

A spider diversity model for the Caucasus Ecoregion

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Received: 27 June 2013 / Accepted: 16 June 2014
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Abstract Precise information on spatial patterns of species richness and endemic species distribution is important for effective species conservation. In the Caucasus Ecoregion such information is virtually non-existent for invertebrate taxa. Using occurrence data from a large database we calculated species distribution models with the GARP algorithm for 471 spider species to visualize the diversity distribution of spider species in this region. Overall species diversity was highest in mountain forests of the North Caucasus, east-central Georgia, the southern slopes of the eastern Great Caucasus and south-east Azerbaijan. A regression tree analysis Chi squared automatic interaction detector method revealed the mean temperature of the driest quarter and precipitation parameters to be the main environmental factors shaping these patterns. Diversity of endemic species was correlated with overall species diversity but hotspots of endemic species (10+ percent of all species) exists in high-mountain areas, suggesting post-glacial speciation events in the high mountains as the main sources of high endemism in Caucasus. Further information on the spatial distribution of species diversity of

invertebrate taxa in the Caucasus Ecoregion is needed to improve conservation efforts in this biodiversity hotspot.

Keywords Araneae · Biodiversity · Climatic variables · Spatial patterns · Altitudinal gradient · Caucasus Ecoregion · Global hotspots

Introduction

In order to halt ongoing biodiversity loss, conservation efforts are often focussed using cross-country conservation plans and biodiversity action plans, which are based on existing threats to biodiversity in the region and precise information on the distribution of species (Ceballos and Brown 1995; García 2006; Newbold et al. 2009; Arponen 2012). Due to a lack of research on arthropod taxa, conservation plans do not normally include arthropod species to an extent reflecting their outstanding contribution to the overall species diversity. This in turn leads to conservation efforts, which do not effectively cover areas important for arthropod diversity (Hernández-Manrique et al. 2012) and therefore probably result in a dramatically increased diversity loss within this taxon, and hence overall species diversity. In order to actually halt current diversity loss, it is therefore necessary to study patterns of arthropod diversity more intensively and use the obtained insights in updated conservation plans and biodiversity action plans (Cardoso et al. 2008; Diniz-Filho et al. 2010; Beck et al. 2012; Hernández-Manrique et al. 2012).

Because of its importance as one of the worldwide Biodiversity Hotspots (Myers et al. 2000; Kier et al. 2005; Foster-Turley and Gokheshvili 2009; Zazanishvili and Mallon 2009), a number of conservation and action plans have been published within the Caucasus Ecoregion (henceforth termed

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CE) (MEPNR 2005; Williams et al. 2006; MEPNR 2011). Despite high total numbers of species and high rates of endemism among arthropods (Aliyev et al. 2009; Kalashian 2009; Konstantinov et al. 2009; Zazanishvili and Mallon 2009), including spiders (Ysnel et al. 2008), knowledge about spatial patterns of arthropod species diversity in the CE is virtually nonexistent. In order to give the arthropods their deserved weight for conservation efforts in this region, it is important to close this data gap by both intensified research as well as by making the existing data available in freely accessible databases. As Otto and Tramp (2012) showed for spiders in the CE, reviewing the existing literature for a given taxon and compiling these occurrence data into a database can dramatically increase the number of known occurrences and update the species lists for the relevant countries in this region (Mikhailov 2002; Marusik et al. 2006; Ysnel et al. 2008).

A large amount of occurrence data of sufficient quality is often insufficient on its own to derive the information needed for effective species conservation. In order to identify hotspots of arthropod diversity, endemic species or threatened species, the occurrence data must be translated into spatial models of distribution for every species, resulting in maps highlighting areas of high arthropod diversity. Macroecological methods like species distribution modeling (SDM) can bridge this gap between existing occurrence data and the final distribution maps (Araújo and Peterson 2012). In SDM, species occurrence data can be correlated with abiotic (scenopoetic), biotic and movement factors (biogeographic and migratory) in the region of interest, in order calculate a spatial model of the area of distribution with suitable conditions for this species (Sypard and Franklin 2009; Graham et al. 2010; Soberón 2010; Zimmermann et al. 2010; Vasconcelos et al. 2012).

Recent algorithms and statistical methods have helped to develop spatial models describing biodiversity including those developed for the prediction of species distributions (Stockwell and Peters 1999; Soberon and Peterson 2005; Fitzpatrick et al. 2007; Ortega-Huerta and Peterson 2008; de Souza Muñoz et al. 2011). In order to identify the spatial pattern of species richness, distribution models for single species are developed and then stacked (García 2006; Newbold et al. 2009; Chaladze 2012). An alternative method is recording species richness at individual localities and modeling richness patterns directly. Newbold et al. (2009) compared the two approaches while modeling the butterfly and mammal fauna of Egypt. They showed that using the former approach (summing individual models) produces more accurate output. Summing individual models is a good approach only when the available distribution data are sufficient to create individual species distribution models.

Species distribution modeling has rarely been applied in the CE to visualize the spatial distribution of an arthropod

taxon. However, a recent study modeled the distribution of ant species richness in Georgia (Chaladze 2012), facilitating new hypotheses on the location of arthropod diversity hotspots in this country. Next to intensified field work, it is important that more studies retrieve the richness of existing occurrence data and provide distribution maps of the diversity of additional arthropod taxa. Using such maps of different arthropod species to create spatial representations of the overall arthropod diversity should yield the information needed to give the highly diverse arthropods their deserved status in future conservation plans for the CE.

In the present paper we aim to contribute to this goal by providing spatial models of overall and endemic spider species diversity based on SDMs. We think that spiders are a good model taxon for this study because regional and continental spider diversity patterns can be explained to a large extent by environmental factors (Jiménez-Valverde and Lobo 2007; Finch et al. 2008; Jiménez-Valverde et al. 2010; Carvalho et al. 2012), commonly included in SDM approaches, e.g. climatic and topographic factors. Here we aim to answer the following questions:

- (1) What is the predicted spatial pattern of spider species richness in the CE?
- (2) Where are predicted hotspots of spider diversity located in the CE?
- (3) Where are predicted hotspots of endemic spider diversity located in the CE?
- (4) Where are regions predicted to show extraordinarily high proportions of endemic spider species in the CE?
- (5) What are the underlying factors shaping these patterns?

Materials and methods

Study area

The study area includes the political territories of Georgia, Armenia, Azerbaijan as well as the countries of the North Caucasus and the rayons Krasnodar and Stavropol in Southern Russia (Fig. 1). The CE is situated on the boundary of temperate and moist-temperate climate belts. Due to the dominance of its mountainous regions, the climatic conditions in the CE are very diverse, ranging from warm and moist regions with a precipitation of more than 2,000 mm per year near the Black Sea Coast to semi-arid regions in Azerbaijan, receiving only 250 mm annual precipitation (see details in Williams et al. (2006).

Together with this orographic and climatic complexity the CE is rich in landscape types of a number of terrestrial ecosystems: mountain forests, freshwater and marine

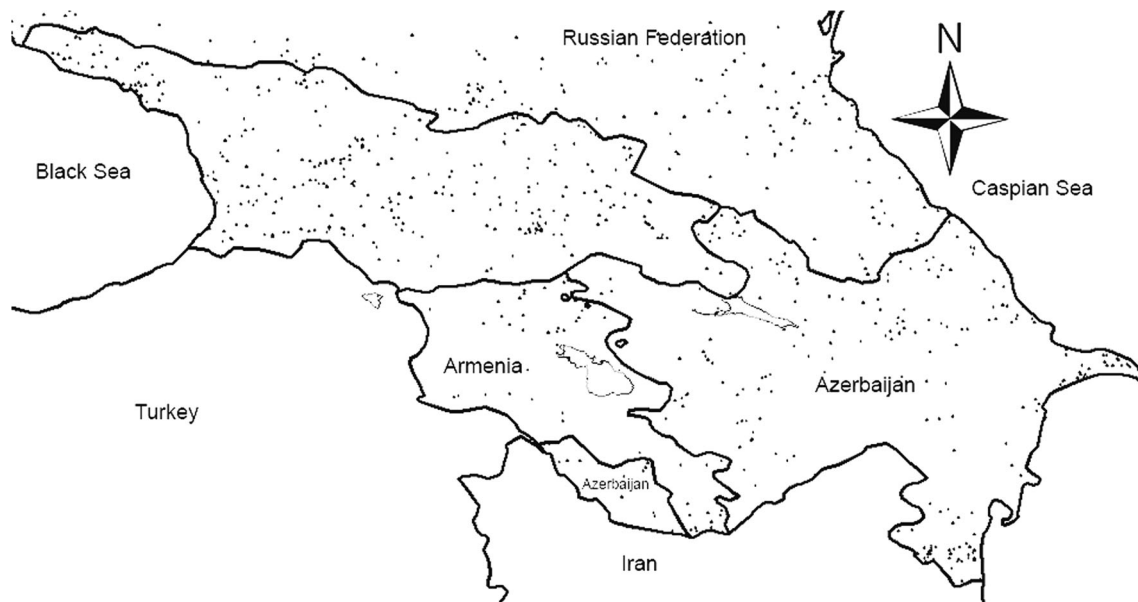


Fig. 1 Study area. *Spots* indicate unique localities with occurrence data

ecosystems, dry mountain shrublands, steppes, semideserts, wetlands and high-mountains, which contribute to the outstanding biodiversity of the CE (Myers et al. 2000; Williams et al. 2006; Foster-Turley and Gokhelashvili 2009; Zazanishvili and Mallon 2009).

Modeling

Species occurrence data was taken from the Caucasian Spiders Database (Otto and Tramp 2012), a collection of 11,418 occurrences of 1,078 spider species from 246 literature sources established since 2006. We excluded oversampled locations (Tbilisi and the Lagodekhi National Park) in order to reduce sampling bias (Hortal et al. 2008). The modeling of species distribution was performed using the software package OpenModeller (de Souza Muñoz et al. 2011). This software helps to model suitable distribution range for individual species and then overlays them in order to estimate a summed model of species richness. The GARP algorithm (Stockwell and Peters 1999; Stockwell 1999) was used to infer the spiders' diversity hotspots.

In total, 19 variables were taken from the WorldClim version 1.4 dataset at a resolution of 5 arcmin (c. 10 km) (Hijmans et al. 2005): (1) Annual mean temperature, (2) mean diurnal range, (3) isothermality, (4) temperature seasonality, (5) maximum temperature of warmest month, (6) minimum temperature of coldest month, (7) temperature annual range, (8) mean temperature of wettest quarter, (9) mean temperature of driest quarter, (10) mean temperature of warmest quarter, (11) mean temperature of coldest quarter, (12) annual precipitation, (13) precipitation of wettest month, (14) precipitation of driest month, (15)

precipitation seasonality, (16) precipitation of wettest quarter, (17) precipitation of driest quarter, (18) precipitation of warmest quarter, and (19) precipitation of coldest quarter.

Range models were developed for each species with at least five records (García 2006). In total, 566 species fit these criteria. Three-quarters of the occurrence locations were used for training the models and one quarter was used for validation. Occurrences were divided randomly as test and training points. The accuracy of each model was assessed using the area under the receiver operator (ROC) curve (AUC); the calculations were performed in OpenModeller with supply of test and training occurrences independently. Following the recommendations made by Swets (1986), species with AUC scores of <0.7 were excluded from further analysis.

Statistical analysis

10,000 random points were generated using Arcview 3.1, covering the whole study area. The following variables were scored for each random point: total inferred species richness, inferred endemic species richness, the 19 bioclimatic variables listed above and elevation was extracted from GIS layers using ArcMap 9.3.

The regression tree analysis with Chi squared automatic interaction detector [CHAID, Kass (1980)] method was used in order to determine the interaction between predicted species richness and the environmental variables. CHAID analysis is a non-parametric procedure and no assumptions about the data distribution need to be made (van Diepen and Franses 2006).

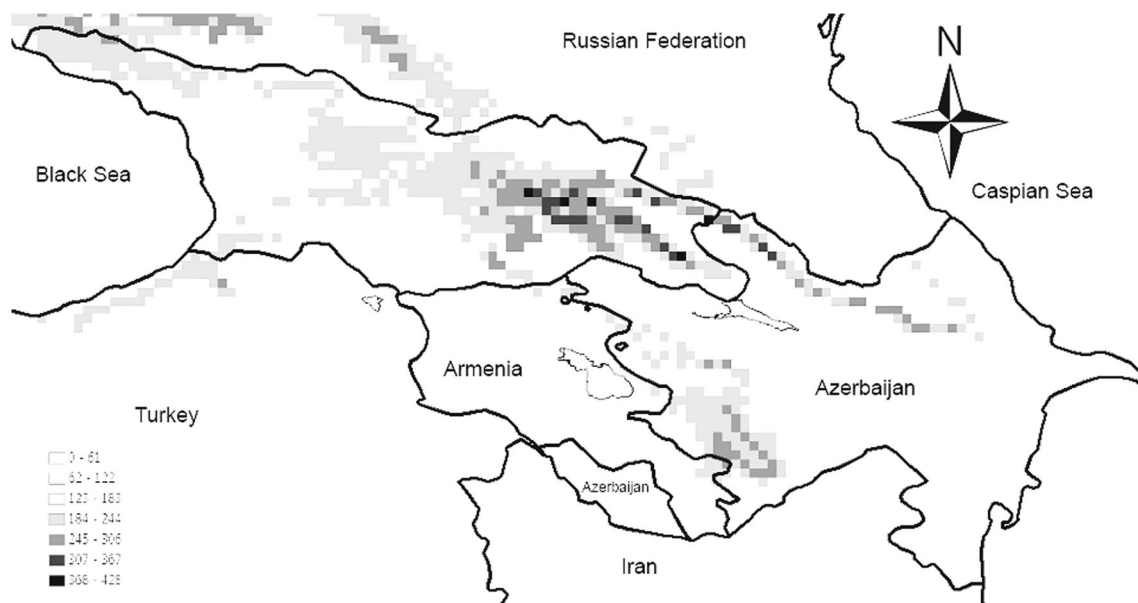


Fig. 2 Distribution of species richness of valid species across the study area. *Darker shades* indicate higher predicted numbers of species

SPSS software (SPSS v.16) was used to carry out the analysis. A significance level of 5 % was used in the F test, the maximum number of levels was established as three, and the minimum number of cases in a node for being a child node was established as 50. Diagrams were compiled using SPSS software (SPSS v.16).

Results

All species

Of all the 566 species included in the analysis 472 passed the cross validation test ($AUC > 0.7$). Total species richness varied from 0 to 446 with an average value of 196.5. Species richness was not distributed uniformly within the study area (Fig. 2). High species richness is predicted for regions with mountain forests, especially in the central parts of the North Caucasus, the Transcaucasus between the Surami Mountains and Gombori Mountains in East Georgia, the southern slopes of the eastern Great Caucasus as well as in mountains in southwestern Azerbaijan.

Total Species richness showed a non linear correlation with elevation, with a well expressed mid-elevation peak (Fig. 3). The lowest richness of endemic species was predicted for very high (>1914 m; Mean 136.9 SD 60.6) and low (<157 m a.s.l.; Mean 152.1 SD 53.5) elevations; highest species richness (Mean 243.3 SD 91.2) was predicted for altitudes between 369 and 1,622 m a.s.l.

The regression tree (CHAID algorithm) including 19 climatic variables revealed seven important discriminators

for predicted species richness: Mean Temperature of Driest Quarter, Temperature Annual Range, Precipitation of Coldest Quarter, Temperature Seasonality, Mean Temperature of Warmest Quarter, Annual Precipitation, Annual Mean Temperature ($R^2 = 0.806$ SEE 36.99, Cross-Validation $R^2 = 0.796$ SEE = 36.45).

Total species richness is best discriminated by the Mean Temperature of Driest Quarter ($P < 0.001$) with the highest diversity value (Mean 299.6 SD 63.5) predicted where temperature range is between -0.74 and 1.93 °C. In those regions with the driest quarter of winter below 0 °C (Armenian Upland, central Transcaucasus and Great Caucasus range) species diversity is positively correlated with mean temperature of driest quarter. At temperatures above 0 °C in the mentioned regions and in the foothills of the study region with a mean temperature of 6 – 15 °C during winter, species diversity is negatively correlated with temperature. On the southeastern Black-Sea Coast and in the Colchis triangle, where summer is the driest part of the year, species diversity is also negatively correlated with temperature in regions with mean temperatures above 15 °C.

At high elevations where Mean Temperature of Driest Quarter is below -4.68 °C Temperature Annual Range is second important parameter, species richness being higher where Temperature annual range is lower (i.e. more even Temperature). Across lowlands of Caspian sea, where Mean Temperature of Driest Quarter is higher than 24.19 °C Annual Mean Temperature is second important parameter. Temperature Seasonality is second important parameter on low elevations (200 – 600 m a.s.l.) and mead elevation ($1,100$ – $1,600$ m a.s.l.) predicted species richness is negatively

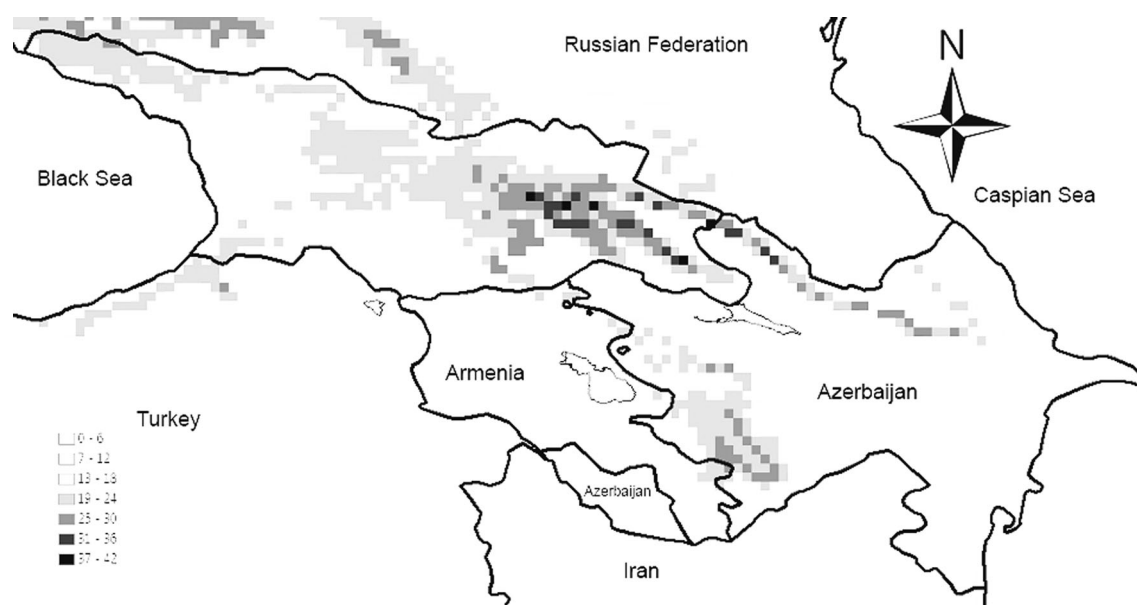


Fig. 5 Distribution of species richness of endemic species across the study area

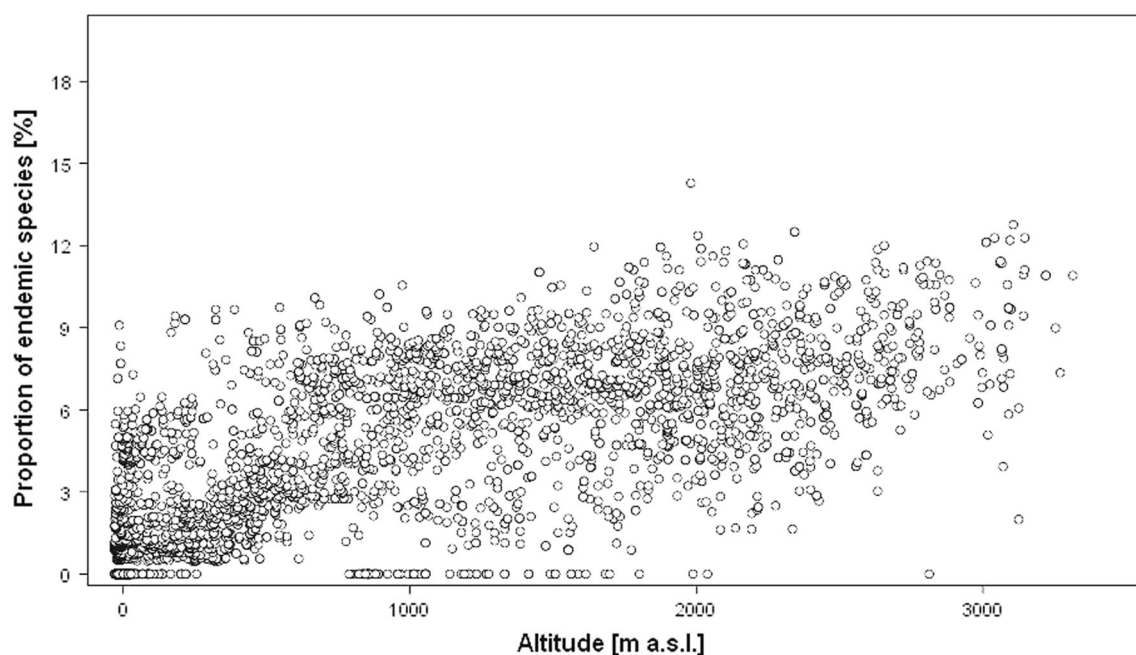


Fig. 6 Proportion of endemic species at different altitudes

of 4.85 %. The proportion of endemic species was positively correlated with elevation ($R^2 = 0.758$, $P < 0.001$). High proportions of endemic species (above 10 %) were predicted for some regions at very low altitudes at very high altitudes, e.g. the Central Greater Caucasus and the Kars-Armavir Region (Figs. 6, 7).

The regression tree including 19 environmental factors revealed four important discriminators for endemic species richness: Mean Temperature of Driest Quarter, Annual

Precipitation, Temperature Annual Range, Mean Temperature of Warmest Quarter ($R^2 = 0.801$, SEE 0.325; Cross-Validation $R^2 = 0.786$, SEE 0.337).

Endemic species richness, similarly to total species richness, is best discriminated by the Mean Temperature of Driest Quarter with the highest diversity value (Mean 19.25, SD 6.43) predicted where temperature range is between -0.74 and 1.93 °C. In those regions with the Mean Temperature of Driest Quarter below 0 °C species

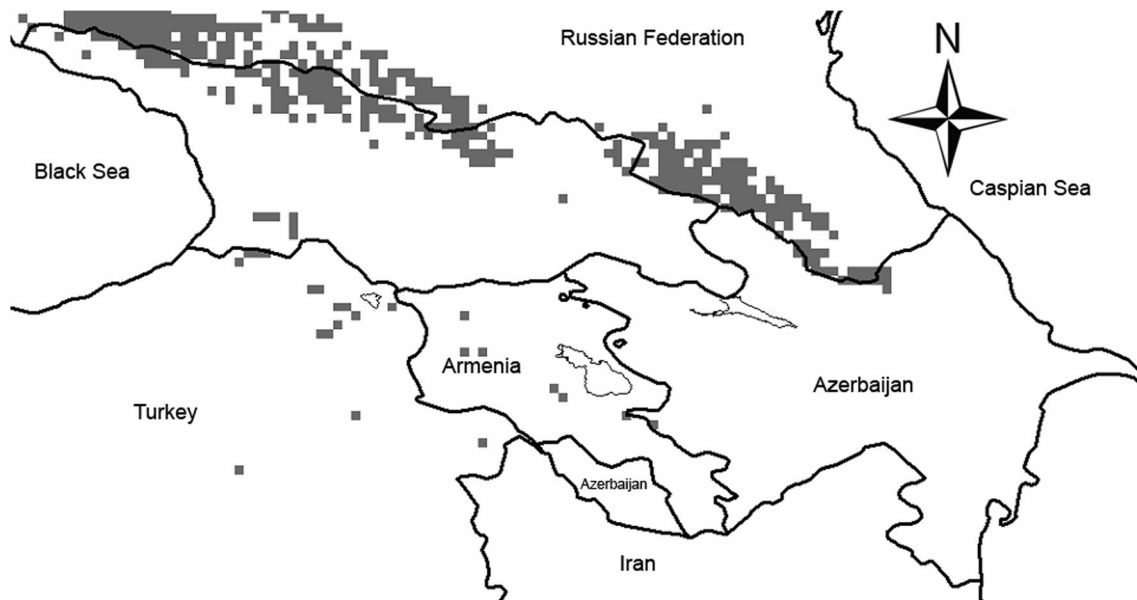


Fig. 7 Regions with high proportions of endemic species in spiders (>10 %)

diversity is positively correlated with the Mean Temperature of Driest Quarter. At temperatures above 0° predicted species diversity is negatively correlated with Mean Temperature of Driest Quarter.

At very low (Mean Temperature of Driest Quarter >24.1 °C) and high elevations (Mean Temperature of Driest Quarter <−4.68 °C) Temperature Annual Range is second important parameter, species richness being higher where Temperature annual range is smaller. Mean Temperature of Warmest Quarter is second important parameter where Mean Temperature of Driest Quarter is between 1.93 and 12.8 °C, geographically this represent low elevation areas between 200 and 600 m.a.s.l. In rest of areas Annual Precipitation is second important parameter, predicted richness is positively correlated, with highest value (Mean 22.91, SD 7.28) between 722 and 938 mm of precipitation.

Discussion

All species

The spatial distribution of spider species richness as predicted by our model confirms a number of hypotheses found in earlier arachnological studies in the CE. First of all, spider diversity in temperate and tropical forests is generally high (Sørensen 2004; Cardoso et al. 2008; Otto and Floren 2010; Blick 2011; Basset et al. 2012); indeed the locations with the highest reported species numbers are situated in the forest zone (e.g. Borjomi-Kharagauli National Park, Lagodekhi National Park). Our model also

confirms the southern slopes of the Eastern Great Caucasus as a hotspot of spider diversity, exemplified by the fact that according to occurrence data Lagdekh National Park is the location with the highest number of spider species (Otto and Tramp 2012). It was not included in the calculation of our model in order to minimize sampling bias but the model predicts high diversity in this forest nonetheless.

Secondly, locations of known Tertiary refugia, which are commonly expected to be hotspots of diversity, according to our model are predicted to exhibit only intermediate levels of spider diversity, e.g. the Black-Sea Coast, the Colchic lowlands and the Hyrcan Forests. It could be that spiders migrated from their refugia to more suitable habitats or climates in other regions as has been shown for other taxa (Graham et al. 2010; Zimmermann et al. 2010), thus increasing diversity outside of the refugia, whereas less motile species became extinct or remained within the refugia (e.g. species of the genus *Raveniola* Zonstein, 1987). Vast parts of the predicted hotspots of spider diversity in the central North Caucasus, central and eastern Georgia and Southwestern Azerbaijan have so far received little attention in arachnological diversity studies (cf. Fig. 1), a data gap in dire need of increased sampling efforts in order to improve our knowledge on the distribution of spider diversity distribution in the CE.

We found the diversity of all species—as well as that of endemic species—to form the typically hump-shaped distribution of species-richness-altitude relationships in spiders and other arthropods (Mikhailov and Mikhailova 2002; Chatzaki et al. 2005; Werenkraut and Ruggiero 2010) with highest species numbers at altitudes of the

mountain forest zone. Spider diversity in north-temperate forests is generally high (Floren et al. 2008; Otto and Floren 2010; Blick 2011) and can increase with altitude when conditions are suitable, e.g. in tropical forests (Russell-Smith and Stork 1994). As habitat structure and suitable climatic conditions dramatically decrease in the higher alto-montane forests and above the forest zone, a negative correlation between altitude and spider species richness is usually observed at high altitudes. Steiner and Thaler (2004) found such a decrease in species richness in arboricolous spiders at altitudes above 1,000 m in the European Alps, whereas our model predicts a reduction of species richness above 1,500 m in the Caucasus (Fig. 3). This difference could possibly be related to the overall warmer climate and thus higher-reaching vegetation zones in the Caucasus as compared to the European Alps.

Some studies found temperature parameters to be good predictors of spider abundance and diversity at various scales (Rypstra 1986; Jiménez-Valverde and Lobo 2007; Finch et al. 2008). This is corroborated by our finding that spider diversity is most strongly affected by the mean temperature of the driest quarter of the year, depending on whether this period occurs in winter or summer. In winter, mild temperatures just below zero represent favorable conditions for diapausing spiders, whereas colder temperatures can decrease survival rates (Schäfer 1987; Foelix 1996). Our findings that mean winter temperatures just above freezing are negatively correlated with species diversity could be attributed to a higher mortality, e.g. due to untimely emergence from diapause, repetitive freezing-thawing events or a combination of raised metabolism and food scarcity in winter (Aitchison 1984; Li and Jackson 1996; Bale and Hayward 2010; Schmalhofer 2011). In the Colchis, with the driest quarter in summer, the negative correlation of the mean temperature with species diversity might be attributed to the higher risk of desiccation at increased temperature levels (Nentwig 1987; DeVito et al. 2004). On an intermediate temperature level we found annual precipitation to be the second most important predictor of spider diversity. Spiders tend to be more abundant in moist habitats (Samu et al. 1996) but a discussion of precipitation is difficult because it does not automatically reflect the amount of water available (Kerr 2001; Finch et al. 2008).

Endemic species

The CE is known for its extraordinarily high rates of endemic species (Foster-Turley and Gokheshvili 2009; Zazanishvili and Mallon 2009); in spiders endemism is estimated at approx. 22–23 % (Marusik et al. 2006; Otto and Tramp 2012), which is the highest rate of endemism in spiders compared to other west Palearctic regions of

similar size (Ysnel et al. 2008). We found, that the local proportion of endemic species is about 4.8 % (SD 3.10) but can reach 10–14+ % in some regions (Fig. 7). Endemic species richness is positively correlated with elevation, suggesting post-glacial speciation events in the high mountains as the main source of high endemism.

The factors influencing overall spider richness and endemic species richness are similar: mean temperature of the driest quarter is the most important climatic factor and annual precipitation, temperature annual range, mean temperature of warmest quarter are the second most important factors.

Implications for species conservation

In our study we identified the altitude zone of the sub-montane to montane forests as harboring the highest species richness in spiders, a pattern similar to the distribution of ant diversity in Georgia (Chaladze 2012). The diversity of endemic species is correlated with total species richness but exhibits especially high proportions at very high altitudes in the central parts of the Greater Caucasus.

Giving forests in the CE priority in conservation efforts would most likely protect the majority of the arthropod species if their distribution patterns prove similar to those of ants and spiders in future studies. However, the effective protection of rare and endemic arthropod species needs more detailed information on the distribution and specific threats to the species in question.

The most urgent activities for filling these gaps in our knowledge are the establishment of extensive databases based on published occurrence data as well as intensified field work on all major arthropod taxa. For example, in our study on spiders, the arthropod taxon with the best data base on occurrence data in the CE, only 471 out of a total of 1,078 recorded species could be included in the SDM because of missing data for the remaining species. Increased data mining and field work is needed to improve SDM in spiders and, even more so, in other arthropod taxa.

Acknowledgments We are indebted to David Tarkhishvili and Alexander Gavashelishvili for productive discussions of species distribution modeling. Jason Dunlop kindly commented our English.

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