

Beyond elevation: testing the climatic variability hypothesis vs. Rapoport's rule in vascular plant and snail species in the Caucasus

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Received 30 January 2017; accepted for publication 1 March 2017

We investigate the generality of Rapoport's rule, that is an increase of elevational range size with increasing elevation, vs. the climatic variability hypothesis, which predicts correlations between the range of variation of climatic parameters tolerated by species and the maximum seasonal variation of these parameters experienced by these species. We tested whether the elevational distributions of vascular plants and land snails along two climatically distinct transects in Lagodekhi in the Greater Caucasus, and Sairme in the Lesser Caucasus, follow these rules. The elevational range size distributions of plants and land snails in Lagodekhi and Sairme do not correspond to Rapoport's rule, but show a maximum at mid-elevations. The mean range of annual temperatures tolerated by the species that have their maximum tolerance of temperature seasonality in the same temperature seasonality category significantly increases with the maximum tolerated temperature seasonality confirming the climatic variability hypothesis. This rule was also confirmed with regard to precipitation, but precipitation had different effects along the two investigated transects. Our results suggest that the investigation of variables that directly affect the studied organisms instead of surrogate variables like elevation or latitude increases our ability to understand the distribution of biodiversity.

ADDITIONAL KEYWORDS: ecogeographical rules – elevational gradient – land snails – macroecology – plants.

INTRODUCTION

Understanding the factors that determine whether a species can exist at a location, and thus determine species ranges and diversity patterns, is a basic goal in ecology and biogeography (Brown, Stevens & Kaufman, 1996; Gaston, 2009; Sexton *et al.*, 2009). Just as species are limited by environmental variables, the study of the ecologist is limited by the knowledge of these variables. The measurement of the variables that may affect species throughout the whole year is difficult, time-consuming and not feasible in studies of larger spatial scales. Therefore, macroecologists and biogeographers tend to use more easily measured variables

that are believed to be highly correlated with the variables that actually affect the investigated species. Two of the most widely used surrogate variables are latitude and elevation. Even if no information about sampling sites other than their location is known, latitude and elevation can easily be determined from maps. No organism can measure latitude or elevation. Thus, it is clear that these variables cannot affect the distribution of organisms directly. These variables are usually highly correlated with temperature, one of the most important ecological determinants (Angilletta, 2009). However, latitude and elevation are compound variables, because other environmental variables, such as precipitation, change with latitude and elevation, albeit in less predictable ways (Körner, 2007). Since climatic data are available now at high resolution, it is no longer necessary to use latitude or elevation as

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simplistic surrogate variables for climate (Hawkins & Diniz-Filho, 2004).

Macroecological rules, like Rapoport's rule, which describes an increase of the latitudinal range of species with increasing latitude (Rapoport, 1975; Stevens, 1989), and its extension to elevation (Stevens, 1992a) are based on these surrogate variables. Stevens (1989, 1992a, b) proposed the climatic (or seasonal) variability hypothesis as a mechanistic explanation of Rapoport's rule. According to this hypothesis, selection favours the evolution of broader climatic tolerances in species that are exposed to a greater annual range of climatic conditions. Conversely, selection for broader climatic tolerances is weaker in species that inhabit regions with little seasonality. The broader climatic tolerances of the species exposed to high seasonality enable these species to colonize regions with more strongly differing climatic conditions than species from regions with little seasonality. Moreover, Stevens (1989, 1992a, b) assumed that the annual range of climatic conditions is generally greater at higher latitudes or elevations. If this and the climatic variability hypothesis are correct, then high-latitude or high-elevation species are expected to colonize broader latitudinal or elevational zones than lower-latitude or lower-elevation species as predicted by Rapoport's rule.

Different aspects of the climatic variability hypothesis have been investigated. Most often the relationships between temperature variables and range size were studied. For example, Snyder & Weathers (1975), Gaston & Chown (1999b), Addo-Bediako, Chown & Gaston (2000), Cruz *et al.* (2005), Compton *et al.* (2007), Calosi *et al.* (2010), Sunday, Bates & Dulvy (2011) and Gutiérrez-Pesquera *et al.* (2016) tested whether physiological thermal tolerance increases with latitude or elevation. Letcher & Harvey (1994), Harcourt (2000), Whitton *et al.* (2012), Sheldon, Leaché & Cruz (2015) and Li *et al.* (2016) investigated whether elevational, latitudinal or geographic range size increases with temperature seasonality. More rarely, the relation between precipitation variables and range size have been examined. Cowlshaw & Hacker (1997), Harcourt (2000), Whitton *et al.* (2012) and Li *et al.* (2016) tested whether range size increases with precipitation seasonality.

However, most of these studies have not considered how climatic variability is actually correlated with latitude or elevation (but see Snyder & Weathers, 1975; Gaston & Chown, 1999b; Pintor, Schwarzkopf & Krockenberger, 2015; Beck *et al.*, 2016), or how wider climatic boundaries scale with wider latitudinal or elevational extent in the geographic ranges. In areas with a steep gradient of a climatic variable, broader climatic tolerance may result in only a small increase of range size, whereas in areas with a shallow gradient of a climatic variable, the same increase in climatic tolerance may result in a much larger increase of range size.

Whereas most of these studies supported predictions of the climatic variability hypothesis, the evidence for Rapoport's rule is mixed. While some studies could confirm the pattern (Rohde, Heap & Heap, 1993; Fleishman, Austin & Weiss, 1998; Sanders, 2002; Hausdorf, 2006; Hawkins & Diniz-Filho, 2006; Ruggiero & Werenkraut, 2007; Pintor *et al.*, 2015), others found little or no support for Rapoport's rule (Rohde *et al.*, 1993; Gaston, Blackburn & Spicer, 1998; Gaston & Chown, 1999a; Ruggiero & Werenkraut, 2007; Whitton *et al.*, 2012; McCain & Bracy Knight, 2013; Pintor *et al.*, 2015; Beck *et al.*, 2016). High-resolution climatic data (Hijmans *et al.*, 2005) permit direct testing of the prediction of the climatic variability hypothesis that the seasonal variability of a climatic parameter experienced by a species in a part of its range positively correlates with wider range boundaries with regard to this parameter. It is no longer necessary to use latitude or elevation as proxies. The examination of the climatic data may also help to understand why distribution patterns do not correspond to Rapoport's rule, although they are in accordance with the climatic variability hypothesis.

The effects of different environmental variables on the distribution of species can be most easily examined along elevational transects where these variables change across short distances within one biogeographic region (Körner, 2000). We examined two elevational transects in the Caucasus Mountains where few studies have explored the elevational distribution patterns of species so far (Murvanidze, Kvavadze & Jgenti, 2004; Chaladze, 2012; Chaladze, Otto & Tramp, 2014; Mumladze *et al.*, 2015), although the Caucasus region is one of the most important biodiversity hotspots worldwide (Myers *et al.*, 2000; Zazanashvili *et al.*, 2004). The two transects were selected to represent contrasting climatic conditions, one in the Lesser Caucasus with subtropical to temperate climate with moderate seasonality, and one in the Greater Caucasus with a continental climate with pronounced seasonality. We have examined the distributions of vascular plants and terrestrial snails along both transects to check the generality of the observed patterns. We investigated the following questions: (1) Does the elevational distribution of plants and snails along the two transects follow Rapoport's rule? (2) Are the predictions of the climatic variability hypothesis fulfilled? (3) Are Rapoport's rule and the climatic variability hypothesis coupled, and if not, why not?

MATERIAL AND METHODS

CHARACTERISTICS OF THE STUDY AREAS

Two elevational gradients in the Greater and the Lesser Caucasus were chosen to represent climatically contrasting conditions. The transect in the Greater Caucasus is located in Lagodekhi National Park on the

south-eastern slopes of Greater Caucasus, in eastern Georgia. This region is characterized by a continental climate with strong seasonal variation, experiencing cold winters, wet springs and dry, hot summers. The park is the oldest protected area in the Caucasus (more than 100 years old) and is covered by old grown primary mixed forest dominated by beech (*Fagus orientalis*). Only at lower elevations (600–700 m a.s.l.) and near the tree line (2200 m a.s.l.) do other tree species (*Carpinus betulus/Quercus* sp. and *Betula/Acer* sp., respectively) proliferate.

The second transect is located in Sairme gorge on the northern slopes of the western Lesser Caucasus. The climate of Sairme gorge is temperate; however, at lower elevations it resembles subtropical climate. Sairme gorge is also covered by old grown primary mixed forest but the composition of the forest is quite different from that in Lagodekhi. At lower elevations *Fagus orientalis* and *Castanea sativa* predominate, whereas conifers (*Abies nordmaniana* and *Picea orientalis*) are mixed with several broadleaf tree species at higher elevations. Furthermore, understory in Sairme gorge is mainly presented by dense rhododendron (*Rhododendron ponticum*) and laurel (*Laurocerasus officinalis*), which are missing in Lagodekhi (Dolukhanov, 2010). In contrast to Lagodekhi, Sairme gorge is outside of protected areas and has been subject to human disturbance

(timber harvest and grazing). However, natural forests are still present at all studied elevations.

Along both transects, mean annual temperature and temperature seasonality almost linearly decrease with increasing elevation (Fig. 1). In Lagodekhi annual precipitation shows a maximum at mid-elevations, whereas precipitation seasonality almost linearly increases with increasing elevation (Fig. 1A). In Sairme there is a minimum in precipitation and a maximum in precipitation seasonality at mid-elevations (Fig. 1B). Annual precipitation is much lower at the plots sampled along the Lagodekhi transect (mean 790 mm) than at the Sairme transect (mean 905 mm). Seasonal variation in precipitation is also much stronger in Lagodekhi (mean coefficient of variation 47 mm) than in Sairme (mean coefficient of variation 19 mm).

SAMPLING DESIGN AND DATA COLLECTION

Along both transects, coordinates of three replicate plots were fixed in the forests at 200 m elevational intervals, starting from 600 m a.s.l. up to 2200 m a.s.l. (upper tree line) using Google Earth without prior knowledge of the area. Thus, 27 sampling plots at each transect were fixed. Both transects were sampled in June 2013. In cases where the predetermined site was

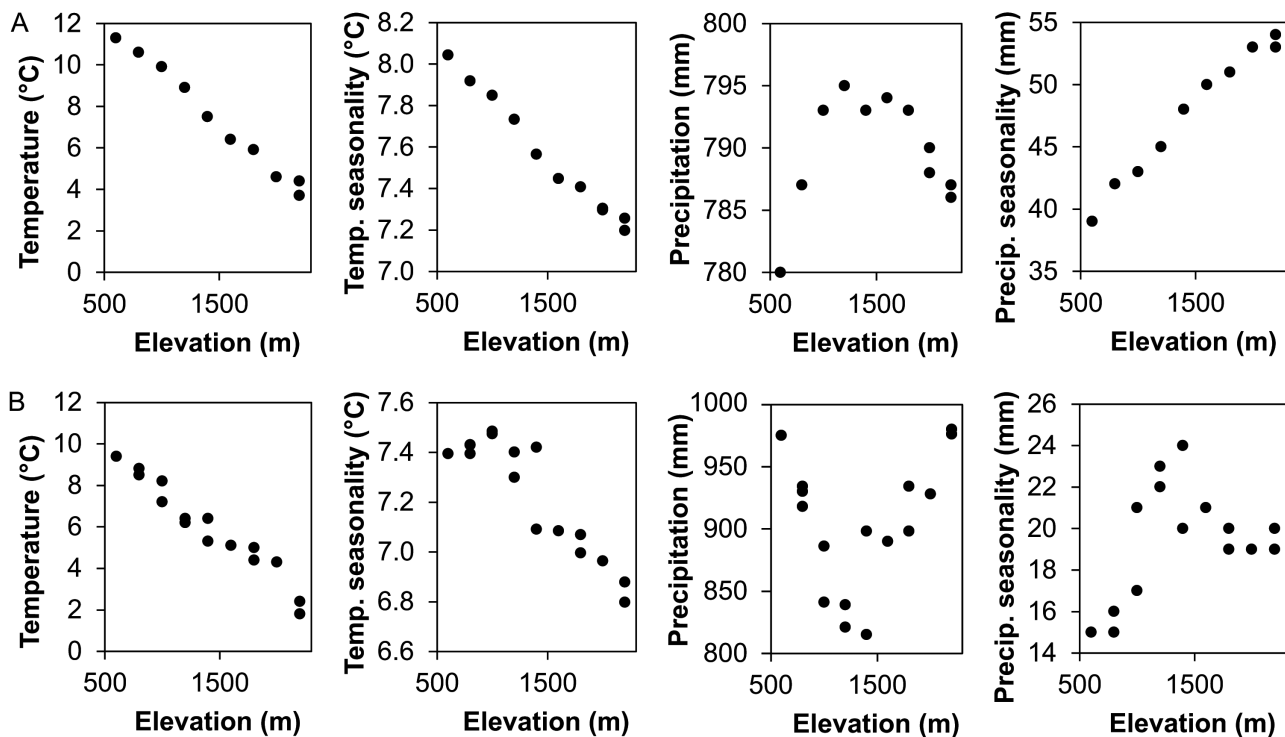


Figure 1. Elevational variation of annual mean temperature, temperature seasonality, annual precipitation and precipitation seasonality in (A) Lagodekhi and (B) Sairme.

not physically accessible, the closest accessible locality was sampled. Distances between plots at each elevation varied from 50 to 150 m.

At each sampling location, a 20 × 20 m area was searched for 2 h by one of us (L.M.) and all living snails and empty shells were collected. Besides this, leaf litter and soil were sieved in the field, and 10 L sieved material was brought to the laboratory for later examination. Sieved soil samples were air dried for 24 h and then sieved again, using sieves with openings of 5 and 2 mm. Each of the fractions was thoroughly searched for shells, with or without stereo microscope depending on particle size. The combination of direct searching and sieving large amounts of litter is time-consuming, but guarantees detecting the rare species in all size classes (Pokryzko & Cameron, 2005). Snail species were identified using the relevant literature (Likharev & Rammelmeier, 1952; Riedel, 1966; Hausdorf, 1996; Schütt, 2005; Sysoev & Schileyko, 2009; Walther, Neiber & Hausdorf, 2016) and the reference collection in the Zoological Museum of the University of Hamburg. Voucher specimens were deposited in the malacological collection of Ilia State University in Tbilisi and the Zoological Museum of the University of Hamburg.

In the same 400 m² plots we also made complete inventories of vascular plant species. Considering the very high diversity of plants (especially in the western Lesser Caucasus), we did not expect to record total plant species richness even for the studied transects. However, the balanced sampling design is sufficient to show general patterns in the distribution of plant species. Most of the plant species were determined in the field, but some doubtful species were transported to the laboratory for precise identification using Dolukhanov (2010) and Ketskhoveli, Kharadze & Gagnidze (2011).

The locations of the sampling plots in Lagodekhi and Sairme and the bioclimatic variables for these plots, which were acquired from the WorldClim database (<http://www.worldclim.org>; c. 1 km² resolution; Hijmans *et al.*, 2005), are listed in Appendix S1.

TEST OF RAPOPORT'S RULE AND THE CLIMATIC VARIABILITY HYPOTHESIS

We used Stevens' (1989) method and the midpoint method of Rohde *et al.* (1993) to check the elevational version of Rapoport's rule. According to Stevens' (1989) method, means of elevational range sizes of all species occurring in the same elevational band were plotted against elevation, whereas according to the midpoint method of Rohde *et al.* (1993) means of elevational range sizes of all species with a midpoint in the same elevational band were plotted against elevation. We used Spearman's rank correlation coefficient to test

whether elevational range size is positively correlated with elevation as predicted by Rapoport's rule.

Colwell & Hurtt (1994) demonstrated that spatial constraints can result in a maximum of the mean range size distribution at intermediate elevations. This mid-domain effect is mainly caused by large-range species that overlap in the middle between the spatial boundaries. The mid-domain effect might obscure Rapoport's rule predicting a maximum of the mean range size distribution at lower elevations. To control for this we applied the quartile method of McCain & Bracy Knight (2013) that examines whether the frequency distribution of the smallest elevational ranges (≤ 400 m in our case) is negatively correlated to elevation.

To test the robustness of our results against under-sampling artefacts that might have affected the determination of the elevational ranges and the range size patterns, we repeated the analyses with datasets from which we excluded all species found only at one elevation (see Beck *et al.*, 2016).

The climatic variability hypothesis predicts that species living at localities with a higher seasonality for a given climatic variable will occupy a broader range of localities with regard to this variable. Thus, we recorded for each species the maximum seasonal variation of a given climatic parameter that it experiences along a transect and the range of this variable at the localities where the species occurs. Analogue to the midpoint method of Rohde *et al.* (1993), we assigned the species into categories with respect to maximum tolerated climatic variability, calculated the mean occupied range of the variable and checked for a correlation between the mean ranges and the tolerated maximum seasonal variation, using Spearman's rank correlation coefficient.

RESULTS

RELATION BETWEEN ELEVATIONAL RANGES AND ELEVATION

We found 80 species of vascular plants along the transect in Lagodekhi (Appendix S2) and 184 along the transect in Sairme (Appendix S3). In Lagodekhi 4573 individuals belonging to 27 land snail species were collected (Appendix S4) and 5435 individuals of 42 species in Sairme (Appendix S5).

In contrast to the prediction of Rapoport's rule, the mean elevational range sizes of plant and snail species do not increase with increasing elevation, regardless whether Stevens' (1989) method or the midpoint method of Rohde *et al.* (1993) was used to investigate the pattern. Stevens' (1989) method (Fig. 2; Appendix S6) shows even an inverse Rapoport pattern, with decreasing mean elevational range sizes with increasing elevation for both plants and snails

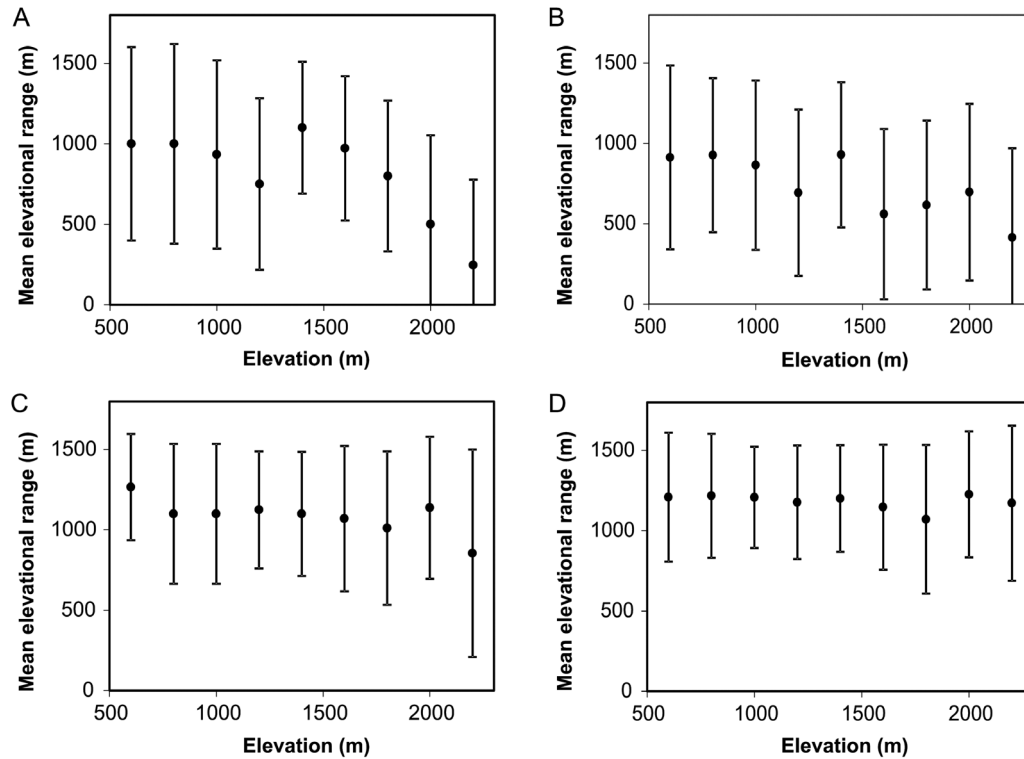


Figure 2. Correlation of mean elevational range of species occurring in an elevational band with elevation. Bars represent standard deviation. (A) Plants in Lagodekhi (numbers of species from left to right: 9, 15, 16, 20, 20, 22, 26, 33, 40). (B) Plants in Sairme (numbers of species from left to right: 34, 38, 34, 54, 31, 78, 63, 54, 43). (C) Snails in Lagodekhi (numbers of species from left to right: 9, 14, 14, 16, 16, 17, 18, 13, 11). (D) Snails in Sairme (numbers of species from left to right: 17, 19, 21, 21, 23, 23, 23, 21, 9).

at both investigated elevational transects. In contrast, unimodal patterns with the largest elevational range sizes at mid-elevations were found with the midpoint method of Rohde *et al.* (1993) (Fig. 3; Appendix S6).

The quartile method which we applied to control for the mid-domain effect revealed an increase rather than a decrease of the number of smallest elevational ranges (≤ 400 m in our case) with increasing elevation, for all examined data sets (Fig. 4; Appendix S6).

The patterns revealed with the mentioned methods were hardly altered by the exclusion of all species found only at one elevation (Appendices S7–S10). This indicates the robustness of the observed patterns with regard to undersampling.

TEST OF THE CLIMATIC VARIABILITY HYPOTHESIS

The annual temperature ranges of plants in Lagodekhi and Sairme and snails in Lagodekhi were significantly correlated with the maximum temperature seasonality tolerated by these species (Fig. 5; Appendix S11). The relationship was not significant for snails in Sairme, but this was probably only due to the low number of different tolerated maxima along this transect. The

rank orders of the plant species that were present in both transects with regard to their maximum tolerated temperature variability in Lagodekhi and Sairme are significantly correlated (Spearman's rank correlation coefficient $r_s = 0.556$, two-sided $P \leq 0.001$).

The annual precipitation ranges of plants in Lagodekhi and Sairme and snails in Sairme were also significantly correlated with the maximum precipitation seasonality tolerated by these species (Fig. 6; Appendix S12). The relationship was not significant for snails in Lagodekhi, probably due to the low number of species, most of which occurred at elevations with high precipitation seasonality. The rank orders of the plant species that were present in both transects with regard to their maximum tolerated precipitation variability in Lagodekhi and Sairme are significantly negatively correlated (Spearman's rank correlation coefficient $r_s = -0.339$, two-sided $P = 0.015$).

DISCUSSION

Both Stevens' (1989) method and the midpoint method of Rohde *et al.* (1993) showed that the elevational

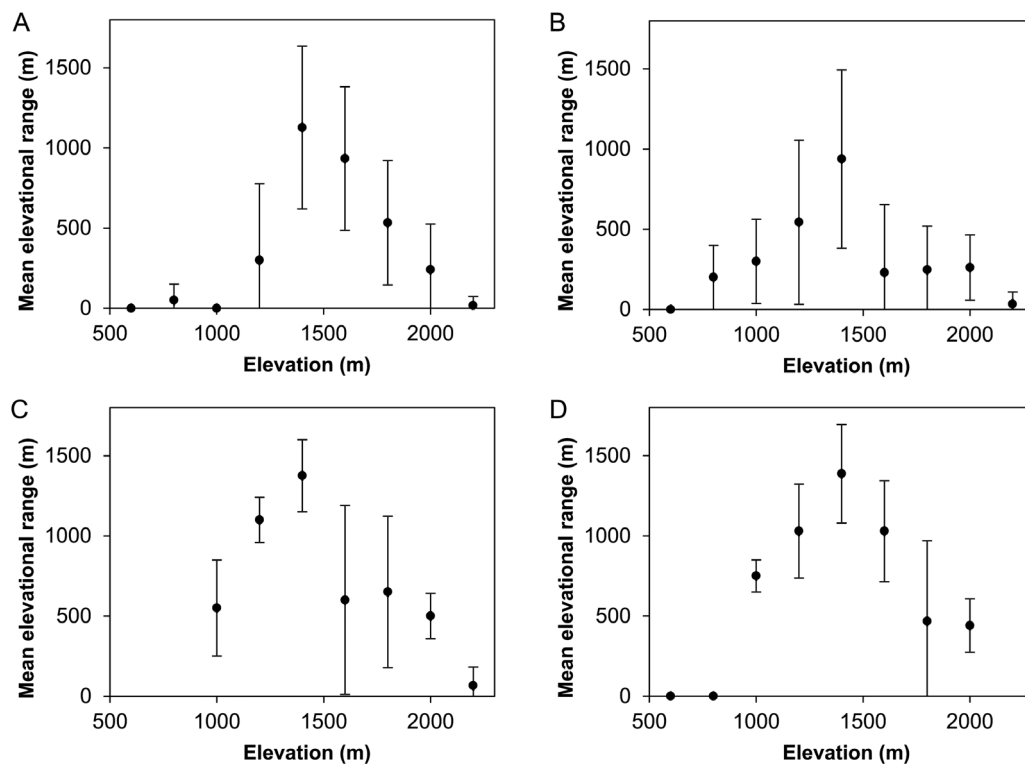


Figure 3. Correlation of mean elevational range of species with their elevational midpoint in the same elevational band with elevation. Bars represent standard deviation. (A) Plants in Lagodekhi (numbers of species from left to right: 1, 4, 3, 4, 11, 9, 9, 15, 24). (B) Plants in Sairme (numbers of species from left to right: 6, 5, 12, 25, 29, 34, 26, 23, 24). (C) Snails in Lagodekhi (numbers of species from left to right: 4, 2, 8, 4, 4, 2, 3). (D) Snails in Sairme (numbers of species from left to right: 1, 1, 4, 7, 15, 7, 3, 5).

distributions of plants and land snails in Lagodekhi and Sairme do not follow Rapoport's rule, that is an increasing elevational range size with increasing elevation. The quartile method indicated that these results are not artefacts resulting from a mid-domain effects caused by large-range species. Furthermore, the exclusion of species found only at one elevation indicated that the results are also robust with regard to potential undersampling artefacts. In contrast, the elevational distributions of plants and land snails in Lagodekhi and Sairme support the climatic variability hypothesis by showing correlations between the range of variation of climatic parameters tolerated by a species and the maximum seasonal variation of the parameters experienced by that species (Stevens, 1989, 1992a, b).

We found high correlations between the mean range of annual temperatures tolerated by the species that have their maximum tolerance of temperature seasonality in the same temperature seasonality category, and the maximum tolerated temperature seasonality for plants in Lagodekhi and Sairme, and snails in Lagodekhi. This result is in line with previous studies that supported some predictions of the climatic

variability hypothesis with regard to temperature for terrestrial, as well as marine, molluscs, arthropods, fish, amphibians, reptiles and mammals (Snyder & Weathers, 1975; Letcher & Harvey, 1994; Gaston & Chown, 1999b; Addo-Bediako *et al.*, 2000; Harcourt, 2000; Cruz *et al.*, 2005; Compton *et al.*, 2007; Calosi *et al.*, 2010; Sunday *et al.*, 2011; Whitton *et al.*, 2012; Pintor *et al.*, 2015; Sheldon *et al.*, 2015; Beck *et al.*, 2016; Gutiérrez-Pesquera *et al.*, 2016; Li *et al.*, 2016).

While the climatic variability hypothesis has been repeatedly confirmed for various taxa with regard to thermal variation, only two studies (Cowlshaw & Hacker, 1997; Harcourt, 2000) found a significant positive correlation between precipitation seasonality and latitudinal range size of African primates. Two other studies (Whitton *et al.*, 2012; Li *et al.*, 2016) found significant negative correlations between precipitation seasonality and range sizes of terrestrial vertebrates, contradicting the climatic variability hypothesis. A possible cause for this discrepancy is that Cowlshaw & Hacker (1997) and Harcourt (2000) used climatic data from the range centre or from a latitudinal band around the range centre, whereas Li *et al.* (2016) used the average value of precipitation seasonality across all

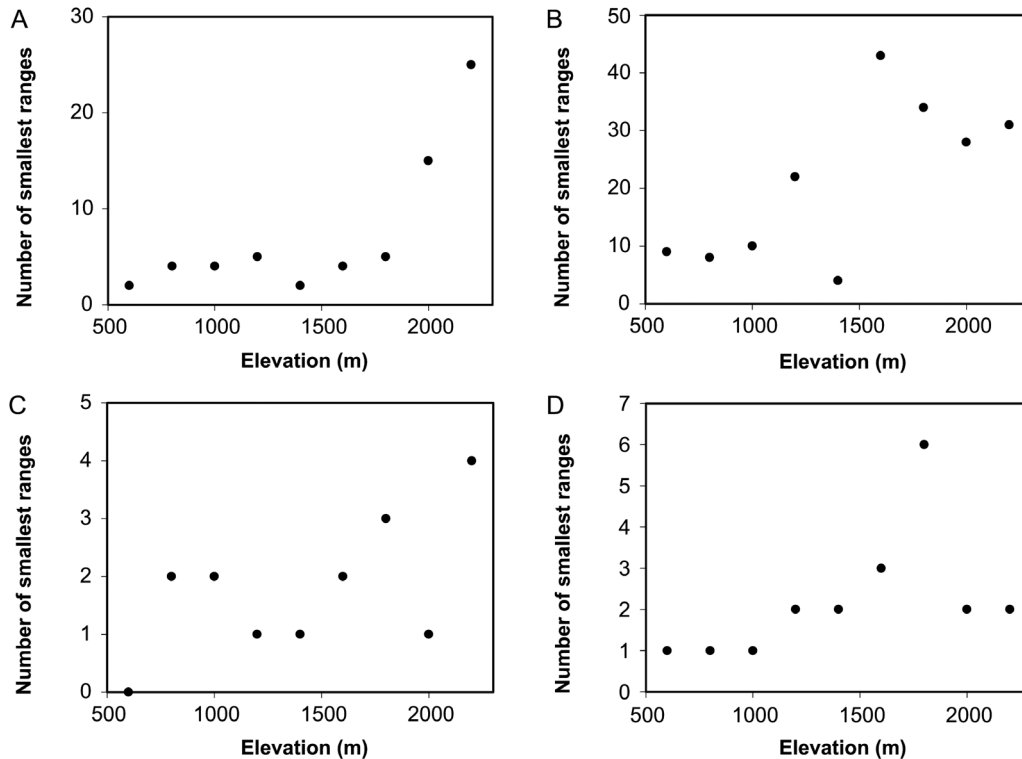


Figure 4. Correlation of the number of smallest elevational ranges (≤ 400 m) with elevation. (A) Plants in Lagodekhi. (B) Plants in Sairme. (C) Snails in Lagodekhi. (D) Snails in Sairme.

grid cells within a species range. The climatic variability hypothesis suggests that species that are exposed to a greater annual range of climatic conditions evolve broader climatic tolerances. The strongest selection for broader climatic tolerances will be in the areas with the greatest annual range of climatic conditions. Thus, the greatest annual range of climatic conditions to which a species is exposed locally rather than the average of climatic seasonality across its whole range determines its climatic tolerance (Pintor *et al.*, 2015). Obviously, the average of climatic seasonality across the whole range of a species will decrease if a species that evolved in areas with a high seasonality expands into areas with lower seasonality. This might explain why average seasonality across whole ranges decreases with increasing range size. This might also explain the results of Whitton *et al.* (2012), which are not based on analyses of interspecific patterns as in the other studies, but on analyses of assemblage patterns in grid cells.

The mean range of annual precipitation tolerated by the plant species in Lagodekhi and Sairme and the snail species in Sairme was significantly positively correlated with the maximum precipitation seasonality experiences by these species. However, contrary to the prediction of the climatic variability hypothesis, the mean occupied precipitation range was much larger in Sairme than in Lagodekhi, although the

precipitation seasonality was higher in Lagodekhi. Thus, the two correlations were caused by different factors. Similarly to elevation or latitude, precipitation may be a proxy for different factors in different surroundings. Precipitation is lower at all sampling localities in Lagodekhi than at those in Sairme. In the drier, and on average, warmer environment in Lagodekhi, available moisture is limited by precipitation, at least during the dry season. In contrast, moisture is practically not limited at the north slope in Sairme with its constantly high precipitation. Rather, the high amount of precipitation in Sairme may result in leaching of minerals and soil acidification. The African primates for which a positive correlation between precipitation seasonality and latitudinal range size has been shown (Cowlshaw & Hacker, 1997; Harcourt, 2000) are most likely not directly affected by precipitation seasonality, but perhaps by their ability to tolerate fluctuations in food availability resulting from precipitation seasonality (Williams & Middleton, 2008). The different effects of different amounts of precipitation affect organisms in different ways. Interestingly, there is a significant negative correlation between the rank orders of the plant species that were present in both transects with regard to their maximum tolerated precipitation variability in Lagodekhi and Sairme. This indicates that sensitive species that are limited in Lagodekhi by

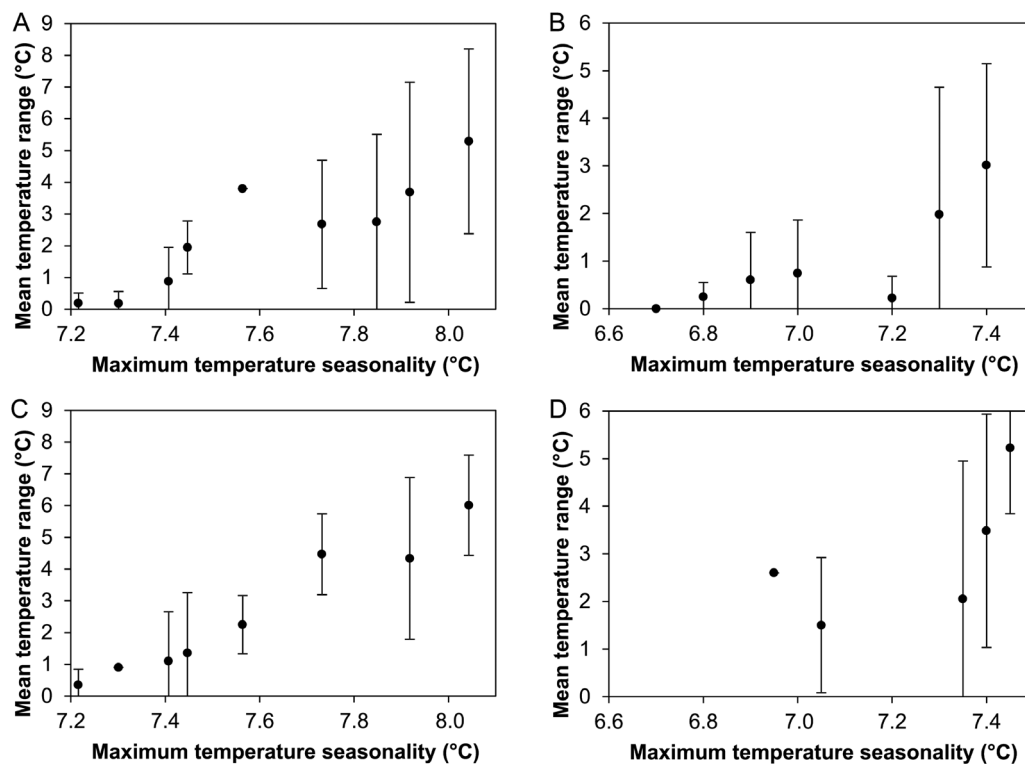


Figure 5. Correlations of mean annual temperature range of species with their temperature seasonality maximum in the same category with temperature seasonality maximum. Bars represent standard deviation. (A) Plants in Lagodekhi (numbers of species from left to right: 9, 7, 8, 9, 2, 9, 4, 10, 22). (B) Plants in Sairme (numbers of species from left to right: 3, 17, 26, 49, 10, 13, 66). (C) Snails in Lagodekhi (numbers of species from left to right: 9, 6, 3, 2, 2, 2, 1, 2). (D) Snails in Sairme (numbers of species from left to right: 2, 5, 2, 7, 27).

drought caused by low precipitation during the dry season tend also to be limited in Sairme, perhaps caused by a shortage of minerals and soil acidification consequent from high precipitation.

Our results show that a lack of a Rapoport effect should not be interpreted as a lack of evidence for the climatic variability hypothesis (see also Pintor *et al.*, 2015). Pintor *et al.* (2015) thought that elevational Rapoport effects might be more reliable indicators of the validity of the climatic variability hypothesis than latitudinal ones, because elevational climate gradients are generally more consistent than latitudinal ones. Our study shows that this is not necessarily the case. The elevational ranges of species along the investigated transects do not increase with elevation as predicted by Rapoport's rule, although the climatic variability hypothesis applies. This may have different causes, namely (1) the seasonality of a climatic variable does not increase with increasing elevation, (2) a lack of correlation of some climatic variables with elevation, (3) the combined influence of several uncorrelated variables on the elevational distribution of organisms.

Stevens (1992a) assumed that the breadth of climatic conditions experienced by mountain residents

increases with increasing elevation, so that there is selection for tolerance of a wide temperature range at high elevations, which entails wider elevational ranges of species from high elevations. However, temperature seasonality is negatively correlated with elevation along both investigated transects (Fig. 1), and precipitation seasonality has a maximum at mid-elevations in Sairme (Fig. 1B). Since the underlying assumptions of Stevens (1992a) are not met, it is not surprising that the elevational range size distributions do not correspond with Rapoport's rule.

In Lagodekhi precipitation seasonality significantly increased with elevation. Although the increased precipitation seasonality actually resulted in wider tolerances for precipitation, again no Rapoport effect could be observed, because (1) there is a steep gradient of mean annual precipitation towards mid-elevations, so that the wider tolerances for precipitation do not result in much wider elevational ranges and (2) the elevational distribution is also affected by the variation of temperature and other environmental parameters.

Pintor *et al.* (2015) investigated the climatic variability hypothesis using the correlation between

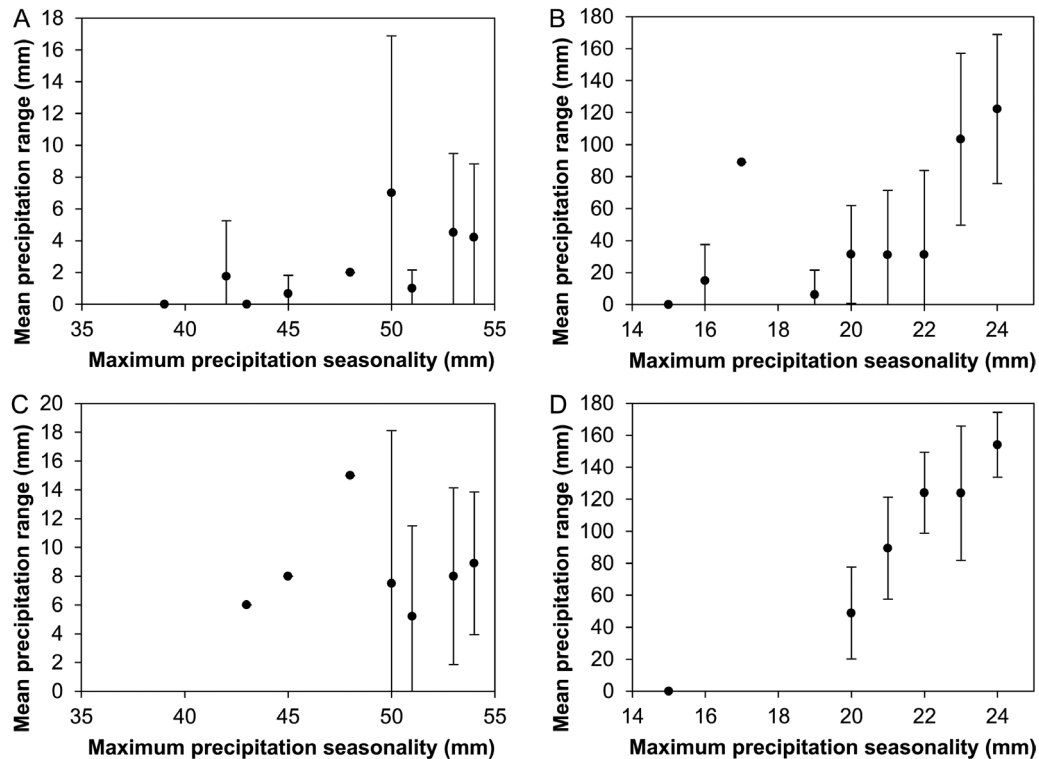


Figure 6. Correlations of mean annual precipitation range of species with their precipitation seasonality maximum in the same category with precipitation seasonality maximum. Bars represent standard deviation. (A) Plants in Lagodekhi (numbers of species from left to right: 1, 4, 3, 3, 2, 2, 4, 33, 28). (B) Plants in Sairme (numbers of species from left to right: 6, 3, 1, 33, 25, 52, 12, 24, 28). (C) Snails in Lagodekhi (numbers of species from left to right: 1, 1, 2, 2, 5, 6, 10). (D) Snails in Sairme (numbers of species from left to right: 2, 7, 5, 3, 4, 22).

maximum annual variability and latitudinal range extent. However, the climatic variability hypothesis predicts that selection favours the evolution of broader climatic tolerances in species that are exposed to a greater annual range of climatic conditions. Broader climatic tolerances enable such species to colonize regions with more diverse climatic conditions, compared to species from regions with little seasonality. Thus, we recommend testing the correlation between the occupied ranges with respect to considered climatic variable and the maximum annual variability of that climatic variable to which a species is exposed. The correlation between maximum tolerated annual variability and latitudinal (or elevational) range extent tested by [Pintor *et al.* \(2015\)](#) may be affected by non-linear relations between climatic variables and latitude or elevation (see [Fig. 1](#)), and by the steepness of climatic gradients across latitude or elevation.

ACKNOWLEDGEMENTS

We are grateful to Cort Anderson for a linguistic revision of the manuscript. The work of L.M. was supported

by Deutscher Akademischer Austauschdienst. We also thank the Volkswagen Stiftung for funding this study within the project 'Biogeography of the land molluscs of the Caucasus region'.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Appendix S1. Location of sampling plots in Lagodekhi and Sairme and climatic variables.

Appendix S2. Vascular plant species recorded in Lagodekhi (0 = absent; 1 = present).

Appendix S3. Vascular plant species recorded in Sairme (0 = absent; 1 = present).

Appendix S4. Land snail species and individuals recorded in Lagodekhi.

Appendix S5. Land snail species and individuals recorded in Sairme.

Appendix S6. Correlations of mean elevational range of species with their elevational midpoint in the same elevational band with elevation (Spearman's rank correlation, two-sided).

Appendix S7. Correlation of mean elevational range of species occurring in an elevational band with elevation. All species found only at one elevation were excluded. Bars represent standard deviation. (A) Plants in Lagodekhi (numbers of species from left to right: 8, 12, 13, 18, 20, 21, 24, 25, 18). (B) Plants in Sairme (numbers of species from left to right: 28, 36, 30, 43, 29, 53, 51, 48, 23). (C) Snails in Lagodekhi (numbers of species from left to right: 9, 14, 14, 16, 16, 16, 17, 13, 9). (D) Snails in Sairme (numbers of species from left to right: 17, 19, 21, 21, 23, 23, 23, 21, 9).

Appendix S8. Correlation of mean elevational range of species with their elevational midpoint in the same elevational band with elevation. All species found only at one elevation were excluded. Bars represent standard deviation. (A) Plants in Lagodekhi (numbers of species from left to right: 1, 2, 11, 8, 7, 7, 2). (B) Plants in Sairme (numbers of species from left to right: 3, 8, 14, 27, 9, 14, 17, 4). (C) Snails in Lagodekhi (numbers of species from left to right: 4, 2, 8, 3, 3, 2, 1). (D) Snails in Sairme (numbers of species from left to right: 4, 7, 15, 7, 2, 5).

Appendix S9. Correlation of the number of smallest elevational ranges (≤ 400 m) with elevation. All species found only at one elevation were excluded. (A) Plants in Lagodekhi. (B) Plants in Sairme. (C) Snails in Lagodekhi. (D) Snails in Sairme.

Appendix S10. Correlations of mean elevational range of species with their elevational midpoint in the same elevational band with elevation (Spearman's rank correlation, two-sided). All species found only at one elevation were excluded.

Appendix S11. Correlations of mean annual temperature range of species with their temperature seasonality maximum in the same category with temperature seasonality maxima (Spearman's rank correlation, two-sided).

Appendix S12. Correlations of mean annual precipitation range of species with their precipitation seasonality maximum in the same category with precipitation seasonality maxima (Spearman's rank correlation, two-sided).