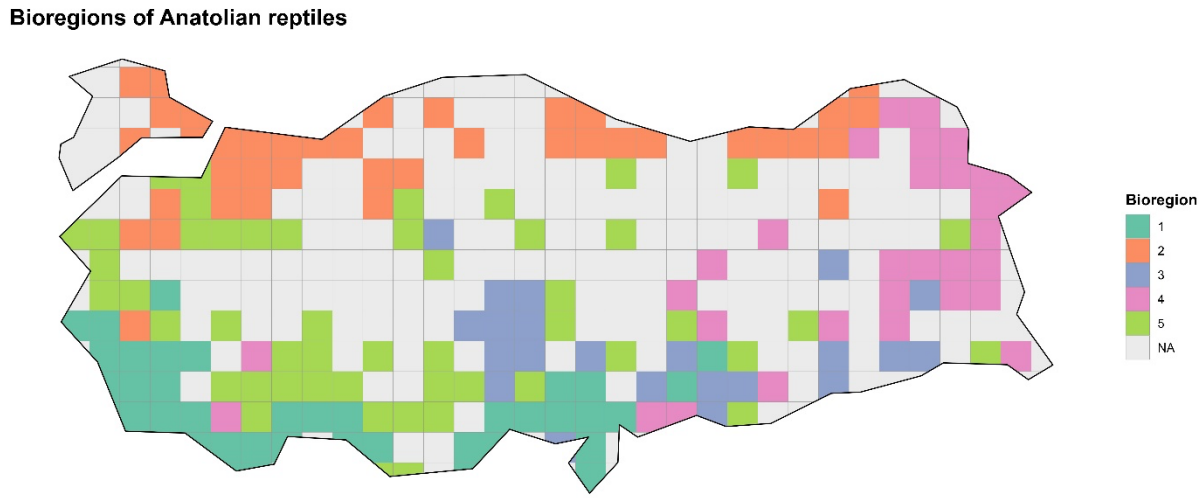

Figure 4. Bioregions of Anatolian reptile assemblages identified using hierarchical clustering analyses. Bioregions were derived from Jaccard dissimilarity matrices based on species presence–absence data using Ward's clustering method. Distinct assemblage regions broadly correspond to major Mediterranean, Irano-Turanian, Euro-Siberian, and montane transition zones across Anatolia.

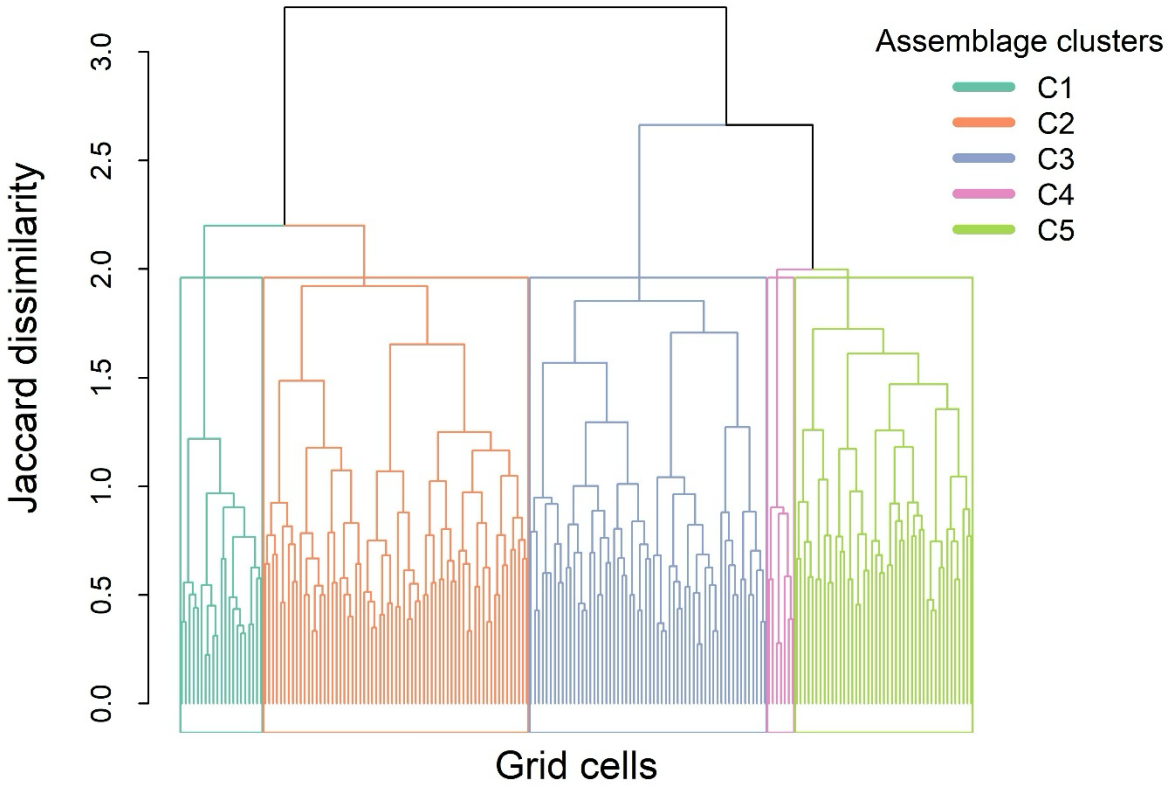

Figure 5. Hierarchical clustering dendrogram of reptile assemblages across Anatolia. The dendrogram was generated using Ward's minimum variance clustering method based on Jaccard dissimilarity matrices derived from species presence–absence data. Major clusters correspond to distinct reptile assemblage regions across Anatolia. Cluster membership is indicated by the same color scheme used for the bioregions in Fig. 4, and cluster labels have been enlarged for legibility.

Null model analysis

Null-model analyses demonstrated that observed reptile assemblage turnover across Türkiye was substantially higher than expected under random community assembly. Observed turnover values (mean βSIM = 0.754) exceeded null expectations generated from randomized assemblages (mean null βSIM = 0.704).

The standardized effect size for turnover was exceptionally high (SES = 14.61), indicating that observed assemblage differentiation was far greater than expected under stochastic assembly processes. In addition, null-model probabilities indicated that observed turnover values were significantly higher than null expectations ($p < 0.001$).

These results demonstrate that reptile assemblages across Türkiye exhibit strong non-random spatial structuring and that assemblage differentiation is primarily driven by deterministic biogeographic and environmental processes rather than random species assembly.

Sampling completeness and bias assessment

Sampling intensity varied considerably across Anatolia, with the highest occurrence densities recorded along Mediterranean coastal areas and parts of western Anatolia, and the lowest densities recorded in portions of central and eastern Anatolia. The Chao2 incidence-based estimator, applied to the final 139-taxon incidence matrix, yielded an asymptotic richness of 169.52 taxa for the study area as a whole, and the estimated sample coverage of the same matrix was 0.9902. The 139 taxa actually recorded therefore correspond to 82.0% of the estimated regional species pool. The two values describe different aspects of sampling completeness: the very high sample coverage indicates that the available records adequately characterize the assemblages they represent, whereas the gap between observed and asymptotic richness indicates that a limited number of additional taxa, predominantly range-restricted or cryptic species of under-sampled regions, remain undetected.

The threshold sensitivity analysis indicated that the overall structure of beta diversity decomposition and the recovered bioregionalization pattern remained qualitatively robust across the three minimum-sampling thresholds tested ($n \geq 5$, $n \geq 10$, and $n \geq 20$). Mean total beta diversity remained high, and the turnover component continued to dominate over nestedness at all thresholds ($n \geq 5$: $\beta SOR = 0.7986$, $\beta SIM = 0.6656$, $\beta SNE = 0.1329$, turnover = 83.3% of total beta diversity; $n \geq 10$: $\beta SOR = 0.7613$, $\beta SIM = 0.6266$, $\beta SNE = 0.1347$, turnover = 82.3%; $n \geq 20$: $\beta SOR = 0.7380$, $\beta SIM = 0.6304$, $\beta SNE = 0.1076$, turnover = 85.4%). Total beta diversity declined only slightly as poorly sampled cells were removed, and the relative contribution of turnover remained essentially unchanged (82–85% at every threshold), indicating that the dominance of compositional turnover is not an artefact of the chosen sampling-effort cutoff.

Spearman rank correlation between species richness per grid cell and the corresponding number of occurrence records was positive and statistically significant (Spearman $\rho = 0.9037$, $p < 0.001$, $n = 309$ grid cells), confirming that some richness variation reflects differences in sampling intensity. Nevertheless, the elevated turnover values, the highly significant null-model deviation (SES = 14.61), and the spatial coherence of recovered bioregions indicate that the principal biogeographic patterns reported here cannot be explained by sampling bias alone.

DISCUSSION

The analyses revealed exceptionally high beta diversity among reptile assemblages across Anatolia, with spatial differentiation overwhelmingly dominated by species turnover rather than nestedness. This result indicates that reptile assemblages across the peninsula are primarily structured by species replacement among regions rather than by ordered species loss along environmental gradients. High turnover values are generally associated with strong environmental heterogeneity, historical isolation, dispersal limitation, and the presence of biogeographic barriers (Baselga 2010). Anatolia exhibits all of these characteristics and therefore represents an ideal system for investigating large-scale assemblage differentiation.

The Anatolian Peninsula is widely recognized as one of the most important biogeographic transition zones in the Western Palearctic, linking Mediterranean, Euro-Siberian, and Irano-Turanian biotas (Zohary 1973, Bilgin 2011). Its complex geological history, highly heterogeneous topography, and strong climatic gradients have created substantial environmental variation over relatively short geographic distances. These conditions have promoted diversification, persistence of refugial populations, and regional differentiation across multiple taxonomic groups (Bilgin 2011, Ambarlı et al. 2016).

The strong dominance of turnover over nestedness observed in this study suggests that reptile assemblages from different regions of Anatolia are not merely species-poor subsets of richer assemblages elsewhere. Instead, assemblages represent distinct faunal compositions associated with different climatic and biogeographic regions. Similar turnover-dominated patterns have been reported in reptile assemblages across the Mediterranean Basin and Western Palearctic, where climatic heterogeneity and historical refugia strongly influence assemblage structure (Ficetola et al. 2018). The results therefore support the hypothesis that Anatolia functions as a major center of faunal replacement between adjacent biogeographic regions.

The null-model analyses further strengthen the interpretation that reptile assemblages across Türkiye are structured by strong deterministic processes. The exceptionally high standardized effect size obtained for turnover indicates that the observed compositional differentiation among assemblages cannot be explained solely by stochastic community assembly. Instead, the observed turnover patterns likely reflect the combined influence of climatic filtering, topographic complexity, dispersal limitation, and historical biogeographic processes operating across Anatolia. The strong deviation from null expectations is consistent with the highly heterogeneous environmental structure of Türkiye, where mountain systems, climatic gradients, and transition zones generate substantial ecological differentiation among regions.

The observed non-random turnover patterns additionally support the hypothesis that Anatolia functions as a major biogeographic transition zone connecting Mediterranean, Euro-Siberian, and Irano-Turanian biotas. Under random assembly, turnover values would be expected to approximate null expectations generated from randomized matrices.

However, the substantially elevated observed turnover detected in this study indicates that reptile assemblages are spatially organized by strong ecological and historical constraints. These findings are also consistent with previous studies emphasizing the importance of Anatolia as both a refugial region and a center of faunal diversification during Quaternary climatic oscillations (Bilgin 2011). Consequently, the observed reptile assemblage structure across Türkiye likely represents the cumulative outcome of long-term historical isolation, environmental filtering, and regional diversification processes.

The spatial patterns recovered by the bioregionalization analyses broadly corresponded to major phytogeographic and climatic divisions across Anatolia. Mediterranean coastal regions formed relatively cohesive assemblages characterized by thermophilic taxa associated with warm and seasonally dry conditions. In contrast, central Anatolian assemblages reflected continental steppe environments, while eastern Anatolian assemblages exhibited additional differentiation likely associated with higher elevations, colder climates, and stronger Irano-Turanian and Caucasian influences. These findings are consistent with previous zoogeographic assessments of Anatolian reptiles emphasizing the mosaic-like structure of Anatolian herpetofauna (Sindaco et al. 2000, Yaşar et al. 2021), and broadly correspond to the chorotype divisions proposed for the Near Eastern fauna within the Western Palearctic framework (Vigna Taglianti et al. 1999).

Topographic complexity likely represents one of the principal drivers underlying the observed compositional turnover. Mountain systems such as the Taurus Mountains, Pontic Mountains, and eastern Anatolian highlands generate strong ecological gradients and may function simultaneously as dispersal barriers, climatic refugia, and centers of diversification. Numerous reptile taxa in Anatolia exhibit restricted distributions associated with montane systems, particularly within genera such as *Darevskia*, *Anatololacerta*, and *Vipera* (Sindaco et al. 2000, Kornilios et al. 2012, Şahin et al. 2022). Such geographically restricted taxa likely contribute substantially to the high levels of regional differentiation observed in this study. Indeed, ecological niche modeling studies have repeatedly demonstrated strong niche divergence among closely related Anatolian taxa, both for amphibians (Kurnaz and Şahin 2021a) and reptiles (Kurnaz and Hosseinian Yousefkhani 2021, Şahin et al. 2021, 2022), supporting the role of climatic heterogeneity in maintaining regional faunal distinctiveness. Ongoing taxonomic work continues to reveal previously hidden lineages within Anatolian reptiles, including the description of new species (Kurnaz and Şahin 2021b) and cryptic species recognized only through integrative morphological and molecular approaches (Arribas et al. 2022), further reinforcing the picture of Anatolia as both a refugial area and a diversification center.

Several transition zones identified in the analyses broadly corresponded to areas associated with the Anatolian Diagonal. The Anatolian Diagonal has long been considered an important biogeographic boundary affecting both floral and faunal distributions across Türkiye (Davis 1971, Çiplak 2003). Previous studies have suggested that this mountain corridor may limit dispersal and promote lineage divergence in multiple vertebrate and invertebrate groups (Çiplak 2003, Bilgin 2011). Although analyses were not specifically designed to test the Anatolian Diagonal hypothesis, the observed spatial discontinuities and rapid assemblage turnover between eastern and western regions are broadly consistent with its proposed biogeographic influence.

The use of GBIF occurrence data enabled a broad-scale macroecological assessment encompassing the entirety of Anatolia. Increasing accessibility of open-access biodiversity databases has substantially expanded opportunities for large-scale biogeographic research. Nevertheless, occurrence databases are associated with well-recognized limitations, including uneven sampling intensity, geographic biases, taxonomic inconsistencies, and spatial uncertainty (Meyer et al. 2016). In the present dataset, occurrence density was clearly higher in western and coastal regions compared to portions of eastern Anatolia, raising legitimate concerns that under-sampling could inflate apparent assemblage turnover by generating spurious single-species cells, and that richness gradients could partly reflect collector effort rather than ecological reality. Several lines of evidence indicate that the principal biogeographic patterns reported here are nevertheless not artefacts of sampling bias. First, extensive coordinate-cleaning procedures were applied, and grid cells with fewer than five records were excluded from ordination and clustering analyses. Second, the threshold sensitivity analysis demonstrated that the dominance of turnover over nestedness and the recovered bioregionalization remained qualitatively consistent when only better-

sampled grid cells were retained. Third, the null-model analyses showed that observed turnover values deviated very strongly from random expectations (SES = 14.61, $p < 0.001$), and such an extreme departure from null distributions is highly unlikely to arise from sampling artefacts alone, which would generally bias observed values toward, rather than away from, null expectations. Fourth, the Chao2 estimator indicated that the dataset captured a substantial proportion of the regional reptile fauna (139 taxa of an estimated 169.52, i.e. 82.0% of the estimated richness, with a sample coverage of 0.9902). Together, these complementary checks suggest that the principal biogeographic signals high compositional turnover, deterministic spatial structuring, and the existence of distinct reptile bioregions reflect genuine ecological and historical processes rather than sampling artefacts. Some residual influence of under-sampling on richness estimates in eastern Anatolia cannot be excluded and warrants targeted field surveys in the future. Overall, these results demonstrate that publicly available biodiversity databases can provide robust insights into large-scale reptile biogeography when combined with appropriate cleaning, sensitivity, and null-model frameworks.

Incompleteness also has a taxonomic dimension that deserves explicit attention. The cleaned dataset recovered 131 of the 151 species (86.8%) included in the harmonized union of the two national checklists, but the species that are missing do not constitute a random subset of the fauna: they are concentrated in south-eastern Anatolia and among recently split or taxonomically contentious lineages. Both biases are conservative with respect to the conclusions drawn here. Range-restricted species absent from south-eastern Anatolia would, if included, increase the compositional distinctiveness of that region and therefore raise rather than lower measured turnover; similarly, occurrences of recently recognized taxa that remain pooled under parental names inflate the apparent ranges of those parental species and thus reduce, rather than exaggerate, the turnover component of beta diversity. Mobilizing the substantial museum material held in Turkish and European collections and updating the taxonomic backbone of existing records would nevertheless considerably improve the resolution of future macroecological analyses in the region, and the synoptic comparison presented in Supplementary Table S1 is intended as a starting point for such an effort.

The high degree of assemblage turnover observed across Anatolia also has important conservation implications. Turnover-dominated systems indicate that different regions contain distinct species assemblages rather than nested subsets of a single regional fauna. Consequently, conservation strategies focused exclusively on species-rich areas may fail to preserve the full spectrum of reptile diversity across Türkiye. Effective conservation planning should therefore incorporate multiple biogeographic regions and transition zones, particularly montane systems, Mediterranean coastal habitats, and eastern Anatolian assemblages, each of which may contain unique faunal components. These conservation priorities are particularly urgent given mounting pressures on Turkish biodiversity from habitat loss, infrastructure development, and climate change, which collectively place much of the country's globally significant herpetofauna at risk (Şekercioğlu et al. 2011).

Overall, this study provides one of the first large-scale quantitative assessments of reptile assemblage structure across Anatolia using publicly available biodiversity occurrence data. The exceptionally high turnover detected among reptile assemblages strongly supports the role of Anatolia as a major biogeographic transition zone connecting Mediterranean, Euro-Siberian, and Irano-Turanian biotas. The findings further highlight the importance of environmental heterogeneity, topographic complexity, and historical biogeographic processes in shaping reptile assemblages across the peninsula.

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DATA AVAILABILITY

All occurrence records used in this study were obtained from the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/) and are

openly accessible through the GBIF download portal. The cleaned occurrence dataset, derived presence–absence matrix, and the R scripts used for data cleaning, beta diversity decomposition, ordination, and clustering analyses are available from the author upon reasonable request.

CONFLICT OF INTEREST

The author declares no competing interests, financial or otherwise, that could have influenced the analyses or conclusions presented in this study.

AUTHOR CONTRIBUTIONS

M.K. designed the study, performed all data collection, cleaning, and analyses, and wrote the manuscript.

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