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Analysis of geographical distribution of the parthenogenetic rock lizard *Darevskia armeniaca* and its parental species (*D. mixta, D. valentini*) based on ecological modelling

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Abstract. Studies of geographical distribution of parthenogenetic *Darevskia armeniaca* and its parental species *D. mixta* and *D. valentini* can extend our knowledge in terms of their biology and prediction of expansion of their ranges owing to increasing anthropogenic impact and global climate change. We studied the rock lizards of the genus *Darevskia* because their ecology, biology and potential ranges have not been well studied. Our objectives were: (1) to create maps of the potential geographical distribution of the lizard species; (2) to identify bioclimatic, topographic and landscape variables that determine their potential ranges; (3) to establish similarities and differences in ecological conditions of lizard localities between the parthenogenetic lizard and its parental species. We extended the available published data set with our own field survey records to assess effects of environmental factors on ecological niches of the lizards and their distribution in Transcaucasia and Asia Minor using methods of ordination and species distribution models (SDMs). Our results show that the main drivers regulating the distribution of *Darevskia* spp. are climatic, topographic and land cover/use. High SDM performance estimated as a Boyce index ~0.917 proved that we had incorporated the most important predictor variables for describing ecological niches of the lizard species. We used an ordination method to compare niches in terms of their overlap, similarity, and niche shifts of the parthenogenetic species relative to its parental species. Habitat preference of *D. mixta* was determined by altitude, vegetation type, high precipitation during the warmest season, low humidity variation, and low insolation. Habitats of *D. valentini* were predicted to be located at the highest altitude in the zone of subalpine meadows, low temperature during the dry months, low precipitation during the warm months, an average coefficient of seasonal variation in humidity, high insolation, and a short distance to roads. We suggest that the centroid of the niche of the "daughter" species, *D. armeniaca,* occupies an intermediate position along environmental gradients relative to that of its parental species with only one exclusion. The coefficient of humidity variation in *D. armeniaca* differed from that of its parental species. In general, we predicted that ecological niches of parthenogenetic and parental species overlapped by 36%, however, the ecological niche of *D. armeniaca* was similar to that of its "paternal" species *D. valentini*. We demonstrate that the parthenogenetic *D. armeniaca* prefers mountain forest, meadow, steppe and human-disturbed habitats, while the "maternal" species *D. mixta* inhabits mainly forest habitats and the "paternal" species *D. valentini* commonly occurs in mountain meadow and mountain steppe habitats in the subalpine zone. These results can be used by environment conservation organizations to preserve the most important habitats of these lizards.

Key words. Squamata, Lacertidae, reticulate evolution, unisexual species, bisexual species, sympatry, modelling.

Introduction

The geographical distribution of the parthenogenetic lacertid *Darevskia armeniaca* (Méhely, 1909) and its parental species *D. mixta* (Méhely, 1909) and *D. valentini* (Boettger, 1892) can elucidate biological and ecological features of these rock lizards. Ranges of lizards are determined by abiotic constituents, such as climate, sunlight, topography and biotic factors, e.g., predators, parasites and competitors, and natural barriers (Gaston 2003). However, the borders of lizard ranges can shift owing to increasing anthropogenic impact caused by the intensified construction of roads, power lines, residential structures in mountainous areas, deforestation, and due to global climate change effects. Since thermoregulation in reptiles depends mainly on thermal determinants in their environment, rock lizards can serve as a sensitive model for studying climate change effects (Shine et al. 2002). In addition, a database of lizard locality records can be a basis for ecological modelling and forecasting potential changes of liz-

ard distribution in response to anthropogenic and climatic changes. Available publications on the rock lizards of the genus *Darevskia* have commonly described their distribution ranges within administrative units, i.e., countries, provinces, districts. These data are carried over from one publication to the next usually without critical verification. At present, the necessity of verifying geographical distributions of lizards arises, requiring re-examination of species records, if they are to provide a basis for studying reticulate evolution and hybrid speciation (Borkin & Darevsky 1980, Vasiliev 1985, Moritz 1991).

Over the past 50 years, unisexual-bisexual complexes of lizard species from different families have been analysed by cytogenetic, molecular-genetic (allozyme, mitochondrial DNA, microsatellite DNA) methods (Darevsky 1966, Uzzell & Darevsky 1975, Kupriyanova 1989, 1997, 1999, Moritz et al. 1992, Darevsky & Kupriyanova 1993, MacCulloch et al. 1995, Murphy et al. 1996, 2000, Kearney et al. 2006, Manríquez-Moran et al. 2014, Freitas et al. 2016). All their results supported a concept of hybridogenetic speciation in vertebrates leading to the appearance of new unisexual hybrid species (carrying parts of genomes inherited from two closely related parent species).

Numerous studies (Kupriyanova 1992, 1997, 1999, 2010, Kupriyanova & Odierna 2002) have revealed that hybridisation is important for evolution due to the instability of the hybrid genome, its rapid changes, and the emergence of unique gene combinations and new alleles that are absent in the parental species. Detailed descriptions of hybridogenetic speciation concepts are given elsewhere (Kupriyanova 2014, Tarkhnishvili et al. 2017). In general, morphological, ecological, cytological and genetic studies have demonstrated that the parthenogenetic species *D. armeniaca* originated from natural hybridisation between the closely related bisexual species *D. mixta* ("maternal" species) and *D. valentini* ("paternal" species) (Darevsky 1967, Darevsky & Danielyan 1968, Uzzell & Darevsky 1975, Moritz et al.1992, MacCulloch et al. 1995, Murphy et al.1996, Fu et al. 2000, Tokarskaya et al. 2001, Martirosyan et al. 2003, Malysheva et al. 2007a, b, Girnyk et al. 2017).

Despite some revelations from studying the mechanisms of unisexual reproduction, the origin and evolution of parthenogenesis in reptiles, clonal diversity, and hypervariable sequences of genomes in the cases of numerous parthenogenetic (*D. armeniaca, D. bendimahiensis, D. dahli, D. rostombekowi, D. sapphirina, D. unisexualis, D. uzzelli*) and its parental (*D. mixta, D. portschinskii, D. raddei, D. valentini*) species, there is no clear evidence of the boundaries of their ranges and species-specific parameters of environmental factors that determine the particular locations of their distribution ranges.

Unfortunately, the species' main habitat requirements are still obscure. In case of the genus *Darevskia,* published data on average annual air temperatures, altitude distributions, and total annual precipitation are scattered over different publications that necessitate their systematisation. Data on other key environment parameters (e.g., daily insolation, wind speed), which characterize the thermal habitat conditions for the lizards, are absent. Still, these factors have significant effects on the activity of the animals and the thermal regimes at places available for oviposition as well as the timing of the start and the duration of the reproductive season (De-Witt 1962, Shine et al. 2002).

Powerful tools for detecting potential ranges in unisexual and bisexual lizards are Species Distribution Models (SDM) based on species' ecological niches. There are several examples of the successful application of SDMs for biogeographic analysis and the detection of potential habitats of rock lizards of the genus *Darevskia* (Tarkhnishvili et al. 2010, 2013, Doronin 2015, Freitas et al. 2016, Ćorović et al. 2018). However, these studies used mainly bioclimatic predictors based on maximum entropy (MaxEnt) (Phillips et al. 2006) whereas topographic and landscape variables were rarely used.

In our study, we used original, published and museum data accumulated over the past 50 years in Armenia, Georgia, Azerbaijan, Nagorno-Karabakh and Turkey. We also applied a high spatial resolution to encompass as much as possible of the variety of lizard habitats with regard to vegetation type, presence or absence of roads and railways, human settlements, rivers, reservoirs and lakes. Modelling with low spatial resolution may result in false predictions of lizard distributions and misapplication of the environmental variables that determine the boundaries of species distribution. We applied maximum-entropy distribution modelling to predict the potential geographic ranges of the parthenogenetic *D. armeniaca* and its parental species (*D. valentini, D. mixta*) and the ordination method to compare ecological niches in terms of their overlap, similarity and niche shift between the "daughter" species and its parental species. We hypothesize that SDMs are able to predict the potential distribution ranges of these species using locality records and a set of climatic, topographic and landscape layers with a resolution of 90 m.

Our objectives were: (1) to devise maps of the geographical distributions of the three lizard species; (2) to identify bioclimatic, topographic and landscape variables that determine their potential ranges; and (3) to establish similarities and differences in the ecological conditions of localities between the parthenogenetic rock lizard and its parental species.

Materials and methods

Field survey and species identification

The datasets of coordinates of *D. armeniaca* and *D. valentini* were collected from extensive surveys across the both species ranges during the period 1967–2018. These datasets were used as original field records. We especially focused on the zones of sympatry of the studied species. In particular, 105 locations of rock lizards were recorded including information on rock sizes, vegetation type, and landscape conditions during the 2018 survey. Lizards were identified in the field based on the extensive experience of our Ar-

menian colleagues and identification guides (Darevsky 1967, Arakelyan et al. 2011) (Fig. 1). Geographical coordinates and altitude of each site were determined using Magellan SporTrak, Garmin Decota 10, Garmin GPSMap 64, and Garmin Montana 680t GPS receivers (Garmin Corp., Olathe, KS, USA) during the various surveys, each with an accuracy of ± 3.65 m.

For accurate species identification, we took photographs of each lizard's anterolateral face, the temporal areas of the head, and the anal region with a Nikon Coolpix B500 digital camera (Nikon Corporation, Tokyo, Japan) (Fig. 1). All these photographs are now kept in the research collection of the Institute of Ecology and Evolution, Russian Academy of Sciences (IEERAS). Sexing of the lizards was performed by visual inspection, distinguishing males from females by the former's enlarged femoral pores, larger heads, brighter colours, and their deep blue markings along the sides of the belly. When in doubt, we carefully checked for the presence of hemipenes without causing any harm. We set the lizards free immediately after having examined them thus. Our 2018 field survey was conducted under permit from the Ministry of Nature Protection of the Republic of Armenia on the basis of Decree (Code 5/22.1/51043) for scientific studies including the capture and/or collection of wild animals.

Vector layers of the species record sites

In addition to original field records collected since 1967, we used museum and published data for creating a valid vector database (VDB) of the species occurrence data in ArcGIS Desktop 10.4.1 (ESRI 2017). In particular, we used museum specimens and record data from the Zoological Museum of the M.V. Lomonosov Moscow State University (ZMMU), Museum of the Zoological Institute, Russian Academy of Sciences (ZISP), and the Canadian Royal Ontario Museum (ROM). ROM data are published in the Global Biodiversity Database (GBIF: *D. armeniaca,* GBIF Species occurrence data doi:10.15468/dl.pzhflc; *D. mixta,* GBIF doi:10.15468/dl.ml4da9; *D. valentini,* GBIF doi:10.15468/dl.howz70). In addition, we analysed and digitised the data gathered from publications from the period 1967–2017. In general, our VBD incorporated three types of locality records. The first type provided geocoordinates (Fu et al. 1999, 2002, Tarkhnishvili et al. 2010, 2013, Gabelaia et al. 2015, Tuniyev et al. 2017). The second type contained maps of locations without geocoordinates (Darevsky 1967, Uzzell & Darevsky 1975). For this type of data, the study area was delimited by geographic coordinates based on georegistration data and matching these maps to the basic vector maps of Armenia, Georgia, Azerbaijan, Rus-

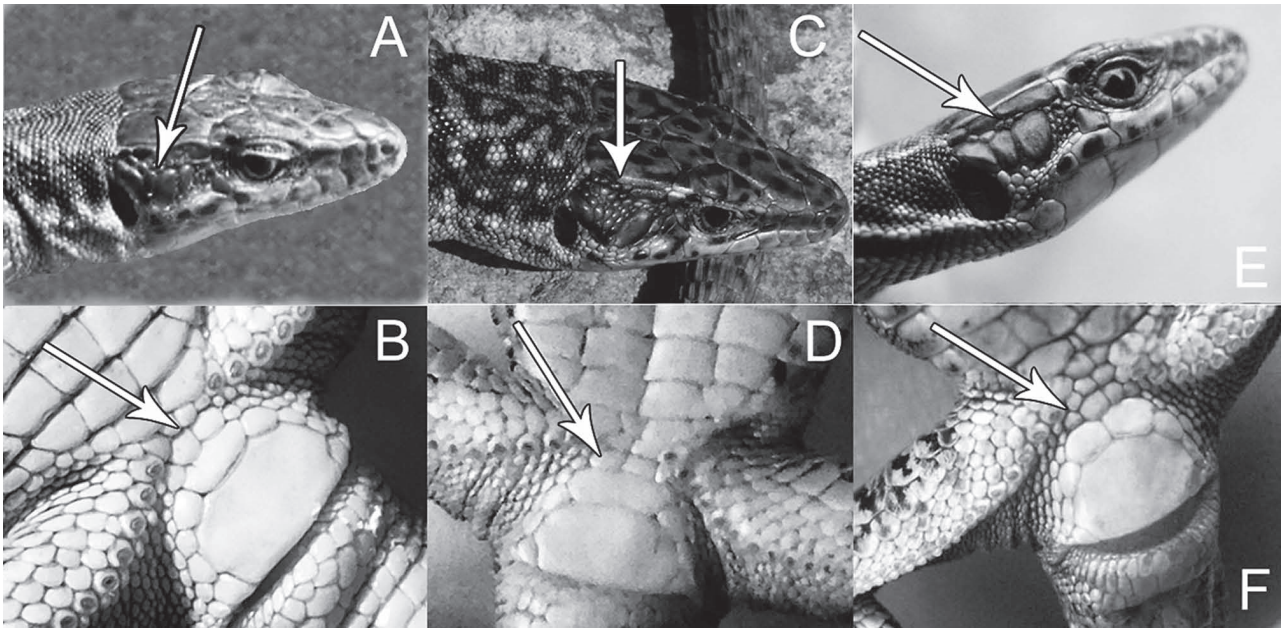

Figure 1. Characters distinguishing *D. armeniaca* (left, from Armenia, photos by F. Osipov), from the bisexual species *D. valentini* (centre, male, from Armenia, photos by M. Arakelyan) and *D. mixta* (right, from Georgia, Tarkhnishvili et al. 2010). A) Two scales of similar size lie between the central temporal and tympanic shields, or the central temporal shield touches the tympanic scale (indicated by arrows). B) In front of the large anal scute, there are one or two enlarged preanal scales of different size than the other preanals (indicated by arrows). C) A group of small scales lies between the central temporal and tympanic shields (indicated by arrows). D) Single (sometimes double) enlarged preanal scale (indicated by arrows). E) There is one large wedge-shaped shield between the central temporal and tympanic shields, often larger than the tympanic shield; if there are two such shields, one of them will be considerably larger than the other. F) There are two slightly enlarged preanal shields in front of the large anal scute, or all preanal shields are small and similar in size.

Table 1. General characteristics of the species' locality records.

Sources	Species	Number of records	Species identification	References
Published data	*D. mixta*	68	Analysis of mt-DNA, morphological features	Tarkhnishvili et al. 2010, 2017, Tuniyev 2014,Gabelaia et al. 2015, Tuniyev et al. 2017
ROM & published data	*D. valentini*	64	Analysis of biochemical markers, morphological features	Darevsky 1967, 1968, Uzzell & Darevsky 1975
Original data	D. valentini	54	Chromosomal analysis, DNA fingerprinting (minisatellite markers), morphological features	Danielyan et al. 2008a, 2008b, Arakelyan et al. 2011
ROM & published data	*D. armeniaca*	29	Analysis of allozyme loci, analysis of mt-DNA, morphological features	MacCulloch et al. 1995, Murphy et al. 1996, Fu et al. 1999, 2000
ZISP & published data	*D. armeniaca*	60	Morphological characteristics, analysis of allozyme loci	Darevsky 1966, 1967, Darevsky & Danielyan 1968, Uzzell & Darevsky 1975
Original data	*D. armeniaca*	127	Multilocus DNA fingerprinting (mini- and microsatellite markers), morphological features	Tokarskaya et al. 2001, Martirosyan et al. 2003, Petrosyan et al. 2003, Malysheva et al. 2007, Arakelyan et al. 2011

Table 2. Average Nearest Neighbour index of species occurrence data. n* is the number of sampling sites, the *Z* score is the statistic value showing the validity of the null hypothesis of a random distribution of points.

Species	Data set	n*	Real means (m)	Expected mean distance (m)	ANNI	Z-score	P-value	Type of distribution
D. armeniaca	All (Fig. 2A)	216	4,259	8,593	0.496	-14.2	<<0.0	Clustered
D. armeniaca	Reduced (Fig. 2B)	99	11,860	1,2693	0.934	-1.25	0.212	Random
D. mixta	All (Fig. 2C)	67	6,691	10,614	0.63	-5.83	<<0.0	Clustered
D. mixta	Reduced (Fig. 2D)	41	12,039	13,669	0.88	-1.46	0.144	Random
D. valentini	All (Fig. 2E)	123	6,764	15,546	0.44	-1.74	<<0.0	Clustered
D. valentini	Reduced (Fig. 2F)	48	17,353	19,707	0.88	-1.58	0.11	Random

sia (obtained from (http://beryllium.gis-lab.info/project/osmshp/) and Turkey (as per "LargeScale 1:10 m" from http://www.naturalearthdata.com; last accessed 21 May 2018) with at least 20 reference points in ArcGIS. For the third type of data, we selected only those species records that enabled us to identify accurate geographical coordinates using Google Earth.

Locality records of 2,148 individuals were analysed to choose only those for which a data set existed from the last 50 years (1967–2017). Three lizard species were identified amongst the ZISP and ROM specimens. General information on lizard locality records from museum, published and original field data is presented in Table 1.

Verification of spatial autocorrelation of species occurrence data

To verify spatial autocorrelation, we used a two-step procedure. First, the points of species occurrences located at distances of less than 1 km from each other were removed using the subsample algorithm available in the spThin package (Aiello-Lammens et al. 2015). Then the dataset was tested by cluster analysis using the Average Nearest Neighbor index (ANNI; spatial statistics toolkit in ArcGIS; Environmental Systems Research Institute, Inc. 2006) (Ebdon 1985). ANNI assesses the degree of data clustering by measuring as a ratio the average distance from each point to its nearest neighbour, divided by the expected average distance for a random distribution. If ANNI = 1, the distribution is random; if ANNI > 1, the distribution is dispersed; if ANNI < 1, the distribution is clustered. Since the original data sets and intermediate subsamples after application of the spThin tool showed clustering, we excluded clustered points from the spThin data set using an interactive process until the distribution became similar to random, i.e., ANNI became close to 1. As a result of our applying such a procedure we obtained reduced data sets for *D. armeniaca, D. mixta,* and *D. valentini*, having excluded autocorrelated points (Table 2, Fig. 2).

Raster layers of environmental predictor variables

We analysed all the available publications to detect the variables controlling the distribution of the studied species (Darevsky 1967, Uzzell & Darevsky 1975, Kaliontzopoulou et al. 2008, Tarkhnishvili et al. 2010, 2013, Do-

RONIN 2015, FREITAS et al. 2016). Selected environmental variables thus included climate, topography and land cover/land use. Spatial climatic variables were taken from the WorldClim 2.0 data set (http://worldclim.org/version2, downloaded 4 April 2018) with a resolution of 30 arc sec. WorldClim data suggested 19 bioclimatic variables manifest in annual trends in seasonality by range of temperature and precipitation variations. In addition to these 19 variables, we also used variables of insolation and wind speed. These were interpolated using meteorological records and then averaged over the period 1970–2000 (HIJMANS et al. 2005).

The raster layers of the relief were created using the digital elevation models from the Shuttle Radar Topography Mission (SRTM), having a resolution of 90 m/pixel (3 arc sec) (https://www2.jpl.nasa.gov/srtm/, downloaded 30 November 2017). Ecological requirements of the lizards were

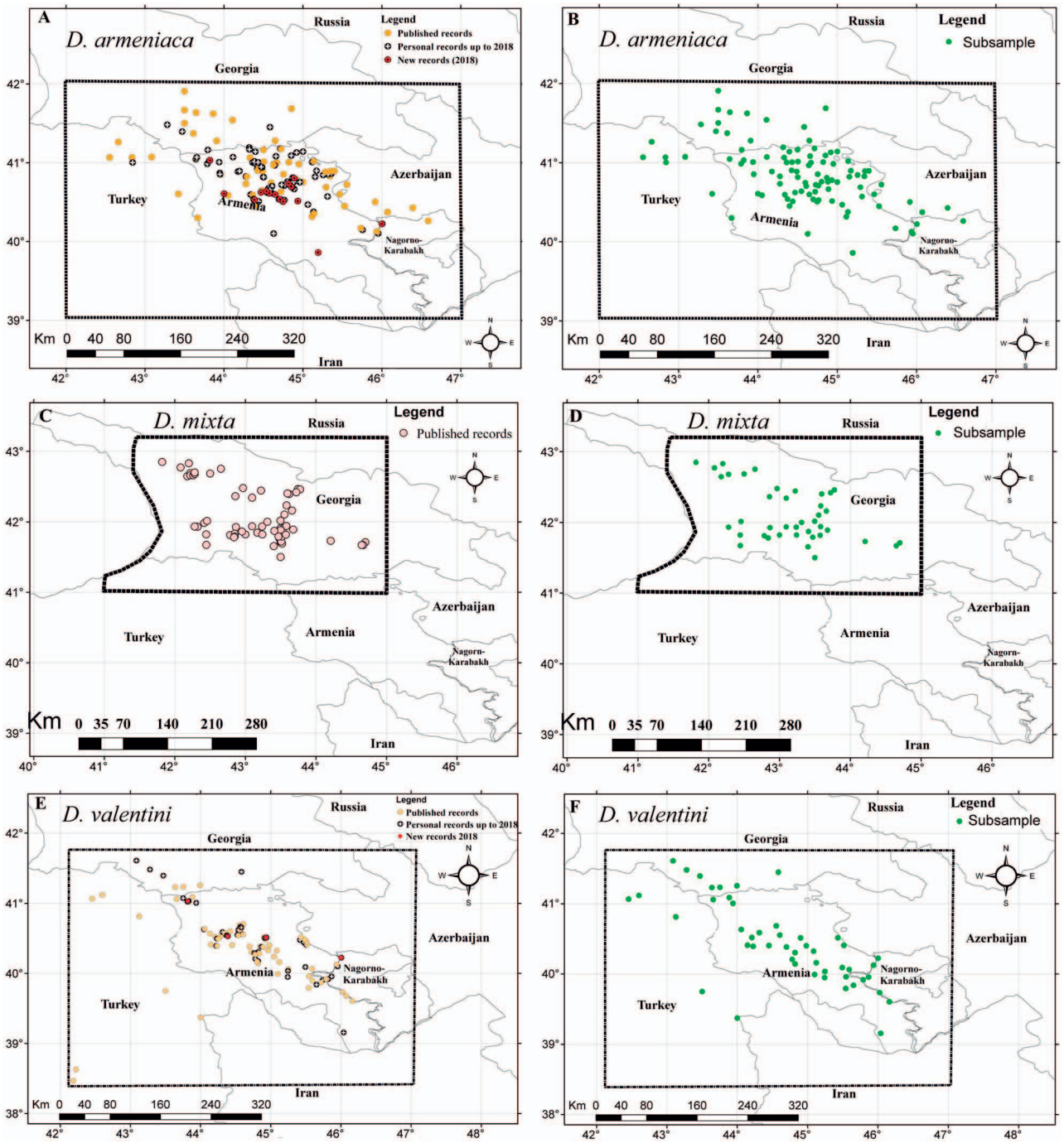

Figure 2. Locations of the study areas based on the available data sets. A, C, E are initial clustered data sets; B, D, F are reduced non–autocorrelated data sets. Dotted areas represent masks used to fit the potential distribution models of *Darevskia* spp.

estimated from raster layers of altitudes above sea level, inclination angles, and exposure aspects of the recorded sites using ArcGIS.

Data on land use, roads and railways, human settlements, rivers, types of vegetation in Armenia, Georgia and Azerbaijan were collected from Open Street Map (http://beryllium.gis-lab.info/project/osmshp/, accessed 17 July 2017; http://ace.aua.am/gis-and-remote-sensing/vector-data/, last accessed 30 November 2017) while data for Turkey were taken from the data set "LargeScale 1:10 m".

Since the raster layers of the relief (3 arc sec) and climatic parameters (30 arc sec) had different resolutions, we used the ArcGIS cubic approximation function to convert the raster data from 30 to 3 arc seconds so that all raster layers had a resolution of 3 arc seconds (Table 3).

SDM building

For predictions of the distributions of *D. armeniaca, D. mixta*, and *D. valentini*, SDMs were constructed using the maximum-entropy method MaxEnt 3.4.1 (Phillips et al. 2006) included in the EcoSpat package for R (Di Cola et al. 2017, R Development Core Team 2017). We chose MaxEnt as the most appropriate modelling approach, because it can be applied in cases of small sample sizes (Elith et al. 2006, Hernandez et al. 2006, Phillips 2008, Kaliontzopoulou et al. 2008, VanDerWal et al. 2009). Moreover, MaxEnt can be used for continuous and categorical predictor variables, which is especially important in cases of small datasets of species records (Pearson et al. 2007). In contrast to ordination methods (Broennimann et al. 2012), the algorithms incorporated in MaxEnt enabled us to select and rank variables depending on their importance for detecting species ranges. Therefore, SDMs that were constructed with MaxEnt could be used to select variables that have great impacts on species distribution. Noteworthy here is that MaxEnt has previously been successfully used for predicting the distribution of other lizard species based on limited and fragmentary distribution data (Kaliontzopoulou et al. 2008, De Pous et al. 2011, Ahmadzadeh et al. 2013).

SDMs were created through 10 MaxEnt runs with a random selection of test and training samples. In all these runs, 80% of the occurrence records were used as training and 20% served as test samples. We calculated the Boyce index (B_{ind}) to assess model performance (Boyce et al. 2002, Hirzel et al. 2006) using the EcoSpat package (Di Cola et al. 2017). Contrary to the AUC index, which is frequently incorporated in various versions of MaxEnt (cf. Lobo et al. 2008), the B_{ind} index measures how much the predictive models differ from random distribution only from species occurrence data. This index varies from -1 to 1. Positive values indicate that the predictive model is consistent with the occurrence data, values close to zero mean that the model does not differ from random distribution, and negative values provide evidence of counter predictions, i.e., predict poor-quality areas where presences are more frequent (Hirzel et al. 2006). We calculated the Boyce index for each of the 10 model replicates for each species, and the averaged its estimates.

Table 3. Habitat variables considered in the lizard distribution models.

Nr	Environmental variables	Code
1	Annual mean temperature (°C)	C_AMT
2	Mean diurnal range (°C)	C_MDR
3	Isothermality (BIO2/BIO7 (x100)), %	C_ISOT
4	Temperature seasonality (standard deviation *100) (%)	C_TSeason
5	Max. temperature in warmest month (°C)	C_MaxTWM
6	Min. temperature in coldest month (°C)	C_MinTCM
7	Annual temperature range (BIO5-BIO6) (°C)	C_TAnR
8	Mean temperature in wettest quarter (°C)	C_MTWetQ
9	Mean temperature in driest quarter (°C)	C_MeanTempDrQ
10	Mean temperature in warmest quarter (°C)	C_MTWarQ
11	Mean temperature in coldest quarter (°C)	C_MTColdQ
12	Annual precipitation (mm)	C_AnP
13	Precipitation in wettest month (mm)	C_PWetM
14	Precipitation in driest month (mm)	C_PDrM
15	Precipitation seasonality (coefficient of variation) (%)	C_PrecipCoefVar
16	Precipitation in wettest quarter (mm)	C_PWetQ
17	Precipitation in driest quarter (mm)	C_PDrQ
18	Precipitation in warmest quarter (mm)	C_PrecWarmQ
19	Precipitation in coldest quarter (mm)	C_PColdQ
20	Solar irradiation (kJ m^{-2} day^{-1})	C_SRad
21	Wind speed (m s^{-1})	C_WindS
22	Altitude (m)	T_EL
23	Exposure aspect (°)	T_EXP
24	Inclination angles (°)	T_INCL
25	Distance to settlements in rural area (m)	L-DSR
26	Distance to water polygons (lakes, reserves) (m)	L_DWP
27	Distance to settlements in urban area (m)	L_DSU
28	Distance to road (m)	L_DHW
29	Distance to river, stream (m)	L_DRS
30	Distance to railway (m)	L_DRW
31	Vegetation type	L_VEG

The importance of each predictor variable on species distribution was assessed by analysis of the MaxEnt variable contribution table using the jackknife method (incorporated in the MaxEnt 3.4.1 software). Variables that had a

great impact on the model, i.e., that produced high values of permutation importance and/or high values of percentile contribution, were considered important (Phillips et al. 2006). To obtain an adequate variable contribution table, we additionally tested the multicollinearity of predictor variables with the Pearson correlation coefficient (R). In SDMs, we used only those variables for which the correlation coefficient was < 0.8. For the finally chosen sets of variables, see Results.

Niche overlap and statistical tests of niche similarity

The ecological niches between closely related species ("daughter" and its parental species) were compared on the basis of the theoretical concept of a realized niche being represented in a grid, depicted by the first two components of the principal component analysis (PCA), which were calibrated using the environmental conditions of the whole study areas (Broennimann et al. 2012). In this environmental space, the numbers of species-presence points were converted into species-occurrence densities with the kernel function to smoothen the distribution of densities (Di Cola et al. 2017). The entire environment, i.e., all available sites within the study area, was graded and converted into densities using the kernel function of the EcoSpat package for R (Di Cola et al. 2017) as well. In this manner, all available environmental conditions can be taken into account by correlating species densities with environmental densities (Petitpierre et al. 2012, Di Cola et al. 2017).

We assessed the extent of niche overlaps between the parental and "daughter" species using Schoener's D index (Warren et al. 2008, Broennimann et al. 2012). This index is measured in the environmental space and depicted by the two axes of the main components, assessing the extent of niche overlap in a range from 0 (no overlap) to 1 (complete overlap). The niche similarity test illustrates whether a niche occupied by a species in one area is more similar to a niche in another area than to a random distribution.

For background points, we used 10,000 randomly sampled spatial points within the study areas. These points were generated using an option to this effect in the MaxEnt 3.4.1 software (Phillips et al. 2006). The most important predictor variables for the PCA were found at the stage of building species distribution models using MaxEnt. We applied the niche similarity test using Schoener's D in the EcoSpat package (Di Cola et al. 2017).

Unoccupied niches and potential expansion

If ranges of "maternal" and "daughter" species overlaped in multidimensional environmental space, we distinguished between three categories of overlapping: (1) stable areas where species occur in both ranges, (2) unoccupied areas that are present only in the range of the parental species, and (3) new areas that are present only in the range of the "daughter" species. We measured three indices to quantify these categories of overlapping using the EcoSpat package (Di Cola et al. 2017). The index of stability is the proportion of the range of the "daughter" species that overlaps with that of a parental species. The index of unoccupied niches is the proportion of the range of a parental species that is absent in that of the "daughter" species. The index of expansion is the proportion of the range of the "daughter" species located in an environment that is different from those of a parental species. Since these indices are estimated in the space of the most important variables controlling species distribution, the expansion index can be considered a measure of niche shifts caused, for example, by the origin of a new hybrid "daughter" species and/or as a result of biotic interactions with the parental species. It must be noted though that the restricted distribution of the parental species can also exert a certain impact.

Statistical test of the significance of shifts in niche centroids along environmental gradients

We estimated shifts of the centre positions (centroids) of species niches along the environmental gradients with the EcoSpat package of Di Cola et al. (2017) based on data obtained using smoothing functions of species densities. The significance of these shifts was assessed with the help of the General Linear Model (GLM) procedure. Centroids were compared on the basis of species occurrence data using one-way analysis of variance (ANOVA) with equal and unequal numbers of replications in the cells. In all cases, we used type I of ANOVA models. Centroids, i.e., means of the most important parameters of the environment, were assigned to three levels (species). If the ANOVA revealed a significant difference between species, a post-hoc Tukey multiple comparison HSD test was used to identify which species differed from each other. If the sample sizes were unequal, i.e., in the case of an unbalanced model of the 1st type, we used a Tukey-Kramer test for a multiple comparison. For a multiple comparison with unequal variances based on the Levene criterion, the Tukey-Kramer test was applied with the Welch modification (Zar 2010). Prior to the analysis, all data were $\log_{10}$-transformed to achieve normal residues and equality of dispersions.

A multiple comparison of proportions of the key vegetation types used by species was performed using the chi-square and the post-hoc tests according to the Tukey procedure (Zar 2010). Graphic representations of centroid shifts in ecological niches along gradients were obtained with the EcoSpat package (Di Cola et al. 2017). Significance of shifts was tested using the Biosystem office package (Petrosyan 2014).

Results

We had available 402 lizard records with geographic coordinates in Armenia, Georgia, Azerbaijan and Turkey. 221

Table 4. Table of contribution of the most important variables obtained by MaxEnt models. Significant contributions of variables are highlighted in bold.

	D. armeniaca		*D. valentini*		*D. mixta*	
Environmental variables	Percent of contribution	Permutation importance	Percent of contribution	Permutation importance	Percent of contribution	Permutation importance
C_MeanTempDrQ	**30.4**	**20.3**	**32.9**	**36.6**	0.4	1.3
C_PrecipCoefVar	**6.3**	**11.4**	2.4	**10.3**	**38**	**40.2**
C_PrecWarmQ	**13.2**	**18.8**	1.1	**5.3**	**33.3**	**20**
C_SRad	**29.6**	**41.6**	**25.3**	**34.5**	**9.2**	**21.6**
T_EL	2.3	3.8	0.9	1.1	**11**	**15.9**
L_DHW	**17.6**	3.8	**21.8**	**11.1**	0.6	0.7
L_VEG	0.6	0.3	**7.5**	0.3	**14.4**	**1.2**

records were taken from published data and 181 were collected during our field surveys. While many of our species records merely confirmed previous ones during our field survey of 2018, we decided to also record the conditions of anthropogenic areas inhabited by *D. armeniaca* and *D. valentini* along roads, human settlements, on cemeteries, church walls, stone bridges, and update data on the species' occurrence in Armenia published without geocoordinates.

After applying the spThin subsampling procedure and the sequential removal of cluster points, we were left with 99, 48 and 41 locality records for *D. armeniaca, D. valentini* and *D. mixta*, respectively (Table 2, Fig. 2), for SDM building and comparisons of their ecological niches.

Model performance and predictor variables

We obtained reliable Boyce index values (B_{ind} ± SD) for all the SDMs (*D. armeniaca*, B_{ind} = 0.926 (± 0.019), *D. valentini,* B_{ind} = 0.917 (± 0.022), *D. mixta*, B_{ind} = 0.908 (± 0.041); Supplementary Table S1). Table 4 shows the contribution table of variables obtained using MaxEnt SDM for the studied species. Variable contributions for 10 different MaxEnt SDMs obtained for test (20%) and training (80%) species occurrence points are presented in Supplementary Table S2.

The most important variables responsible for the suitability of habitats for *D. armeniaca* were the mean air temperature in the dry season quarter (C_MeanTempDrQ-Bio9), the seasonal coefficient of humidity variation (C_PrecipCoefVar-Bio15), precipitation in the warm season quarter (C_PWarmQ-Bio18), and insolation (C_SRad). In addition to these variables, distances from roads were responsible for more than 0.5 suitability of the habitat (L_DHW) (Table 4, Supplementary Table S2).

For the bisexual "paternal" species *D. valentini*, a set of the most important variables included air temperature in the dry season quarter (C_MeanTempDrQ-Bio9), seasonal coefficient of humidity variation (C_PrecipCoefVar-Bio15), precipitation in the warm season quarter (C_PWarmQ-Bio18), insolation (C_SRad), distance from roads (L_DHW), and vegetation type (L_VEG) (Table 4, Supplementary Table S2).

For the "maternal" species *D. mixta*, the most important variables in habitat preference were seasonal coefficient of humidity variation (C_PrecipCoefVar-Bio15), precipitation in the warm season quarter (C_PWarmQ-Bio18), insolation (C_SRad), altitude above sea level (T_EL), and vegetation type (L_VEG) (Tables 4 and S2). The remaining variables accounted for less than 5% in our SDMs, yet their contributions were also estimated.

Supplementary Figs S1–S3 illustrate the relationships between the most important environmental predictors and the probabilities of species' occurrence. For all rock lizard species, the curves of dependencies of climatic and topographic variables on the probabilities of habitat preferences were bell-shaped with P-values > 0.5.

Potential range of the studied species

The map of preferred habitats of *D. armeniaca* (Fig. 3A) shows that its range covers northwestern Armenia, western Azerbaijan, and southern Georgia. In addition, there are some suitable habitats in northeastern Turkey. Records of *D. valentini* give evidence that its range consists of three extensive, isolated areas, comprising the highland meadow and steppe zones of Armenia, Nagorno-Karabakh, southern Georgia, and eastern Turkey (Fig. 3B). The range of *D. mixta* is located in the south-to-north gorges from the Lesser to the Greater Caucasus (Fig. 3C).

Niche overlaps and tests of niche similarity

Our ordination methods provided estimates of ecological niche overlaps between the parthenogenetic species and its parental species. The first axis correlated with precipitation in the warm season quarter while the second axis was related to altitude above sea level. Supplementary Fig. S4 shows the correlation parameters between the predictor variables and the first two principle components, which had been calibrated along the environmental gradients for the parental and "daughter" species, respectively. The first and second components accounted for 84.18% of the total variation.

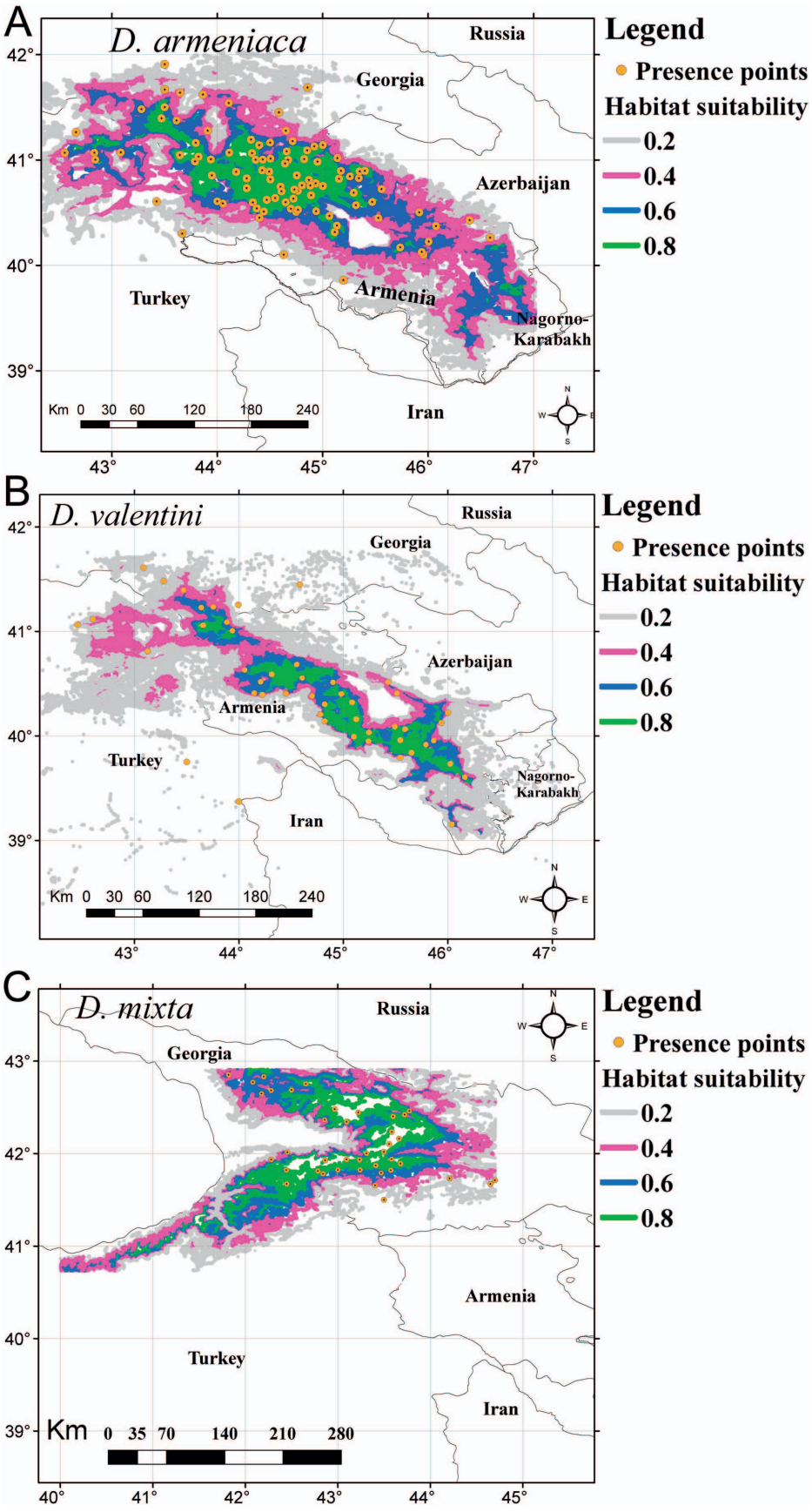

Figure 3. Maps of habitats suitable for the lizards studied.

We did not include the other axes in the analysis because they explained the minor proportion of the total variation. Figure 4 illustrates the niche overlaps between *D. armeniaca* and its "maternal" species *D. mixta* and between *D. armeniaca* and its "paternal" species *D. valentini*. The niche centroid of *D. armeniaca* is shifted upwards, however, in that precipitation in the warm quarter is located lower relative to the corresponding centroids of *D. mixta*. Centroids of *D. valentini* and *D. armeniaca* are located inversely to each other as compared to the positions of centroids of *D. armeniaca* and its "maternal" species. Quantitative assessments of niche overlapping based on Schoener's D index are presented in Table 5.

According to Table 5, *D. armeniaca* exploits about 36% of the habitats also occupied by *D. mixta*, while 64% of its habitats are located outside the realized ecological niche of the "maternal" species. There is a significant difference between the realized ecological niches of *D. armeniaca* and *D. mixta* (test of niche similarities P = 0.42). However, *D. armeniaca* exploits 80% of the habitats of the "paternal" species *D. valentini* and 20% of *D. armeniaca* habitats are located outside the realized ecological niche of its "paternal" species. The test of similarities between the ecological niches of *D. armeniaca* and *D. valentini* shows them to be insignificantly different (P = 0.03).

Table 5. Niche overlap using Schoener's D indices between "daughter" (*D. armeniaca*) and parental (*D. mixta, D. valentini*) ranges. Where E is expansion, S – stability, U – unoccupied, and p-values of niche similarity are given for each comparison.

Parental species	Schoener's D	P-value	E	S	U
D. mixta	0.08	0.42	0.64	0.36	0.82
D. valentini	0.41	**0.03**	0.20	0.80	0.15

Shifts of the realized ecological niche centroids along environmental gradients

Niche centroid shifts in *D. armeniaca* along the environmental gradients relative to centroids of the parental species was measured based on one-dimensional graphs. In these graphs, the X-axis represents the predictor variable plotted against the density of a species' occurrence (terms adopted from Di Cola et al. 2017) in the multidimensional space of the environment (Supplementary Figs S5, S6). The niche centroid of *D. armeniaca* appears shifted in terms of both individual variables and the entire set of predictor variables relative to those of its parental species. The centroid of *D. armeniaca* in terms of altitude is shifted upwards relative to that of *D. mixta* and downward relative to that of *D. valen-*

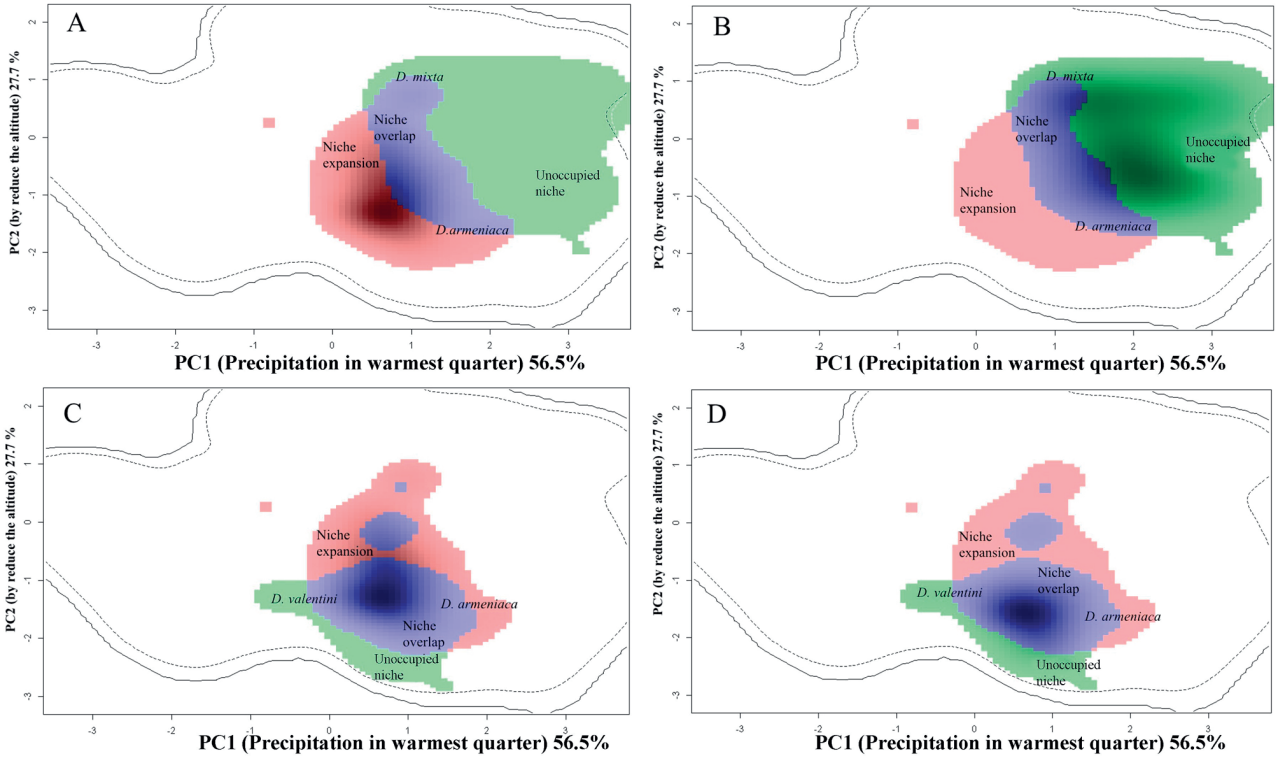

Figure 4. Niche overlaps of *D. armeniaca, D. mixta* and *D. valentini* in the multidimensional space of climatic, topographic and land cover/use variables assessed using PCA. A) and B) show the niche overlap between *D. armeniaca* and *D. mixta* along the first two axes of the PCA; C) and D) show the niche overlap between *D. armeniaca* and *D. valentini*. Colored areas indicate densities of *D. armeniaca* (A, C), *D. mixta* (B), and *D. valentini* (D), respectively. The solid and dashed lines designate, respectively, 100% and 90% of the available (background) environment.

tini (Supplementary Figs S5E, S6E). The centroid of *D. armeniaca* in terms of minimum temperature in the dry season quarter is lower than that of *D. mixta* and higher than that of *D. valentini* (Supplementary Figs S5A, S6A). With regard to the coefficient of humidity variation, the centroid of *D. armeniaca* is located higher than that of *D. mixta*, but it is shifted both upwards and downwards compared with *D. valentini* (Supplementary Figs S5B, S6B). The position of the centroid of *D. armeniaca* in terms of humidity in the warmest season quarter indicated that *D. armeniaca* preferred drier habitats compared to *D. mixta* and more humid habitats compared to *D. valentini* (Supplementary Figs S5C, S6C). The centroid within the gradient of insolation shows that *D. armeniaca* prefers an intermediate position between the corresponding centroids of *D. mixta* and *D. valentini* (Supplementary Figs S5D, S6D). It is noteworthy that while the insolation curves are monomodal throughout the ecological space in *D. mixta* and *D. valentini*, this curve is polymodal in *D. armeniaca* (Supplementary Figs S5D, S6D). The centroid of distance from roads in *D. armeniaca* occupies an intermediate position between the corresponding parameters in the parental species (Fig. 5F). *D. mixta* habitats are farther from roads than those of the parental species (Supplementary Figs S5E, S6E). In general, *D. armeniaca* dwells in diverse habitats including forest vegetation (1), mountain meadows (2), mountain steppe (3), semi-desert (6), and urban areas (10) (Supplementary Fig. S5G) whereas *D. mixta* prefers the forest zone (Supplementary Fig. S6G) and *D. valentini* mainly occurs in habitats 1, 2, 3 (Supplementary Fig. S5G). From amongst these habitats, mountain meadows (vegetation type 2) are most preferred by *D. valentini*.

Statistical tests of the shifts in niche centroids

For the final verification of the statistical significance of niche shifts, we conducted an additional analysis for each variable separately (ANOVA, GLM model). Figure 5 dem-

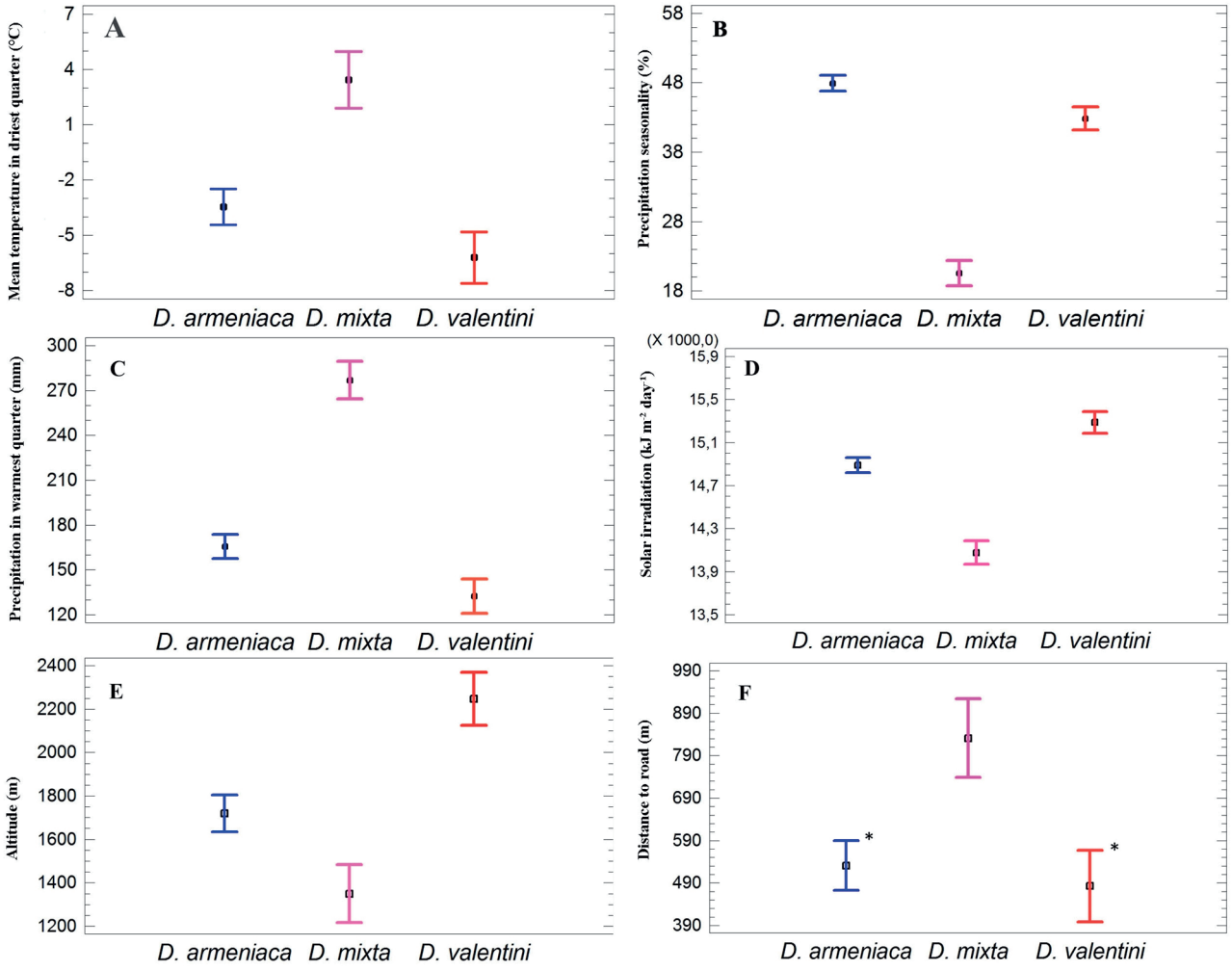

Figure 5. The positions of the centroids of the ecological niches of the lizard species along the environmental gradients with 95% confidence intervals of Tukey HSD. GLM ANOVA tested the main effects on the species. A) $F = 31.9$; $P < 0.01$; B) $F = 226.8$; $P < 0.01$; C) $F = 111.3$, $P < 0.01$; D) $F = 96.8$; $P < 0.01$; E) $F = 35.83$, $P < 0.01$; F) $F = 13.03$; $P < 0.01$ (F is Fisher's test; P value is given for the factor effects). Absence of significant differences between the means is marked with *.

onstrates that the niche centroid of *D. mixta* in terms of habitat altitude corresponds to the temperate forest zone (1,350 ± 80 m). Its centroids with regard to the other variables tend to conform to high temperatures in the dry season quarter (3.4 ± 0.9°C), a low coefficient of variation of humidity (20.5 ± 1.1%), heavy precipitation in the warm season quarter (276 ± 7.5 mm), low daily amounts of solar irradiation (14,076 ± 65 kJ m^{-2} day^{-1}), and large distances from roads (831 ± 55.5 m).

The niche centroid of the "paternal" species *D. valentini* in terms of altitude has a high position in the landscape (2,247 ± 73 m). The niche centroids with regard to the other variables comply with low temperatures in the dry season quarter (-6.2 ± 0.84°C), low amounts of precipitation in the warm season quarter (132.4 ± 6.9 mm), high coefficient of humidity variation (42.8 ± 1.0%), high daily amount of solar irradiation (15,286 ± 59.6 kJ m^{-2} day^{-1}), and an intermediate distance from roads (483 ± 50.6 m) (Fig. 5).

The niche centroids of *D. armeniaca* for our six environmental variables are located between the corresponding centroids of its two parental species. Only one predictor variable does not differ from that of its "paternal" species *D. valentini* (Fig. 5). Intermediate positions of the niche centroids of *D. armeniaca* relative to those of its parental species are found in altitude (1,719 ± 51 m), temperature in the dry season quarter of (-3.5 ± 0.6°C), precipitation in the warm season quarter of (166 ± 5 mm), daily amount of solar irradiation (14,889 ± 42 kJ m^{-2} day^{-1}), and distance from roads of (531 ± 35 m). The realized niche of *D. armeniaca* shows that, contrary to its parental species, it inhabits biotopes characterized by high coefficients of humidity variation (48 ± 1%).

With regard to preferred vegetation types (qualitative predictor), *D. armeniaca* also takes an intermediate position. Figure 6 demonstrates that *D. armeniaca* exploits mountain forests less efficiently than its "maternal" species *D. mixta*, but more efficiently than its "paternal" species *D. valentini*. To the contrary, *D. armeniaca* exploits mountain meadows and steppes less efficiently than *D. valentini*, but more efficiently than *D. mixta*.

To conclude, *D. armeniaca* inhabits a great variety of biotopes: mountain forests (51%), subalpine meadows (27%), steppes (18%), semi-deserts (2%), and urbanized situations (2%) (Supplementary Figs S5G, S6G), i.e., the preferred habitats of this species are located in mountain forests and mountain steppes.

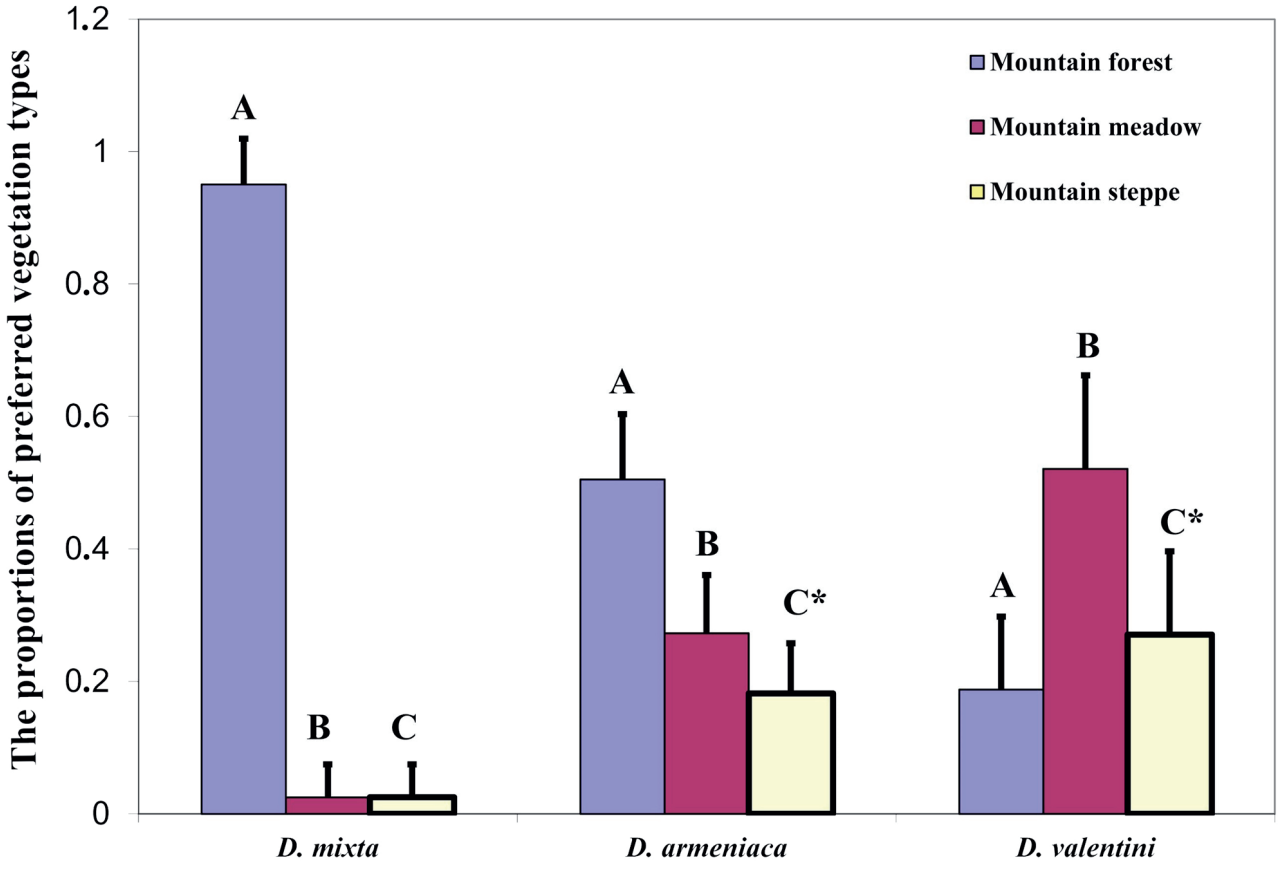

Figure 6. The proportions of preferred vegetation types with 95% Wald's confidence intervals. A multiple comparison of proportions for each type was performed using chi-square (A: 50.97, DF = 2, P << 0.001; B: 26.53, DF = 2, P << 0.001; C: 9.47, DF = 2, P = 0.009) and Tukey's Post Hoc tests. Absence of significant differences between the means is marked with *.

Discussion

Species distribution modelling is an important tool for the assessments of lizard habitat requirements and the selection of the most important variables that determine their spatial distribution. Moreover, we can compare ecological niches of "daughter" and parental species with the help of an ordination method to measure their overlap, similarity and dissimilarity. These two methods permit to estimate the extent of niche partitioning between competing and/or coexisting species and predict areas of their occurrence. Based on our results, we can suggest a set of environmental drivers that control the distribution of rock lizards in Asia Minor and Transcaucasia and assess ecological niche partitioning in lizard species in the multidimensional space of predictor variables.

Predicted distribution range

The available data on the distribution of the three lizard species studied here in Transcaucasia and Asia Minor are still very limited, especially, with regard to *D. mixta* in northeastern Georgia and northeastern Turkey (Fig. 3C). Although Gabelaia et al. (2015) indicated that the occurrence of *D. mixta* in northeastern Turkey was not supported by field studies, our assessments provide evidence that this region harbours environments that would be quite suitable for *D. mixta*. The results of five field studies on the fauna of northeastern Turkey in 1995, 1996, 2007, 2011 and 2012 validated our prediction that *D. mixta* would occur in this region (Tuniyev et al. 2014). Unfortunately, these surveys only confirmed the occurrence of this species without specifying the exact sites of the records. Our assessments of its range also agrees with the data of Tuniyev et al. (2017) who found *D. mixta* in the Republic of South Ossetia far away (40–60 km) from the nearest known habitats in the Borjomi Gorge (Lesser Caucasus) and on the tributaries of the Rioni River (Greater Caucasus) in Georgia. Data on the *D. mixta* records in South Ossetia are very important for clarifying the boundaries of this species' range. The predicted occurrence and records from central Georgia show that there is a high correlation between past and recently published data on the distribution of *D. mixta* (Tarkhnishvili et al. 2010, 2013, 2017, Gabelaia et al. 2015). The estimated range of this species and its records indicate that *D. mixta* lives in the mountain forest zone south-to-north between the Lesser and Greater Caucasus, i.e., that this species inhabits three large regions: (1) the central part of the Meskheti Range; (2) the Borjomi Gorge; and (3) the Greater Caucasus Mountains.

Records and the predicted range of *D. armeniaca* indicate that this species is widely distributed in the Transcaucasian region in northwestern Armenia, western Azerbaijan, southern Georgia, and the northeastern part of Turkey (Fig. 3A). Most of the habitats where *D. armeniaca* was previously found (Darevsky 1967, Uzzell & Darevsky 1975) were predicted by SDMs. The model also predicted a wider distribution range for *D. armeniaca*, i.e. beyond already-known areas due to its expanding its range. SDMs provided evidence of suitable habitats on the southern border of Georgia, the southwestern part of Nagorno-Karabakh, and on the northeastern border of Turkey (in the valleys of Trabzon, Ardahan and Kars). These areas should be checked for previously unknown populations to verify the predictive power of the model.

Species records and SDM showed that the range of *D. valentini* is divided into several, quite expansive, yet isolated areas, including mountain meadows and mountain steppes in Armenia, Nagorno-Karabakh, southern Georgia, and eastern Turkey (Fig. 3B). The most expansive areas of its occurrence are located in the mountain zone of the Gegham Range stretching to Lake Sevan, the mountain region of Mount Aragats, northwestern Armenia, and adjacent areas of southern Georgia. The northern distributional border of *D. valentini* from west to east lies approximately at the latitude of Akhalkalaki in Georgia (from where field records exist). Unfortunately, the western border limits of the range in Turkey is not exactly known, however, the model predicted that this species is widely distributed in northeastern Asia Minor, which is in accordance with Darevsky (1967). The model predicted a wider range for *D. valentini*, i.e., beyond the already-known habitats in the territory of Nagorno-Karabakh. Therefore, the regions of northeastern Turkey and southern Nagorno-Karabakh should be explored to verify the predictive power of the model and specify the boundaries of this species' range.

Ecological predictors of SDM

Our MaxEnt approach showed that there are three variables common to all SDMs, namely, coefficient of humidity variation (C_PrecipCoefVar-Bio15), total precipitation in the warm season quarter (C_PWarmQ-Bio18) and insolation (C_SRad) (Table 3). The vegetation type variable (L_VEG) appeared to be important only for *D. mixta* and *D. valentini*. MaxEnt and EcoSpat estimates indicate a high occurrence probability of *D. mixta* and high population density of in forest zones (Supplementary Figs S3E, S5G). These estimates are consistent with a number of published data (Darevsky 1967, Uzzell & Darevsky 1975, Tarkhnishvili et. al 2010).

D valentini usually dwells in mountain meadows and mountain steppes, preferring the subalpine zone (Supplementary Fig. S6G). It is found more frequently in mountain meadows and mountain steppes than *D. armeniaca* (Fig. 6). Estimates of the proportion of preferred vegetation types are in accordance with data published elsewhere (Darevsky 1967, Uzzell & Darevsky 1975, Arakelyan et al. 2011) and they are supported by our field survey (Petrosyan et al. 2019).

The altitude above sea level variable (T_EL) was important for *D. mixta* (Table 4), demonstrating its preference of the mountain forests of the Transcaucasus, which are characterized by a quite humid climate and low insolation

(Fig. 5). This is consistent with data published elsewhere (Darevsky 1967, Uzzell & Darevsky 1975, Tarkhnishvili et al. 2010).

In the case of *D. valentini,* besides three common variables, the contributions to SDM of temperature in the dry season quarter (C_MeanTempDrQ-Bio9) and distance from roads (L_DHW) were also high (Table 4). Distance from roads contributed 21.8% to SDM. The records that were used for this species in SDM were from on rocks, large stones, and clay cliffs in mountain gorges, and our models showed that favourable conditions for this lizard were located about 483 m on average away from roads (Fig. 5). This finding is in accordance with the results of our 2018 field survey that was discussed elsewhere (Darevsky 1967, Arakelyan et al. 2011, Petrosyan et al. 2019). These variables could help detect the most suitable environmental conditions for *D. valentini* based on our MaxEnt approach amongst which, there are high solar irradiation, a moderate coefficient of humidity variation, and intermediate humidity in the warm season quarter in the subalpine zone (Fig. 5).

MaxEnt selected the variables responsible for *D. armeniaca* niche occupation, which included the three abovementioned common variables, temperature in the dry season quarter (C_MeanTempDrQ-Bio9), and distance from roads (L_DHW), i.e., the same variables that were important for *D. valentini* (Table 4). With regard to *D. armeniaca,* the contribution of distance from roads was 17.6%, i.e., intermediate relative to the parental species (Fig. 5). Favourable habitats for this species are on average located 531 m from roads. Due to the ecological plasticity of *D. armeniaca,* this species can occur in all habitats where its parental species dwell. In addition, this species can be found in human-disturbed places (on stone bridges, church walls, tombstones on cemeteries, fences in settlements, and roadsides with stone mounds in the mountains) (Supplementary Figs S5G, S6G) (Petrosyan et al. 2019). Therefore, the parthenogenetic species can occupy human-disturbed habitats, enlarging its potential range (Supplementary Figs S5F, S6G). This result is well supported by the theory of "geographical parthenogenesis" (Vandel 1928) and the "weed hypothesis" (Wright & Lowe 1968). The coefficient of humidity variation (C_PrecipCoefVar-Bio15) appeared to be the highest compared to those in the two parental species. Hence, *D. armeniaca* can inhabit both wet and dry regions whereas *D. mixta* occurs only in wet habitats and *D. valentini* is found only in dry places (Table 4, Fig. 5). This result is consistent with published data illustrating that *D. armeniaca* can live in drier habitats than both its parental species.

In contrast to its paternal species, the type of vegetation is not important for the occurrence of the parthenogenetic species *D. armeniaca*, because this variable contributed only 0.6% to the SDM (Table 4). This means that *D. armeniaca* does not pose great demands on the vegetation type. The ecological plasticity of this species was demonstrated through the introduction of *D. armeniaca* to Ukraine from Armenia by I. S. Darevsky and N. N. Shcherbak in 1963 (Darevsky & Shcherbak 1967, Darevsky et al. 1998). The initial population of *D. armeniaca* was represented by 126 mature females from the Semyonovsky Mountain Pass near the city of Stepanovan in northern Armenia. These lizards were released in the canyon of the Teterev River, 22 km upstream from Zhitomir city. Despite the significant differences in climate (temperature, humidity) and topography (altitude above sea level), the introduction was successful. The range of the Ukrainian population had increased approximately 10-fold by 1998 although a great part of the initial population had perished during the first severe winter in 1963–1964 (Darevsky et al. 1998, Dotsenko et al. 2007). *D. armeniaca* formed a new isolated population about 8.5 km away from the site of its original release along the left bank of the Teterev River (Nekrasova & Koistiushyn 2016). However, it is still unclear whether the introduction of this species here was intentional or accidental. The introduction of *D. mixta* to this region in 1968, in contrast, was unsuccessful. We believe that this lizard could not form a sustainable population because the initial recruitment size was insufficient, consisting only of 11 males. If this introduction had been successful, we could have expected the appearance of triploid lizards as a result of crossing *D. armeniaca* × *D. mixta*. However, later studies on the allelic and genotypic diversity of Ukrainian and Armenian populations of the parthenogenetic lizard *D. armeniaca* confirmed its successful adaptation and revealed that two new genotypes had appeared in the Ukrainian population (Omelchenko et al. 2016).

The ecological niches of predictor variables in multidimensional space

Identifying the ecological niches of the rock lizards investigated here provide robust information on overlaps and similarities as well as on niche shifts of the parthenogenetic lizard relative to its parental species (Fig. 4, Supplementary Figs S5, S6, Table 5). Our results prove that niche overlaps can be accurately assessed if we select a set of the most important variables for SDM (Fig. 4, Table 5). Therefore, an SDM approach and the method of ordination enable us to select the most important variables and assess their contribution to species' ecological niches.

The statistically insignificant similarity (P = 0.42) of the niches of *D. armeniaca* and *D. mixta* and a low overlap index (0.08) between the niches of these species indicate an allopatric distribution of *D. mixta* and considerable geographical separation of the range of the "daughter" species from that of the maternal species (Figs 3A, C, 4A, B, Table 5). Indeed, *D. armeniaca* has expanded its range by 64% relative to that of *D. mixta*. Therefore, an existence of sympatric zones of these species is unlikely. Although one sympatric area was recorded from near Bakuriani city, no other field studies have supported this (Uzzel & Darevsky 1975).

The high overlap index (0.41) between the niches of the "daughter" species *D. armeniaca* and the "paternal"

D. valentini and their significant similarity (P = 0.03) suggest the existence of a large number of sympatric zones (Figs 4C, D, Table 5). The range of *D. armeniaca* was expanded beyond the "paternal" range only by 20%. Although the centroid of *D. armeniaca* is shifted downward along the altitude variable compared to that of *D. valentini* (Fig. 5E, Supplementary Fig. S5E), we identified six zones of sympatry of these species during our field survey in 2018 (Petrosyan et al. 2019). Centroids of niches of *D. valentini* and *D. armeniaca* along the altitude variable did not significantly differ from the mean altitude of the sympatric zones (1,935 ± 144 m) (t = 2.25, P = 0.07 and t = -1.58, P = 0.16, respectively). These zones are usually located close to the lower boundaries of the *D. valentini* range and the upper boundaries of the *D. armeniaca* range. These results are consistent with the field data of Danielyan et al. (2008b), illustrating that sympatry zones of these lizards are located in the mountainous regions of Central Armenia at an altitude of 1,800–2,000 m above sea level.

Our study suggests that climatic, topographic and landscape variables are the main drivers of lizard distributions. They determine overlaps of ecological niches and/or their similarities. The rock size and soil types can be referred to as minor factors in comparison with climatic factors (Tarkhnishvili et al. 2010). This finding is in accordance with studies that noted differences in climatic tolerance constraints between bisexual and parthenogenetic lizards (Kearney & Shine 2004). The abiotic requirements of *D. armeniaca* are intermediate between those of its two parental species, which is a result of its hybrid origin (Fig. 5). This finding is consistent with data on other parthenogenetic species (Moore et al. 1970, Tarkhnishvili et al. 2010).

In conclusion, we have enhanced our knowledge on the distribution of the parthenogenetic and its parental species in the Transcaucasus and Asia Minor. We assessed niche overlaps and/or their similarities, measured ecologically significant niche shifts of the parthenogenetic species relative the niches of the parental species along environmental gradients. The high indices of the model performance for all studied species (*D. armeniaca* - B_{ind} = 0.926; *D. valentini* - B_{ind} = 0.917, *D. mixta* : B_{ind} = 0.908) based on 10 runs of the model reassured us that we had involved all the most significant environmental factors that determined their ecological niches. We found that the parthenogenetic species *D. armeniaca* is associated with forest, steppe and human-disturbed habitats, whereas one parental species, *D. mixta*, prefers forest habitats, and the other parental species, *D. valentini*, exploits mainly mountain meadow and steppe habitats in the subalpine zone. For each species, we selected the most significant predictors that constrain their spread beyond the zones of tolerance, namely, climatic, topographic and landscape variables. Since we used a moderate resolution of 90 m, we were able to assess the contribution of human-disturbed areas to the distribution patterns of *D. armeniaca* and *D. valentini*. These results can facilitate future surveys and can be used as a guideline for conservation organisations and decision-makers.

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Supplementary data

Supplementary Table S1. Boyce index assessment using the *EcoSpat* package for the ten *D. armeniaca, D. valentini*, and *D. mixta* MaxEnt models.

Supplementary Table S2. Variable percentile contribution table obtained from MaxEnt ecological niche models for the 10 different replications.

Supplementary Figure S1. Relationships between each of the most important environmental predictors (see Table 3) and the likelihood of *D. armeniaca* occurrence.

Supplementary Figure S2. Relationships between each of the most important environmental predictors (see Table 3) and the likelihood of *D. valentini* occurrence.

Supplementary Figure S3. Relationships between each of the most important environmental predictors (see Table 3) and the likelihood of *D. mixta* occurrence.

Supplementary Figure S4. Correlation between predictor variables and the first two components of the principal component analysis.

Supplementary Figure S5. Graphic representation of the shifts of the niche centroids of the "daughter" species *D. armeniaca* relative to the maternal species *D. mixta* along the most important environmental gradients.

Supplementary Figure S6. Graphic representation of the shifts of the niche centroids of the "daughter" species *D. armeniaca* relative to the "paternal" species *D. valentini* along the most important environmental gradients.