RESEARCH ARTICLE

Journal of Biogeography WILEY

Diversity patterns and evolutionary history of Arabian squamates

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Abstract

Aim: Deserts are generally perceived as areas of low diversity, and hence receive little attention from researchers and conservationists. Squamates are the dominant group of vertebrates in arid regions, and as such represent an ideal model to study biodiversity patterns in these areas. We examine spatial patterns of diversity, evolutionary history and endemism of terrestrial squamates of the Arabian Peninsula and test hypotheses on the role of topography and history of isolation so as to identify possible environmental drivers of diversification.

Location: The Arabian Peninsula.

Taxon: Squamate reptiles (Squamata; lizards and snakes).

Methods: We generated distribution maps for all Arabian squamate species (including yet undescribed) and reconstructed their phylogenetic relationships using existing and newly produced genetic data for nearly all the species. We assessed patterns of the distribution of species richness, phylogenetic diversity and phylogenetic endemism across the peninsula to identify areas that could be considered evolutionary or endemicity hotspots for squamates. We evaluated community turnover across the peninsula and assessed the possible environmental drivers affecting the diversity of Arabian squamates in a regression framework.

Results: The main hotspots of Arabian squamate diversity are mostly along the mountains that rim the peninsula while the most arid, central regions support a low diversity of species. The distribution of the phylogenetic diversity mirrors that of the species richness. Phylogenetic endemism is also highest in the mountains, especially when only endemic species are analysed. The deserts of northern Arabia are poor in terms of species richness and they show low connectivity to the peninsular communities. Topographic heterogeneity is the strongest predictor for Arabian squamates, followed by elevation. There is no correlation between richness and temperature.

Main conclusions: The mountains of Arabia support rich and unique squamate communities that are dominated by local radiations of closely related and narrow-ranging species. In particular, the Asir Mountains of SW Arabia, Dhofar Province of Oman and

the Hajar Mountains of northern Oman and UAE show unprecedented levels of squamate endemism and phylogenetic endemism. While many generalist species range across Arabia, a low number of species is shared between the peninsula and mainland Asia, indicating an effective isolation of the Arabian fauna. Squamate richness is highest in heterogeneous, topographically complex habitats.

KEYWORDS
deserts, diversification, Middle East, phylogenetic diversity, phylogenetic endemism, reptiles, Squamata

1 | INTRODUCTION

The distribution of biodiversity on Earth is neither even nor random. Different processes determine biodiversity variation at different scales. At the global scale, the most prominent pattern is the tendency for most groups to have more species in the tropics, the so-called latitudinal diversity gradient, a trend that has been recognized for over two centuries in most groups of organisms and whose explanation still remains a matter of debate (Mittelbach et al., 2007; Pianka, 1966; Rabosky et al., 2018; Wiens et al., 2006; Willig et al., 2003). At more local scales, richness gradients have been attributed to manifold sources such as ambient temperature (Allen et al., 2002), habitat heterogeneity (Badgley et al., 2017), aridification (Richardson et al., 2001) and water availability (Hawkins et al., 2003). Extreme environments such as hyper-arid deserts rank in this respect among the most challenging, yet least studied habitats.

Deserts cover nearly one fifth of the world's land mass and are generally perceived as uniform areas that support low diversity of life. Yet they support very specific biota perfectly adapted to their harsh environmental conditions and often showing a high degree of endemism (e.g. Brito et al., 2014; Lewin et al., 2016; Simmons et al., 1998). At the same time, however, arid regions tend to be among the most difficult to access for researchers (Ficetola et al., 2013) and suffer from the lack of precise data on species distributions and community structure. Thus, biodiversity of such areas is often underestimated and poorly represented in conservation actions and main drivers shaping its distribution remain little understood (Brito et al., 2014; Durant et al., 2012).

Squamate reptiles (lizards and snakes) are unusually diverse in arid and semi-arid regions of the world compared to other groups of vertebrates (Powney et al., 2010; Roll et al., 2017). It is hypothesized that, being ectotherms, squamates achieve high species richness in deserts because thermoregulation is cheap there and times of stress may be overcome by inactivity (Schall & Pianka, 1978). Therefore, they represent an ideal model to study how the extreme desert environments affect the distribution of biodiversity in space and time. The diversity of desert reptiles and the factors influencing it have been studied across continents (Lewin et al., 2016; Pianka, 1986; Powney et al., 2010; Vale et al., 2020), yet the results they provide are not congruent. In Africa, the alpha (species richness) and beta (species turnover) diversity patterns of squamates match those of

other terrestrial vertebrate groups (amphibians, birds and mammals), perhaps as a result of similar responses to environmental variables (Lewin et al., 2016; Vale et al., 2020). The richness of African lizards is strongly influenced by topographic heterogeneity, reflecting their ability to specialize in diverse ecoregions. On the other hand, in Australia, squamate species richness differs from other vertebrates. While the richness of Australian amphibians, birds and mammals increases with evapotranspiration, squamate richness is predicted by different factors, being highest in dry and hot regions (Powney et al., 2010).

The Arabian Peninsula is a biogeographically complex region with historical affinities to the African continent. While the north of the peninsula was traditionally considered to be part of the Palearctic zoogeographic realm and the south of the Afrotropical realm, recent studies show the entire peninsula to be rather a transition zone between the two, termed the Saharo-Arabian realm (Ficetola et al., 2018; Holt et al., 2013; Kreft & Jetz, 2013). The mountains rimming the peninsula in the west, south and east have been shown to hold exceptional diversity of species and especially endemics, which contrasts with the relatively depauperate interior (Arnold, 1986; Cox et al., 2012; Gasperetti, 1988). These diversity patterns have, however, never been examined in detail and explanations have relied on *ad hoc* collected data. It is therefore unclear to what extent this pattern can be attributed to varying sampling efforts in different parts of Arabia. The last two decades have brought major improvements to our knowledge of the distributions, taxonomy, species limits, systematics and phylogenetic relationships of most groups of Arabian squamates. For example, many new species have been described or documented for the first time in the Arabian Peninsula (e.g. Carranza & Arnold, 2012; Machado et al., 2019; Sindaco et al., 2018; Šmíd, Moravec, et al., 2017; Šmíd et al., 2015; Tamar, Mitsi, et al., 2019), subspecies have been raised to the species level (Šmíd et al., 2021), generic reassignments have been made (Nazarov et al., 2018; de Pous et al., 2016), candidate species have been delimited (Garcia-Porta et al., 2017; Simó-Riudalbas et al., 2019), results of regional surveys have been published (e.g. Alshammari et al., 2017; Alshammari & Ibrahim, 2015), previously unexplored areas have been surveyed (Metallinou et al., 2014; Šmíd, 2010), and detailed atlases have been compiled (Sindaco & Jeremčenko, 2008; Gardner, 2013; Sindaco et al., 2013; Cogălniceanu et al., 2014; Carranza et al.,

2018; Burriel-Carranza et al., 2019; see Appendix S1 for a complete list of references). As a result of all these efforts, we now have unprecedented knowledge on the composition and distribution of the unique fauna of Arabian squamates, yet a synthesis is still lacking.

In this study, we assess spatial patterns in the distribution of squamates across the Arabian Peninsula to identify and delineate hotspots of their diversity and evolutionary history. First, we examine the species richness pattern to confirm previous findings reporting high diversity in the peripheral mountains. Second, with the knowledge on the evolutionary relationships among Arabian squamates, we test whether the regions of high species richness also serve as reservoirs of evolutionary history. If species in the mountains are mostly a product of recent diversification events, which seems to be the case at least in some groups (Garcia-Porta et al., 2017; Šmíd, Shobrak, et al., 2017), then phylogenetic diversity of such places would be low compared to lowland areas. Alternatively, if mountain communities are not dominated by young species or if the mountain and lowland biota experience frequent transitions, then phylogenetic diversity would grow linearly with species richness. Third, we map the distribution of phylogenetic endemism to find out which parts of Arabia support spatially restricted evolutionary history. We hypothesize that the mountains will be the most important hotspots for endemic squamates. Fourth, we examine the distribution of squamate diversity in major Arabian ecoregions to assess their importance as local diversity hotspots. The degree of turnover between the ecoregions is used as an indicator of their mutual differentiation and as a gauge to measure each ecoregion's separation. Lastly, we investigate the possible drivers of species richness in Arabian squamates. Considering previous reports on the extraordinarily high richness of squamates in the mountains, we hypothesize that species richness will positively correlate with elevation. Based on findings from communities of Australian squamates we hypothesize that the Arabian squamate richness will be influenced by ambient temperature, and that the level of endemism will scale positively with topographic heterogeneity. To tackle these goals, we compiled a comprehensive dataset of species distribution records for all native terrestrial squamate species of Arabia, totalling over 18,000 records, and generated species distribution models for each species. Moreover, using a multilocus genetic dataset generated for this study, we inferred a nearly fully sampled phylogeny that included described species and well-supported candidate species to account for cryptic diversity.

2 | MATERIALS AND METHODS

2.1 | Study area delineation

We follow the political definition of Arabia that defines the peninsula as comprising the following countries: Bahrain, Kuwait, Oman, Qatar, Saudi Arabia, the United Arab Emirates (UAE) and Yemen. We did not include the Socotra Archipelago politically belonging to Yemen for its remoteness from mainland Arabia.

2.2 | Baseline taxonomy

Since the focus of this study were terrestrial squamates native to Arabia, we excluded from our analyses species that have been introduced by human-mediated transport (i.e. *Calotes versicolor* [Agamidae], *Hemidactylus flaviviridis*, *H. leschenaultii* [Gekkonidae] and *Indotyphlops braminus* [Typhlopidae]). We did not include the following species previously recorded from Arabia for reasons provided: *Acanthodactylus yemenicus* (Lacertidae) – although the species is listed in the Reptile Database (Uetz et al., 2020), we follow Sindaco and Jeremčenko (2008) and consider it conspecific with *A. felicis*; *Myriopholis yemenica* (Leptotyphlopidae) – there is only one known specimen, which is the holotype, and the type locality was in the original description described only vaguely as 'Yemen' (Scortecci, 1933), hence the systematic status and details on its distribution remain unknown; *Mesalina* sp. B (Lacertidae) – only one specimen has ever been collected (Arnold, 1980) and its phylogenetic affinities are uncertain; *Pristurus mazbah* (Sphaerodactylidae) – although listed in the Reptile Database (Uetz et al., 2020), Arnold (2009) did not consider it a valid species; and *Trapelus jayakari* (Agamidae) – listed in the Reptile Database, but Arnold (1986) considered it a younger synonym of *T. flavimaculatus* and it is still treated as such (Carranza et al., 2018). We retained *Chalcides ocellatus* (Scincidae) in the dataset but it must be noted that its native status is under question (Kornilios et al., 2010). The taxonomy of the genus *Platyceps* (Colubridae) is convoluted and various names are used to refer to similar species in the literature. We use the nomen *Platyceps rogersi* for the Arabian Gulf species, which is sometimes referred to as *P. ventromaculatus* (Burriel-Carranza et al., 2019; Gardner, 2013) or *P. chesnei* (Sindaco et al., 2013) based on Schätti's (2006) indication of the conspecificity of these species. Although *rogersi* was later considered a subspecies of *P. karelini* by the same author (Schätti et al., 2012), the two taxa belong to different clades within the genus' phylogeny (Sinaiko et al., 2018).

The list of native terrestrial squamates of Arabia contains 176 described species and 12 additional candidate species that were delimited in previous studies as well as ongoing projects (Badiane et al., 2014; Garcia-Porta et al., 2017; Metallinou et al., 2015; Sindaco et al., 2018; Tamar, Chirio, et al., 2019) and are awaiting description (work in progress). In total, the final list comprises 188 species from 56 genera of 15 families (Table S1).

2.3 | Analysis of spatial data

We compiled a dataset of georeferenced distribution records for all Arabian squamates by searching published literature, public biodiversity databases and citizen science websites, museum catalogues (see Appendix S1 for a complete list of collections and references),

gathering unpublished field observations provided by colleagues, and conducting targeted field work in different parts of Arabia (Oman, Saudi Arabia, UAE).

The original raw dataset was carefully curated for outlying and dubious records. Records that could not be assigned with certainty to species level due to recent taxonomic changes were removed. We used the R package *CoordinateCleaner* (Zizka et al., 2019) to flag potentially erroneous coordinates. We found and removed eight records placed in country centroids. The final dataset used for downstream spatial processing contained 18,053 records (Figure S1). The number of species-specific unique records ranged between 1 and 565 records (mean = 69, median = 31; Table S1).

2.3.1 | Species distribution modelling

We used a species distribution modelling (SDM) approach to derive the distribution ranges. Of the 188 species used in the analyses, 26 species had less than five unique records (Table S1). Small sample size may negatively influence modelling success (Rissler et al., 2006), and we therefore did not develop SDM for these species. Instead, their distributions were inferred as described below in the section *Environmentally informed buffer design*. We used the maximum entropy approach implemented in Maxent 3.3 (Phillips et al., 2006) to estimate the distribution of the potentially suitable habitat for each species. The spatial background defined for developing the models matched the study area defined above.

We used a set of 23 environmental and topographic variables as predictors to capture the diverse habitat preferences across species of such a heterogeneous group as squamates. The variables included: (a) 19 bioclimatic variables (CHELSA; Karger et al., 2017); (b) elevation and slope; (c) mean monthly potential evapotranspiration (averaged over 12 monthly layers; Trabucco & Zomer, 2019) and (d) mean monthly solar radiation (averaged over 12 monthly layers; Fick & Hijmans, 2017). All layers were downloaded at the resolution of or were rescaled to 2.5-arcmin (~4.6 × 3.9–4.5 km at the latitude of Arabia). Some of the variables presented obvious spatial artefacts with inconsistent spatial patterns, likely due to interpolations, and were removed (BIO8, BIO9 and BIO18). The remaining variables were tested for collinearity using ENMTools (Warren et al., 2010), and of those with strong correlation (Pearson's $r > 0.7$) we retained the biologically more meaningful ones (Elith & Leathwick, 2009).

The final set of uncorrelated variables that were used for the modelling included [units in brackets]: elevation [m], slope [degrees], BIO15 – precipitation seasonality [coefficient of variation], BIO17 – precipitation of driest quarter [mm/quarter], mean monthly potential evapotranspiration [mm/month] and mean annual solar radiation [kJ×m^{-2}×day^{-1}]. We ran Maxent with the following settings: random seed, regularization multiplier = 1, maximum number of background points = 10,000, number of replicates = 10, replicated run type = cross validate and maximum iterations = 5000. To account for the bias in sampling effort in different parts of Arabia, we generated a Gaussian kernel density layer based on the complete

curated dataset of all squamate records and a search radius 0.5°, and used this layer as a bias file in the modelling process (Kramer-Schadt et al., 2013). Model accuracy was determined by means of the area under the receiver-operating curve (AUC) and the true skill statistic (TSS; Allouche et al., 2006). AUC was classified according to Araújo et al. (2005). The distribution model of each species was evaluated based on the two metrics and on how realistic it was given our expert knowledge on the species ecology and habitat requirements (Table S1). Predictive models were reclassified to binary presence/absence maps using the maximum training sensitivity plus specificity threshold. Models of potential species distribution may be over-predicted as they are built using abiotic environmental predictors while relevant biotic factors such as species dispersal limitations or interspecific interactions are ignored (Graham & Hijmans, 2006; Peterson, 2011b; Vasconcelos et al., 2012). To at least partially alleviate the model over-prediction, we followed Kremen et al. (2008) and cropped away species ranges lying more than 100 km from each species' localities.

2.3.2 | Environmentally informed buffer design

Distributions of 59 species could not be modelled by the SDM approach. This concerned three categories of species: species with less than five unique records (26 species); species whose ranges could not be predicted for poor model performance or an unrealistic range estimate (30 species) and island endemics (3 species). We buffered all localities of these species by 50 km buffers and applied the deductive approach to species distribution modelling that uses species ecological requirements to extrapolate suitable areas from the environmental variable layers (Corsi et al., 2000; Rondinini et al., 2006). We used the distribution data to extract values of key environmental predictors as detailed below.

To account for the elevational preference of each species, we extracted the information on the elevation of all its Arabian records and we calculated the mean and standard deviation (SD) of it. We then cropped out parts of the buffers laying outside the elevational tolerance of the species, defined as mean ±2×SD. For species that only had one known record within Arabia and for which the SD could not be calculated, we applied hard boundaries of 250 m of elevation around it. This procedure was repeated with the slope, cropping out flat and steep surfaces that are unsuitable for the various species. Finally, because there are many habitat specialists among the Arabian squamates (e.g. strict sand-dwellers such as *Eryx jayakari* [Boidae] or *Trigonodactylus arabicus* [Gekkonidae]), we used soil type as a factor determining species distribution. We first classified Arabia into soil classes based on the global soil type layer (ISRIC World Soil Information; https://www.isric.org/). There are 15 main soil types present in Arabia (Appendix S2). We classified records of each species according to the soil type using the *SpGeoCod* function of the *SpeciesGeoCoder* R package (Töpel et al., 2016). Soils present in more than 10% of a species records were considered suitable for that species and other soil types were removed from the buffer.

Our approach was not followed for habitat generalists that are not selective of a particular soil type (e.g. *Varanus griseus* [Varanidae]), or for species with a broad range of elevational preferences within Arabia (e.g. *Acanthodactylus schmidti* [Lacertidae]), or island endemics (*Hemidactylus masirahensis* [Gekkonidae], *Pristurus masirahensis* and *P. schneiderii* [Sphaerodactylidae]). The final range estimate for each species was a carefully considered and environmentally informed combination of these variables.

2.3.3 | Species grid maps

The species distribution maps were intersected with a grid of 10-arcmin (~18 × 15.7–18.1 km at the latitude of Arabia) to create species grid maps. Although it is difficult to avoid species richness overestimation when combining range maps produced by SDM (Guisan & Rahbek, 2011), we attempted to reduce this bias by applying a criterion according to which, when the species range covered less than 1% of a grid cell area then that cell was not considered to be occupied by that species.

2.3.4 | Alternative distribution range estimates

To inspect the robustness of our conclusions, we compared our range estimates with two other sets of maps. To account for the varying geographical precision of the records, we developed a new set of maps following the SDM method detailed above, but this time using only records with spatial resolution of 1 km or better (13,898 records; 135 species with more than 5 unique records; hereafter referred to as the GPS maps). Moreover, we applied a strict radius of 50 km around each species' localities to crop its predictive range. The strictness of this approach produced narrow ranges that tightly encompassed the precise locality data. Second, we compared our maps with previously published ones. We extracted species occurring in Arabia from the maps by Roll et al. (2017) (189 squamates). It must be noted that Roll et al.'s and our datasets differed considerably in the species composition. This was most notably due to many taxonomic changes having been done since 2017, the fact that we include candidate species that have not yet been described, and less strict criteria applied by Roll et al. to derive species ranges that resulted in species never recorded from Arabia being shown as present (typically, the presence of extralimital species at the northern border of the peninsula).

2.4 | Phylogenetic data and analyses

2.4.1 | Sequence data and DNA sequencing

We compiled DNA sequence data for as many of the 188 species as possible. We gleaned the literature and used Geneious 11.1 (Kearse et al., 2012) to search GenBank for published sequences. We targeted loci customarily used in squamate phylogenetic studies.

Sequence data were available for 170 of the 188 species, for which we downloaded a total of 928 sequences of 16 genetic markers, seven mitochondrial (12S, 16S, CYTB, COI, ND1, ND2 and ND4) and nine nuclear (ACM4, BDNF, CMOS, MC1R, NT3, PDC, PRLR and RAG1, RAG2). Each species was represented by one specimen in the phylogenetic analyses. Whenever possible, we downloaded sequences of the same specimen in order not to create chimeric samples. Species for which there were no data available on GenBank were sequenced *de novo*, targeting markers that had been sequenced before for other species of their respective families. Primers used for the amplification are given in Table S2. We produced 83 new DNA sequences of 12 genetic markers for 25 species (GenBank accessions MW198193–MW198209 and MW204503–MW204568; Tables S3 and S4). Particularly noteworthy are the species that have been sequenced for the first time for this study: *Eirenis coronella*, *Platyceps thomasi* (Colubridae), *Walterinnesia morgani* (Elapidae), *Tropiocolotes wolfgangboehmei* (Gekkonidae) and *Pristurus ornithocephalus* (Sphaerodactylidae). The final genetic dataset contained sequences of 177 species (94% taxon sampling), ranging from one to twelve sequences per species with the mean of 5.8 sequences. All Arabian squamate families were represented, of the 56 genera only *Philochortus* (Lacertidae) and *Agamodon* (Trogonophidae) were missing.

2.4.2 | Phylogenetic analyses

We aligned all genes independently using MAFFT 7 (Katoh & Standley, 2013) using the default settings. We trimmed long ragged ends manually to reduce incomplete data. Mitochondrial tRNAs and flanking regions were removed. We checked all newly produced mitochondrial sequences of protein-coding genes for stop codons to detect potential amplification of nuclear pseudogenes. None were detected. Alignments of all markers were concatenated for the analyses, producing an alignment of 16,706 bp in length. Each marker was treated as a separate partition.

We inferred the phylogenetic relationships using maximum likelihood (ML) and Bayesian inference (BI) approaches. For the ML analysis we used RAxML 7.3 (Stamatakis, 2006) with a heuristic search of 10 random addition replicates and 100 bootstrap pseudoreplicates and the GTRGAMMA substitution model applied to all partitions. For the BI analysis we used BEAST 2.5.2 (Bouckaert et al., 2014) with the following parameterization: ambiguous nucleotide positions indicating heterozygotes in the nuclear markers were included; nucleotide substitution models were estimated by the reversible-jump–based method (RB model; Bouckaert et al., 2013) with four gamma-distributed rate categories; relaxed lognormal clock model; Yule process tree prior with a uniformly distributed prior on the birth rate (lower: 0, upper = 10); clock parameters with lognormal distributions for the mitochondrial markers (mean = 0.1, SD = 1.25) and exponential distribution for the nuclear ones (mean = 0.5); among-lineage rate heterogeneity parameters with gamma distributions (α = 0.5396, β = 0.3819); five independent runs each of 2×10^{8} generations

with logs and trees sampled every 2×10^4 generations. Preliminary analyses had problems to reconstruct the geckos (Gekkota) as a monophyletic group so we enforced monophyly of the group containing the three gecko families (Gekkonidae, Phyllodactylidae and Sphaerodactylidae). Stationarity, convergence of the five runs and effective sample size of all parameters was assessed using Tracer 1.5 (Rambaut et al., 2014) and output tree files were combined in LogCombiner after discarding 10% of the posterior trees of each as burnin. Maximum clade credibility tree was generated using TreeAnnotator (both programs are part of the BEAST package). All phylogenetic analyses were run through CIPRES (Miller et al., 2010).

2.5 | Spatial analyses

2.5.1 | Diversity and phylodiversity metrics

A map of species richness (SR) was produced by overlaying maps of all species. Phylogenetic diversity (PD; Faith, 1992) of each grid cell was calculated using the *picante* package of R (Kembel et al., 2010). Following recommendations of Rodrigues and Gaston (2002), the root of the tree was included in the PD calculation. Phylogenetic endemism (PE; Rosauer et al., 2009) was calculated with the *PDcalc* R package (Faith, 2013). All diversity metrics were calculated for two sets of species, one containing all species (188 species) and one of Arabian endemics only (120 species; Table S1). To explore the relationships between the diversity metrics (PD ~ SR, PE ~ PD), we used local regression with nonparametric smoothing implemented in the *loess* function in R (smoothing parameter α = 0.75).

2.5.2 | Ecoregion classification

Ecoregions of Arabia were obtained from the map of terrestrial ecoregions of the world (Dinerstein et al., 2017; Olson et al., 2001). Some of the ecoregions were very marginal to Arabia. Those were merged with larger ones based on their distribution and ecological relevance. This way we produced a map of 10 dominant ecoregions of Arabia: The Hajar Mountains; Central Arabian Desert; Arabian sand Desert; Arabian-Persian Gulf Desert; The Sharqiya Sands; North Arabian Desert; Red Sea Desert Shrublands; South Arabian Plains and Plateau Desert; SW Arabian Escarpment and Highlands; The Tihama Desert.

Species were assigned to ecoregions based on the degree of overlap between their ranges with each ecoregion. A species was considered to be present in an ecoregion when at least 10% of its range was found within that ecoregion, or when at least 10% of the ecoregion area was occupied by that species. Ecoregion turnover was visualized using functions from the R packages *geosphere* and *rgdal* (Bivand et al., 2014; Hijmans et al., 2016). PD and PE was calculated for each ecoregion using the methods described above for the grid-level analysis. Each metric was again

inferred for two sets of species: one of all species and one of Arabian endemics. To incorporate phylogenetic uncertainty, the ecoregion PD and PE calculations were run 1000 times with 1000 posterior trees drawn randomly from the BI results. Additionally, to account for the effect of ecoregion area (larger ecoregions may acquire higher diversity only as a function of their area), we divided the PD and PE metrics of each ecoregion by its area (square root transformed).

2.6 | Identifying possible determinants of squamate species richness

A number of studies have indicated that species richness has a strong association with climate (Field et al., 2005; Jetz & Rahbek, 2002; Kreft & Jetz, 2007; among others). We tested three potential predictors that capture the multidimensionality of climatic space to explain squamate species richness in Arabia: elevation, topographic heterogeneity and mean annual temperature. The comparisons were conducted at the 10-arcmin grid scale. The elevation and temperature (BIO1) variables were upscaled from their original resolution (2.5-arcmin) by averaging the finer-scale raster values contained in each 10-arcmin grid cell. Topographic heterogeneity was calculated as the standard deviation of the elevation values contained in each 10-arcmin grid cell. Although the elevation range is commonly used as a measure of topographic heterogeneity (e.g. Lewin et al., 2016), the standard deviation of the elevation is less prone to be biased by the presence of extreme values of a few narrow areas within the grid cell and should better describe the dominant pattern of heterogeneity. Species richness was regressed against each of the three determinant variables using the *loess* regression (α = 0.75). Each comparison was done twice, for all species and for endemics only. We used Pearson's correlation coefficient (*r*) to assess the dependence of species richness on each of the variables.

3 | RESULTS

3.1 | Phylogenetic reconstructions

Topologies of the ML and BI trees were largely congruent (Figures S2 and S3; Appendix S4). All genera were recovered monophyletic with strong support with one exception, which was *Eryx* (ML bootstrap = 62, BI posterior probability = 0.92), most likely owing to the limited overlap of markers available for the two species included in the analyses. All squamate families were recovered as monophyletic with the exception of Lamprophiidae (Figure 1), which has not been convincingly supported as monophyletic in previous studies either (Pyron et al., 2013; Zheng & Wiens, 2016). All downstream spatial analyses produced similar results regardless of the input tree (not shown) and we report only results obtained using the BI tree.

3.2 | Spatial patterns of SR, PD and PE

The species distribution maps produced in this study are available as figures in Appendix S2 and as shapefiles in Appendix S3. Hotspots of squamate SR in Arabia are distributed mostly in the coastal mountainous regions, the richest being south-western Yemen and the Asir Mountains of Saudi Arabia, Dhofar Province of Oman and the Hajar Mountains of northern Oman and UAE (Figure 2a). Another important area of high richness was found in central Saudi Arabia. In contrast to these species-rich regions, most of the Arabian interior shows rather depauperate squamate communities. The distribution of PD showed a similar spatial pattern to that of SR, which is a result of the two metrics being tightly correlated (Figure 2c; Pearson's $r = 0.970$ [confidence interval (CI): 0.969–0.971], $p < 0.001$). The PE analysis also recovered the peripheral mountain systems of Arabia as important PE hotspots. In addition to these regions, the extreme northeast (Kuwait) and

northwest (Tabuk region of Saudi Arabia) of the peninsula came out as areas with high PE (Figure 2e). PE and PD were not as tightly correlated as SR and PD, although the trend was still clearly positive and significant (Pearson's $r = 0.773$ [CI: 0.764–0.781], $p < 0.001$).

The pattern of SR distribution of endemics remained largely similar to that of all species, with the southwest of the peninsula, Dhofar, and the Hajars being the most endemic-rich areas (Figure 2b). Central Arabia, however, was not as species rich as in the analysis of all species. SR and PD of endemics only were also tightly correlated (Figure 2d; Pearson's $r = 0.969$ [CI: 0.968–0.970], $p < 0.001$), resulting in their matching spatial patterns. PE of endemics identified the southern and eastern peripheral mountains as high PE areas (Figure 2f), whereas the north-eastern and north-western parts of the peninsula did not appear to harbour any substantial PE compared to the analysis of all species. PE and PD of endemic species were also positively and significantly correlated (Pearson's $r = 0.766$ [CI: 0.757–0.775], $p < 0.001$).
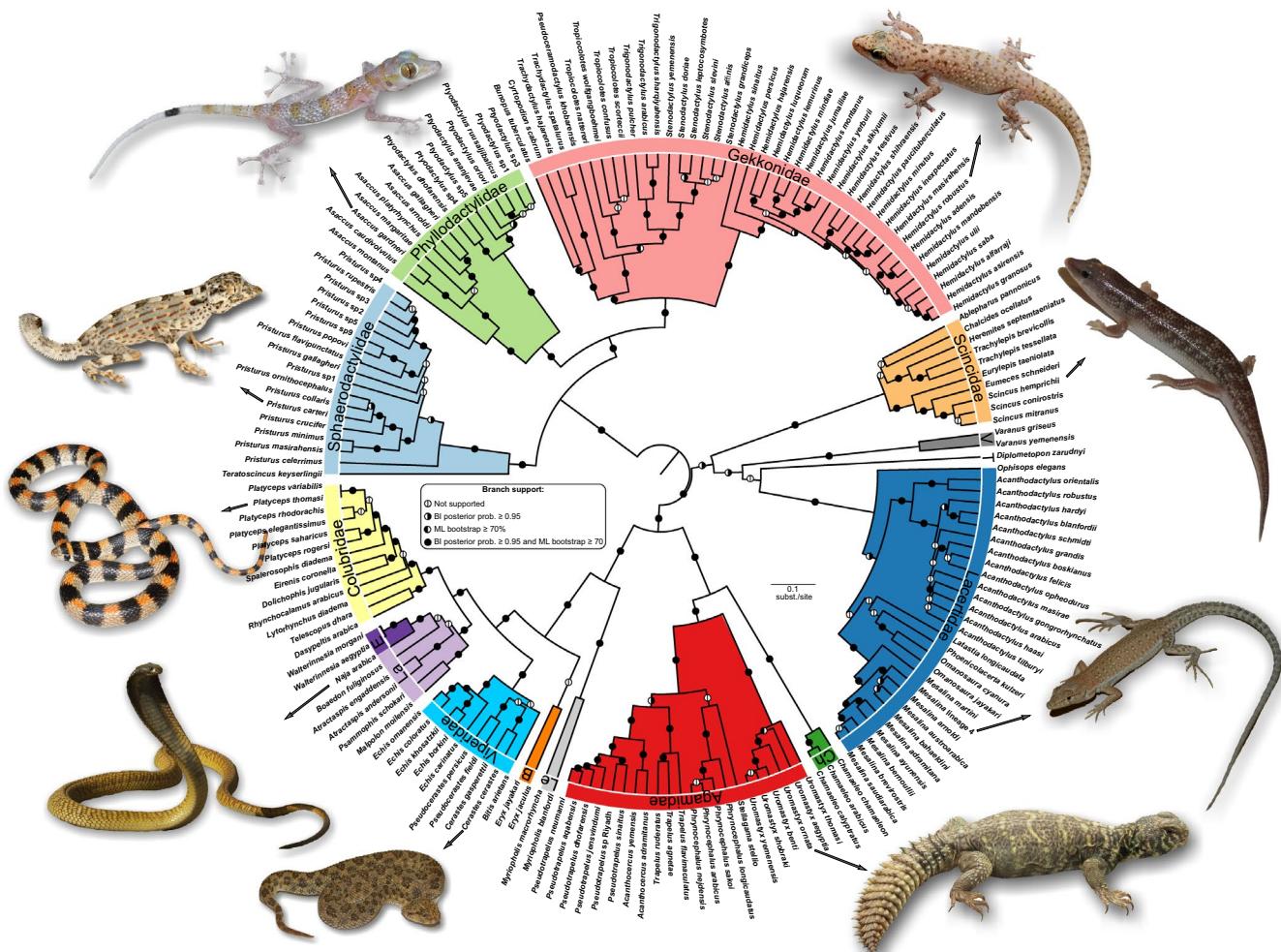
FIGURE 1 Phylogenetic tree of Arabian squamates. Families are highlighted in colours with names shown at the perimeter. Some family names have been abbreviated as follows: B – Boidae, Ch – Chamaeleonidae, E – Elapidae, La – Lamprophiidae, Le – Leptotyphlopidae, T – Trogonophidae, V – Varanidae. The photographs show the phenotypic diversity represented by the tree. The arrows indicate the species depicted; note that not all families are represented by a photograph. Branches supported by the ML and BI analyses are marked with the left and right filled semicircles, respectively. For detailed ML and BI trees including branch support see Supplementary Figures S5 and S6.
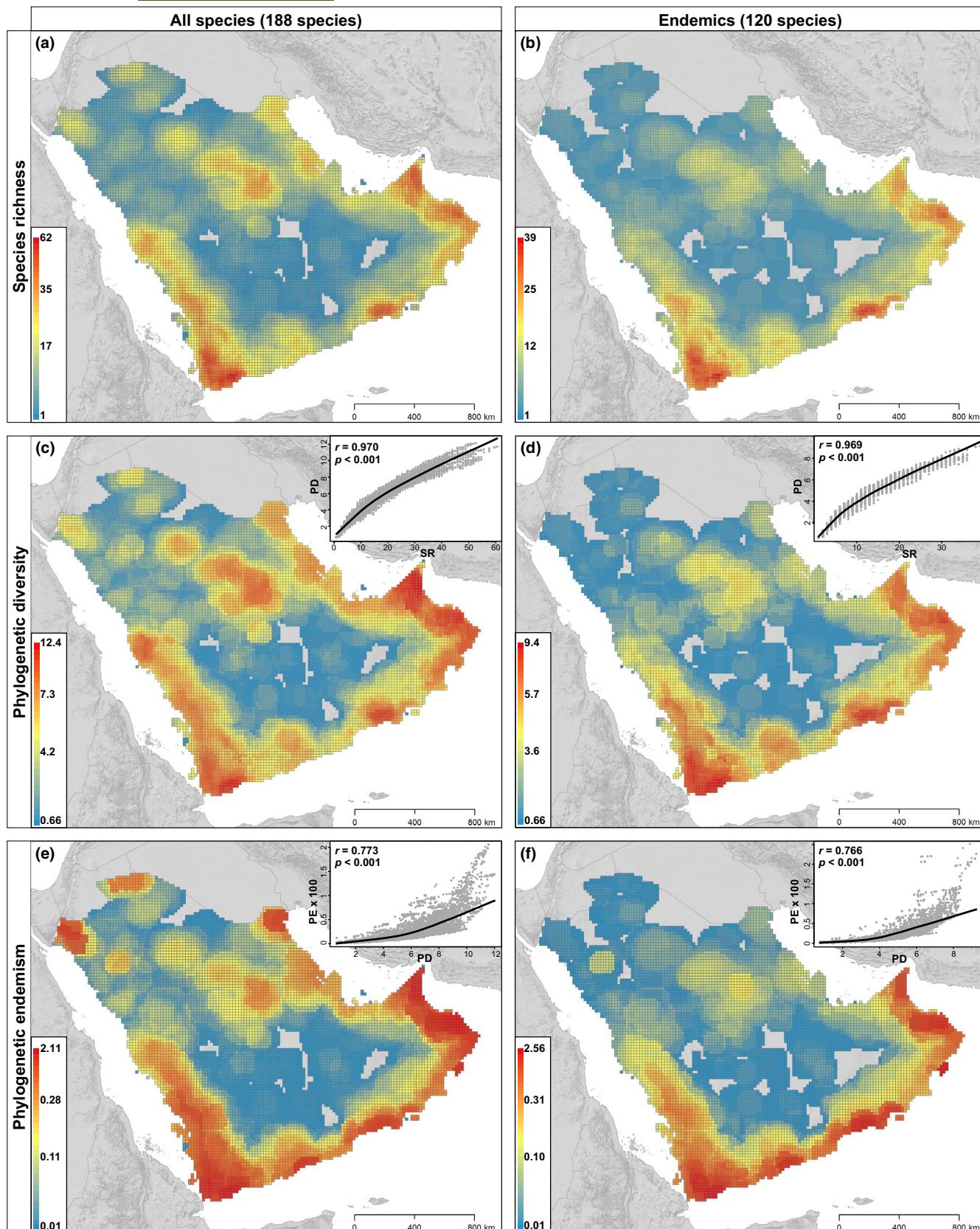
FIGURE 2 Maps of species richness (SR), phylogenetic diversity (PD) and phylogenetic endemism (PE) of squamates of the Arabian Peninsula. Maps in the left column are based on analyses of all species (188 species), right column shows maps for Arabian endemics (120 species). Plots in the insets of (c) and (d) show the relationship between PD (*y* axis) and SR (*x* axis), those in (e) and (f) show the relationship between PE (*y* axis) and PD (*x* axis), with the *loess* regression lines in black. Correlation of the metrics (Pearson's *r*), as well as its statistical significance, is in the upper left corner of each plot. Confidence intervals are given in the Results.

Analyses of the GPS maps (135 species in total) produced similar spatial patterns for all the metrics to those described above (Figure S4). Albeit many parts of Arabia lacked any predicted squamates due to the absence of precise occurrence data and the strict criteria applied to estimate the GPS maps, the mountains along the south-western, southern and eastern margins of the peninsula had the highest SR, PD and PE regardless of whether all species or only endemics were analysed. In accord with our results were also those based on the Roll et al. (2017) maps (189 species in total) that resulted in mostly corresponding diversity patterns (Figure S5). All metrics highlighted the peripheral mountains as diversity hotspots, both for all species and for endemics only. The highlands of central to north-western Saudi Arabia were also identified as a SR and PD hotspot, which also confirmed our findings. On the other hand, the Roll et al. (2017) maps predicted intermediate diversity of species in most of Arabia's interior (ca. 15–25 species) even in regions void of any squamate records (e.g. the Rub' al Khali Desert; Figure S1).

At the ecoregion scale, the highest species richness was found in the South Arabian plains and plateau desert, the South-western Arabian escarpment and highlands, and the Tihama Desert, with 69, 68 and 64 species respectively (Figure 3a). The species-poorest ecoregions were the North Arabian Desert and the Sharqiya Sands with 23 and 39 species respectively (Figure 3a). The North Arabian Desert is isolated from the rest of the peninsula with a low degree of diversity overlap with the other ecoregions (16 species shared with the Central Arabian Desert [29% of diversity] and 10 with each of the Red Sea Desert Shrubland [20% of diversity] and the Arabian-Persian Gulf [20% of diversity]). The rest of the peninsula, on the contrary, shows a relatively high species overlap, especially between adjoining ecoregions (mean proportion of shared species 55 ± 15% SD, min-max: 26–87%; Figure 3b).

In contrast to their low SR, the Sharqiya Sands were consistently found as the highest PD and PE ecoregion relative to its area, followed by the Tihama Desert, the Hajar Mountains and the Arabian-Persian Gulf Desert (Figure 4). In fact, the Sharqiyah Sands' PE values were nearly twice as high as those of the Tihama Desert, the second ecoregion in rank. When the effect of ecoregion area was not accounted for, the ecoregions mostly overlapped in their PD values, with the exception of the North Arabian Desert (Figure S6). In the PE comparisons, the Sharqiya Sands stood out again as the highest PE ecoregion for all species and together with the South Arabian plains and plateau desert, the Tihama Desert and the Arabian-Persian Gulf Desert, as PE hotspots for endemics. The North Arabian Desert ecoregion was extremely depauperate in terms of both PD and PE for all species and for endemics as well.

3.3 | Species richness determinants

Species richness showed a slight positive correlation with elevation, but the *loess* regression was convex shaped. Correlation between species richness and topographic heterogeneity was stronger. On the contrary, mean annual temperature was not found to determine the number of species (Figure 5; details in Table 1). The relationships between the three determinant variables showed that topographic heterogeneity and elevation were positively correlated, while mean annual temperature declined with both topographic heterogeneity and elevation (Figure S7).

4 | DISCUSSION

In this study we provide the first insights into the patterns and processes shaping the distribution of squamate diversity and evolutionary history in the environmentally extreme conditions of the Arabian
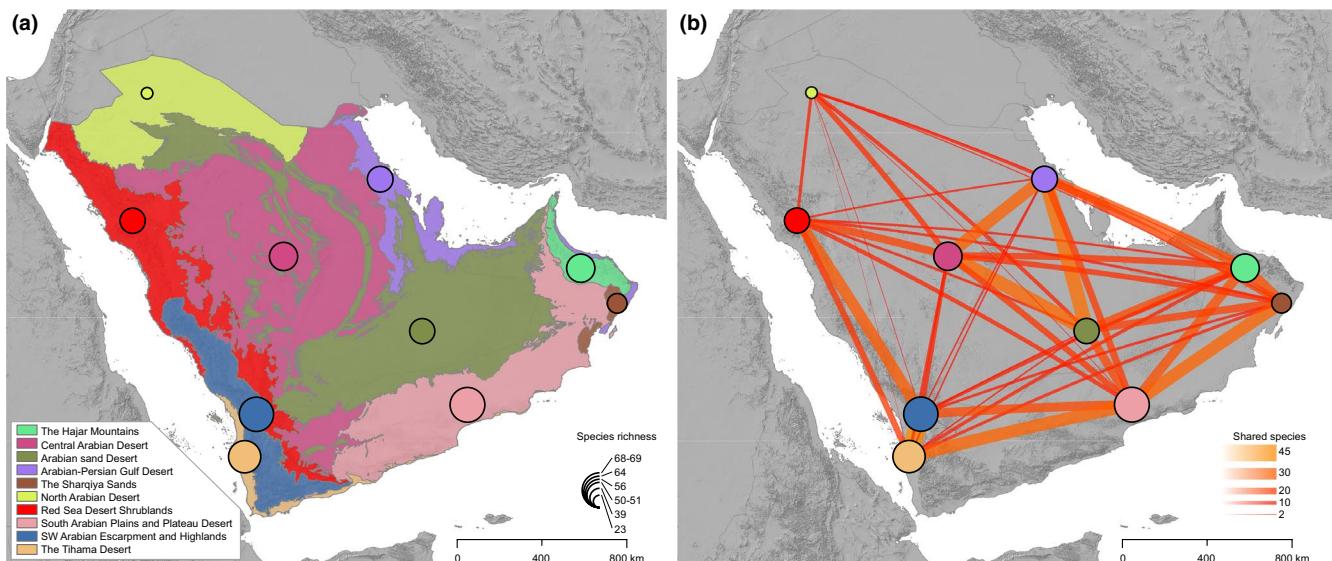
FIGURE 3 Diversity of squamates and their turnover among Arabian ecoregions. (a) Ecoregion diversity. Circles are placed in ecoregion centroids and their radii correspond to the respective species richness of each ecoregion. (b) Ecoregion turnover. Lines show the number of species common to two ecoregions; thicker, brighter lines indicate more shared species.
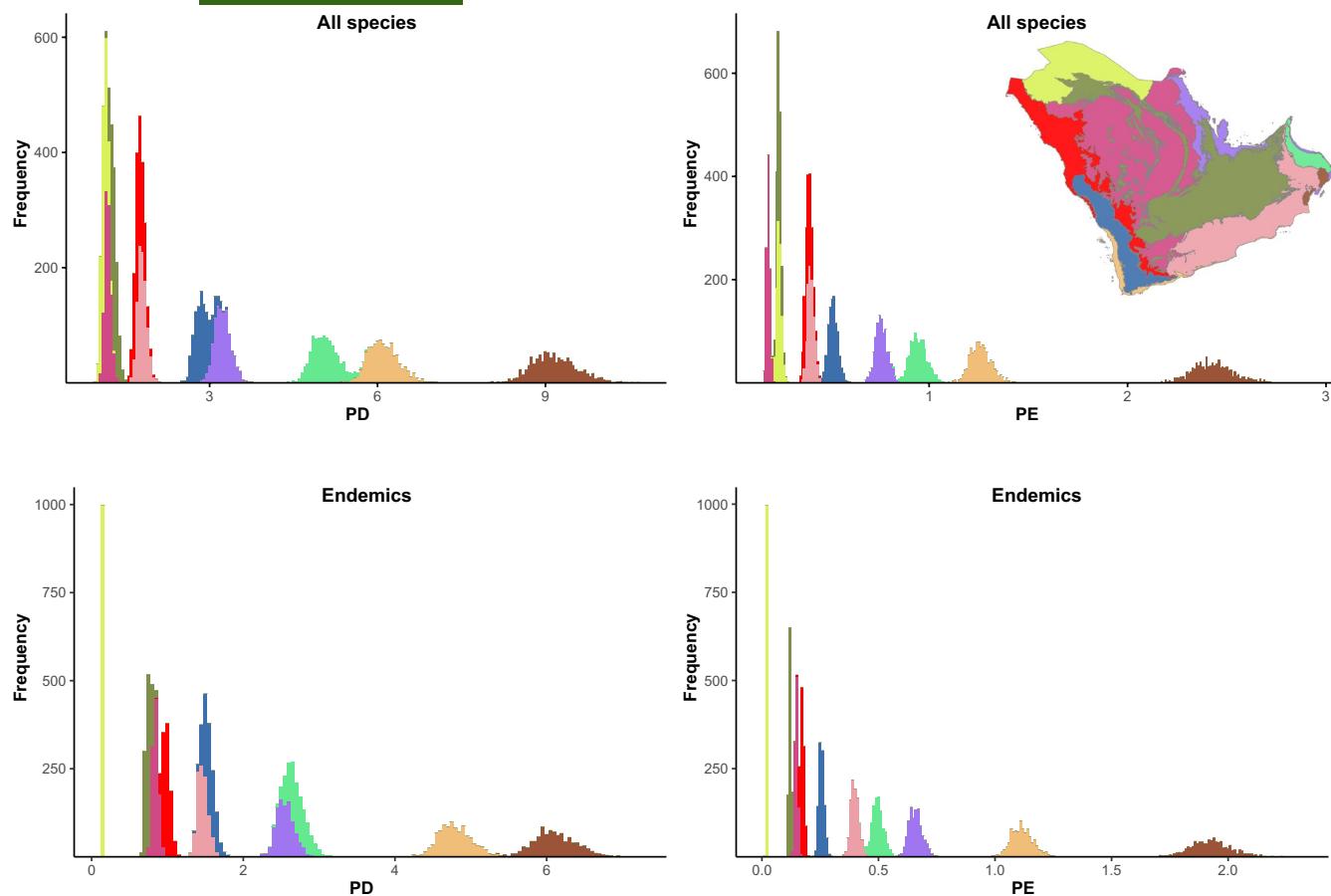
**FIGURE 4** Frequency histograms of phylogenetic diversity (PD) and phylogenetic endemism (PE) of Arabian squamates in ecoregions generated with 1000 randomly sampled trees from the posterior of the Bayesian phylogenetic analysis and accounting for the ecoregion area. Plots in the upper panes are based on analyses of all species, lower panes show plots for Arabian endemics only. Histogram colours correspond to the different ecoregions plotted in the upper right corner. For ecoregion names see Figure 3.

Peninsula. The species distributions and genetic datasets compiled in this study are the most comprehensive to date and allow in-depth examination of the spatial distribution patterns of Arabian squamates. Additionally, the results also pinpoint areas where more field work is required or can be used as a foundation for improving local conservation planning and management.

4.1 | Patterns of Arabian squamate distribution

The distributions of SR and PD show that most squamate diversity and evolutionary history is concentrated in the mountains along the south-western, southern and eastern edges of the peninsula, and along the Arabian Gulf coast and central Saudi Arabia. However, only the mountains emerge as diversity hotspots when endemics are analysed. Although this pattern is mirrored in other groups of vertebrates, such as amphibians (Fritz & Rahbek, 2012), birds (Jetz et al., 2012), mammals (Ceballos & Ehrlich, 2006) and turtles (Roll et al., 2017), none of them achieves richness levels comparable to those observed in squamates. This further stresses the uniqueness of squamate communities in arid environments and highlights the need

for their independent treatment in biodiversity and conservation assessments. The matching spatial patterns of SR and PD and the close correlation of the metrics indicate that, at the geographic scale of Arabia and phylogenetic scale of squamates, species richness can be considered a good surrogate for the community's evolutionary history. In general, species diversity has been shown to be an adequate surrogate for PD when the phylogenetic tree is not extremely unbalanced, i.e. all clades of the tree have more or less equivalent number of taxa, and old species occur in species-rich areas (Rodrigues et al., 2005), both of which conditions are met by Arabian squamates.

The Arabian mountains are not only species richness hotspots but they also show high levels of PE, especially for endemic species. In other words, the rich diversity and deep evolutionary history of the mountains are spatially restricted and confined to particular mountain ranges. Indeed, the mountain fauna is mostly composed of local radiations of closely related and narrow-ranging species (Garcia-Porta et al., 2017; Simó-Riudalbas et al., 2018; Šmíd, Shobrak, et al., 2017), and although there are species whose distributions cover several mountain ranges, these are rarely high-elevation specialists. The mountains of south-western Arabia and the Hajar Mountains have already been recognized as areas of pronounced reptile endemism
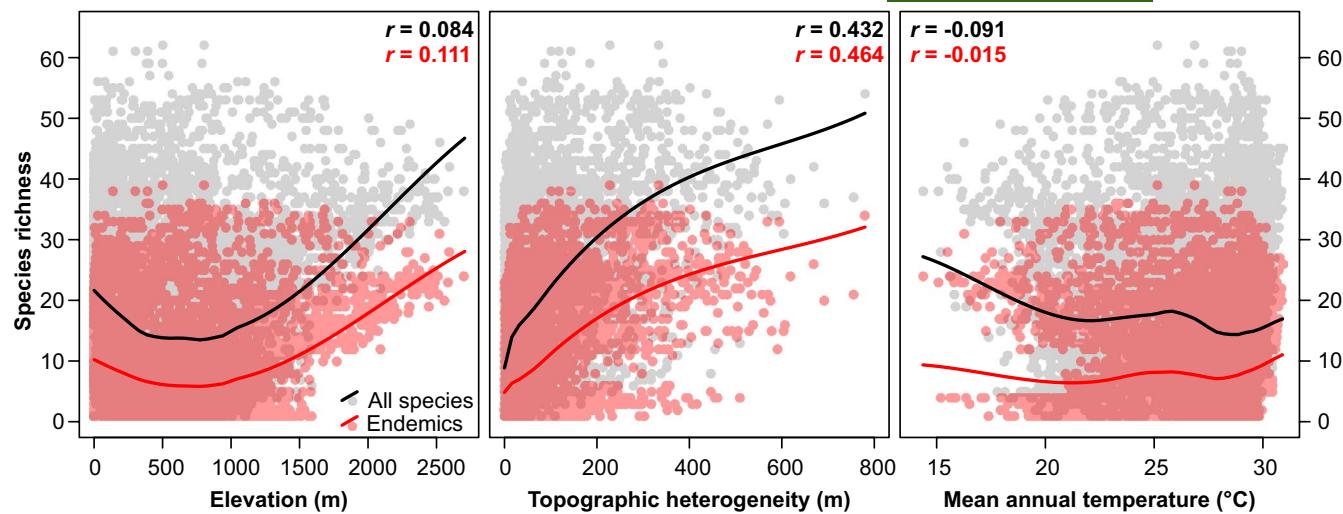
FIGURE 5 Relationships between three environmental predictors and species richness of Arabian squamates. Values for all species are shown as grey points, for endemics only as red points. Black and red lines indicate fit of the *loess* regression models for all species and endemics only, respectively. Variable correlations (Pearson's *r*) are in the upper corner of each plot; for all species in black, for endemics in red. Confidence intervals are given in the Results.

TABLE 1 Correlation of Arabian squamate species richness with three environmental predictors. Each correlation was calculated for richness of all species and of richness of endemics only. Pearson's correlation coefficients values are shown along with their confidence intervals and statistical significance.

	Pearson's *r*	Confidence interval	*p*
Elevation			
All species	0.084	0.063–0.104	<0.001
Endemics	0.111	0.090–0.132	<0.001
Topographic heterogeneity			
All species	0.432	0.415–0.449	<0.001
Endemics	0.464	0.447–0.480	<0.001
Mean annual temperature			
All species	−0.091	−0.112 to −0.070	<0.001
Endemics	−0.015	−0.036 to 0.006	0.165

(Ficetola et al., 2018). Moreover, south-western Arabia is known to present exceptional levels of diversity and endemicity of both plants and animals and, hence, was recognized as part of two global biodiversity hotspots (Mittermeier et al., 2004). The fine-scale resolution of our analyses allowed more detailed delineation of these hotspots and identification of other areas of endemic diversity, as the Hajar Mountains and Masirah Island off the coast of central Oman.

Some areas of the interior of Arabia that were identified as poor in SR, PD and PE may be a result of insufficient sampling effort. This applies, for example, to the Rub' al Khali and An-Nafud sand deserts of southern and northern Arabia respectively. Guisan and Rahbek (2011) have shown that when species richness is estimated based on stacked SDMs, local diversity tends to be overestimated. However, given that the number of species predicted to occur in these deserts never exceeds five (and is actually zero in nearly 3% of the grid cells),

it is rather unlikely that we are dealing with diversity overestimates. Instead, the conservative approach applied here to estimate species distributions produced spatial ranges that are likely narrower than they in fact are, which in turn resulted in that the diversity in these areas is more prone to underestimation. We are aware of this limitation of the species range maps we produced and that they might underestimate the richness of squamates locally, but our intention was to map distributions that are supported by actual locality data with as little interpolation as possible. Nevertheless, the two alternative sets of maps confirm that the overall diversity patterns across the peninsula hold and are not distorted. In the case of the Rub' al Khali, which is the largest continuous sand desert in the world, the low predicted diversity is likely genuine and may be imposed by the harshness of the environment that is composed of vast stretches of barren sand dunes (Edgell, 2006). On the other hand, the relatively low predicted diversity of the mountains of north-western Saudi Arabia that are topographically and environmentally considerably more complex than the sand deserts (Vincent, 2008) may truly be a result of sampling bias. These regions have received little attention of herpetologists despite the potential they hold, and more discoveries are to be expected from there (Aloufi et al., 2020).

4.2 | Ecoregion richness and turnover

The ecoregions show a variance in SR, with the north of Arabia being the poorest and the ecoregions in the south of the peninsula the richest. Ecoregions with the highest PD and PE (relative to their area) are the Sharqiya Sands, the Tihama Desert, the Hajar Mountains and the Arabian-Persian Gulf Desert, which, to a certain degree, mirrors the results obtained in the analyses at the grid scale. The sand dunes of the Sharqiya Sands and the coastal Tihama Desert particularly achieve high PD and PE values even if the effect of area

is not accounted for. Their diversity and endemism levels are comparable (and even higher in case of PD) to those in much larger ecoregions like, for instance, the South Arabian plains and plateau desert, stressing their significance as important hotspots of diversity and endemism. Given their limited geographical extent in combination with their unique habitat they represent potential targets for future conservation efforts in Oman (the Sharqiya Sands) and Saudi Arabia and Yemen (the Tihama Desert).

An important biodiversity region is the Hajar Mountains of northern Oman and UAE that shows high levels of diversity and endemicity within a geographically well-delineated area. The Hajars are not as high in terms of endemic SR as are the south-western mountains, but their PD and PE are among the highest. This suggests that for the same number of species, the Hajars achieve relatively longer evolutionary history and higher endemism, meaning that local communities are phylogenetically diverse and comprise species with smaller average ranges than those in the southwest. Albeit the Hajars are not among the globally recognized hotspots, their level of squamate endemism is comparable to other renowned biodiversity hotspots in the world, such as the Eastern Arc Mountains of Tanzania or the Ethiopian highlands (Burgess et al., 2007). Considering that only a fraction of the Hajars is covered by protected areas either in Oman or UAE (Burriel-Carranza et al., 2019; Carranza et al., 2018) and that they face massive transformations (Carranza et al., 2016) some measures should be taken to improve the protection of this unique biodiversity hotspot.

The North Arabian Desert stands out as the invariably poorest of the ecoregions in all metrics calculated and regardless of whether all species or only endemics were analysed. Also, the proportion of species shared between this and the other ecoregions is much lower in comparison with the rest of Arabia where, on average, 55% of species are shared between adjoining ecoregions. All this suggests that Arabia is very effectively isolated from mainland Asia by the deserts in the north of the peninsula, even though the north served as a colonization route for several squamate groups (Simó-Riudalbas et al., 2019; Tamar et al., 2016, 2018). The low rates of ecoregion isolation within the peninsula may seem to contradict the above-described pattern of mountains swarming with local radiations of narrow-ranging endemics. However, considering the squamate richness of the Arabian mountains where a community of 50 species is not uncommon, a diversity overlap of 55% between ecoregions still leaves over 22 species (on average) that are ecoregion specific and generate the high levels of endemism and phylogenetic endemism. In consequence, the mountain hotspots thus support balanced communities of both local endemics and broad-ranging species.

4.3 | Determinants of Arabian squamate richness

In light of the above-described findings that the Arabian mountains harbour the greatest diversity, one might expect that the key determinant of richness would be the elevation. However, elevation does not seem to be the main driver as its correlation with SR (both for all species and endemics alone) is not exceptionally strong, and the regression lines do not show a constant growth. This suggests that our hypothesis of species richness being dependent on elevation is not supported.

Instead, SR scales better with topographic heterogeneity. Although heterogeneity is linearly related to the elevation (Figure S7), for Arabian squamates it is a more substantial determinant of species richness than elevation. This is in line with the many studies that have documented greater diversity in heterogeneous, topographically complex habitats, both at global and regional scales (Badgley et al., 2017; Cowling & Lombard, 2002; Kreft & Jetz, 2007; Szabo et al., 2009), including studies on squamates from multiple continents (Lewin et al., 2016; Nogueira et al., 2009; Powney et al., 2010; Whiting & Fox, 2020). Heterogeneous environments provide a large number of available habitat types and thus numerous opportunities for niche partitioning, population isolation and allopatric speciation. Tilman (1982) hypothesized that selection in these environments should favour narrow-ranging specialists over generalists, which should translate into these regions being dominated by endemics. Our results of the PE distribution comply with this hypothesis and, together with previous studies (Garcia-Porta et al., 2017; Šmíd, Shobrak, et al., 2017), support the key role of topographic complexity as one of the main drivers of Arabian squamate richness and endemicity.

Given that thermoregulation for squamates is largely dependent on ambient temperature, warm climates are expected to harbour more species than cold climates. Although previous studies support the supposition that richness is higher where temperatures are higher (Powney et al., 2010; Schall & Pianka, 1978; Whiting & Fox, 2020), this pattern is not supported by our results. We find no correlation between SR and mean annual temperature, indicating that temperature does not determine squamate richness in Arabia, which suggests that the supposed pattern of high diversity in warm regions does not apply to all parts of the globe. For example, richness of African lizards cannot be explained by temperature-related variables (Lewin et al., 2016). It thus appears that the dependence of richness on temperature is more clade or region specific, whereas the dependence on topographic complexity could be a largely global phenomenon.

4.4 | Limitations and potential caveats

A word of caution is needed when interpreting spatial and phylogenetic results from broad and historically neglected regions, such as those presented here. Despite applying very strict criteria to generate species ranges, one must bear in mind that the range maps are still only estimates based on the data available and the methods incorporated. Ideally, range maps should be based on verified point localities without the need of using predictive modelling to fill in the intervening gaps, which always introduces some degree of error (Peterson, 2011a). Unfortunately, such detailed data are rarely available even for the best surveyed regions of the world, not to mention climatically extreme, barren and difficult-to-access deserts.

However, by comparing our results with those based on the two alternative sets of maps (GPS and maps from Roll et al., 2017) we confirm that the squamate diversity patterns across the peninsula hold regardless of the input range maps, which lends credence to our conclusions.

Another caveat is that the PD and PE values may be affected by the phylogenetic tree used to estimate them (Rodrigues et al., 2005). Although we have inferred the tree using two independent methods that yielded mostly similar topologies with most relevant nodes supported, we acknowledge that we did not account for phylogenetic uncertainty in the grid-scale analysis. This could have been done, for example, by using a set of trees as we did in the ecoregion-scale analysis. This would allow measuring local variance in PD and PE, thus pointing out grid cells where these metrics vary with the tree topology, and which could be translated into a stability measure. This should, however, be addressed in a stand-alone study.

DATA AVAILABILITY STATEMENT

Appended to this article is a list of museum catalogues, online and published sources that were used to assemble the distribution records (Appendix S1), distribution maps for Arabian squamates available as figures (Appendix S2) and shapefiles (Appendix S3) at the resolution of 10-arcmin grid cells, and the phylogenetic trees resulting from both ML and BI analyses (Appendix S4). Permits to carry out field work and to collect tissue samples in Oman were issued by the Nature Conservation Department of the Ministry of Environment and Climate Affairs (Refs 08/2005; 16/2008; 38/2010; 12/2011; 13/2013; 21/2013; 37/2014; 31/2016), in Saudi Arabia by Saudi Wildlife Authority (Ref: 04/2019), and in Yemen by Environment Protection Agency (Ref 10/2007).

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BIOSKETCH

Jiří Šmíd is a herpetologist, whose main research aim is to understand the phylogenetics, systematics and the dynamics in the evolutionary and diversification history of the unique fauna of squamate reptiles of the arid regions of Arabia, the Middle East and Africa.

Author contributions: JŠ and SC designed the project; JŠ, RS, MS, SB, MS-R, PG, P-AC, JE and SC conducted field work to collect distribution data and samples for genetic analysis; RS collected, computerized and georeferenced data from the literature; KT, TA, MS-R and BB-C did laboratory work and DNA sequence analysis; JŠ conducted phylogenetic analyses; JŠ, PT, BB-C and HT-C analysed the spatial data; JŠ led the writing with contributions from all authors.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

SUPPLEMENTARY MATERIALS

Diversity patterns and evolutionary history of Arabian squamates

Jiří Šmíd, Roberto Sindaco, Mohammed Shobrak, Salem Busais, Karin Tamar, Tatiana Aghová, Marc Simó-Riudalbas, Pedro Tarroso, Philippe Geniez, Pierre-André Crochet, Johannes Els, Bernat Burriel-Carranza, Héctor Tejero-Cicuéndez, Salvador Carranza

Contents

Figure S1. Map of squamate records for the Arabian Peninsula assembled for this study (18,053 records in total).
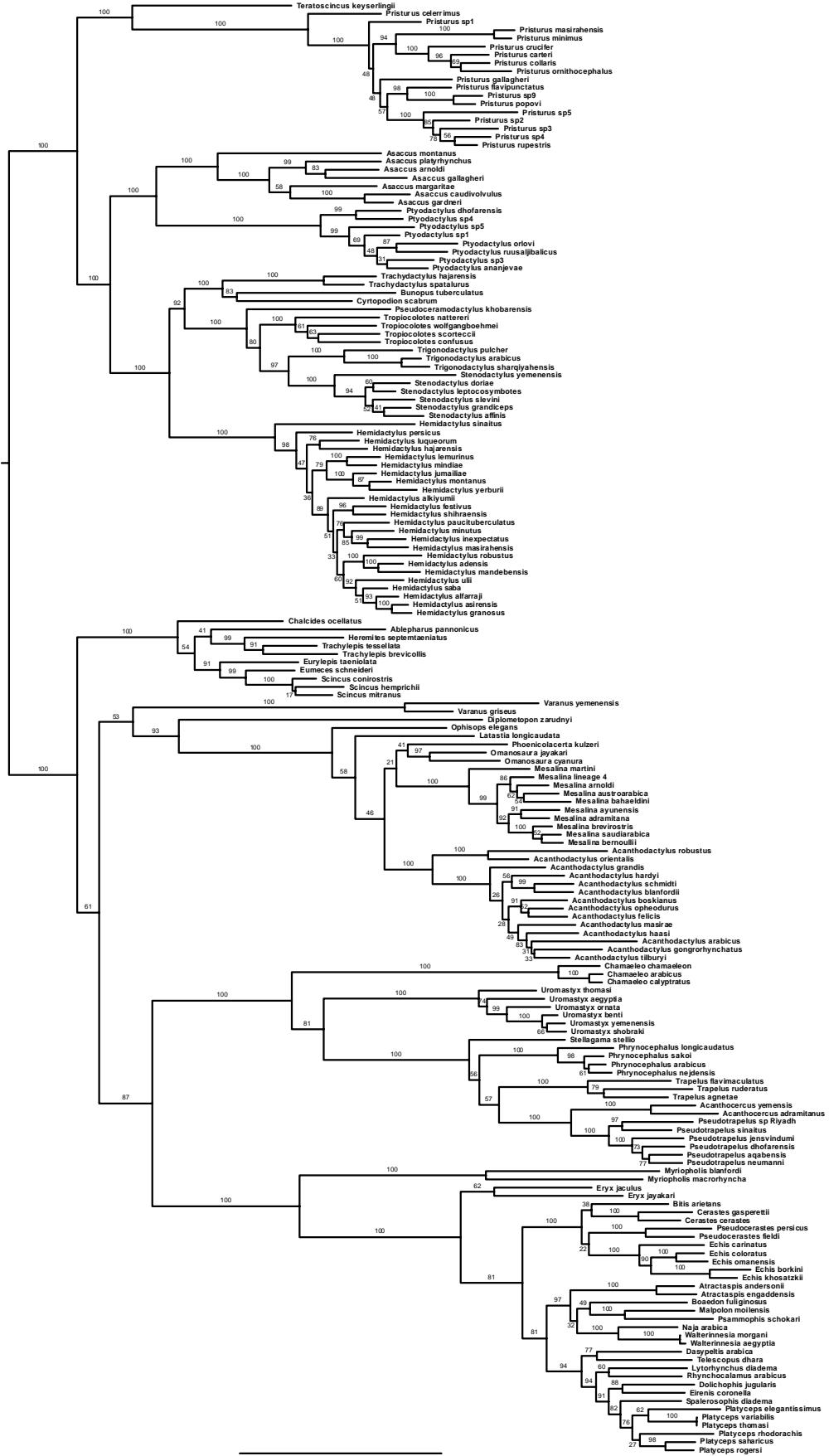
Figure S2. Phylogenetic tree of Arabian squamates resulting from the ML analysis. Numbers by branches indicate bootstrap support.
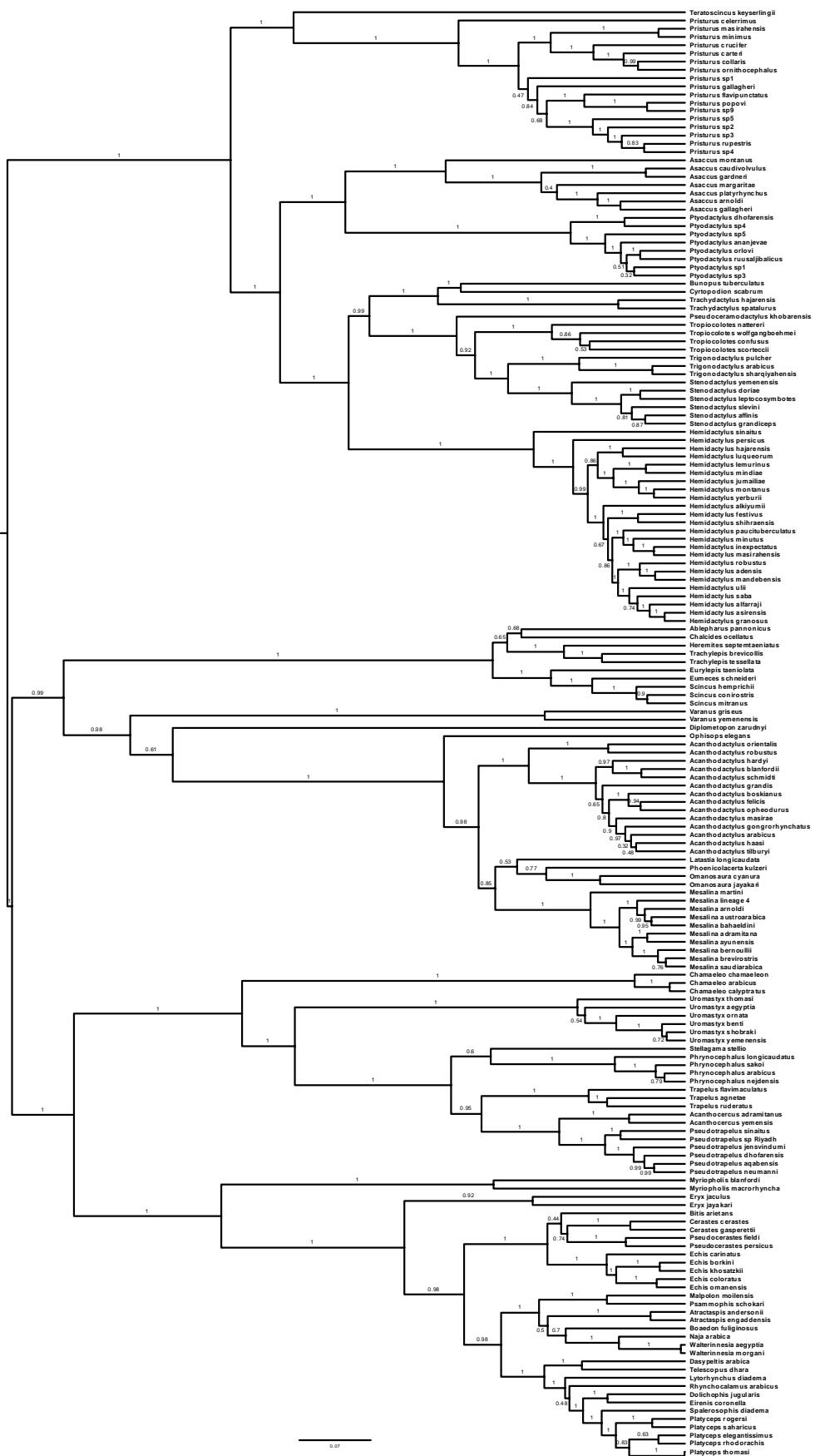
Figure S3. Maximum clade credibility tree of Arabian squamates resulting from the Bayesian analysis. Numbers by branches indicate posterior probabilities.
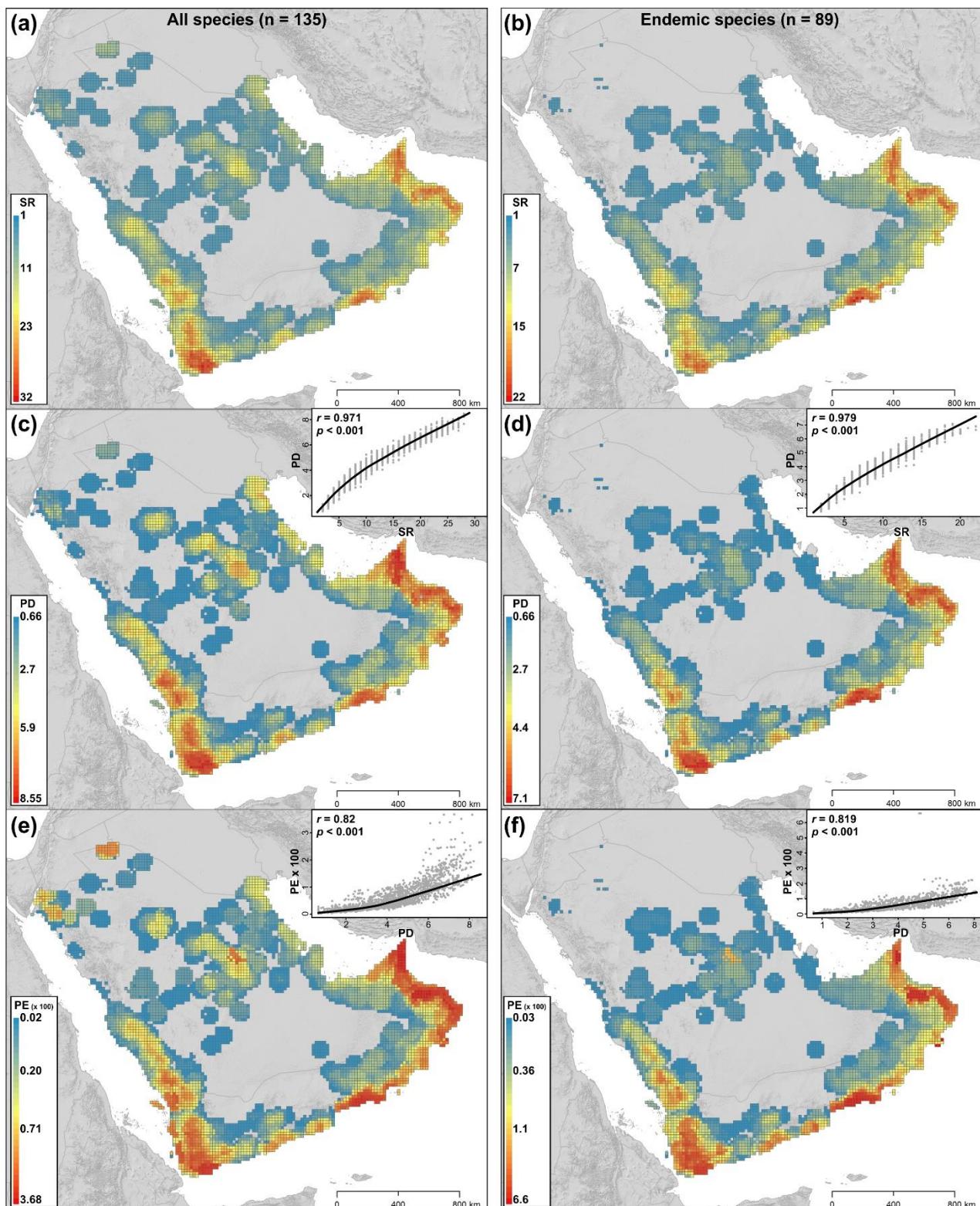
Figure S4. Arabian squamate species richness (SR), phylogenetic diversity (PD), and phylogenetic endemism (PE) based on the GPS maps (distribution records with precision ~ 1km or better; 13,898 records). Maps in the left column (a, c, e) are based on analyses of all species, right column (b, d, f) shows maps for Arabian endemics. Plots in the insets of (c) and (d) show the relationship between PD (y axis) and SR (x axis), those in (e) and (f) show the relationship between PE (y axis) and PD (x axis), with the *loess* regression lines in black. Correlation of the metrics (Pearson's *r*), as well as its statistical significance, is in the upper left corner of each plot.
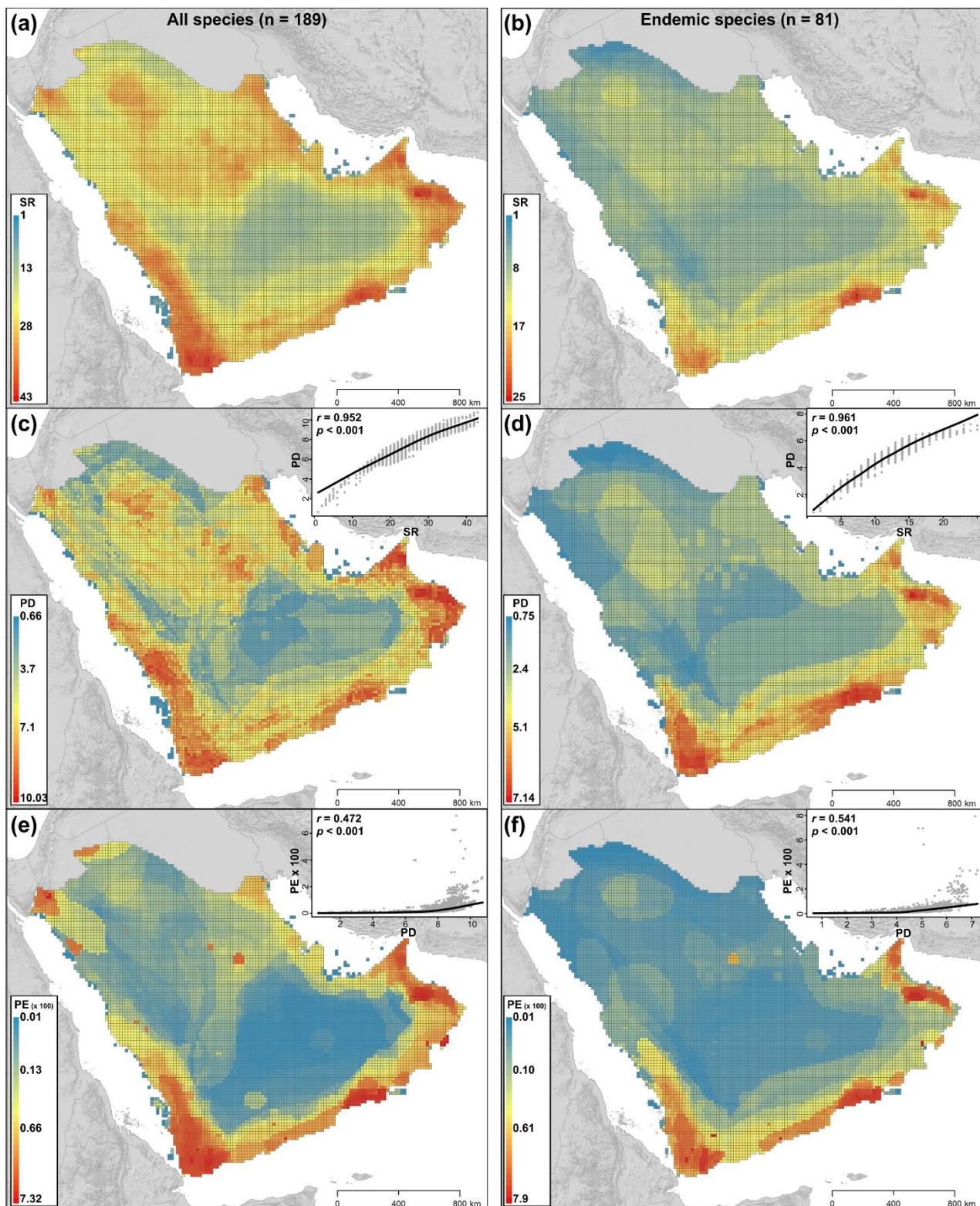
Figure S5. Arabian squamate species richness (SR), phylogenetic diversity (PD), and phylogenetic endemism (PE) based on distribution maps published by Roll et al. (2017). Maps in the left column (a, c, e) are based on analyses of all species, right column (b, d, f) shows maps for Arabian endemics. Plots in the insets of (c) and (d) show the relationship between PD (y axis) and SR (x axis), those in (e) and (f) show the relationship between PE (y axis) and PD (x axis), with the *loess* regression lines in black. Correlation of the metrics (Pearson's *r*), as well as its statistical significance, is in the upper left corner of each plot.
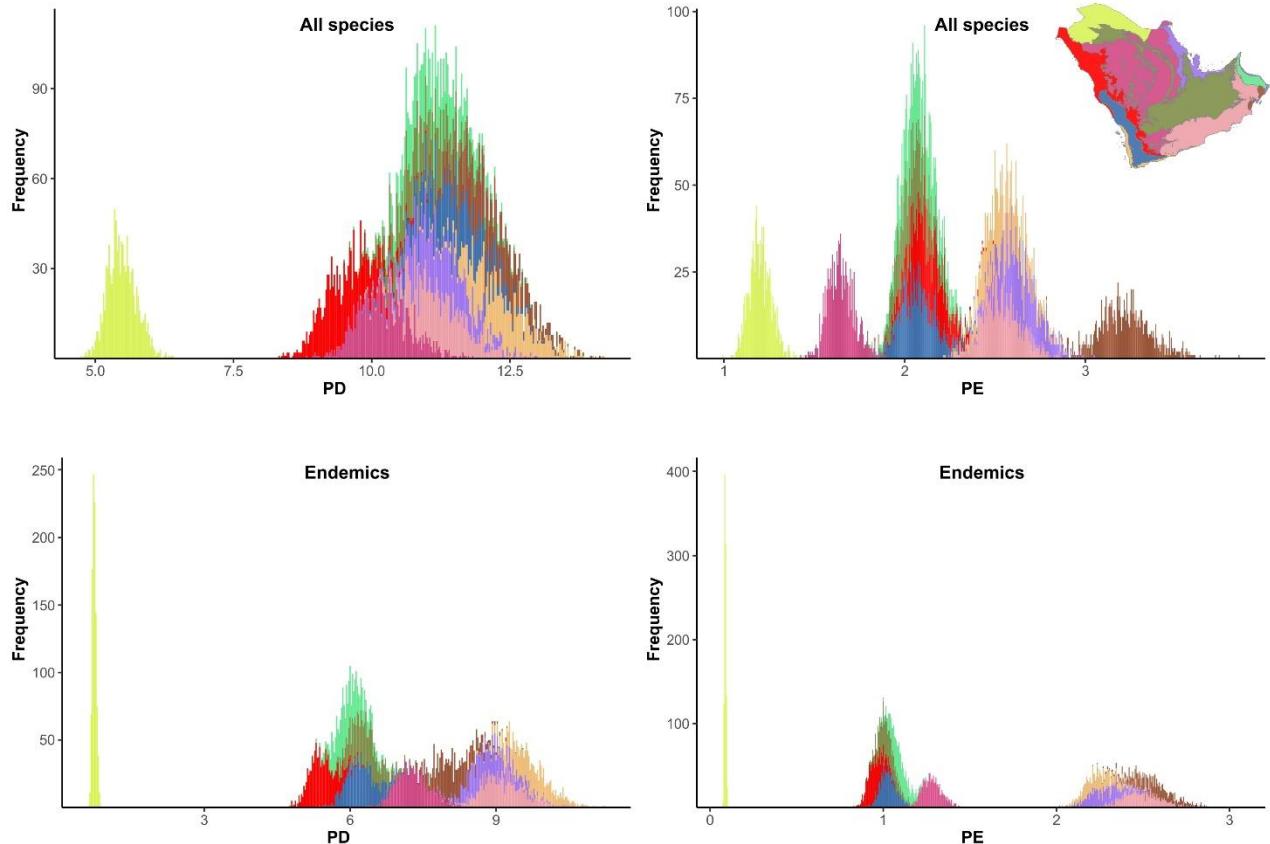
Figure S6. Frequency histograms of phylogenetic diversity (PD; units = sum of the branch lengths in the phylogeny that connect all species present in a ecoregion) and phylogenetic endemism (PE; units = sum of the branch lengths divided by clade ranges) of Arabian ecoregions generated with 1,000 randomly sampled trees from the posterior of the BI phylogenetic analysis without accounting for the ecoregion area. Plots in the upper panes are based on analyses of all species, lower panes show plots for Arabian endemics. Histogram colors correspond to the different ecoregions plotted in the upper right corner. For ecoregion names see Fig. 2 in the main text.
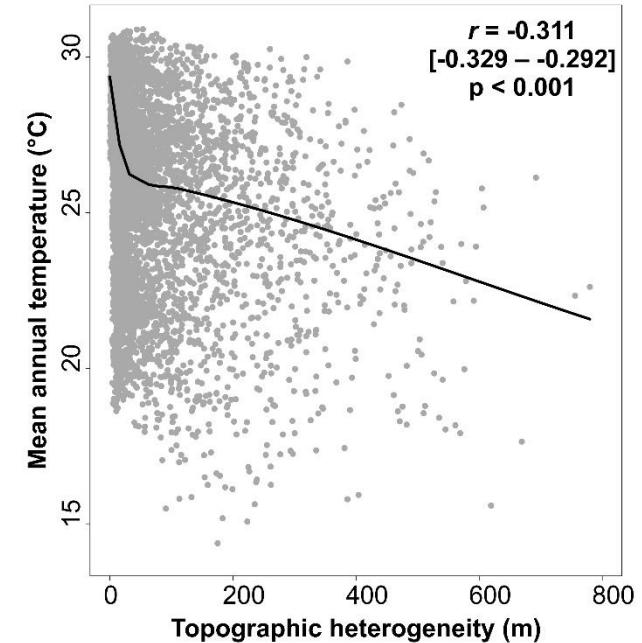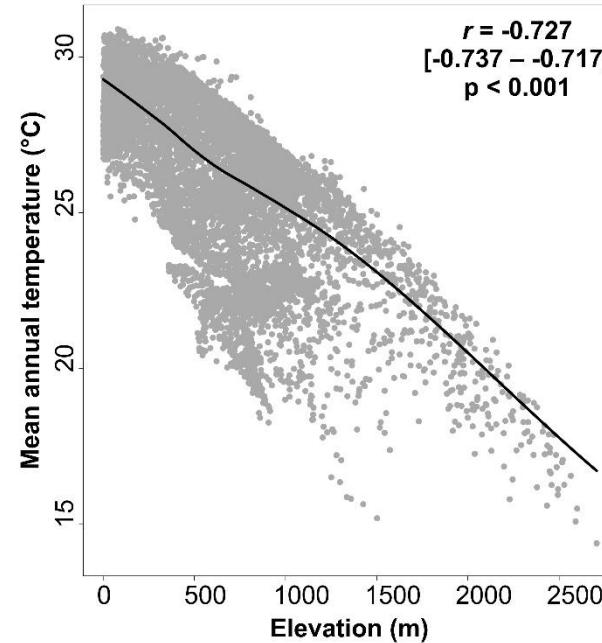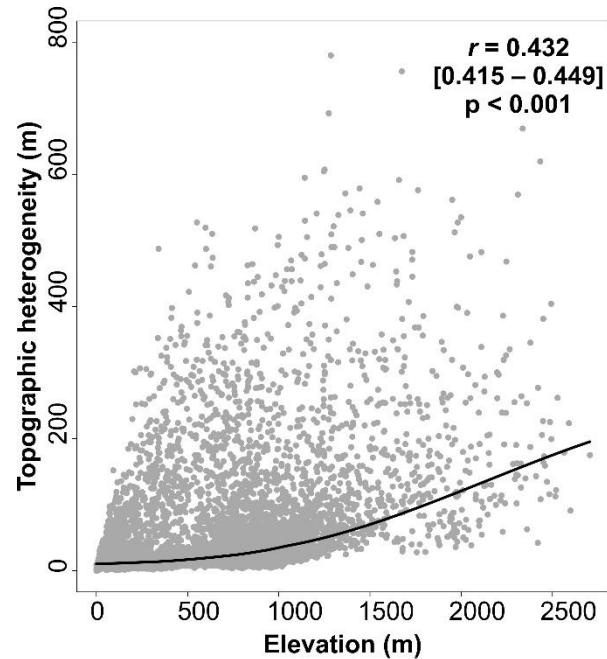
Figure S7. Relationships between elevation, topographic heterogeneity and mean annual temperature in the Arabian Peninsula. Solid black lines indicate fit of the *loess* regression models. Variable correlations (Pearson's *r*) are in the upper right corners, followed by confidence intervals in brackets and statistical significance.

Table S1. List of native terrestrial squamate species of Arabia. Together with described taxa the list includes also candidate, but yet undescribed species for which original reference is given in the *Reference* column. The column *Unique records* shows the number of unique locality points available for each species. The *Mean AUC* column shows the area under the curve of the receiver operating characteristics curve plot indicating the overall fit of the model and model accuracy. The *Mean TSS* columns shows true skill statistic values, another model evaluation metric that is immune to prevalence. Species with five and less unique records or species endemic to islands were not modelled. Ranges of species that were not modelled or whose predictions were unrealistic were estimated using environmentally informed buffers (see Materials and Methods). Specific environmental buffers were applied to each species depending on the species' habitat requirements and ecology (column *Range inference method*).

Family	Species	Reference	Endemic to Arabia	Unique records	Mean AUC	Mean TSS	Range inference method	Notes; model performance classes follow Araújo et al. (2005)
Agamidae	*Acanthocercus adramitanus*		YES	139	0.952	0.799	SDM	
Agamidae	*Acanthocercus yemensis*		YES	53	0.983	0.824	SDM	
Agamidae	*Phrynocephalus arabicus*		YES	242	0.766	0.531	50km buffer + slope + soil cropped	
Agamidae	*Phrynocephalus longicaudatus*		NO	69	0.82	0.491	SDM	
Agamidae	*Phrynocephalus nejdensis*		YES	7	0.773	0.455	SDM	Model performance 'fair', but model realistic
Agamidae	*Phrynocephalus sakoi*		YES	29	0.994	0.792	SDM	
Agamidae	*Pseudotrapelus aqabensis*		NO	25	0.902	0.609	SDM	
Agamidae	*Pseudotrapelus dhofarensis*		YES	104	0.949	0.758	SDM	
Agamidae	*Pseudotrapelus jensvindumi*		YES	161	0.965	0.841	SDM	
Agamidae	*Pseudotrapelus neumanni*		YES	77	0.938	0.721	SDM	
Agamidae	*Pseudotrapelus sinaitus*		NO	8	0.881	0.445	SDM	
Agamidae	*Pseudotrapelus* sp_Riyadh	Tamar et al. (2019)	YES	14	0.968	0.858	SDM	
Agamidae	*Stellagama stellio*		NO	13	0.935	0.755	SDM	
Agamidae	*Trapelus agnetae*		NO	51	0.801	0.527	SDM	
Agamidae	*Trapelus flavimaculatus*		YES	163	0.693	0.322	50km buffer + alt + slope cropped	
Agamidae	*Trapelus ruderatus*		NO	62	0.878	0.592	SDM	
Agamidae	*Uromastyx aegyptia*		NO	494	0.7	0.333	50km buffer + slope cropped	
Agamidae	*Uromastyx benti*		YES	20	0.924	0.715	SDM	
Agamidae	*Uromastyx ornata*		NO	33	0.884	0.677	SDM	
Agamidae	*Uromastyx shobraki*		YES	9	0.85	0.811	SDM	
Agamidae	*Uromastyx thomasi*		YES	19	0.958	0.778	SDM	
Agamidae	*Uromastyx yemenensis*		YES	9	0.955	0.75	SDM	
Boidae	*Eryx jaculus*		NO	5	0.856	0.37	SDM	
Boidae	*Eryx jayakari*		YES	233	0.691	0.258	SDM	Model performance 'poor', but model realistic
Chamaeleonidae	*Chamaeleo arabicus*		YES	69	0.958	0.738	SDM	
Chamaeleonidae	*Chamaeleo calyptratus*		YES	63	0.958	0.81	SDM	
Chamaeleonidae	*Chamaeleo chamaeleon*		NO	72	0.919	0.682	SDM	
Colubridae	*Dasypeltis arabica*		YES	11	0.948	0.728	SDM	
Colubridae	*Dolichophis jugularis*		NO	1	*na*	*na*	50km buffer + alt (±250m) cropped	
Colubridae	*Eirenis coronella*		NO	20	0.808	0.511	50km buffer + alt + slope cropped	Model performance 'good', but model unrealistic
Colubridae	*Lytorhynchus diadema*		NO	142	0.673	0.285	50km buffer + alt + slope + soil cropped	
Colubridae	*Lytorhynchus gasperetti*		YES	9	0.953	0.664	SDM	
Colubridae	*Platyceps elegantissimus*		YES	38	0.786	0.397	SDM	Model performance 'fair', but model realistic
Colubridae	*Platyceps insulanus*		YES	1	*na*	*na*	50km buffer + alt (±250m) cropped	
Colubridae	*Platyceps rhodorachis*		NO	310	0.881	0.602	SDM	
Colubridae	*Platyceps rogersi*		NO	49	0.946	0.724	SDM	
Colubridae	*Platyceps saharicus*		NO	3	*na*	*na*	50km buffer + alt cropped	
Colubridae	*Platyceps thomasi*		YES	15	0.933	0.589	SDM	
Colubridae	*Platyceps variabilis*		YES	20	0.953	0.766	SDM	
Colubridae	*Rhynchocalamus arabicus*		YES	4	*na*	*na*	50km buffer + alt + slope cropped	

Family	Species	Reference	Endemic to Arabia	Unique records	Mean AUC	Mean TSS	Range inference method	Notes; model performance classes follow Araújo et al. (2005)
Colubridae	*Spalerosophis diadema*		NO	153	0.687	0.289	SDM	Model performance 'poor', but model realistic
Colubridae	*Telescopus dhara*		NO	157	0.849	0.538	SDM	
Elapidae	*Naja arabica*		YES	109	0.893	0.648	SDM	
Elapidae	*Walterinnesia aegyptia*		NO	10	0.878	0.531	SDM	
Elapidae	*Walterinnesia morgani*		NO	33	0.805	0.467	SDM	
Gekkonidae	*Bunopus tuberculatus*		NO	565	0.624	0.285	50km buffer + slope cropped	
Gekkonidae	*Cyrtopodion scabrum*		NO	141	0.812	0.453	50km buffer + slope cropped	Model performance 'good', but model unrealistic
Gekkonidae	*Hemidactylus adensis*		YES	4	*na*	*na*	50km buffer + alt + slope + soil cropped	
Gekkonidae	*Hemidactylus alfarraji*		YES	3	*na*	*na*	50km buffer + alt + slope + soil cropped	
Gekkonidae	*Hemidactylus alkiyumii*		YES	75	0.985	0.828	SDM	
Gekkonidae	*Hemidactylus asirensis*		YES	18	0.99	0.875	SDM	
Gekkonidae	*Hemidactylus endophis*		YES	1	*na*	*na*	50km buffer + alt (±250m) cropped	
Gekkonidae	*Hemidactylus festivus*		YES	43	0.882	0.545	SDM	
Gekkonidae	*Hemidactylus granosus*		NO	18	0.786	0.406	50km buffer + alt + slope + soil cropped	
Gekkonidae	*Hemidactylus hajarensis*		YES	50	0.967	0.783	SDM	
Gekkonidae	*Hemidactylus inexpectatus*		YES	15	0.993	0.929	SDM	
Gekkonidae	*Hemidactylus jumailiae*		YES	21	0.969	0.773	SDM	
Gekkonidae	*Hemidactylus lemurinus*		YES	28	0.956	0.78	SDM	
Gekkonidae	*Hemidactylus luqueorum*		YES	31	0.994	0.885	SDM	
Gekkonidae	*Hemidactylus mandebensis*		YES	2	*na*	*na*	50km buffer + alt + slope cropped	
Gekkonidae	*Hemidactylus masirahensis*		YES	7	0.999	0.499	confined to Masirah Island	Endemic to Masirah Island
Gekkonidae	*Hemidactylus mindiae*		NO	1	*na*	*na*	50km buffer + alt (±250m) cropped	
Gekkonidae	*Hemidactylus minutus*		YES	65	0.972	0.777	SDM	
Gekkonidae	*Hemidactylus montanus*		YES	37	0.987	0.839	SDM	
Gekkonidae	*Hemidactylus paucituberculatus*		YES	34	0.989	0.857	SDM	
Gekkonidae	*Hemidactylus persicus*		NO	22	0.875	0.658	SDM	
Gekkonidae	*Hemidactylus robustus*		NO	228	0.857	0.622	SDM	
Gekkonidae	*Hemidactylus saba*		YES	1	*na*	*na*	50km buffer + alt (±250m) cropped	
Gekkonidae	*Hemidactylus shihraensis*		YES	5	*na*	*na*	50km buffer + alt cropped	
Gekkonidae	*Hemidactylus sinaitus*		NO	1	*na*	*na*	50km buffer + alt (±250m) cropped	
Gekkonidae	*Hemidactylus ulii*		YES	12	0.878	0.516	50km buffer + alt + slope + soil cropped	Model performance 'good', but model unrealistic
Gekkonidae	*Hemidactylus yerburii*		YES	36	0.981	0.888	SDM	
Gekkonidae	*Pseudoceramodactylus khobarensis*		NO	59	0.919	0.564	SDM	
Gekkonidae	*Stenodactylus affinis*		NO	5	*na*	*na*	50km buffer + alt + slope + soil cropped	
Gekkonidae	*Stenodactylus doriae*		NO	260	0.668	0.264	50km buffer + slope + soil cropped	
Gekkonidae	*Stenodactylus grandiceps*		NO	1	*na*	*na*	50km buffer + alt (±250m) cropped	
Gekkonidae	*Stenodactylus leptocosymbotes*		YES	163	0.905	0.744	SDM	
Gekkonidae	*Stenodactylus slevini*		YES	129	0.704	0.266	50km buffer + alt + slope + soil cropped	
Gekkonidae	*Stenodactylus yemenensis*		YES	32	0.988	0.733	SDM	
Gekkonidae	*Trachydactylus hajarensis*		YES	122	0.963	0.834	SDM	
Gekkonidae	*Trachydactylus spatalurus*		YES	23	0.829	0.459	SDM	
Gekkonidae	*Trigonodactylus arabicus*		YES	157	0.803	0.506	50km buffer + slope + soil cropped	
Gekkonidae	*Trigonodactylus pulcher*		YES	9	0.986	0.597	SDM	
Gekkonidae	*Trigonodactylus sharqiyahensis*		YES	42	0.983	0.855	SDM	
Gekkonidae	*Tropiocolotes confusus*		YES	11	0.901	0.553	SDM	
Gekkonidae	*Tropiocolotes nattereri*		NO	5	0.864	0.278	SDM	
Gekkonidae	*Tropiocolotes scorteccii*		YES	36	0.861	0.577	SDM	
Gekkonidae	*Tropiocolotes wolfgangboehmei*		YES	3	*na*	*na*	50km buffer + alt cropped	
Lacertidae	*Acanthodactylus arabicus*		YES	25	0.965	0.767	SDM	
Lacertidae	*Acanthodactylus blanfordii*		NO	26	0.979	0.853	SDM	
Lacertidae	*Acanthodactylus boskianus*		NO	224	0.592	0.162	50km buffer + alt + slope + soil cropped	
Lacertidae	*Acanthodactylus felicis*		YES	41	0.944	0.622	SDM	
Lacertidae	*Acanthodactylus gongrorhynchatus*		YES	74	0.909	0.661	50km buffer + slope + soil cropped	

Family	Species	Reference	Endemic to Arabia	Unique records	Mean AUC	Mean TSS	Range inference method	Notes; model performance classes follow Araújo et al. (2005)
Lacertidae	*Acanthodactylus grandis*		NO	9	0.963	0.66	SDM	
Lacertidae	*Acanthodactylus haasi*		YES	25	0.783	0.369	50km buffer + alt + slope + soil cropped	
Lacertidae	*Acanthodactylus hardyi*		NO	41	0.865	0.635	SDM	
Lacertidae	*Acanthodactylus masirae*		YES	30	0.966	0.842	SDM	
Lacertidae	*Acanthodactylus opheodurus*		YES	164	0.603	0.162	50km buffer + alt + slope cropped	
Lacertidae	*Acanthodactylus orientalis*		NO	8	0.984	0.854	SDM	
Lacertidae	*Acanthodactylus robustus*		NO	9	0.982	0.813	SDM	
Lacertidae	*Acanthodactylus schmidti*		YES	460	0.717	0.365	50km buffer + slope + soil cropped	
Lacertidae	*Acanthodactylus tilburyi*		YES	10	0.791	0.318	50km buffer + alt + slope cropped	
Lacertidae	*Latastia longicaudata*		NO	9	0.94	0.573	SDM	
Lacertidae	*Mesalina adramitana*		YES	178	0.84	0.593	SDM	
Lacertidae	*Mesalina arnoldi*		YES	38	0.967	0.799	SDM	
Lacertidae	*Mesalina austroarabica*		YES	28	0.917	0.637	SDM	
Lacertidae	*Mesalina ayunensis*		YES	7	0.864	0.671	50km buffer + alt + slope + soil cropped	Model performance 'good', but model unrealistic
Lacertidae	*Mesalina bahaeldini*		NO	4	*na*	*na*	50km buffer + alt + slope + soil cropped	
Lacertidae	*Mesalina bernoullii*		NO	38	0.901	0.591	SDM	
Lacertidae	*Mesalina brevirostris*		NO	78	0.991	0.939	SDM	
Lacertidae	*Mesalina* lineage 4	Sindaco et al. (2018)	YES	39	0.935	0.744	SDM	
Lacertidae	*Mesalina martini*		NO	4	*na*	*na*	50km buffer + alt + slope + soil cropped	
Lacertidae	*Mesalina saudiarabica*		YES	11	0.815	0.56	SDM	
Lacertidae	*Omanosaura cyanura*		YES	61	0.987	0.882	SDM	
Lacertidae	*Omanosaura jayakari*		YES	151	0.975	0.883	SDM	
Lacertidae	*Ophisops elbaensis*		YES	11	0.948	0.624	SDM	
Lacertidae	*Ophisops elegans*		NO	1	*na*	*na*	50km buffer + alt (±250m) cropped	
Lacertidae	*Philochortus neumanni*		YES	15	0.959	0.777	SDM	
Lacertidae	*Phoenicolacerta kulzeri*		NO	1	*na*	*na*	50km buffer + alt (±250m) cropped	
Lamprophiidae	*Atractaspis andersonii*		YES	64	0.709	0.315	SDM	Model performance 'fair', but model realistic
Lamprophiidae	*Atractaspis engaddensis*		NO	2	*na*	*na*	50km buffer + alt cropped	
Lamprophiidae	*Boaedon fuliginosus*		NO	17	0.958	0.787	SDM	
Lamprophiidae	*Malpolon moilensis*		NO	244	0.581	0.118	50km buffer + alt + slope cropped	
Lamprophiidae	*Psammophis schokari*		NO	386	0.626	0.178	50km buffer + alt + slope cropped	
Leptotyphlopidae	*Myriopholis blanfordi*		YES	2	*na*	*na*	50km buffer + alt + slope + soil cropped	
Leptotyphlopidae	*Myriopholis burii*		YES	2	*na*	*na*	50km buffer + alt + slope cropped	
Leptotyphlopidae	*Myriopholis macrorhyncha*		NO	44	0.717	0.367	50km buffer + alt + slope cropped	
Leptotyphlopidae	*Myriopholis nursii*		YES	43	0.9	0.648	SDM	
Phyllodactylidae	*Asaccus arnoldi*		YES	14	0.978	0.855	SDM	
Phyllodactylidae	*Asaccus caudivolvulus*		YES	4	*na*	*na*	50km buffer + alt + slope cropped	
Phyllodactylidae	*Asaccus gallagheri*		YES	66	0.984	0.852	SDM	
Phyllodactylidae	*Asaccus gardneri*		YES	27	0.996	0.881	SDM	
Phyllodactylidae	*Asaccus margaritae*		YES	9	0.998	0.711	SDM	
Phyllodactylidae	*Asaccus montanus*		YES	29	0.992	0.929	SDM	
Phyllodactylidae	*Asaccus platyrhynchus*		YES	40	0.98	0.784	SDM	
Phyllodactylidae	*Ptyodactylus ananjevae*		YES	1	*na*	*na*	50km buffer + alt (±250m) cropped	
Phyllodactylidae	*Ptyodactylus dhofarensis*		YES	96	0.947	0.755	SDM	
Phyllodactylidae	*Ptyodactylus orlovi*		YES	203	0.952	0.768	SDM	
Phyllodactylidae	*Ptyodactylus ruusaljibalicus*		YES	29	0.996	0.942	SDM	
Phyllodactylidae	*Ptyodactylus* sp1	Metallinou et al. (2015)	YES	19	0.838	0.441	SDM	
Phyllodactylidae	*Ptyodactylus* sp3	Metallinou et al. (2015)	YES	30	0.873	0.578	SDM	
Phyllodactylidae	*Ptyodactylus* sp4	Metallinou et al. (2015)	YES	37	0.962	0.817	SDM	
Phyllodactylidae	*Ptyodactylus* sp5	Metallinou et al. (2015)	YES	10	0.906	0.538	SDM	
Scincidae	*Ablepharus pannonicus*		NO	37	0.867	0.725	SDM	
Scincidae	*Chalcides levitoni*		YES	3	*na*	*na*	50km buffer + alt + slope + soil cropped	
Scincidae	*Chalcides ocellatus*		NO	114	0.797	0.427	50km buffer + alt + slope + soil cropped	

Family	Species	Reference	Endemic to Arabia	Unique records	Mean AUC	Mean TSS	Range inference method	Notes; model performance classes follow Araújo et al. (2005)
Scincidae	*Eumeces schneideri*		NO	7	0.543	0.018	50km buffer + alt + slope + soil cropped	
Scincidae	*Eurylepis taeniolata*		NO	21	0.826	0.435	SDM	
Scincidae	*Heremites septemtaeniatus*		NO	22	0.985	0.868	SDM	
Scincidae	*Scincus conirostris*		NO	60	0.56	0.135	50km buffer + alt + slope + soil cropped	
Scincidae	*Scincus hemprichii*		YES	36	0.992	0.88	SDM	
Scincidae	*Scincus mitranus*		YES	342	0.717	0.353	50km buffer + slope + soil cropped	
Scincidae	*Trachylepis brevicollis*		NO	159	0.845	0.565	SDM	
Scincidae	*Trachylepis tessellata*		YES	93	0.931	0.735	SDM	
Sphaerodactylidae	*Pristurus carteri*		YES	260	0.93	0.757	SDM	
Sphaerodactylidae	*Pristurus celerrimus*		YES	195	0.985	0.872	SDM	
Sphaerodactylidae	*Pristurus collaris*		YES	29	0.982	0.864	SDM	
Sphaerodactylidae	*Pristurus crucifer*		YES	20	0.937	0.773	SDM	
Sphaerodactylidae	*Pristurus flavipunctatus*		NO	83	0.936	0.758	SDM	
Sphaerodactylidae	*Pristurus gallagheri*		YES	44	0.989	0.795	SDM	
Sphaerodactylidae	*Pristurus masirahensis*		YES	7	*na*	*na*	confined to Masirah Island	Endemic to Masirah Island
Sphaerodactylidae	*Pristurus minimus*		YES	142	0.94	0.857	SDM	
Sphaerodactylidae	*Pristurus ornithocephalus*		YES	16	0.97	0.787	SDM	
Sphaerodactylidae	*Pristurus popovi*		YES	24	0.991	0.888	SDM	
Sphaerodactylidae	*Pristurus rupestris*		NO	187	0.976	0.873	SDM	
Sphaerodactylidae	*Pristurus saada*		YES	6	0.981	0.8	SDM	
Sphaerodactylidae	*Pristurus schneideri*		YES	1	*na*	*na*	confined to Hanish Islands	Endemic to Hanish Islands
Sphaerodactylidae	*Pristurus* sp1	Badiane et al. (2014)	YES	384	0.868	0.6	SDM	
Sphaerodactylidae	*Pristurus* sp2	Garcia-Porta et al. (2017)	YES	29	0.999	0.899	SDM	
Sphaerodactylidae	*Pristurus* sp3	Garcia-Porta et al. (2017)	YES	197	0.96	0.786	SDM	
Sphaerodactylidae	*Pristurus* sp4	Garcia-Porta et al. (2017)	YES	2	*na*	*na*	50km buffer + alt (±250m) cropped	
Sphaerodactylidae	*Pristurus* sp5	Garcia-Porta et al. (2017)	YES	72	0.931	0.672	SDM	
Sphaerodactylidae	*Pristurus* sp9	Ongoing *Pristurus* project	YES	1	*na*	*na*	50km buffer + alt (±250m) cropped	
Sphaerodactylidae	*Teratoscincus keyserlingii*		NO	63	0.998	0.945	SDM	
Trogonophidae	*Agamodon arabicus*		YES	8	0.994	0.792	SDM	
Trogonophidae	*Diplometopon zarudnyi*		NO	110	0.88	0.624	SDM	
Varanidae	*Varanus griseus*		NO	201	0.608	0.207	50km buffer + alt + slope cropped	
Varanidae	*Varanus yemenensis*		YES	37	0.959	0.813	SDM	
Viperidae	*Bitis arietans*		NO	62	0.923	0.711	SDM	
Viperidae	*Cerastes cerastes*		NO	28	0.987	0.82	SDM	
Viperidae	*Cerastes gasperettii*		YES	270	0.503	0.052	50km buffer + alt + slope + soil cropped	
Viperidae	*Echis borkini*		YES	46	0.961	0.827	SDM	
Viperidae	*Echis carinatus*		NO	78	0.973	0.85	SDM	
Viperidae	*Echis coloratus*		NO	163	0.666	0.257	50km buffer + alt + slope + soil cropped	
Viperidae	*Echis khosatzkii*		YES	37	0.924	0.623	SDM	
Viperidae	*Echis omanensis*		YES	97	0.97	0.813	SDM	
Viperidae	*Pseudocerastes fieldi*		NO	6	0.952	0.546	SDM	
Viperidae	*Pseudocerastes persicus*		NO	31	0.985	0.824	SDM	

Table S2. Primers used to amplify and sequence the genetic markers targeted in this study. The table shows information on the genome type, gene and primer name, primer orientation (forward [F] or reverse [R]), primer nucleotide sequence (5' to 3'), length of the fragment amplified, annealing temperature used for the amplification, and original reference.

Genome	Gene	Primer	Orientation	Sequence	Amplicon length	Annealing Temp	Primer source
mtDNA	12S	12S268	F	GTGCCAGCGACCGCGGTTACACG	ca. 620bp	65°C	Schätti and Utiger (2001)
		12S916	R	GTACGCTTACCATGTTACGACTTGCCCTG			
		12Sa	F	AAACTGGGATTAGATACCCCACTAT	ca. 400bp	48°C	Kocher et al. (1989)
		12Sb	R	GAGGGTGACGGGCGGTGTGT			
	16S	16Sa	F	CGCCTGTTTAACAAAAACAT	ca. 500bp	48°C	Palumbi et al. (1991)
		16Sb	R	CCGGTCTGAACTCAGATCACGT			
	cytb	L14910	F	GACCTGTGATMTGAAAACCAYCGTTGT	ca. 1100bp	46°C	Burbrink et al. (2000)
		H16064	R	CTTTGGTTTACAAGAACAATGCTTTA			
		cytb1	F	CCATCCAACATCTCAGCATGATGAAA	307bp	46°C	Kocher et al. (1989)
		cytb2	R	CCCTCAGAATGATATTTGTCCTCA			
	COI	COIb	F	TAAATAATATAAGCTTCTGACTGCTACCACC	642bp	65°C	Schätti and Utiger (2001)
		COIbdeg	R	ATTATTGTTGCYGCTGTRAARTAGGCTCG			
		RepCOI_F	F	TNTTMTCAACNAACCACAAAGA	664bp	48.5°C	Nagy et al. (2012)
		RepCOI_R	R	ACTTCTGGRTGKCCAAARAATCA			
	ND2	L4437	F	AAGCTTTCGGGCCCATACC	983bp	50°C	Macey et al. (1997)
		H5540	R	TTTAGGGCTTTGAAGGC			
	ND4	ND4_F	F	CACCTATGACTACCAAAAGCTCATGTAGAAGC	696bp + 167bp flanking tRNAs	48°C	Arèvalo et al. (1994)
		Leu_R	R	CATTACTTTTACTTGGATTTGCACCA			
nDNA	acm4	Int-F	F	TTTYCTGAAGAGCCCTCTGGTC	364 bp	55°C	Gamble, Simons, et al. (2008)
		Int-R	R	CAAATTTCCTGGCAACATTRGC			
	cmos	FUF	F	TTTGGTTCKGTCTACAAGGCTAC	ca. 400bp	53°C	Gamble, Bauer, et al. (2008)
		FUR	R	AGGGAACATCCAAAGTCTCCAAT			
		S77	F	CATGGACTGGGGATCAGTTATG	567bp	53°C	Lawson et al. (2005)
		S78	R	CCTTGGGTGTGATTTTCTCACCT			
	mc1r	MC1RF	F	AGGCNGCCATYGTCAAGAACCGGAACC	ca. 670bp	56°C	Pinho et al. (2010)
		MC1RR	R	CTCCGRAAGGCRTAAATGATGGGGTCCAC			
	NT3	F3	F	ATATTTCTGGCTTTTCTCTGTGGC	ca. 480bp	50°C	Noonan and Chippindale (2006)
		R4	R	GCGTTTCATAAAAATATTGTTTGACCGG			
	rag1	R13	F	TCTGAATGGAAATTCAAGCTGTT	ca. 1000bp	58°C	Groth and Barrowclough (1999)
		R18	R	GATGCTGCCTCGGTCGGCCACCTTT			
	rag2	PY1F	F	CCCTGAGTTTGGATGCTGTACTT	410bp	53°C	Gamble, Bauer, et al. (2008)
		PY1R	R	AACTGCCTRTTGTCCCCTGGTAT			

Table S3. Specimens newly sequenced for this study, with their sample and collection codes and locality details. Museum acronyms are as follows: IBES – Institute of Evolutionary Biology, Barcelona, Spain; NMP – National Museum in Prague, Czech Republic; SMNH - Steinhardt Museum of Natural History, Tel Aviv, Israel.

Family	Genus	Species	Sample code	Collection number	Country	GPS	Markers sequenced *de novo*
Agamidae	*Trapelus*	*agnetae*	BEV10192	-	Israel	31.0413N, 34.7376E	16S, CYTB, ND4, ACM4, CMOS, MC1R
Agamidae	*Trapelus*	*flavimaculatus*	CN8128	IBE CN8128	Oman	21.48861N, 58.25798E	16S, ND4, ACM4, CMOS, MC1R
Agamidae	*Trapelus*	*ruderatus*	BEV10064	-	Kuwait	28.7467N, 48.3366E	16S, CYTB, ND4, ACM4, CMOS, MC1R
Boidae	*Eryx*	*jayakari*	CN5907	-	Oman	22.16556N, 58.58795E	12S, 16S, CYTB
Colubridae	*Eirenis*	*coronella*	R17839	SMNH R17839	Israel	31.27N, 35.218E	12S, 16S, CYTB, ND2, ND4, CMOS, NT3
Colubridae	*Platyceps*	*thomasi*	OM137	NMP 74279	Oman	16.8859N, 53.7775E	12S, CYTB
Colubridae	*Platyceps*	*variabilis*	OM60	-	Oman	16.8859N, 53.7775E	12S, CYTB
Elapidae	*Walterinnesia*	*morgani*	CN12091	-	Saudi Arabia	-	12S, 16S, CYTB, ND2, ND4, CMOS, RAG1
Gekkonidae	*Bunopus*	*tuberculatus*	CN819	-	UAE	24.99638N, 55.66103E	12S, COI
Gekkonidae	*Tropiocolotes*	*wolfgangboehmei*	CN15783	NMP 76035	Saudi Arabia	25.45933N, 46.56276E	16S, CMOS, MC1R
Lamprophiidae	*Atractaspis*	*andersonii*	JIR22	-	Oman	17.172866N, 54.091813E	CYTB
Lamprophiidae	*Atractaspis*	*andersonii*	CN5950	-	Oman	17.10531N, 54.454563E	12S, 16S, ND4, CMOS
Sphaerodactylidae	*Pristurus*	*carteri*	S7195	-	Oman	17.04136N, 54.32605E	MC1R
Sphaerodactylidae	*Pristurus*	*celerrimus*	AO72	-	Oman	23.17333N, 57.43194E	CMOS
Sphaerodactylidae	*Pristurus*	*collaris*	JEM593	-	Yemen	14.38N, 49.2E	CMOS, MC1R
Sphaerodactylidae	*Pristurus*	*flavipunctatus*	JEM228	-	Yemen	13.31N, 43.57E	ACM4, MC1R
Sphaerodactylidae	*Pristurus*	*gallagheri*	AO19	-	Oman	22.78667N, 57.59389E	MC1R
Sphaerodactylidae	*Pristurus*	*ornithocephalus*	JEM646	-	Yemen	14N, 48.19E	12S, ACM4, MC1R, RAG1, RAG2
Sphaerodactylidae	*Pristurus*	*popovi*	S10506	IBES10506	Saudi Arabia	18.26042N, 42.37877E	ACM4, CMOS, MC1R
Sphaerodactylidae	*Pristurus*	*rupestris*	S7553	IBES7553	Oman	23.13167N, 58.61889E	ACM4
Sphaerodactylidae	*Pristurus*	sp1	JEM305	-	Yemen	16.39N, 53.05E	CMOS, MC1R
Sphaerodactylidae	*Pristurus*	sp2	S7264	-	Oman	22.84549N, 59.13829E	ACM4, CMOS, MC1R, RAG1, RAG2
Sphaerodactylidae	*Pristurus*	sp3	S7475	IBES7475	Oman	23.13968N, 57.8442E	ACM4, CMOS, MC1R, RAG1, RAG2
Sphaerodactylidae	*Pristurus*	sp4	S7257	IBES7257	Oman	23.13167N, 58.61889E	ACM4
Sphaerodactylidae	*Pristurus*	sp5	S7552	IBES7552	Oman	22.76253N, 58.85312E	ACM4
Sphaerodactylidae	*Pristurus*	sp9	JEM248	-	Yemen	13.52N, 45.48E	12S, ACM4, MC1R, RAG1, RAG2

Table S4. List of Arabian squamates used in this study along with information on whether each species was included in the phylogenetic analysis (column 'In tree') and GenBank accession numbers of the DNA sequences. Locality data and collection numbers of the newly sequenced specimens are detailed in Table S3. GenBank accessions of sequences newly generated for this study are in the ranges MW198193–MW198209 and MW204503–MW204568.

Family	Genus	Species	In tree	12S	16S	CYTB	COI	ND1	ND2	ND4	ACM4	BDNF	CMOS	MC1R	NT3	PDC	PRLR	RAG1	RAG2
Agamidae	*Acanthocercus*	*adramitanus*	YES		KU097507					KU169222			KU097582	KU097645					
Agamidae	*Acanthocercus*	*yemensis*	YES		KU097509					KU169224			KU097581	KU097646					
Agamidae	*Phrynocephalus*	*arabicus*	YES				KT182055		KF691651	KF691675		KJ363434						KJ363507	
Agamidae	*Phrynocephalus*	*longicaudatus*	YES			KF691623	KF691707		KF691650	KF691674		KJ363433							
Agamidae	*Phrynocephalus*	*nejdensis*	YES				KT182061												
Agamidae	*Phrynocephalus*	*sakoi*	YES				KT182047	KJ195909										KJ195950	
Agamidae	*Pseudotrapelus*	*aqabensis*	YES		KU097464		KP994947			KU169191			KU097554	KU097630				KP994934	
Agamidae	*Pseudotrapelus*	*dhofarensis*	YES		KU097450		KP979759			KU169176			KU097574	KU097590				KP994932	
Agamidae	*Pseudotrapelus*	*jensvindumi*	YES		KU097476		KP979760			KU169202			KU097533	KU097607				KP994936	
Agamidae	*Pseudotrapelus*	*neumanni*	YES		KU097474					KU169200			KU097556	KU097638					
Agamidae	*Pseudotrapelus*	*sinaitus*	YES		KU097434		KP994943			KU169157			KU097526	KU097643	JX839249			KP994929	
Agamidae	*Pseudotrapelus*	*sp_Riyadh*	YES		MK176908					MK176910			MK176912	MK176914					
Agamidae	*Stellagama*	*stellio*	YES		GU128464					GU128500			JX838986		JX839247				
Agamidae	*Trapelus*	*agnetae*	YES		MW198205	MW204509				MW204517	MW204529		MW204542	MW204556					
Agamidae	*Trapelus*	*flavimaculatus*	YES		MW198206					MW204519	MW204530		MW204544	MW204558					
Agamidae	*Trapelus*	*ruderatus*	YES		MW198207	MW204510				MW204518	MW204531		MW204543	MW204557					
Agamidae	*Uromastyx*	*aegyptia*	YES	FJ639658	FJ639620	MF960631				MF993250	MF960319			MF960419	MF960515				
Agamidae	*Uromastyx*	*benti*	YES		EF081056	MF960603				MF993220	MF960288			MF960393	MF960496				
Agamidae	*Uromastyx*	*ornata*	YES	AB641361	EF081046	MF960626			AB641376	MF993245	MF960313			MF960413	MF960510				
Agamidae	*Uromastyx*	*shobraki*	YES		EF081068	MF960599				MF993215	MF960286			MF960392	MF960494				
Agamidae	*Uromastyx*	*thomasi*	YES		MF980217	MF960591				MF993210	MF960280			MF960388	MF960490				
Agamidae	*Uromastyx*	*yemenensis*	YES	AB114447	AB114447	AB114447	AB114447	AB114447	AB114447	AB114447	MF960295			MF960396	MF960499				
Boidae	*Eryx*	*jayakari*	YES	MW198196	MW198204	MW204508						DQ465566	DQ465565						
Boidae	*Eryx*	*jaculus*	YES			KJ841055	KU986317												
Colubridae	*Dasypeltis*	*arabica*	YES		AY611854	AY612036							AY611945						
Colubridae	*Dolichophis*	*jugularis*	YES			AY486917		AY486968	AY487007	AY487046			AY486941						
Colubridae	*Eirenis*	*coronella*	YES	MW198195	MW198203	MW204505			MW204512	MW204515			MW204534		MW204559				
Colubridae	*Lytorhynchus*	*diadema*	YES	KX909259	KX909293	KX909324							KX909363						
Colubridae	*Lytorhynchus*	*gasperetti*	NO																
Colubridae	*Platyceps*	*elegantissimus*	YES	AY039147			AY039185												
Colubridae	*Platyceps*	*insulanus*	NO																
Colubridae	*Platyceps*	*rhodorachis*	YES			AY486921		AY486973	AY487012	AY487051			AY486945						
Colubridae	*Platyceps*	*rogersi*	YES		AY188082	AY188041		AY486974	AY487013	AY487052			AY188002						
Colubridae	*Platyceps*	*saharicus*	YES	MF767311		MF767373	MF767350												
Colubridae	*Platyceps*	*variabilis*	YES	MW198200		MW204506													
Colubridae	*Platyceps*	*thomasi*	YES	MW198199		MW204507													
Colubridae	*Rhynchocalamus*	*arabicus*	YES	KT878842	KT878847	KT878854							KT878851						
Colubridae	*Spalerosophis*	*diadema*	YES	KX694605	KX694668	KX694865					KX694764		KX694820					KX695051	
Colubridae	*Telescopus*	*dhara*	YES	MK372073	MK372111	MK373062			MK373097	MK373132			MK373171		MK373243			MK373211	
Elapidae	*Naja*	*arabica*	YES	GQ359663	GQ359749	GQ359500				GQ359582									
Elapidae	*Walterinnesia*	*aegyptia*	YES	U96807		AF217838		AY058963	AY059001	AY058988			AY058943						
Elapidae	*Walterinnesia*	*morgani*	YES	MW198201	MW198209	MW204504			MW204513	MW204516			MW204533						MW204564
Gekkonidae	*Bunopus*	*tuberculatus*	YES	MW198194			MW204511		JX041317		JQ945641		JQ945535			JQ945355		JQ945287	JQ945427
Gekkonidae	*Cyrtopodion*	*scabrum*	YES	AB661665	AB661665	AB661665	AB661665	AB661665	AB661665	AB661665	HQ426355		HQ426532		HQ426186			HQ426275	HQ426448
Gekkonidae	*Hemidactylus*	*adensis*	YES	KC818735		KC818886							KC818791	KC818944				KC819003	KC819063
Gekkonidae	*Hemidactylus*	*alfarraji*	YES	KX263482		KX263646							KX263624	KX263587				KX263546	KX263522
Gekkonidae	*Hemidactylus*	*alkiyumii*	YES	JQ957038		JQ957168					KU749838		JQ957121	JQ957236	KU749870			KU749908	JQ957401
Gekkonidae	*Hemidactylus*	*asirensis*	YES	KX263492		KX263656							KX263628	KX263598				KX263556	KX263526
Gekkonidae	*Hemidactylus*	*endophis*	NO																
Gekkonidae	*Hemidactylus*	*festivus*	YES			JQ957179				JQ957322	KU749839		JQ957125	JQ957249	KU749874			KU749912	JQ957408
Gekkonidae	*Hemidactylus*	*granosus*	YES	KF647568		KF647584							KF647576	KF647588				KF647595	KF647609
Gekkonidae	*Hemidactylus*	*hajarensis*	YES	JQ957053		JQ957188				JQ957336	KU749848		JQ957128		KU749878			KU749916	KU749934
Gekkonidae	*Hemidactylus*	*inexpectatus*	YES	JQ957066		JQ957206				JQ957364	KU749843		JQ957141	JQ957274	KU749880			KU749918	JQ957427
Gekkonidae	*Hemidactylus*	*jumailiae*	YES	KC818682		KC818837							KC818770	KC818918				KC818975	KC819038
Gekkonidae	*Hemidactylus*	*lemurinus*	YES	JQ957061		JQ957199				JQ957351	KU749842		JQ957137	JQ957267	KU749882			KU749920	JQ957423
Gekkonidae	*Hemidactylus*	*luqueorum*	YES	JQ957069		JQ957213							JQ957145	JQ957281	KU749883			KU749921	JQ957430
Gekkonidae	*Hemidactylus*	*mandebensis*	YES	KC818732		KC818883							KC818790	KP238244				KP238241	JQ957409
Gekkonidae	*Hemidactylus*	*masirahensis*	YES	JQ957063		JQ957202				JQ957357	KU749844		JQ957139		KU749884				
Gekkonidae	*Hemidactylus*	*mindiae*	YES	KC818686		HQ833747							JQ957128					KC818980	JQ957423
Gekkonidae	*Hemidactylus*	*minutus*	YES	KJ189804		KJ189773				KJ189841			KJ189864	KJ189902				KJ189923	KU749936
Gekkonidae	*Hemidactylus*	*montanus*	YES	KX263476		KX263677							KX263640	KX263617				KX263579	KX263542
Gekkonidae	*Hemidactylus*	*paucituberculatus*	YES	JQ957072		JQ957217				JQ957376	KU749840		JQ957151	JQ957285	KU749886			KU749925	JQ957425
Gekkonidae	*Hemidactylus*	*persicus*	YES	JQ957075		JQ957223					KU749849		JQ957152		KU749887			KU749926	KU749938

Family	Genus	Species	In tree	12S	16S	CYTB	COI	ND1	ND2	ND4	ACM4	BDNF	CMOS	MC1R	NT3	PDC	PRLR	RAG1	RAG2
Gekkonidae	Hemidactylus	robustus	YES	KC818701		KC818852							KC818779	KC818928				KC818987	JQ957409
Gekkonidae	Hemidactylus	saba	YES	KF647567									KF647573	KF647587				KF647594	KF647605
Gekkonidae	Hemidactylus	shihraensis	YES	KC818710		KU955721							KC818783	KC818932				KC818990	KC819053
Gekkonidae	Hemidactylus	sinaitus	YES	KC818712		KC818866							JQ957164	KC818935				KC818993	JQ957446
Gekkonidae	Hemidactylus	ulii	YES	KC818725		KC818874							KC818787	KC818940				KC818999	KC819059
Gekkonidae	Hemidactylus	yerburii	YES	JQ957086		KC818897							JQ957166	JQ957307				KC819014	JQ957448
Gekkonidae	Pseudoceramodactylus	khobarensis	YES	KC190703	KC190897				MG990918		MG990811		KC191005			MG990881		MG990896	KC191123
Gekkonidae	Stenodactylus	affinis	YES	KC190675	KC190869								KC190946						KC191054
Gekkonidae	Stenodactylus	doriae	YES	KC190649	KC190843								KC190940						KC191046
Gekkonidae	Stenodactylus	grandiceps	YES	KC190667	KC190861								KC190951						KC191061
Gekkonidae	Stenodactylus	leptocosymbotes	YES	KC190657	KC190851								KC190942						KC191048
Gekkonidae	Stenodactylus	slevini	YES	KC190680	KC190874								KC190950						KC191057
Gekkonidae	Stenodactylus	yemenensis	YES	KC190640	KC190834								KC190991						KC191064
Gekkonidae	Trachydactylus	hajarensis	YES	KT302073					MG990922		KT302096		KT302105			KT302133		KT302135	KT302141
Gekkonidae	Trachydactylus	spatalurus	YES	KT302092							KT302098		KT302124			KT302131		KT302137	KT302143
Gekkonidae	Trigonodactylus	arabicus	YES	KC190692	KC190886								KC191001	KF898504					KC191113
Gekkonidae	Trigonodactylus	pulcher	YES	KC190701	KC190895				MG990920		MG990813		KC191003			MG990883		MG990898	KC191120
Gekkonidae	Trigonodactylus	sharqiyahensis	YES	KC190696	KC190890				MG990921		MG990814		KC190998	KF898479		MG990884		MG990899	KC191116
Gekkonidae	Tropiocolotes	confusus	YES	MG990746	MG990790	MG990829			MG990926		MG990817		MG990768	MG990855		MG990887		MG990903	MG990914
Gekkonidae	Tropiocolotes	nattereri	YES	KC190708	KC190901	MG990834			MG990927		MG990818			MG990861				MG990904	KC191128
Gekkonidae	Tropiocolotes	scortecii	YES	MG990763	MG990807	MG990843			MG990930		MG990820		MG990770	MG990874		MG990890		MG990907	MG990916
Gekkonidae	Tropiocolotes	wolfgangboehmei	YES		MW198208								MW204541	MW204555					
Chamaeleonidae	Chamaeleo	arabicus	YES	EF222194	EF222194	EF222194	EF222194	EF222194	EF222194	EF222194			HF570665				HF570854	HF570765	
Chamaeleonidae	Chamaeleo	calyptratus	YES	EF222192	EF222192	EF222192	EF222192	EF222192	EF222192	EF222192		GU457847	HF570667		GU456003		JN880819		
Chamaeleonidae	Chamaeleo	chamaeleon	YES	EF222199	EF222199	EF222199	EF222199	EF222199	EF222199	EF222199				KY762250				FJ984184	
Lacertidae	Acanthodactylus	arabicus	YES	KX296920		KX297031													
Lacertidae	Acanthodactylus	blanfordii	YES	KX296906	AF197482	KX297017					KX297380		KX297575	KX297305					
Lacertidae	Acanthodactylus	boskianus	YES	KX296880		KX296996					KX297373		KX297555	KX297275					
Lacertidae	Acanthodactylus	felicis	YES	KX296883		KX297011					KX297396		KX297573	KX297294					
Lacertidae	Acanthodactylus	gongrorhynchatus	YES	KX296909	AF080343	KX297125					KX297459		KX297586	KX297310					
Lacertidae	Acanthodactylus	grandis	YES	KX296918	JX847521	KX297022					KX297377		KX297582	KX297286					
Lacertidae	Acanthodactylus	haasi	YES	KX296904		KX297030					KX297405		KX297584	KX297283					
Lacertidae	Acanthodactylus	hardyi	YES	KX296901		KX297029					KX297541		KX297292	KX297581					
Lacertidae	Acanthodactylus	masirae	YES	KJ567753	AF197504	KJ567849					KJ547925		KJ548093	KJ548095					
Lacertidae	Acanthodactylus	opheodurus	YES	KX296891	KX528727	KX296997					KX297385		KX297558	KX297276					
Lacertidae	Acanthodactylus	orientalis	YES	KX296979		KX297183					KX297424		KX297606	KX297356					
Lacertidae	Acanthodactylus	robustus	YES		KX528787	KX528899													
Lacertidae	Acanthodactylus	schmidti	YES	KX296911		KX297020				KJ652832	KX297384		KX297583	KX297308					
Lacertidae	Acanthodactylus	tilburyi	YES	KX296890		KX297014					KX297544		KX297585	KX297303					
Lacertidae	Latastia	longicaudata	YES	JX962891	JX962911	JX962946							EF632272				JX963015	EF632229	JX963053
Lacertidae	Mesalina	adramitana	YES	MK533809	MK533881	MK551683					MK551564		MK551585	MK551606				MK551671	
Lacertidae	Mesalina	arnoldi	YES	MH039917	MH039965	MH040010								MH040053					
Lacertidae	Mesalina	austroarabica	YES	MK533831	MK533932	MK551730					MK551578		MK551601	MK551659					
Lacertidae	Mesalina	ayunensis	YES	MK533832	MK533899	MK551692							MK551591	MK551624				MK551677	
Lacertidae	Mesalina	bahaeldini	YES	MH039929	MH039984	MH040022								MH040065					
Lacertidae	Mesalina	bernoullii	YES	KY967189	KY967141	KY967172							KY967095	KY967114					
Lacertidae	Mesalina	brevirostris	YES	KY967187	KY967128	KY967153					MK551570		KY967087	KY967109				MK551679	
Lacertidae	Mesalina	martini	YES	MH039952	KM410953	KM411105								MH040084					
Lacertidae	Mesalina	saudiarabica	YES	KY967181	KY967121	KM411151							KY967086	KY967104					
Lacertidae	Mesalina	lineage 4	YES	MK533865	MK533928	MK551726					MK551574		MK551597	MK551655					
Lacertidae	Omanosaura	cyanura	YES	MG672311		MG672357				MG672404			MG672334	MG672382					
Lacertidae	Omanosaura	jayakari	YES	MG672308		MG672354				MG672402			MG672331	MG672379					
Lacertidae	Ophisops	elegans	YES	GQ142069	EU081719	EU081647	EU081564			KJ652838			EF632278				JX963016	EF632235	JX963054
Lacertidae	Ophisops	elbaensis	NO																
Lacertidae	Philochortus	neumanni	NO																
Lacertidae	Phoenicolacerta	kulzeri	YES	KR082565		KR082619							KR082731		KR082721				
Lamprophiidae	Atractaspis	andersonii	YES	MW198193	MW198202	MW204503				MW204514			MW204532						
Lamprophiidae	Atractaspis	engaddensis	YES		MK621476	MK621612				MK621555			MK621669					MK621519	
Lamprophiidae	Boaedon	fuliginosus	YES	AY122681	AY188079	KM519701	AY122663			KM519682		EU402646	KM519735		EU390926		JN880847	KM519720	EF144104
Lamprophiidae	Psammophis	schokari	YES			MG002980				MG003046			MG002915						MG003101
Lamprophiidae	Malpolon	moilensis	YES	AY643313	AY643355	AY643397				DQ486309			DQ486157						
Leptotyphlopidae	Myriopholis	blanfordi	YES	GQ469241	GQ469241	GQ469104					GQ469176		GQ469061						
Leptotyphlopidae	Myriopholis	burii	NO																
Leptotyphlopidae	Myriopholis	macrorhyncha	YES	GQ469245	GQ469245	GQ469115					GQ469187		GQ469072			GQ469026			
Leptotyphlopidae	Myriopholis	nursii	NO																
Phyllodactylidae	Asaccus	arnoldi	YES	MG019482		MG019710					KX550621		MG019554	MG019630					
Phyllodactylidae	Asaccus	caudivolvulus	YES	KX550493		KX550586					KX550673		KX550760	KX550846					
Phyllodactylidae	Asaccus	gallagheri	YES	MG019428		MG019683					MH752977		MG019564	MG019640					
Phyllodactylidae	Asaccus	gardneri	YES	KX550485		KX550578					KX550665		KX550752	KX550838					
Phyllodactylidae	Asaccus	margaritae	YES	KX550523		KX550616					KX550702		KX550789	KX550875					
Phyllodactylidae	Asaccus	montanus	YES	KX550530		KX550537					KX550625		KX550711	KX550798					
Phyllodactylidae	Asaccus	platyrhynchus	YES	KX550525		KX550533					KX550620		KX550706	KX550793					
Phyllodactylidae	Ptyodactylus	ananjevae	YES	KP858394		KP868017					KP868255		KP868144	KP868438					KP868335
Phyllodactylidae	Ptyodactylus	dhofarensis	YES	KP858444		KP868005					KP868271		KP868163	KP868423					KP868319

Family	Genus	Species	In tree	12S	16S	CYTB	COI	ND1	ND2	ND4	ACM4	BDNF	CMOS	MC1R	NT3	PDC	PRLR	RAG1	RAG2
Phyllodactylidae	*Ptyodactylus*	sp4	YES	KP858327		KP868012					KP868240		KP868129	KP868432					KP868328
Phyllodactylidae	*Ptyodactylus*	sp5	YES	KP858365		KP868015					KP868248		KP868138	KP868436					KP868333
Phyllodactylidae	*Ptyodactylus*	sp3	YES	KP858300		KP868036					KP868235		KP868124	KP868463					KP868360
Phyllodactylidae	*Ptyodactylus*	sp1	YES	KP858401		KP868030					KP868257		KP868146	KP868457					KP868354
Phyllodactylidae	*Ptyodactylus*	orlovi	YES	MF084420		MF084662					MF084541		MF084480	MF084715					MF084601
Phyllodactylidae	*Ptyodactylus*	ruusaljibalicus	YES	MF084456		MF084691					MF084578		MF084517	MF084751					MF084638
Scincidae	*Ablepharus*	pannonicus	YES		KX591474	KX591438		AY607280	AY607280			AF039466		KX591399					
Scincidae	*Eumeces*	schneideri	YES	JQ344280	JQ344269	JQ344289		JQ344312		JQ344301		JQ344214	JQ344225					JQ344255	
Scincidae	*Eurylepis*	taeniolata	YES	JQ344279	JQ344268	JQ344291		JQ344313		JQ344302		JQ344213	JQ344224					JQ344259	
Scincidae	*Heremites*	septemtaeniatus	YES	AY159062	KX364964							KX364972	KX364996	KX365022				KX365050	
Scincidae	*Chalcides*	levitoni	NO																
Scincidae	*Chalcides*	ocellatus	YES	JQ344273	JQ344262	JQ344283		JQ344306		JQ344295		JQ344207	JQ344218					JQ344257	
Scincidae	*Scincus*	hemprichii	YES	MW192581	MW192549	MW204302							MW204332	MW204366					
Scincidae	*Scincus*	mitranus	YES	MW192596	MW192564	MW204314							MW204347	MW204379					
Scincidae	*Scincus*	conirostris	YES	EU278016	EU278081	EU278248							MW204329	MW204364					
Scincidae	*Trachylepis*	brevicollis	YES	AY907712	AY907714	AY907716	MG700105												
Scincidae	*Trachylepis*	tessellata	YES	JQ598777	JQ598789														
Sphaerodactylidae	*Pristurus*	carteri	YES	KJ849846							KJ849923		KJ849978	MW204545				KJ850039	KJ850114
Sphaerodactylidae	*Pristurus*	celerrimus	YES	KJ849850							KJ849927		MW204535	MK751381				KJ850043	KJ850118
Sphaerodactylidae	*Pristurus*	collaris	YES	KJ849857							KJ849933		MW204536	MW204547				KJ850048	KJ850123
Sphaerodactylidae	*Pristurus*	crucifer	YES	KJ849859							KJ849935		KJ849886	MK729396				KJ850050	KJ850125
Sphaerodactylidae	*Pristurus*	gallagheri	YES	KJ849874							KJ849940		KU749866	MW204552				KJ850064	KJ850139
Sphaerodactylidae	*Pristurus*	sp1	YES	KJ849897							KJ849958		MW204537	MW204551				KJ850088	KJ850161
Sphaerodactylidae	*Pristurus*	minimus	YES	KJ849885							KJ849949		KJ850005	MK729412				KJ850075	KJ850148
Sphaerodactylidae	*Pristurus*	masirahensis	YES	KJ849881							KJ849945		KJ850001	MK729385				KJ850071	KJ850144
Sphaerodactylidae	*Pristurus*	ornithocephalus	YES	MW198197							MW204521			MW204546				MW204560	MW204565
Sphaerodactylidae	*Pristurus*	popovi	YES	KJ849888							MW204522		MW204538	MW204549				KJ850078	KJ850151
Sphaerodactylidae	*Pristurus*	rupestris	YES	KY023590							MW204523		KY023914	KY023999				KY024056	KY024126
Sphaerodactylidae	*Pristurus*	sp5	YES	KY023794							MW204527		KY023941	KY024026				KY024072	KY024142
Sphaerodactylidae	*Pristurus*	sp2	YES	KY023727							MW204524		MW204539	MW204553				MW204561	MW204566
Sphaerodactylidae	*Pristurus*	sp3	YES	KY023399							MW204525		MW204540	MW204554				MW204562	MW204567
Sphaerodactylidae	*Pristurus*	sp4	YES	KY023453							MW204526		KY023953	KY023979				KY024044	KY024117
Sphaerodactylidae	*Pristurus*	saada	NO																
Sphaerodactylidae	*Pristurus*	schneideri	NO																
Sphaerodactylidae	*Pristurus*	sp9	YES	MW198198							MW204528			MW204550				MW204563	MW204568
Sphaerodactylidae	*Pristurus*	flavipunctatus	YES	KJ849868							MW204520		KJ849992	MW204548				KJ850059	KJ850132
Sphaerodactylidae	*Teratoscincus*	keyserlingii	YES	AY753545	AY753545	AY753545	AY753545	AY753545	AY753545	AY753545	HQ426418		HQ426589						HQ426508
Trogonophidae	*Agamodon*	arabicus	NO																
Trogonophidae	*Diplometopon*	zarudnyi	YES	AY605474	AY605474	AY605474	AY605474	AY605474	AY605474	AY605474		JN654798	AF148709		JN568326		JN880828		MG661258
Varanidae	*Varanus*	griseus	YES	KU746369	KU746383			AF407503	AF407503									AY662608	
Varanidae	*Varanus*	yemenensis	YES					JN673354											JN673367
Viperidae	*Bitis*	arietans	YES	KX694571	MK387629	JX114014	EU852310		MK387428	JX114185					KX694996			JX073299	
Viperidae	*Cerastes*	cerastes	YES	KX694540	KX694629	AF471028	EU852311			EU852305		KX694706	KX694830		KX695003			HM623449	
Viperidae	*Cerastes*	gasperettii	YES	HQ658415		AJ275756	AJ275704												
Viperidae	*Echis*	borkini	YES	GQ359644	GQ359734	GQ359485				GQ359569									
Viperidae	*Echis*	carinatus	YES	EU852313	EU852319	GQ359433	EU852307			GQ359569								HM623447	
Viperidae	*Echis*	coloratus	YES	EU852315	HQ658452	EU852297	EU852309			EU852303								HM623444	
Viperidae	*Echis*	khosatzkii	YES	GQ359617	GQ359698	GQ359449				GQ359534									
Viperidae	*Echis*	omanensis	YES	GQ359631	GQ359723	GQ359466				GQ359550									
Viperidae	*Pseudocerastes*	fieldi	YES	EU624264	AJ275769	AJ275716													
Viperidae	*Pseudocerastes*	persicus	YES		AJ275770	AJ275717													

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Appendix I.

List of museum catalogues, online sources, and published literature that were used to glean distribution records of Arabian squamates.

Museum catalogues and citizen science websites.

Acronym	Collection/ Website
CAS	California Academy of Sciences, San Francisco, USA
GBIF	Global Biodiversity Information Facility (https://www.gbif.org/)
IBES	Institute of Evolutionary Biology Collection, Barcelona, Spain
iNaturalist	https://www.inaturalist.org/
LACM	Natural History Museum of Los Angeles County, Los Angeles, USA
LSUMZ	Louisiana Museum of Natural History, Baton Rouge, Louisiana, USA
MCCI	Museo Civico di Storia Naturale, Carmagnola, Italy
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
MVZ	University of California, Museum of Vertebrate Zoology, Berkeley, USA
MZUT	Museo di Zoologia, University of Turin, Torino, Italy
Naturgucker	https://www.naturgucker.de/
NHMUK	Natural History Museum, London, UK
NMP	National Museum Prague, Czech Republic
RBINS	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
SMF	Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt, Germany
TAU	Tel Aviv University, National Museum of Natural History, Tel Aviv, Israel
USNM	National Museum of Natural History, Smithsonian Institution, Department of Vertebrate Zoology, Washington D.C., USA
ZFMK	Zoologisches Forschung Institut und Museum Alexander Koenig Bonn, Germany
ZMA	Zoological Museum Amsterdam, Amsterdam, the Netherlands
ZMB	Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität, Berlin, Germany

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