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The oribatid mite (Acari: Oribatida) community of a high-Andean cushion peatland in southern Peru

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Original research

ABSTRACT

The oribatid mites of a high-Andean cushion peatland in southern Peru were investigated. A total of 17 oribatid mite species, belonging to eight families, could be identified in five different microhabitats. A rarefaction analysis showed a potential mite community of maximum 18 taxa per 1000 specimens for this peatland site. Ranked species abundance analysis revealed three dominant, five subdominant, three recedent, two subrecedent and four sporadic occurring taxa. The abundance of oribatid mites was 3.0 specimens cm^{-3} (SD = 5.9) in mean. However, significantly higher oribatid mite densities were detected in muddy soils and scarcely vegetated parts in comparison to soils covered by dense vegetation cushions. The identification of deposited and damaged remains of oribatid mites is discussed.

Keywords bofedales; paleoenvironmental indicator; species richness

Introduction

The oribatid mite's species of high-Andean cushion peatlands were initially explored by the groundbreaking work of Hammer (1958, 1961), but recent studies are only available for cushion peatlands of northern and central Chile (Covarrubias and Mellado 2003; Covarrubias 2004a, b, 2009; Figueroa and Covarrubias 2005). In contrast, the oribatid fauna of the Peruvian peatlands is largely unknown.

The cushion peatlands of the high Andes above ~3000 m a.s.l., locally called *bofedales*, are a unique ecosystem, characterised by extreme environmental conditions with seasonal drought, diurnal frost-thaw cycles, hypoxia, strong winds and intense solar radiation (Ruthsatz 1993; Squeo *et al.* 2006; Schittek *et al.* 2012). As a direct consequence of these harsh environmental conditions, parts of the cushion peatland regularly die off, or are infrequently covered by debris from erosion and landslides. This results in a dynamic mosaic of ecotopes. More recently, anthropogenic impacts, especially land-use as pasture dramatically increased the disturbance intensity of cushion peatlands (Ruthsatz 1995; Ramsar-Convention 2005, Poblete 2007), leading to an extremely heterogenous and dynamic mosaic of different successional stages (Schittek *et al.* 2012, 2015). In general, habitat heterogeneity is a major driving force of species richness (Adams 2009). This connection is well studied in above-ground settings (Mittelbach *et al.* 2001), but it has been only rarely addressed for below-ground communities (Nielsen *et al.* 2010). Moreover, habitat heterogeneity is changing in time and its implications, amplitude, and temporal characteristics are the main research focus of the paleoenvironmental discipline. In

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order to advance paleoenvironmental analyses, it is claimed to intensify multiproxy approaches where different indicators of habitat change are combined (Birks and Birks 2006). In the last two decades, Oribatid mites gained more interest as paleoenvironmental indicators (Erickson and Platt 2013) but were used only once in the Neotropics (Chepstow-Lusty *et al.* 2007). High-Andean cushion peatlands showed high potential as archives for paleoenvironmental analyses and subfossil oribatid mites are deposited and well preserved over time (Schittek *et al.* 2015).

Considering the lack of knowledge on oribatid mites of Peruvian peatlands and a need of new paleoenvironmental indicators, the aim of this study was: (i) to characterise the taxonomic richness of oribatid mites in a cushion peatland; (ii) to describe changes in community composition within the soil heterogeneity of the peatland; and (iii) to test if identification to species level can be attained using deposited and damaged dead specimens.

Material and Methods

Study site

The Cerro Llamoca peatland (referred later as CLP) is situated in the western Cordillera of the Andes of southern Peru (14°10′S, 74°44′W) at an altitude between 4150 and 4250 m a.s.l., southward of the name giving mountain peak 'Cerro Llamoca', and covers an area of 11.6 hectares (Figure 1). It comprises a part of the unique cushion peatland ("*bofedal*") ecosystems situated on slopes, in wet brooks or valley bottoms at 4000-4900 m a.s.l. in the Andes. The cushion peatlands are of significant importance for the local human population: they represent pastureland for wild and domestic animals and are important water reservoirs during drought periods (Ruthsatz 1995).

The study area is characterised by a tropical climate (Lauer 1993), in the sense where extreme diurnal temperature fluctuations, due to the high altitude, are overlaid by distinct annual fluctuations of temperature and precipitation. The ERA-Interim model, renders a mean annual precipitation of 349 mm for the CLP with a marked seasonal pattern (Dee at al. 2011), of which about 90% falls during the austral summer (December to March). Within this wet season, rainy days are distinctly clustered with short periods of thunderstorms and heavy rain, followed by longer dry periods (Garreaud 2000). This precipitation pattern could be termed as "monsoon-like" (Zhou and Lau 1998). The peatlands act as an important buffer by absorbing all precipitation and releasing it throughout the year (Verzijl and Quispe 2013). The main cushion-forming plants of the CLP are the Juncaceae *Distichia muscoides* Nees & Meyen 1834 and *Oxychloe andina* Phil. 1860 (Schittek *et al.* 2012, 2015). Overall, the uppermost part of the CLP shows clearly visible transitions between the following ecotopes: (i) Springs in the upper area are bordered by large *Distichia muscoides* cushions, although most of them are degraded by trampling of hoofed herbivores, such as cattle. Trampling destroys the vital uppermost plants and hence exposes the underlying peat, which fosters stronger evaporation or direct drainage of stored water from the peat cushions and facilitates further vegetation damage and vulnerability to erosion (Schittek *et al.* 2012): (ii) Due to erosion on the surrounding slopes, transportation of eroded sediments and further accumulation processes in the valley bottoms, the middle section is characterised by a large debris fan covering the peatland. Solely *Oxychloe andina* inhabits some of the wet debris layers of this area. (iii) The lowest section is less affected by degradation and shows a typical mosaic-like pattern of well-established large *Distichia muscoides* cushions, interspersed by several accompanying species e.g. *Zameioscirpus muticus*, *Plantago tubulosa*, *Gentiana prostrata* and *Werneria pygmaea*. The cushions are often encircled by a frame of *Deyeuxia chrysantha* reeds and are usually separated by small and shallow pools (Schittek *et al.* 2012).

Sampling strategy and preparation

The sampling aimed to get a full overview of the oribatid mite community of the Cerro Llamoca peatland. Accordingly, five representative ecotopes characterizing distinct microhabitats within the peatland were sampled (Figure 1d). From each ecotope, one core was taken on 28/10/2011 with a soil-corer (5cm diameter x 15cm length). Depending on the depth of the bedrock and other soil characteristics, varying core length from 8 - 24 cm could be retrieved. The cores were immediately divided into two equal halves of the length and stored in half-shell plastic tubes. One half was injected immediately with ca. 0.5 ml ethanol (96%) cm^{-1} to preserve and fix the soil fauna and to avoid spatial displacements of the invertebrates. The other half was used for the characterization of the soil substrates and categorized as: (i) dense *Distichia muscoides*-cushion (Figure 2a); (ii) mineral debris (Figure 2b); (iii) silty peat of *Oxychloe andina* plant material (Figure 2c); (iv) humous silty mud (Figure 2d); and (v) dry peat of dead (*Distichia muscoides*) material (Figure 2e).

In the laboratory, each half soil core was subsampled into layers of 1 cm thickness. From all five subsampled cores, the samples of each second centimetre (n=41) were chosen for the examination of the mesofauna (see Figure 2). For the analysis, the volume of every sample was quantified by placing the soil in a graduated measuring cylinder and filling it up with distilled H_2O to a fixed volume of 10 ml with accuracy 0.1 ml. The samples were then macerated in 10% KOH for at least four hours at 4 °C before being separated by wet sieving into two fractions of <112-250µm and >250µm, respectively. Subsequently, the individual fractions were diluted in water, spread out on a white picking tray (10 x 6cm) and completely scanned in multiple steps under a dissecting microscope at 10-12x magnification. All mesofaunistic individuals or fragments of these were picked out and stored in ethanol (96%) until mounting. In this study, only the data on oribatid mites is presented. Juvenile oribatid mites were not included in the data.

Mounting and identification of oribatid mites

The oribatid mites were cleared in gently heated lactic acid (96%), following the procedure of Weigmann (2006) and mounted in Hoyer's medium (Baker and Wharton 1952), which was stained with potassium iodide and iodine to increase the contrast (Faraji and Bakker 2008). For identification, different light microscopes with magnifications from 50-400x, and literature by Hammer (1958, 1961, 1962a, b), Balogh and Balogh (1988, 1990), Balogh (1972), Norton and Behan-Pelletier (2009) and an interactive glossary by Hunt *et al.* (1998) were used. The nomenclature is based on Subías (2004, update 2021).

Photos were taken with a Canon EOS 600D mounted on a Zeiss Axio Scope A1 light microscope with differential interference contrast (DIC) illumination, using the remote-control software SmartShooter v.1.1.14. Multi-layer stacking with 10-30 pictures per specimen was performed by the Zerene Stacker v.1.04 software with image processing and measuring width and length by Adobe Photoshop CS4.

According to their species rank-abundance distribution, the species were subdivided according to the abundance classification criteria of Engelmann (1978) into dominant (>10%), subdominant (<10%), recendent (< 2%), subrecendent (<1%) and sporadic (<0.3%) taxa. These ratios refer to all individuals of a single oribatid mite species in relation to all the total abundance.

Statistical Analyses

The species richness was calculated by rarefaction analysis using the software EstimateS ver. 9.10 (Colwell 2013) and BioDiversity Pro (McAleece *et al.* 1997), following the procedures by Gotelli and Colwell (2011) and Colwell *et al.* (2012). For all other statistical analyses, the software R (R Core Team 2018) was used.

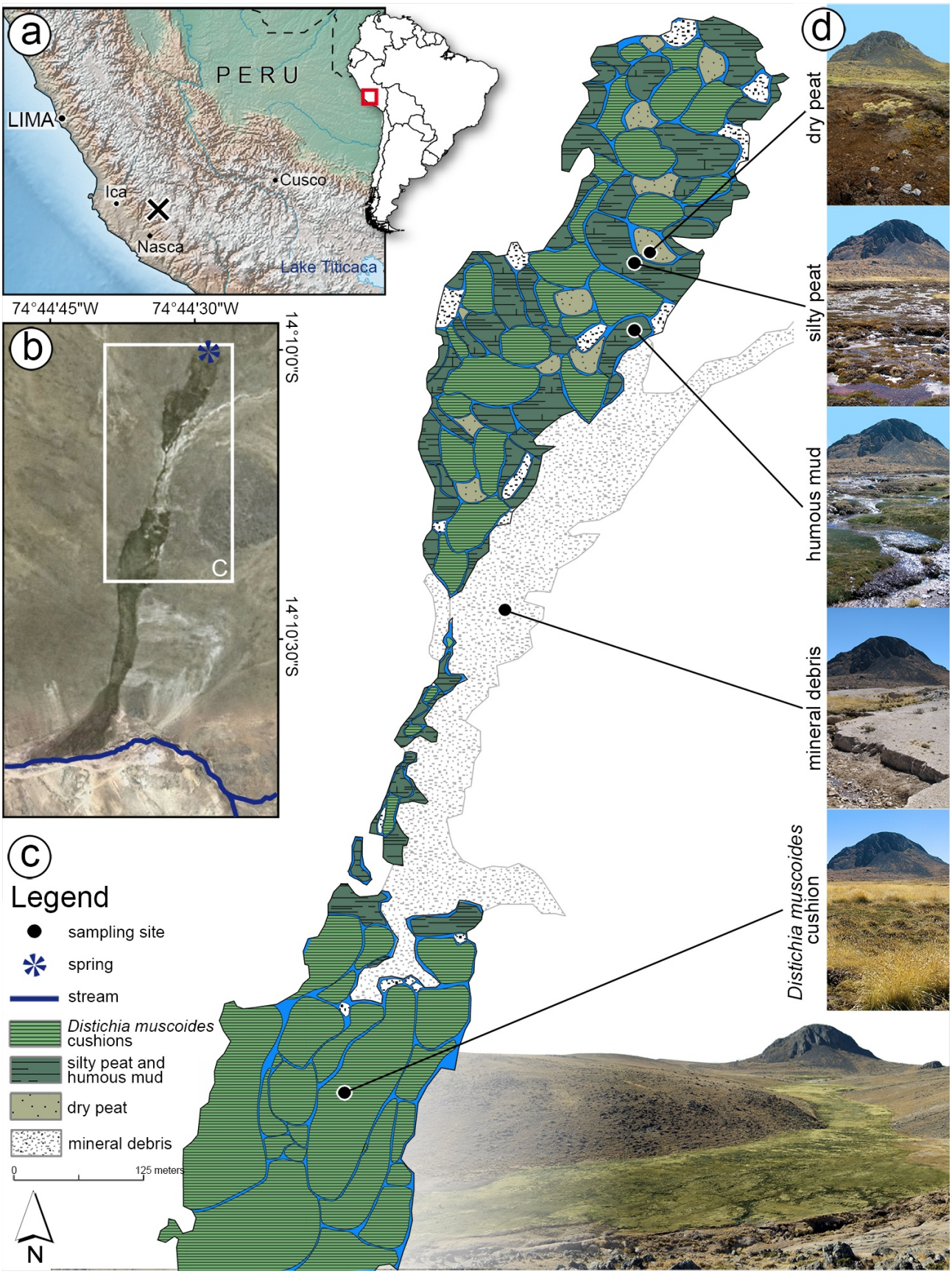


Figure 1 Localisation of the Cerro Llamoca peatland (a), satellite image total view (b), spatial representation of microhabitats on the basis of satellite images (c) and examples of the different substrates and microhabitats along the sampled transect (d).

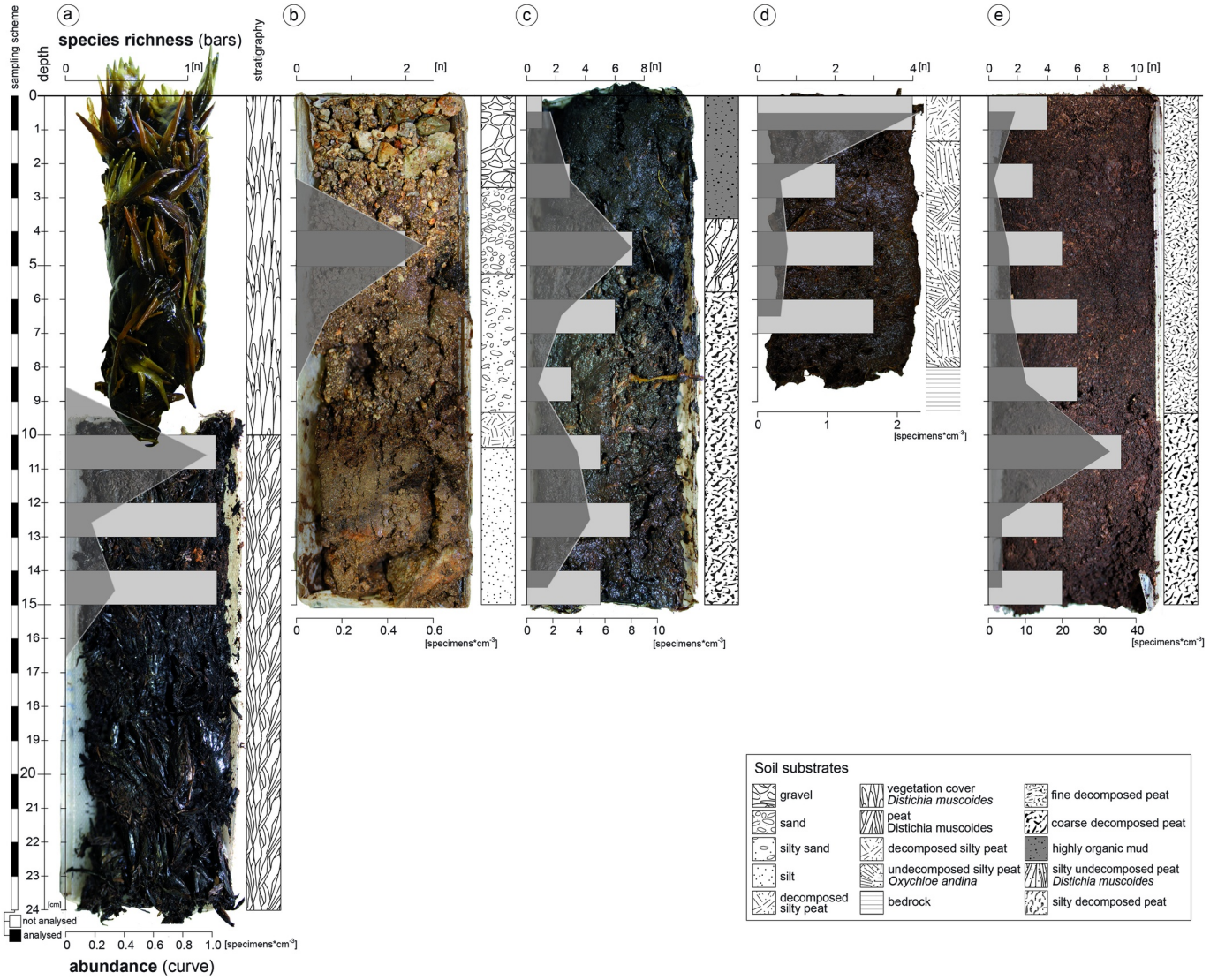


Figure 2 Soil cores stratigraphy and depth changes in abundances and species richness of oribatid mites in (a) dense *Distichia muscoides*-cushion; (b) mineral debris; (c) silty peat of *Oxychloe andina* plant material; (d) humous silty mud; and (e) dry peat of dead (*Distichia muscoides*) material. The stratigraphy of soil substrates is indicated next to the core photos. Oribatid mite species richness is drawn as grey bars on the upper axis and total oribatid mite abundances as grey curve on the bottom axis.

Comparisons of multiple, independent and non-parametric datasets were achieved using the Kruskal-Wallis-test with a subsequent post-hoc procedure corrected by the number of tests (Giraudoux 2015). The influences of different parameters on the oribatid mite community were tested by multiple regressions.

To characterise the ranked abundance distribution, different models were fitted to the curve using maximum likelihood estimation with the vegan package (Oksanen *et al.* 2019). In this package, five models (brokenstick, pre-emption, log-normal, Zipf and Zipf-Mandelbrot) are implemented. The best model fit was determined by the lowest Akaike information criterion (AIC) value.

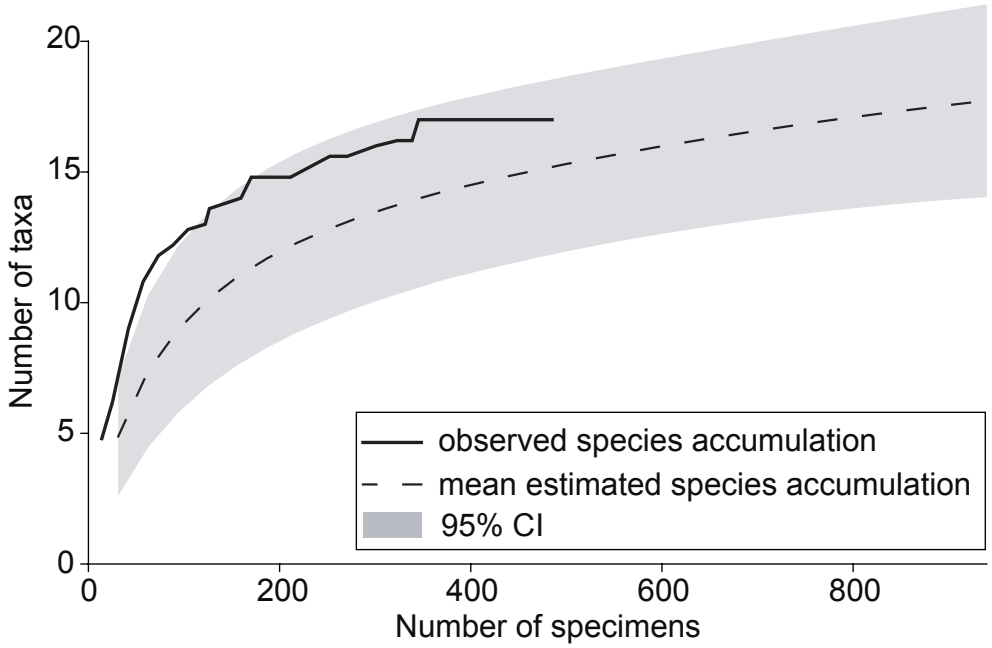


Figure 3 Rarefaction analysis of oribatid mite species. The solid line shows the observed detection of additional species with increasing number of examined specimens. The dashed curve indicates the estimated species accumulation achieved by rarefaction analysis, and the grey area the 95% confidence interval (CI) of the model.

Results

In total, 17 oribatid mite species were identified, by investigating of 689 adult specimens or remains of these from all 41 samples. The community comprised eight families, of which the most diverse families were the Ceratozetidae with six taxa and the Scheloribatidae with three taxa. Only 85 (12.4%) of the 689 oribatid mite specimens could not be identified because of damage to taxonomically important structures. A mean richness of 2.5 species per sample (SD= 2.7) was discovered, ranging from only one species (*Zetomimus furcatus*) in the *Distichia muscoides* cushion substrate to up to 11 species in the dry peat substrate (see Figure 4b). A full overview of the identified oribatid mite community is given in Table 1.

For all samples, the rarefaction analysis shows a non-saturating estimation curve reaching 18 taxa at 1000 counted specimens (Figure 3). The real species accumulation runs in accordance with the upper limit of the 95% confidence interval (CI), which ranges from 13 to 21 species at 1000 counted specimens. The community structure of the peatland inhabiting oribatid mites showed a best fit to a niche preemption model with an AIC support of 59.75 (Figure 5). For the other fitted models, higher AICs were estimated (Zipf-Mandelbrot: 62.3; Lognormal: 63.6; Brokenstick: 64.3; Zipf: 69.4). *Tectocepheus* sp. (23.8%), *Edwardzetes armatus* (17.0%) and *Trichoribates hammerae* (13.7%) were the dominant species of the oribatid mite community. These most abundant species were accompanied by a group of subdominant species: *Neoamerioppia notata* (9.5%), *Malaconothrus monodactylus* (5.6%), *Nanhermannia elegantissima* (5.3%), *Scheloribates confundatus* (3.5%) and *S. pallidulus* (3.5%). In addition, there are some recedent species like *Zetomimus furcatus* (1.4%), *Tyrphonothrus maior* (1.1%) and *Scheloribates elegantulus* (1.0%). Two subrecendet species *Sphaerozetes chavinensis* and *Oxyoppia suramericana* with <1% abundance and four sporadically occurring taxa (*Zetomimus nigrisetosus*, *Aquanothrus* sp., *Ceratozetes (Magellozetes)* sp. and *Oripoda* sp.) with <0.32% complete the species inventory.

Distribution within the ecotopes

In mean, the oribatid mite community showed an abundance of 3.0 specimens per cm^3 (SD= 5.9) (Figure 4a). However, the abundance of oribatid mites differed significantly within different microhabitats of the peatland ($H(4)= 27.3$, $p<0.001$). Post hoc comparisons showed higher densities specimens cm^{-3} in the degraded dry *Distichia muscoides* peat substrate (M= 8.96, SD=10.11) and in the humous silty mud (M= 3.40, SD= 2.30) (see Figure 4a). The different microhabitats had a significant influence ($\beta=0.62$, $p<0.001$) on the density of oribatids ($F_{(2,32)}= 7.4$, $p<0.001$, $R^2=.27$) and explained 27.33% of the overall variation. In the investigated soil cores, the abundance of oribatid mites varied with depth (Figure 2), however, the sample depth had no significant influence on the inhabiting oribatid mite density ($\beta=0.18$, $p=0.27$).

Discussion

The rarefaction analysis of the oribatid mite fauna indicates sufficient sampling density in the current study. The confirmed (17 species) and by rarefaction estimated species richness (18 species) lies within the range of 18 and 13 species per 1000 specimens reported in Chilean cushion peatlands (Covarrubias 2004a; Figueroa and Covarrubias 2005). However, the oribatid mite communities of other cushion peatlands, such as a *Patosia clandestina*-dominated type in northern Chile, with only seven species are distinctly less diverse (Covarrubias 2009). Nevertheless, cushion peatlands are species rich in comparison to other ecosystems of the high Andes (forest, cactus zone, dwarf shrub heath, tussock grass steppe, and cushion plant zone), which achieve only a mean of 5.4 oribatid species (Covarrubias 2004a).

According to the classification of Engelmann (1978), *Tectocepheus* sp., *Edwardzetes armatus* and *Trichoribates hammerae* were the dominant species of the oribatid mite community. Species of the genus *Tectocepheus* are extremely ubiquitous, favored by parthenogenetic

Table 1 Systematic overview of the oribatid mite community identified in soil samples of the Cerro Llamoca peatland in the western cordillera of the Andes of southern Peru. The classification of the abundance ranks follows Engelmann (1978).

	Taxon	No. of examined specimens	Abundance rank
	Trhypochthoniidae		
1	*Malaconothrus monodactylus* (Michael, 1888)	44	subdominant
2	*Tyrphonothrus maior* (Berlese, 1910)	8	recedent
	Nanhermannidae		
3	*Nanhermannia* cf. *elegantissima*	35	subdominant
	Opiidae		
4	*Oxyoppia suramericana* (Hammer, 1958)	3	subrecedent
5	*Neoamerioppia notata* (Hammer, 1958)	74	subdominant
	Tectocepheidae		
6	*Tectocepheus* sp.	181	dominant
	Ameronothridae		
7	*Aquanothrus* sp.	1	sporadic
	Ceratozetidae		
8	*Ceratozetes* (*Magellozetes*) sp.	1	sporadic
9	*Edwardzetes armatus* (Hammer, 1958)	104	dominant
10	*Sphaerozetes chavinensis* (Hammer, 1961)	6	subrecedent
11	*Trichoribates hammerae* (Subías, 2010)	88	dominant
12	*Zetomimus furcatus* (Warburton & Pearce, 1905)	7	recedent
13	*Zetomimus nigrisetosus* (Hammer, 1958)	2	sporadic
	Scheloribatidae		
14	*Scheloribates confundatus* (sensu Hammer 1961)	23	subdominant
15	*Scheloribates* cf. *elegantulus*	8	recedent
16	*Scheloribates pallidulus* (Koch, 1841)	27	subdominant
	Oripodidae		
17	*Oripoda* sp.	1	sporadic

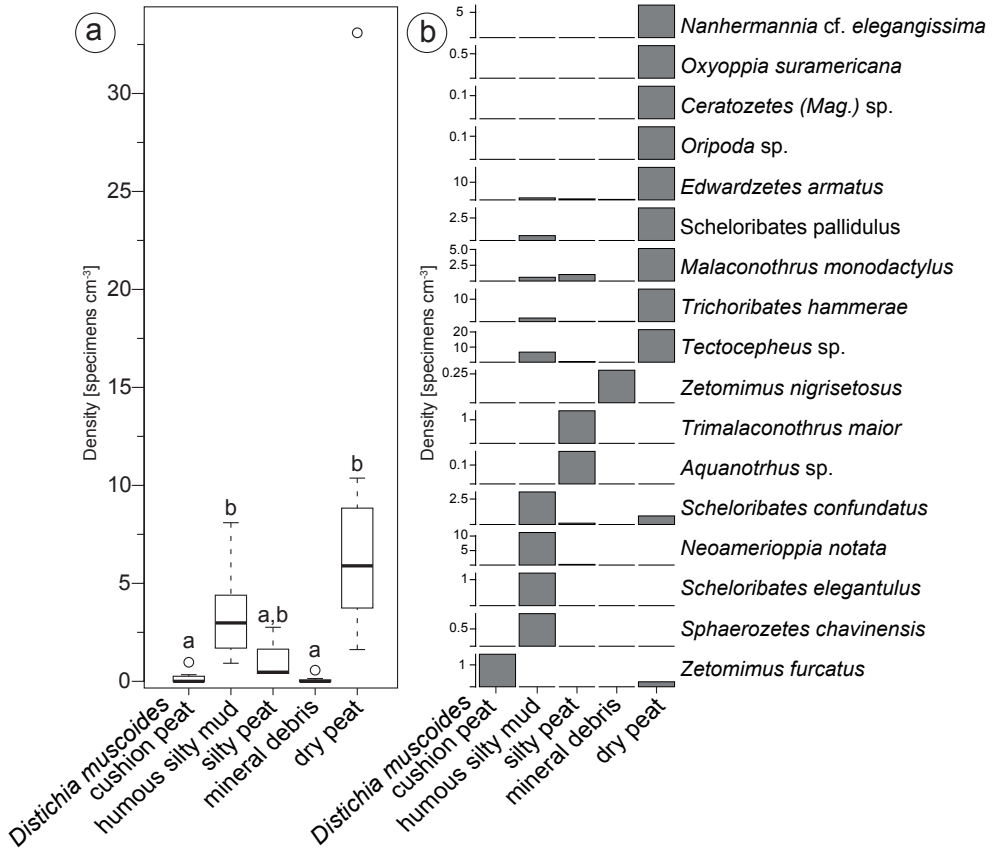


Figure 4 Oribatid mite distribution patterns within the different soil substrates of CLP: (a) boxplot on total densities of oribatid mites. Significant differences are marked by different letters (post hoc Kruskal-Wallis comparisons: observed difference>critical difference, α= 0.05, corrected for the number of tests). Solid lines show the median and circles extreme values; (b) abundance plot of oribatid mite species.

reproduction and belong to the most common oribatid mites throughout the world (Nübel-Reidelbach 1994; Hajmová and Smrž 2001; Subías 2004, update 2021; Weigmann 2002, 2006). *Tectocepheus* sp. is reported from cushion peatlands in Chile (Covarrubias 2004a; Figueroa and Covarrubias 2005). In contrast, *Edwardzetes armatus* and *Trichoribates hammerae* were exclusively found at altitudes >4200 m a.s.l. inhabiting wet habitats (Hammer 1958, 1961; Balogh and Balogh 1990). *Trichoribates hammerae* is endemic to Peru, but *Edwardzetes armatus* is occurring thoughout the Neotropical region (Subías 2004, update 2021).

The dominant species were accompanied by a group of subdominant species: *Neoamerioppia notata*, *Malaconothrus monodactylus*, *Nanhermannia elegantissima*, *Scheloribates confundatus* and *S. pallidulus*. Among these, *Neoamerioppia notata* is known from moist to wet habitats in the high Andes of Bolivia (Hammer 1958). *Malaconothrus monodactylus* was reported at high densities from a cushion peatland in Chile (Covarrubias 2004a, 2009). However, it is frequently found in bogs and peatlands throughout the Holarctic and Neotropic ecozones (Subías 2004, update 2021; Weigmann 2006). *Nanhermannia elegantissima* is a well-known species from the entire Neotropic and other regions (Subías 2004, update 2021) and also from high-Andean cushion peatlands (Hammer 1958; Covarrubias 2004a, b; Figueroa and Covarrubias 2005). The genus *Nanhermannia* is composed of secondary decomposers feeding mainly on fungi (Schneider *et al.* 2004; Ermilov and Łochyńska 2008) and show a slow development despite being parthenogenetic. *Scheloribates confundatus* was found in very wet habitats in Peru and Argentina (Hammer 1961), whereas *S. pallidulus* is a cosmopolitan

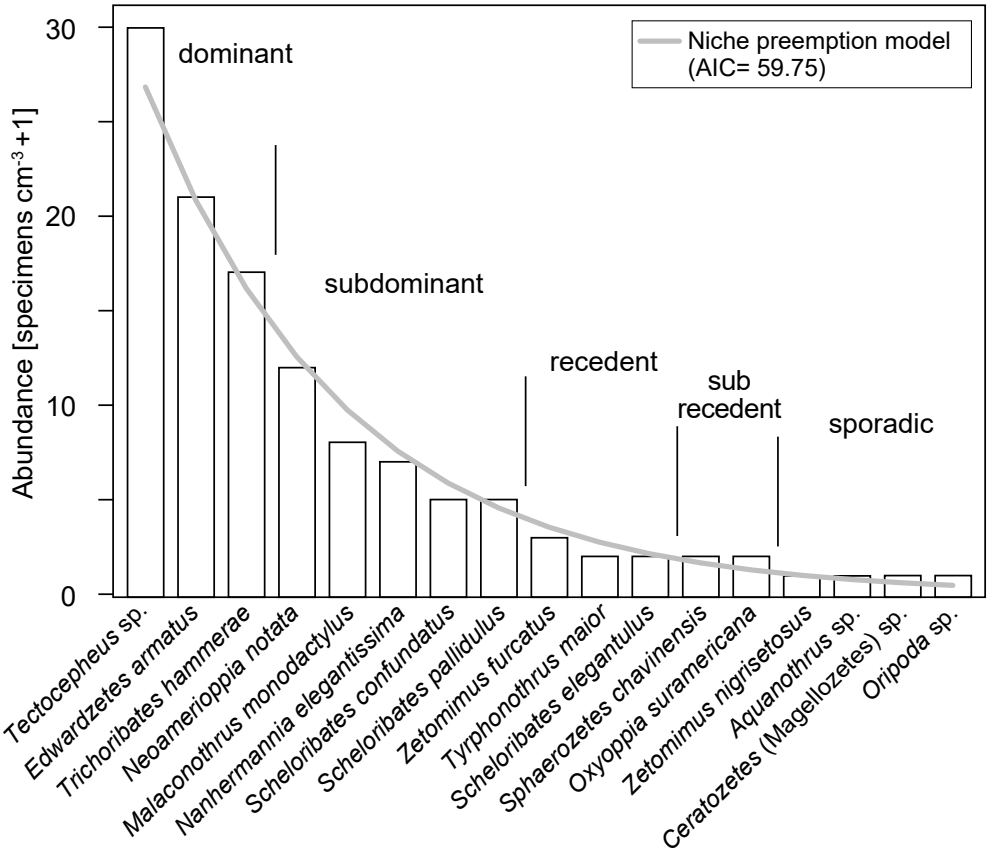


Figure 5 Ranked species abundance plot (Whittaker plot) of CLP's oribatid mite community. The grey curve fits the calculated niche preemption model (geometric series). The species were subdivided by the abundance classification criteria according to Engelmann (1978).

species and typical for peat bogs and forest soils in Europe, Eurasia and North America (Ivan *et al.* 1997; Subías 2004, update 2021; Weigmann 2006; Murvanidze and Kvavadze 2010; Barreto and Lindo 2018; Behan-Pelletier and Lindo 2019).

In addition, some recedent species like *Zetomimus furcatus*, *Tyrphonothrus maior* and *Scheloribates elegantulus* could be determined.

Zetomimus furcatus is one of the few fully aquatic oribatids (Fischer and Schatz 2010), characterised as a specialist of oligotrophic Holarctic peat bogs and other swampy habitats (Schelvis and van Geel 1989; Murvanidze and Kvavadze 2010; Weigmann 2006). Similarly, *Tyrphonothrus maior* is a semi-aquatic, semi-cosmopolitan and parthenogenetically reproducing species, occurring in very wet habitats (Balogh and Balogh 1988; Palmer and Norton 1991; Subías 2004, update 2021; Schatz and Behan-Pelletier 2008; Lehmitz and Maraun 2016; Minor *et al.* 2019; Barreto and Lindo 2021). In contrast, *Scheloribates elegantulus* was found in moss between heathery shrubs (Hammer 1961) and in semi-deciduous forest fragments surrounded by savanna (Ferreira *et al.* 2012). This species shows a Neotropical distribution (Subías 2004, update 2021).

The community structure showed a best fit to a niche preemption model (Wilson 1991). This fit characterises a community in which each species arrives randomly and preempts a constant fraction of the remaining resources. This is typical for small, stressed or pioneer communities (May 1975). Together with the frequent occurrence of parthenogenetic species, the composition and structure of the oribatid community likely reflects the selective forces acting in the extremely harsh environmental conditions of the high Andean cushion peatlands such as extreme diurnal temperature fluctuations, intense solar radiation and seasonal droughts

(Ruthsatz 1993; Squeo *et al.* 2006; Schittek *et al.* 2012).

The oribatid density in our study ranged from 0.08 specimens cm^{-3} in the debris ecotope to 8.96 specimens cm^{-3} in the degraded ecotope, and it was much higher than reported in the soils of other cushion peatlands with densities ranging between 0.2-1.4 specimens cm^{-3} (Figueroa and Covarrubias 2005; Covarrubias 2009). These latter values, however, were obtained by Berlese-Tullgren funnel extraction of the living oribatid mites, while we handpicked all dead and damaged specimens from the sample. In particular the relatively high oribatid densities in dry peat likely indicate higher availability of food resources (e.g. fungi) due to higher decomposition rates in the degraded parts of the peatlands. Unpublished data on high fungi spore concentrations in the dry peat samples supports this hypothesis (Dzakovic, unpublished data). If this connection can be confirmed in future studies, the density of oribatid mites may thus be used as an indicator of peatland degradation.

In view of the extremely low abundances of mites in cushion peatland soils we consider the hand-picking procedure described in this study as superior. In addition, by including the remains of dead specimens, we could obtain a much more complete species inventory of the oribatid mite community. Most importantly, we were able to identify even heavily damaged oribatid mites with the existing literature. This gives us a good precondition to use dead and preserved specimens from older soil deposits as indicators of the past changes in ecotone composition in future studies.

Conclusion

This investigation represents the first comprehensive study of the oribatid mite fauna of a high-Andean cushion peatland from Peru. The oribatid mites inhabit only distinct substrates within the full range of the peatland's heterogeneous ecotopes. In the dense *Distichia muscoides* cushions, almost no oribatids could be observed, but relatively high densities in dry peatland parts may indicate increased degradation of the peatlands due to increased decomposer activity caused by trampling of cows.

It is demonstrated that the identification of oribatid mites is also possible using *in situ* dead specimens obtained from the soil samples by hand-picking. Identification of dead species was particularly important to complement the species inventory by rare taxa. For taxonomic determination, the absence of the legs, which is often the case in dead oribatid mite specimens, is only a problem for specific taxa. However, the absence of legs requires an adapted use of the available identification keys for South America. The comments on morphological features, given in this study, provide a means to ease the use of fossil remains as indicators for environmental change in these habitats. With the synthesis of the taxonomic, distributional and autecological data, a useful tool for (paleo-)environmental research could be developed. More research on oribatid mites of the high Andes and especially for Peru is needed to obtain a complete species inventory of this region. On account of the age, and due to the remoteness and isolation of the cushion peatland ecosystems, its oribatid mite fauna may serve as an ideal model system for evolutionary studies.

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