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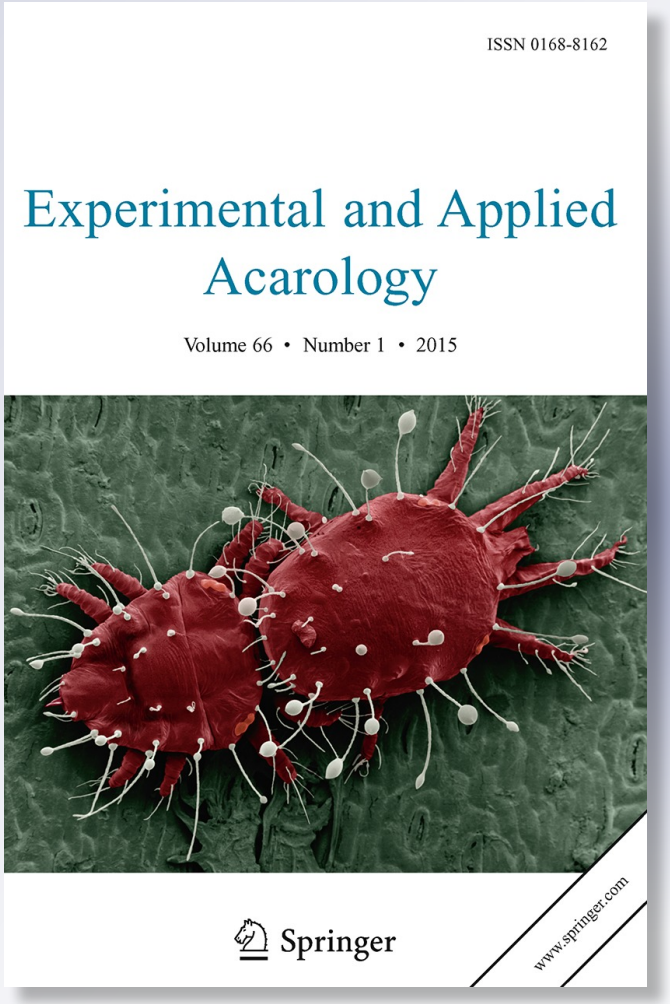

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Abstract Many aboveground animals and plant communities have been studied along elevational gradients whereas studies on soil animals are scarce. Here, we studied oribatid mite community distribution along an elevational gradient from 600 to 2200 m in forest ecosystems of the Western Lesser Caucasus Mountains in Georgia. Overall, 86 oribatid mite species were found at the study sites. Oribatid mite densities were generally low ($\sim$9800 ind./m^2), and 74 % of all species reproduced sexually indicating that resource conditions at the study sites are generally poor. Oribatids mainly comprised Brachypylina (76 %), Mixonomata (13 %), Desmonomata (6 %) and Enarthronota (5 %). Oribatid mite community structure changed along the elevational gradient and the changes correlated with temperature, pH, litter thickness and density of the herb layer. The dominance of sexually reproducing taxa and low overall abundance indicate that the studied elevational gradient is characterized by poor resource conditions for soil microarthropods. Oribatid mite species richness and density declined with elevation suggesting that decreasing temperature in concert with resource limitation is a main driver of oribatid mite communities whereas stochastic factors (such as mid-domain effects) are of minor importance.

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Introduction

Understanding animal communities along natural gradients is one of the central research focuses of ecology and biogeography (Gaston 2000; Lomolino et al. 2006). In terms of the distribution of species diversity the most striking and well documented gradients are latitudinal and elevation gradients (Rohde 1992; Rahbek 1995, 2005; Willig et al. 2003; Fischer et al. 2011; Guo et al. 2013) which are mirroring each other in many ways. Therefore, hypotheses explaining the diversity distributions in both gradients are used interchangeably (Lomolino 2001; Lomolino et al. 2006; Adams 2009). Since mountains are much easier to investigate (in terms of scale) than latitudinal bends, investigation of biodiversity distribution along elevation gradients is suggested as a good proxy to understand the patterns of distribution along latitudinal gradients as well (Körner 2000).

Despite numerous studies reporting patterns and potential drivers of biodiversity distribution along elevation gradients, there is no unifying theory explaining those patterns (Lomolino et al. 2006; Adams 2009). Most studies have shown a hump-shape diversity response to elevation, but there are a number of investigations suggesting monotonic decreases in species diversity, while few provide evidence of increasing, flattened, bimodal or unclear pattern in diversity distribution (Rahbek 2005; Fischer et al. 2011; Kessler et al. 2011; Guo et al. 2013). The offered explanations or hypotheses vary greatly, and the most promising ones indicate that the general explanation of the diversity distribution along either elevation or latitude is a result of complex interactions of historical, spatial and temporal (biotic and abiotic) factors (Lomolino et al. 2006; Romdal and Grytnes 2007). However, there is an important gap in our knowledge about the distribution of biodiversity which in turn can easily distort the view of general patterns. The first one is about the representative taxon sampling. Most of the studies concentrated on plants and vertebrates (Fischer et al. 2011) whereas invertebrates, especially belowground animals, fungi and prokaryotes are understudied. Second, the location on the earth surface, peculiar history and characteristics of each mountain system can result in differences in biodiversity composition. Some mountain systems, such as the Caucasus, are hardly studied in terms of species diversity in elevational gradient. In order to generalize the biogeographic patterns, those regions need to be more thoroughly investigated (Andrew et al. 2003; Fischer et al. 2011). Another difficulty is associated with the methods used to obtain elevational diversity data. Many studies only provide partial coverage of the respective gradients which may result in biased estimation of a true pattern (Kessler et al. 2011). Further, the design of the study in terms of e.g., sampling strategies and grain size may also affect the results significantly (Willig et al. 2003).

In the present study, we report results of the first case of investigation of oribatid mites species diversity along an elevation transect of a forest from the Lesser Caucasus Mountains. Despite several studies on vertical distribution of oribatid mites in mountain regions of Caucasus (Tarba 1993; Shtanchaeva 2003; Arabuli et al. 2004; Murvanidze et al. 2004; Davudova 2013), incomplete sampling design did not allow to discuss the obtained results in a general framework. The Caucasus Mountain region is one of the global biodiversity hotspots (Mittermeier et al. 2004). Invertebrate biodiversity of the Caucasus is largely unexplored. Almost all studies (including the current project) with the aim of an

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inventory of particular groups of invertebrates in the Caucasus region resulted in one or several new species either for the studied area or for science. Deficiency in high quality data on invertebrate taxonomy and distribution in the Caucasus area makes it impossible to conduct regional scale biogeographical analyses with few exceptions (Pokryszko et al. 2011; Ghobad-Nejhad and Hallenberg 2012). Hence, the primary aim of this study was to evaluate the oribatid mite community structure along an elevational transect in the mountain forests of Western Lesser Caucasus and reveal possible drivers of the observed pattern. We addressed four major questions: (1) Does oribatid mite density decrease with increasing elevation? Resource limitation, i.e. the quality of food resources is a possible driver of soil and litter dwelling microarthropod densities at higher elevations, whereas abiotic conditions play a minor role (Illig et al. 2010; Wehner et al. 2014). Hence, we suppose that resource limitation along with more harsh environmental conditions at high elevations act as limiting factors for population density. (2) Is the species number highest at mid-elevations? The hump-shaped distribution of species richness along the elevation gradient is supposed to be due to deterministic (intermediate productivity, climate and disturbance) or stochastic (Mid-Domain Effect) factors. (3) Does the proportion of sexually reproducing taxa in oribatid mite communities change with elevation? Sexual reproduction is considered advantageous in resource limited habitats (Maraun et al. 2013; Fischer et al. 2014). As higher elevations are expected to provide low quality food for decomposer taxa (Leuschner et al. 2007; Illig and Schatz 2008), we expect the proportion of sexually reproducing oribatids to increase at higher elevations. (4) Are changes in the community structure of oribatid mites at higher elevations related to their trophic ecology? Recent study showed that decomposer mites dominate at lower elevations whereas other feeding groups, including lichen-feeders, predators and scavengers, dominate at higher elevations (Fischer et al. 2014).

Materials and methods

Sampling area and data collection

We established an elevational transect in the northern slopes of the Georgian part of the Western Lesser Caucasus (Sairme gorge—41.88°N and 42.76°E) spanning from 600 to 2200 m. The climate of the study area is temperate, however, at lower elevations it resembles subtropical climate with mean annual temperatures of around 14 °C that decline with elevation by ~0.65 °C every 100 m (Neidze 2003; Dolukhanov 2010). The upper limit of the transect is at the timberline of the Lesser Caucasus (Nakhutsrishvili 2013). Sairme gorge harbors old-growth natural mixed forests which existed throughout Pleistocene glaciations (Shatilova et al. 2011). Dominant tree species include *Abies nordmaniana* (Stev.), *Picea orientalis* (L.), *Fagus orientalis* Lipsky, *Tilia begonifolia* Stev., *Carpinus betulus* L., *Castanea sativa* Mill., *Alnus barbata* C. A. Mey, *Acer* ssp., *Quercus* ssp. The understory vegetation is dominated by evergreen bushes, e.g. *Rhododendron ponticum* L. and *Laurocerasus officinalis* Roem. (Dolukhanov 2010; Nakhutsrishvili 2013). Sairme gorge is not a protected area and is subject of anthropogenic disturbances such as timber logging and grazing, however, human influence is not strong.

Samples were taken at 600, 800, 1000, 1200, 1400, 1600, 1800, 2000 and 2200 m (for coordinates see Supplementary Material—Table 1). At each elevation, three plots were established at least 50 m distant from each other and from each of those three plots three

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100 cm^3 soil samples were collected from different microhabitats including leaf litter, soil under dead wood and under moss. Those three subsamples were pooled resulting in three replicates per elevation.

Oribatid mites were extracted using modified Berlese–Tullgren apparatus for 1 week (Coleman et al. 2004). After extraction, mites were stored in 70 % ethanol, and for microscopic inspection mounted on slides with lactic acid. Adult oribatid mites were identified at species level using Ghilarov and Krivolutsky (1975) and Weigmann (2006) and counted. A full list of species with authors is given in the Supplementary Material (Table 1); voucher specimens are kept at the Agricultural University of Georgia. Reproductive mode was ascribed to the species according to literature (Norton et al. 1993; Cianciolo and Norton 2006; Domes et al. 2007; Domes-Wehner 2009; Wehner et al. 2014). If the reproductive mode was not known for the studied species we inferred it from a closely related species of the same genus. Feeding strategy of oribatid mites was defined using mainly Fischer et al. (2014) and Schneider et al. (2004a, b).

During field sampling environmental variables were measured, including plant richness (20 × 20 m around each plot), slope, exposition, soil pH, depth of leaf litter, amount of dead wood, coverage by herbaceous plants and human impact (for details see Supplementary Material—Table 2). Temperature and precipitation for each elevation was calculated using WorldClim v1.4 data base (Hijmans et al. 2005). The WorldClim data have ~ 1 km^2 resolution and is the only available climate data for the region. We calculated the mean value of five horizontal adjacent grid cells to obtain the best estimate of mean annual temperature and mean annual precipitation for each elevation. All variables (Supplementary Material—Table 3) were then used in subsequent statistical analyses to identify determinants of oribatid species diversity.

Data analyses

Plot species richness and densities as well as pooled species richness (for each elevation) were subjected to simple and multiple linear (stepwise) regression analyses to reveal the relationship and test for significance with elevation and other habitat variables. Before the multiple regression we calculate intervariable correlations (Spearman's r). Significant but moderate correlation were detected between pH and temperature ($r = 0.5$, $p = 0.006$) and between litter amount and human impact ($r = -0.5$, $p = 0.005$) and precipitation ($r = -0.46$, $p = 0.017$). Since there were not strong relationships between variables (all are <0.7) we assumed independence of the environmental factors in regression analyses.

Elevational range distributions were further explored using mid-domain effect (MDE) null model (Colwell and Hurtt 1994) to test the potential effect of random processes on the pattern of oribatid species richness using RangeModel 5 (Colwell 2008).

We calculated the proportions of the individual density and species numbers of parthenogenetic species for each sampling plot following one way ANOVA, to investigate the effect of elevation (as fixed factor) on the proportion of parthenogenetic individual and species numbers. The community structure of oribatid mites was studied using canonical correspondence analyses (CCA) using CANOCO v5 (Jongman et al. 1995; Ter Braak and Šmilauer 2002). If not otherwise stated all analyses were performed using SPSS for Windows v.18 (SPSS, Chicago, IL, USA).

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Results

A total of 2064 oribatid mite individuals belonging to 86 species were identified (Supplementary Material—Table 1). Two species, *Suctobelbella tuberculata* (Strenzke) and *Oribatella tenuis* Csiszar were new for Georgia. Overall, mean abundance of oribatid mites was low (9844 ± 13,713 ind./m^2). Lowest densities occurred at 1800 m (1320 ± 1933 ind./m^2) whereas densities were highest at 1000 m (22,900 ± 32,189 ind./m^2) (Supplementary Material—Table 3). Generally, densities significantly declined with elevation, however, this relationship was weak ($r^2 = 0.15$; $F_{1,25} = 2.33$; $p = 0.045$; Fig. 1).

Species richness also declined with elevation ($r^2 = -0.46$; $F_{2,24} = 5.98$, $p = 0.044$; Fig. 2). Only two variables, elevation and slope, contributed to the multiple regression models. Temperature was also significantly correlated with oribatid mite species richness; however, it was inter-correlated with elevation (Pearson's $r = 0.97$, $p < 0.001$). There was no correlation between plant and mite species richness (Pearson's $r = 0.2$; $p > 0.05$).

MDE simulation produced hump-shaped diversity distribution with the peak of richness at 1200 m and was not correlated with observed richness ($r^2 = 0.28$; $p > 0.05$). When species occurrences within range minima and maxima were interpolated (default function of RangeModel software) the MDE effect was the strongest predictor of derived empirical richness ($r^2 = 0.37$; $p < 0.01$ for whole fauna, and $r^2 = 0.62$; $p < 0.01$ for species with a range size of more than 200 m).

Parthenogenetic species comprised 26 % of total oribatid mite species but only 6 % of all individuals. The proportion of parthenogenetic individuals and species did not change significantly with elevation ($F_{1,25} = 0.69$; $p > 0.05$ and $F_{1,25} = 0.29$; $p > 0.05$, respectively). Average density of parthenogenetic individuals was 530 ± 569 ind./m^2 and species number per elevation was 5 ± 4.

According to CCA, oribatid mite community structure strongly changed with elevation (length of gradient = 4.0; Fig. 3). The first axis of the CCA represented the altitudinal gradient. Most abundant species at lower elevations (600–800 m) were *Minunthozetes pseudofusiger* (Schweizer), *Phthiracarus crassus* Niedbala, *Phthiracarus ferrugineus* (Koch), *Damaeolus ornatissimus* Csiszár, *Quadroppia quadricarinata* (Michael) and *Oribatula tibialis* (Nicolet), and at higher elevations (2000-2200 m) *Parachipteria georgica* Murvanidze and Weigmann, *Suctobelbella acutidens* (Forsslund) and *Trichoribates caucasicus* Shaldybina dominated. Temperature, soil pH and herb cover corresponded mainly with the first axis, with higher temperatures and higher pH at lower elevations and

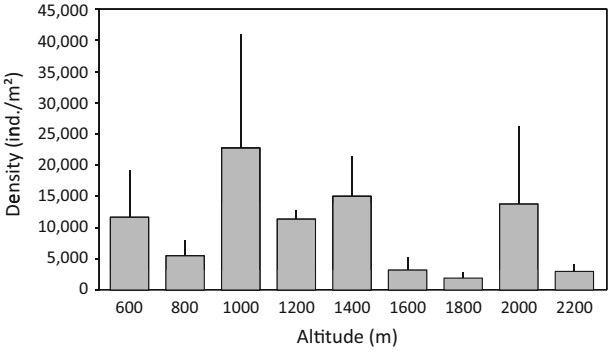

Fig. 1 Densities of oribatid mites (ind./m^2 ± SD) along the altitudinal gradient from 600 to 2200 m in Sairme gorge (Georgia)

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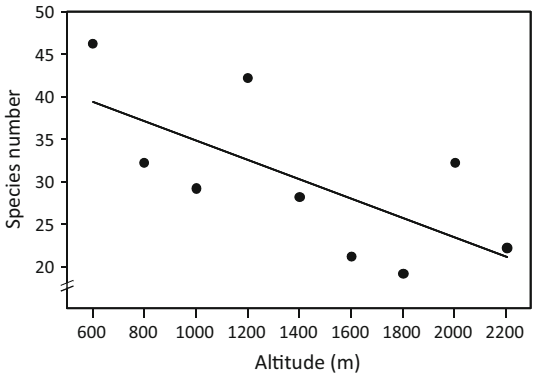

Fig. 2 Relationship between oribatid mite species richness and elevation in Sairme gorge (Georgia)

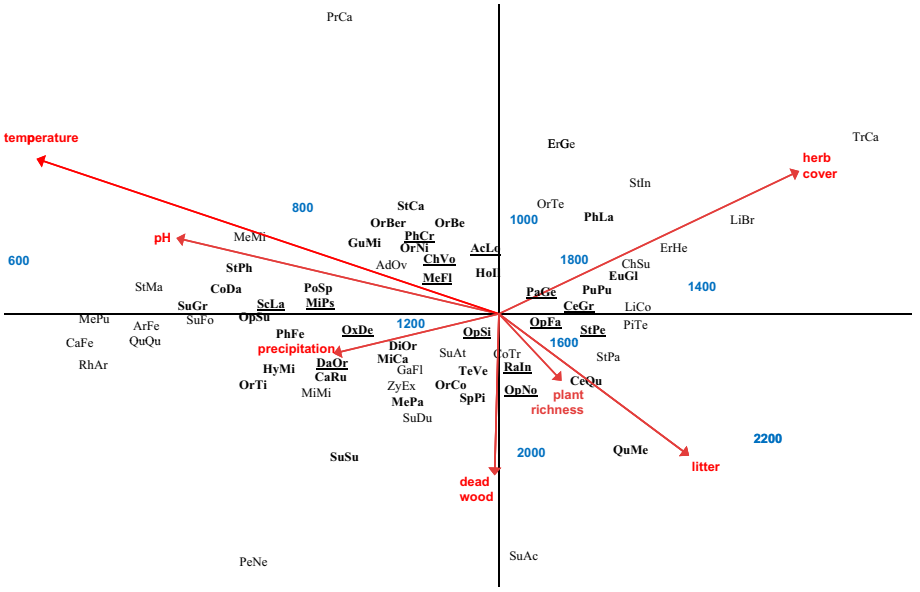

Fig. 3 CCA (canonical correspondence analyses) ordination diagram of oribatid mite species communities along the altitudinal gradient from 600 to 2200 m in Sairme gorge (elevation was included as passive variable). *Red arrows* represent environmental variables. For full species names see Supplementary Material. Eigenvalues of axes 1 and 2 were 0.27 and 0.20, respectively. Data were log transformed prior to the analysis. The 15 most abundant taxa are *underlined* and species with more than 10 % of occurrence are in *bold* face

higher herb cover at higher elevations. The second axis of the CCA was mainly represented by a high amount of dead wood (especially at 2000 m) which corresponded with the occurrence of certain oribatid mite species such as *Sphaerozetes piriformis* (Nicolet) and *Metabelba papillipes* (Nicolet). Environmental variables accounted for a total of 28.4 % of the variation in the dataset, with pH (8.2 %), dead wood (5.9 %) and temperature (5.6 %) being most important. Overall, the most species rich taxa of oribatid mites at the study sites were Brachypylina (76 %), Mixonomata (13 %), Desmonomata (6 %) and Enarthronota

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(5 %). These proportions did not differ significantly between the elevations (MANOVA: Wilks' Lambda = 0.14; $F_{32,56} = 1.24$, $p = 0.24$).

Discussion

Oribatid mite density

Generally, at the study sites density of oribatid mites was low compared to other temperate forests and resembled that of tropical rain forests (Olson 1994; Maraun and Scheu 2000; Hasegawa et al. 2006; Maraun et al. 2008; Illig et al. 2010). In agreement with other studies oribatid mite density generally declined with elevation (Maraun et al. 2008; Illig et al. 2010) although highest density was detected at intermediate elevations (1000, 1400 and 2000). The low overall density can be attributed either to abiotic severity (Olson 1994) or resource limitation (Illig et al. 2010). The first is less likely to be true since at our study sites at lower elevations environmental conditions are more benign (i.e. higher temperature in winter season) than in higher elevations as well as in most temperate regions (Neidze 2003). Furthermore, none of the studied variables was correlated with oribatid mite density. This indicates that climate factors or habitat characteristics are of little importance for the observed changes in oribatid mite density. The amount (or availability) of resources as measured by the thickness of the leaf litter layer may also determine oribatid mite density (Maraun and Scheu 2000). Indeed the thickness of leaf litter at the studied plots was on average 5.4 cm (1.6 SD) which is quite low, however, the thickness of the litter layer varied only slightly across the study sites and did not have significant effects on the mite communities. Hence, the amount of litter layer alone cannot explain the elevational variation in mite density. The dominance of Brachypylina (which are mainly reproducing sexually; Norton et al. 1993) at all elevations suggests that resource limitation (in terms of quality or availability) may be of prime importance (Maraun et al. 2009; Illig et al. 2010). Hence the interaction of these two factors could provide an explanation for the variation in oribatid mite density along an elevation.

Oribatid mite species richness

Only few studies have addressed the problem of diversity changes of oribatid mite species (and soil animals in general) along an elevational gradient. One of the most comprehensive studies in Japan suggested oribatid mite diversity to change in a unimodal pattern with elevation (Mori et al. 2013). In contrast, Hasegawa et al. (2006) found oribatid mite diversity to decrease monotonically with elevation in Malaysian forests. However, the study from Japan only spanned gradient from 0 to 1200 m, whereas the study in Malaysia spanned a large gradient from 700 to 3100 m. In another study in mountain ranges in Tasmania and New Zealand no consistent pattern in changes in oribatid mite diversity was observed (Andrew et al. 2003). Other studies investigating sections of elevational gradients usually found oribatid mite diversity to monotonically decrease with elevation (Schatz 1978; Olson 1994; Lamoncha and Crossley 1998; Jing et al. 2005; Illig et al. 2010; Fischer and Schatz 2013; Fischer et al. 2014). Consistent with these findings we found oribatid mite species richness to decrease along a gradient of forest ecosystems spanning from 600 to 2200 m. The decrease in mite species richness was not linear (peaks were found at 600, 1200 and 2000 m) which can be a result of sampling bias in concert with population dynamics. However, the linear model was the most parsimonious one. Interestingly, there

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was no relationship between the density and richness of oribatid mite species suggesting that different processes can be responsible of the patterns.

Among the environmental variables that were studied, temperature (or elevation) and slope contributed to the regression models. The influence of slope on species richness is rather straightforward since more flattened areas maintain thicker leaf litter layers providing more space and more habitat for oribatid mites, whereas at steeper slopes the litter layer is eroded by wind and precipitation. Absence of species widespread in western Georgia preferring high humidity, such as *Nanhermannia nana* (Nicolet), *Oppia nitens* Koch and *Pergalumna minor* Willmann (Murvanidze et al. 2004, 2011; Murvanidze and Kvavadze 2009), supports this interpretation.

The influence of temperature on the distribution of oribatid mite species or communities is rather difficult to explain. At lower temperature (or high elevation) decomposition processes are slow resulting in thicker organic layers (Leuschner et al. 2007; Illig and Schatz 2008). However, slow litter decomposition may also be due to low resource quality (Illig and Schatz 2008). Although the temperature at our study site declined with increasing elevation, we did not detect significant changes in organic layer thickness. This suggests that the decomposition rate changes little with elevation or that the input of litter material decreases at higher elevation. Furthermore, low temperatures may hamper the ontogenetic development of oribatid species thereby limiting their distribution (Olson 1994; Hasegawa et al. 2006). This suggests that even though the amount of leaf litter is similar, fewer species colonize higher elevations due to climatic harshness.

Similar to other studies (Zapata et al. 2003; Currie and Kerr 2008) we did not find the species richness distribution of oribatid mites to follow predictions of the MDE. This suggests that deterministic factors override stochastic factors in structuring oribatid mite communities (Mori et al. 2013; Mumladze et al. 2013; Zaitsev et al. 2013).

Variation of reproductive modes along with elevation

Typically, in temperate forests the proportion of parthenogenetic species and individuals in oribatid mite communities is high (Maraun et al. 2003, 2012; Fischer et al. 2010). The dominance of parthenogenesis has been ascribed to stressful environmental conditions (Glesener and Tilman 1978; Kearney 2005) or to low population density (Gerritsen 1980). However, there also is evidence that environmental severity favors sexual rather than parthenogenetic reproduction and results in low population density (Maraun et al. 2013; Fischer et al. 2014), while high population density is associated with a high frequency of parthenogenesis (Maraun et al. 2012). In Sairme gorge, dominant sexually reproducing taxa comprised mainly secondary decomposers (*Nothrus silvestris* (Hammer), Damaeidae, Oribatulidae, Chamobatidae) as well as predators and scavengers (*Hypochthonius rufulus* Koch, Oppiidae, Suctobelbidae, Galumnidae) feeding on high quality resources in short supply (Schneider et al. 2004 a, b). Primary decomposers [Ptyctima, Liacaridae, Oribatellidae, *Euzetes globulus* (Nicolet), *Platynothrus peltifer* (Koch)] reproducing often by parthenogenesis (Fischer et al. 2014) were scarce. Recent theoretical (Scheu and Drossel 2007; Song et al. 2011, 2012) and experimental investigations (Fischer et al. 2010, 2014; Maraun et al. 2013) suggest that this pattern may be due to changes in the availability of resources. Accordingly, the low density of oribatid mites at the study area could be an indicator of resource limitation (quality and/or amount of litter material) similar to tropical rain forests (Illig et al. 2010; Maraun et al. 2013).

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Changes in oribatid mite community structure with elevation

We observed changes in oribatid mite community structure along the studied elevation gradient. However, despite these differences the fraction of parthenogenetic taxa, trophic guild composition and composition of phylogenetic lineages remained similar which is in contrast to other studies (Maraun et al. 2009; Fischer et al. 2014). This indicates that general community characteristics changed little with elevation suggesting that structuring forces of oribatid mite communities also changed little with elevation, e.g., the availability (i.e. thickness of litter layer) of resources presumably was poor and less variable at each elevation. Overall, the oribatid mite community was dominated by Brachypylina. Typical decomposer taxa such as *P. peltifer*, Achipteriidae or *Tectocepheus* spp. were rare or absent at each elevation indicating that only a very small fraction of the oribatid mite community is feeding on the dead organic material as such. This pattern is again supporting the view that resource limitation is of prime importance at the study sites. A similar community structure has been found in tropical regions where Brachypylina also dominate and where resource conditions are poor (Maraun et al. 2008). This underpins the assumptions that the whole studied altitudinal gradient is a resource poor site where only few decomposer taxa can survive and most oribatid mite species feed on fungi or animals.

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