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RESEARCH NOTE

An inverse elevational species richness gradient of Caucasian vascular plants and Encyrtidae (Hymenoptera, Chalcidoidea)

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ABSTRACT
The elevational gradient in biodiversity, i.e. the decrease in species richness with increasing altitude, is well established in ecology. Here, we examined the respective gradient of parasitic hymenopterans (Encyrtidae) and plants in the Lagodekhi National Park (Country of Georgia) across an elevational gradient from 665 m to 2559 m a.s.l. by means of a year-round sampling of insects and a seasonal sampling of plants. Contrary to expectation, we found species richness of both taxa to peak at highest elevations. This unusual pattern was related to particular shifts in vegetation types, from relatively species-poor forests over rich grasslands towards poorer highland scrub vegetation. Our results call for a closer look at elevational gradients and highlights the need for including vegetation types in the assessment of altitudinal diversity gradients.

RÉSUMÉ
Le gradient altitudinal de biodiversité, c.-à-d. la diminution de la richesse spécifique suivant l'augmentation de l'altitude, est bien connu en écologie. Nous avons examiné les gradients d'hyménoptères parasites (Encyrtidae) et de plantes dans le Parc National de Lagodekhi (Georgie), entre 665 et 2559 m a.s.l., par un échantillonnage annuel d'insectes et saisonnier de plantes. Contrairement aux attentes, nous avons trouvé que la richesse spécifique des deux taxa était plus élevée aux plus hautes altitudes. Ce patron inhabituel était lié à des changements particuliers des types de végétation, passant de forêts relativement pauvres en espèces, à des prairies riches, jusqu'à des arbustaies pauvres. Nos résultats indiquent l'importance de mieux évaluer les gradients altitudinaux et soulignent la nécessité d'inclure les types de végétation dans l'analyse des gradients altitudinaux de biodiversité.

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Introduction

The decrease in species richness with increasing latitude is well established for many animal and plant taxa, thus forming one of the main biogeographical rules (reviewed in Brown (2014)). Among the few known examples with inverse latitudinal gradients are at least two taxa of Hymenoptera, the phytophagous Symphyta (Kouki et al., 1994) and the parasitoid Inchneumonidae (Timms et al., 2016; but see Veijalainen et al., 2012; 2014). This is in sharp contrast with the well-established and pronounced increase in species richness in other insect taxa, like Coleoptera, Lepidoptera, Diptera (Crowson, 1981; Holloway, 1987; Lobo, 2000; Larocque et al., 2006), but also non-parasitoid Hymenoptera (Apocrita: Abrahamczyk et al., 2011).

The functional equivalent of the latitudinal richness gradient is the elevational decrease in species richness (McCain & Grytnes, 2010; Fischer et al., 2011; Guo et al., 2013), although the underlying ecological and evolutionary causes might differ. While latitudinal richness gradients are apparently triggered by temperature dependence of ecological and evolutionary rates (Brown 2014), altitudinal richness gradients are more under the control of ecological processes driven by climate, resource availability, reduced habitat size and variability (McCain & Grytnes, 2010). This interplay of mechanisms can result either in the typical altitudinal richness decrease or in mid-altitudinal richness peaks (McCain & Grytnes, 2010; Guo et al., 2013). In any case, the elevational gradient seems to be more 'universal' than the latitudinal gradient, and so far no counterexample has been described (Fischer et al., 2011).

In this study, we show that the local diversity of encyrtid wasps and plant communities forms a

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Supplemental data for this article can be accessed here.

counterexample to the elevational gradient rule. Encyrtidae are a hyper-diverse Chalcidoid family containing more than 3000 species worldwide, which mainly attack lepidopteran, aphid, and scale insect hosts (Noyes, 2016). We measured encyrtid and plant richness along an elevational gradient in the Eastern Caucasian Mountains. Prior studies from these and surrounding areas have shown hump-shaped patterns or decreases in richness with increasing elevation in various arthropod groups (Murvanidze et al., 2004; Chaladze, 2012; Chaladze et al., 2014; Mumladze et al., 2015; Aslan et al., forthcoming 2017), plants and snails (Mumladze et al., 2017). Thus, the increase in plant and encyrtid richness contrasts with the general diversity pattern in this specific region.

Materials and methods

The Lagodekhi National Park (Country of Georgia) is the oldest protected area in the Caucasus (more than 100 years old) and covered by old-growth primary mixed forests dominated by beech (*Fagus orientalis*). Only at lower elevations (600–700 m) and near the tree line (2200 m) are other tree species (*Carpinus betulus*/*Quercus* ssp. and *Betulla*/*Acer* ssp., respectively) predominant. In the forested area, five small, naturally open sites (forest edges) with dense herbaceous vegetation along an elevational transect spanning from 665 m to 1900 m a.s.l. were selected for sampling (Table 1; Figure 1). We chose this ecotone in order to increase efficiency of sampling species associated exclusively with forests and meadows. In addition, we established two extra sites above tree line (in subalpine/alpine areas). At each location, a single Malaise trap was set up from early spring to the end of the vegetation season to collect Encyrtidae. Samples we collected every 10 days resulted in a total of 1080 trap-days, with 190 trap-days at the lowest (665 m) and 130 trap-days at the highest elevation (2559 m).

In each plot, we assessed the richness of vascular plants using total counts in four randomly located 10 × 10 m^2 plots within an area of 2500 m^2 around each Malaise trap. Plant inventories were performed in May, June, and September. The Encyrtidae were identified using the keys of Trjapitzin (1989), Gibson et al. (1997), Hayat (2006), and Guerrieri and Noyes (2000, 2005).

Table 1. Summary data on the studied sites and species diversity for each sampling elevation.

Sampling site	Elevation	Longitude	Latitude	Herb richness	Woody plant richness	Total encyrtid abundance	Encyrtid richness
p1	665	41.85248	46.28776	39	12	228	27
p2	845	41.85585	46.29273	35	14	65	22
p3	1345	41.87146	46.31153	28	10	330	51
p4	1850	41.88273	46.32185	22	10	70	29
p5	1900	41.88557	46.32413	69	17	193	50
p6	2230	41.89805	46.33387	127	7	131	34
p7	2559	41.90616	46.33340	112	3	252	48

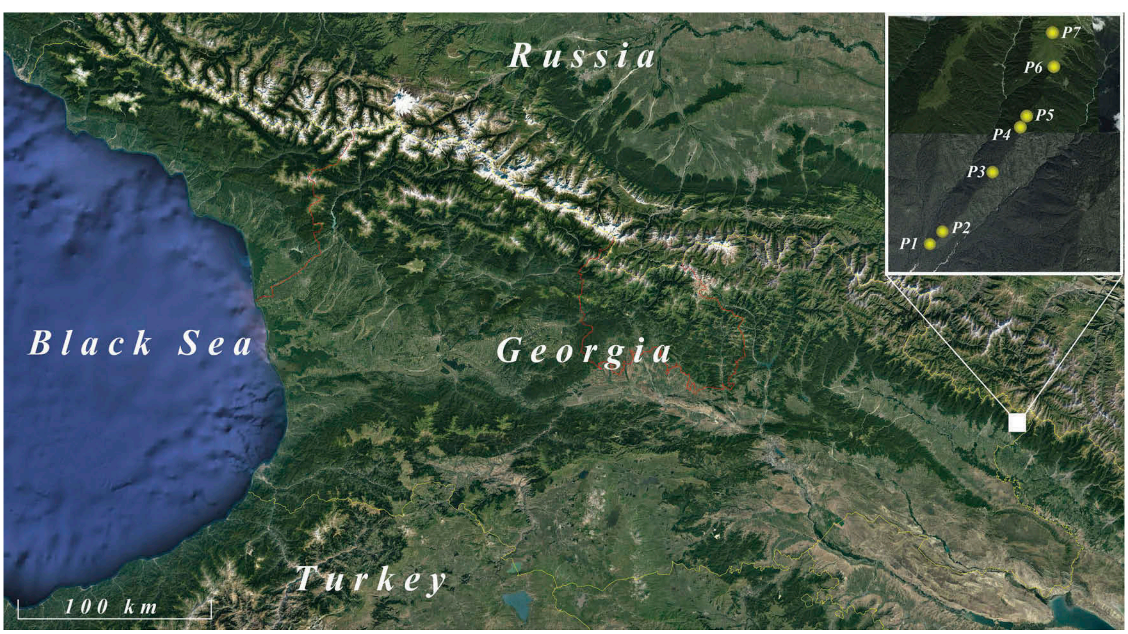

Figure 1. Location of the study area and sites in Georgia.

Several singletons and doubletons are typical in arthropod inventories (Coddington et al., 2009) and our study is no exception. Therefore, we used abundance-based asymptotic richness estimation to obtain expected Encyrtid species data according to the estimators of Chao et al. (2014) and Chao et al. (2016), using the pooled abundance data represented in all traps for each sampling elevation. For plant species, we used incidence data of four plots at each sampling elevation to estimate asymptotic expected richness. We tested the strength of the altitudinal gradients using ordinary least squares regression (OLS).

Results and discussion

In total we found 54 woody and 244 herbaceous plant species (Supplementary Material Tables S1, S2). Woody species richness decreased with altitude, while herbs had lowest richness at intermediate altitude and highest richness above 2200 m (Figure 2(a); Table 1). Interestingly, a recent study on plant diversity from a nearby mountain (Mumladze et al., 2017) revealed a linear increase of total plant richness from 600 to 2200 m. However, this study dealt with forest plots only, while our data include forest edges and subalpine/alpine meadows. Consequently, the linear increase in plant richness reported by Mumladze et al. (2017) is closely linked to the increased canopy opening at higher elevation.

A total of 1348 individuals representing 103 named species and 16 morpho-species of Encyrtidae were captured (Supplementary Material Table S3), among which 45 species are new records for the country. Observed and estimated encyrtid species richness increased with increasing elevation (Figure 2(b)). At 665 m we found 29 and expected 33 species, while these values increased to 48 and 70 species, respectively at 2559 m (Figure 2(b)). The vast majority of Encyrtidae depend on phytophagous arthropod host species. Consequently, encyrtid richness should increase with plant diversity. This was not the case (Figure 2(c)). In contrast, the proportion of Encyrtidae with respect to plant species was highest at intermediate altitude, where herbaceous plant richness was lowest. Of course, the host range of most of the encyrtid species is unknown, and thus the plant richness is only a crude proxy to the potential number of hosts. Nevertheless, this result combined with the increase in total encyrtid richness contrasts to the common altitudinal richness gradient. Clearly, parasitoid Hymenoptera need further studies with respect to common biogeographic patterns. Possibly the parasitoid way of life counteracts common climatic constraints on richness, making less favourable habitats still attractive for a larger number of parasitoid species.

Our study design cannot exclude differences in sample coverage among the study sites. Decreasing woody

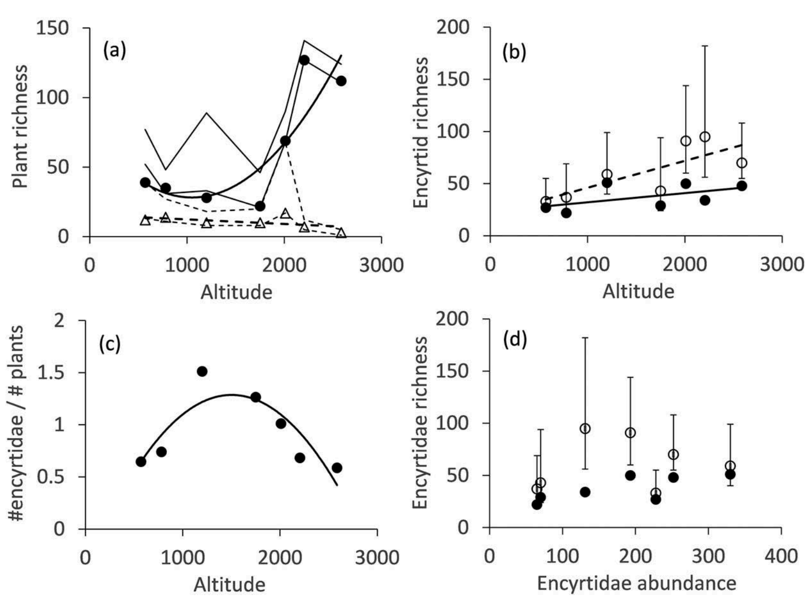

Figure 2. (a) Observed herbaceous plant (black circles: second order polynomial OLS regression $r^2 = 0.74$, $p(F_{1,5}) = 0.07$) and woody plant (light triangles: linear OLS $r^2 = 0.28$, $p(F_{1,5}) > 0.10$) species richness in relation to elevation. Straight and broken lines respectively show the 95% upper and lower confidence intervals of the estimated richness. Note that lower confidence limits are very close to actual values. (b) Observed (black circles) and estimated (open circles, error bars indicate the 95% confidence limits of estimation) increase with elevation (observation linear OLS $r^2 = 0.30$, $p(F_{1,5}) > 0.10$, estimate $r^2 = 0.60$, $p(F_{1,5}) = 0.04$). (c) The ratio of encyrtid/plant species richness was highest at intermediate altitude (second order polynomial OLS regression $r^2 = 0.73$, $p(F_{1,5}) = 0.07$). d) Estimated encyrtid species richness did not increase with total abundance (d) $p(F_{1,5}) > 0.30$).

plant cover might increase the effectivity of Malaise traps, although we do not have any indication for such an effect. Prior studies on Ichneumonidae (Timms et al., 2016) and Parasitica as a whole (Ulrich, 2005) have found a strong positive allometric dependence of species richness with local abundance, and we expected to see a similar pattern if sampling coverage had biased our richness results. Surprisingly, sampling efficacy was independent of elevation, as richness did not co-vary with abundance (Figure 2(d)). The observed altitudinal increase in species richness (Figures. 2(a,b)) was linked to reduced average abundances per species at higher altitude, dropping from 4.5 individuals per species and trap below 1000 m to 2.7 individuals per species and trap above 2000 m. Consequently, our data suggest a change in the pattern of species abundances towards an increased proportion of relatively rare species at higher altitude. However, due to the limited sample size future studies have to verify this alleged altitudinal abundance gradient.

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Disclosure statement

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