

Climate-based model of spatial pattern of the species richness of ants in Georgia

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Abstract For optimal planning of conservation and monitoring measures, it is important to know the spatial pattern of species richness and especially areas with high species richness. A spatial pattern of the species richness of ants in Georgia (Caucasus) was modeled, areas with the highest number of ant's species were inferred, and climatic factors that influence the pattern of ant diversity were identified. A database was created by accumulating occurrences for 63 ant species, including 256 localities and 2,018 species/occurrences. Species richness was positively correlated with variables associated with temperature and negatively correlated with variables associated with precipitation. Species richness reaches a maximum at the elevations 800–1,200 m a.s.l. and declines at both lower and higher altitudes. The role of climatic variables and geography of the study area in determining the observed pattern of species richness is discussed.

Keywords Biodiversity · Climatic variables · Formicidae · Spatial pattern · Altitudinal gradient · Ground moisture

Introduction

For optimal planning of conservation and ecological monitoring, it is important to know geographic areas with particularly high species richness (Ceballos and Brown 1995; Garcia 2006; Myers et al. 2000; Newbold et al. 2009). However, development of biodiversity inventories is a very time and effort consuming process, especially for

highly diverse species groups such as insects, because it requires intensive sampling and taxonomic expertise (Agosti et al. 2000). An alternative is to develop spatial models based on the limited occurrence data which are already compiled in literature and online databases (Garcia 2006; Newbold et al. 2009).

Understanding spatial pattern of species richness in Georgia is important at the global scale as the whole territory of Georgia is part of the Caucasus biodiversity hotspot, which is one of 25 global biodiversity hotspots. These global biodiversity hotspots comprise only 1.4% of the land surface of the Earth and contain as many as 44% of vascular plant species and more than 30% of vertebrate species (Myers et al. 2000).

Knowing the dependence of species richness on environmental variables is important for understanding the formation of modern species richness distribution and for the prediction of how species richness would be affected by climate change (Kerr 2001; Kienasta et al. 1998; Iverson and Prasad 2001). Dunn et al. (2009) showed that ant species richness is positively correlated with temperature, and negatively correlated with precipitation at a global scale. The use of ants as bio-indicators is also growing in Australia (Andersen and Majer 2004), tropical location (e.g. Bestelmeyer and Wiens 2001; Van Hamburg et al. 2004) and temperate areas (Kaspari and Majer 2000; Sauberer et al. 2004).

Taxonomic studies of ants in Georgia started in the late nineteenth century (Gratiashvili and Barjadze 2008). The studies collected much data on the occurrences of ant species (Gratiashvili and Barjadze 2008) but did not identify spatial patterns of the species richness.

Recent algorithms and statistical methods have helped to develop spatial models describing biodiversity including those developed for the prediction of species distributions (Fitzpatrick et al. 2007; Muñoz et al. 2009; Ortega-Huerta

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and Peterson 2008; Soberon and Peterson 2005; Stockwell 1999; Stockwell and Peters 1999). In order to identify the spatial pattern of species richness, distribution models for single species are developed and then those models are summed (Garcia 2006; Newbold et al. 2009). 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.

In this study, spatial patterns of the species richness of ants in Georgia were modeled and the factors of spatial and altitudinal variation of species richness were inferred.

Methods

Study area

The study area included the entire territory of Georgia (Fig. 1). The elevation within the area varies between -1 and $4,550$ m. a.s.l., mean annual temperature between -9.7 and 15°C , and annual precipitation between 439 and $2,376$ mm (Hijmans et al. 2005). The country has a broad variety of landscapes, from temperate mountain rainforests to semi-deserts and alpine tundra, including agricultural and alpine landscapes covering nearly half of the country (Tarkhishvili et al. 2010).

Modeling

A database was created by compiling data on the locations of Georgian ant species (Gratiashvili and Barjadze 2008).

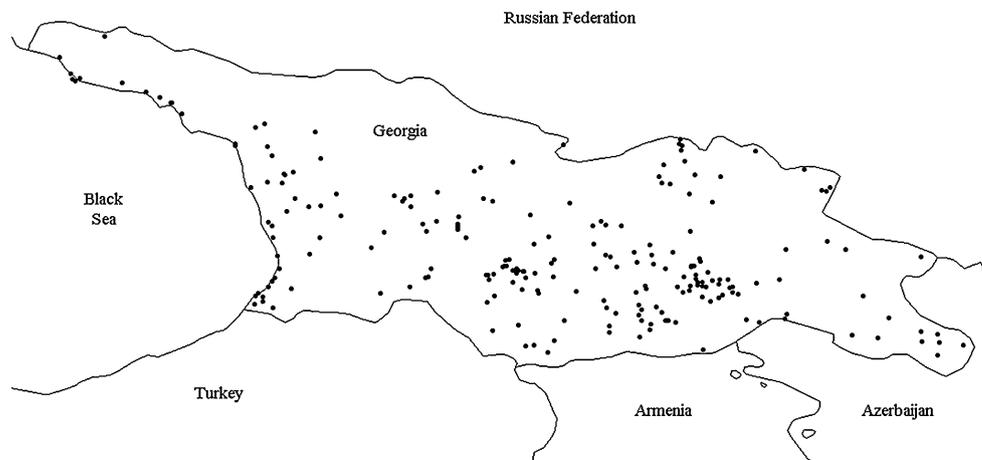
Geographic coordinates of individual locations were scored from the GeoNames database (<http://www.geonames.org/>). In total, 2,018 species/locations were analyzed, providing data on 72 ant species and 258 unique localities (Fig. 1).

The modeling of species distribution was performed using openModeller (Muñoz et al. 2009). This software helps to model suitable habitats for individual species and then overlay them in order to estimate summed model of species richness (Muñoz et al. 2009). The GARP algorithm (ecological niche model) was used in order to infer the ant diversity hotspots (Stockwell 1999; Stockwell and Peters 1999).

In total, 19 variables were taken from the WorldClim version 1.4 dataset at a resolution of 30 arcsec (c. 1 km) (Hijmans et al. 2005). These were: (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 (Garcia 2006). In total, 72 species met this criteria. Seventy five percent of occurrence locations were used for training the models and 25% was used for validation. Occurrences were divided into test and training points randomly. 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),

Fig. 1 Study area and localities of ant species



nine species with the AUC scores of <0.7 were excluded from the further analysis.

The individual binary models of species ranges predicted by the GARP system were overlaid and summed for producing map of species richness.

Statistical analysis

Thousand random points were generated using Arcview 3.1, covering whole study area. The following variables were scored for each random point: inferred species richness index, the 19 bioclimatic variables listed above, elevation and Annual Potential Ground Moisture (PGM). Data was extracted from GIS layers using Grid Pig tools extension of ArcView 3.1.

Annual PGM was calculated as: $\text{Annual PGM} = \text{MP} - \text{PET}$; Where MP = Monthly precipitation, PET = Potential Evapotranspiration; $\text{PET} = \text{Monthly temperature mean above } 0^{\circ}\text{C} \times 4.910833333$, otherwise = 0 (Thornthwaite 1948; Thornthwaite and Mather 1957).

The regression tree analysis with CHAID (Chi-squared Automatic Interaction Detector, Kass 1980) method was used in order to determine the interaction between 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).

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 at 50. Analysis was performed (1) for each variable separately and (2) including all variables.

Results

From 72 species included in the analysis 63 passed cross validation test (AUC >0.7). Average AUC value of

validated models was 0.87 and average prediction accuracy 80%. Inferred species richness varied from 2 to 63 with an average value of 36. Inferred Species richness was not uniform within the study area (Fig. 2).

Species richness in this study showed non linear correlation with elevation, with a well expressed mid-elevation (~ 800 m) peak (Fig. 3). The lowest richness was predicted for high elevation ($>2,500$ m) and low species richness was predicted for the Colchis lowland and Black Sea Coast. The highest richness was predicted for the elevation between 500 and 1,500 m.

Species richness was positively correlated with variables associated with temperature and negatively with variables associated with precipitation (Table 1; Fig. 4); only a few variables had no significant correlation with species richness (Table 1).

The regression tree analysis for each variable separately is given in Table 1. Most of the variables were useful for discrimination of species richness except: Precipitation of Coldest Quarter, Precipitation of Driest Quarter and

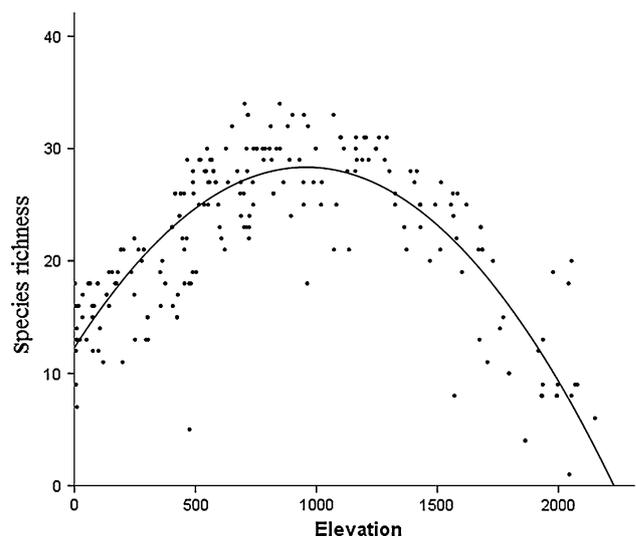
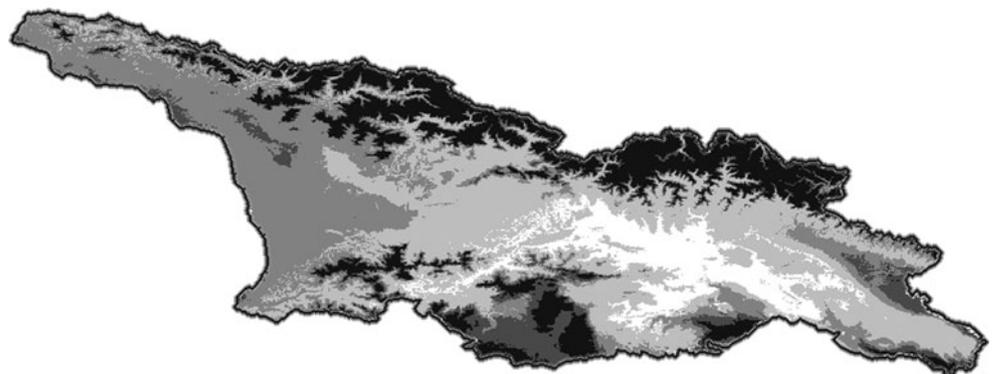


Fig. 3 Distribution of ant species richness along altitudinal gradient with line of best fit

Fig. 2 Ant species richness generated by summing individual predictions of the distributions of species. *Lighter tones* indicate high predicted species richness and *darker tones* indicate lower species richness



Precipitation of Driest Month. In General Variables associated with precipitation were less useful for discrimination of species richness using single factor. Variables associated with temperature were more predictive for species richness (Table 1).

The regression tree including 21 environmental factors revealed four important discriminators for species richness:

Elevation, Precipitation of driest quarter, Precipitation of coldest quarter and Annual precipitation ($R^2 = 0.827$, $SEE = 3.006$). Figure 5 provides an overall picture of the relative importance of the variables. The first most important discriminator is elevation ($P < 0.001$). The second splitter is precipitation, however different season precipitations are important at different elevations: (1) for

Table 1 Summary table of regression tree analysis using CHAID algorithm for single variables and correlation of species richness with those variables

Variables	Correlation coefficient	Regression tree analysis using CHAID algorithm	
		R ²	SEE
Mean temperature of driest quarter	0.311*	0.673	6.36
Mean temperature of wettest quarter	0.435*	0.389	7.123
Temperature annual range	0.221*	0.295	9.304
Min temperature of coldest month	0.409*	0.685	5.649
Max temperature of warmest month	0.562*	0.659	5.194
Temperature seasonality	0.391*	0.337	8.045
Isothermality	-0.272*	0.252	9.372
Mean diurnal range	-0.022		
Precipitation of coldest quarter	0.008		
Precipitation of warmest quarter	-0.309*	0.243	9.31
Precipitation of driest quarter	0.004		
Precipitation of wettest quarter	-0.260*	0.256	8.635
Precipitation seasonality	-0.219*	0.17	9.578
Precipitation of driest month	0.013		
Precipitation of wettest month	-0.232*	0.245	8.573
Mean temperature of coldest quarter	0.436*	0.724	5.539
Mean temperature of warmest quarter	0.548*	0.694	4.71
Annual precipitation	-0.144*	0.225	9.696
Mean annual temperature	0.510*	0.777	3.491
Elevation	-0.538*	0.777	3.86
Annual potential ground moisture	-0.417*	0.445	7.715

Significant correlations ($P < 0.005$) are marked with asterisk (*)

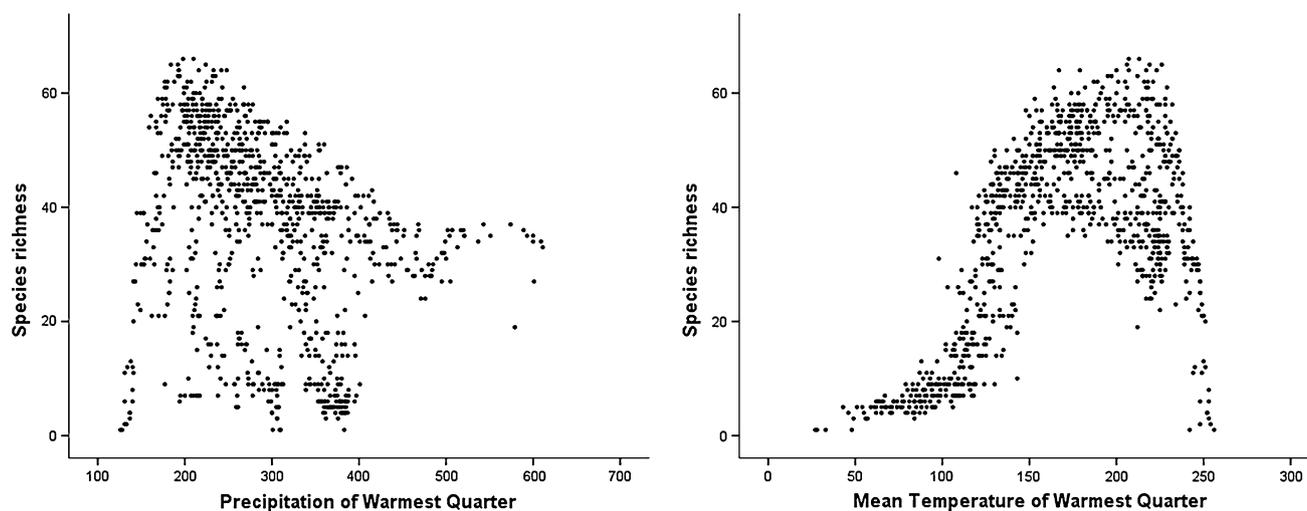
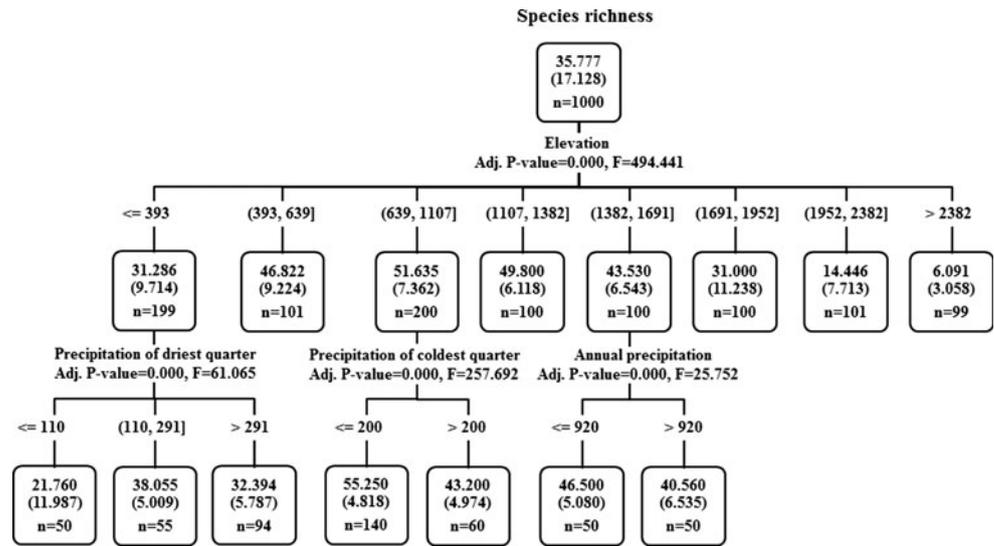


Fig. 4 Correlation of inferred species richness with precipitation of warmest month and mean temperature of warmest quarter

Fig. 5 Regression tree using CHAID algorithm and 21 environmental variables. The numbers in the boxes represent the predicted mean and the standard deviation (between brackets) of species richness. *n* is the number of points in each branch



lower elevation (≤ 393 m) precipitation of the driest quarter is the second important splitter, highest species richness (Mean 38.055, SD 5.009) is predicted where precipitation during the driest quarter is between 110 and 291 mm; (2) for mid elevation (639–1,107 m) precipitation during the coldest month is the second important splitter—highest species richness (Mean 55.25, SD 4.818) is predicted where the precipitation of the coldest quarter is less or equal to 200 mm; (3) for high elevations (1,382–1,691 m) annual precipitation is the second important splitter—highest species richness (Mean 46.5, SD 5.08) is predicted where annual precipitation is less than or equal to 920 mm.

Discussion

Variation of species richness with climatic variables

Ant’s species richness, similar to other animal groups, is strongly correlated with climate. Whereas pattern varies by region, the general trend is that richness is positively correlated with temperature and negatively correlated with precipitation and temperature range. This pattern is observed both at a global (Dunn et al. 2007; Dunn et al. 2009) and at a local scale (Wielgoss et al. 2010).

In this study, species richness was negatively correlated with variables associated with precipitation and positively correlated with variables associated with temperature (Table 1; Fig. 4). However, the combination of variables is more important than the individual predictors. Table 2 shows the distribution of average species richness dependent on different combinations of annual precipitation and mean annual temperature. There is a well expressed area (Table 2, cells with black background) which favors high species richness and species richness decreases in any

direction from this area. Given the same temperature values, the species richness is higher if precipitation is low. Given the same precipitation level, richness increases with temperature. However, above a certain threshold temperature, species richness decreases. This may reflect dependence of the richness on the evaporation level: if the temperature is high, water evaporation increases and soil moisture decreases.

Figure 6 shows the dependence of species richness on annual potential ground moisture (Thornthwaite 1948; Thornthwaite and Mather 1957). Species richness decreases on both sides of the optimal moisture. Many ant species are able to change the moisture within the nest so that nest moisture is significantly different compared to the surrounding soil (Frouz 2000; Frouz and Finer 2007; McCa-hon and Lockwood 1990). This is achieved either by creating drainage near the nest so that water can quickly go into deeper layers thus reducing moisture or by construction ditches where water accumulates and creates constantly wet zones in the anthill (Green et al. 1999; Frouz and Jilkova 2008). Despite the fact that many species of ants are able to affect anthill moisture, this study shows that soil moisture is a very strong delimiting factor for the species richness of ants at a large scale.

Spatial variation of species richness

Many publications indicate that the number and abundance of species correlates with elevation; Brühl et al. (1999) studied leaf litter ant communities along an elevation gradient on Mount Kinabalu, Malaysia. The number of ant species in the leaf litter decreased exponentially without evidence of a peak in species richness at mid-elevations. Fisher (1999) showed that species richness decreased with elevation linearly in Madagascar ant communities. Samson

Table 2 Mean annual precipitation (mm), Annual temperature (°C) and Average species richness

Annual Mean Temperature	-2	-1	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Annual Precipitation																		
400																	4	1
500													43	33	35	29	21	4
600						8	12	22	39	40	38	44	40	43	43	35	18	14
700				4	7	11	25	34	41	44	47	46	45	42	38	30		
800		2	2	3	13	17	32	37	43	44	44	42	39	37	37			
900	3	3	3	3	14	13	33	33	40	41	41	40	39					
1000	3	3	3	4	7	15	23	32	39	39	41	37	35	36	37			
1100				5	5	8	19	36	34	33	39	37	36		36			
1200					8	16			34	27	34	33	33	34	36	38		
1300												33	34	34	27	37	35	
1400														32	28	28	30	29
1500															30	30	27	23
1600															30	26	26	25
1700															25	24	24	27
1800																27	30	28
1900																25	26	25
2000																22	24	
2100																		23
2200																		21
2300																		10
2400																		17
Average Elevation (m)	2983	2811	2644	2465	2262	2048	1834	1681	1450	1292	1096	953	814	724	571	397	175	53

Darker tones indicate highest species richness; lighter tones indicate lowest species richness. The numbers in the cells indicate the average number of species at a combination of precipitation and temperature

et al. (1997) surveyed how species richness and abundance in ant communities changes along an elevation gradient in Philippines. Measures of species richness and relative abundances peaked at mid-elevations and declined sharply with increasing elevation. Ants were extremely rare above 1,500 m. Similar patterns were observed in a number of other studies (Olson 1994; Sanders et al. 2003; Sabu et al. 2008). Sanders et al. (2003) surveyed species richness in three canyons in Spring Mountains, Southern Nevada. Ant

species richness increased linearly with elevation along two transects and peaked at mid-elevation along a third transect.

Several explanations have been suggested to explain the dependence of species richness on the altitudinal gradient: direct effect of climate (Krebs 2001); indirect effect of climate through net primary productivity—a high net primary production permits consumers to maintain high population densities, thereby reducing the probability of

local extinction (Janzen 1973; Siemann 1998; Srivastava and Lawton 1998; Kaspari and Majer 2000); human impact (Sanders et al. 2003).

Species richness in this study showed a mid-elevation peak (800–1,200 m). The drop of species richness at high elevations was expected in this study because temperature decreases with increase of elevation and after a certain value it would directly limit development of ants. However, ant species richness also declines at lower elevations, where the temperature is high and when it is known that ants species richness is positively correlated with temperature. Explanation of why species richness is low at lower elevations (<500 m) derives from the geographic conditions of Georgia. Figure 7 illustrates changes in mean annual temperature and annual precipitation with elevation within the study area.

Annual mean temperature linearly decreases with increase of elevation. Annual precipitation at lower elevations (<700 m) has two basic trends: it either increases or decrease with with a decrease of altitude. This means that low elevation areas in Georgia are either too wet or too dry. After 700 m precipitation varies across mean (900 mm).

Figure 8 shows exponentiated elevation with an optimal value 1,000 m as the mean. Those locations that show decreasing precipitation with elevation (<500) correspond to the Colchis lowland (Fig. 8 area 1). Locations below 600 m and with low annual precipitation are basically arid or semi-arid sites in the south-eastern part of Georgia (Fig. 7, area 3). Generally then, sites below 500 meters in Georgia are out of the optimal humidity levels for ants.

The white color in Fig. 8 shows the optimal altitudinal range for ants in space. Even it is not the only factor

affecting the spatial pattern of species richness—some basic trends can be observed. The highest species richness (Fig. 8, area 6, marked with quadratic pattern) is concentrated at the biggest and central patch of optimal space. But the optimal spaces which are remote and enclosed by below-optimal space have a lower species richness (Fig. 8, areas 4, 5, 7, 8).

Ant species are very strongly bound within the high elevation mountain ranges of the Great Caucasus from the north and the Lesser Caucasus and arid places in Armenia from the south. Most probably, species turnover within Georgia will be higher than from adjacent territories. Species turnover within Georgia might be limited by the Likhi Range (Fig. 8, area 2) which connects the Great and Lesser Caucasus ranges. This will increase re-colonization times in the western part of optimal space, resulting in lower species richness.

Usage of spatial model of species richness for conservation

Spatial distribution of species richness might be different for other taxa, but many studies have shown that that species numbers of different taxa in the same area correlate with each other (Toranza and Arim 2010; Newbold et al. 2009, Garcia 2006). Therefore, it is logical to expect that species in other groups will show similar spatial distributions to that of ants in Georgia. The area which was shown in this study to have the highest number of ants might be the core area for Georgian biodiversity. Unfortunately, there are no studies on spatial distribution of species

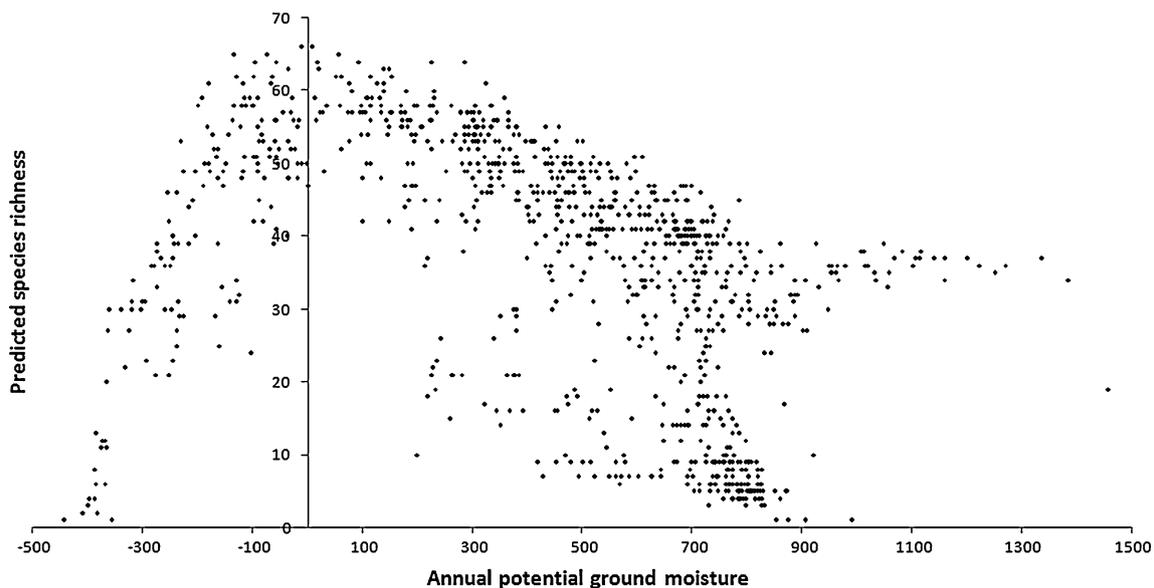


Fig. 6 Dependence of species richness on annual potential ground moisture

Fig. 7 Distribution of mean annual temperature ($^{\circ}\text{C} \times 10$) and annual precipitation (mm) across altitudinal gradient in Georgia. Data collected from 1,000 randomly generated points across study area

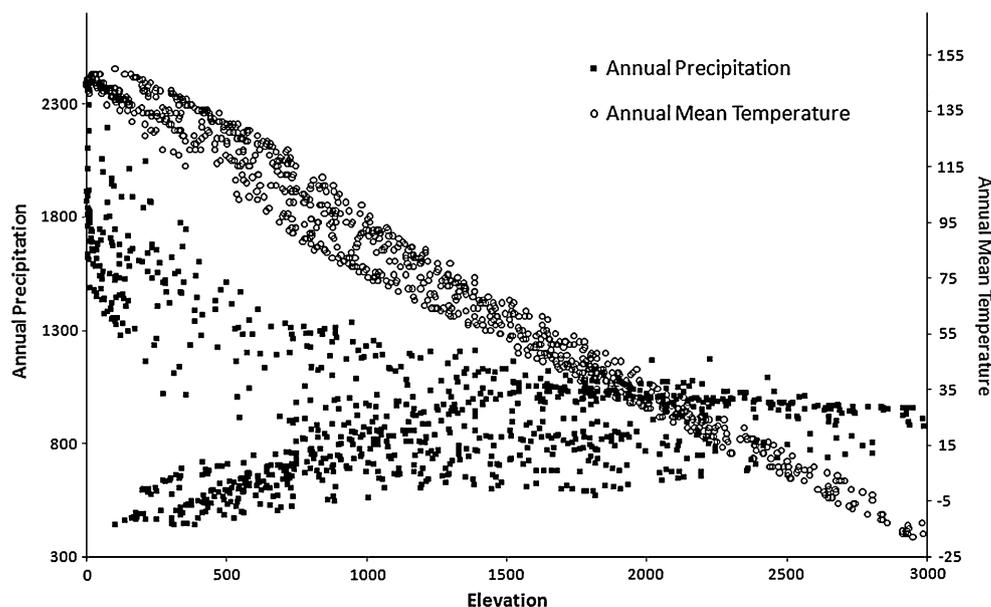
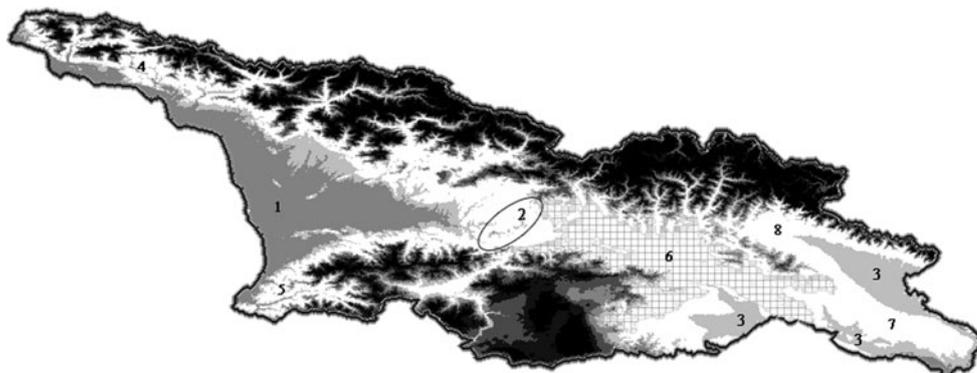


Fig. 8 Exponentiated elevation. *Lighter tones* show areas near to the mean elevation (800 m) of highest predicted species richness and *darker tones* show deviation from mean elevation. 1, 3 Unfavorable climatic conditions; 2 Likhi range; 4, 5, 7, 8 suitable climatic conditions, enclosed with unfavorable areas; 6 central patch of suitable climatic conditions, quadratic pattern shows highest species richness



richness conducted for other groups in Georgia to test this hypothesis. But, if this turns out to be true, it will be an important outcome for practical conservational. Georgia is still undergoing a process of creation of National Parks. Information about spatial pattern of species richness would be helpful for such planning. Single taxa may not be sufficient for usage as indicators of biodiversity (Oliver et al. 1998) or for detection of overall biodiversity change (Lawton et al. 1998). However, data on species occurrences is accumulated in the literature and in online which can be used for determining important sites for conservation. Distribution data for more than 10 thousand species is available for Georgia (Eliava et al. 2007, Tarkhnishvili et al. 2010), and this study is a first attempt to understand the primary drivers of the spatial pattern of species richness in Georgia. The methods here, can be applied to other taxa and can be used to assist in the decision making processes surrounding where conservation efforts needs to be focused.

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References

- Agosti D, Majer JD, Alonso LE, Schultz TR (2000) *Ants: standard methods for measuring and monitoring biological diversity*. Smithsonian Institution Press, Washington, DC
- Andersen AN, Majer JD (2004) Ants show the way down-under: invertebrates as bioindicators in land management. *Front Ecol Environ* 2:218–291
- Bestelmeyer BT, Wiens JA (2001) Ant biodiversity in semi-arid landscape mosaics: the consequences of grazing vs. natural heterogeneity. *Ecol Appl* 11:1123–1140
- Brühl CA, Mohamed M, Linsenmair KE (1999) Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. *J Trop Ecol* 15:265–277

- Ceballos G, Brown JH (1995) Global patterns of mammalian diversity, endemism, and endangerment. *Conserv Biol* 9:559–568
- Dunn RR, Sanders NJ, Fitzpatrick MC, Laurent E, Lessard J-P, Agosti D, Andersen AN, Bruhl C, Cerda X, Ellison AM, Fisher BL, Gibb H, Gotelli NJ, Gove A, Guenard B, Janda M, Kaspari M, Longino JT, Majer J, Mcglynn TP, Menke SB, Parr CL, Philpott SM, Pfeiffer M, Retana J, Suarez AV, Vasconcelos HL (2007) Global ant (Hymenoptera: Formicidae) biodiversity and biogeography—a new database and its possibilities. *Myrmecological News* 10:77–83
- Dunn RR, Sanders NJ, Menke SB, Weiser MD, Fitzpatrick MC, Laurent E, Lessard J-P, Agosti D, Andersen A, Bruhl C, Cerda X, Ellison A, Fisher B, Gibb H, Gotelli H, Gove A, Guénard B, Janda M, Kaspari M, Longino JT, Majer J, McGlynn TP, Menke SB, Parr C, Philpott S, Pfeiffer M, Retana J, Suarez A, Vasconcelos H (2009) Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. *Ecol Lett* 12:324–333
- Eliava I, Cholokava A, Kvavadze E, Bakhtadze G, Bukhnikashvili A (2007) New data on animal biodiversity of Georgia. *Bulletin of the Georgian National Academy of Sciences* 175(2):115–119
- Fisher BL (1999) Ant diversity patterns along an elevational gradient in the reserve *Naturalle Integrale d'Andohalela*, Madagascar. *Fieldiana Zool* 94:129–147
- Fitzpatrick MC, Weltzin JF, Sanders NJ, Dunn RR (2007) The biogeography of prediction error: why does the introduced range of the fire ant over-predict its native range? *Glob Ecol Biogeogr* 16(1):24
- Frouz J (2000) The effect of nest moisture on daily temperature regime in the nest of *Formica polyctena* wood ants. *Insect Soc* 47:229–235
- Frouz J, Finer L (2007) Diurnal and seasonal fluctuations in wood ant (*Formica polyctena*) nest temperature in two geographically distant populations along a south - north gradient. *Insect Soci* 54:251–259
- Frouz J, Jilkova V (2008) The effect of ants on soil properties and processes (Hymenoptera: Formicidae). *Myrmecol News* 11:191–199
- Garcia A (2006) Using ecological niche modelling to identify diversity hotspots for the herpetofauna of Pacific lowlands and adjacent interior valleys of Mexico. *Biol Conserv* 130:25–46
- Gratiashvili N, Barjadze Sh (2008) Checklist of the ants (FORMICIDAE LATREILLE, 1809) of Georgia. *Proc Instit Zool* 23:130–146
- Green WP, Pettry DE, Switzer RE (1999) Structure and hydrology of mounds of the imported fire ants in the south-eastern United States. *Geoderma* 93:1–17
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climogy* 25:1965–1978
- Iverson LR, Prasad MA (2001) Potential changes in tree species richness and forest community types following climate change. *Ecosystems* 4:186–199
- Janzen DH (1973) Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology* 54:687–708
- Kaspari M, Majer JD (2000) Using ants to monitor environmental change. In: Agosti D, Majer JD, Alonso LE, Schultz TR (eds) *Ants: standard methods for measuring and monitoring biodiversity*. Smithsonian Institution Press, Washington, pp 89–98
- Kass G (1980) An exploratory technique for investigating large quantities of categorical data. *Appl Stat* 29:119–127
- Kerr JT (2001) Butterfly species richness patterns in Canada: energy, heterogeneity, and the potential consequences of climate change. *Conserv Ecol* 5(1):10. [Online] URL: <http://www.consecol.org/vol5/iss1/art10/>
- Kienasta F, Wildia O, Brzezieckib B (1998) Potential impacts of climate change on species richness in mountain forests—an ecological risk assessment. *Bioll Conserv* 83:291–305
- Krebs CJ (2001) *Ecology: the experimental analysis of distribution and abundance*. Benjamin Cummings, San Francisco
- Lawton JH, Bifnell DE, Bolton B, Blowmers GF, Eggleton P, Hammond PM, Hodda M, Holt RD, Larsen TB, Mawdsley NA, Stork NE, Srivastava DS, Watt AD (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* 391:72–76
- McCahon TJ, Lockwood JA (1990) Nest architecture and pedoturbation of *Formica obscuripes* FOREL (Hymenoptera, Formicidae). *Pan-Pac Entomol* 66:147–156
- Muñoz MES, Giovanni R, Siqueira MF, Sutton T, Brewer P, Pereira RS, Canhos DAL, Canhos VP (2009) openModeller: a generic approach to species' potential distribution modelling. *Geoinformatica* 15:111–135
- Myers N, Mittermier RA, Mittermier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858
- Newbold T, Gilbert F, Zalat S, El-Gabbas A, Reader T (2009) Climate-based models of spatial patterns of species richness in Egypt's butterfly and mammal fauna. *J Biogeog* 36:2085–2095
- Oliver I, Beattie AJ, York A (1998) Spatial fidelity of plants, vertebrate and invertebrate assemblages in multiple-use forest in Eastern Australia. *Conserv Biol* 12:822–835
- Olson DM (1994) The distribution of leaf litter invertebrates along a neotropical altitudinal gradient. *J Trop Ecol* 10:129–150
- Ortega-Huerta MA, Peterson AT (2008) Modeling ecological niches and predicting geographic distributions - a test of six presence-only methods. *Rev Mex Biodivers* 79:205–216
- Sabu TK, Vineesh PJ, Vinod KV (2008) Diversity of forest litter-inhabiting ants along elevations in the Wayanad region of the Western Ghats. *J Insect Sci* 8:69. Available online: insect-science.org/8.69
- Samson DA, Rickart EA, Gonzales PC (1997) Ant diversity and abundance along an elevational gradient in the Philippines. *Biotropica* 29(3):349–363
- Sanders NJ, Moss J, Wagner D (2003) Patterns of ant species richness along elevational gradients in an arid ecosystem. *Global Ecol Biogeog* 12:93–102
- Sauberer N, Zulka KP, Abensperg-Traun M, Berg HM, Bieringer G, Milasowsky N, Moser D, Storch C, Trostl R, Zechmeister H, Grabherr G (2004) Surrogate taxa for biodiversity in agricultural landscapes of eastern Austria. *Biol Conser* 117:181–190
- Siemann E (1998) Experimental tests of effects of plant productivity and diversity on grassland Arthropod diversity. *Ecology* 79:2057–2070
- Soberon J, Peterson AT (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodivers Inform* 2:1–10
- Srivastava DS, Lawton JH (1998) Why more productive sites have more species: an experimental test of theory using tree-hole communities. *Am Nat* 152:510–529
- Stockwell DRB (1999) Genetic algorithms II. In: Fielding AH (ed) *Machine learning methods for ecological applications*. Kluwer Academic Publishers, Boston, pp 123–144
- Stockwell DRB, Peters DP (1999) The GARP modeling system: problems and solutions to automated spatial prediction. *Int J Geogr Infn Syst* 13:143–158
- Swets JA (1986) Indexes of discrimination or diagnostic accuracy—their ROCs and implied models. *Psychol Bull* 99:100–117

- Tarkhishvili D, Chaladze G, Gavashelishvili L, Javakhishvili Z, Mumladze L (2010) Georgian biodiversity database. Internet: <http://www.biodiversity-georgia.net/>. Accessed 12 Feb 2011
- Thornthwaite CW (1948) An approach toward a rational classification of climate. *Geogr Rev* 38:55–94
- Thornthwaite CW, Mather JR (1957) Instructions and tables for computing potential evapotranspiration and the water balance. *Publ Climatol* 10:311
- Toranza C, Arim M (2010) Cross-taxon congruence and environmental conditions. *Ecology* 10:18
- Van Diepen MV, Franses HP (2006) Evaluating Chi-squared automatic interaction detection. *Inf Syst* 31:814–831
- Van Hamburg H, Andersen AN, Meyer WJ, Robertson HG (2004) Ant community development on rehabilitated ash dams in South African Highveld. *Restor Ecol* 12:552–558
- Wielgoss A, Tschardtke T, Buchori D, Fiala B, Clough Y (2010) Temperature and a dominant dolichoderine ant species affect ant diversity in Indonesian cacao plantations. *Agr Ecosyst Environ* 135:253–259