Oribatid mite (Acari: Oribatida) and Chironomid (Diptera: Chironomidae) communities from a high-Andean cushion peatland in Peru (14°S) and their use for palaeoenvironmental reconstruction during the Nasca cultural period

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Abbreviations

a.s.l.	above sea level
A(1,2,3,a)	area porosae 1,2,3 or adalar
AIC	Akaike information criterion
ANOVA	analysis of variance
BP	before present
cal.	calibrated
CCA	canonical correspondence analysis
cf.	lat. conferre
CI	confidence interval
CLP	Cerro Llamoca peatland
Cond.	conductivity
CONISS	constrained hierarchical clustering
crit.diff.	critical difference - post-hoc Kruskal-Wallis comparison statistics
CV	cross-validation
DIC	differential interference contrast
DJF	austral summer season (December, January, February)
ENSO	El Niño-Southern Oscillation
F	F-test statistics
H	Kruskal-Wallis test statistics
HOF	Huisman-Olff-Fresco models
hPa	hectopascal
IKFA	Imbrie & Kipp Factor Analysis
IndVal	indicator value
ITCZ	Intertropical Convergence Zone
JJA	austral winter season (June, July, August)
k	kernel of smoothing by gaussian weights
MANOVA	multivariate analysis of variance
MAT	modern analogue technique
MLRC	Maximum Likelihood Response Surfaces analysis
MRT	multivariate regression tree analysis
myr	million years
NMDS	non-metric multidimensional scaling
obs.diff.	observed difference - post-hoc Kruskal-Wallis comparison statistics
Opt.	optimum
RMSE	root mean squared error
s.l.	lat. sensu lato
S(9,10)	setal socket 9,10
SASM	South American Summer Monsoon
SD	standard deviation
SE	standard error
SSm	submental seta
Syn.	synonym
T	matrix temperature
V	Pillai-Bartlett trace test statistics
VIF	variance inflation factor
VP	ventral pores
WA	weighted averaging
Water con.	water content
XRF	X-ray fluorescence spectroscopy
$\boldsymbol{\beta_i}$	effect size revealed by a Kruskal-Wallis test
$\boldsymbol{\omega}$	effect size revealed by a one-way independent ANOVA

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1 | Chapter I – Introduction

1.1 | Preface

Anthropogenic climate change is one of the biggest challenges of the 21st century (Peters et al., 2013; UN, 2015), with research remaining an ongoing priority into its implications for the biosphere and on society (Walther et al., 2002; Adger et al., 2013; Taylor et al., 2013). However, the main key to confront this challenge and the basis of climate change research is to understand the climates and the environments of the past (Overpeck et al., 2011), which highlights the need for further advances in the field of palaeoclimatology and palaeoecology.

In this context, high-Andean peatlands stand out as valuable model systems as mountainous regions are highly sensitive to climatic fluctuations (e.g. Gottfried et al., 2012), while the investigation of (semi-)aquatic ecosystems can reveal important information on water availability, which is crucial for both ecosystems and society (Taylor et al., 2013).

1.1.1 | Aims & Objectives

In order to advance palaeoenvironmental research, it is often claimed to intensify that efforts using so called "multiproxy" approaches need to be intensified (e.g. Birks & Birks, 2006; Lotter, 2003). This term describes the combination of different proxies, i.e. records of change, from single or more palaeo-archives (Lotter, 2003). A multiproxy approach aims to account for the vast complexity of biotic and abiotic relationships in an ecosystem (NRC, 2005).

To emphasise the effect that should be achieved by a multiproxy approach, an augmented terminology is proposed. The main advantage of combining different proxies from the same archive is to expand the research to a likewise "multiscale" approach. This approach widens the combination of various palaeo-indicators, which acquire different positions within a frame of contrasting dimensions: i) different spatial prediction ranges (local – global); ii) different detection sensitivities (idly – dynamic); iii) different immediacies of impact (indirect – direct). Such a synthesis of proxies would highlight their strengths and expose the weaknesses of single proxies (Lotter, 2003).

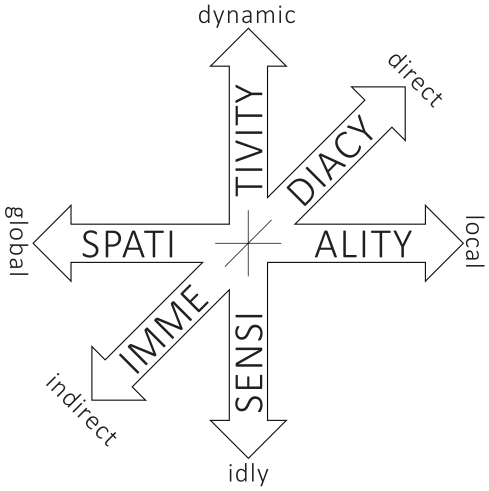


Figure 1.1 | Different dimensions of a "multiscale" approach in palaeoenvironmental research.

Hence, this thesis attempts to extend the range of palaeoproxies by investigating high-Andean cushion peatlands and to broaden the view on palaeoenvironments within a more multiscale approach.

For this purpose, taxa from the Oribatid mites (Arachnida, Oribatida) and the Chironomids (Diptera, Chironomidae) appear to be useful for palaeoenvironmental research since both are commonly deposited and preserved in peatland sediments as investigations e.g. by Schittek et al. (2015) have already revealed.

In this thesis, Oribatid mites and Chironomids from high-Andean cushion peatlands were analysed for their potential as soil condition indicators and palaeo-proxies.

In order to test for a proxy's applicability, different pre-investigations were obligatory:

- the establishment of a peatland's succession model as a theoretical foundation;
- the assessment of modern on-site Oribatid mite and Chironomid communities;
- an advanced taxonomic clarification of all taxa;
- a comprehensive investigation on the ecology of both groups.

Following the structure stated above, the investigation was guided by the following hypotheses:

- **The ecosystem of a high-Andean cushion peatland is characterised by a subset of different ecotopes, which can be connected according to successional processes.**
- **The ecotopes of a high-Andean cushion peatland are inhabited by distinct Oribatid mite and Chironomid communities.**
- **The Oribatid mite and Chironomid communities are associated with specific microhabitats, defined by geochemical soil parameters.**
- **Oribatid mite and Chironomid taxa can be used as significant soil condition indicators.**
- **The preserved Oribatid mite and Chironomid assemblages in the peat deposits of CLP show significant changes in time.**
- **Oribatid mite and Chironomid proxies and indicator functions combined quantitatively reveal environmental changes in time.**

1.1.2 | Thesis structure

Chapter I presents the theoretical foundation of the thesis. In that regard, the ecosystem of high-Andean cushion peatlands is introduced in general by giving information on their occurrence, typical plants associated, hydrology and other important characteristics, e.g. the ecosystem's heterogeneity and dynamics. Subsequently, the reader is introduced to the biology of Oribatid mites and Chironomids, while retrieving an overview of the phylogeny, systematics, morphology, and biogeography, as well as different aspects of their ecology and behaviour, such as habitat preferences or dispersal pathways.

Chapter II provides detailed information on the study site, describing its geographical setting, climate conditions, soils, surrounding vegetation and floral composition. In this part, information on the climatic mechanisms influencing the precipitation at the study site is of particular importance.

In Chapter III, the results of the modern Oribatid mite and Chironomid community analyses are presented. Before the description of the fauna is given, different ecotopes characterising the study site are identified, delimited from each other and ranked in a succession model. This characterisation forms the basis for further analyses in this thesis. Subsequently, information on sample preparation and classification of Oribatid mites and Chironomids is provided, before both communities are described in terms of their taxa composition, taxonomy and distribution patterns within the peatland.

In the subsequent Chapter IV, additional information on the biogeography of Oribatid mites from the high Andes in general and from cushion peatlands in particular is presented. Characteristic species for cushion peatlands are identified and the community composition in relation to changing environmental conditions is discussed.

Based on the communities presented in Chapter III, Chapter V reveals ecological information on these. First, the geochemical results are described from the peatland's ecotopes, which are afterwards merged to provide a habitat characterisation for the Oribatid mites and Chironomids. Finally, this ecological information is tested on indicator functionality.

In Chapter VI, the overall findings of the palaeoenvironmental investigation are recorded. Based on analysis of the subfossil assemblages, all information presented in the previous chapters are synthesised into a palaeoecological interpretation.

In the last Chapter VII, a synopsis for the entire thesis is given, from which conclusions can be reached.

Figure 1.2 | Different perspectives on high Andean landscapes and on cushion peatlands: A) gives a typical impression of a landscape characterised by Puna ecosystems; (B) Satellite image showing cushion peatlands as green ribbons in the landscape © 2016 TerraMetrics; (C) shows a cushion peatland in a valley bottom and (D) at a lake shore; (E) exposes the thickness of peat deposition at a incised and dried-out peatland

1.2 | High-Andean cushion peatlands

Cushion peatlands, locally called 'bofedales' or 'vegas', are an azonal floral element in the high Andes occurring from the Paramos of Venezuela and Colombia across the Puna ecoregions of Peru, Bolivia and northern-Chile and -Argentina to the southern Andean steppes of mid-Chile and -Argentina. They are an unique ecosystem, which is not comparable to northern hemispheric or magellanic (true) bogs, as they are neither dominated by *Sphagnum* mosses nor ombrogenous. Cushion peatlands are restricted to the high Andes ranging in the sub-alpine and low alpine belt from 3200-5000 m a.s.l. in the northern Andes, from 4000-4900 m a.s.l. in the central Andes and down to 2800 m a.s.l. at the southern distribution limit in mid-Chile and -Argentina (Ruthsatz, 2000; Succow & Joosten, 2001; Squeo et al., 2006) (see Figure 2.2)

1.2.1 | Floral composition of cushion peatlands

Despite the extreme environmental conditions of the high-Andes, with numerous factors operating to restrict plant growth, including (hyper-)aridity, intense solar radiation, strong winds, reduced oxygen air content, minimal atmospheric humidity and diurnal freeze-thaw cycles, some plants of the families Juncaceae and Cyperaceae are capable of establishing peatlands, which cover areas of up to hundreds of hectares in favourable conditions (Squeo et al., 2006).

As adaptions to the extreme environmental conditions, some plants show a distinct shortening of the internodes, a reduction of the short-lived leaves, acrotony of the branches, consistent length growth, and a dense array of regularly branched sprouts, whereby a compact, sheared-looking hard surface is formed. Only the outermost few centimeters of the sprouts are alive. Those living parts can grow 0.96-5.37 cm yr^{-1} and produce organic carbon with up to 4 kg m^{-2} yr^{-1} in the case of Distichia cushions in Bolivia, which is one of the highest carbon production rate of higher altitudes (Cooper et al., 2015). Underneath the living outermost centimetres of the plant, the rear parts die and build up peat or humus layers on which new sprouts with adventitious roots can grow. Through this mechanism, the plants build up circular sided- and upwards growing cushions of flattened hemispherical shape in cross section. This growth habit is referred to as '(woody) cushion plants' (sensu Du Rietz, 1931). Indeed, cushion growth is known from several representatives of 35 families of flowering plants, of which two-thirds occur in the Andes and sub-Antarctica (Rauh, 1988).

This unique growth form enables the plants to resist the extreme environmental conditions in the high Andes in several ways. For example, dense growth creates a microclimate in the small air spaces between the sprouts, which prevents frost damages and retains the humidity. Meanwhile, water and nutrients are stored in the encircled dead plant material. In addition, the compact and homogenous surface in combination with, in some species, pointed and sclerenchyma cap protected sprouts, impedes serious damage by rodents, birds or large herbivores (Ruthsatz, 2000).

While a lot of cushion building species, e.g. of the genus *Azorella*, are terrestrial plants, a specific floral community can colonise wet raw soils at groundwater-saturated sites such as springs, valleys, that are watered by shallow streams or on the shores of lakes and lagoons. As these semiaquatic plants build up cushions, the decomposition of dead submerged organic material is prohibited by the exclusion of oxygen. Because of this, massive, more than ten meters thick layers of undecomposed plant material (i.e. peat) can be established over long periods of time and hence characterise this habitat as a peatland (Succow & Joosten, 2001). The accumulation rates of high-Andean bofedales are high in comparison to other montane wetlands and growth can exceed up to 2 mm per year (Earle et al., 2003). The accumulated peat body acts as a long-term storage for water and nutrients, which are also exploited by a number of small epiphytes settling in gaps of the cushions or by accompanying wetland species at the borders of the cushions (Rauh, 1988).

The main peat accumulating species of high-Andean cushion peatlands are *Distichia muscoides*, *Oxychloe andina* and *Patosia clandestina* of the family Juncaceae, which are all dioecian, anemophilous and spread by birds attracted to their coloured fruits (Ruthsatz, 2000). The peatland's vegetation composition is determined by: i) water availability and seasonal distribution; ii) temperature regimes (i.e. diurnal amplitudes and frost frequency); iii) water chemistry (i.e. availability of nutrients, content of toxic elements, etc.), and; iv) biotic influences, such as seed dispersal or anthropogenic impact, in-

Figure 1.3 | Some cushion forming plants of high-Andean peatlands: (A) ***Distichia muscoides*** with (B) the typical growth habit (B); and (C) ***Oxychloe andina*** with (D) its typical growth habit

cluding intense grazing (Squeo et al., 2006). As a consequence of individual resilience and adaptions, the three Juncaceae species show different distribution patterns within the north-to-south extension of the Andes. *Distichia muscoides* is typical for peatlands of the more humid Andes, from Venezuela and Colombia to southern Peru, Bolivia and to north-western Argentina. In contrast, *Oxychloe andina* is adapted to drier, colder and saltier conditions and occurs in the semiarid mountains from southern Peru across Bolivia and northern Chile to the distribution limit of cushion peatlands in mid-Argentina and -Chile. Meanwhile, *Patosia clandestina* shows an insular distribution pattern with separated areas in mid-Chile to north-western Argentina and northern Bolivia to southern Peru. Only under extreme environmental conditions are other cushion forming plant species, such as *Scirpus atacamensis* (Cyperaceae) or *Plantago tubulosa* (Plantaginaceae) able to comprise larger areas of the peatland, though they are not normally the main peat accumulating vegetation. Under sub-optimal habitat conditions, several accompanying species have the ability to settle between leaves, sprouts and cushions (Ruthsatz, 2000).

1.2.2 | Hydrology

High-Andean bofedales are percolation peatlands mainly supplied by groundwater, rather than precipitation, which characterises the peatlands as minerotrophic (Succow & Joosten, 2001) and the term “bog” should not be applied to describe bofedales (Cooper et al., 2010).

The cushion peatlands located west of the Andean watershed and draining towards the Pacific Ocean are of exceptional hydrological importance. They represent the main water source for the rivers of the western Andean slopes and, further downwards, also for the river oases located in the deserts between the Andean foothills and the Pacific coast (Fehren-Schmitz et al., 2014). In the distinct seasonal precipitation regime of the central high Andes, the cushion peatlands have an important regulating effect on the water drainage. The water perlocates through the fine grained peat layers, which significantly reduces the runoff velocity. Through this mechanism, the cushion peatlands store water, weaken the runoff during the pooled rain events in the wet season and prolong the water supply for the westwards draining river systems into the dry season (Ramsar-Convention, 2005; Cepeda et al., 2006; Schittek et al., 2012).

Figure 1.4 | Different aspects of the same high-Andean cushion peatland

1.2.3 | Heterogeneity and dynamics of the ecosystem

High-Andean cushion peatlands appear as green, dense oases in the valley bottoms and other places with a shallow relief, and contrast with the surrounding scattered yellowish to brownish Puna vegetation. The naturally occurring circular cushions are often interlaced with each other by the prolonged ends of single cushions, and build an undulating micro relief. The typical aspect of a cushion peatland is generated by the combination of well established cushions and water filled or dried out pools in between (Coronel et al., 2004). At a certain growth height, the slightly elevated centres of the hard cushions are particularly exposed to wind erosion or the influence of frost, especially at unprotected sites. This leads to damage of the living surface layer, uncovering the underlying peat which desiccates and gets blown out. The hollows created are often filled up with groundwater and become small to medium sized pools of less than one or up to several tens of square meters in size. However, because of the distinct radial growth of the cushion plants and their ability to colonise shallow water, the pools are resettled and transformed into cushions again (Rauh & Falk, 1959). Through these dynamic processes, the surface of high-Andean cushion peatlands is constantly changing and shows a great heterogeneity.

Figure 1.5 | An *Oxychloe andina*-cushion showing natural degradation in the central part

Another basic reason for the great heterogeneity of high-Andean cushion peatlands is the strong influence of the highly mobile soils in the catchment of the peatlands. Because of intense frost disintegration, substantial wind erosion and the sparse vegetation cover of the surroundings, the influx of mineral particles by aeolian or fluviatile transport is considerable. Pooled precipitation events can produce huge debris flows, which are able to cover large parts of the peatlands (Schittek et al., 2012). Nevertheless, even under unexceptional climatic conditions, the peat matrices are mixed with a significant amount of mineral particles, which characterises high-Andean cushion peatlands as soligenous peatlands (Succow & Joosten, 2001).

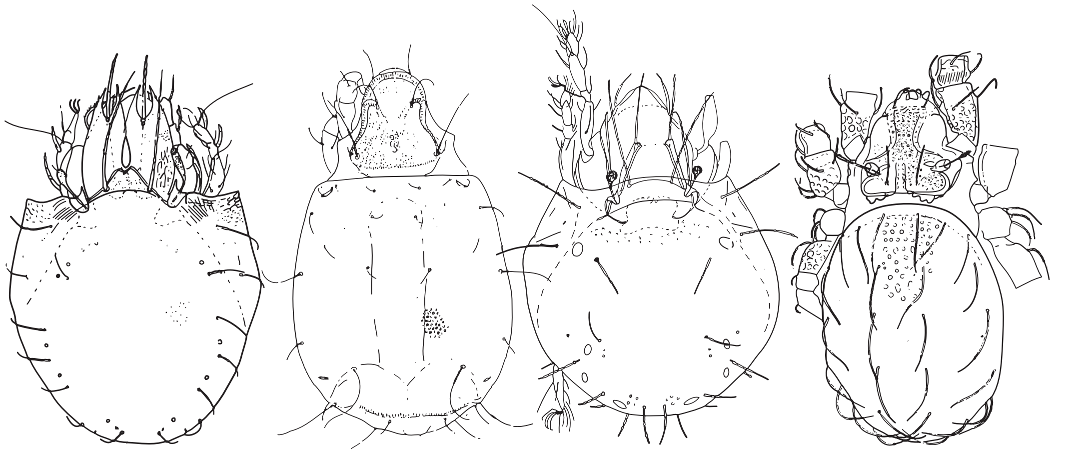


Figure 1.6 | Illustration of Oribatid mites diversity. All drawings by Hammer (1958, 1961, 1962). Species from left to right: *Oribatella illuminata*, *Trimalaconothrus cajamarcensis*, *Jugatala armata* & *Nanhermannia nana*

1.3 | Biology of Oribatid Mites

The compound term "Oribatid mite" can be affiliated to the Greek words "oreos" (mountain) and "batein" (travel) ("those that travel around in the mountains" (De La Riva-Caballero, 2011)) and the Old English meaning of "mite" as a very small creature (Walter & Proctor, 2013). The term refers to a taxonomical group, the Oribatida, of which the basic biological aspects are described in this chapter.

1.3.1 | Phylogeny & Systematics

Systematically, the Oribatida belong to the Arthropoda and within to the most numerous chelicerate class, the Arachnida (Krantz, 2009). The Arachnida are separated into 18 orders, of which, e.g. the Araneae includes the spiders and the Scorpiones the scorpions (Roskov et al., 2015). Modern systematics divide the mites into several orders which can be distinguished further into the two superorders: i) Parasitiformes, which include e.g. all Mesostigmata and the ticks (Ixodida); and ii) Acariformes, which include the Trombidiformes and Sarcoptiformes (Lindquist et al., 2009). Traditionally, both superorders are treated as a subclass of the Arachnida called "Acari" (Walter & Proctor, 2013). The Oribatida form a suborder of the Sarcoptiformes (besides the Endeostigmata) for which Subìas (2004) lists 164 families, 1262 genera and 10,695 species and subspecies in his worldwide catalogue (most recently updated in March 2015). 50,000 to 100,000 existing species of Oribatida are estimated to occur (Schatz, 2002).

1.3.2 | Origin of Oribatid mites

The earliest fossil evidence of acariform mites is known from the Early Devonian ca. 410 myr at Gilboa, USA (Shear et al., 1984), but molecular dating methods suggest an earlier origin of Oribatid mites from the Cambrian era (571±37 myr) (Schaefer et al., 2010). Thus, acariform mites can be considered among the first colonisers of land. Indeed, Labandeira (2005) hypothesises a colonisation through the interstitial route. It is likely that detritivorous acariform mites played an important role in early terrestrial ecosystems as they strongly enhanced the recycling of nutrients in coal swamp forests and facilitated further invasion of terrestrial habitats by colonisers at higher trophic levels (Labandeira et al., 1997).

1.3.3 | Classification and Morphology

Mites and arachnids in general can be distinguished from other arthropods by using crucial morphological differences. The body plan is characterised by two regions. On the anterior part, the "prosoma", structures for feeding, locomotion and sensing are present. Forked, tweezer-like mouthparts (chelicerae), pedipalps for feeding and sensing and four pairs of walking legs are morphological characteristics of the prosoma. The posterior body part, or "opisthosoma", comprises organs for digestions, gamete production and gaseous exchange. In contrast to all other arachnids, mites show a unique body separation with a "gnathosoma" containing the feeding apparatus, and the "idiosoma", composed by all other structures (Walter & Proctor, 2013).

Within the mites, the Acariformes are characterised by, e.g. having genital papillae, a plate-like tritosternum and prodorsal trichobotria, consisting of a bothridium and a sensillus. Many taxa show an obvious division of the body into the "proterosoma", bearing the pedipalps, chelicerae and both anterior leg pairs, and the "hysterosoma", comprising the idiosoma and the posterior two leg pairs (Walter & Proctor, 2013). Typical for many Oribatid mites is an extensive and continuous sclerotisation of the cuticle in adults, which produces hard body plates (Norton & Behan-Pelletier, 2009). However, the cuticle can also reveal distinct porous areas for secretory or respiratory functions and polymorphic setae. The size of Oribatid mite species predominantly ranges from 300 to 700 µm in general, with some taxa merely reaching 150 µm, while others can be up to 2000 µm (Norton & Behan-Pelletier, 2009).

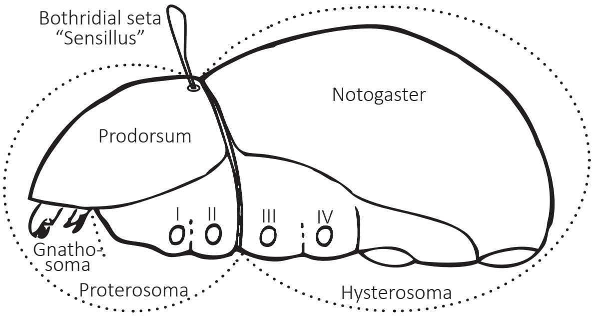


Figure 1.7 | Schematic acariform mite showing the general body form in lateral aspect. The circles I-IV indicate the base of appendages. Drawing modified from Weigmann, 2006.

1.3.4 | General biogeography

Cosmopolitans among the Oribatid mites are rare (16% of the genera (Hammer & Wallwork, 1979)) while only a few taxa have a semicosmopolitan distribution (less than 1% of the species and only 12% of the genera). In fact, 90% of all species are found in one biogeographical region. In 2015, 2126 species were known from the Neotropical zoogeographical region, which represents the third richest zoogeographical region after the Palearctic and Oriental regions (Subìas, 2004). Ca. 1000 species are confined to South America (Schatz, 2004). Summing up all available faunal investigations for Peru up to present (June 2015), 490 species are reported (Balogh & Balogh, 1988, 1990; Wunderle, 1992; Schatz, 1997, 2006; Maraun et al., 2007; Ermilov & Gwiazdowicz, 2015; H. Schatz, pers. comm., 2015).

The Oribatid mite fauna of temperate South America differs strikingly from the tropical areas (Hammer & Wallwork, 1979). As the Andean fauna corresponds closely to the fauna of the Falklands, the Sub-Antarctic Islands and New-Zealand, the establishment of an Andean zoogeographical region can therefore be supported based on Oribatid mite distribution data (Stary & Block, 1998; Morrone, 2002).

1.3.5 | Habitat

Oribatid mites often dominate the arthropod community in soil-litter systems. Highly organic temperate forest soils can contain more than 100 Oribatid mite species and can reach densities up to 100,000 specimens per square meter (Norton & Behan-Pelletier, 2009). Oribatid mites are mainly soil dwelling but can also be found in other habitats, such as mosses and lichens, and on the surface of vascular plants while many species inhabit the bark of trees and shrubs (Walter & Proctor, 2013). Oribatid mites are primarily terrestrial; only about 1% of known species can be described as truly aquatic (Schatz & Behan-Pelletier, 2008). The aquatic and semi-aquatic species can be found in bogs, peatlands, lakes, streams and at the seashore (Walter & Proctor, 2013).

1.3.6 | Dispersal pathways

Dispersal, i.e. the movement of individuals from their home site (Kendeigh, 1961) and colonisation, i.e. successful establishment of a species in a habitat (Allaby, 1994) are two stages in the invasion of new habitats by species. Dispersal is a precondition of colonisation which can be separated in active and passive forms (Lehmitz et al., 2012). In active dispersal, Oribatid mites spread above as well as below ground by locomotion and can move with a speed of between 0.3 to 2.1 cm per day (Lehmitz et al., 2012). In passive dispersal, Oribatid mites are spread by the wind, phoretic on birds, mammals, insects and humans or by water (Karasawa et al., 2005). Of these types, wind transport (even over very long distances) has been demonstrated to be an important mechanism for spreading Oribatid mites (Wallwork, 1972). Lehmitz et al. (2011) showed the relative importance of active and passive dispersal pathways for Oribatid mites, and their ability to inhabit new habitats in a short period of time (Lehmitz et al., 2012).

1.3.7 | Food web position

Among the Oribatid mites, different feeding guilds occur at different trophic levels with the occupation of distinct trophic niches by different taxa verifiable by stable isotope ratio ($^{15}N/^{14}N$ and $^{13}C/^{12}C$) measurement (Schneider et al., 2004b; Maraun et al., 2011). At the lowest level, phycophages or fungiphages feed on algae or lichens. Primary decomposers are feeding on litter, whereas secondary decomposers ingest fungi. The highest tropic level is occupied by the carnivores, scavengers or omnivores, which feed on living and dead animals (e.g. nematodes or collembolans) and fungi (Schneider et al., 2004a). Most Oribatid mite species are particle or fungal-feeding primary or secondary decomposers (Norton & Behan-Pelletier, 2009).

1.3.8 | Reproduction and life history trait

Different types of reproduction, development, synchronisation and dispersal define the life history tactics of microarthropods (Siepel, 1994). Oribatid mites typically show K-style life history traits with low reproduction output and long life cycles of 1-5 years (Norton & Behan-Pelletier, 2009) and up to seven years in extreme habitats of the Arctic (Søvik et al., 2003). Oribatid mites exhibit an acariform plesiotypic life cycle, which includes seven stages: egg, calyptostatic prelarva, six-legged larva, protonymph, deutonymph, tritonymph and adult (Walter & Proctor, 2013). Deposition of eggs is the normal case in Oribatida, but in some aquatic or semi-aquatic species embryogenesis and even partial larval development proceeds internally (Norton, 1994). Thelytokous parthenogenesis plays an important role in Oribatida (Norton & Palmer, 1991) and its occurrence in potential parthenogenetic species is mainly controlled by the availability of resources and not by unfavourable environmental conditions (Maraun et al., 2013).

1.4 | Biology of the Chironomidae

In this chapter, basic biological aspects of the multifarious Chironomids, generally known as the "non-biting midges", are described.

1.4.1 | Systematics & Phylogeny

The family Chironomidae belongs to the Arthropoda and the mandibulate class Insecta. Within, the taxon is a member of the Diptera (Roskov et al., 2015). The Chironomidae are placed in the paraphyletic but traditionally established suborder Nematocera (the "lower" Diptera), in which they, together with the Ceratopogenidae (the "biting midges"), form a sister group to the Simuliidae (the "black flies") (Cranston, 1997c; Courtney & Merritt, 2009). The earliest known fossils of Chironomidae are known from Lower Cretaceous amber in Lebanon (Schlee & Dietrich, 1970) and Mongolia (Lukashevich & Przhiboro, 2015). Recent phylogenetic investigations reveal a Permian origin for the family (Cranston et al., 2012), while global Chironomid species richness is estimated at 8,000-20,000 species (Coffman, 1997). Although, the current number of described species is unclear, due to the lack of a worldwide species catalogue, Ferrington (2008) quotes, that 4147 aquatic species are described worldwide. In the Neotropical zoogeographic region, a total of nine of the global 11 subfamilies, 155 genera and 709 species are recorded (Spies & Reiss, 1996; Paggi, 2009). Ashe et al. (1987) list 187 species as restricted to the Andean/Patagonian region, of which the majority belongs to the subfamilies Podonominae (87 species) and Orthocladiinae (85 species).

1.4.2 | Larval Morphology and Classification

The larval body of Chironomidae is vermiform, in the sense of being cylindrical and elongated (Courtney & Merritt, 2009), with the body length ranging from 1 to 30mm in mature larvae; albeit the larvae of only a few species exceed 10 mm (Oliver & Roussel, 1983). The head is highlighted by a well-developed, non-retractile and complete sclerotised head capsule, which is typical for nemantocerous Dipterans. The soft and often hyaline body is segmented into equally shaped three thoracic and nine abdominal segments, which demarcate the transition between the thorax and abdomen. Usually, a pair of parapods can be found on the first and last segments. The last segment additionally shows seta-bearing procerci. The paired parapods, the characteristic procerci and the absence of spiracles are the features that distinguish the Chironomidae from other nematocerous larvae (Cranston, 1997b).

The head capsule consisting of three heavily sclerotised plates, a dorsal apotome and a pair of lateral genae, is enclosing the complete cranium. The most prominent ventral feature on the head capsule is the mentum. Its shape and number of teeth are important for identification. Other important features are the ventromental plates, posterior of the mentum and the mandibles and premandibles, anterior of the mentum. In Tanypodinae, the mentum is weakly developed and hyaline. In this subfamily the most noticeable feature is the ligula, a modified structure of the premento-hypopharyngeal complex (Epler, 2001).

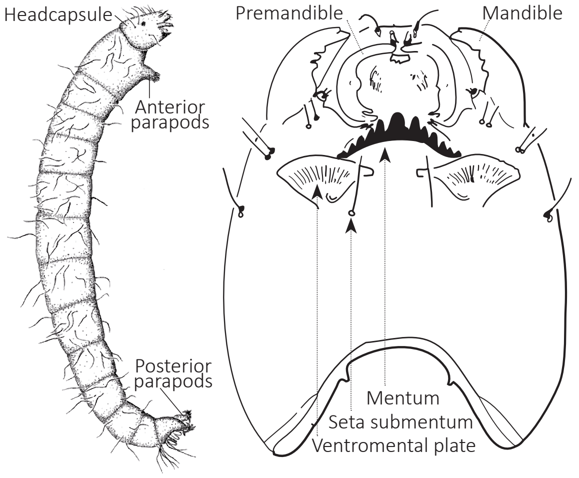


Figure 1.8 | Morphology of a Chironomid larva. For illustration, a Orthocladiinae-larva (left) and details of the corresponding headcapsule (right) are depicted. Drawings by Epler, 2001.

1.4.3 | General Biogeography

Chironomids are the most widely distributed free-living holometabolous insects (Cranston, 1997a). They occur from Antarctica at 68°S latitude (Sugg et al., 1983) to the Arctic at 81°N latitude (Oliver & Corbet, 1966). Only 38 Chironomid genera show a cosmopolitan distribution, representing four subfamilies. In general, the data on the Neotropical distribution of Chironomids is very sparse (Ashe et al., 1987).

Regarding the Chironomid taxa, the Nearctic and Neotropical biogeographic regions are zoogeographically interrelated (Coffman, 1997) connected by the mountain chains of the Rocky Mountains and the Andes, which stretch from Alaska to Patagonia, facilitating a migration pathway for cold adapted species. A similar exchange is possible through the lowlands and the Caribbean Islands for warm adapted species (Ashe et al., 1987).

As a general rule, the diversity of Chironominae and Tanypodinae increases from polar to equatorial regions and from high to low altitude, whereas diversity of Orthocladiinae, Podonominae, Diamesinae and Prodiamesinae decreases (Ashe et al., 1987).

1.4.4 | Habitats

Chironomid larvae are one of the most tolerant insects. They are preferably found in an aquatic habitat, inhabiting the majority of freshwater environments ranging from flowing and standing waters to temporary pools, phytotelmata and thin water layers on ice. Some species occur in brackish or saline water including intertidal and marine habitats (Cranston, 1997a). Immature Chironomids are found at 1000 m depth in Lake Baikal to 5600 m altitude on glaciers in Nepal (Linevich, 1959; Koshima, 1984). Some species even occur in hot springs with temperatures of 38°C (Hayford et al., 1995), while others tolerate temperatures of -20°C (Bouchard et al., 2006). In favourable aquatic habitats, larval densities of over 30,000 specimens per square metre are not unusual (Oliver & Roussel, 1983). Nevertheless, although most of the species are truly aquatic, some species are semi-aquatic or terrestrial and inhabit wetlands, wet areas next to water bodies, wet leaf litter or dung (Oliver & Roussel, 1983). All Chironomid larvae, except of some predaceous species, construct a case, lined by silk-like threads, on or in the substrate. The substrate is usually only penetrated a few centimetres. In lotic and lentic habitats, 95% of the larvae can be found in the uppermost 10 cm of the substrate (Ford, 1962).

1.4.5 | Dispersal pathways

Chironomids spread to new habitats mainly by passive dispersal of fertilised females (Armitage, 1997). However, long distance wind drifting is possible as observations suggest, including adult Chironomids from high elevations (*Cricotopus* sp. and *Pentaneura* sp. at >600 m above ground Glick,

1960) and over oceans (up to 80 km from the nearest coast line Holzapfel et al., 1969).

1.4.6 | Reproduction & life-cycle

The Chironomidae show a holometabolic life-cycle with four stages: egg, four larval instars, pupa and imago. The ovoid eggs are laid singly (in Telmatogetoninae) or clustered in numbers up to several hundred. Egg development to hatching is strongly influenced by temperature and takes 2.5-6 days under mid-European summer conditions (Thienemann, 1974). The first instar larva is transparent, but the head becomes sclerotised after a short time. However, the head capsule differs in distinct features, e.g. dentation of mentum, from later instars. The first instar larvae are free-swimming and highly mobile. After the first moulting, the morphological features resemble later larval instars (Pinder, 1997a). The duration of the last larval instar is often the longest. However, the overall duration of larval development is strongly effected by environmental conditions and mostly by temperature. At constant conditions with uniform high temperatures, e.g. in the tropics, an Amazonian species completes the larval development in seven days (Nolte, 1996). In the less stable conditions of temperate or polar regions, the larval development is slowed down or interrupted during unfavourable winter conditions (Oliver, 1971). In an extreme case and under Arctic conditions, larval development, requiring seven years to complete was found in two *Chironomus* species (Butler, 1982).

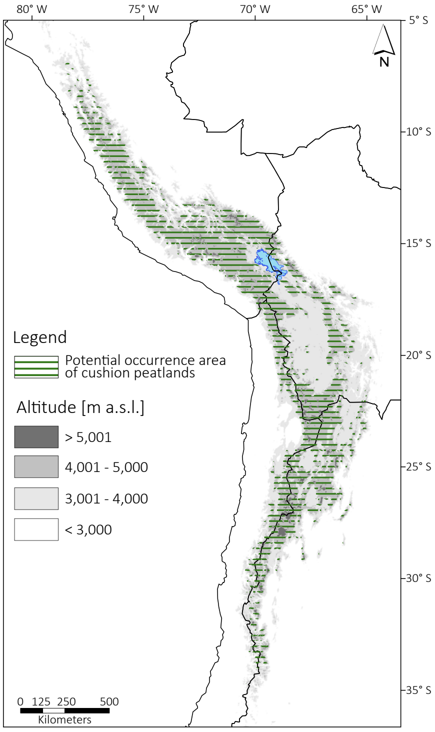
After complete larval development, the final instar larva produces a pupa, which is either free-living (in Tanypodinae, Aphroteniidae and some genera of Podonominae) or sedentary in a tube or covering film (in all other subfamilies). Pupation lasts only for a few hours or up to several days. The mature pupa, induced by specific stimuli, moves to the surface of the water and the imago emerges (Langton, 1997). Some species show hibernation during the pupal stage, by which seasonally unfavourable environmental conditions, such as droughts, are outlasted (Pinder, 1997b). The adult stage lasts several weeks in which reproduction takes place. Most of the species do not feed as imagines (Oliver, 1971). Parthenogenesis is not common in Chironomidae (Armitage, 1997).

The Chironomid species show different life cycle patterns, mainly governed by distinctions in larval development as adaptions to specific environmental conditions. The differences are expressed in specific numbers of generations that a species produces in a year (or voltinism). Most of the species show a voltinism of 1-2, with the bivoltine pattern being the most dominant (Tokeshi, 1997). Some species, mainly from cold environments, produce less than one generation per year, e.g. 1/7 in *Chironomus* (Butler, 1982), or 1/2-3 in six genera or species from an Arctic lake (Welch, 1976). For other species, multivoltine patterns with more than two generations per year are reported, e.g. five in *Cricotopus* in an eutrophic stream (LeSage & Harrison, 1980). Four or more generations per year are suggested mainly for lotic species. In general, the higher developed taxa such as the Orthocladiinae show higher voltine patterns in comparison to lower taxa like Chironominae (Tokeshi, 1997).

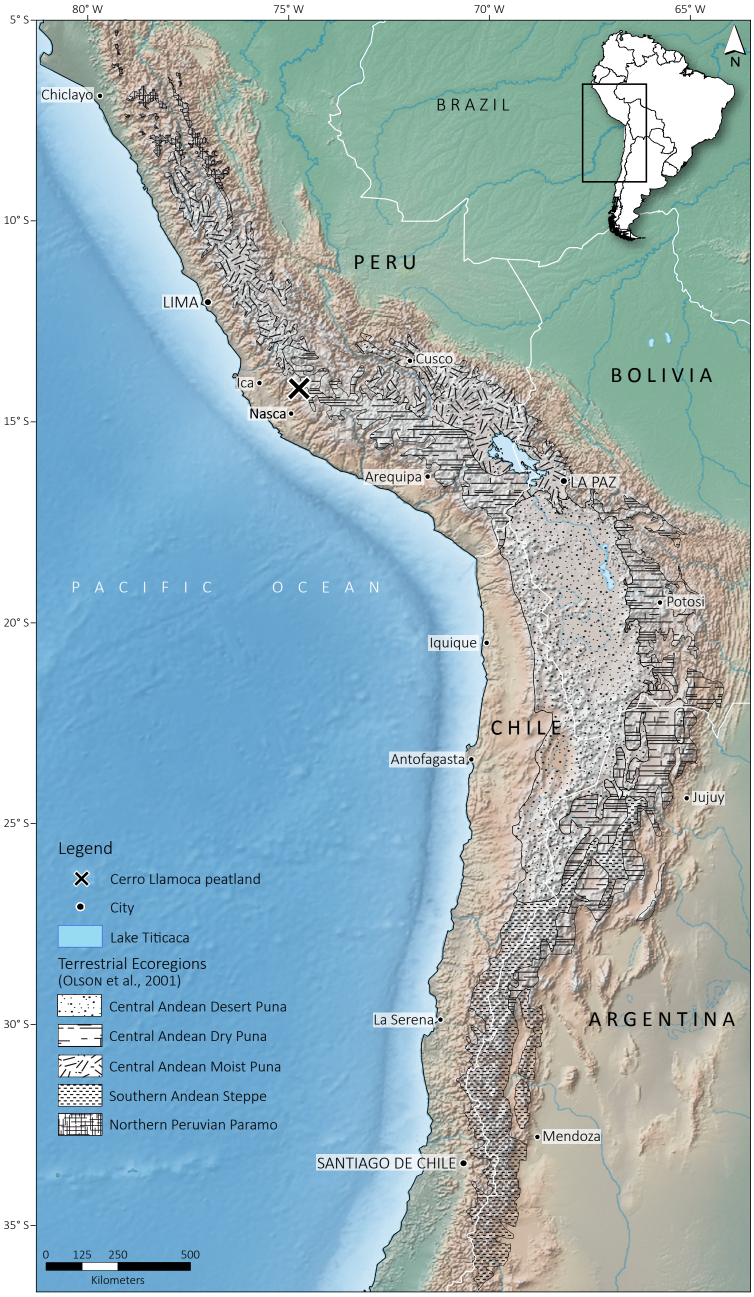
1.4.7 | Food web position

Chironomids larvae feature a wide range of feeding types from detritivores to herbivores and predators (Courtney & Merritt, 2009). The free-living predaceous species, most Tanypodinae and some other species, feed on larger invertebrates such as chironomid larvae, oligochaetes and copepods. All other chironomid species ingest food from their immediate environment, feeding on detritus, plant particles or algae (Oliver & Roussel, 1983). Chironomids play an important role in nutrient recycling in freshwater ecosystems and represent a connection between primary and secondary consumers (Porinchu & MacDonald, 2003).

2 | Chapter II - Study area



▲**Figure 2.1 |** Distribution map of cushion peatlands in the Puna and steppe ecoregions of the high Andes. The striped pattern indicates a simplified depiction of the potential occurrence area, corresponding to the altitudinal level between 4000-5000 m a.s.l..



◀**Figure 2.2 |** Map showing the geographical setting of the Cerro Llamoca peatland in southern Peru. The classification of ecoregions in the area corresponds to Olsen et al., 2001.

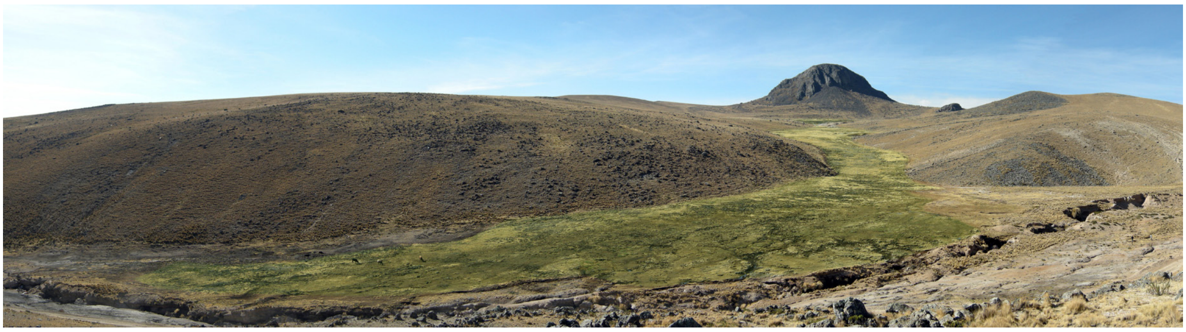


Figure 2.3 | Overview of the “Cerro Llamoca” peatland. In the background, the name giving mountain peak can be seen.

2.1 | Geographical Setting

The Cerro Llamoca peatland (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', about 100 km east of the city Ica. The peatland distinctly stretches north-to-south with an approximately length of 1.3 km and covers an area of 11.6 hectares. It is located west of the continental watershed in the Río Viscas catchment area and drains towards the Pacific Ocean.

The CLP is located in the transition zone between the Moist and the Dry Puna (Troll, 1968), where diurnal freeze-thaw cycles, high solar radiation and a seasonal precipitation regime are of high ecological significance (Cabrera, 1968).

Puna ecosystems are found between approximately 8°S to 29°S in the high altitude belt of the Andes from 3800 to and maximal up to 6000 m a.s.l. in the case of the Desert Puna in northern Chile. The Moist Puna or 'Puna húmeda' of mid-Peru and the eastern cordillera of southern Peru and Bolivia, found in the altitudinal belt between 3800 and 4700 (max. 5500) m a.s.l., is characterized by an annual precipitation of more than 400 mm. In contrast, the Dry Puna or 'Puna seca' of the western cordillera of Southern Peru, the eastern cordillera of Bolivia and northern Argentina is affected by fewer humid months per year and an annual precipitation between 100 and 400 mm and can be found in altitudes between 4000 and 5500 (max. 5700) m a.s.l. (Cabrera, 1968; Troll, 1968; Olson et al., 2001).

2.2 | Climate Conditions

The study area is characterised by a tropical climate (Lauer, 1993) shaped by distinct temperature and precipitation fluctuations on daily and yearly patterns.

2.2.1 | Precipitation

An accurate measure of yearly precipitation is not possible for the study area, because on-site measurements or local weather stations are not available. Nevertheless, different climate models estimate an annual amount of 200-400 mm precipitation per year (Bookhagen & Strecker, 2008) or up to 600 mm per year (Hijmans et al., 2005). The currently most advanced climate model, the ERA-Interim model (ECMWF, 2014), renders a mean annual precipitation of 349 mm per year for the location of the CLP (see Figure 2.4).

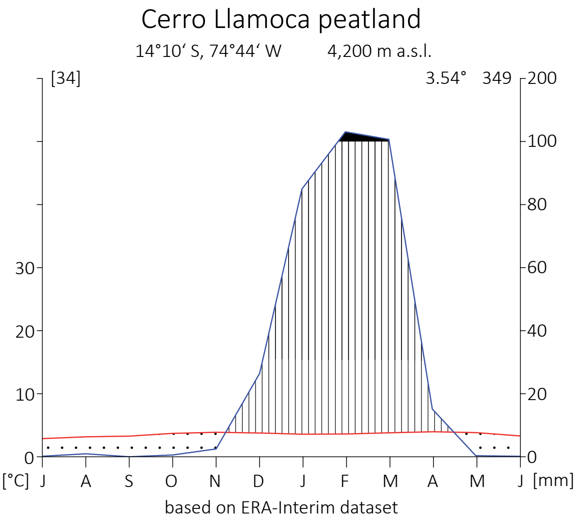


Figure 2.4 | Climate diagram for the study area, based on the ERA-Interim model. Data were obtained using Climate Reanalyzer (http://cci-reanalyzer.org), Climate Change Institute, University of Maine, USA.

The modelled climate data show a marked seasonal precipitation pattern. About 90% of the annual precipitation falls during the austral summer (December to March). Within the wet season, rainy days are distinctly clustered in short periods of about seven days with thunderstorms and heavy rain, followed by longer dry periods (Garreaud, 2000). This concentration of precipitation during distinct periods of the year could be termed as a "monsoon-like" precipitation pattern (Zhou & Lau, 1998).

This precipitation regime in the study area is triggered by a complex interplay of several key features: i) the position of the Intertropical Convergence Zone (ITCZ); ii) the intensity of the South American Summer Monsoon (SASM), and; iii) the strength of El Niño-Southern Oscillation (ENSO) (Garreaud et al., 2009). The influences of these climatic features change throughout the year and between years, and lead to inter- and intra-seasonal variation in precipitation.

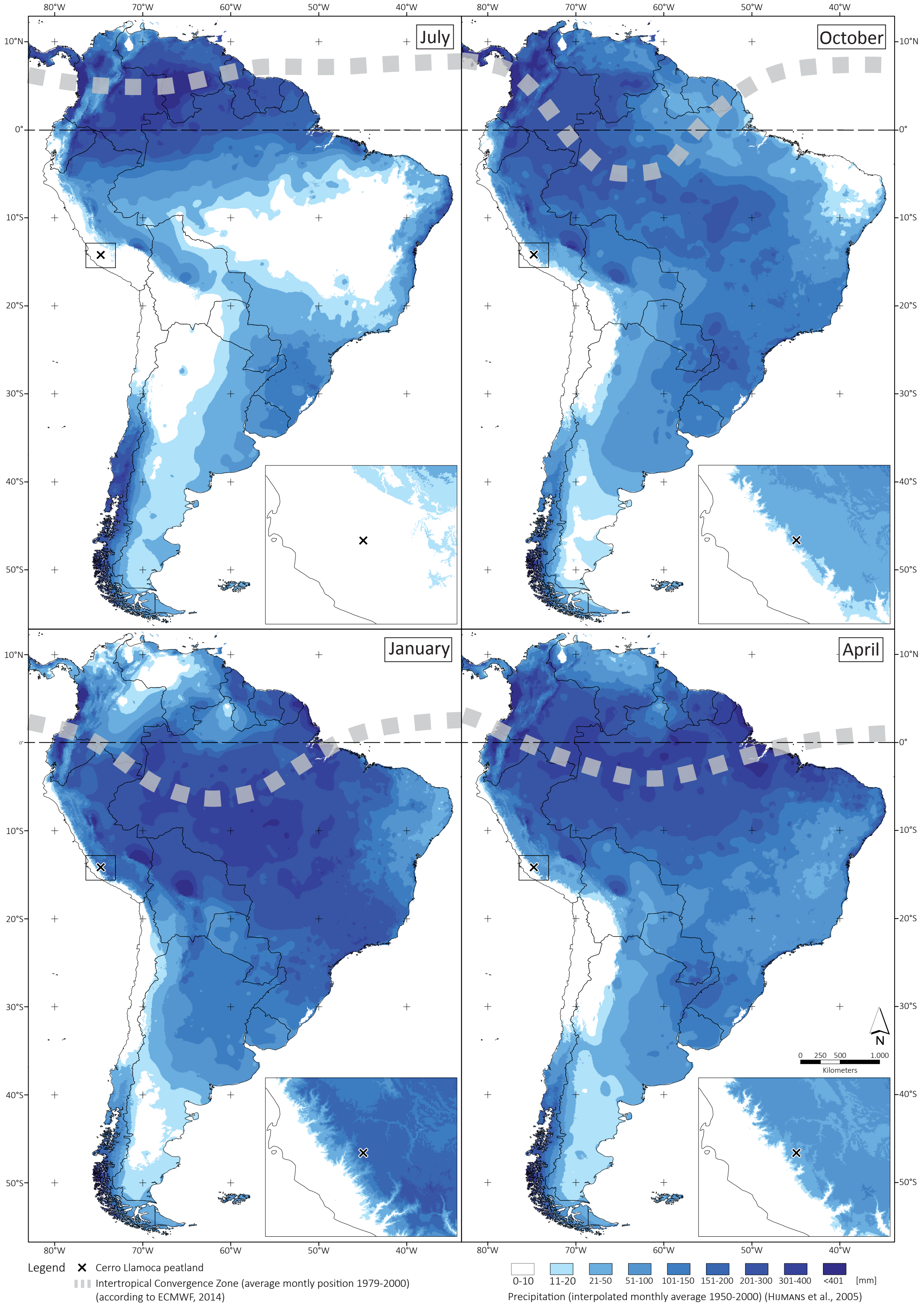


Figure 2.5 | Precipitation fluctuations on the South American landmass and in the study area in detail (each bottom right corner) depicted by precipitation patterns in austral winter (July), spring (October), summer (January) and autumn (April). To map precipitation conditions, the WorldClim v.1.4 (release 3) dataset was used (HIJMANS et al., 2005). The Intertropical Convergence Zone (ITCZ), indicated by the grey dotted line, was drawn by an alignment of monthly average water column and vertical velocity (omega) data from 1979-2013 by the ERA-Interim source (ECMWF, 2014) based on the procedure of LORREY (2012). Data were obtained using Climate Reanalyzer (http://cci-reanalyser.org), Climate Change Institute, University of Maine, USA.

Throughout the year, moisture transport from the Pacific Ocean to the central Andes is completely impeded by a southeast Pacific anticyclone in combination with cold sea water, transported far northwards along the western shore of South America by the Humboldt Current. Both phenomena together are the reason for a large-scale subsidence and a temperature inversion at 1000 m a.s.l. along the shore line, which cause the very dry climatic conditions on the Peruvian and Chilean coasts (Vuille, 1999; Rutllant et al., 2003).

In austral winter, the ITCZ, whose low pressure belt produces convective precipitation, is located at about 5°N, leading to a distinct concentration of precipitation in the northern part of the continent. The tropospheric conditions lead to a constant easterly air flow in the study area, receiving dry air masses from the eastern part of the continent (Garreaud et al., 2009).

The situation changes in austral summer. The ITCZ shifts southwards (see Figure 2.5). The core zone of this convection reaches as far as 5-10°S over the central continent. Simultaneously, the near-ground wind system changes. A low over the Chaco region in northern Argentina (at about 25°S) causes a low-level jet flow of moist air masses from the Amazon basin southwards along the easterly side of the Andes, as far south as 35°S. Additionally, a high pressure cell is established at 200 hPa level (12 km a.s.l.) over the Altiplano, which pulls moist air masses up the eastern slopes, fostering precipitation events in the central high Andes (Vuille, 1999; Seltzer et al., 2000; Garreaud et al., 2003; Seluchi et al., 2003; Garreaud et al., 2009).

Intraseasonal variability in the amount of precipitation reaching the central high Andes are ascribed to the winter position of the ITCZ. A distinctly southerly position intensifies moisture transport in the Amazon basin which strengthens the SASM and the movement of moist air masses upwards over the high Andes (Maslin & Burns, 2000; Bird et al., 2011a, b; Maslin et al., 2011; Vuille et al., 2012). Additionally, the intensity of ENSO with increased precipitation during La Niña conditions affects precipitation in the study area (Garreaud et al., 2009).

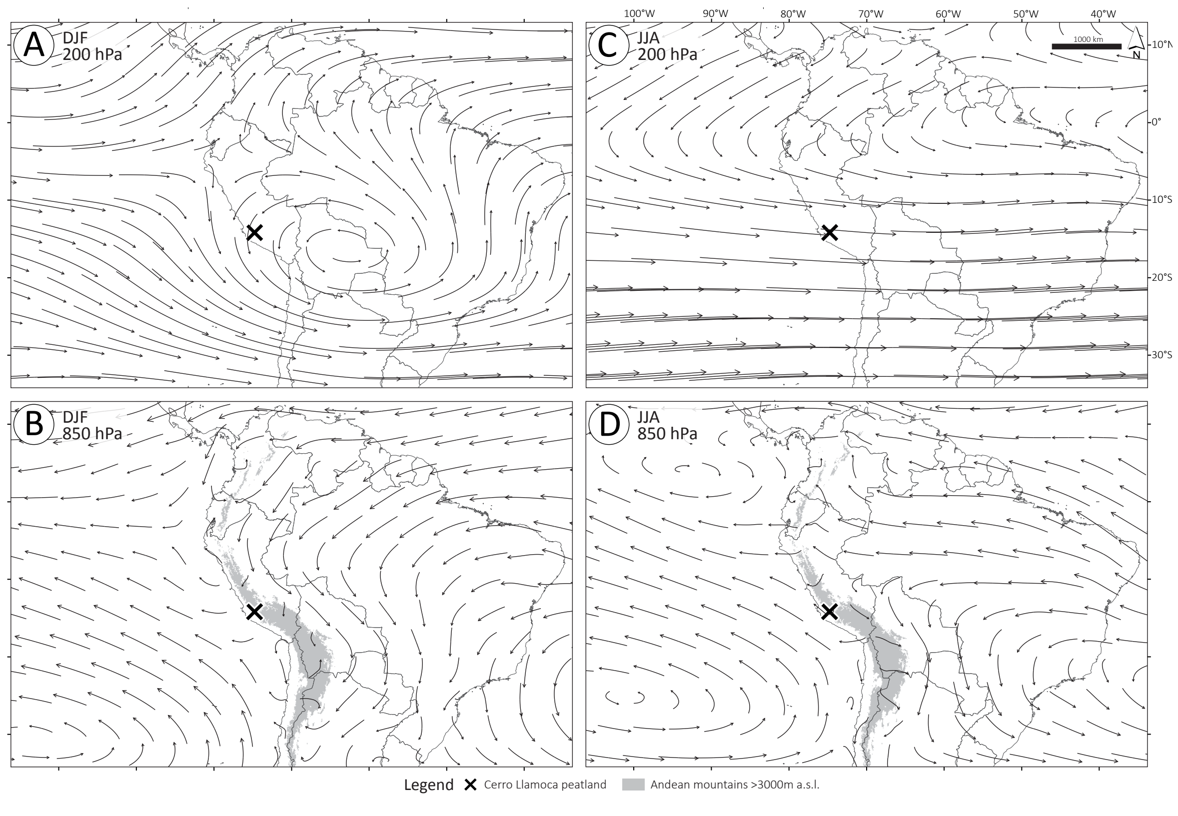


Figure 2.6 | Windfields over northern and central South America in the austral summer season (December-February) at A) 200 hPa level and B) 850 hPa level, and in the austral winter season (June-August) at C) 200 hPa and D) 850 hPa, respectively. Wind speed is indicated by the length of arrows. Long term average wind speed conditions have been reconstructed with the data from 1979-2013 by the ERA-Interim source (ECMWF, 2014), based on the procedure by Vuille (1999). Data were obtained using Climate Reanalyzer (http://cci-reanalyser.org), Climate Change Institute, University of Maine, USA.

2.2.2 | Temperatures

The ERA-Interim model (ECMWF, 2014) renders a mean temperature of 3.54°C for the location of the CLP (see Figure 2.4). To get accurate near ground data for the CLP, the temperatures were hourly recorded from September 2010 to the end of October 2011 with an EBRO EB1 10-T100 data logger, located a few centimeters above the ground in a wind and sun protected shelter (see Figure 2.7). The measured mean temperature for this period amounted to 8.1°C with a low annual standard deviation (*SD*= 2.3). The mean daily minimum temperature during this period was 1.2°C, ranging from -4.0°C at the lowest to +5.2°C at the highest. Frost occurred during the entire year (94 days in the season 2010/11), but mainly from June to November (in average on 12 days/month, min. 7 days/month - max. 18 days/month in the season 2010/11). From January to April only on single days did the temperature drop below 0°C (in average on 1 d/month, min. 0 days/month - max. 2 days/month in the season 2010/11). The study area showed a pronounced diurnal temperature regime with extreme amplitudes attaining 28.2°C during 24 hours and an average day amplitude of 13.8°C. Temperature amplitudes were highest from September to December.

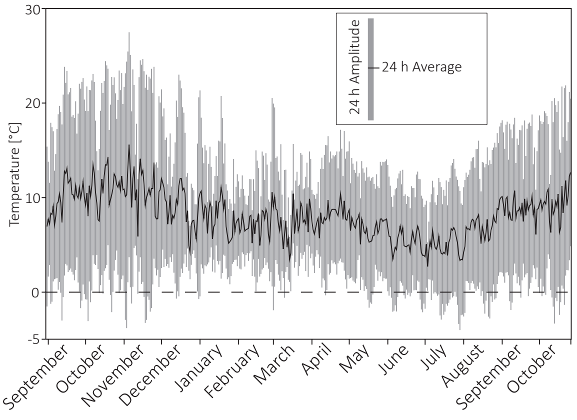


Figure 2.7 | Air temperature at the CLP at ca. 4250 m a.s.l. recorded from 09/2010 to 10/2011. Grey bars show maximal 24 hour amplitude and the black line the 24 hour average temperature fluctuations. Data were hourly logged by an EBRO EB1 10-T100 data logger in a wind and direct sun protected shelter, a few centimeters above ground.

The annual temperature fluctuations show a typical tropical pattern with higher diurnal changes than annual changes (Lauer, 1993). The temperature data of a previous timespan from the same location, showing a similar pattern, were published by Schittek et al. (2012).

2.3 | Soils

The soils in the catchment area of the CLP have been investigated by F. Leceta (pers. comm., 2014), and are classified as vitric Andosols following the classification by WRB (2006); vitric Andosols represent a young soil development stage derived from volcanic raw material. Soil mineralisation is not far advanced. Southern exposed slopes show an Ah-2Ah-Bwt-C soil profile, whereas northern exposed slopes are characterised by the loss of the Ah horizon. The Ah horizon is interspersed by a mixed loess/sand matrix originating from weathering of volcanic material (Miller et al., 1993).

2.4 | Vegetation of the study site and its surroundings

The Puna ecoregions of the high Andes, occurring above 3800 m altitude, are naturally formed from potentially an uninterrupted cover of bunch grasses (e.g. *Stipa* or *Festuca*) in the Moist Puna, or by a scattered mixture of Tola shrubs (e.g. *Lepidophyllum*) and bunch grasses in the Dry Puna. The vegetation of both ecosystems gradually becomes more open with increasing altitude and changes to a frost desert above the snow line (Cabrera, 1968). Single small sized patches of *Polylepis*-woodlands can occur up to altitudes of 4800-5000 m a.s.l., which ascends the absolute upper tree-line worldwide (Troll, 1968). Nowadays, the vegetation is heavily influenced by intense pasture for cattle, domestic camelids, horses and donkeys, while *Polylepis*-woodlands have disappeared almost completely due to anthropogenic deforestation (Serpa, 1974). Another characteristic feature of the Puna flora are the distinct growth forms, which can be interpreted as being advantageous to survive the harsh conditions at high altitudes (see also Chapter 1.2). Typically adapted plants include tussock grasses, small woody shrubs, rosette-forming perennials and cushion plants (Cabrera, 1968; Rauh, 1988). The surrounding areas of the peatland are characterised by sparsely distributed stiff bunch grasses such as *Festuca dolichophylla*, *Stipa brachyphylla* and *S. ichu*, in combination with xerophilic woody dwarf-shrubs, including *Senecio spinosus*, *Baccharis tola* and *Parastrephia quadrangularis*, which together form a dry savanna-like grassland. On northern exposed slopes, where the soil is less stable, the vegetation is noticeably different, consisting only of single specimens of *Pycnophyllum molle*, *Junellia minima* and *Azorella diapensioides*. Overall, the vegetation is limited by grazing to ca. 30% coverage. Only a few inaccessible sites, where grazing is prevented, show the natural dense growing vegetation, with up to 1 m tall *Festuca*- and *Stipa*-tussocks (Schittek et al., 2012).

The CLP's floristic composition reflects its position in the transition zone between two different ecoregions. According to Schittek et al. (2012), the main cushion-forming plants at the site are *Distichia muscoides* and *Oxychloe andina*. Ruthsatz (2000) has identified *Distichia muscoides* and several other associated species as typical peatland elements of the more humid northern tropical Andes. *Distichia muscoides* reaches its southwestern distribution limit at the site, whereas *Oxychloe andina*, the main cushion-forming peatland plant of the drier ecoregions of the southern Andes, gets to its northernmost distribution limit.

Overall, the uppermost half of the CLP shows a gradiently merged but clearly visible tripartite separation into different parts:

In the upper area, next to the spring, large *Distichia muscoides* cushions can be found, of which the majority are degraded by the trampling of hoofed herbivores, such as cattle in this area (see Figure 2.8-A). Trampling destroys the vital uppermost plants and hence exposes the underlying peat. This 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).

The middle section is characterised by a large debris fan covering the peatland (see Figure 2.8-B). In this area, solely *Oxychloe andina* inhabits some of the wet debris layers.

The lowest section is less affected by degradation and shows a typical mosaic-like pattern of well-established large *Distichia muscoides* cushions, accompanied by several epiphytic species e.g. *Zameioscirpus muticus*, *Plantago tubulosa*, *Gentiana prostrata* and *Werneria pygmaea* growing on the cushion between the dense *Distichia* sprouts (see Figure 2.8-C). The cushions are often encircled by a frame of *Deyeuxia chrysantha* reeds and are usually separated by small pools (Schittek et al., 2012).

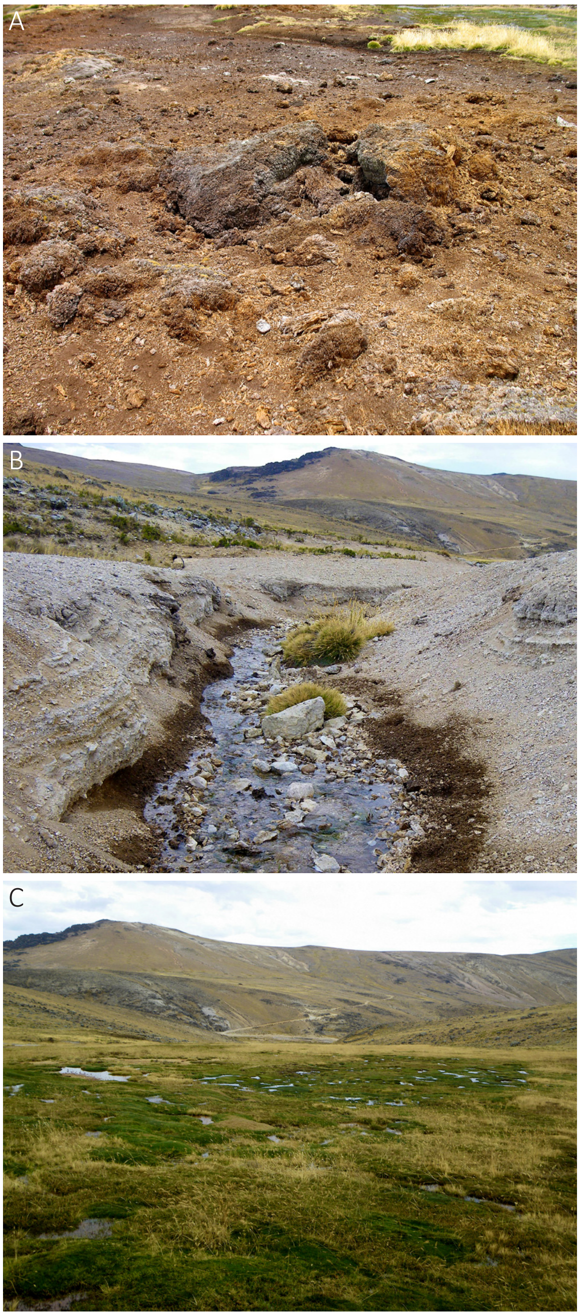


Figure 2.8 | Different aspects of the upper half of the CLP: (A) the upper area is characterised by degraded ***Distichia muscoides*** cushions; (B) the middle section is covered by a debris fan with sparsely occurring ***Oxychloe andina*** cushions; (C) the lower section shows the typical mosaic-like pattern of fully established ***Distichia muscoides*** cushions and small pools

3 | Chapter III - Community Analyses

The Oribatid mites (Acari: Oribatida) and Chironomidae (Insecta: Diptera) fauna within the ecotope heterogeneity of a high-Andean cushion peatland

Abstract

The Oribatid mites and Chironomid larvae of five different successional stages of a high-Andean cushion peatland in southern Peru have been investigated. In total, 17 Oribatid mite taxa, belonging to eight families could be identified. Four species are new for Peru. Taxonomical remarks are provided for the found species. A rarefaction analysis shows a potential mite community of maximum 18 taxa per 1000 specimens for this ecosystem. Ranked species abundance analysis reveals three dominant, five subdominant, three recedent, two subrecedent and four sporadic occurrence patterns of the taxa. The investigation shows significantly higher Oribatid mite densities in early and medium successional stages in comparison to the successional climax ecotope. Additionally, specific distributional patterns are detected: *Jugatala montana, J. armata, Scheloribates pallidulus* and *Nanhermannia elegantissima* have their distributional main area in the degraded peatland parts, while *Scheloribates elegantulus*, *S. confundatus* and *Neoamerioppia notata* dwell in mid-successional areas of the peatland.

In total, 11 taxa of Chironomids, belonging to three subfamilies, could be identified. For the taxa found, taxonomical descriptions are provided. Rarefaction analysis estimates an α-diversity of maximum 12 taxa for 300 specimens. Ranked species abundance analysis reveals two dominant, subdominant and recedent taxa accompanied by four subrecedent and a single sporadic occurring taxa. Within the successional rank order of the peatland, the abundance of Chironomids is higher in pioneer soils followed by mid-successional and degraded soils. Significant distribution patterns are identified for *Apsectrotanypus/Alotanypus*, *Parametriocnemus/Paraphaenocladius*, *Parochlus*, *Paracricotopus* and *Cricotopus/Paratrichocladius* type II, which primarily dwell in pioneer soils.

3.1 | Introduction

The cushion peatlands of the high Andes above ~3000 m a.s.l. are an unique ecosystem, heavily influenced by the harsh environment with hyperaridity, diurnal frost-thaw cycles, hypoxia, strong winds and intense solar insulation (Ruthsatz, 1993; Squeo et al., 2006). As a direct consequence of these environmental influences and additionally due to anthropogenic impact, especially through land-use for pasture (Ruthsatz, 1995; Ramsar-Convention, 2005; Poblete, 2007), the ecosystem is highly heterogenous in soil types and vegetational composition (Schittek et al., 2012) and is very dynamic over time (Schittek et al., 2015).

Heterogeneity is a major driving force of species richness. This connection is well studied in above-ground settings (Mittelbach et al., 2001; Adams, 2009), but for below-ground communities and conditions, the first investigations have been conducted only recently and many processes remain unknown (Nielsen et al., 2010). For high-Andean cushion peatlands, the effect of heterogeneity on species richness has been studied on aquatic Cladocerans, inhabiting peatland water pools (Declerck et al., 2011), but no other data, e.g. on soil organisms are available.

The aim of this study is: i) to capture the Oribatid mite and Chironomid richness of a cushion peatland; ii) to clarify the taxonomy of the organisms to ensure reliable identification; iii) to characterise the communities, and; iv) to reveal community variability within the heterogeneity of the ecosystem.

3.1.1 | Current state of knowledge

Due to the mainly terrestrial mode of life of Oribatid mites, research on this taxon, focussing on wetland occurrences, is relatively sparse in general (Fischer & Schatz, 2010). Oribatid mites from cushion peatlands have only been investigated in northern and central Chile (Covarrubias & Mellado, 2003; Covarrubias, 2004a, b; Figueroa & Covarrubias, 2005; Covarrubias, 2009).

For Chironomids, Ferrington (2008) names high-elevation springs and seeps as one of the most underrepresented habitats in research, with presumably high numbers of undescribed species. In the Central Andes, research on Chironomid assemblages has been conducted in stream (Brundin, 1966; Turcotte & Harper, 1982; Roback & Coffman, 1983; Tejerina & Molineri, 2007; Acosta & Prat, 2010; Prat & Rieradevall, 2011; Prat et al., 2011; Tejerina & Malizia, 2012; Scheibler et al., 2014) and lake ecosystems (Matthews-Bird et al., 2016), but not in high altitude peatland ecosystems so far.

This study represents the first investigation on high-Andean cushion peatland-inhabiting Chironomid assemblages, as well as Oribatid mites from a Peruvian cushion peatland.

3.1.2 | Succession model for the Cerro Llamoca cushion peatland

For the foundation of this work, a theoretical succession model based on key features such as vegetation, microtopography and soil types (Rydin & Jeglum, 2013) was developed (see Figure 3.1). The model is based on observations by Ruthsatz (2008) and has been adjusted to the study area with the work by Schittek et al. (2012) and own observations.

In general, five ecotopes could be separated in the field which are named as “debris ecotope”, “pioneer ecotope”, “successional ecotope”, “fully developed ecotope” and “degraded ecotope”. These ecotopes

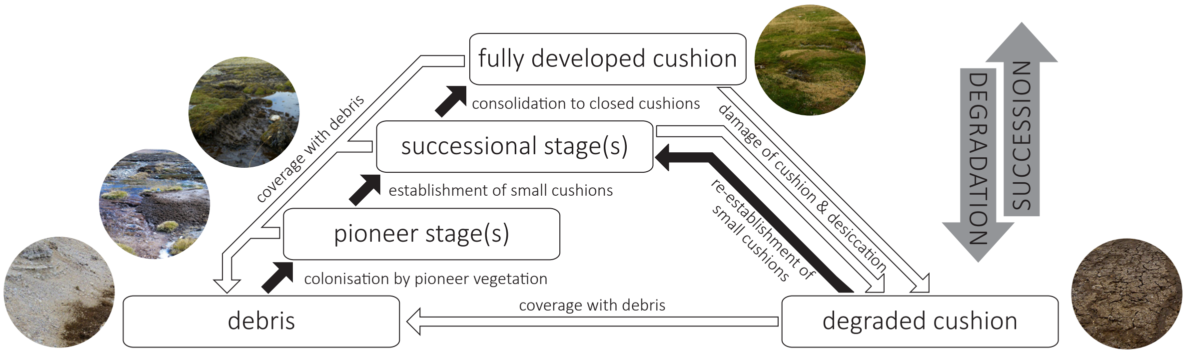


Figure 3.1 | Theoretical succession model of a high-Andean cushion peatland. Upwards moving processes (solid arrows) can be classified as successional developments and downwards moving processes (hollow arrows) as degradation influences.

are connected in the different stages of the succession model:

Sandy to gravelly and soaking wet mineral debris serves as a raw substrate which is first of all inhabited by pioneer vegetation. In CLP, this is mainly achieved by the more frost and dry tolerant *Oxychloe andina* (Ruthsatz, 1993). After the first pioneer colonisation and with ongoing succession, other cushion-forming plants species migrate to the freshly inhabited areas. Concomitant with an increasing displacement of the pioneer vegetation, small sized cushions of *Distichia muscoides* are formed in early successional stages, but still leave blank spots of muddy, organic soil and rivulets between the cushions. The transition from pioneer to successional ecotopes constitutes a continuum and cannot be defined clearly. If the *Distichia muscoides* cushion growth proceeds, the successional climax vegetation is reached with fully developed and narrow standing *Distichia muscoides* cushions, interspersed with ponds and rivulets, but no blank soil spots are visible. Due to physical damage by animals, weather effects or through changes in the landscape hydrology, the living vegetation layer can die off, causing degradation of the peatland. If sufficient rewetting occurs, new cushions may re-establish on those degraded areas and restart the succession with early successional stages (Ruthsatz, 2008). Meanwhile, coverage with debris deposition from the surrounding slopes is possible at every stage of the succession, which restarts the succession with pioneer colonisation.

3.1.3 | Hypotheses

In this investigation, two main hypotheses are tested:

- The ecosystem of a high-Andean cushion peatland is characterised by a subset of different ecotopes, which can be connected according to successional processes.
- The ecotopes of a high-Andean cushion peatland are inhabited by distinct Oribatid mite and Chironomid communities.

3.2 | Material & Methods

3.2.1 | Study site

For a full description of the study area, see Chapter 2.

3.2.2 | Sampling and sub-sampling strategy

The sampling was planned and performed in order to cover the full ecotope heterogeneity of the Cerro Llamoca peatland. To guarantee this, representatives of all five stages within the succession model were sampled (see Figure 3.2). The surface samples were extracted on 28/10/2011 with a MacFadyen-

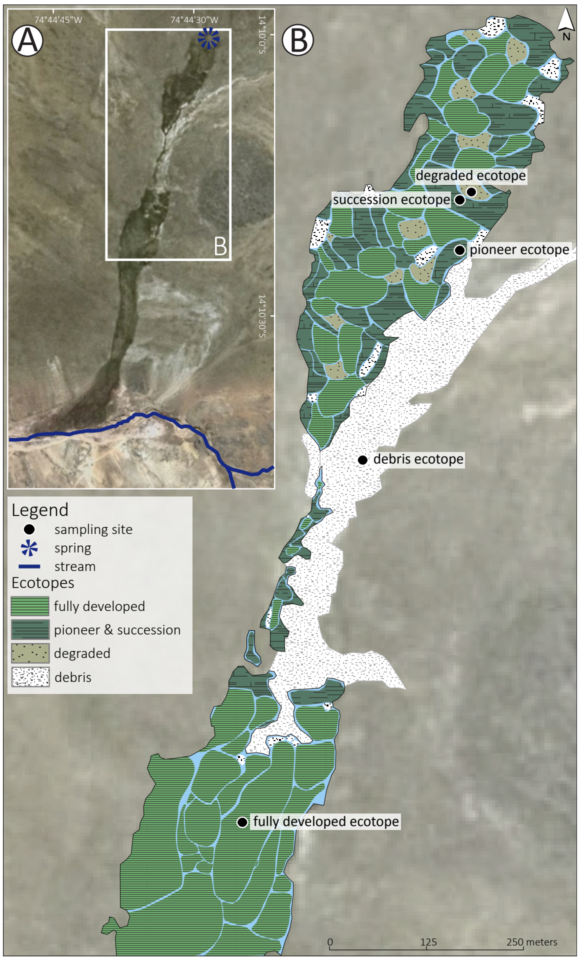


Figure 3.2 | The study site: the Cerro Llamoca peatland. A) shows a sattelite image of the peatland with the spring area and draining stream indicated. B) provides an overview of the northern half of the CLP while schematically implying the surface structure of the peatland, and indicates the sampling locations.

corer (MacFadyen, 1961). The cores were split equally lengthways and stored in half-shell plastic tubes. One half was injected immediately with ca. 0.5 ml ethanol (96%) each centimeter to kill the soil arthropods and to avoid spatial displacements of the invertebrate biocoenosis. The sedimentological description of the cores was performed using the German nomenclature (Blume et al., 2002).

3.2.3 | Sample preparation

To examine the Oribatids and Chironomids from the soils, a subsample was extracted from the cores each second centimeter, starting at the surface (see Figure 3.3). The bypassed core samples and the parallel core half were used for different geochemical analyses. The volume of every sample for mesofaunistic analysis was ascertained by filling with a specific amount of distilled H_2O in a graduated measuring cylinder (accuracy 0.1 ml). The samples were macerated in KOH (10%) for at least four hours at 4°C before being divided by wet sieving into their respective >250µm and <250>112µm fractions using analytical aluminum sieves (10 cm diameter). Subsequently, the different fractions were diluted in water, spread out on a white picking tray (10 x 6 cm) and scanned completely in multiple steps under a dissecting microscope (BonnTec Zoom Advanced 2) with a 10-12x magnification. All Oribatid mites, Chironomid head capsules or fragments of these were picked out of the sample material by using fine forceps, a preparation needle or a small noose made of a thin wire wound around a wooden stick. The picked specimens of a sample were stored in about 2 ml ethanol (96%) in labelled and sealed plastic containers.

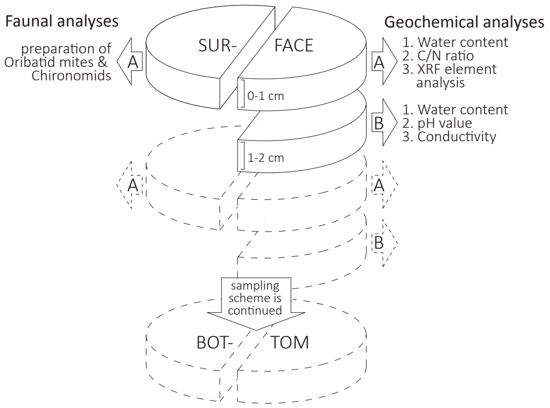


Figure 3.3 | Subsampling scheme and analysis strategy of the surface cores.

3.2.4 | Preparation & mounting of Oribatid mites and Chironomid head capsules

Before mounting, the Oribatid mites and Chironomid head capsules were cleared by immersion in gently heated lactic acid (96%), following the procedure of Weigmann (2006). Hoyer's medium was used for mounting (Baker & Wharton, 1952). Due to some very pale sub-fossil specimen the medium was modified and stained with 1 g potassium iodide and 0.3 g iodine (resublimated) in proportion to 100 g Hoyer's solution to increase the contrast of the mounted specimen and medium (Faraji & Bakker, 2008). To avoid dilution of the mounting medium, the Oribatid mites and Chironomid head capsules were transferred from lactic acid into a drop of Hoyer's medium, before being final placed on the microscope slide in another drop of the medium. The samples were covered with a cover slip (18x18 mm), labeled and dried in a well-ventilated compartment dryer at 50°C for at least 24 hours. After drying, the slides were sealed with two layers of clear nail polish. For identification different light microscopes (Zeiss Axio Scope A1, Zeiss Primo Star & Leica DMLS), with magnifications from 50-400x and optional phase contrast, were used. All photos were taken with a Canon EOS 600D mounted on the Zeiss Axio Scope A1 light microscope with differential interference contrast (DIC) illumination, using the remote control software SmartShooter ver. 1.1.14. Multi-layer stacking with 10-30 pictures per specimen was performed by the Zerene Stacker ver. 1.04 software with image processing and measuring by Adobe Photoshop CS4.

3.2.5 | Identification

For the identification of Oribatid mites, literature by Hammer (1958, 1961, 1962a, b), Balogh & Balogh (1988), Balogh (1972, 1990), Norton & Behan-Pelletier (2009) and an interactive glossary by Hunt et al. (1998) were used. For Chironomid identification, literature by Williams et al. (2012), Prat & Rieradevall (2011), Dieffenbacher-Krall et al. (2008), Brooks et al. (2007), Epler (2001), McAlpine et al. (1981) and Sæther (1980), as well as an online identification key (http://chirokey.skullisland.info, last accessed in November 2014) were used.

3.2.6 | Numerical 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 & Colwell (2011) and Colwell et al. (2012). For all other statistical analyses, the software R ver. 3.1.2 (R Core Team, 2014) was used. The indicator species analysis was performed with the Indicspecies package ver. 1.7.1 (De Caceres & Legendre, 2009). The results were tested on significance by running 999 random permutations, using the permute package ver. 0.8.3 (Simpson, 2014).

3.3 | Results

3.3.1 | Ecotope description and stratigraphy

The "debris" ecotope

The uppermost 3 cm of this core (see Figure 3.4-A) contained gravel with a maximum particle size of ~2 cm. Between 3-6 cm depth, the gravels were underlaid by sand. Starting at 6 cm depth, silt filled up the cavities in the sandy framework and changed the colour of the sediment from yellowish to greyish brown. A single $1\ cm^2$ large, blackish organic rich spot at 5.5 cm was embedded at the transition between the overlying sand and the silty sand matrix.

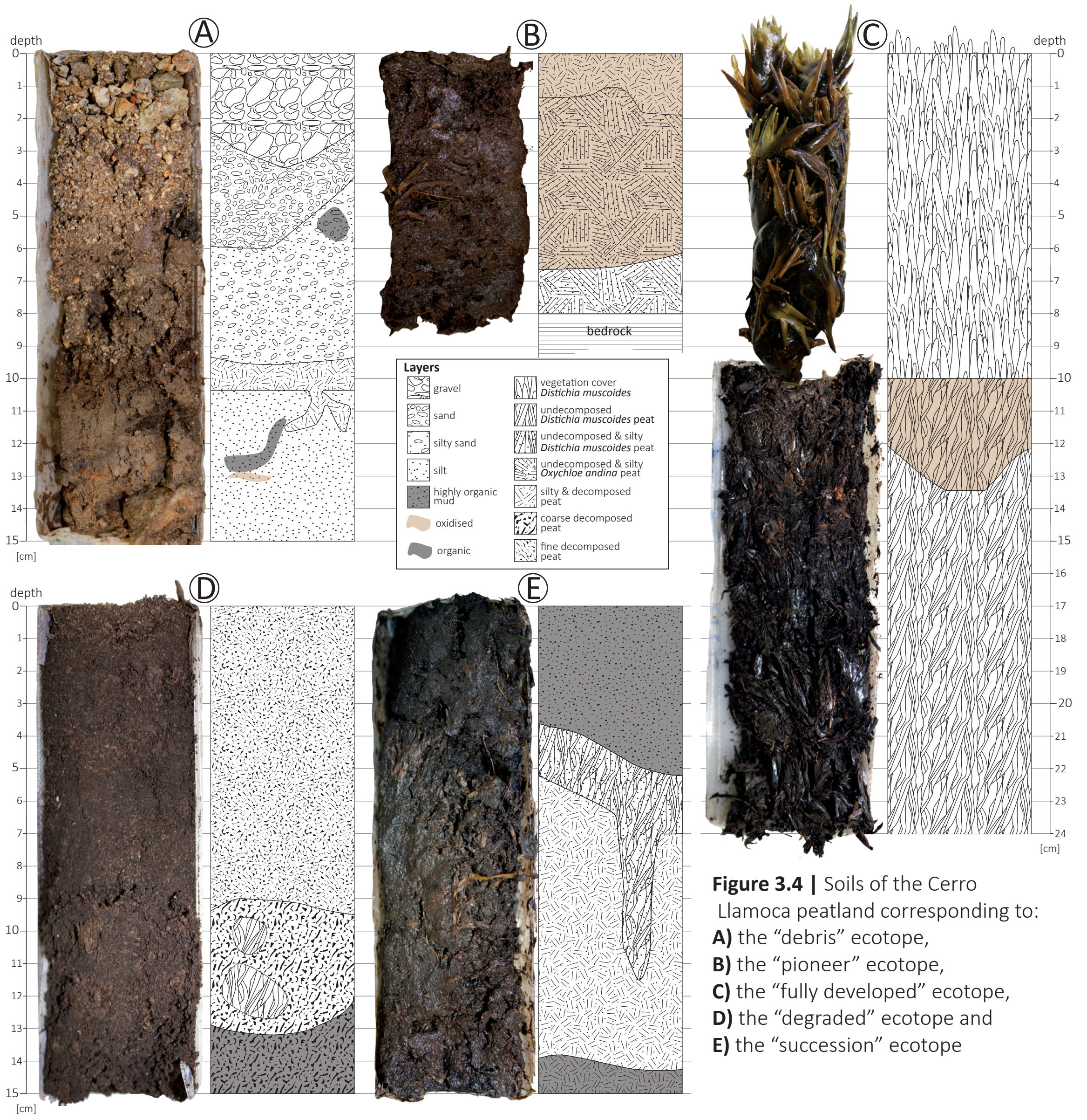


Figure 3.4 | Soils of the Cerro Llamoca peatland corresponding to:
A) the "debris" ecotope,
B) the "pioneer" ecotope,
C) the "fully developed" ecotope,
D) the "degraded" ecotope and
E) the "succession" ecotope

The silty sand layer was interrupted at 9-10 cm by a brown silty peat layer which formed a single small sized offshoot down to 11.5 cm. The peat consisted of undecomposed, but fragmented plant material. Underneath the silty peat, the core consisted of light brownish silt till 15 cm depth. Within this matrix, an elongated, organic rich greyish spot at between 11 and 12.5 cm, and a small sized reddish spot at 13 cm occurred. In total, the core was 15 cm long.

The “pioneer” ecotope

The sediment of this 8 cm long core consisted invariably of a brownish to reddish silty peat matrix (see Figure 3.4-B). The uppermost 2.5 cm were characterised by stronger decomposed peat, whereas the underlying sediment was built up by undecomposed *Oxychloe andina* plant material. From the top until 6.5 cm depth, the sediment appeared noticeably reddish, but between 6.5 to 8 cm the peat matrix was rather brownish. At ~8 cm depth, the bedrock prohibited deeper coring.

The “fully developed” ecotope

This 24 cm long core (see Figure 3.4-C) showed a distinct two-part structure. The uppermost 10 cm represented the living vegetation cover at that site, which consisted completely of *Distichia muscoides*. From 10-24 cm, the sediment was built up of undecomposed peat of *D. muscoides* plant material. Between 10 and 13 cm depth, the undecomposed peat appeared slightly reddish.

The “degraded” ecotope

The whole 15 cm long core was consistently built up by peat in different decompositional conditions (see Figure 3.4-D). From 0-9 cm, the sediment could be characterised as fine decomposed peat with a friable structure. From 9 cm downwards the decomposed peat was noticeably coarser and two 1-2 cm^2-large spots of undecomposed plant material of *D. muscoides* were interspersed in the peat matrix at 9.5-10.5 cm and 11-12.5 cm depth. Between 13 cm and the bottom of the core, the decomposed peat showed a darker colour by comparison to the overlying material.

The “succession” ecotope

The top of this 15 cm core (see Figure 3.4-E) was characterised by a thick mud layer, consisting of a fine silt matrix strongly enriched with humus. This uppermost layer transitioned diagonally between 4-5 cm into a silty-undecomposed peat matrix, consisting of *D. muscoides* plant material. The peat band ran obliquely between 4-5 cm at the top edge to 5-7 cm at the lower edge, and formed a vertical offshoot of 1 cm width into the underlying layer as low as 11.5 cm. Underneath the peat layer, till 15 cm depth, the core consisted of silty decomposed peat which showed a more blackish colour between 14-15 cm.

3.3.2 | The Oribatid mite community

In total, 17 Oribatid mite taxa could be identified, by investigating 689 specimens from 41 modern surface samples. The community comprised eight families, of which the Ceratozetidae with six taxa and the Scheloribatidae with three taxa were the most diverse families. Only 12.4% of the picked Oribatid mite specimens could not be identified because of damage to taxonomically important structures. Four species (*Neoamerioppia notata*, *Ceratozetes nigrisetosus*, *Jugatala armata* and *Zetomimus furcatus*) were identified in Peru for the first time. A full overview of the identified Oribatid mite community is presented in Table 3.1.

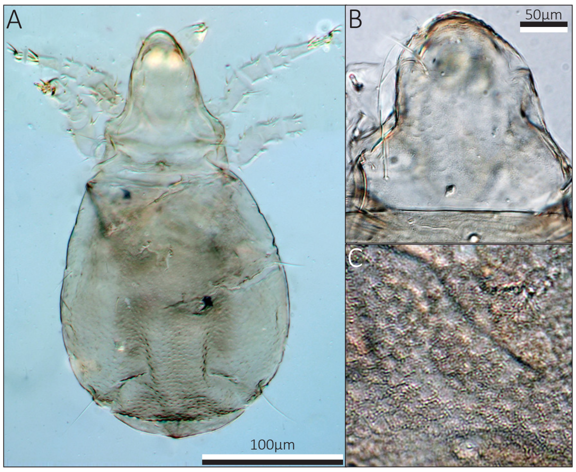


Figure 3.5 | *Tyrphonothrus maior*: dorsal view (A), details of the prodorsum (B) and notogastral structure (C)

Table 3.1 | Systematic overview of the identified Oribatid mite community of the CLP

Family ***Species***	**Author**
Trhypochthoniidae	
1. *Malaconothrus monodactylus*	Michael, 1888
2. *Tyrphonothrus maior*	Berlese, 1910
Nanhermannidae	
3. *Nanhermannia* cf. *elegantissima*	Hammer, 1958
Opiidae	
4. *Oxyoppia suramericana*	Hammer, 1958
5. *Neoamerioppia* cf. *notata*	Hammer, 1958
Tectocepheidae	
6. *Tectocepheus* sp.	Berlese, 1896
Ameronothridae	
7. Ameronothroid *Aquanothrus*-type	
Ceratozetidae	
8. *Ceratozetes nigrisetosus*	Hammer, 1958
9. *Ceratozetes* (*Magellozetes*)-type	
10. *Jugatala armata* *Syn. Edwardzetes armatus*	Hammer, 1958
11. *Jugatala chavinensis* *Syn. Sphaerozetes chavinensis*	Hammer, 1961
12. *Jugatala montana* *Syn. Trichoribates hammerae*	Hammer, 1961 Subías, 2010
13. *Zetomimus furcatus*	Warburton & Pearce, 1905
Scheloribatidae	
14. *Scheloribates confundatus*	Hammer, 1961; non sensu Berlese, 1908
15. *Scheloribates* cf. *elegantulus*	Hammer, 1961
16. *Scheloribates pallidulus*	Hammer, 1958; non sensu Koch, 1841
Oripodidae	
17. *Oripoda* sp.	Banks, 1904

3.3.2.1 | Taxonomy, zoogeography and autecology of the Oribatid mite taxa

1. *Malaconothrus monodactylus* Michael, 1888

Zoogeography & autecology: *Malaconothrus monodacytlus* is found frequently in bogs and peatlands throughout the Holarctic and Neotropic ecozones (Subìas, 2004; Weigmann, 2006). Although, representatives of the genus inhabit freshwater habitats, however, *Malaconothrus* is not truly aquatic because saturated air is needed for reproduction (Schatz & Behan-Pelletier, 2008). The species is reported with high densities of up to 0.02 specimens cm^{-3} from high-Andean cushion peatlands in northern Chile (Covarrubias, 2004a, 2009). The species is known to reproduce parthenogenetically (Palmer & Norton, 1991), and the whole genus is characterised using stable isotope ratio measurements as litter/fungal feeders, predominantly feeding on litter (Schneider et al., 2004).

2. *Tyrphonothrus maior* Berlese, 1910

Taxonomy: all eight examined specimens showed great resemblance to *Tyrphonothrus novus* Sellnick, 1921. This evidence supports merging of the taxa into the basionym *T. maior* Berlese, 1910 (Subìas, 2004). Furthermore the status of *T. cajamarcensis* Hammer, 1961 as a valid species or a variety of *T. maior* remains in doubt.

Zoogeography & autecology: *Tyrphonothrus maior* is a semicosmopolitan species, occurring in the Holarctic, the Nearctic and New Zealand (Subìas, 2004). This parthenogenetically reproducing species (Palmer & Norton, 1991) is common in very wet habitats (Balogh & Balogh, 1988) and requires relatively high water temperatures (Solhøy & Solhøy, 2000). However, the species can be characterised as semi-aquatic as saturated air is needed at least for reproduction (Schatz & Behan-Pelletier, 2008).

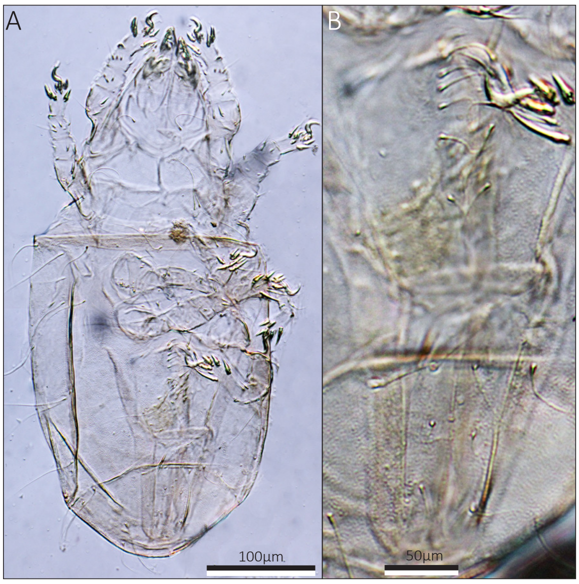


Figure 3.6 | *Malaconothrus monodactylus:* ventral view (left) and details of the ano-genital region (right)

3. *Nanhermannia* cf. *elegantissima* Hammer, 1958

Taxonomy: the status of *Nanhermannia elegantissima* should be reviewed because of the morphological similarity to the Palaearctic species

N. elegantula Berlese, 1913 (Weigmann, 2006; Schäffer et al., 2010). All collected 35 specimens showed a wide range in the variety of key features, e.g. the posterior protuberance of the prodorsum or the ornamentation of the notogaster (Balogh & Balogh, 1988).

Zoogeography & autecology: *N. elegantissima* is known from the entire Neotropic (Subìas, 2004). The species was found at high densities in a high-Andean cushion peatland from northern Chile (Covarrubias, 2004a, b) and in central Chile (Figueroa & Covarrubias, 2005). According to the taxonomic description by Hammer (1958), *N. elegantissima* was found in Argentina and Bolivia between 1600 and 3800 m a.s.l., with the habitat described as meadow vegetation, comprising grass tussocks, clover, *Juncus* and other wet to dripping moss and grasses. At a site which probably corresponds to a high-Andean cushion peatland, the species was found at high densities of 8.3 specimens cm^{-2} (Hammer, 1958). In Europe, one *Nanhermannia* species was found to be the most dominant oribatid mite in a Sphagnum peat bog (Murvandize & Kvavadze, 2010). The genus *Nanhermannia* is supposed to reproduce completely parthenogenetically (Palmer & Norton, 1991). Investigations on other species of this genus (*N. nana* and *N.* cf. *coronota*) show, that the development is slow and needs more than 100 days for completion at >22°C. The development even decelerates with decreasing temperatures (170 days at 19°C in *N.* cf. *coronota*) (Ermilov & Łochyńska, 2008). Some representatives of the genus *Nanhermannia* are categorised to be secondary decomposers, feeding predominately on fungi and in part on litter (Schneider et al., 2004).

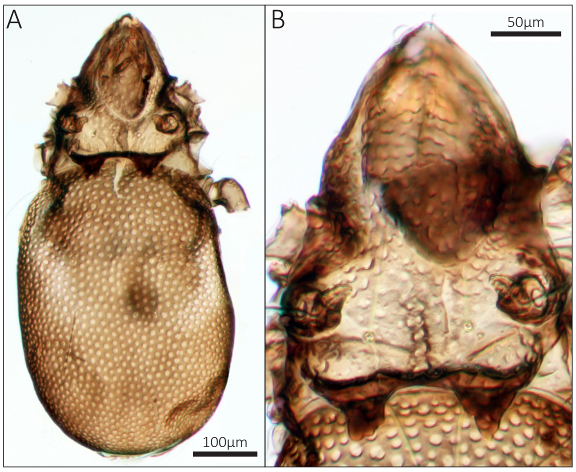


Figure 3.7 | *Nanhermannia* cf. *elegantissima:* dorsal view (A) and details of the prodorsum (B)

4. *Oxyoppia suramericana* Hammer, 1958

Zoogeography & autecology: *Oxyoppia suramericana* is known from the Neotropic, India and Australiana (Subìas, 2004). Hammer (1958) describes the species as common in every kind of habitat, but high densities are reached only in dry locations. The author found 1510 specimens m^{-2} in hard cushions of the dry adapted *Pycnophyllum bryoides* at high altitudes in Bolivia and central Argentina.

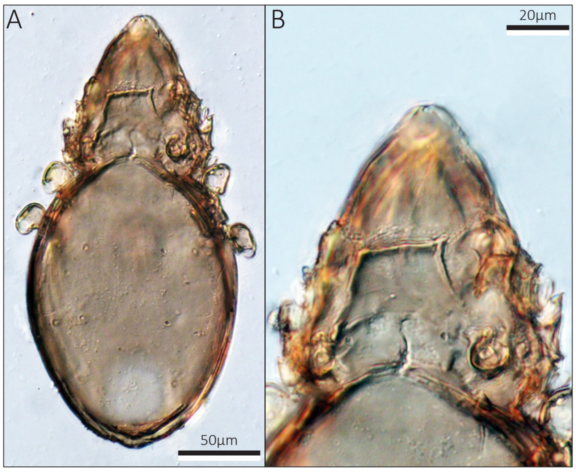


Figure 3.8 | *Oxyoppia suramericana:* dorsal view (A) and details of the prodorsum (B)

5. *Neoamerioppia* cf. *notata* Hammer, 1958

Taxonomy: the lanceolate shape of the pseudostigmatic organ, the close-set rostral setae, a small incision at the tip of the rostrum and a lateral spinose process of the coxisternum between epimera III and IV indicated rather *Neoamerioppia notata* than *N. pectigera*, which generally shows very similar features (Hammer, 1958, 1961; Balogh & Balogh, 1988). This observation was based on 104 specimens.

Zoogeography & autecology: *Neoamerioppia notata* is only known from Bolivia (Subìas, 2004). The species was described by Hammer (1958) from moist wet habitats in the high Andes of Bolivia. Members of the genus are pantropical or subtropical in their distribution. From the Neotropic, 16 species are known, of which two are distributed throughout the entire zoogeographical region, two only occur in the northern part and 12 only in the southern part, respectively (Martínez & Velis, 2000; Subìas, 2004).

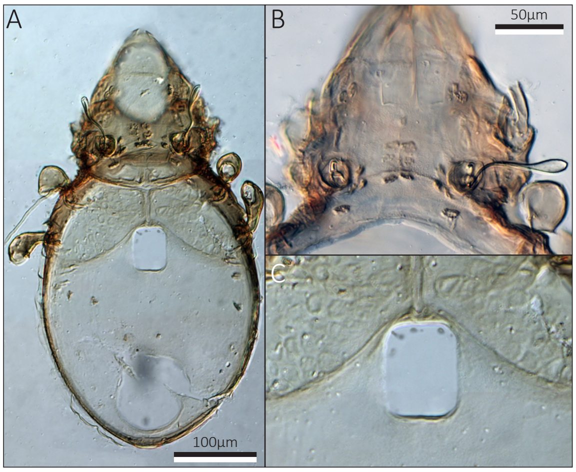


Figure 3.9 | *Neoamerioppia* cf. *notata:* dorsal view on the ventral plate (A), details of the prodorsum (B) and the characteristic genital aperature (C)

Figure 3.10 | *Tectocepheus* sp.*:* dorsal view

Figure 3.11 | Ameronothroid *Aquanothrus*-type*:* dorsal view on the fused notogaster and prodosum

6. *Tectocepheus* sp. Berlese, 1896

<u>Taxonomy</u>: all taxonomical surveys discussing the genus *Tectocepheus* in the Neotropic conclude the described specimen as "species inquirenda", because the occurrence of all possible combinations of morphological characters prevents a separation of species (Hammer, 1958, 1961, 1962a, b; Balogh & Balogh, 1988). However, all 181 examined specimens of this study showed a high morphological similarity to *Tectocepheus velatus* s.l. Michael, 1880 (Weigmann, 2006). Further investigations are needed to assess the status of the Neotropical Tectocepheida.

<u>Zoogeography & autecology:</u> some species of the genus *Tectocepheus* belong to the most common Oribatid species throughout the world (Hajmová & Smrž, 2001). In general, members of this genus are cosmopolitan (Subìas, 2004), extremely ubiquitous (Nübel-Reidelbach, 1994) and completely parthenogenetic (Weigmann, 2006). Due to a lack of knowledge of the Neotropical morphotypes of *Tectocepheus*, species determination was only possible at a few sites in Argentina (Martínez & Velis, 2000; Accattoli et al., 2010). The genus has been identified at numerous locations in the high Andes of Peru, Bolivia, Chile and Argentina (Hammer, 1958, 1961; Covarrubias, 2004a; Figueroa & Covarrubias, 2005; Covarrubias, 2009). In the hard cushions of the dry adapted *Pycnophyllum bryoides, Tectocepheus* reaches high densities of >1.6 specimens cm^{-3} (Covarrubias, 2009). The taxon was reported from cushion peatlands in northern (19°S) and central Chile (33°S) (Covarrubias, 2004a; Figueroa & Covarrubias, 2005). However, representatives of the *T. velatus* complex, to which the examined specimens of this study show the greatest resemblance, are found in a wide range of environmental conditions (Nübel-Reidelbach, 1994; Hajmová & Smrž, 2001). Thus, the adults and juveniles of *T. velatus* are known to be extremely tolerant to humidity and dryness as they have been observed in flooded areas (Hammer, 1966; Weigmann, 2006), yet can also survive soil temperatures of >40°C (Haarløv, 1960). However, Hammer (1958) only found representatives of *Tectocepheus* in Argentina and Bolivia in not particularly wet habitats. *T. velatus* is one of the first colonisers of young soils in glacier forelands (Hågvar et al., 2009) and an unspecialised feeder, ingesting plant particles, bacteria, fungal spores and hyphae (Hajmová & Smrž, 2001), with a focus on primary decomposition, as stable isotope ratio investigations have revealed (Maraun et al., 2011).

7. Ameronothroid *Aquanothrus*-type

<u>Taxonomy</u>: only one fused notogaster and prodorsum was found in the samples and an accurate determination was not possible. Probably because of the acidic conditions during sample treatment or deposition in peat, the cerotegument was detached from the cuticle. The Ameronothroidae appear susceptible to be damaged in acid conditions as they are weakly sclerotised on the ventral body parts (Krantz & Walter, 2009). However, some characteristics, such as the coalesced prodorsum, resemble the family Ameronothridae (Schubart, 1975). An

incomplete dorso-sejungal arch, extremely small bothridia, lamellar slopes on the lateral sides of the prodorsum and a faint translamellar slope are reminiscent of the genus *Aquanothrus* (Engelbrecht, 1975; Wallwork, 1981). An obvious lenticulus, sensilli and notogastral setation could not be found in the investigated specimen, which would provide helpful information for further classification. A special search for living and undistorted mites should be carried out to resolve the taxonomic uncertainty or to enable the description of probably a new species.

Zoogeography & autecology: due to taxonomic difficulties, no exact biogeographic and ecological specifications can be listed for the Ameronothroid *Aquanothrus*-type examined in this investigation. However, more than half of the Ameronothridae species are restricted to (sub-)(Ant)arctic islands and are known to be truly aquatic (Schatz & Behan-Pelletier, 2008). Many of the species of this taxa have the ability to inhabit extreme habitats, e.g. salt marshes, mangroves, intertidal rocky shores or high altitudinal rock pools or can survive under (sub)polar climate conditions (Marshall & Convey, 2004). Only two species of the family Ameronothridae are recorded from the southern Neotropic (Tierra del Fuego and southern Chile) (Subìas, 2004). So far, the genus *Aquanothrus* is only known from rock pools in South Africa (Engelbrecht, 1975).

Remarks on the taxa of the family Ceratozetidae

The value of typically used diagnostic characters within the “Higher Oribatida”, or Brachyplina, is questionable in several cases. The mosaic-like distribution of determining characters (e.g. presence or absence of area porosae, sacculi or pteromorphae, shape of tutorium, etc.) hampers a selective classification of genera and profound association of taxa (Woas, 1998). Recent molecular genetic data support different ancestral states as derived by diagnostic morphological characters (Schäffer et al., 2010). The three investigated species of the genus *Jugatala* have been allocated each to different genera *Edwardzetes*, *Trichoribates* and *Sphaerozetes* by Subìas (2004, 2010). Nevertheless, alternative concepts of taxonomic classification are available (e.g. Bayartogtokh & Schatz, 2008). Because of these systematic difficulties, the Ceratozetid taxa identified here are compared to the original descriptions to avoid further ambiguities in genera allocations.

Figure 3.12 | *Ceratozetes nigrisetosus:* dorsal view on ventral plate

Figure 3.13 | *Ceratozetes (Magellozetes)*-type*:* dorsal view on ventral plate

8. *Ceratozetes nigrisetosus* Hammer, 1958

Zoogeography & autecology: *Ceratozetes nigrisetosus* is only known from high Bolivia (Subìas, 2004) and from *Araucaria araucana* forest in central Chile (38°S) (Martínez & Casanueva, 1995). In Bolivia, the species was found by Hammer (1958) in the dripping wet vegetation of a cushion peatland at an altitude of 5000 m a.s.l.. In general, the genus *Ceratozetes* is known to be semiaquatic (Schatz & Behan-Pelletier, 2008) and the members of the Ceratozetidae seem to not inhabit dry and warm habitats, but are restricted to cold-temperate climates (Behan-Pelletier, 1986).

9. *Ceratozetes (Magellozetes)*-type

Taxonomy: the tutorium of the found specimen projected far anteriorward and was shaped like a blade, which refers to the Ceratozetes (Magellozetes) genus group (Woas, 2002). The description was based on only one ventral plate of a single specimen. Further identification was not possible.

Zoogeography & autecology: due to insufficient sample material, determination of the *Ceratozetes (Magellozetes)* taxon was only possible to subgenus level. Two *C. (Magellozetes)* species are known and listed from the very southern Neotropical and Antarctic regions (Subìas, 2004). *C. (Magellozetes) processus* is known from black, peaty soils in southern Chile (Hammer, 1962a) and *C. (Magellozetes) antarcticus* from lichens and mosses on stones (Block & Stary, 1996).

10. *Jugatala armata* sensu Hammer, 1958

Taxonomy: a good morphological character for the separation of *Jugatala armata* from *J. montana* is the location of the area porosae A1, which was situated in its entirety medial of an imaginary line from Aa to A2. This feature was recorded in all 104 examined specimens of this taxon. Additionally, the equal size of Aa and A3 was a specific morphological character (Hammer, 1961; Balogh & Balogh, 1990).

Zoogeography & autecology: *Jugatala armata* (Syn. *Edwardzetes armatus*) is only known from Bolivia and Chile (Subìas, 2004) and at high altitudes between 4200-5400 m a.s.l. (Balogh & Balogh, 1990). Hammer (1958) reported the species from very wet habitats within Bolivian cushion peatlands. In northern Chilean peatlands, *J. armata* was found at densities of 0.006-0.007 specimens cm^{-3} (Covarrubias, 2004a, 2009).

11. *Jugatala chavinensis* sensu Hammer, 1961

Taxonomy: the shape of the space between the cuspides was very similar to *Jugatala montana*, which was stated as a distinguishing character by Hammer (1961). Efficient morphological characters are the teeth on both sides of the rostrum and the specific shape of the cuspides, with a long and pointed outer tooth and a shorter and pointed inner tooth. The shape of the sensillus is rather variable and could not be reconciled with the descriptions given by Hammer (1961) and Balogh & Balogh (1990). The description here was based on six specimens.

Zoogeography & autecology: *Jugatala chavinensis* (Syn. *Sphaerozetes chavinensis*) is endemic to Peru (Subìas, 2004) and has been found in moist-wet moss at an altitude of >3000 m a.s.l. (Hammer, 1961).

12. *Jugatala montana* sensu Hammer, 1961

Taxonomy: one of the most prominent morphological characteristics listed by Balogh & Balogh (1990) for *Jugatala montana* appeared very variable within all the examined specimens of this taxon: the space between the cuspides was not U-shaped with parallel sides in almost all cases. This feature was very similar to the morphology of *J. chavinensis* and was therefore inappropriate for species separation. This observation was based on 88 specimens.

Zoogeography & autecology: *Jugatala montana* (Syn. *Trichoribates hammerae*) is endemic to Peru (Subìas, 2004) and was only found at altitudes >4500 m a.s.l. in wet black soils and in mosses (Hammer, 1961).

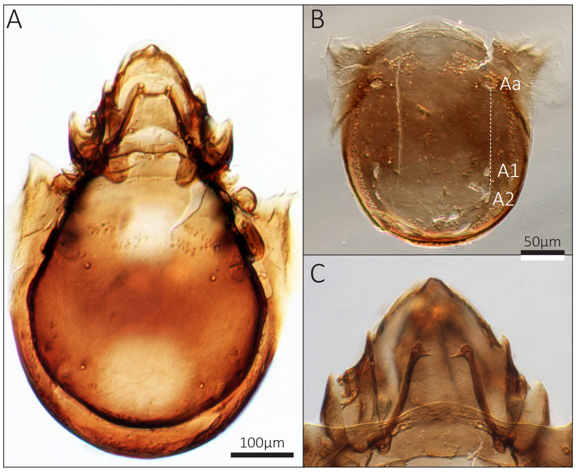


Figure 3.14 | *Jugatala armata:* dorsal view (A), view on a separated notogaster (B) and details of the prodorsum (C)

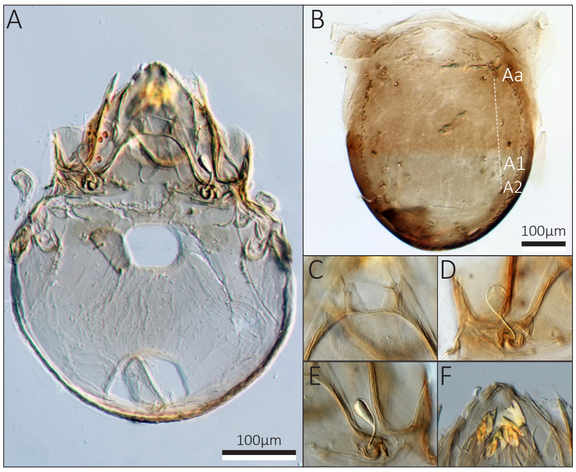


Figure 3.15 | *Jugatala chavinensis:* dorsal view on ventral plate (A), view on a separated notogaster (B), and detailed view on the cuspides (C), different sensilli (D,E) and on the tip of the rostrum (F)

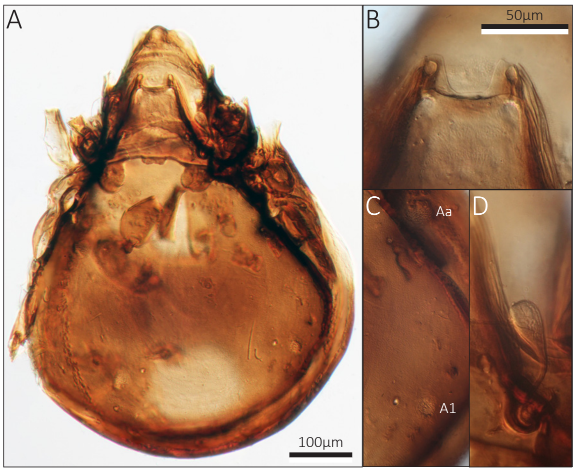


Figure 3.16 | *Jugatala montana:* dorsal view (A) and details of the cuspides (B), the area porosae (C) and of a sensillus (D)

Zoogeography & autecology of the genus *Jugatala*

Following the taxonomic classification by Bayartogtokh & Schatz (2008), the genus *Jugatala* comprises only seven species, which are distributed in the Americas (four species) and in central and southern Europe (three species). From stable isotope ratio measurements ($^{15}N/^{14}N$ and $^{13}C/^{12}C$), members of the genus *Jugatala* are determined to be lichen-feeders (Fischer et al., 2014). A *Jugatala* sp. has also been found inhabiting lichens by Lindo & Stevenson (2007). However, these results have to be interpreted carefully because stable isotope signatures can significantly differ within species of the same genus, and feeding types should not be derived directly (Schneider et al., 2004). In Subìas (2004), the three original *Jugatala* species by Hammer (1958, 1961) were each re-classified into the different genera *Edwardzetes*, *Sphaerozetes* and *Trichoribates*, which hinders an ecological description. Despite refusing the rearrangement of the species, the ecological data available for the other genera are listed here:

Members of the genus *Edwardzetes* are distributed in temperate climates mainly in the Neotropic and the Antarctic, but also in New Zealand, Europe and Greenland (Subìas, 2004). Stable isotope ratios indicate a soil food web position of *Edwardzetes*-species as secondary decomposers (Fischer et al., 2014). Similar to the distribution of *Jugatala* in the European Alps, *Edwardzetes* is restricted to high altitudes (Fischer & Schatz, 2013).

Representatives of the genus *Sphaerozetes* are mainly distributed in the Holarctic, Neotropical and Australian regions (Subìas, 2004). Some members of the *Sphaerozetes* are known to be euryoecious and associated with wet forest soils and springs (Wild et al., 2008).

Trichoribates-species are primarily distributed in the Palaearctic and Nearctic (comprising 52 species), but three species are distributed in the Neotropic and one in the Oriental region. Most representatives of this genus inhabit litter systems in various types of forests (Bayartogtokh & Schatz, 2008). Nevertheless, some species are found in mosses, lichens, decaying wood, and also arboreal habitats and arid soils (e.g. Bayartogtokh, 2005).

13. *Zetomimus furcatus* Warburton & Pearce, 1905

Zoogeography & autecology: *Zetomimus furcatus* is listed to be typical of oligotrophic Holarctic peat bogs (Murvandize & Kvavadze, 2010), swampy meadows, reedland (Schelvis & van Geel, 1989) and swamp forests (Weigmann, 2006). *Z. furcatus* is one of the few species of Oribatid mites that is fully aquatic, which implies not living in free water but on submerged vegetation or sediment (Fischer & Schatz, 2010). Nevertheless, *Z. furcatus* is known to be able to walk on water surface tension (Schelvis & van Geel, 1989).

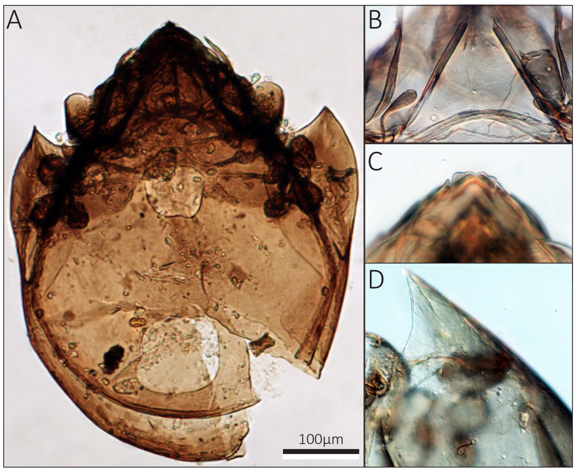


Figure 3.17 | *Zetomimus furcatus:* dorsal view (A) and details of the cuspides and sensilli (B), the tip of the rostrum (C), and the pteromorphs (D)

Remarks on the taxa of the family Scheloribatidae

All examined Scheloribatid mites covered in this study showed particular features, which divide the Neotropical Scheloribatids from European species. All specimens showed a fine translamellar ridge and differently arranged maculae on the anterior third of the notogaster. The morphological traits to classify the genus Scheloribates seemed to be uncertain at least for the Neotropical species (Badejo et al., 2002). To avoid taxonomical pitfalls, the species of Scheloribatidae found are compared with the descriptions and drawings of Hammer (1958, 1961). The ecological traits of the large genus *Scheloribates* (containing 221 species: Subìas, 2004) are extremely diverse, and it is therefore impossible to generalise for the whole genus.

14. *Scheloribates confundatus* sensu Hammer, 1961 non sensu Berlese, 1908

Taxonomy: *Scheloribates confundatus* Sellnick, 1928 is used as a synonym for *Hemileius initialis* Berlese, 1908 (Forsslund, 1963; Subìas, 2004). In contrast to the descriptions given for *Hemileius initialis* (Weigmann, 2006), all 23 examined specimens in this investigation showed two rows of maculae on the anterior part of the notogaster and undulating sublamellae. These morphological features were drawn by Hammer (1961) on *Scheloribates confundatus*. This morphological conspicuousness regarding the taxonomic status of the Neotropical representatives of *S. confundatus* in comparison to *H. initialis,* and the status of the genus *Hemileius* in general, needs further clarification (Bayartogtokh et al., 2011).

<u>Zoogeography & autecology</u>: due to the distinct taxonomical problems of this taxon, revealed in this investigation, the distribution range and ecology of *Scheloribates confundatus* is difficult to assess. In the taxonomic literature, this taxon is usually quoted as a synonym of *Hemileius initialis* sensu Berlese, 1908. To get at least some distributional and ecological information, all data referring to Neotropical findings of this taxon are cited: Balogh & Balogh (1990) name Chile and Argentina as the distribution area, with the habitats described as spring localities, wet grasses, mosses and mouldering or dripping wet soils (Hammer, 1961). *H. initialis* is characterised as a secondary decomposer, feeding predominantly on fungi and litter in part, but also predacious feeding on nematodes was observed (Schneider et al., 2004). The ecology is described as hygrophilous and tyrphobiotic (Schatz & Gerecke, 1996).

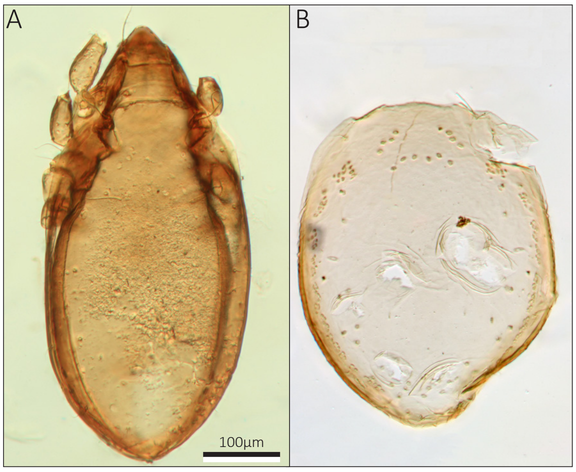


Figure 3.18 | *Scheloribates confundatus:* dorsal view (A) and details of a separated notogaster (B)

15. *Scheloribates* cf. *elegantulus* Hammer, 1961

<u>Taxonomy</u>: equivalent to the description given by Hammer (1961), the pseudostigmatic organs reached beyond the edge of the pteromorphae and showed a very distinct shape with a thickening at the distal half and a thin prolonged tip. A sublamella was also indicated in the taxonomic drawings, though additionally all eight investigated specimens showed maculae on the notogaster.

<u>Zoogeography & autecology</u>: *Scheloribates elegantulus* shows a Neotropical distribution (Subìas, 2004). The species was found in moss between heathery shrubs (Hammer, 1961) and in semideciduous forest fragments surrounded by savanna (Ferreira et al., 2012).

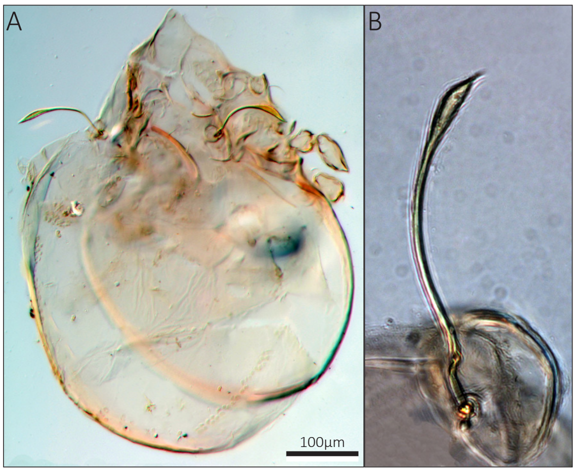


Figure 3.19 | *Scheloribates* cf. *elegantulus:* dorsal view (A) and details of a sensillus (B)

16. *Scheloribates pallidulus* sensu Hammer 1958

<u>Taxonomy</u>: all 27 examined mites of this taxon showed two rows of maculae on the notogaster and a fine translamellar ridge which was not found in European *S. pallidulus* (Weigmann, 2006). Because of this, the classification infers Hammer (1958) to emphasise a morphological divergence.

<u>Zoogeography & autecology</u>: *Scheloribates pallidulus* is a cosmopolitan species (Subìas, 2004) and typical for wooded *Sphagnum* peat bogs and forest

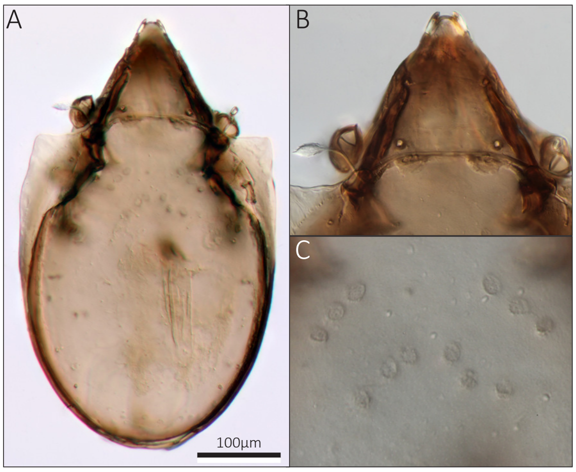


Figure 3.20 | *Scheloribates pallidulus:* dorsal view (A), details of the prodorsum (B), and the rows of maculae on the notogaster (C)

soils in Europe and Eurasia (Ivan et al., 1997; Weigmann, 2006; Murvandize & Kvavadze, 2010). Investigations on stable isotope ratios reveal some species of the Scheloribatidae as secondary decomposers (Schneider et al., 2004).

17. *Oripoda* sp. Banks, 1904

Taxonomy: an exact determination could not be implemented, as the only found specimen was badly damaged. However, some available features referred to the genus *Oripoda*: the genital aperture is situated strikingly anterior on the ventral plate and adjoins apodema I and II. The genital aperture was about half the size of the anal aperture and the body length was approximately twice as long as the width. Bothridia and sensilli were completely covered by the anterior margin of the notogaster. Furthermore, the notogastral integument was very smooth (Wooley, 1966; Krantz & Walter, 2009). The examined specimen resembled most likely *Oripoda trilabiata* Hammer, 1961.

Zoogeography & autecology: due to insufficient sample material, determination of the *Oripoda* taxon was only possible to genus level. Members of the genus have a cosmopolitan distribution, with a tropical and sub-tropical focus (Subìas, 2004). In the Neotropics, *Oripoda* species are recorded from the eastern lowlands and southern Argentina (Martínez & Velis, 2000), as well as from the tropical rainforests of Ecuador (Illig et al., 2007). Four species are known from the high Andes (>3000 m a.s.l.) of Bolivia and Peru (Hammer, 1962b; Balogh & Mahunka, 1969). Ecological information can not be provided because only a high taxonomic rank could be determined.

3.3.3 | The Chironomid community

In total, 801 specimens from 41 modern surface samples were investigated of which 85.5% could be identified. On 14.5% of all specimens, taxonomically important structures were damaged which prohibited identification. Altogether, 11 taxa could be identified. However, it was only possible to determine to species level in one case. All other taxa are determined to genus or genus-group level. The most diverse subfamily was the Orthocladiinae with nine associated taxa. The subfamilies Tanypodinae and Podonominae were represented each by a single taxon. An overview on the Chironomid fauna of the CLP is given in Table 3.2:

Table 3.2 | Systematic overview of the Chironomid community of the CLP

Sub-family *Species*	**Author**	**Taxonomic description**
Tanypodinae		
1. *Apsectrotanypus/Alotanypus*	Johannsen-Roback	Williams et al., 2012; Prat & Rieradevall, 2011
Podonominae		
2. *Parochlus*	Enderlin	Prat & Rieradevall, 2011; Brooks et al., 2007
Orthocladiinae		
3. *Metriocnemus eurynotus*	Holmgren, 1883	Prat & Rieradevall, 2011
4. *Limnophyes/Paralimnophyes*	Eaton	Williams et al., 2012; Brooks et al., 2007
5. *Epoicocladius*	Zavrel	Brooks et al., 2007
6. *Cricotopus/Paratrichocladius* type I	van der Wulp	Matthews-Bird et al., 2016; Williams et al., 2012
7. *Cricotopus/Paratrichocladius* type II	van der Wulp	Matthews-Bird et al., 2016; Williams et al., 2012
8. *Paracricotopus*	Thienemann & Harnisch	Brooks et al., 2007
9. *Pseudosmittia*	Goetghebuer	Brooks et al., 2007
10. *Pseudorthocladius*	Goetghebuer	Brooks et al., 2007
11. *Parametriocnemus/Paraphaenocladius*	Goetghebuer-Thienemann	Prat & Rieradevall, 2011; Brooks et al., 2007

3.3.3.1 | Taxonomical remarks and ecology of the Chironomid taxa

1. *Apsectrotanypus/Alotanypus* Johannsen-Roback

Taxonomic remarks: the taxonomic features were nearly identical to the description of Williams et al. (2012) and Prat & Rieradevall (2011): the ligula had five teeth of which the central tooth is the shortest and the outer teeth are the longest. The basis of the ligula showed a distinct granulation. The paraligula was bifid and five dorsomentral teeth were present. The pecten hypopharyngis had 15 tiny and weakly sclerosed teeth on each side. The setal sockets (S) on the ventral side were roughly the same size. S9 and S10 were located close to each other and S10 was mesial to S9. The ventral pore (VP) was located posterolateral to S9 and S10 and about twice the distance S9-S10 away from S10. The seta socket (SSm) was positioned between S9 and S10 but further mesial, about the same distance from S9 as VP was apart from S9. The tip of the basal tooth of the mandible was bent inwards and the accessory tooth is very small and pointed. The description was based on 31 specimens. With reference to both identical descriptions given by Williams et al. (2012) and Prat & Rieradevall (2011), an assembled taxon type name of *Apsectrotanypus/Alotanypus* was chosen.

Ecology: Tanypodinae larvae are generally occurring in warmer conditions, preferring standing water and can survive oxygen-poor conditions (Ashe et al., 1987).

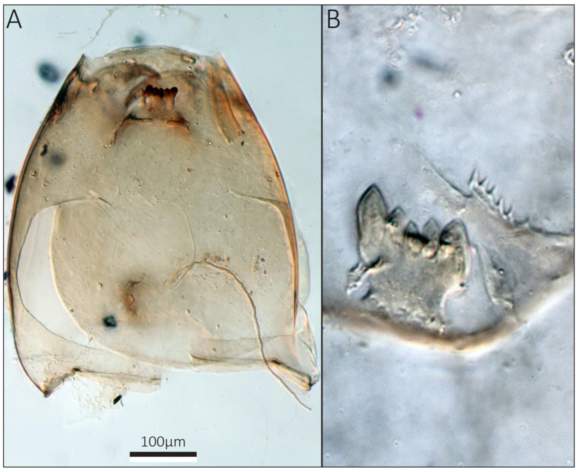


Figure 3.21 | *Apsectrotanypus/Alotanypus:* ventral view on the headcapsule (A) and details of the ligula (B)

2. *Parochlus* Enderlin

Taxonomic remarks: the taxonomic description refers to Brooks et al. (2007): The mentum showed one median tooth and seven lateral teeth. The first and second lateral were shorter than the median tooth and the first lateral was partly fused to the median tooth. The third lateral tooth was nearly as long as the median tooth. The forth to seventh lateral teeth decreased in size. The head capsules of *Parochlus* appeared distinctly smaller than other taxa in this survey and show a dark pigmentation. Another characteristic feature for determination of this genus was the distinct premento-hypopharyngeal complex and the shape of the mandibles, which showed six teeth in total, with a short first and a large second tooth (Ruiz-Moreno et al., 2000). The description was based on 14 specimens.

Ecology & zoogeography: *Parochlus* is referred to as a cold stenotherm taxon (Brooks et al., 2007) and representatives of the genus inhabit cool springs and running water (Brundin, 1983). The taxon *Parochlus* is distributed in the southernmost part of South America, the southern Atlantic islands and the high Andean regions of Chile and Argentina, ending at the desert zone of northern Chile. Further north, an endemic population is known from the tropical high mountains of Bolivia, Peru and Ecuador (Brundin, 1966).

Figure 3.22 | *Parochlus:* ventral view on the headcapsule

3. *Metriocnemus eurynotus* Holmgren, 1883

Taxonomic remarks: the taxonomic description refers to Prat & Rieradevall (2011) and Brooks et al. (2007): the mentum of the genus Metriocnemus featured paired median teeth and five lateral teeth, of which the paired median teeth were distinctly shorter in comparison to the lat-

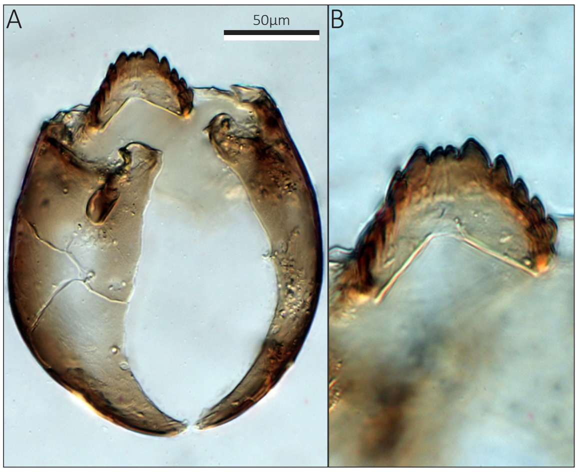


Figure 3.23 | *Metriocnemus eurynotus:* ventral view on the headcapsule (A) and details of the mentum (B)

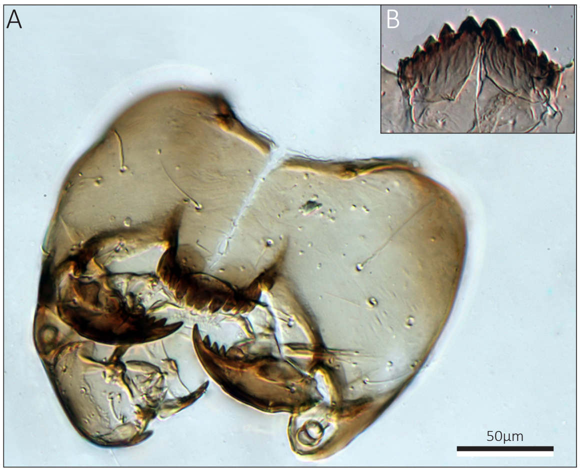


Figure 3.24 | *Limnophyes/Paralimnophyes:* ventral view on the headcapsule (A) and details of the mentum (B)

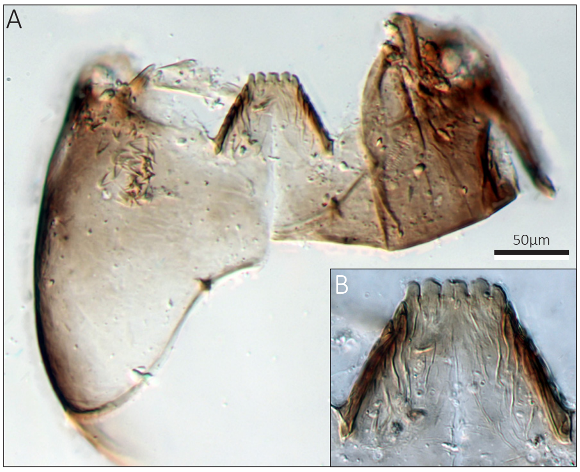


Figure 3.25 | *Epoicocladius:* ventral view on the headcapsule (A) and details of the mentum (B)

eral teeth. The third to fifth lateral teeth decreased gradually in size. The described taxon was assigned as *Metriocnemus eurynotus* in reference to Epler (2001), because the longest tooth was at first lateral position in comparison to the second lateral position, as recorded in e.g. *Metriocnemus* 1 by Prat & Rieradevall (2011). The description was based on two specimens.

Ecology: *M. eurynotus* occurs in madicolous (also known as hygropetric) environments, i.e. in <2 mm thin water layers, for example where water runs over a rock (Armitage et al., 1997), organic enriched habitats (Epler, 2001) or amongst plants (Brooks et al., 2007).

4. *Limnophyes/Paralimnophyes* Eaton

Taxonomic remarks: the taxonomic description refers closely to e.g. Williams et al. (2012): the mentum of this taxon showed a pair of median teeth and five lateral teeth, which decreased in size. However, the forth and fifth lateral teeth were of the same size. The median pair of teeth were distinctly bigger than all other teeth on the mentum. The description was based on 95 specimens.

Ecology: *Limnophyes* is associated with very shallow waters in the littoral zone of lakes and can be used as an indicator for lake-level changes (Massaferro & Brooks, 2002). Other authors report *Limnophyes/Paralimnophyes* larvae as the dominant species in water saturated, peat soils (Strenzke, 1951).

5. *Epoicocladius* Zavrel

Taxonomic remarks: the taxonomic description refers to Epler (2001) and Brooks et al. (2007): the mentum was strongly arched and showed six (4-8) equally shaped median teeth in a row. Five lateral teeth were present, which were positioned behind one another so that the lateral dentation of the mentum was hardly visible. The description was based on a single specimen.

Ecology: In Europe and North America, *Epoicocladius* is parasitic or phoretic on mayflies (Epler, 2001) which occur in gravelly streams (Cranston et al., 1983).

6. & 7. *Cricotopus/Paratrichocladius* type I & II van der Wulp

Taxonomic remarks: the taxonomic description is based on Matthews-Bird et al. (2016) and Williams et al. (2012): the mentum of this genus showed a single median tooth and six lateral teeth. The first lateral teeth were noticeably rounded and wider than the other lateral teeth. The second tooth was shorter than the third and a gap between the second and third was typical. To specify morphotypes, the shape of the ventromental plates was

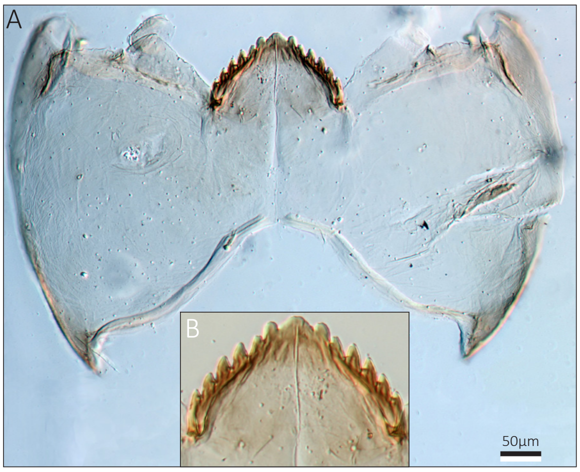


Figure 3.26 | *Cricotopus/Paratrichocladius* type I*:* ventral view on the headcapsule (A) and details of the mentum (B)

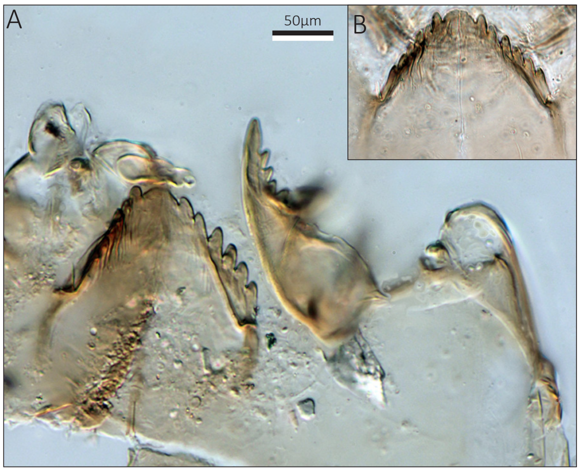


Figure 3.27 | *Cricotopus/Paratrichocladius* type II*:* ventral view on the headcapsule (A) and details of the mentum (B)

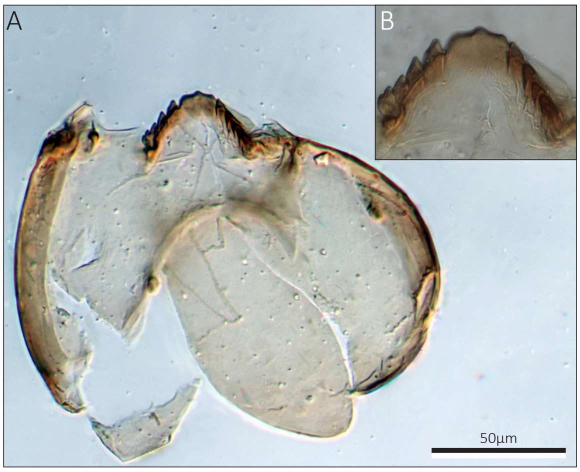


Figure 3.28 | *Paracricotopus:* ventral view on the headcapsule (A) and details of the mentum (B)

used. In *Cricotopus/Paratrichocladius* type I, the ventromental plates did not protrude much posterior than the bases of the sixth lateral teeth. The description was based on four specimens. *Cricotopus/Paratrichocladius* type II was identical to *C./P.* type I, except for the shape of the ventromental plates. In morphotype II, the ventromental plates showed a long spike originating at the bases of the sixth lateral teeth and reached far caudally. The description was based on 97 specimens.

Ecology: The Orthocladiinae is the biggest and the ecologically most broadly adapted subfamily. Because of the large number of species in the *Cricotopus/Paratrichocladius* group, statements on the ecology are difficult to summarise. In general, members of this taxon are adopted to cold stenothermic conditions and become more frequent with increasing altitude (Ashe et al., 1987). Epler (2001) states that the genus occurs in running water habitats. However, in Brooks et al. (2007), the habitat of this taxon is indicated as running and standing water, with the group characterised as ubiquitous and frequently found in lake sediments. In contrast, some *Cricotopus* species are common in warm tropical waters (Ashe et al., 1987). Nevertheless, the subfamily Orthocladinae in general is a taxa adapted to cold stenothermic conditions (Cranston, 1997).

8. *Paracricotopus* Thienemann & Harnisch

Taxonomic remarks: the taxonomic description is similar to Williams et al. (2012) and Brooks et al. (2007): The mentum had a single broad median tooth and five lateral teeth. The median tooth was often pointed in the middle and shows distinct shoulders. The lateral teeth gradually decreased in size and the fifth is often hardly visible. The outer margin of the fifth lateral tooth was curved and points inwards. The sockets of SSm were located clearly posterior of an imaginary line between the origins of both side's fifth lateral tooth. The description was based on ten specimens.

Ecology: *Paracricotopus* inhabits mosses, liverworts and algae in springs, bogs and small rivulets (Cranston et al., 1983; Epler, 2001).

9. *Pseudosmittia* Goetghebuer

Taxonomic remarks: the taxonomic description is similar to Williams et al. (2012) and Brooks et al. (2007): the mentum featured a single and broad median tooth and four lateral teeth. The sockets of SSm were located distinctly posterior of an imaginary line between the bases of both fourth lateral teeth. The description was based on two specimens.

Ecology: many species of this taxon are terrestrial or semi-terrestrial (Strenzke, 1951; Epler, 2001). Some species are also common in the well vegetated littoral zone of lakes (Brodin, 1986).

Figure 3.29 | *Pseudosmittia:* ventral view on the headcapsule (A) and details of the mentum and a mandible (B)

Figure 3.30 | *Parametriocnemus/Paraphaenocladius:* ventral view on the headcapsule

10. *Pseudorthocladius* Goetghebuer

<u>Taxonomic remarks</u>: the taxonomic description refers to Brooks et al. (2007): the mentum of Pseudorthocladius featured two well divided, paired median teeth and four lateral teeth, which were not obviously decreasing in size. The description was based on three specimens.

<u>Ecology</u>: *Pseudorthocladius* inhabits shallow waters of lakes or streams and is often associated with mosses (Strenzke, 1951). Furthermore, Epler (2001) states the occurrence of *Pseudorthocladius* in bogs of southern North America.

11. *Parametriocnemus/Paraphaenocladius* Goetghebuer-Thienemann

<u>Taxonomic remarks</u>: the taxonomic description refers to Prat & Rieradevall (2011) and Brooks et al. (2007): the mentum showed a single or weakly incised, broad median tooth and five lateral teeth. The first lateral teeth were distinctly longer than all the other lateral teeth and the tip was almost on the same level as the median ones. The third, fourth and fifth lateral teeth were considerably smaller in comparison to the first and second. The dull-edged third and the fifth lateral teeth were smaller than fourth. The fifth lateral tooth was partly fused to the fourth lateral. Because of nearly indistinguishable similarities between the genera *Parametriocnemus* and *Paraphaenocladius*, both were consolidated in one taxon group (Epler, 2001). The description was based on two specimens.

<u>Ecology</u>: some species of *Parametriocnemus* are terrestrial (Cranston et al., 1983), but the taxon is also common in streams and springs (Epler, 2001).

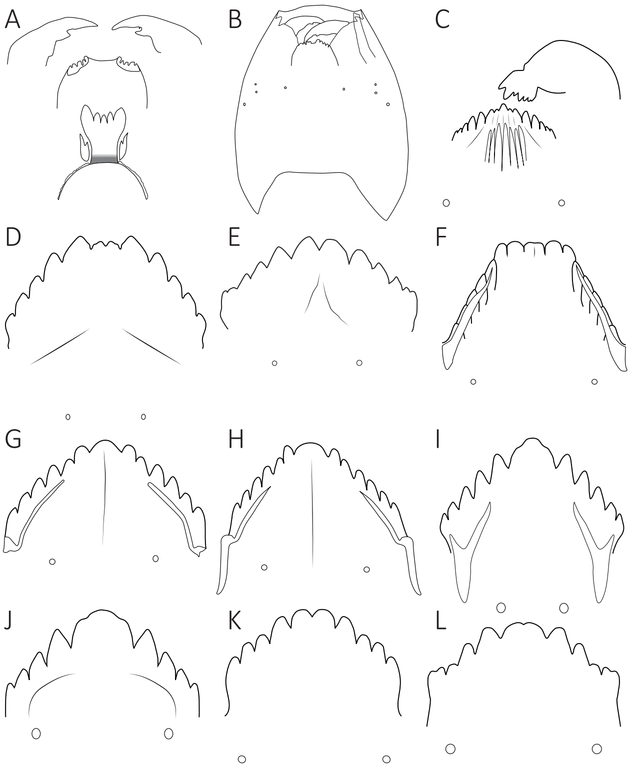


Figure 3.31 | Characteristic features of the Chironomid taxa, summarised as schematic drawings:
A) ligula, paraligula, pecten hypopharyngis and mandibles, and **B)** dorsal setation of *Apsectrotanypus/Alotanypus*
C) mandible and mentum of *Parochlus*
D) mentum of *Metriocnemus eurynotus*
E) mentum of *Limnophyes/Paralimnophyes*;
F) mentum of *Epoicocladius*;
G) mentum of *Cricotopus/Paratrichocladius* type I;
H) mentum of *Cricotopus/Paratrichocladius* type II;
I) mentum of *Paracricotopus*;
J) mentum of *Pseudosmittia*;
K) mentum of *Pseudorthocladius*;
L) mentum of *Parametriocnemus/Paraphaenocladius*

3.4 | Discussion

3.4.1 | Analysis of the Oribatid mite community

A rarefaction analysis of the Oribatid mite fauna indicates sufficient sampling density, regarding the total amount of species in relation to specimen numbers (see Figure 3.32). The analysis shows an infinite rising estimation curve which reaches 18 taxa at 1000 counted specimens. 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.

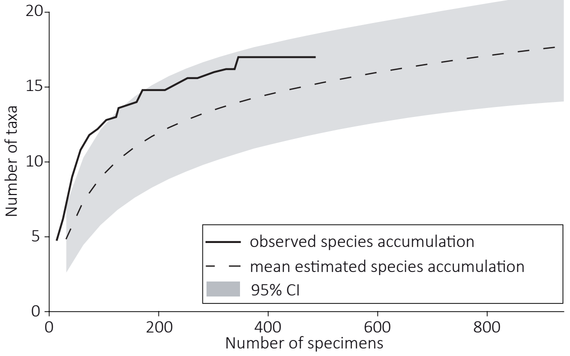


Figure 3.32 | Oribatid mite species richness estimation. The solid line shows the observed development of species number with increasing examined specimens. The dashed curve indicates the estimated species accumulation, achieved by rarefaction analysis, and the grey area the 95% CI of the model.

In comparison to other sampled cushion peatlands, the Oribatid mite richness of the CLP is similar to a peatland in central Chile (33°S) at 3200 m a.s.l. with 18 identified species (Figueroa & Covarrubias, 2005) or still comparable to a sampling site in northern Chile (19°S) from which 13 species are known (Covarrubias, 2004a). The latter study reveals also the higher Oribatid mite richness of the bofedal ecosystem in comparison to six other ecotopes 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 species.

Nevertheless, the Oribatid mite community of other bofedales, such as a *Patosia clandestina*-dominated cushion peatland in northern Chile (18°S) at 4580 m a.s.l., consisting of only seven species, turn out to be distinctly less diverse (Covarrubias, 2009).

3.4.1.1 | Community structure

Referring to the classification criteria by Engelmann (1978), *Tectocepheus* sp. (23.8%), *Jugatala armata* (17.0%) and *J. montana* (13.7%) are the dominant species of the Oribatid mite community, followed by a group of subdominant species: *Neoamerioppia* cf. *notata* (9.5%), Malaconothrus monodactylus (5.6%), *Nanhermannia elegantissima* (5.3%), *Scheloribates confundatus* (3.5%) and *S. pallidulus* (3.5%). Recedent species are *Zetomimus furcatus* (1.4%), *Tyrphonotrhus maior* (1.1%) and *Scheloribates elegantulus* (1.0%). *Jugatala chavinensis*, *Oxyoppia suramericana* with <1.0% can be considered as subrecedent while all other taxa (*Ceratozetes nigrisetosus*, Ameronothroid *Aquanothrus*-type, *Ceratozetes (Magellozetes)*-type and *Oripoda* sp.) with less than 0.32% occur sporadically. The community data shows a best fit to a niche preemption model with a AIC support of 59.75 (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).

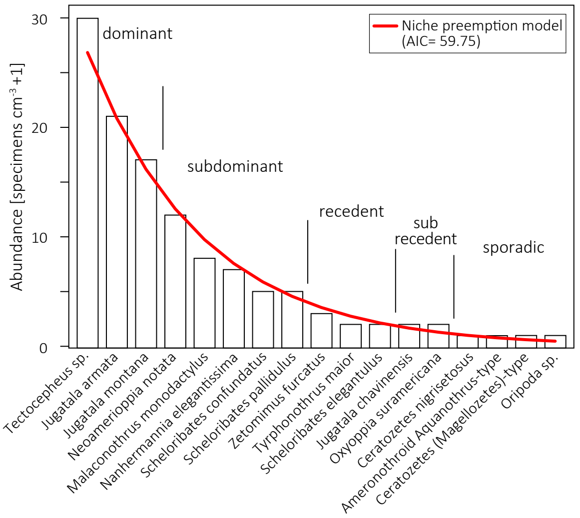


Figure 3.33 | Ranked species abundance plot (Whittaker plot) of CLP's Oribatid mite community. Red curve shows the calculated preemption model. The species are subdivided by the abundance classification criteria according to Engelmann (1978).

3.4.1.2 | Density distribution in the peatland

Overall, a mean density of Oribatid mites of 3.0 specimens cm^{-3} (*SD*= 5.9) was found in CLP, ranging from 0.08 specimens cm^{-3} in the debris ecotope to 8.96 specimens cm^{-3} in the degraded ecotope (see Figure 3.34). The density is much higher than in the soils of other cushion peatland sampling sites, which have densities ranging between 0.2-1.4 specimens cm^{-3} (Figueroa & Covarrubias, 2005; Covarrubias, 2009). However, these values are not comparable, because of methodological differences; despite using a Berlese-Tullgren funnel to extract the living Oribatid mites, dead specimens were also hand-picked from the samples in this study. Most likely, the method used here achieves a much higher number of Oribatid mite specimens.

In addition, the density of Oribatid mites differs significantly within the investigated ecotopes (H(4)= 27.3, p<0.001). However, the sample depth appears to have no influence on the inhabiting Oribatid mite density (p=0.27). In contrast, the relationship with the different ecotopes shows a significant influence on the density (p<0.001), but explains only 27.3% of the overall variability. Post hoc comparisons show similar Oribatid mite densities (observed differences= 1.8-7.8) in the fully developed, pioneer and debris ecotopes (α=0.05, corrected with the number of tests: critical differences= 14.9-18.0) and in the succession, pioneer and degraded ecotope (observed differences= 4.8-7.5; critical differences= 14.4-17.6).

3.4.1.3 | Habitat analysis

The indicator species analysis, using the Oribatid mite density data (see Figure 3.35), reveals a full coverage (proportion of site in which one or more indicators were found) for the degraded ecotope which is the main distribution area for *Jugatala montana* (indicator value: IndVal= 0.937, p<0.001), *J. armata* (IndVal= 0.937, p<0.001), *Nanhermannia elegantissima* (IndVal= 0.866, p<0.001) and *Scheloribates pallidulus* (IndVal= 0.660, p<0.05). *Nanhermannia elegantissima* is fully specific (i.e. 100% probability, that the surveyed sample belongs to the targeted ecotope, if this species has been found in it) to this ecotope, while its sensitivity (i.e. the probability of finding the species in the sample belonging to the ecotope) is 0.75. Vice versa, *Jugatala montana* and *J. armata* are fully sensitive to this ecotope and both show specificities of about 0.88. For *Scheloribates pallidulus* the specificity is 0.87 and the sensitivity 0.5. The succession ecotope was significantly more inhabited by *Neoamerioppia notata* (IndVal= 0.916, p<0.001), *Scheloribates elegantulus* (IndVal= 0.707, p<0.01) and *S. confundatus* (IndVal= 0.682, p<0.05) which represent a coverage of 0.875. *Neoamerioppia notata* shows high specificity and sensitivity for this ecotope (0.96 and 0.88) while *Scheloribates elegantulus* reveals full specificity and mid sensitivity (0.5). For *S. confundatus* a specificity of 0.74 and a sensitivity of 0.63 were computed.

Tectocepheus sp. (IndVal= 0.921, p<0.001) is characteristic of both the degraded and the succession ecotope, with a high specificity (0.97) and sensitivity (0.88). The coverage of the "degraded ecotope and succession ecotope"-combination is calculated as 0.88 for this single indicator species.

Malaconothrus monodacytlus (IndVal= 0.671, p<0.05) is an indicator for a combined "degraded, succession and pioneer ecotope", with a coverage of 0.45. *M. monodactylus* shows full specificity for this combination of three ecotopes, but with a low sensitivity (0.45). See Appendix 1 for all results of the indicator species analysis.

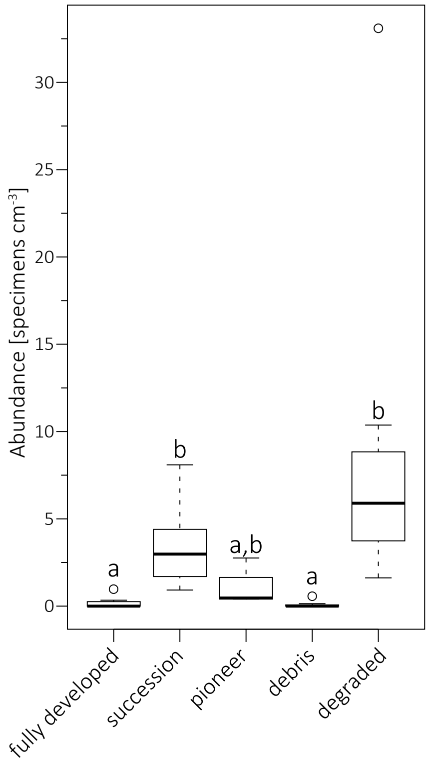


Figure 3.34 | Abundance of Oribatid mites in the ecotopes of CLP. Not significantly different ecotopes (post hoc Kruskal-Wallis comparisons: observed difference>critical difference, α= 0.05, corrected for the number of tests) are marked with same letters. Solid lines mark the median and circles extreme values.

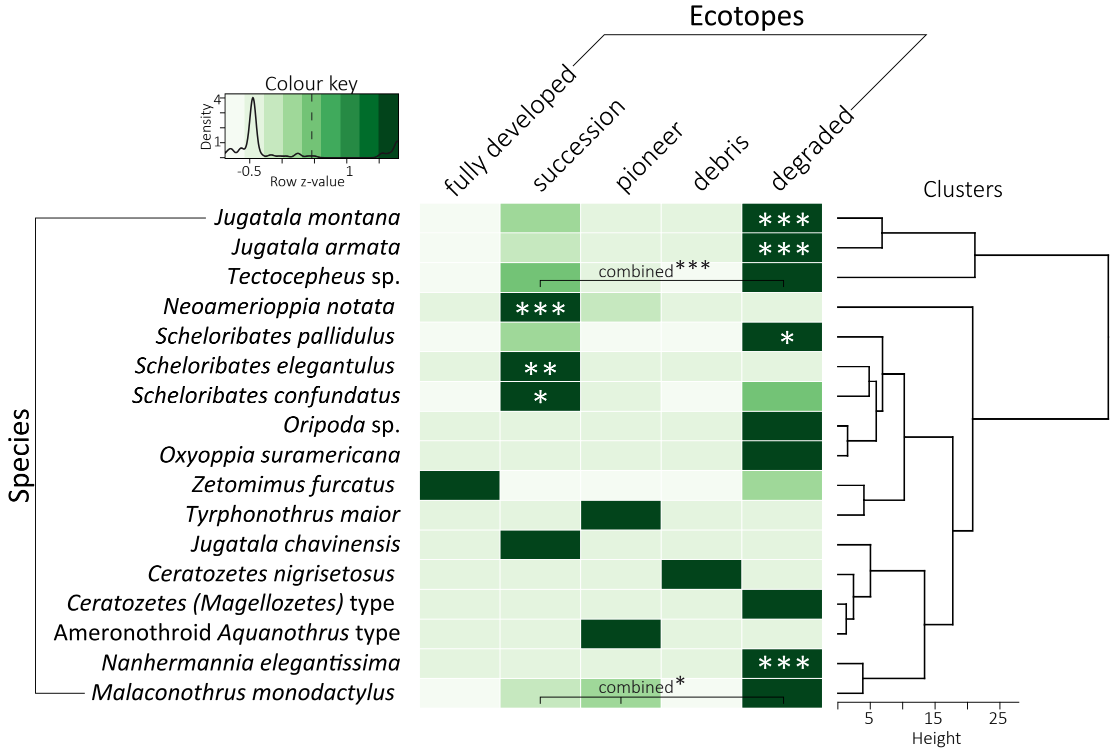


Figure 3.35 | Heatmap showing Oribatid mite taxa distribution within the ecotopes. Darker colours indicate focal points of distribution by high positive mean value derivation (positive z-values). Data were square root transformed to accentuate low values, and z-values refer separately to the single taxon distribution. Significant indicator species for different ecotopes or ecotope combinations are indicated by: ***= p<0.001; **= p<0.01; *= p<0.05; p was tested with 999 random permutations.

3.4.2 | Analysis of the Chironomid community

The rarefaction analysis of the Chironomid data shows an estimated taxa accumulation that approaches the asymptote at about 12 species (see Figure 3.36). The 95% CI ranges from 9-14 species. In general, the Chironomid community of the CLP shows low species richness in comparison to stream ecosystems of the same altitude, which are inhabited by >30 taxa (Acosta & Prat, 2010).

The community is strongly dominated by taxa of the Orthocladiinae with a relative abundance of 83.6%. Similar dominant occurrences of Orthocladiinae, comprising 57-76% of all the Chironomid taxa, are also reported from several other investigations (e.g. Acosta & Prat, 2010). In contrast, the community of the CLP is characterised by a total absence of taxa from the subfamily Chironominae, which represents the most numerous subfamily in lake ecosystems (Matthews-Bird et al., 2016) of the Central Andes and reaches relative abundances between 3-23% in stream ecosystems (Acosta & Prat, 2010). Another difference to the stream communities investigated by Acosta & Prat (2010) is represented by the not so evident dominance of specimens belonging to the *Cricotopus* complex. In the CLP community, the *Limnophyes* taxon shows higher abundances than *Cricotopus*.

The most unique feature of the CLP Chironomid community is the occurrence of *Parochlus* with a relative abundance of 5.4%, which has not been recorded so far from stream or lake ecosystems in the Central Andes (Acosta & Prat, 2010; Matthews-Bird et al., 2016). In Patagonian rivers, specimens of this genus can represent >38% of the total communities (Brundin, 1966). It can be assumed that the endemic populations of this genus in the high Andes of Bolivia, Peru and Ecuador inhabit different habitats from the southern populations, which could explain such relatively high numbers in a peatland.

Likewise, the subfamily Tanypodinae, with a relative abundance of 10.9%, is overrepresented in the CLP community in comparison to stream and lake ecosystems of the same region (Acosta & Prat, 2010; Matthews-Bird et al., 2016).

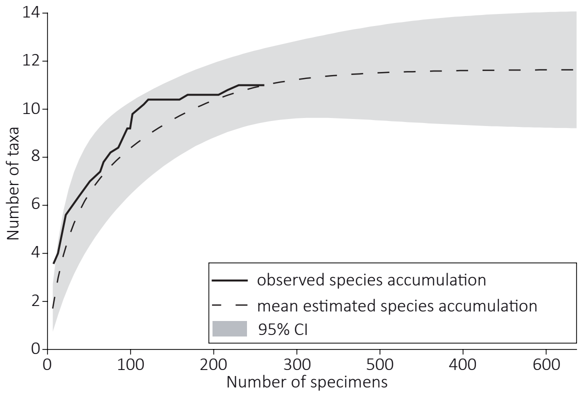


Figure 3.36 | Chironomid taxa richness estimation. The solid line shows the observed development of taxa number with increasing examined specimens. The dashed curve indicates the estimated taxa accumulation, achieved by rarefaction analysis, and the grey area the 95% CI of the model.

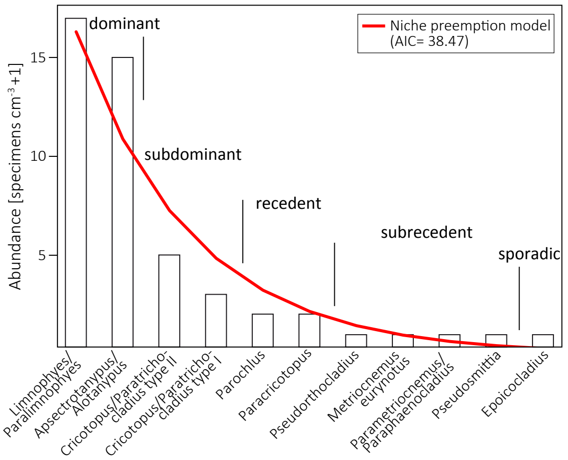


Figure 3.37 | Ranked species abundance plot (Whittaker plot) of CLP's Chironomid mite community. The red curve shows the calculated preemption model. The species are subdivided by the abundance classification criteria according to Engelmann (1978).

3.4.2.1 | Community structure

Regarding the classification criteria by Engelmann (1978), *Limnophyes/Paralimnophyes* (31.9%) and *Cricotopus/Orthocladius* type II (28.7%) are dominant in the Chironomid community (see Figure 3.37). Subdominant taxa are *Apsectrotanypus/Alotanypus* (8.8%) and *Parochlus* (4.4%), accompanied by the recedent taxa *Paracricotopus* (3%), and *Cricotopus/Orthocladius* type I (1.3%). All other taxa are subrecedent: *Metriocnemus eurynotus* (0.9%), *Pseudorthocladius* (0.8%), *Parametriocnemus/Paraphaenocladius* (0.5%), *Pseudosmittia* (0.5%); or occur only sporadically, such as *Epoicocladius* (0.2%).

The community data show best fit to the niche preemption model with a AIC support of 38.47 (Wilson, 1991). The 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).

3.4.2.2 | Density distribution in the peatland

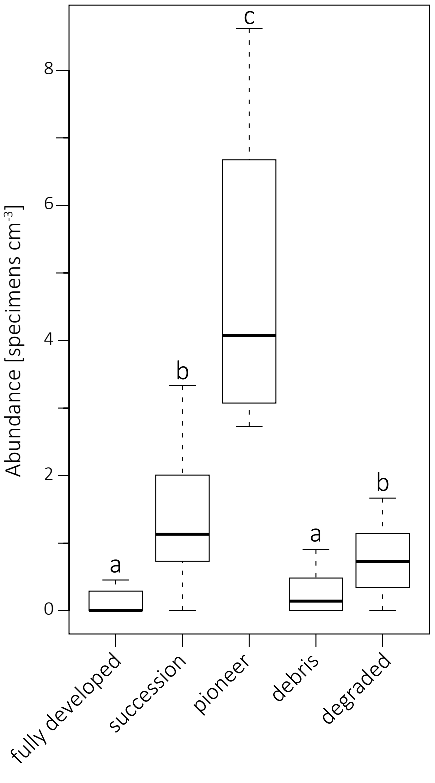


Figure 3.38 | Abundance of Chironomids in the ecotopes of CLP. Not significantly different ecotopes (Bonferroni comparisons, p>0.05) are marked with the same letters. Solid lines mark the median values.

Overall a mean density of Chironomids of 0.98 specimens cm^{-3} (*SD*= 1.64) was found in CLP, ranging from 0.11 specimens cm^{-3} in the fully developed ecotope to 4.88 specimens cm^{-3} in the pioneer ecotope (see Figure 3.38). The density of Oribatid mites differs significantly within the investigated ecotopes (F(1, 39)= 10.2, p=0.003, ω=0.18). Sample depth appears to have no influence on the inhabiting Oribatid mite density (p=0.50). In contrast, the relationship with the different ecotopes shows a significant influence on the density (p<0.01), yet explains only 17.53% of the overall variability. Bonferroni tests show similar (p>0.05) Chironomid densities in the fully developed and debris ecotope, and in the succession and degraded ecotope.

3.4.2.3 | Habitat analysis

The pioneer ecotope is significantly more inhabited by *Cricotopus/Orthocladius* type II (IndVal= 0.948, p<0.001), *Apsectrotanypus/Alotanypus* (IndVal= 0.902, p<0.001), *Parochlus* (IndVal= 0.861, p<0.001), *Parametriocnemus/Paraphaenocladius* (IndVal= 0.707, p<0.01) and *Paracricotopus* (IndVal= 0.698, p<0.01), which represents full coverage for this ecotope (see Figure 3.39). *Cricotopus/Orthocladius* type II shows full sensitivity for the pioneer ecotope and high specificity (0.948). The same applies to *Apsectrotanypus/Alotanypus* (specificity 0.814) and with a mid specificity of 0.707 for *Parochlus*. In contrast, *Parametriocnemus/Paraphaenocladius* shows full specificity and only a low sensitivity of 0.5. For *Paracricotopus*, a specificity of 0.65 and a sensitivity of 0.75 were calculated. The genus *Limnophyes/Paralimnophyes* is significantly more represented (IndVal= 0.91 p<0.001) in the habitats of the degraded, pioneer and succession ecotope, which correspond to a coverage of 0.85 for this ecotope combination. Therefore, *Limnophyes/Paralimnophyes* shows high specificity (0.974) and sensitivity (0.85). For complete results of the indicator species analysis of the Chironomid taxa, see Appendix 2.

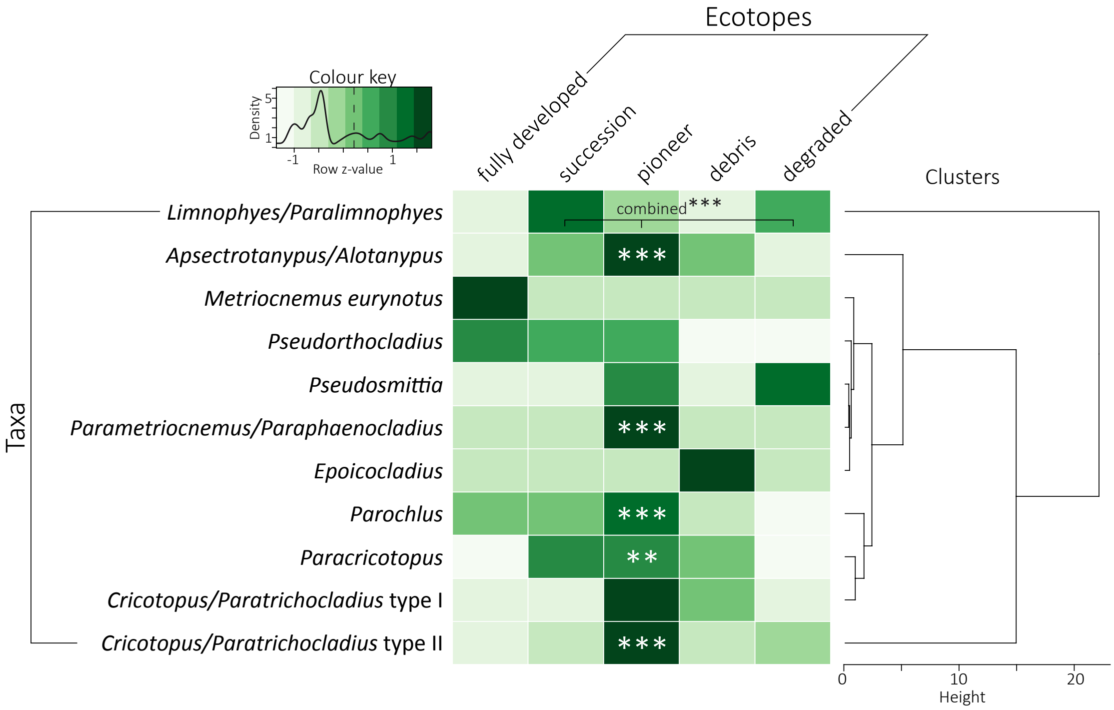


Figure 3.39 | Heatmap showing Chironomid taxa distribution within the ecotopes. Darker colours indicate focal points of distribution by high positive mean value derivation (positive z-values). Data were square root transformed to accentuate low values and z-values refer separately to the single taxon distribution. Significant indicator species for different ecotopes or ecotope combinations are indicated by: ***= p<0.001; **= p<0.01; *= p<0.05; p was tested with 999 random permutations.

3.5 | Conclusion

This investigation represents the first comprehensive study of the Oribatid mite and Chironomid fauna of a high-Andean cushion peatlands from Peru and reveals their distribution in the different soils of the study site. Both taxa inhabit only distinct ecotopes within the full range of peatland's heterogeneity. At the successional climax, almost no mesofauna could be observed.

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. For taxonomic determination, the absence of the legs, which is often the case in dead Oribatid mite specimens, is only a problem for single taxa. However, this damage requires an adapted use of the available identification keys for South America. The remarks on morphological features, provided in this study, could contribute to further taxonomic research on Oribatid mites in general, and the special community of cushion peatlands in particular. More research on Oribatid mites of the high Andes and especially for Peru is needed to get a complete species inventory of this region. For Chironomids, the identification to generic level was possible without any problems, using global keys, provided by palaeoenvironmental investigations, combined with the literature available from local investigations on high-Andean rivers and streams. However, some distinct morphological features require greater examination, which could be useful for future research. This is especially the case for further investigations on high-Andean cushion peatlands, as these are inhabited by a special community.

This investigation could form the foundation for expanding this research approach. A next step should focus on providing autecology data for the taxa found as this is currently nearly completely lacking. The main areas of distribution within the heterogeneity of the peatland, revealed in this study, should be tested to understand the most influential environmental parameters which describe best the (micro-)habitats of the Oribatid mites and Chironomids. With the synthesis of the taxonomic, distributional and the autecological data, a useful tool for palaeoenvironmental research could be developed.

4 | Chapter IV - Biogeography

The Oribatid mite diversity (Acari: Oribatida) of the high Andes with special reference to cushion peatlands (bofedales)

Abstract

The Oribatid mite fauna of the high Andes is under-collected in general. Only 39 sampling sites, ranging from 3000-5200 m altitude from southern Ecuador (4°S) to mid-Argentina (34°S), have been sampled. Six of these sampling sites can be assigned to cushion peatlands. For these sampling sites, diversity analyses have been performed.

From the high Andes >3000 m a.s.l., 219 species from 116 genera and 51 families are reported. The most common taxa are *Tectocepheus* sp., *Oxyoppia suramericana*, *Malaconothrus translamellatus* and *Camisa khencensis*, occurring each in >25% of all the sampling sites. The α-diversity ranges from a single taxon up to 45 species (median=10 taxa).

For high-Andean cushion peatlands, 48 taxa from 34 genera and 18 families are identified, of which only nine taxa are found in two or more sampling sites. The most prominent species are *Jugatala armata* and *Nanhermannia elegantissima* which are present each at four peatlands.

In the high Andes, the γ-diversity of Oribatid mites shows evident fluctuations with latitude. At low latitudes <10°S, species richness is high with >30 species. With increasing latitude, the richness declines to 7 species at 19°S before it increases again to 14 species at >30°S. This fluctuation can partly be associated with changes in precipitation.

Community analyses reveal the high Andean Oribatid mite community as highly nested both at genera- and species-level, and show a zonal character of the community in contrast to the azonal occurrence of cushion peatlands; a significant change in the taxonomic composition of the community is indicated at about 4-7°S.

4.1 | Introduction

Approaches to regionalise species distributions in the world and to classify biogeographical regions go back to the early days of Buffon & Daubenton (1766), von Humboldt & Bonpl and (1807) and Wallace (1876), and are regularly under reconsideration (Cox, 2001; Kreft & Jetz, 2010). One of the new approaches, a meta-analysis of cladistic investigations on numerous taxa, claims an independent biogeographic region for the Andes, within the classic region of the Neotropics (Morrone, 2001, 2002).

For Oribatid mites, biogeographical studies from the Andes are sparse, with a few investigations noting the connected sub-antarctic to mid-Andean distribution ranges of some species (Stary & Block, 1996, 1998). Nevertheless, although less studies exist within this taxonomic group, their potential for biogeographical research was recognised, for example, by Hammer & Wallwork (1979), who were able to trace continental drift from the distribution areas of Oribatid mite species.

In recent years, changes in Oribatid mite communities along altitudinal gradients have been of particular interest, with some remarkable patterns observed, for example: a decrease of species richness with altitude, and different community compositions within altitudinal levels (Fischer & Schatz, 2013; Mumladze et al., 2015); a higher ratio of sexual reproduction at high altitudes (Maraun et al., 2013); and a different distribution of feeding strategies, with more decomposers at low altitudes but a greater number of species feeding on living resources at high altitudes (Fischer et al., 2014).

Despite the general interest in altitudinal gradients, investigations in extreme environments above 3000 m a.s.l. remain rare. Some studies are available from the Himalayas, revealing altitudinal gradients (Jing et al., 2005; Moitra et al., 2008) or the community composition of high altitudinal ecosystems from the Andes (Beck, 1963; Covarrubias & Mellado, 2003; Covarrubias, 2004a, 2009). Meanwhile, in Central America, altitudinal distribution was limited at about 2600-2800 m a.s.l., with a specific species poor and cold adapted community taking over from a species rich tropical lowland community (Schatz, 2007).

Due to the lack of a biogeographic overview for the Oribatid mites of the high altitudes, this study is the first attempt to capture the Oribatid mite community of the Andean belts >3000 m a.s.l. over a large area. The hard cushion peatlands are highlighted in this study as they represent a special ecosystem of the high Andes, with unique faunal characteristics (Covarrubias, 2004a), while a species inventory for this ecosystem is urgently needed. For further investigation, considering the predominance of harsh climate conditions in the high montane regions of the Andes, the interplay of environmental conditions and community composition should be taken into account as being influential on biogeographic patterns.

The aims of this study are: i) to characterise the Oribatid mite community of the high Andes; ii) to contrast the community of the special high Andean ecosystem of cushion peatlands with other ecosystems, and; iii) to investigate the environmental control of γ-diversity of the high Andean Oribatid mite community.

4.1.1 | Hypothesis

For this investigation, a hypothesis tested in the first chapter is modified and re-analysed considering the above mentioned aims:

- High-Andean cushion peatlands are inhabited by a distinct Oribatid mite community which is different to the communities occurring in other ecosystems of the high Andes.

4.2 | Material & Methods

4.2.1 | Sampling sites of the high Andes with special reference to cushion peatlands

For the assessment of the Oribatid mite community of cushion peatlands, available studies which have been carried out in the high Andes have been analysed. To harmonise the different species inventories of many authors and to avoid synonym listings, Subìas (2004) was used as a reference. Cushion peatlands have been sampled in six sites (Covarrubias & Mellado, 2003; Covarrubias, 2004a, b; Figueroa & Covarrubias, 2005; Covarrubias, 2009). The studies by Hammer (1958, 1961) were analysed very conservatively. The data were only included if the term "bog" or "peat" was mentioned in the site descriptions and the altitude of the locality fits into the distribution range of cushion peatlands in the Andes (see Chapter 1.2). Sampling sites which are described as "stiff *Juncus*", or "Umbellifera cushions" have been

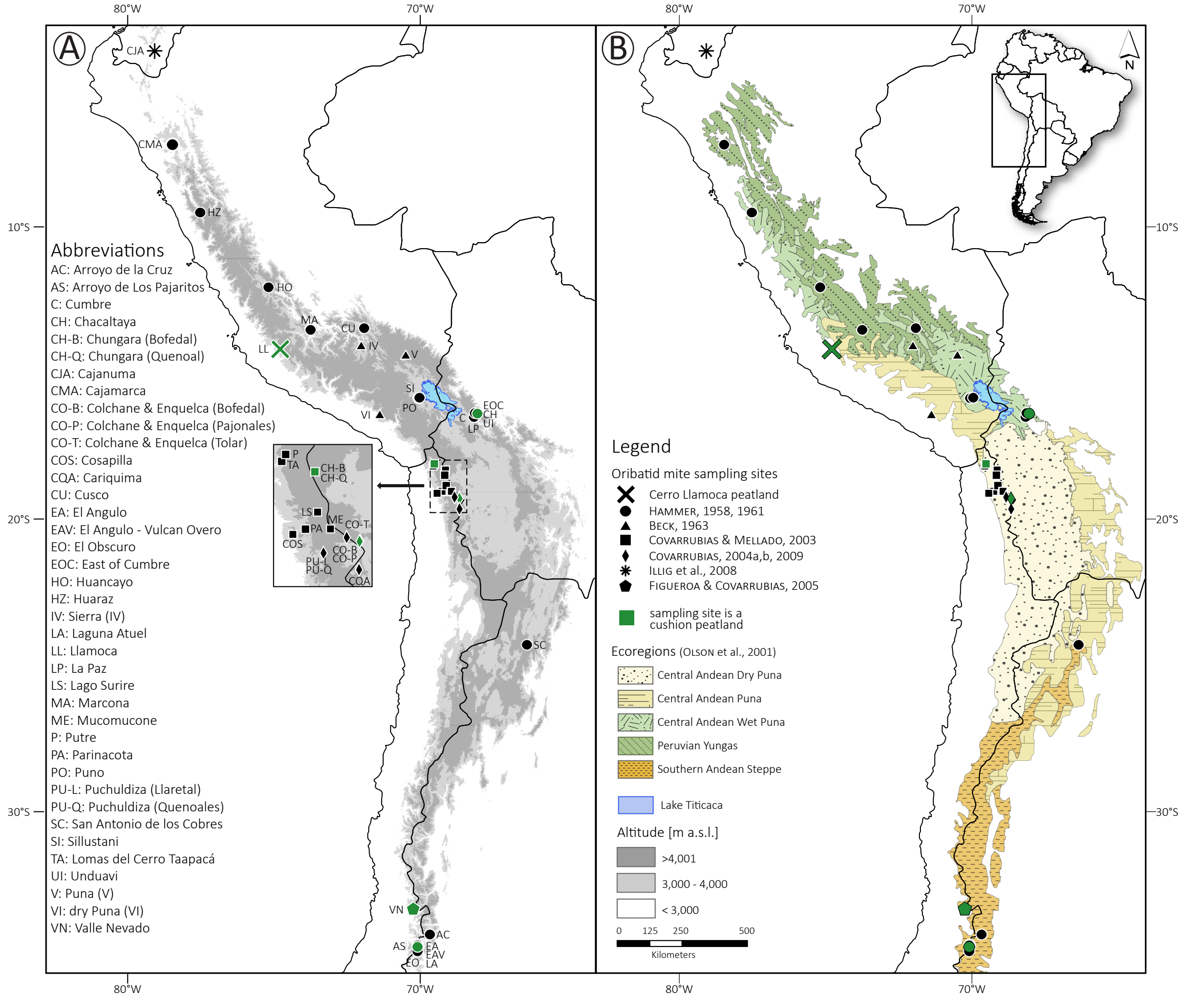


Figure 4.1 | Map of all Oribatid mite sampling sites (N=39) available from the high Andes >3000 m a.s.l.. In A), the height above sea level is indicated by grey shadings and all names of the sampling sites are given. In B) the corresponding ecoregions are shown in individual colours. Cushion peatlands are highlighted by a green symbol colour.

added to the assessment as well, but only if the given photo of the sites could indicate a cushion peatland vegetation. Additionally, unpublished data from the Cerro Llamoca peatland in southern Peru (see Chapter 3.3.2) have been added to the assessment.

For general comparison, all other high Andean sampling sites have been added to the dataset. From southern Ecuador (4°S) to central Argentina (34°S), 39 sampling sites from seven authors are available, ranging from 3000 to 5200 m a.s.l. (Hammer, 1958, 1961; Beck, 1963; Covarrubias & Mellado, 2003; Covarrubias, 2004a; Figueroa & Covarrubias, 2005; Illig et al., 2007; Covarrubias, 2009). To test the influence of different assignments to an ecoregion, the sampling sites where grouped following the classification by Olson et al. (2001). The entire list of available sampling sites with further details is given in Appendix 3.

4.2.2 | Numerical Analyses

For statistical analyses the software R ver. 3.1.2 (R Core Team, 2014) was used. Spline curve smoothness was estimated using a generalised additive model with the mgcv package ver. 1.8.6, following the procedure by Wood (2011). Environmental variables for regression modelling, precipitation, mean annual temperature and mean diurnal temperature, were derived from Hijmans et al. (2005). Nestedness was analysed with the bipartite package ver. 2.04 (Dormann et al., 2014) and the BINMATNEST-software ver. 3, following the procedures by Rodríguez-Gironés & Santamaría (2006), Almeida-Neto et al. (2007) and Dormann et al. (2008). Taxonomic diversity (taxonomic distinctness) has been measured using the Vegan package ver. 2.2.1 (Oksanen et al., 2015), based on the methodology by Clarke & Warwick (2001).

4.3 | Results

4.3.1 | The Oribatid mite fauna of high-Andean cushion peatlands

In total, 48 taxa from 34 genera and 18 families have been identified from high-Andean cushion peatlands, including the four above mentioned investigations of six sites, and the unpublished data from this study (see Table 4.1). Of the total 48 taxa, 38 species occurred only in one locality. Only nine species were found in two or more sites. *Jugatala armata* (Syn. *Edwardzetes armatus*) and *Nanhermannia elegantissima* were represented most, each occurring in four sites. No species have been found at all sites.

4.3.2 | Characterisation of the Oribatid mite fauna of the high Andes >3000 m a.s.l.

Overall 219 species from 116 genera and 51 families were reported. The number per site ranged from only a single species in an alfalfa plantation in northern Chile (Covarrubias, 2009) to 45 species in the Cusco area in Peru (Hammer, 1961), with a median of 10 species per site (*SD*=10.0). The most common taxon was *Tectocepheus* sp., which was present in 59% of all sampling sites, followed by *Oxyoppia suramericana* (36%), *Malaconothrus translamellatus* (31%) and *Camisia khencensis* (26%).

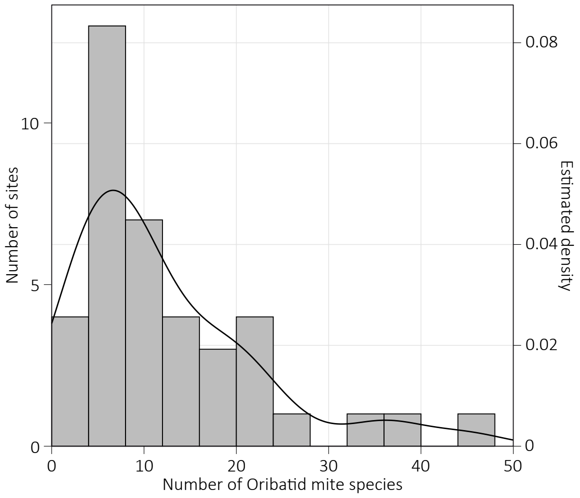


Figure 4.2 | Histogram showing the distribution of species diversity per site. The black line indicates the estimated density of species per site.

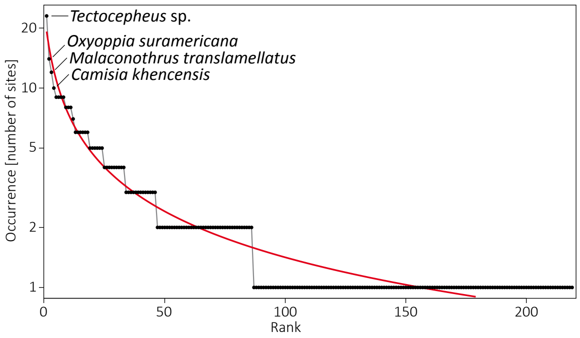


Figure 4.3 | Whittaker plot of the high Andean Oribatid mite community. A Zipf-Mandelbrot model (red line) shows best fit for the community data (AIC=549.1).

Table 4.1 | Overview of all Oribatid mites species identified from high-Andean cushion peatlands, with locations and references; [1]sensu Hammer, 1958 (Syn. ***Edwardzetes armatus***), [2]sensu Hammer, 1961 (Syn. ***Sphaerozetes chavinensis***), [3]sensu Hammer, 1961 (Syn. ***Trichoribates hammerae***)

Family		Taxon	Peatland location	Reference
Brachychthoniidae				
	1	*Liochthonius rigidisetosus*	northern Chile (18°S	Covarrubias, 2009
	2	*Sellnickochthonius foliatus*	northern Chile (18°S)	Covarrubias, 2009
Trhypochthoniidae				
	3	*Mainothrus breviclava*	central Chile (33°S)	Figueroa & Covarrubias, 2005
	4	*Mucronothrus nasalis*	central Chile (33°S)	Figueroa & Covarrubias, 2005
	5	*Malaconothrus translamellatus*	northern Chile (19°S)	Covarrubias, 2004a
			central Chile (33°S)	Figueroa & Covarrubias, 2005
			southern Peru (14°S)	own, unpublished data
	6	*Malaconothrus monodactylus*	northern Chile (18°S)	Covarrubias, 2009
			northern Chile (19°S)	Covarrubias, 2004a
	7	*Malaconothrus sylvaticus*	central Chile (33°S)	Figueroa & Covarrubias, 2005
	8	*Tryphonothrus australis*	northern Chile (19°S)	Covarrubias, 2004a
	9	*Tyrphonothrus maior*	southern Peru (14°S)	own, unpublished data
	10	*Tyrphonothrus novus*	central Chile (33°S)	Figueroa & Covarrubias, 2005

Table 4.1... continued

Family		Taxon	Peatland location	Reference
Nothrus				
	11	*Nothrus suramericanus*	Bolivia (16°S)	Hammer, 1958
			central Chile (33°S)	Figueroa & Covarrubias, 2005
			central Argentina (34°S)	Hammer, 1958
Crotoniidae				
	12	*Camisia khencensis*	northern Chile (18°S)	Covarrubias, 2009
			northern Chile (19°S)	Covarrubias, 2004a
Nanhermanniidae				
	13	*Nanhermannia elegantissima*	southern Peru (14°S)	own, unpublished data
			northern Chile (19°S)	Covarrubias, 2004a
			central Chile (33°S)	Figueroa & Covarrubias, 2005
			central Argentina (34°S)	Hammer, 1958
Oppiidae				
	14	*Globoppia trichosus*	northern Chile (19°S)	Covarrubias, 2004a
	15	*Lanceoppia nodosa*	central Chile (33°S)	Figueroa & Covarrubias, 2005
	16	*Multioppia insularis*	northern Chile (19°S)	Covarrubias, 2004a
	17	*Brachioppiella periculosa*	northern Chile (19°S)	Covarrubias, 2004a
	18	*Oxyoppia cubana*	northern Chile (18°S)	Covarrubias, 2009
	19	*Oxyoppia suramericana*	southern Peru (14°S)	own, unpublished data
			central Chile (33°S)	Figueroa & Covarrubias, 2005
	20	*Neoamerioppia* cf. *notata*	southern Peru (14°S)	own, unpublished data
	21	*Neoamerioppia trichosa*	Bolivia (16°S)	Hammer, 1958
Tectocepheidae				
	22	*Tectocepheus* sp.	southern Peru (14°S)	own, unpublished data
			northern Chile (19°S)	Covarrubias, 2004a
			central Chile (33°S)	Figueroa & Covarrubias, 2005
Ameronothridae				
	23	Ameronothroid *Aquanothrus*-type	southern Peru (14°S)	own, unpublished data
Tegoribatidae				
	24	*Wiliamszetes elsosneadensis*	central Argentina (33°S)	Hammer, 1958
			central Chile (33°S)	Figueroa & Covarrubias, 2005
Oribatellidae				
	25	*Oribatella illuminata*	central Chile (33°S)	Figueroa & Covarrubias, 2005
Ceratozetidae				
	26	*Ceratozetella thienemanni*	central Argentina (33°S)	Hammer, 1958
	27	*Ceratozetes nigrisetosus*	southern Peru (14°S)	own, unpublished data
			Bolivia (16°S)	Hammer, 1958
	28	*Ceratozetes (Magellozetes)*-type	southern Peru (14°S)	own, unpublished data
	29	*Edwardzetes andicola*	central Chile (33°S)	Figueroa & Covarrubias, 2005
	30	*Hydrozetes lemnae*	northern Chile (19°S)	Covarrubias, 2004a
	31	*Jugatala armata*[1]	southern Peru (14°S)	own, unpublished data
			Bolivia (16°S)	Hammer, 1958
			northern Chile (18°S)	Covarrubias, 2009
			northern Chile (19°S)	Covarrubias, 2004a
	32	*Jugatala chavinensis*[2]	southern Peru (14°S)	own, unpublished data
	33	*Jugatala montana*[3]	southern Peru (14°S)	own, unpublished data
	34	*Pedunculozetes andinus*	central Chile (33°S)	Figueroa & Covarrubias, 2005
	35	*Zetomimus furcatus*	southern Peru (14°S)	own, unpublished data
Zetomotrichidae				
	36	*Ghilarovus* sp.	central Chile (33°S)	Figueroa & Covarrubias, 2005

Table 4.1... continued

Family		Taxon	Peatland location	Reference
Oribatulidae				
	37	*Oribatula gracilis*	northern Chile (19°S)	Covarrubias, 2004a
	38	*Oribatula lata*	northern Chile (19°S)	Covarrubias, 2004a
Hemileiidae				
	39	*Hemileius suramericanus*	central Chile (33°S)	Figueroa & Covarrubias, 2005
Liebstadiidae				
	40	*Cordiozetes* sp.	central Chile (33°S)	Figueroa & Covarrubias, 2005
Scheloribatidae				
	41	*Scheloribates confundatus*	southern Peru (14°S)	own, unpublished data
	42	*Scheloribates diversidactylus*	northern Chile (18°S)	Covarrubias, 2009
	43	*Scheloribates* cf. *elegantulus*	southern Peru (14°S)	own, unpublished data
	44	*Scheloribates pallidulus*	southern Peru (14°S)	own, unpublished data
	45	*Scheloribates rugosus*	Bolivia (16°S)	Hammer, 1958
	46	*Scheloribates striatus*	Bolivia (16°S)	Hammer, 1958
Oripodidae				
	47	*Oripoda* sp.	southern Peru (14°S)	own, unpublished data
Protoribatidae				
	48	*Tuxenia manantialis*	central Chile (33°S)	Figueroa & Covarrubias, 2005

4.3.3 | Diversity changes along large scale environmental gradients in the high Andes

In the high-Andes, the number of species per site showed distinct fluctuations with latitude. At 3-10°S, the number of species accounted >30 before the fauna got less species-rich with a minimum at ca. 19°S with about seven species. Further southwards, the number of species increased again to ca. 14 species at 32°S (see Figure 4.4).

Precipitation had a significant influence on the Oribatid mite species number in high-Andean sampling sites, F(1, 37)=12.34, p<0.01, R^2=0.25. Temperature parameters (mean diurnal temperature range and mean annual temperature) showed no significant effect on the number of species (ΔR^2=0.003, p=0.85). The complete test statistics are denoted in Appendix 4.

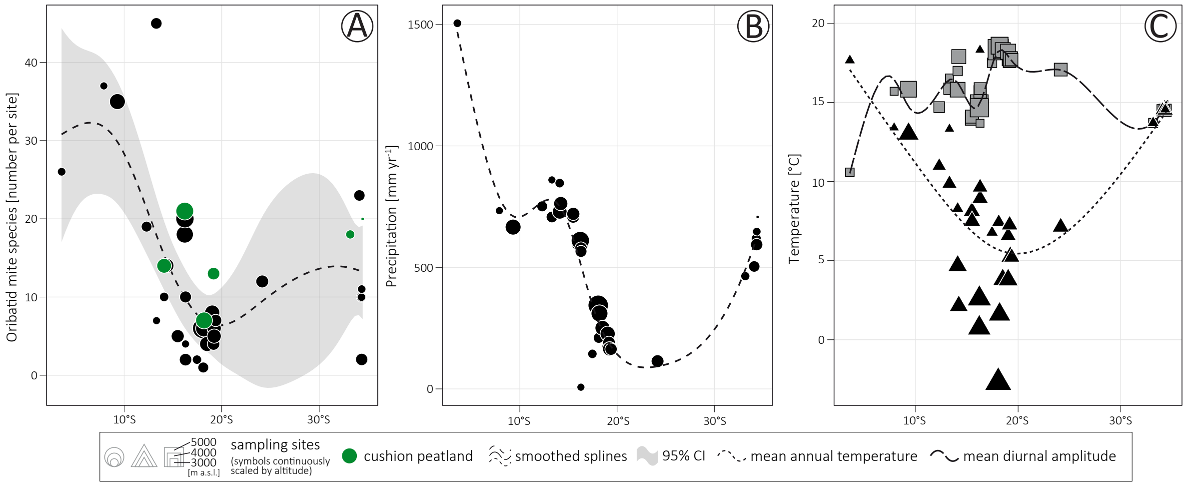


Figure 4.4 | Latitudinal Oribatid mite diversity changes and environmental fluctuations in the high Andes (>3000 m a.s.l). In **A**), the Oribatid mite species numbers of all available sampling sites in a latitudinal order are depicted. For the same sites, **B**) gives the amount of precipitation and **C**) the mean annual and mean diurnal temperature amplitude. General additive (gam) models have been used to estimate the degree of smoothness of the splines from the data. The grey area denotes the 95% probability interval. The altitudes of the sampling sites are shown by the continuous scaling of symbols. Green symbols indicate cushion peatland sampling sites. The environmental data were retrieved from Hijmans et al. (2005).

4.4 | Discussion

The analysis shows that precipitation is the only environmental factor of the tested dataset which has influences Oribatid mite diversity in the study area. In the high Andes, the amount of precipitation cannot be exclusively assigned to a latitudinal gradient (F(1, 37)= 2.1, p=0.16), because different climate systems, operating independently from each other, influence the precipitation in the study area: the northern part of the study area receives water by a southwards movement of the ITCZ (Garreaud et al., 2009), while the mid-Chilean area is supplied by a northwards transport of moist air masses of the westerlies airflow (Vuille & Ammann, 1997). Both areas are separated by the arid diagonal (Abraham et al., 2000).

Temperature variations show no significant effect on Oribatid mite richness in the high Andes. Some studies provide evidence that this is the case for soil dwelling microarthropod communities in general, except through an indirect effect of temperature on soil wetness (Kardol et al., 2011).

For Oribatid mites, a latitudinal gradient with increasing diversity from the boreal to the warm temperate latitudes, but without a further increase towards the tropics has been described by Maraun et al. (2007). In the analysis of this study, it is shown, that this general pattern cannot be applied to extreme habitats close to the environmental distribution limits of Oribatid mites. For these habitats, the analysis shows a significant environmental control of species richness which has also been revealed by several other studies, e.g. by Gough et al. (1994).

However, only 25% of the overall variation of species numbers can be explained by the influence of precipitation. Considering these results and those of some other studies (Hansen, 2000; Maraun & Scheu, 2000; Wardle, 2002; Nielsen et al., 2010), local factors, e.g. soil or vegetation, can be assumed to have the highest effect on belowground diversity.

4.4.1 | Inter-faunal comparison of high Andean Oribatid mite communities.

The comparison of high-Andean Oribatid mite communities, based on the Bray-Curtis dissimilarity, reveals a distinct pattern (see Figure 4.5). Most dissimilar to all other sampling sites is the community of the Cajanuma sampling site from the Ecuadorian Eastern Cordillera montane forests (Illig et al., 2007) and the sampling site "El Angulo" at the Vulcan Overo in mid-Chile (Hammer, 1958). A cluster analysis separates ten significant inter-site communities (p<0.05) within the high Andean study area. Some communities are characterised by a homogenous association with the sampling site's ecoregion. That applies to: i) the sampling sites of the Central Andean Dry Puna of which the majority (78% of total) are grouped in one community cluster; ii) the sites of the southern Andean steppe (75% of total), and; iii) the sites of Central Andean Wet Puna (44% of total).

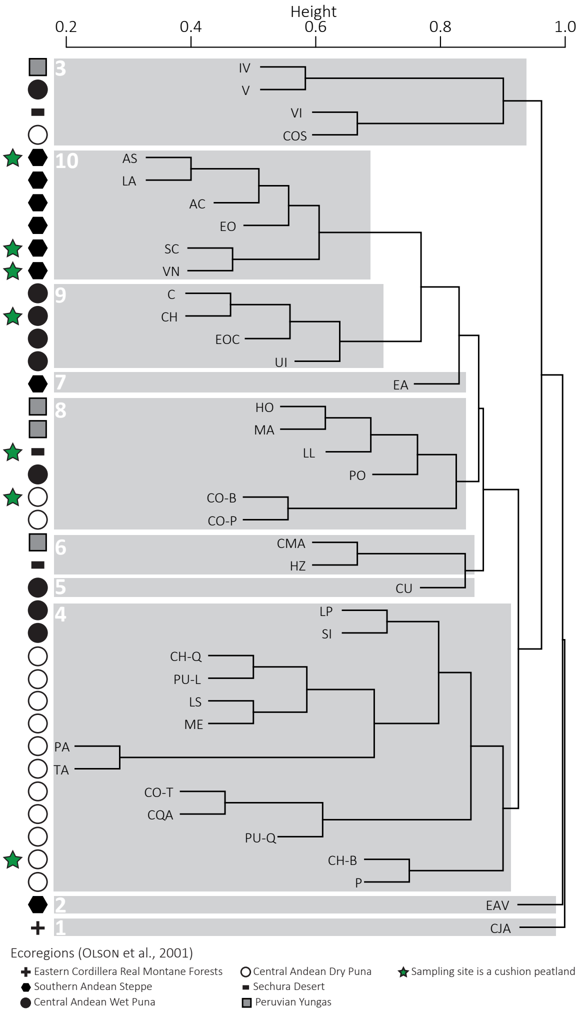


Figure 4.5 | Cluster analysis of Oribatid mite species presence/absence data for all 39 sampling sites available from the high Andes. Clustering was performed with average linkage analysis based on a Bray-Curtis dissimilarity matrix. Grey areas indicate significant clusters (p<0.05) and different symbols show the ecoregion in which the site is situated, following the classification by Olson et al. (2001). Abbreviations of sampling sites are given in Figure 4.1.

However, the cushion peatland sampling sites show no clear assignment to a separate cluster and are, to the contrary, arbitrarily placed through all clusters. This could be interpreted as evidence for a closer connectivity of cushion peatland Oribatid mite communities to the related ecoregion and against a distinct peatland inhabiting community. This proposed zonal character of the Oribatid mite community differs strikingly from the azonal distribution of the cushion forming plant species of the peatlands (Ruthsatz, 2008).

4.4.2 | Community nestedness

The nestedness of the Oribatid mite fauna regarding the 39 sites is high at both genera- (T=5.79 p<0.001) and species-level (T=3.75 p<0.001), indicating an insular rather than a continuous distribution of species and genera within the study area. For the interpretation of these results, the very low coverage of Oribatid mite sampling sites in the high Andes has to be taken into account. Only one sampling site >3000 m a.s.l., "San Antonio de los Cobres" (Hammer, 1958), is available between 20°S and 34°S, which represents a sampling gap of ca. 500 km in southern Bolivia or northern Chile and of ca. 1000km towards mid-Argentina and Chile. Therefore, the analysis of sampling sites, which are extremely scattered in this study, can reveal only a selective view of the Oribatid mite community.

In general, faunal and floral montane and peatland communities are known to be nested (Mumladze et al., 2013) and Oribatid mites have the potential to form a nested soil community as they have a relatively high passive (Karasawa et al., 2005; Lebedeva & Lebedev, 2007; Lehmitz et al., 2011, 2012) and active dispersal ability (Skubala, 1999; Skubala & Gulvik, 2005; Lindo & Winchester, 2009; Lehmitz et al., 2012). However, it is evident that Oribatid mite communities are not only shaped by their dispersal ability and random ecological drift (Rosindell et al., 2011); other possible factors have to be considered to explain the distinct nestedness of the high Andean Oribatid mite community.

In general, strong niche differentiation on a local scale, e.g. food resources (Caruso et al., 2012), climate, vegetation, land cover, soil and topography (Stein et al., 2014) can generate nested communities. Meanwhile, another phenomenon which can affect on species richness is ecological disturbance. A moderate ecological disturbance, i.e. neither at a high frequency which no species can survive, nor at a low frequency which lets single strong competitors dominate, can generate either high species richness or high heterogeneity between communities (Adams, 2009). In comparison to other ecosystems, species richness in the high Andes is low (Norton & Behan-Pelletier, 2009) leading to the assumption that high disturbance at high altitudes could have (partially) caused the measured high nestedness of the community. Additionally, the differential effect of post-glacial colonisation of previously uninhabited soils on the community has to be taken into account for large parts of the high Andean area (Mumladze et al., 2013). Overall, the factors responsible for shaping a local Oribatid mite community are still not well studied and remain enigmatic.

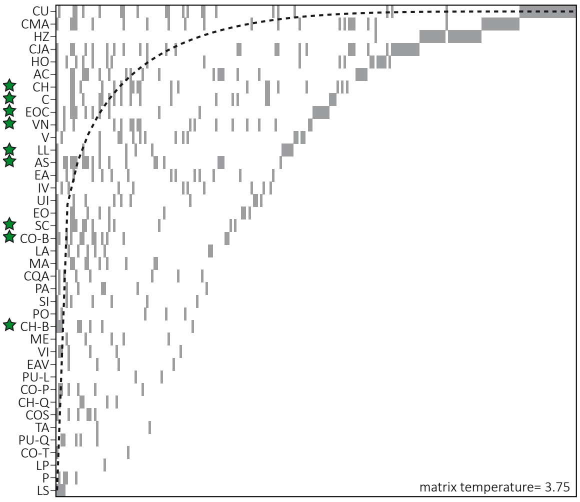


Figure 4.6 | Nestedness plot showing ranked Oribatid mite species (n=219) from 39 sites in the high Andes >3000 m a.s.l. and total nestedness. The green stars characterise the sampling site as a cushion peatland. Grey fields indicate presence; blank fields indicate absence of species; the dashed line represents the isocline of perfect order. Ranked configuration of species differs significantly (p<0.001) from random.

4.4.3 | Taxonomic diversity

The examination of the distribution areas of several Oribatid mite taxa reveals a biogeographic relationship between the grassland ecosystems of the Andean mountains, Tierra del Fuego and southern Patagonia and the South Atlantic Islands - Islas Malvinas/Falkland and South Georgia, and even New Zealand (Wallwork, 1972; Hammer & Wallwork, 1979; Stary & Block, 1996). These results can be verified by a taxonomic diversity analysis of the Oribatid mite inventories compared in this study, at least for the central and southern

Andes. Only two sampling sites show significantly different ($p<0.05$) taxonomic compositions (see Figure 4.7). Whereas the diverging composition of the sampling site "Cariquima" (Covarrubias, 2004a) may be associated with a low test accuracy at <10 species, the significantly different composition of the northernmost site "Cajanuma" (Illig et al., 2007) could indicate a transition of the Oribatid mite community between 4° and 7°S. Those latitudes are characterised by a distinct depression in the Andean mountains, named the "Huancabamba Depression", in which few peaks reach 3000 m a.s.l. This depression is known to be a biogeographic barrier for montane plant taxa (Weigend, 2002, 2004), reptiles and amphibians (Duellmann, 1979).

Another important feature at these latitudes is a shift in the precipitation regime from seasonal rain in the south to all-year precipitation in the north. This is reflected by a change in vegetation from Puna to Paramo ecosystems at approximately 8°S (Olson et al., 2001).

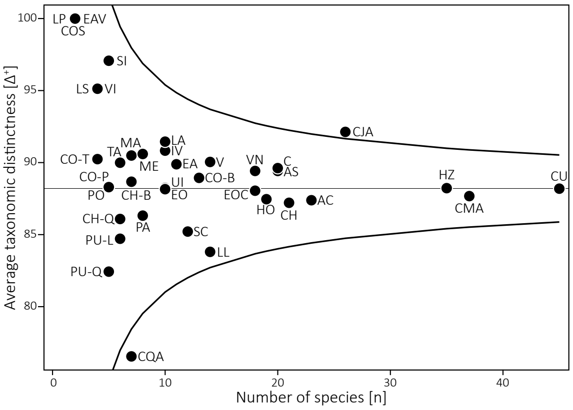


Figure 4.7 | Oribatid mites taxonomic diversity shown as average taxonomic distinctness (Δ^+) for species inventories from 39 sites in the high Andes >3000 m a.s.l.. A 95% probability funnel is indicated by thick lines and theoretical mean taxonomic diversity for randomly selected subsets of the total 219 species.

4.5 | Conclusion

This study is a first attempt to derive biogeographic patterns for the Oribatid mite community of the high Andes from a very scattered sampling site distribution and, in comparison to other studies, a small database. However, with careful interpretation of the analyses results, some noteworthy aspects become evident:

The Oribatid mite community of the high Andes is distinctly nested which is often found in montane and/or peatland communities. The nestedness could be ascribed to great heterogeneity on a local scale, most likely fostered by strong niche differentiation, the impact of disturbance and, in terms of geological times, the young age of high-Andean ecosystems, which emerged through deglaciation of the high altitudes after the Last Glacial Maximum. From the data of the high Andes, a community shift is evident between 4°S-7°S. Nevertheless only one sampling site is available from the high Andes north of the transition. Hence, further sampling effort is needed to confirm this finding.

In contrast to the azonal occurrence of cushion peatlands in the high Andes, this study gives evidence that the peatland-inhabiting Oribatid mite community shows a greater zonal character and is (at least partly) influenced by the ecoregion that the peatland is situated in.

5 | Chapter V - Ecology

Ecology of edaphic Oribatid mites and Chironomids from a high-Andean cushion peatland and their potential as soil condition indicators

Abstract

The soil conditions (water content, C/N ratios, conductivity, pH and element content) of 38 samples from five ecotopes of a high-Andean cushion peatland in southern Peru (14°S) have been analysed. The data show the ecological heterogeneity of the peatland with strong variations in nutrient availability (very poorly oligotrophic - strongly mesotrophic), soil wetness (dry - saturated) and element content (e.g. in As, Cr, Cu, Fe, K, Pb and Rb). On the basis of these results, an advanced succession model is proposed for the different peatland ecotopes.

Furthermore, the geochemical data were used to reveal microhabitat descriptions and the soil condition indicator potential of the Oribatid mite (17 taxa) and Chironomid (11 taxa) communities. The Oribatid mite community showed monotonous responses to N and Zr content, skewed unimodal responses to Cu, Rb, and Ti and bimodal responses to Fe, As, Zn, Ca, Pb, water content and pH, of which iron and copper content had the highest impact. At the species level, seven indicator taxa were assessed: i) *Malaconothrus monodactylus*, *Scheloribates pallidulus*, *Nanhermannia elegantissima*, *Tectocepheus* sp., *Jugatala montana* and *J. armata* indicate low soil wetness <58%, and; ii) *Neoamerioppia notata* indicates high soil wetness >73%.

The Chironomid community showed a monotonous response to Fe, a symmetric unimodal response to Rb and bimodal responses to C, Cu, N, As, Zn, Pb, pH, and conductivity, of which the carbon and nitrogen content had the highest impact. At the genus level, five indicator taxa were revealed: i) *Cricotopus/Paratrichocladius* type II, *Parochlus*, *Apsectrotanypus/Alotanypus* and *Parametriocnemus/Paraphaenocladius* indicate soil wetness of 80-81%, and; ii) *Limnophyes/Paralimnophyes* indicates soil wetness >81%.

5.1 | Introduction

Soils are sometimes called the 'poor man's tropical rainforest' (Giller, 1996), which insinuates the extreme high biodiversity that the majority of soils host. This high biodiversity has a key influence on the overall performance of ecosystems and therefore also on ecosystem services on which society depends, such as decomposition or nutrient cycling and retention (Wagg et al., 2014). The belowground diversity is mostly attributable to the vast amount of nested ecological habitats derived by the complex physical and chemical nature, the huge surface area and variable availability of organic materials, food or water within the soil (Giller, 1996; Orgiazzi et al., 2016). Concerning these soil conditions, which dynamically shape the environments for the diverse soil communities, research is still lacking but of great importance for understanding future challenges such as the impact of biodiversity loss through climate change or environmental pollution (Orgiazzi et al., 2016).

This investigation is a first attempt to provide information on the soil environments of a high-Andean cushion peatland, which have never been investigated. Until recently, solely water chemistry data from the peatland-supplying springs have been used for research on peatland classification, modelling of plant species range and floral β-diversity (Ruthsatz, 1993; Coronel et al., 2004; Figueroa & Covarrubias, 2005; Squeo et al., 2006; Ruthsatz, 2008; Cooper et al., 2010; Ruthsatz, 2012).

Additionally, this investigation aims to investigate small-scale microhabitat differentiation rather than coherences over a wide area, which has been nearly exclusively the focus of ecosystem research on high-Andean cushion peatlands so far. Only Coronel et al. (2004) report a high variation., e.g. in water chemistry or aquatic flora, between different pools of the same peatland. However, the geochemistry and soil dwelling faunal variability within one peatland have never been assessed. This is especially the case for the soil mesofauna, on which this investigation focusses, with local variability and microhabitat differentiation being highly influential on α-diversity and community structure (Hansen & Coleman, 1998; Maraun & Scheu, 2000).

5.1.1 | Research on the ecology of Oribatid mites

Oribatid mites are known to be controlled by various environmental drivers such as soil humidity (Borcard & Legendre, 1994; Gao et al., 2016) but with complex responses (O'Lear & Blair, 1999), C/N ratios, concentration of organic content and pH (Straalen & Verhoef, 1997; Haq, 2001; Gao et al., 2014; Zhang et al., 2015), soil temperature (Bokhorst et al., 2008) and heavy metal concentration of Cd, Cu, Zn and Pb (Seniczak et al., 2005, 2009; Owojori & Sicciliano, 2012). Indeed, the potential of Oribatid mites as indicators for soil conditions is broadly discussed and developed in different contexts (Lebrun & Straalen, 1995; Straalen & Verhoef, 1997; van Straalen, 1998; Ruf et al., 2003; Gulvik, 2007; Gergócs & Hufnagel, 2009; Bedano et al., 2011; Shimano, 2011).

However, explanations for patterns in Oribatid mite abundances, diversity or community composition are missing and further research should be carried out to improve the knowledge on species autecology (Maraun & Scheu, 2000). Additionally, a usable indicator system needs to be adapted to each environment. In this context, this investigation is the first approach to provide ecological data for the community of a high-Andean cushion peatland and to develop an indicator system for this ecosystem.

5.1.2 | Research on the ecology of the Chironomidae

Similarly, Chironomids are known to respond to a variety of environmental drivers on a very local scale or up to continental scales, which include precipitation (Matthews-Bird et al., 2016), temperature (Jacobsen et al., 1997; Jacobsen, 2004; Eggermont & Heiri, 2011; Matthews-Bird et al., 2016), salinity (Eggermont et al., 2006), oxygen availability and phosphorus content (Brooks et al., 2001), pH (Lebrun & Straalen, 1995; Nyman et al., 2005), substrate type (Entrekin et al., 2007) or vegetation (Brodersen et al., 2001). However, most of these investigations focus on lake and river ecosystems. Much rarer are ecological studies on wetland, peatland or soil-dwelling Chironomids (Bendell-Young et al., 1994; Woodcock et al., 2005; Carew et al., 2007; King & Richardson, 2007; Liston et al., 2008).

From the central Andes, ecological information on Chironomids is available from lakes and streams (Acosta Rivas, 2009; Acosta & Prat, 2010; Matthews-Bird et al., 2016), but additional autecology data are urgently needed, especially for the interpretation of palaeoenvironmental investigations (Matthews-Bird et al., 2016). Thus, many aspects of Chironomid ecology remain unknown and not a single ecological study on Chironomids from neotropical cushion peatlands exists. This investigation is the first attempt to understand the autecology of the Chironomids from a high-Andean cushion peatland.

The aim of this study is to show soil condition variability within different ecotopes of a single cushion peatland and on the basis of this, define microhabitats for soil-dwelling Oribatid mites and Chironomids. By using these data, environmental limits and indicator functions for single taxa are tried to be determined.

5.1.3 | Hypotheses

Considering the mentioned aims, the hypotheses of this investigation are:

- The Oribatid mite and Chironomid communities are associated with specific microhabitats, defined by geochemical soil parameters.
- Oribatid mite and Chironomid taxa can be used as significant soil condition indicators.

5.2 | Materials & Methods

5.2.1 | Sample set

In total, 38 (67 for water content analysis) soil samples from five different ecotopes of the Cerro Llamoca peatland (CLP) in southern Peru (14°S), covering each ecotope from the surface to maximal depth, were processed for geochemical analysis. For further information on the sedimentology, coring technique and sample conservation, see Chapter 3.2. For ecological analysis, the Oribatid mite and Chironomid abundance data from 41 samples of the same sampling set have been used. For the description of these data, see Chapter 3.3.

5.2.2 | Geochemical analyses

For the analysis of the water content, the thermogravimetric method by Topp et al. (2008) was performed. The sample water content [% H_2O of dry weight] was obtained after drying for at least 48 hours at 105°C in a well-ventilated oven with an accuracy of 0.1 mg using an ultra-fine scale, and noting the loss in weight. The measurements of carbon and nitrogen content were carried out at the Geobotany Lab, University of Trier. For preparation, the samples were dried at 105°C for at least 48 hours, subsequently freeze-dried, and milled with a high-speed grinder for 1 hour. Two portions of 8-30 mg, depending on the proposed carbon content of each sample, were placed in tin capsules and analysed with an Elementar Vario EL CHNOS. The two results obtained were used to calculate mean values only if the values did not differ more than 5%. The classification of trophic stages derived by C/N ratios follows Bock et al. (2007).

Table 5.1 | Classification of trophic stages by C/N ratio according to Bock et al. (2007)

C/N ratio	Classification	Description
> 40	oligotrophic	very poor
33 - 40		poor
26 - 33	mesotrophic	rather poor
20 - 26		medium
13 - 20	eutrophic	strong
10 - 13		rich
7 - 10	polytrophic	very rich
< 7		extremely rich

Table 5.2 | Classification of soil pH values according to Succow & Joosten (2001). The conversion between pH measured in KCl and H_2O follows Bock et al. (2007)

pH(KCl)-value	pH(H_2O)-value	Classification	Description
< 2.4	< 2.0	acidic	extremely acidic
2.4 - 3.2	2.0 - 2.7		very strongly acidic
3.2 - 4.0	2.7 - 3.4		strongly acidic
4.0 - 4.8	3.4 - 4.0		moderately acidic
4.8 - 5.6	4.0 - 4.7	subneutral	slightly acidic
5.6 - 6.4	4.7 - 5.4		very slightly acidic
6.4 - 7.2	5.4 - 6.0	alkaline	neutral
> 7.2	> 6.0		basic

The pH-values [$-\log_{10}(H^+)$] and conductivity [µS cm^{-1}] were analysed at the Physical Geography Lab, University of Cologne. The soil solution was prepared with a fixed sample volume and 2.5 x double-distilled water. The solution was mixed in a horizontal shaker for two hours and measured with a WTW inoLab pH/ION/Cond 750, connected to a SenTix 81 electrode for pH and a TetraCon 325 electrode for conductivity. Every sample was analysed twice with a constant delay and was arithmetically averaged (Hendershot & Lalande, 2008; Miller & Curtin, 2008).

The classification of pH-values follows the scheme of Succow & Joosten (2001) for peatland ecosystems. The $pH(H_2O)$-value was calculated using the pedotransfer function ($pH(KCl)= 0.87\ pH(H_2O)$, $R^2=0.93$) derived from the global dataset (Bock et al., 2007).

5.2.3 | Element content analysis

To obtain element contents of the soil samples, X-ray fluorescence spectroscopy was performed at the Physical Geography Lab, University of Cologne, using a Niton XL3t pXRF-Analyser. For the measurements, freeze-dried and fine-ground sample material was used. The powder was pressed into circular sleeves of 1 cm diameter under high pressure, using a compactor piston in order to ensure a plain surface for accurate measurements. Every sample was measured at least twice to achieve an accuracy of <5% relative standard deviation between the measurements. For all non-diverging measurements, the mean values were calculated. Data by Knight et al. (2013) have been used to calculate post-measurement calibration and to assess test accuracy and limitations (denoted in Appendix 8). According to these data, the measurements are only reliable for 18 elements, of which Sr, Zn, Ca, Fe, K, Mn, Rb, Zr, As, Cu, Ba, Ti, Cr and Pb are of importance for this investigation.

5.2.4 | Numerical analyses

All numerical analyses have been performed in R ver. 3.1.2 (R Core Team, 2014). For trend analysis of the geochemical data, the Jonckheere-Terpstra test was used. The collinearity analysis of the environmental data was performed using the variance inflation factor (VIF) and procedures for pairwise comparisons by Zuur et al. (2009). Community changes in relation to environmental factors were determined with a general additive model using cubic splines, obtained by the mgcv package ver. 1.8-6 (Wood, 2015). The type of community response was evaluated with the procedures of the eHOF package ver. 1.7 (Jansen & Oksanen, 2016).

Because normality of the Oribatid mite and Chironomid abundance data was denied in a Shapiro-Wilk test ($p<0.001$), the data were transformed using the "Hellinger" method (Legendre & Gallagher, 2001), before calculating the multivariate regression tree with the mvpart package ver. 1.6-2 (De'ath, 2014). Optimal tree size was determined with the "1-SE rule" by Breimann et al. (1984) after 100 cross-validations. Indicator species analysis was carried out with the Indicspecies package ver. 1.7.1 (De Caceres & Legendre, 2009). Cluster analysis and ordination were performed with the Vegan package ver. 2.2.1 (Oksanen et al., 2015). The depth zonation with constrained hierarchical clustering (CONISS), including significance testing with the 'broken stick model', were achieved with the Rioja package ver. 0.9-5 (Juggins, 2015).

5.3 | Results

5.3.1 | Geochemical description of the peatland's ecotopes

5.3.1.1 | Analysis of inter-ecotope soil parameter variability

The **water content**, with a combined mean of 66.8% (min.=12.4%, max.=88.6%, *SD*=23.3) varied significantly (H(4)= 58.88, p<0.001) within

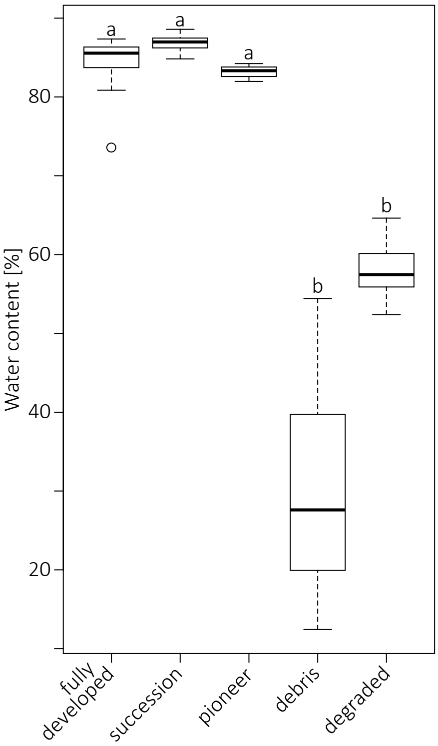


Figure 5.1 | Water contents of the ecotopes. Not significantly different ecotopes (post hoc Kruskal-Wallis comparisons: observed difference > critical difference, α= 0.05, corrected for the number of tests) are marked with the same letters. Solid lines mark median, and the circle an extreme value.

the investigated ecosystem (see Figure 5.1). The comparison with the median of 82.4% revealed the distinct skewness of the distribution, emphasising the overrepresentation of water content values >80%. A sample's depth had a significant effect on water content ($p<0.001$), but in comparison to the effect of its relationship with a distinct ecotope (β_i= 1.7-14.2), the impact of sample depth was very small (β_i= 0.05). Together, both factors explained 93% of the variability in the water content. Post hoc comparisons revealed that the water contents of the fully developed, the succession and the pioneer ecotopes (observed differences= 9.5-19.7) did not differ significantly ($\alpha=0.05$, corrected with the number of tests, critical differences= 20.3-24.2). The debris ecotope (observed difference= 29.2-49.0) and degraded ecotope (obs.diff.= 14.0-34.3) were not significantly different from each other, but both could be separated from the other three ecotopes (crit.diff.= 17.7-19.9).

In relation to all ecotopes, the average **pH-value** of 4.9 indicated very slightly acidic conditions but was significantly different between the ecotopes ($H(4)= 19.94$, $p<0.001$) (see Figure 5.2). Indeed, across the spectrum of all samples, the pH ranged from moderately acidic (pH 3.97) to basic (pH 6.13) conditions and did not change significantly with depth ($p=0.75$) or by affiliation to different ecotopes ($p=0.06$-0.62). The pH conditions of the fully developed ecotope (obs.diff.= 6.5-17.7) did not differ significantly from the succession and pioneer ecotopes (crit.diff.= 15.1-17.7), though markedly from the debris and degraded ecotopes (obs. diff.= 16.3-23.6; crit.diff.= 15.1-16.1). In contrast, the succession, pioneer, debris and degraded ecotopes did not differ from each other (obs.diff.= 1.6-17.0; crit.diff.= 14.7-18.3).

Overall, the trophic stages derived by the **C/N ratios** varied significantly ($H(4)= 29.9$, $p<0.001$) from very poor (6.98, oligotrophic) to extremely rich (62.64, polytrophic) within the heterogeneity of the peatland (see Figure 5.3). Additionally, the C/N ratios were significantly influenced by depth ($p<0.01$). Together, both factors explained 88% of C/N variability, but sample depth had a rather small impact on the C/N ratio (β_i= 0.2) in comparison to which ecotope the sample belonged (β_i= 0.7-13.6). The C/N ratio of the fully developed ecotope didn't differ significantly from the succession ecotope (obs.diff.= 10.6; crit.diff.= 13.9) but was different (obs.diff.= 14.5-27.3) from all other ecotopes (crit. diff.= 13.5-15.8). A comparison of the C/N ratios revealed neither a significant difference between the succession, pioneer and degraded ecotopes (obs. diff.= 3.9-13.1; crit.diff.= 15.6-17.8), nor between the pioneer, debris and degraded ecotope (obs. diff.= 3.5-12.8; crit.diff.= 15.2-17.8).

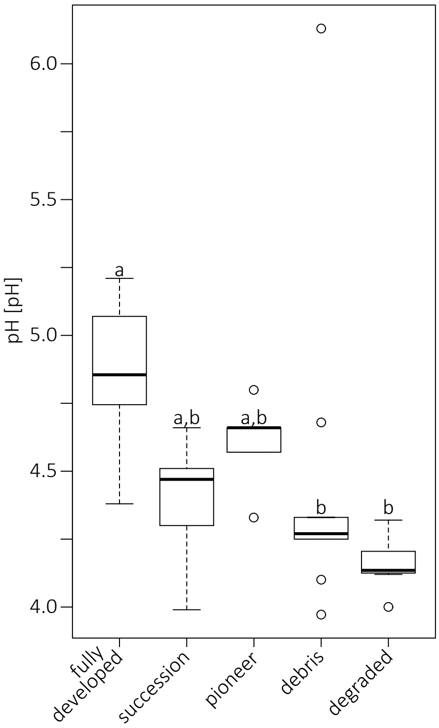


Figure 5.2 | Soil pH of the ecotopes. Symbols as in Figure 5.1

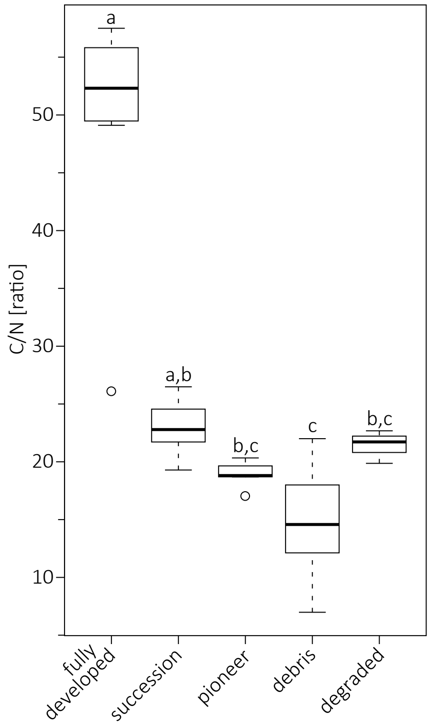


Figure 5.3 | C/N ratios of the ecotopes. Symbols as in Figure 5.1

In general, the **conductivity** showed a mean of 51.4 µS cm^{-1}, varying from 38.2-320.5 µS cm^{-1} between the ecotopes (see Figure 5.4). A Kruskal-Wallis test revealed a significant difference in the conductivity of the peatland soils (H(4)= 9.58, p=0.048), but corrected post-hoc comparisons did not confirm these findings and showed no significant differences between the ecotopes. However, the overall observed changes in total ion content could significantly be associated to a sample's affiliation only in the case of the succession ecotope ($p<0.05$). Sample depth had also a significant influence ($p<0.05$) but the effect was small (β_i= -0.13) in comparison to the effect of samples belonging to the succession ecotope (β_i= -6.5). Together, both factors explained 20% of the variation in conductivity.

5.3.2 | Soil characterisation by element contents

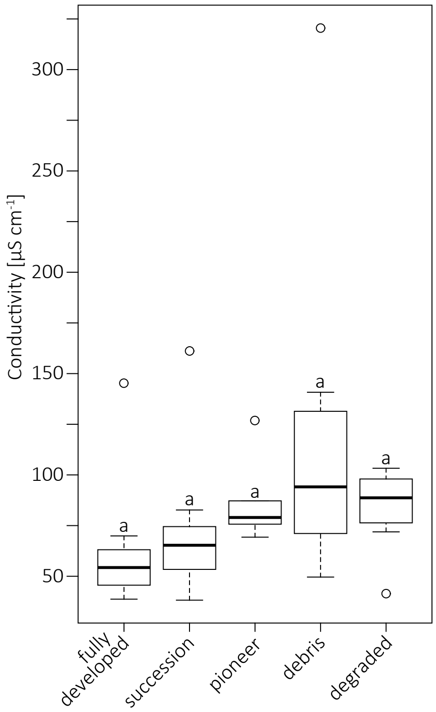


Figure 5.4 | Soil conductivity of the ecotopes. Symbols as in Figure 5.1

The **debris ecotope** was characterised by the highest amounts of strontium, potassium, rubidium, zirconium, barium and titanium. In particular, the contents of K (mean=50,000 ppm) and Rb (mean=171 ppm) were much higher in the soils of this ecotope in comparison with the other ecotopes. Conversely, the contents of calcium, copper, chromium, iron, arsenic, lead and manganese content were very low or undetectable.

The soils of the **pioneer ecotope** showed high amounts of arsenic, lead, potassium, rubidium, zirconium, copper and titanium, of which As (mean= 7200 ppm) and Pb (mean= 20 ppm) concentrations were the highest of those assessed in this investigation. Barium, manganese and zinc were not evident or showed very low content in this ecotope.
The **succession ecotope** revealed high content of arsenic and copper. The measured Cu concentration (mean= 650 ppm) represented the highest value at the study site. In contrast, strontium, zinc, iron, barium, manganese and lead showed very low values or were not evident in the samples.
In the soils of the **degraded ecotope**, the concentrations of zinc, calcium and barium were high. In particular, Zn (mean= 56 ppm) and Ca (mean= 12,000 ppm) were notably more concentrated in this ecotope than in the other investigated ecotopes. Other elements such as potassium, arsenic, lead, titanium and manganese showed very low contents or were undetectable in the samples.
The fully **developed ecotope** showed the highest concentrations of iron (mean= 42,000 ppm), manganese (mean= 156 ppm) and chromium (mean= 121 ppm). Additionally, the contents of zinc and calcium were high. However, strontium, copper, titanium, barium and lead showed very low concentrations or were undetectable.

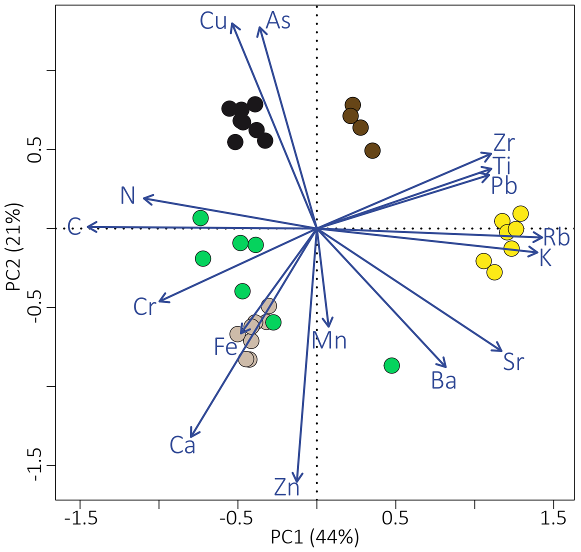


Figure 5.5 | Principal component analysis (PCA) of the soil element content of all investigated ecotopes of the CLP. The different ecotopes are indicated by colours (grey= degraded, yellow= debris, brown= pioneer, black= succession, green= fully developed)

5.3.3 | Analysis of intra-ecotope soil parameter variation

Debris ecotope

The debris ecotope (see Figure 5.6) showed the lowest **water content** (mean= 30.37%, min.= 12.4% at 1-2 cm depth) and the highest variability in water content (*SD*=13.0) of all the investigated ecotopes. Within the uppermost 8 cm of the sediment, the water content rose constantly from 14.1% to nearly 25%, before rapidly peaking at 9-10 cm with 54.4%. Downwards of 10 cm depth, the water content decreased slowly to 33.0%. The maximum water content in the debris soil (54.4% at 9-10 cm depth) confirmed that it had approximately the lowest water content compared to all the other ecotopes (52.4% in the degraded ecotope at 1-2 cm depth).

In the debris ecotope, the highest variability of acidity was also detected (*SD*=0.61). The **pH values** changed from moderately acidic (pH 3.97) to basic (pH 6.13) conditions within the core. The maximum pH of 6.13 was found in the uppermost layer, but it decreased very rapidly to 4.68 at 1.5 cm depth. Further down, the pH decreased slightly more to the minimum of pH 3.97 at 14.5 cm depth. Additionally, the debris ecotope showed the highest **conductivity** (mean= 118 µS cm^{-1}) and the highest variability (*SD*=76.9) of all investigated ecotopes. The highest conductivity was found in the top layer (0-1 cm) with 320.5 µS cm^{-1}. Further down, the values declined first rapidly to 140.8 µS cm^{-1} at 1.5 cm depth, and subsequently more gradually to 70.7 µS cm^{-1} towards the bottom of the core.

With an average of 14.51, the debris ecotope displayed the narrowest **C/N** ratios of all the investigated ecotopes and a medium variability (*SD*=4.66). The measured ratio indicated a high availability

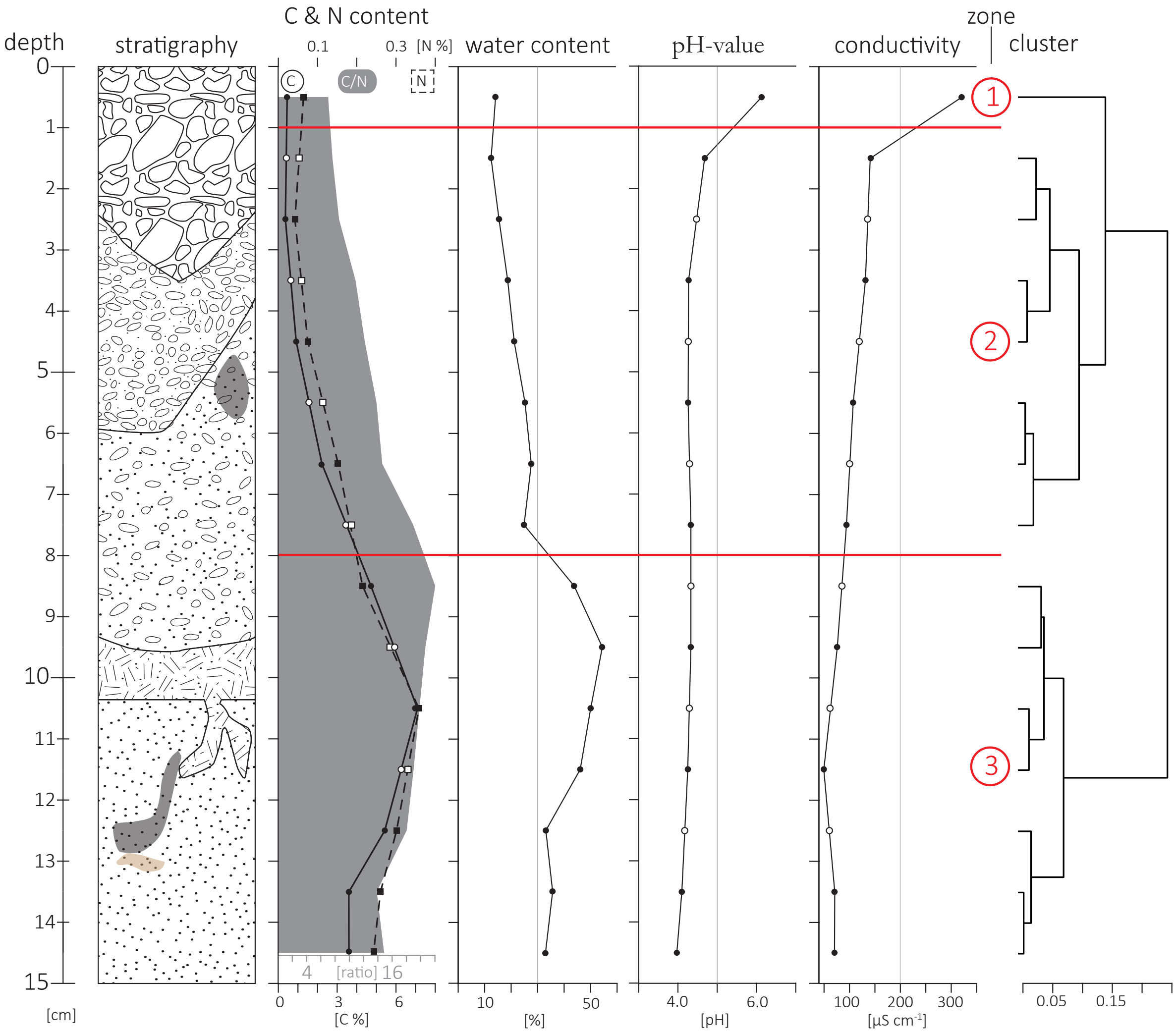


Figure 5.6 | Soil condition variations in the debris ecotope. The stratigraphy refers to Chapter 3.3.1. The depth zonation was achieved using the CONISS method.

of nutrients in the soil (eutrophic). From the uppermost layer, the C/N ratios increased constantly from 6.98 to 22.0 at 8.5 cm depth. Subsequently, until the bottom of the core, the C/N ratios decreased again to 14.83. The soil layers from 0 to 3.5 cm depth could be characterised as very rich in nutrients (polytrophic), whereas from 4.5 to 7.5 cm and from 10.5 to 14.5 cm, the C/N ratios indicated eutrophic conditions and from 8.5 to 9.5 cm mesotrophic conditions occurred.

Three significantly different **depth zones** could be identified in the debris ecotope. The top layer (0-1 cm) was characterised by high conductivity, high pH and low water content and C/N ratios. The rapid decrease in conductivity and pH marked the second zone from 1-8 cm, which showed slightly increasing C/N ratios and water content, accompanied by further decreasing pH and conductivity values. The last zone, ranging from 8-15 cm was characterised by first rapidly increasing and subsequently stable C/N ratios and water content, and slightly decreasing pH and conductivity.

Degraded ecotope

For the degraded ecotope (see Figure 5.7), an average **water content** of 57.95%, which represented the second lowest value, and a medium variability (*SD*=3.1) were measured. Within the stratigraphy, the water content of this ecotope revealed an increase with depth from ca. 54% to ca. 60%; however, some minor deviations from the main trend were noticeable. At the direct surface of the

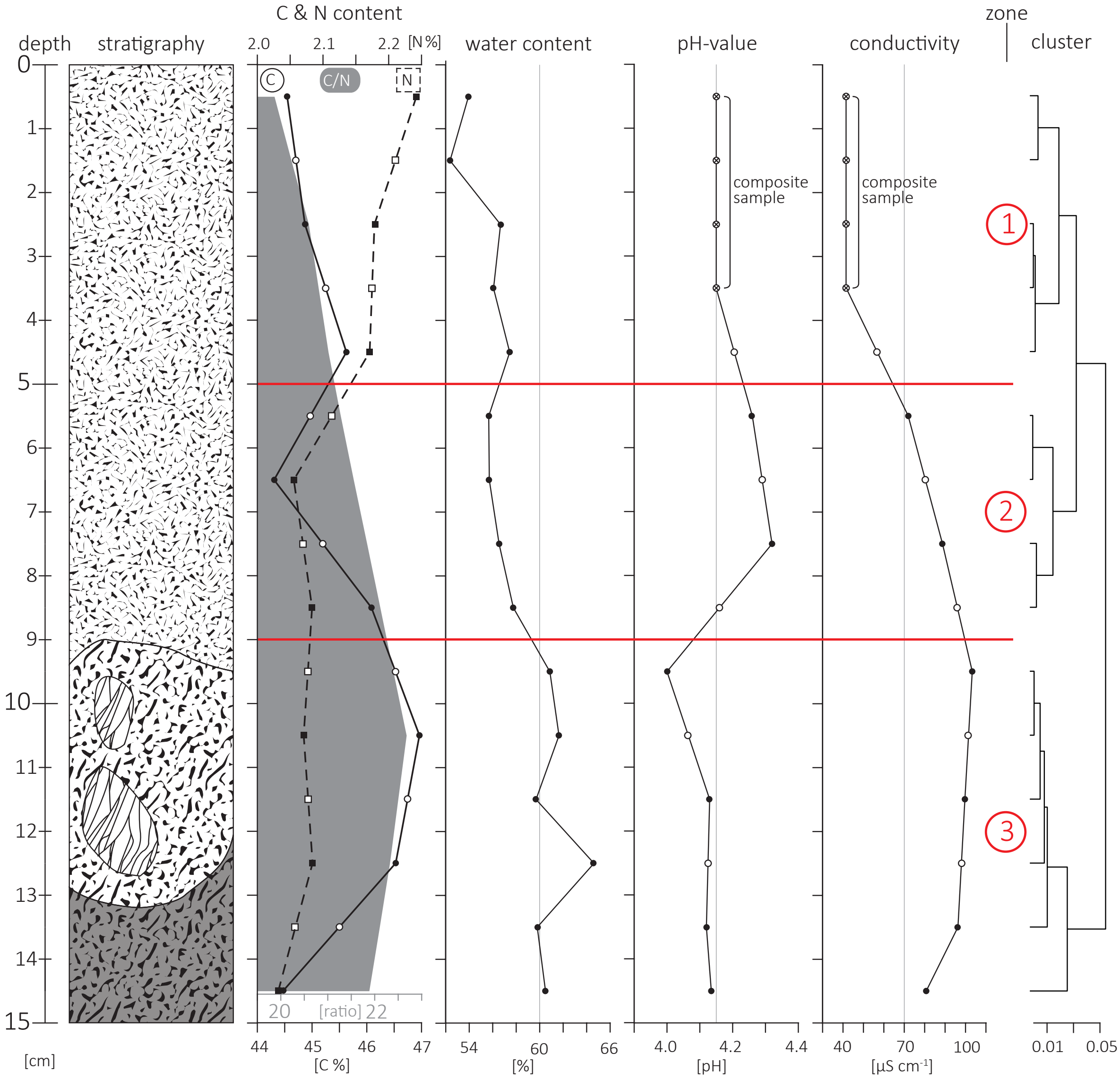


Figure 5.7 | Soil condition variations in the degraded ecotope. The stratigraphy refers to Chapter 3.3.1. The depth zonation was achieved using the CONISS method.

degraded ecotope, the water content was 53.9%, but dropped to a minimum of 52.4% at 1-2 cm depth. Further down, between 2-5 cm depth, the water content rose slightly to a stable level around 56.7%, before decreasing to 55.5% at 5-6 cm and again increasing to an average of 60.7% between 9-12 cm. At 12-13 cm depth, the water content ascended abruptly to the maximum value of 64.6%, whereupon the content declined again to a mean of 60.1% at the bottom of the core between 13-15 cm.

Investigating the **pH values**, the degraded ecotope appeared to be the most acidic of the sampling set (average of pH 4.16) and showed the smallest variability (*SD*=0.10). The core material of the uppermost 5 cm had to be consolidated for pH measurement due to insufficient quantity, which yielded a composite pH value of 4.15 for 0.5-5.5 cm depth. Further down, the pH increased slightly to 4.32 at 8.5 cm before decreasing to 4.0 at 9.5 cm, and plateaued at pH 4.12-4.14 from 11.5 to 14.5 cm depth. In general, this ecotope could be characterised as slightly acidic.

The degraded ecotope showed very stable trophic conditions (*SD*=0.89) with an average **C/N** ratio of 21.51, which indicated a medium nutrient availability (mesotrophic). From the uppermost layer, the C/N ratios increased constantly from 19.87 to 22.68 at 10.5 cm depth. Subsequently, until the bottom of the core, the C/N ratios decreased again to 21.89. Additionally, this ecotope showed a medium **conductivity** (average of 83.16 µS cm^{-1}) with a very low variability (*SD*=19.82). As for investigating pH, the soil of the uppermost 5 cm had to be consolidated for conductivity measurement due to insufficient sample volume. The composite sample showed a conductivity of 41.5 µS cm^{-1}. From 4.5 cm downwards, the values increased to a maximum of 103.3 µS cm^{-1} at 9.5 cm before they decreased again towards 14.5 cm depth with 80.8 µS cm^{-1}.

The soil core of the degraded ecotope was divided into three significant **depth zones**. The first zone (0-5 cm) was characterised by stable pH and conductivity values with a slightly fluctuating water content and increasing C/N ratio due to decreasing N content combined with rising C content. The second zone (5-9 cm) showed stable water content and fluctuating pH values, accompanied by increasing conductivity and C/N ratios. The C/N ratios were influenced by further decreasing N content and a fluctuating C content. The deepest zone (9-15 cm) was characterised by a fluctuation in the water content around a stable mean, stable conductivity and pH values, and by peaking and subsequently decreasing C/N ratios, could be associated with a strongly changing C content.

Pioneer ecotope

In the pioneer ecotope (see Figure 5.8), the **water content** was high (mean= 83.21%) and showed very little variability (*SD*=0.74). On average, the

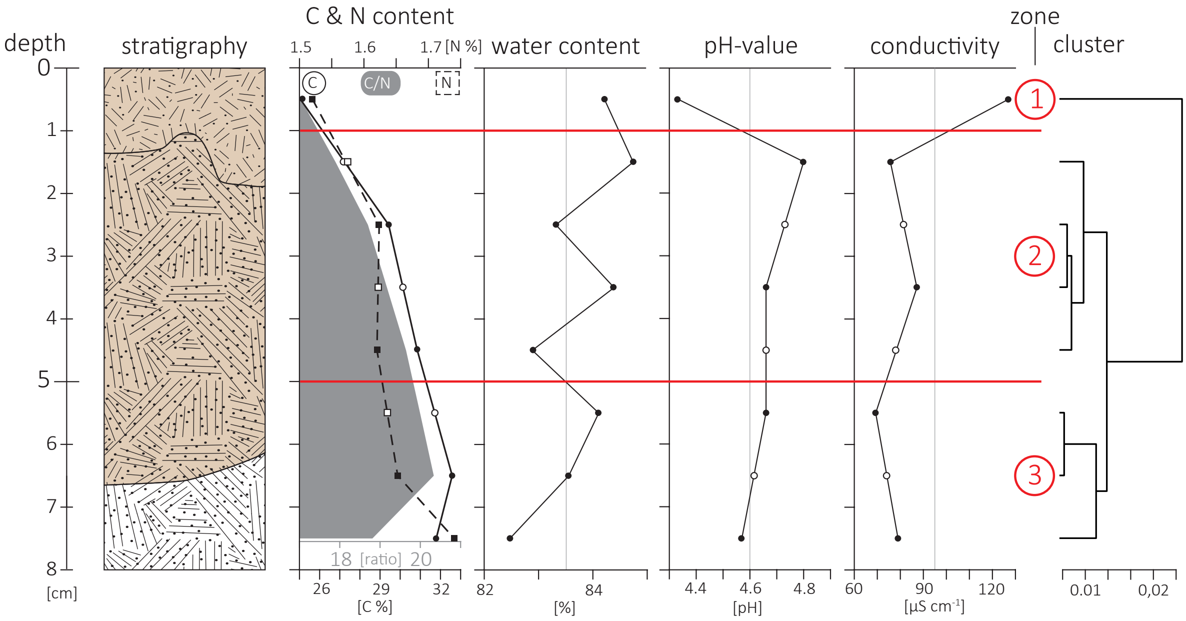


Figure 5.8 | Soil condition variations in the pioneer ecotope. The stratigraphy refers to Chapter 3.3.1. The depth zonation was achieved using the CONISS method.

water content decreased very slightly from the surface to the bottom of the core, changing from 83.7% to 81.9%, with three peaks at 1-2 cm, 3-4 cm and 5-6 cm (84.2%, 83.9% and 83.6%) and two local minima in between at 2-3 cm and 4-5 cm (82.8% and 82.4%). The pioneer ecotope showed also little variability in **pH** (*SD*=0.16) and represents slightly acidic conditions (average pH 4.6). Within the uppermost centimetre, the pH rose from slightly acidic to very slightly acidic conditions, with values increasing from 4.3 to 4.8. Below 1.5 cm depth, the pH decreased constantly and attains 4.57 at 7.5 cm.

The **C/N ratios** were very consistent in this ecotope (*SD*=1.11). They only increased evenly from 17.0 at the top to 20.3 at 6 cm depth and decreased slightly to 18.8 towards 7 cm depth. With a mean of 18.91, this part of the peatland could be characterised as a strong eutrophic environment. The soil of the pioneer ecotope showed a medium **conductivity** (mean of 87.6 µS cm^{-1}), which was very stable in the 8 cm core (*SD*=20.45). In the top layer, the conductivity decreased rapidly from 126.9 to 75.7 µS cm^{-1} at 1.5 cm depth. Further downwards to 7.5 cm, the values were stable between 69.3-79.0 µS cm^{-1}.

Three significantly different **depth zones** were separated in this core. The first zone, ranging from 0-1 cm was characterised by a strongly decreasing conductivity combined with an increasing pH. The second zone (1-5 cm) showed increasing C/N ratios, stable conductivity and slightly decreasing pH-values and water content. The deepest zone (5-7.5 cm) was marked first by rising and then falling C/N ratios, combined with decreasing water content, and stable pH and conductivity conditions.

Succession ecotope

With a mean of 86.9%, the succession ecotope (see Figure 5.9) featured the highest **water con-**

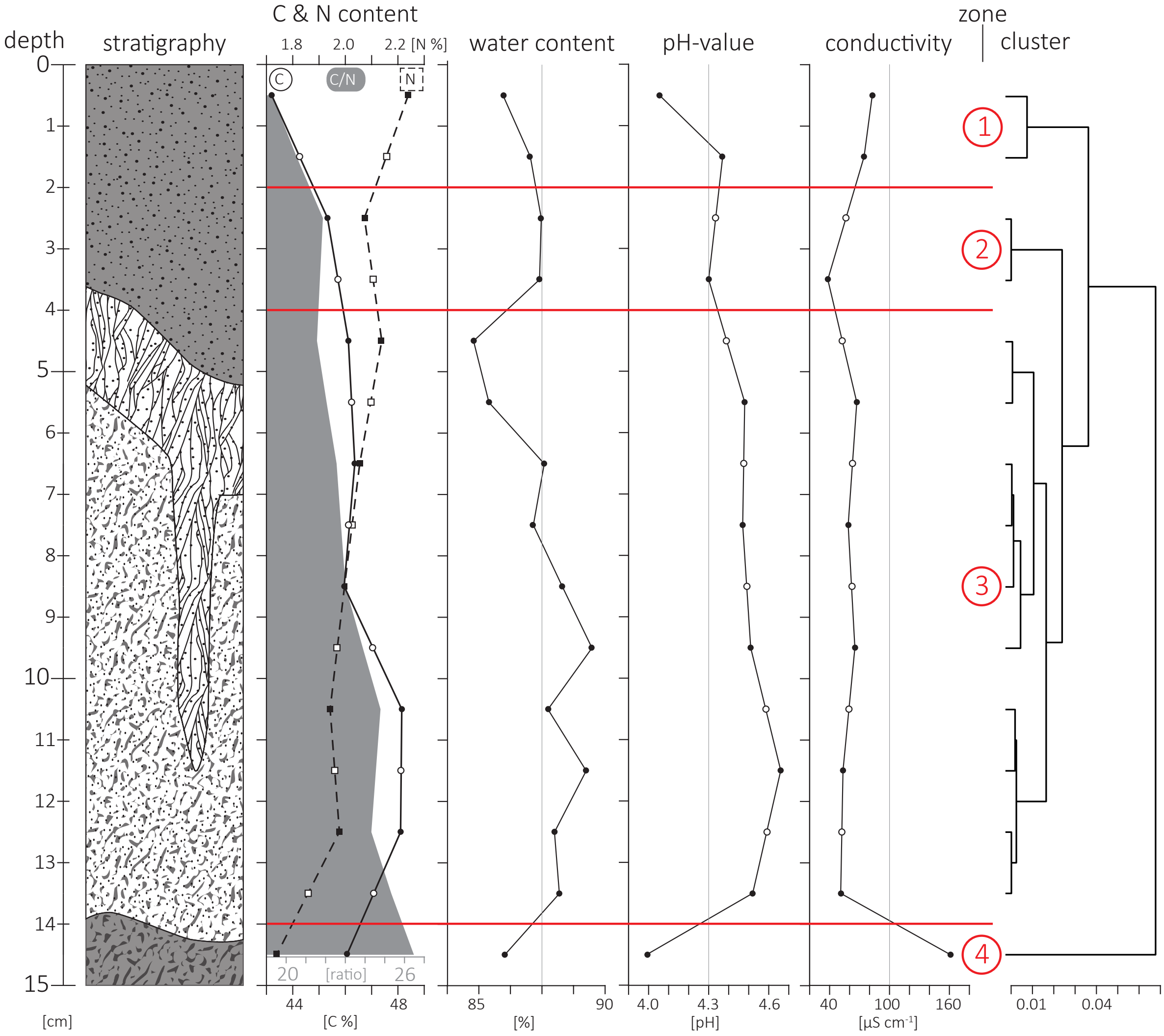


Figure 5.9 | Soil condition variations in the succession ecotope. The stratigraphy refers to Chapter 3.3.1. The depth zonation was achieved using the CONISS method.

tent within the Cerro Llamoca peatland, and little variability in this parameter (*SD*=1.02). In the uppermost 4 cm, the water content slightly rose from 85.8% to 86.9%, followed by a minor decrease to the minimum values at 4-6 cm depth, but still with an average of 85.1%. Further down, at 6-7 cm the water content increased again to the previous level with 87.1%. Within the next six centimetres, the water content fluctuated around an average of 87.5%, before a minor reduction to 85.8% at the bottom of the core.

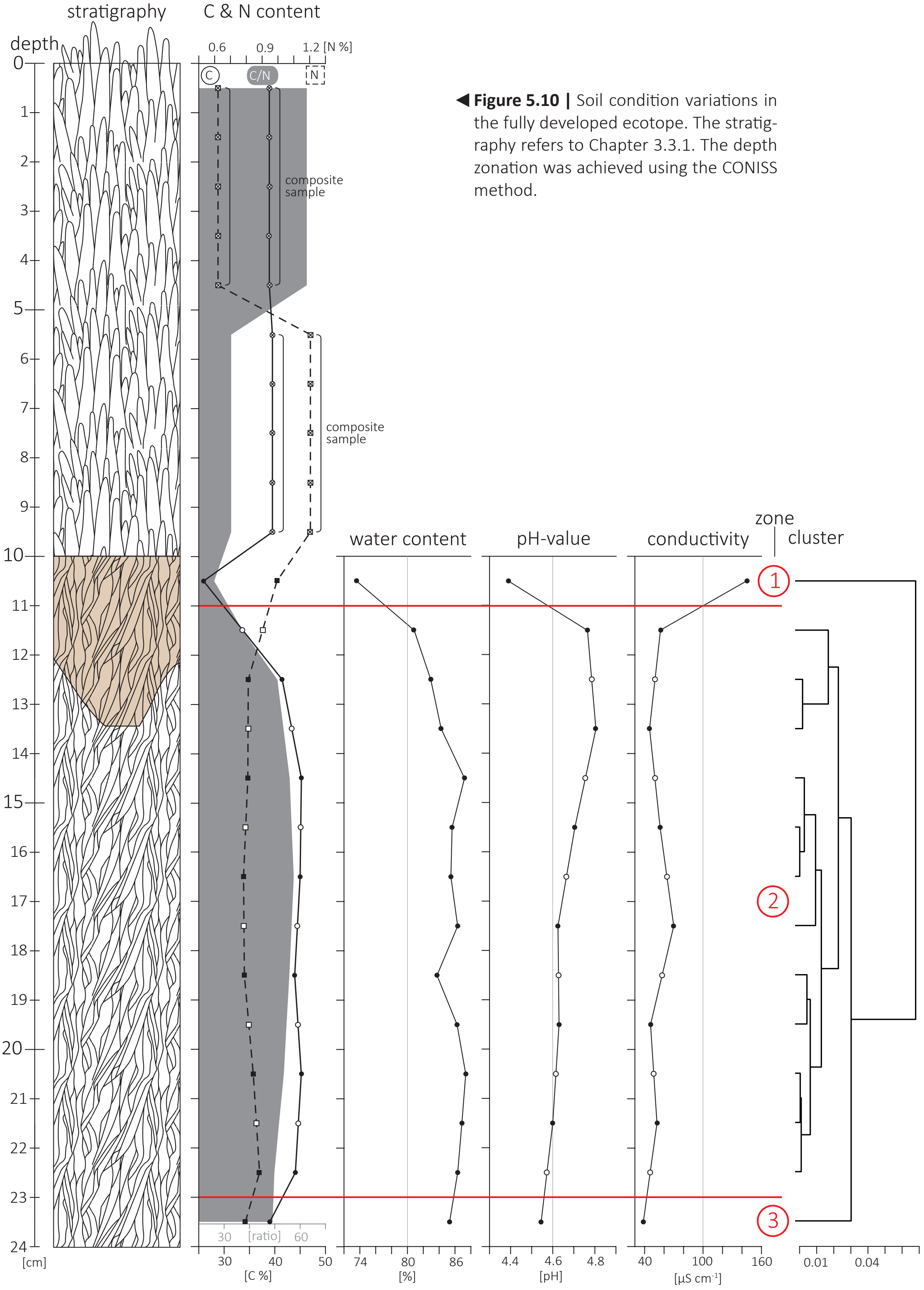
An average **pH value** of 4.37 characterised the succession ecotope as slightly acidic. In the core, the pH increased rapidly from 4.06 at 0.5 cm to 4.37 at 1.5 cm. Further down, the pH increased constantly but only slightly to a value of 4.66 at 11.5 cm depth. From 11.5 to 14.5 cm depth, the pH decreased to 3.99, which represented moderately acidic conditions. The variability of the **C/N ratios** was quite low (*SD*=2.0), but increased from 19.3 to 26.5 from the top to the bottom of the core. Regarding this change with depth, the surface of the ecotope (0-1 cm) could be characterised as strongly eutrophic in comparison to the remaining 14 cm towards the bottom of the core with a mean C/N ratio of 22.9, which represented medium mesotrophic conditions. The **conductivity** of the succession ecotope was the smallest (mean= 72.46 µS cm^{-1}) of all the sampled ecotopes. The values slightly decreased from the top of the core to 13.5 cm depth, ranging from 82.7 µS cm^{-1} to 51.1 µS cm^{-1}. At the bottom of the core, at 14.5 cm depth the conductivity peaked rapidly to 161.2 µS cm^{-1}.

Fully developed ecotope

In the fully developed ecotope (see Figure 5.10), the **water content** was high (mean 84.44%) with a medium variability (*SD*=3.48). Due to the very small sample size, measurement of water content was not possible between 0-10 cm. Between 10-11 cm, the sediment showed the minimum water content of 73.6%, before it increased to the overall mean of ca. 84% at 13-14 cm depth. From 14-24 cm downwards, the water content remained largely constant with an average of 85.9%, except for one distinct decline to 83.7% at 18-19 cm depth. The fully developed ecotope was determined by very slightly acidic **pH** conditions (average of pH 4.87). Because of too little sample material, pH measurement was not possible for the top 0-10 cm. Between 10.5 to 11.5 cm depth, the pH increased rapidly from 4.38 to 5.13, and reached a maximum of 5.21 at 13.5 cm depth, then decreased constantly to pH 4.69 at the bottom of the core.

The fully developed ecotope showed by far the highest **C/N ratio** with a mean of 49.4, but displayed also the highest variability (*SD*=10.8). The C/N ratios were very high from 0-5 cm reaching 62.6, which indicated very poor oligotrophic conditions. Between 5 and 11 cm depth, the C/N ratios decreased to 26.1 (mesotrophic trophic conditions), before increasing rapidly at 11 cm depth and fluctuating around 53 with a maximum of 57.5. The bottom part of the core from 11 to 24 cm depth could also be characterised by very poor oligotrophic conditions. The **conductivity** in this ecotope showed the lowest values (mean of 63.74 µS cm^{-1}) compared to all other sample sets. The conductivity decreased strongly from 145.2 to 56.3 µS cm^{-1} between 10.5 and 11.5 cm depth. From 11.5 cm to the bottom of the core at 23.5 cm, the values remained stable around an average of 52.1 µS cm^{-1} with a local peak of 69.9 µS cm^{-1} at 17.5 cm depth.

The interval between 10-24 cm depth of the fully developed ecotope could be divided into three significant **depth zones**. The first zone (10-11 cm) was characterised by strongly increasing C/N ratios, water content, pH-values and a decreasing conductivity. Further down, a zone ranging from 11-23 cm showed stable C/N ratios and conductivity conditions, whereas the water content was slightly increased and the pH values decrease. A third zone (23-24 cm) was marked by synchronously decreasing N and C content.



◀ **Figure 5.10 |** Soil condition variations in the fully developed ecotope. The stratigraphy refers to Chapter 3.3.1. The depth zonation was achieved using the CONISS method.

5.3.4 | Geochemical classification of peatland ecotopes and microhabitat separation

The revealed soil conditions of the five investigated ecotopes are summarised in Table 5.3.

Table 5.3 | Summary of the heterogeneity of soil conditions in the five ecotopes of the CLP

	Trophic stage	Acidity	Wetness
Debris ecotope	strongly eutrophic	slightly acidic (4.48)	dry (30.3%)
Degraded ecotope	medium mesotrophic	slightly acidic (4.16)	semidry (57.9%)
Pioneer ecotope	strongly eutrophic	slightly acidic (4.6)	saturated (83.3%)
Succession ecotope	medium mesotrophic	slightly acidic (4.37)	saturated (86.8%)
Fully developed ecotope	very poorly oligotrophic	very slightly acidic (4.87)	saturated (84.4%)

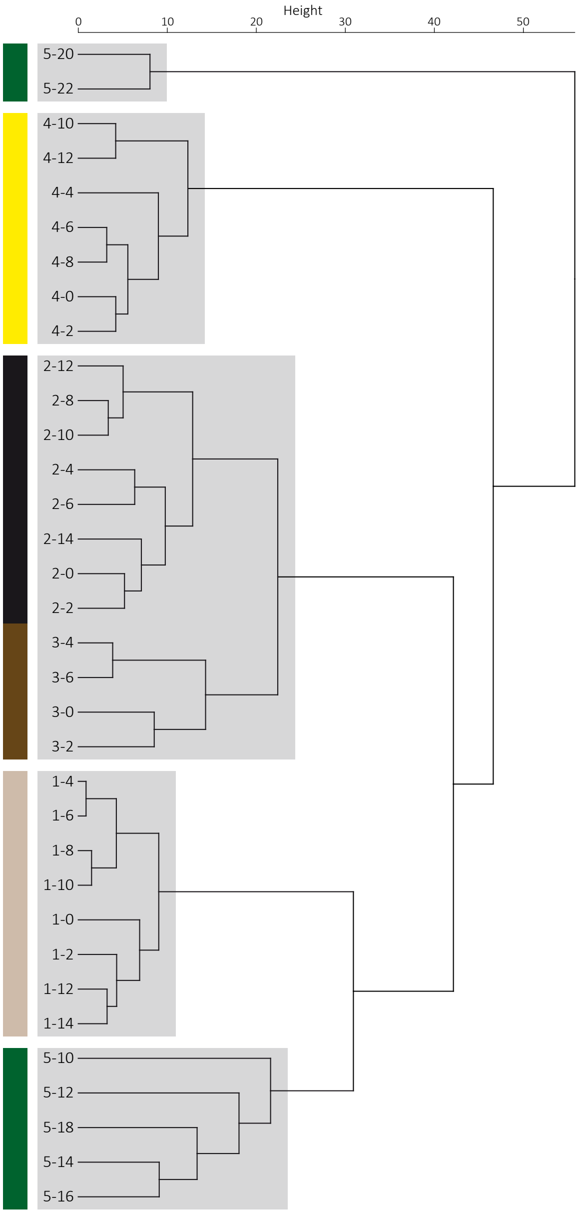


Figure 5.11 | Cluster analysis of the complete geochemical dataset with water content, conductivity, C/N ratios, pH and all element contents. The analysis is based on Manhattan dissimilarities and uses the average linkage clustering method. The grey frames show the significant cluster solution derived by 500 permutations and the coloured sidebar shows sample affiliation to ecotopes (grey= degraded, yellow= debris, brown= pioneer, black= succession, green= fully developed). The agglomerative coefficient of the tree is 0.91.

The average linkage cluster analysis, tested on significance by 500 permutations, of the entire geochemical dataset (Water content, conductivity, C/N ratios and the contents of Sr, Zn, Ca, Fe, K, Mn, Rb, Zr, As, Cu, Ba, Ti, Cr and Pb) grouped the samples in five clusters (see Figure 5.11). In this significant cluster solution, all samples retrieved from the same ecotopes were placed in the same cluster with two exceptions: the deepest samples from the fully developed ecotope (20-21 cm and 22-23 cm) were out-grouped and placed in a separate cluster, while all samples of the pioneer and the succession ecotopes were clustered together. The clustering process put the clusters in a specific order. In the first cluster, the two deepest samples of the fully developed ecotope were identified, followed by the debris ecotope samples. The third cluster was the combined cluster of the succession and pioneer ecotopes. The forth cluster contained the remaining samples of the fully developed ecotope, while the last contained all samples of the degraded ecotope.

To verify the results of the cluster analysis, a non-metric multidimensional scaling (NMDS) analyses was performed using the complete geochemical dataset. The results are depicted in Figure 5.12. It shows the close allocation of the samples from each ecotope. The only anomaly was one sample (10-11 cm depth) of the fully developed ecotope, which was more closely related to samples from the pioneer and the debris ecotopes than to the other samples of its own ecotope. This feature of the individual sample was mainly attributable to a diverging high conductivity value, which resulted in an allocation closer to the conductivity variable centrum in ordination space. A division of the total sample set as belonging to the different ecotopes was highly supported by a MANOVA analysis using a Pillai-Bartlett trace (V=0.99, F(1, 18)= 88.3, p<0.001).

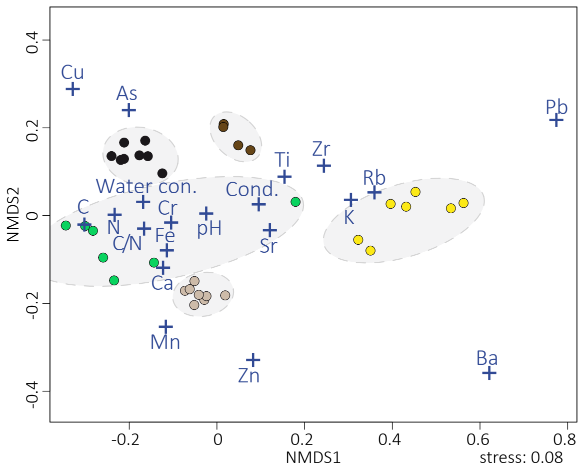


Figure 5.12 | Non-metric multidimensional scaling (NMDS) analysis of the complete geochemical dataset with water content, conductivity, C/N ratios, pH and all element contents. Samples are shown as circles with different colours indicating the affiliation to the ecotopes (grey= degraded, yellow= debris, brown= pioneer, black= succession, green= fully developed). Grey areas divide the sample set in accordance to ecotope differentiation. This subdivision is highly supported by a Pillai-Bartlett trace MANOVA analysis, V=0.99, F(1, 18)= 88.3, p<0.001.

To conclude, the cluster arrangement and the NMDS results characterised the ecotopes, which were classified in the field by surface soil texture or vegetation, as significantly different microhabitats with different environments, shaped by diverging geochemical conditions. The results of these analyses verified the subdivision of the peatlands into different ecotopes and showed that the environmental heterogeneity within the peatland was (at least partly) captured by the derived samples.

5.4 | Discussion

The results presented in this study, are the first analysis of small-scale soil condition variability of a high-Andean cushion peatland. Based on these data, an ecological analysis of the peatland inhabiting Oribatid mite and Chironomid communities can be done. Certainly, some restrictions for further analysis have to be taken into account.

The results of the XRF spectrometry are taken as equivalents for element concentration in this study, because all possible techniques to ensure accurate measurements, (i.e. pre-treatment of samples to avoid wetness deviations, thorough mixing of soil components, provision of a very smooth impinging surface and post-measurement data calibration), were carefully followed. However, for the assessment of toxicity or element deficiencies, the test results are not adequate as they provide the total amount and do not quantify the plant- and animal-available concentrations of those elements. This availability depends on several other factors besides the total amount, such as the pH or the local redox potential (Alloway & Trevors, 2013).

Despite much evidence for the strong influence of physical disturbance on soil communities (Wardle, 2006; Cole et al., 2008), this impact has been discounted in this investigation, in order to focus on the influence of geochemical variables on soil-dwelling Oribatid mites and Chironomids. Nevertheless, there are some indications of disturbance in the data if the degraded ecotope is considered as a disturbed soil. However, closer investigations are needed to derive the level of disturbance, such as to what extent trampling of hoofed animals impacts on the soil communities of a high-Andean cushion peatland.

5.4.1 | Verification of the succession model by geochemical data

In general, the results of the cluster analysis, indicating an allocation of the samples within ecotope homogenous clusters (see Figure 5.11) support the differentiation of distinct stages as proposed by the model (see Chapter 3.1.2).

Apart from the general verification of the succession model, the pioneer and succession ecotopes are not significantly distinguishable in the cluster analysis. This indicates a continuous transition between the debris ecotope and the fully developed ecotope, after the initiation of succession, rather than separate intermediary stages. However, the samples of both proposed ecotopes are homogeneously grouped in separate sub-clusters within the significant superior cluster. Therefore, it can be hypothesised that an enhanced sampling scheme might reveal significantly different pioneer and successional stages.

The order of revealed clusters also gives information on the proposed succession model, with the exception of the first cluster, containing two samples of the fully developed ecotope, which can be regarded as an out-group. The order of the remaining four clusters (1. debris ecotope, 2. combined pioneer/succession ecotope, 3. fully developed ecotope, 4. degraded ecotope) confirms the array of stages proposed in the succession model. Furthermore, the outsourced position of the de-

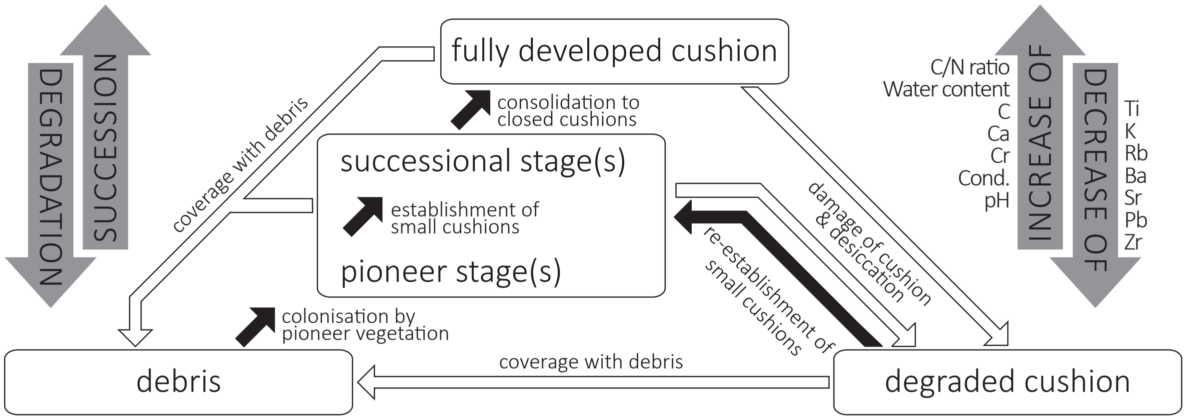


Figure 5.13 | Revised succession model for the succession model of a high-Andean cushion peatland. Upwards moving processes (solid arrows) can be classified as successional developments and downwards moving processes (hollow arrows) as degradation influences. On the right side, processes of enrichment and depletion are indicated as grey arrows.

graded ecotope from the successional order can be supported. Nevertheless, a closer connection to the fully developed ecotope, as revealed in the cluster solution, should be taken into account for the succession model. The sequence of the clusters is a result of trends in the geochemical data, which can be revealed by Jonckheere-Terpstra tests. Significant trends with an increase of geochemical parameters or an enrichment of an element in line with higher successional order are inferred for C/N ratios, Ca, Cr, water content, C, conductivity and pH. Meanwhile, decreasing or depleting trends are evident for Ti, K, Rb, Ba, Sr, Pb and Zr.

All results of the trend analysis are denoted in Appendix 5.

5.4.2 | Collinearity of the geochemical variables

The comparison of the geochemical variables reveals a high collinearity of the different parameters. The variance inflation factor (VIF) is very high for the entire dataset and nearly all parameters exceed the critical range of 5-10 (Zuur et al., 2007). Only the VIF of the pH variable with 4.5 comes below the critical limit. The results of the VIF analysis are confirmed by pairwise correlation comparisons of all variables, which reveals high ($r>0.75$) and significant ($p<0.05$) correlations between different parameters. As an example and as a basis for further discussions, the correlation of all variables to the water content is given (see Table 5.4).

Table 5.4 | Results of the collinearity assessment within the environmental and geochemical variables comprised by the variance inflation factors (VIF). Additionally, the correlation of all parameters to the water content is denoted with Pearson's r and the ANOVA results.

Variable	VIF	r	F	p
Rb	1732.6	-0.8	58.8	<0.001
K	1162.1	-0.8	52.8	<0.001
C	662.9	0.8	49.0	<0.001
N	465.8	0.5	12.9	0.001
C/N ratio	259.8	0.6	0.3	0.591
Water con.	185.5	-	-	-
Sr	117.3	-0.7	24.9	<0.001
Ti	53.1	-0.3	4.1	0.052
Fe	45.3	0.3	2.1	0.153
Zn	40.8	-0.2	1.9	0.174
Mn	35.8	0.1	0.6	0.464
Pb	33.8	-0.3	3.3	0.079
Ca	33.1	0.1	14.7	<0.001
Cr	26.7	0.5	13.8	<0.001
As	26.5	0.7	26.4	<0.001
Ba	21.4	-0.9	118.2	<0.001
Cu	20.0	0.5	12.3	0.001
Zr	15.0	-0.5	9.5	0.004
Cond.	10.3	-0.5	10.3	0.003
pH	4.5	0.0	1.1	0.908

5.4.3 | Ecology of the Oribatid mite community and derivation of soil condition indicators

5.4.3.1 | Community response to the environment

Based on gam models (using cubic splines), which provides the community response to local environments, and on the classification by HOF-models (Huismann et al., 1993; Oksanen & Minchin, 2002; Jansen & Oksanen, 2013), the Oribatid mite community shows various responses to changing environments (see Figure 5.14): A) Monotonous responses are evident for nitrogen (positive response to rising N content) and zirconium content (negative response to rising Zr content) in the local environment; B) Skewed unimodal responses are revealed for Cu (Optimum= 100 ppm), Rb (Opt.= 25 ppm) and Ti (Opt.= 600 ppm); C) Bimodal responses are indicated for Fe, As, Zn, Water content, Ca, Pb and the pH value. Of the influencing environmental parameters, nitrogen content (R^2= 0.54), iron content (R^2=0.47)

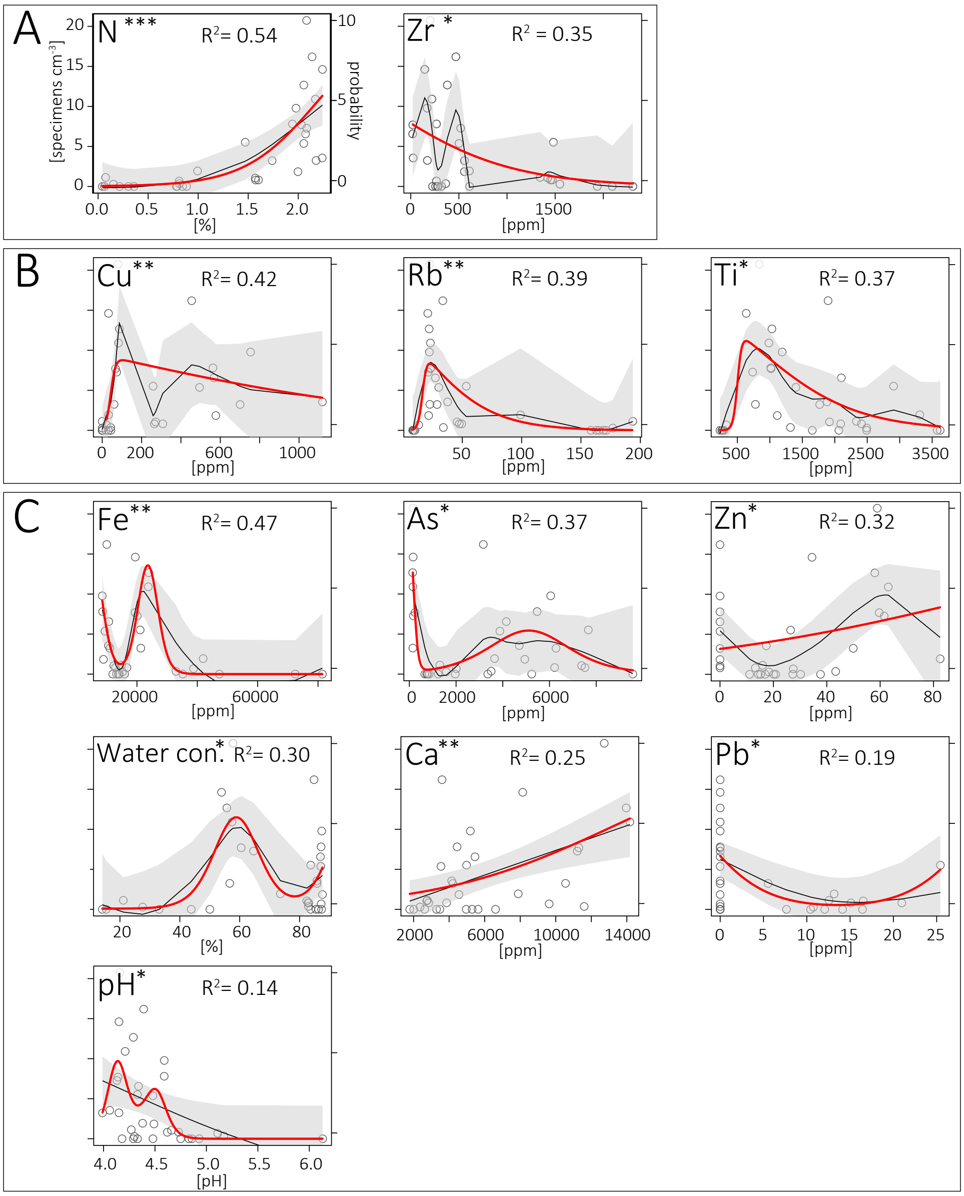


Figure 5.14 | Response of the Oribatid mite community to various environmental factors. The graphs show the development of Oribatid mite density in specimens cm^{-3} (first y-axis) in relation to different parameters. The results are grouped by: **A)** monotonous; **B)** skewed unimodal, and; **C)** bimodal responses to the relevant factor, following the classification by Huismann et al. (1993), Oksanen & Minchin (2002) and Jansen & Oksanen (2013). The best supported response HOF-model is given in red (probability values are denoted on the secondary y-axis). The impact curve (solid black line) and the 95% CI (grey area) are provided by a general additive model using cubic splines. Only significant factors are shown (*: p<0.05, **: p<0.01, ***: p<0.001). For each factor, the adjusted R^2 is denoted.

and copper content (R^2=0.42) have the highest impact on the Oribatid mite community. All test results are denoted in Appendix 6.

Some of the community responses reported above can be linked with specific impact mechanisms that are well known to science. For example, the skewed unimodal response of the Oribatid mite community to higher copper concentrations in the soil could be ascribed to the hormesis effect, implying a stimulated reproduction of organisms at low concentrations of toxic substances (Stebbing, 1982), which is also evident for Oribatid mites (Denneman & van Straalen, 1991). Another example is the association of rubidium with medium abundances of Oribatid mites, which can be assigned as a secondary response, as in soil-dwelling animals the Rb^+ uptake is significantly triggered by soil pH (Tyler, 1997).

In general, many environmental parameters that influenced Oribatid mite communities in this study, such as pH, nitrogen content, soil humidity and heavy metals concentrations, including Cu, Zn and Pb, were also reported in other studies (Borcard & Legendre, 1994; Straalen & Verhoef, 1997; O'Lear & Blair, 1999; Haq, 2001; Seniczak et al., 2005, 2009; Owojori & Sicciliano, 2012; Gao et al., 2014; Zhang et al., 2015; Gao et al., 2016). However, some new or not so well-studied impacts were also discovered, such as the impact of iron and arsenic in particular. Further studies based on these heavy metals may provide new insights into ecological shaping in naturally enriched environments. For future investigations, high-Andean cushion peatlands represent suitable study sites as many are fed by heavy metal-enriched spring waters, originating from the weathering of volcanic rocks (Schittek et al., 2015). Indeed, the phenomenon that As is trapped in anoxic peat, intensifies the enrichment in peatland ecosystems (Langner et al., 2012).

The response analysis of the Oribatid mite community data reveals more bimodal responses to the different environmental variables than other types. This evident deviation from the Gaussian response curve along a gradient indicates a disparate response of different members within the community or enhanced ecological shaping of the response curve, e.g. due to competition, rather than physiological shaping (Austin, 1985).

5.4.3.2 | Ecological constraints on Oribatid mite species

The previous data analyses point out the strong collinearity of the environmental variables. To take account of this inter-dependence, the element content variables, except for carbon and nitrogen content, were excluded from further analyses. Furthermore and due to evidence for a pronounced ecological shaping of the Oribatid mite community response, the abundance of the individual species instead of the summarised community density was used in the subsequent multivariate analyses in order to derive suitable indicators for soil conditions.

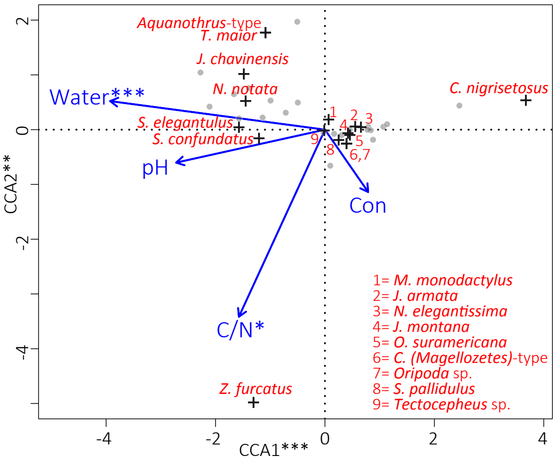


Figure 5.15 | Canonical correspondence analysis (CCA) of Oribatid mite fauna including the environmental variables - water content, pH values, C/N ratios and conductivity as constraints. Species ordinations are marked by black crosses and sites as pale grey circles. Results of ANOVA permutation tests of the CCA axes and constraints are indicated as ***: $p<0.001$, **: $p<0.01$, *: $p<0.05$. Before analysis, rare species with <0.5 specimens cm^{-3} have been down-weighted. Species score have been scaled by eigenvalues.

A canonical correspondence analysis (CCA, see Figure 5.15) based on the four variables - water content, C/N ratios, pH values and conductivity, significantly reflects the variance of the Oribatid mite community (F(4, 20)= 3.1, $p<0.001$). A sequential permutation test on significant constraints reveals the water content (F(1, 20)= 5.7, $p<0.001$) and C/N ratios (F(1, 20)=3.07, p=0.014) as the driving environmental parameters. This result is confirmed by a type III test with marginal effects, which reveals that the water content (F(1, 20)= 3.8, p=0.004) and C/N ratios (F(1, 20)= 3.0, p=0.016) remain as driving parameters. Additionally, an AIC test underlies these results. The first and second axes are only significant (CCA1 $p<0.001$, CCA2 p=0.007) with high species environment correlation on the first two axes (CCA1=0.92, CCA2=0.66). In contrast to the results of the complete environmental variable set, the variance inflation factors are low (water=1.9, conductivity=1.7, pH=2.8, C/N ratios=1.2), indicating a highly independent effect of each variable on the species.

The CCA analysis marks two species as outsiders, living on the one hand in a very dry and eutrophic environment (*Ceratozetes nigrisetosus*) and on the other hand in a moderately wet but poorly oligotrophic environment (*Zetomimus furcatus*). Besides the two deviant species, two groups of species can be identified. One group of taxa, consisting of *Tectocepheus* sp., *Malaconothrus monodactylus*, *Jugatala armata*, *J. montana*, *Oxyoppia suramericana*, *Ceratozetes* (*Magellozetes*)-type, *Oripoda* sp. and *Scheloribates pallidulus*, is indifferently located around the origin of CCA axes 1 and 2. The second group of taxa, consisting of *Scheloribates confundatus*, *S. elegantulus*, *Neoamerioppia notata*, *Jugatala chavinensis*, *Tyrphonothrus maior* and Ameronothroid *Aquanothrus*-type, are located at a higher environment wetness level of >80% water content in comparison to the first group of taxa. This wetness-associated group is internally differentiated by C/N ratios, spreading the taxa by increasing trophic conditions in the above stated order.

5.4.3.3 | Assessment of soil condition indicators

A multivariate regression tree analysis (MRT, see Figure 5.16) reveals a five leaved tree with four nodes regarding water content, C/N ratios, conductivity and pH values as environmental variables. The model shows an error of 0.39 which means that the correlation of the model is R^2=0.61. The standardised community data has been back transformed to generate ecologically meaningful values for MRT nodes. For that purpose, a linear regression model was used. The first split of the MRT is defined by a limit in C/N ratios at 29.54 (back transformation: R^2=0.79, F(1, 33)= 126.7, p<0.001) and the first leaf with C/N ratios ≥29.54 includes nine samples with a very low error of 0.002. The second node is built by a limit in conductivity at 101.65 µS cm^{-1} (back transformation R^2=0.61, F(1, 33)= 54.1, p<0.001). The leaf ≥101.65 µS cm^{-1} comprises eight samples and shows an error of 0.02. The last two nodes are characterised by limits in water content at 73.21% (back transformation: R^2=0.71, F(1, 33)= 85.33, p<0.001) and 57.9%. The leaf ≥73.21% is built from 11 samples and shows an error of 0.06, the leaf ≥57.9% by five samples with an error of 0.03 and the leaf <57.9% by two samples with an error of 0.02.

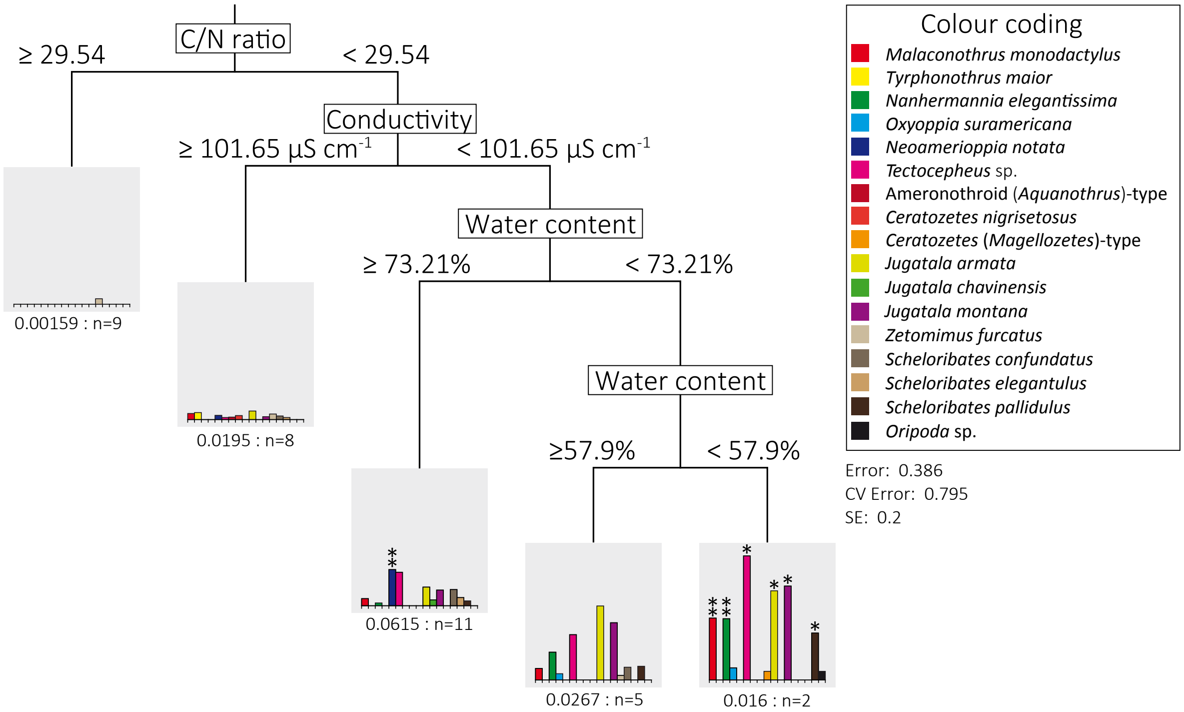


Figure 5.16 | Multivariate regression tree relating the Oribatid mite community with the soil variables - C/N ratios, water content, conductivity and pH. The error given below the colour codings represents the reciprocal fit of the model which is R^2= 0.61. At each leaf, the individual error and included number of samples are given. Significant indicator taxa are marked by *: p<0.05, **: p<0.01, ***: p<0.001.

An indicator species analysis on the basis of the MRT results exposes the significant indicator species in the dataset connected with an indicating environmental parameter. In the Oribatid mite community these are for low soil wetness (<57.9%): *Malaconothrus monodactylus* (IndVal= 0.72, p=0.007), *Scheloribates pallidulus* (IndVal= 0.72, p=0.016), *Nanhermannia elegantissima* (IndVal= 0.67, p=0.006), *Tectocepheus* sp. (IndVal= 0.61, p=0.011), *Jugatala montana* (IndVal= 0.55, p=0.014) and *J. armata* (IndVal= 0.47, p=0.038). For high soil wetness (≥73.2%), the only significant indicator species is *Neoamerioppia notata* (IndVal=0.65, p=0.010).

5.4.4 | Ecology of the Chironomid community and derivation of soil condition indicators

5.4.4.1 | Community response to the environment

Based on the gam models (using cubic splines), which provide the community response to local environments, and on the classification by HOF-models (Huismann et al., 1993; Oksanen & Minchin, 2002; Jansen & Oksanen, 2013), the Chironomid community shows various response types to changing environments: A) Monotonous response is evident for the iron content (negative response to rising Fe concentration); B) Symmetric unimodal response can be revealed by changing rubidium content (Optimum= 60 ppm); C) Bimodal responses are indicated for C, Cu, N, pH, As, conductivity, Zn, and Pb.

Of these influencing environmental parameters, the carbon content (R^2= 0.80), copper content (R^2=0.77) and nitrogen content (R^2=0.69) have the highest impact on the Chironomid community. All test results are denoted in Appendix 7.

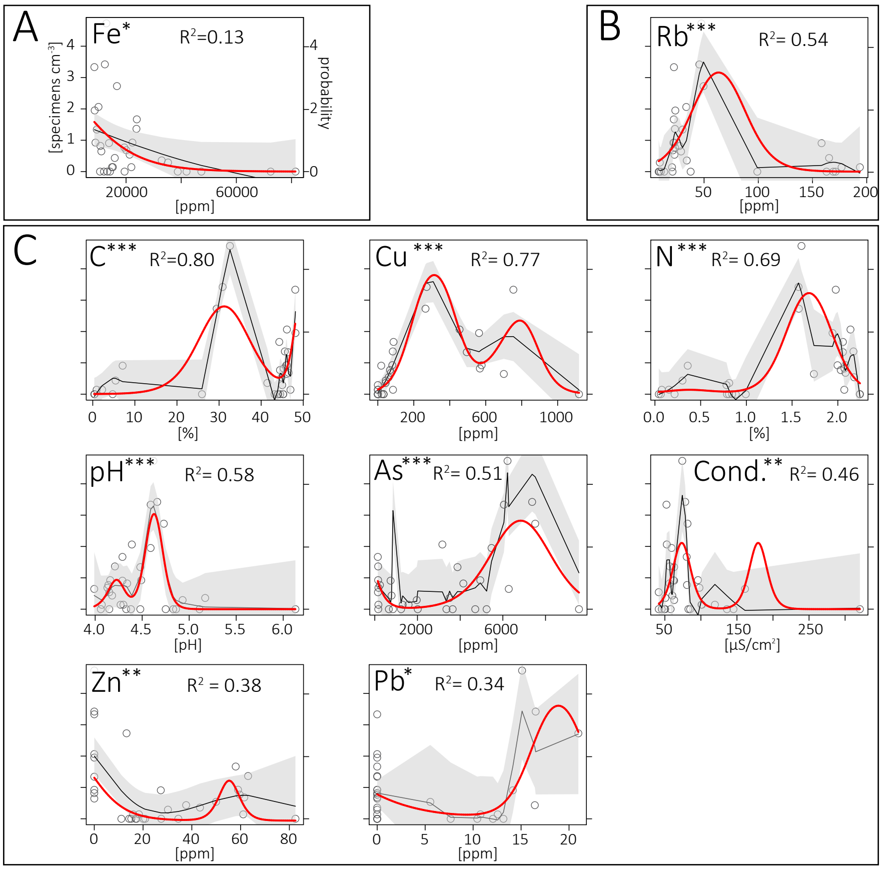


Figure 5.17 | Response of the Chironomid community to various environmental factors. The graphs show the development of Chironomid density in specimens cm^{-3} (first y-axis) in relation to different parameters. The results are grouped by: **A)** monotonous, **B)** skewed unimodal and **C)** bimodal responses to the relevant factor, following the classification by Huismann et al. (1993), Oksanen & Minchin (2002) and Jansen & Oksanen (2013). The best supported response HOF-model is given in red (probability values are denoted on the secondary y-axis). The impact curve (solid black line) and the 95% CI (grey area) are provided by a general additive model using cubic splines. Only significant factors are shown (*: $p<0.05$, **: $p<0.01$, ***: $p<0.001$). For each factor, the adjusted R^2 is denoted.

Similar to the results for the Oribatid mite community, the Chironomids show more bimodal responses to the environment than linear or unimodal responses. Of the ten verifiable responses, the Chironomid community shows a bimodal character for eight of them. As already described for the Oribatid mite community, this kind of reaction to environmental gradients indicates a disparate response of different members within the community or a stronger ecological shaping of the response curve, e.g. due to competition, rather than a physiological shaping (Austin, 1985).

5.4.5 | Ecological constraints on the Chironomid genera

The same data characteristics as stated for the indicator assessment for the Oribatid mites (see Chapter 5.4.3.1) are evident for the Chironomid data. Due to the high collinearity, the environmental variables were reduced to water content, conductivity, C/N ratios and pH for further analyses. The strong ecological shaping of the environmental response implies the usage of genera abundance data for the assessment of soil condition indicators for the Chironomids.

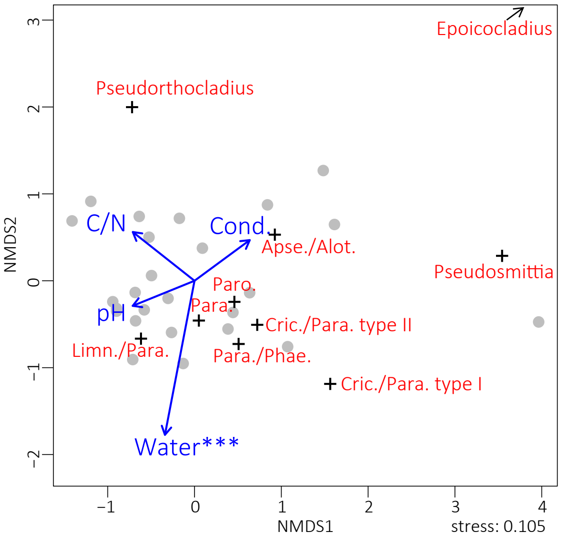


Figure 5.18 | Non-metric multidimensional scaling (NMDS) ordination of the Chironomid community. The analysis is based on Bray-Curtis-dissimilarity and the soil variables C/N ratios, water content, conductivity and pH have been fitted to the ordination. The black crosses mark taxa allocations and the grey circles represent the samples. The significant environmental parameter is marked by ***: $p<0.001$.

A non-metric multidimensional scaling (NMDS) ordination, based on the environmental parameters C/N ratios, water content, conductivity and pH values, depicts the variance of the Chironomid community (see Figure 5.18). Three taxa, *Epoicocladius*, *Pseudosmittia* and *Pseudorthocladius* can be regarded as outsiders. Some taxa, e.g. *Limnophyes/Paralimnophyes* or *Parametriocnemus/Paraphaenocladius*, show a closer relation to the only significant environmental parameter (water content: $R^2= 0.49$, $p<0.001$). However, clear assignments regarding indicator potential of the taxa cannot be made based on this NMDS.

5.4.5.1 | Assessment of soil condition indicators

The best fitting multivariate regression tree analysis (MRT) reveals a tripartite tree with two nodes separating the community by the water content. The regression tree shows a correlation of $R^2=0.38$. The standardised data have been back transformed to ecologically meaningful data for the MRT nodes with a linear regression model. The first split is defined by a limit in water content of 80.2% (back transformation: $R^2=0.70$, $F(1, 33)=80.4$, $p<0.001$). The first leaf with a water content <80.2% is built up by 26 samples with a medium error of 0.06 and comprises nine taxa. The second node is characterised by a split in water content at 81.2%. Following this classification, the second leaf, comprising three samples and eight taxa at a water content of 80.2-81.2% with a very small error of 0.003, is mainly dominated by *Cricotopus/Paratrichocladius* type II. The community of the last leaf, defined by the highest water content ≥81.2% and an error of only 0.007, is built up by six species from six samples and dominated by the *Limnophyes/Paralimnophyes* taxon. In the Chironomid community the indicator taxa for soil wetness between 80.2-81.2% are: *Cricotopus/Paratrichocladius* type II (IndVal=0.79, $p=0.007$), *Parochlus* (IndVal= 0.74, $p=0.008$), *Apsectrotanypus/Alotanypus* (IndVal=0.72, $p=0.008$) and *Parametriocnemus/Paraphaenocladius* (IndVal= 0.67, $p=0.004$). For high soil water content (≥81.2%), the only significant indicator taxon is *Limnophyes/Paralimnophes* (IndVal=0.53, $p=0.05$).

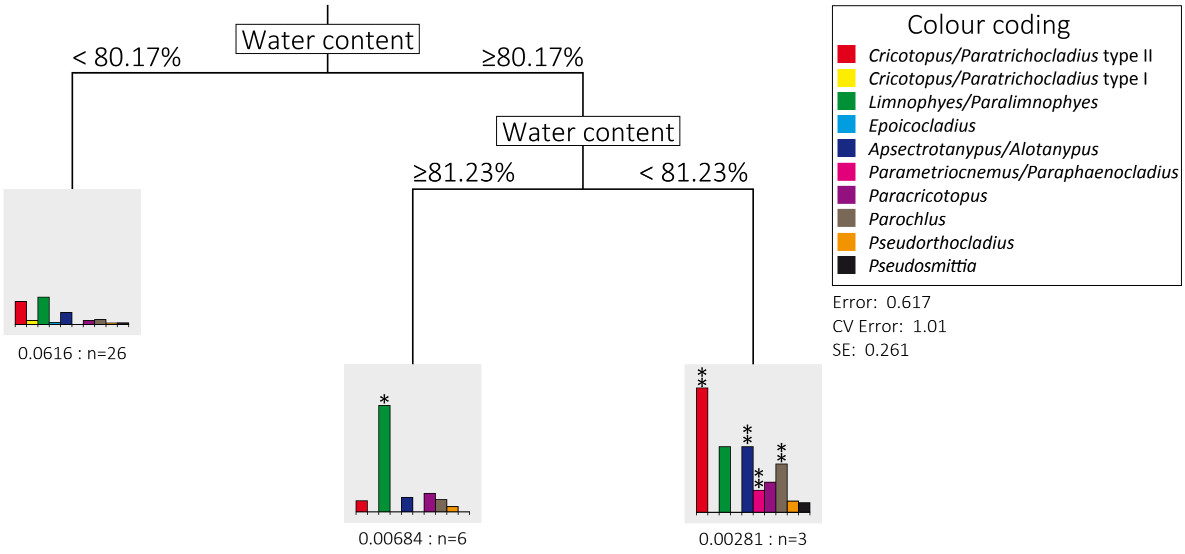


Figure 5.19 | Multivariate regression tree relating the Oribatid mite community with the soil variables - C/N ratios, water content, conductivity and pH. The error given below the colour codings represents the reciprocal fit of the model which is $R^2 = 0.38$. At each leaf, the individual error and included number of samples are given. Significant indicator taxa are marked by *: $p<0.05$, **: $p<0.01$, ***: $p<0.001$.

5.5 | Conclusion

This investigation reveals an indicator system, which comprises seven Oribatid mite species and five Chironomid genera, and gives information on the soil water content. These autecology data on the presented species could provide the basis for palaeoenvironmental interpretation, on the precondition that the identified indicator taxa can be obtained from palaeo-archives. However, on the basis of this ecological assessment, only information on soil wetness conditions is available for the Oribatid mites and Chironomids of high-Andean cushion peatlands. To verify and refine the revealed indicator functionality, further faunal sampling and geochemical analyses should be applied in future investigations from a wider range of peatland and adjacent habitats.

The geochemical analysis reveals remarkably variable soil conditions between the different ecotopes of the peatland. In particular, the concentration of heavy metal ions appears noticeable. As such, the very high As content could be the basis for future research, which investigates, for example, the behaviour of heavy metal ions during episodic wetting and/or rewetting of the peat. This may contribute to conservational strategies and efforts for securing reliable supplies of drinking water.

6 | Chapter VI - Palaeoecology

Palaeoenvironmental reconstruction of a high-Andean cushion peatland during the Nasca-Wari cultural transition (1920-860 yr BP) based on Oribatid mites (Acari, Oribatida) and Chironomids (Diptera, Chironomidae)

Abstract

The Oribatid mites and Chironomid subfossil assemblages were investigated in a 152 cm-long core, retrieved from a high-Andean cushion peatland in southern Peru, which represents a record covering 1064 years (1924-860 cal yr BP). 16 Oribatid mite species and 12 Chironomid taxa could be identified, with five significant indicator taxa from each being used to reconstruct soil wetness quantitatively, by employing a modern analogue technique (MAT) model. The model predicts a humid period from 1924-1426±22 yr BP with a significant dry spell occurring from 1601±35-1543±24 yr BP, which was fully established by 1567 yr BP. After 1426±22 yr BP, the soil wetness shifted to drier conditions and remained stable until 860 yr BP. The archeological implications of the results are discussed.

6.1 | Introduction

The impact of climatic and environmental changes is well accepted as a driving factor for societal development and dispersal in ancient times (Eriksson et al., 2012), and nowadays (Stephenson et al., 2010; Adger et al., 2013). However, precise mechanisms in the coupling between climate and environmental change are poorly understood and remain of great interest for palaeoecological research, especially the impact of short-term climatic changes on cultural development (e.g. Chepstow-Lusty et al., 2003).

The pre-Colombian cultures in the Peruvian coastal deserts offer a unique chance to investigate the human-environment relationship. In particular, the Nasca region in southern Peru, known for the Nasca culture and its famous geoglyphs in the desert floor, provides good advantageous preconditions for research (Fehren-Schmitz et al., 2014): prominent climatic changes have taken place since the Pleistocene-Holocene transition (Sandweiss et al., 2001); an excellent cultural chronology exists since this area was first settled ca. 5700 yr BP (Unkel et al., 2012); and the area between the Pacific and the Andean foothills can be characterised as a low-resilience and fragile ecosystem (Mächtle & Eitel, 2013). In addition, the Nasca region is geographically dominated by an extremely dry desert representing the northern extension of the Atacama (Mächtle, 2007); in the northern part of the region, pre-Colombian settlement areas were located in three converging river valleys, which supplied the lowlands with sufficient water for agriculture.

These rivers are fed by summer rains in the Andean catchment area, in which the high Andean cushion peatlands, located at the headwaters of the rivers, play a vital role in the hydrological drainage control (Cepeda et al., 2006). The outstanding quality of these peatlands as sensitive palaeoecological archives for the high Andes has been repeatedly demonstrated several times (see Chapter 6.1.2.3); recently, they revealed the first evidence for socio-environmental fluctuations (Schittek et al., 2015). However, to study short-term changes, additional interpretation of local peatland condition related data is needed to verify and reinforce the available data on pollen- and geochemistry-based reconstructions. This study provides a new approach by using Oribatid mites and Chironomids as strictly local proxies for environmental reconstruction and combines these with regional signals to produce a fine-scale multiproxy palaeoecological interpretation.

6.1.1 | A multiproxy palaeoecological approach

Modern palaeoecological research should be open to a variety of new proxies and their integration into older and established proxy analyses. Hence, a fuller multiproxy view on past ecological or climate changes can be obtained by capturing interactions of the biotic and abiotic components in an ecosystem (NRC, 2005; Birks & Birks, 2006).

Proxy data from an archive can be retrieved from fossil organisms or sediment characteristics. A combination of both biotic and abiotic counterparts, and intra- (local) and extra-ecosystem (regional) proxies can provide a more robust interpretation and hence allow a better reconstruction of ecosystem changes (e.g. floral and faunal communities, on-site environmental conditions, etc.), landscape changes (e.g. vegetation coverage or belt shifts) and climate changes (precipitation, temperature).

Long-term studies with a focus on biodiversity responses to environmental and climate influences are essential to face the challenges of modern nature conservation. These studies should exceed a few decades of recorded changes and reach a century or millennial timeframe (Willis & Birks, 2006). However, the main requirement for such investigations is the attainment of high resolutions in time, which enables the reconstruction of minor population fluctuations and concomitant environmental variables.

Especially for the study of socio-ecological systems in the Anthropocene (in terms of Crutzen, 2002), it is indispensable to work at a regional scale and with high resolution records. Only under these conditions is it possible to model socio-ecological systems and to detect environmental fluctuations with the appropriate accuracy (Dearing et al., 2015).

6.1.2 | Palaeoecological studies

6.1.2.1 | Archives & Proxies from the Central Andes

For the Central Andes of Peru, northern Chile and Bolivia, a variety of published palaeostudies (N=63) is available (see Figure 6.1). A full overview of investigated sites is given in Appendix 9. The best studied areas are the Western Cordillera of mid-Peru between 9-12°S and the Eastern Cordillera of northern Bolivia between 15-18°S.

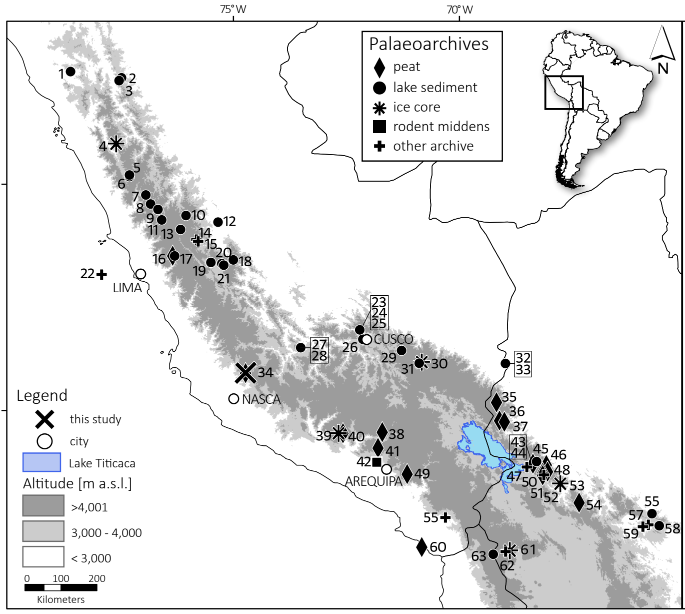


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Figure 6.1 | Location map of palaeoclimate records available from the Central Andes. Black symbols indicate different sites and archive types.

Table 6.1 | Overview and relative importance of all proxies used in palaeoecological investigations in the Central Andes.

Biological proxies	Relative importance	Geophysical and -chemical proxies	Relative importance
Pollen	61.3%	Carbon content (TIC/TOC)	22.6%
Charcoal	8.1%	Magnetic susceptibility	19.4%
Diatoms	8.1%	Isotope analysis	16.1%
Chironomids	3.2%	Bulk density	12.9%
Oribatid mites	3.2%	Clastic influx	12.9%
Spores	3.2%	Element analysis (XRF)	8.1%
Macrofossils	1.6%	Biogenic silica	4.8%
Phytoliths	1.6%	Spectral analysis	4.8%
		Nitrogen content	3.2%
		Loss on ignition (LOI)	3.2%
		Ammonium content	1.6%

Additionally, the Cusco area and the Arequipa areas are well studied. Half of the records were derived from lake sediments, 29% from peat deposits and 8% from glaciers. In addition, 13% of all records were obtained from various archives such as speleothems (Kanner et al., 2012, 2013), lake and river terraces (Graf, 1979, 1992), lacustrine sediments (Placzek et al., 2001), cushion plants (Graf, 1992) or rodent middens (Holmgren et al., 2001). The investigated timespans of all records range from 1055 cal. yr (Sterken et al., 2006) to 80,000 cal. yr (Graf, 1992) with a mean of ca. 15,500 cal. yr.

6.1.2.2 | Meta-analysis of palaeoclimate investigations

Of the 63 palaeoclimatic investigations available from the Central Andes, the majority (n=37) use only a single proxy to indicate climate variations, especially many carried out in the 1980s and 1990s. The more recent investigations (n=22) use multiproxy approaches for palaeoecological or climate reconstructions. These studies employ an average of 3.6 proxies for reconstructions, although two investigations provide six proxies (Williams et al., 2011, 2012). In general, very different proxies were sued for palaeoecological reconstructions. An overview is given in Table 6.1.

75% of all records cover a maximal age of ca. 5700-12,000 cal. yr BP with a median of 10,000 cal. yr BP and attain a resolution of 130-530 yr sample^{-1}, with a median of 260 yr sample^{-1} (see Figure 6.2). Only a few investigations reach a resolution <100 yr sample^{-1} (Ostria, 1987; Sterken et al., 2006; Chepstow-Lusty et al., 2007; Kuentz et al., 2011; Mosblech et al., 2012; Schittek et al., 2015). This highlights the need for further high-resolution palaeoenvironmental investigations in the Central Andes.

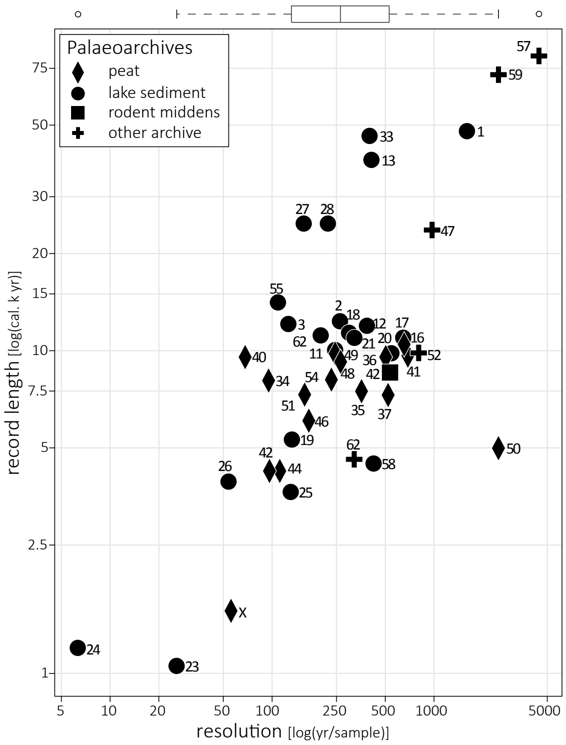


Figure 6.2 | Meta-analysis of palaeoclimate investigations (n=43) from the Central Andes using biological proxies (e.g. pollen, charcoal, Chironomids, Oribatid mites,...) showing a scatterplot of the record length and the resolution. Both axes are log-transformed. The site numbers are in accordance with Figure 6.1 and Appendix 9.

6.1.2.3 | Cushion peatlands as archives for palaeoenvironmental reconstruction

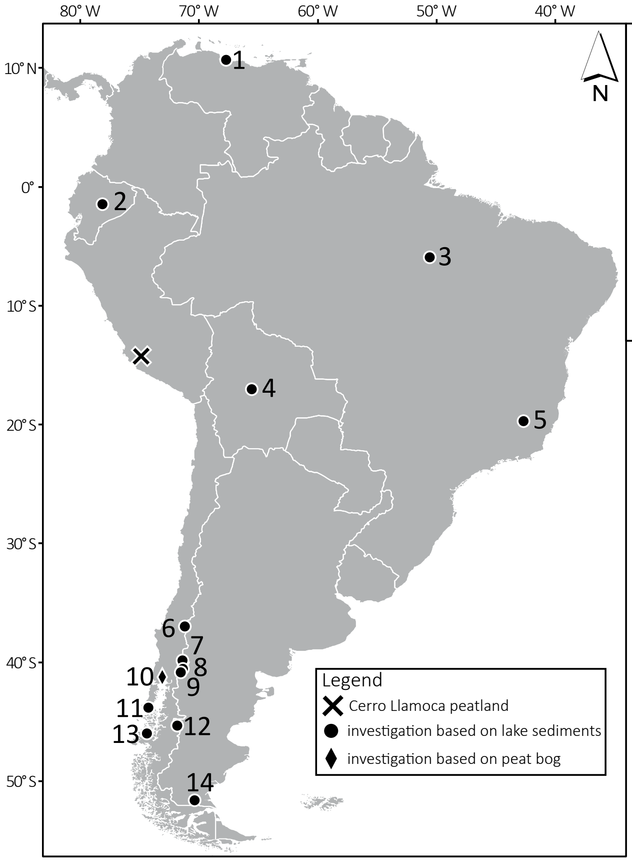
Cushion peatlands in the high Andes are an understudied ecosystem in general and have not been widely used as archives for palaeoreconstruction. Only recently have cushion peatlands aroused increasing interest as palaeoarchives (Skrzypek et al., 2011; Schittek et al., 2012; Engel et al., 2014; Schittek, 2014; Schittek et al., 2015, 2016). These investigations mainly deal with pollen, stable isotopes, and charcoal as palaeoproxies. However, Schittek (2014, 2016) indicated the potential of other subfossil remains as palaeoproxies, such as Oribatid mites, Chironomid head capsules, Heleomyzid pupae, fungal spores and the eggs of Neorhabdocoela and Copoepoda, which are all well preserved in the peat layers.

6.1.3 | Faunistic proxies in palaeoenvironmental research

6.1.3.1 | Oribatid mites in palaeoecology

The use of Oribatids or mites in general is a relatively new discipline in the palaeosciences. The first recognition of subfossil Oribatid mites and interpretations were presented by Knülle (1957) and Karppinen et al. (1979). However, it was not until the late 1980s that more attention was directed on the utility in archaeological settings. Initially, these findings contributed to the interpretation of human activities, such as agro-pastoralism using predatory mites as indicators for dung (Schelvis, 1987, 1989, 1990a; Schelvis & Ervynck, 1992; Schelvis, 1992). Soon after, the first environmental reconstructions were undertaken by Schelvis & van Geel (1989) and Schelvis (1990b). An excellent overview on the usage of Oribatid mites in palaeoecology and archaeology is given in Drouk (1997), Solhøy (2002), Baker (2009) and Erickson & Platt (2013).

Since 2000, Oribatid mites have been used to investigate palaeoenvironments: in the Northern Hemisphere in Norway by Solhøy & Solhøy (2000), Larsen et al. (2006) and De La Riva-Caballero et al. (2010); in Greenland by Presthus et al. (2010); in Turkey by Schelvis et al. (2005); in the USA by Erickson et al. (2003) and Erickson & Solod (2007); and in the southern Hemisphere on Antarctic Islands by Hodgson & Convey (2005). Oribatid mites as proxies derived from peat cores have been used in Europe by Wild et al. (2008). However, the usage of Oribatid mites as palaeoproxies in a neotropical context is virtually non-existent, besides being mentioned as non-pollen palynomorphs (Rull et al., 2008). Only one lake sediment investigation by Chepstow-Lusty et al. (2007), using Oribatid mites as potential indicators for ancient domestic animal densities is available, but lacks taxonomic definition. No palaeoecological study using Oribatid mites as a proxy for environmental reconstruction has ever been carried out from a peatland in this region.



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3. Andrade-Morraye, 1999
4. Williams et al., 2012
5. Andrade-Morraye, 1994
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8. Bianchi et al., 1999
9. Massaferro et al., 2005b
10. Massaferro et al., 2014
11. Araneda et al., 2013
12. Massaferro et al., 2005a
13. Massaferro & Brooks, 2002
14. Massaferro & Larocque-Tobler, 2013

Figure 6.3 | Palaeoenvironmental sites investigated in South America for Chironomids. For location data, the studies reviewed by Massaferro (2009), Massaferro & Vandergoes (2013), Verschuren & Eggermont (2006) and additional studies are depicted.

6.1.3.2 | Chironomids in palaeoecology

The usage of Chironomids in palaeoecology is a discipline with a long tradition and first attempts go back to Einar Naumann (Sweden) and August Thienemann (Germany), and the beginning of limnology in the 1920s. Both used Chironomid assemblages to describe lake ontogeny but without considering the effect of climate on the ecosystems (Walker, 2013). The first palaeoenvironmental study using Chironomids as a proxy was carried out by Gams (1928). However, only since the 1980s and 1990s Chironomids were commonly used as palaeoproxies, in studies focussing on the qualitative reconstruction of palaeotemperatures, lake levels, palaeosalinity and human impact, including eutrophication and acidification (Hofmann, 1988). Full reviews of the development of Chironomid palaeoenvironmental research are given in Walker (2013) and Walker (2002).

Recently, Chironomids became a widely used proxy, primarily due to the easy availability of surface samples in Europe and North America, and the establishment of transfer functions (Walker, 2002). In particular, the quantitative reconstruction of temperatures has been demonstrated to be robust and sensitive using Chironomids as a proxy, at least for European or Northern American settings (Lotter et al., 1999; Brooks, 2000). Using this approach, Chironomids analysis were applied to reconstruct summer surface-water temperatures (e.g. Walker et al., 1991) and mean July air temperatures (e.g. Brooks & Birks, 2000b).

In South America (see Figure 6.3), Chironomids were not used as a palaeoproxy until Binford (1982) studied sediments from Lake Valencia in Venezuela. Since the late 1990s and due to the success of Chironomid reconstructions in Europe, they have acquired increasing importance in palaeoenvironmental investigations: glacial lake archives from Northern Patagonia (Ariztegui et al., 1997; Bianchi et al., 1999; Massaferro et al., 2005b; Urrutia et al., 2010); Southern Patagonia (Massaferro & Larocque-Tobler, 2013); the Chilean archipelago (Massaferro & Brooks, 2002; Massaferro et al., 2005a); swampy lakes in Eastern Amazonia (Andrade-Morraye, 1994, 1999); as well as high Andean lakes in Bolivia (Williams et al., 2012) and Ecuador (Matthews-Bird et al., 2016).

In general, peat archives are rarely used for chironomid analyses (Chambers et al., 2012), with only a few studies undertaken, e.g. in Scotland by Brooks & Birks (2000a) and in Poland by Płóciennik et al. (2011). In South America, the only palaeoenvironmental investigation on Chironomids from peat cores was carried out by Massaferro et al. (2014) (see Figure 6.3, site no. 10). This study site can be characterised as a Magellanic ombrotrophic moorland (Moreno & Léon, 2003).

6.1.3.3 | Comparison of palaeoproxy properties of Oribatid mites and Chironomids

In the following Table 6.2, a comprehensive comparison of the potential applicability of both Oribatid mites and Chironomids as proxies for palaeoenvironmental investigations is given. This table summarises important factors such as ecological tolerance, habitat, abundance and sensitivity, and gives information on global diversity, identification literature, preservation in archives and sample preparation effort, the possible taxonomic accuracy in identification of subfossil specimens and the range of the proxy signal derived from both taxa.

Table 6.2 | Comprehensive comparison of Oribatid mites and Chironomids regarding their potential applicability for palaeoenvironmental investigations

	Oribatid mites	**Chironomids**
Ecological tolerance	Various ecological traits (Weigmann, 2006; Walter & Proctor, 2013)	Large proportion of stenotopic taxa (Brooks et al., 2007)
Habitats	Occur mainly in terrestrial habitats, ~1% of the species are truly aquatic (Schatz & Behan-Pelletier, 2008)	Larvae cover virtually all kind of aquatic, a wide range of semiaquatic and in rare exeptions terrestrial biotopes (Oliver & Roussel, 1983)
Abundance in habitats	Very abundant: densities >100,000 specimens m^{-2} are common in favourable habitats (Norton & Behan-Pelletier, 2009)	Very abundant: densities >30,000 specimens m^{-2} are common in favourable habitats (Oliver & Roussel, 1983)
Sensitivity (dispersal, generation cycle & reproduction mode)	Slow dispersers, but passive dispersal over long distances known (Wallwork, 1972; Lehmitz et al., 2011); relatively fast colonisation of new habitats (Lehmitz et al., 2012); K-style life history traits with low reproduction and long life cycles of 1-5 years (Norton & Behan-Pelletier, 2009)	Relatively fast dispersers, passive dispersal over long distances is common (Armitage, 1997); rapid colonisation of new habitats is possible due to direct choice of favourable sites for oviposition by flying adult females (Frouz, 1997); most taxa show two generations per year, heavily depending on the environmental conditions (Tokeshi, 1997)
Global number of species	>10,000 species described (Subías, 2004) from an estimated number of 50,000-100,000 species (Schatz, 2002)	>4,000 aquatic species described (Ferrington, 2008) from an estimated number of 8,000-20,000 species (Coffman, 1997)
Identification literature	Literature for the identification of modern taxa is available, but no adjusted keys for the identification of subfossil Oribatid mites are provided (Solhøy, 2002)	Sufficient taxonomic literature available for subfossil remains (Walker, 2002)
Preservation	In general, all morphological features for identification on sclerotised body are well preserved (Drouk, 1997; Solhøy & Solhøy, 2000; De La Riva-Caballero et al., 2010); the density of preserved Oribatid mites is reported as 0.3 specimens cm^{-3} from Russian peat deposits (Drouk, 1997) and 0.5 specimens cm^{-3} in lake sediments from Norway (Solhøy & Solhøy, 2000)	In general, all morphological features for identification on the sclerotised head capsules are preserved (Brooks et al., 2007); head capsules are preserved in high numbers; only small sample volumes are needed (Brooks et al., 2007)
Sample preparation effort	In comparison to other palaeoecological proxies, the analysis of Oribatid mites is time consuming if any sediment separation technique works (Drouk, 1997)	In comparison to other palaeoecological proxies, the analysis of Chironomid is time consuming (Brooks et al., 2007)
Identification level of subfossil specimen	Mainly to species level, if not possible, at least to genus level (De La Riva-Caballero et al., 2010)	Mainly to genus level, sometimes a species-group is possible (Brooks et al., 2007)
Range of proxy signal	Mainly a very local signal (De La Riva-Caballero et al., 2010), but artificial influx from surroundings has to be considered (Drouk, 1997)	Local signal, giving information for one ecosystem, e.g. a lake (Walker, 2002)

6.1.4 | Climate history of the Central Andes

The most important force for long-term climate variations in the Central Andes during the Holocene is the Inter-Tropical Convergence Zone (ITCZ) (Haug et al., 2001; Ledru et al., 2009; Bird et al., 2011a, b; Vuille et al., 2012; Flantua et al., 2016). Additionally, ocean-atmosphere interactions can strongly effect the large-scale circulations over the entire continent, which are also responsible for fluctuating climatic conditions on an inter-seasonal to -decadal scale (Flantua et al., 2016). For further information on the impact of the position of the ITCZ in relation to precipitation in the Central Andes, see Chapter 2.2.1.

Various palaeoclimatic investigations in the Central Andes revealed evidence for the changing interplay of the above listed climatic drivers through time. The studies show distinct periods of significantly different climatic conditions in the Holocene. Of relevance for this study are the climatic fluctuations of the timeframe between 2000-500 yr BP:

Starting before 2000 and lasting until 1800 yr BP, a period of dry (Chepstow-Lusty et al., 2003; Mosblech et al., 2012; Schittek et al., 2015) and relatively warm conditions (Chepstow-Lusty et al., 2003) are inferred in the Central Andes, accompanied by evidence of cultural adaptions to climate through cultivation of more drought tolerant crops such as quinoa (Ledru et al., 2013). However, beginning from 1850 yr BP, a decline of agriculture becomes evident in the pollen spectrum (Chepstow-Lusty et al., 2003).

From 1800 yr BP, a distinctly wetter and more stable period begins, indicated by changes in the pollen spectrum and Mn/Fe element ratios derived from a peat deposit at high altitudes (Schittek et al., 2015). This is supported by evidence from a marine sediment core of high runoff towards the Pacific Ocean (Rein et al., 2004), and a relatively high water level in an Andean lake from 1700-1300 yr BP (Placzek et al., 2001). Additionally, starting from 1800 yr BP, changes in pollen spectrum (Chepstow-Lusty et al., 2009) and evidence for glacial growth (Wright et al., 1989; Rodbell, 1992; Abbott et al., 1997b) characterise the climatic conditions as distinctly colder. This period of humid and cooler climate lasts until ca. 1200 yr BP (Mosblech et al., 2012; Schittek et al., 2015). The first evidence for reduced precipitation are traceable as early as 1300 yr BP through geochemistry changes in peat deposits (Schittek et al., 2015), a reduction in Titicaca's lake-level (Abbott et al., 1997a; Binford et al., 1997) and the re-establishment of drought tolerant crop cultivation (Ledru et al., 2013). Nearly simultaneously, the first indication of a temperature increase is given at 1290 yr BP from a lacustrine pollen record in the Cusco area (Chepstow-Lusty et al., 1998).

At 1175 yr BP, the peat archive from >4000 m altitude indicates a harsh transition to drier conditions and a fully established dry period starting at 1050 yr BP (Schittek et al., 2015). Beginning from 1050 yr BP, many studies report markedly arid conditions, e.g. as indicated by pollen records (Chepstow-Lusty et al., 2003, 2009), calcite records (Bird et al., 2011b) and ice cores (Thompson et al., 1995). Other evidence for dry and warm climate conditions during the following period are inferred from reduced river runoff into the Pacific starting from 1150 yr BP (Rein et al., 2004), changes in oxygen isotopes from a calcite deposit indicating an extreme drought around 1000 yr BP (Bird et al., 2011b), together with a high dust content in the Quelcaya ice cores (960-830 yr BP Thompson et al., 1988). In addition, the resurgence of agriculture at altitudes >3000 m at 920 yr BP due to warmer conditions (Chepstow-Lusty et al., 2003), and low lake-levels at Titicaca at 850 yr BP (Abbott et al., 1997a; Binford et al., 1997) and other Central Andean lakes at 750 yr BP (Hillyer et al., 2009) support these patterns of increasing aridity and warmth at this time. In contrast, colder conditions in combination with a dry climate are solely reported by Kuentz et al. (2011) from pollen analysis in the timeframe between 980-820 yr BP. The end of this arid period is less clear, ranging from 750 yr BP (Schittek et al., 2015), through to 700 yr BP (Rein et al., 2004), and until 650 yr BP (Thompson et al., 1995).

After this transition from 750-650 yr BP, more humid but highly unstable climatic conditions occur (Schittek et al., 2015), including a temporary decrease in precipitation, e.g. around 660 yr BP (Schittek et al., 2015), extremely strong summer monsoons at 550 yr BP (Bird et al., 2011b), and heavy clastic influx into Andean lakes at about 500 yr BP (Rodbell et al., 2008). Additionally, this period is characterised by distinctly lower temperatures, e.g. with evidence of glacial advance starting at around 600 yr BP (Stansell et al., 2013). A marked change in the isotopic composition of a calcite record at about 650 yr BP suggests a significant

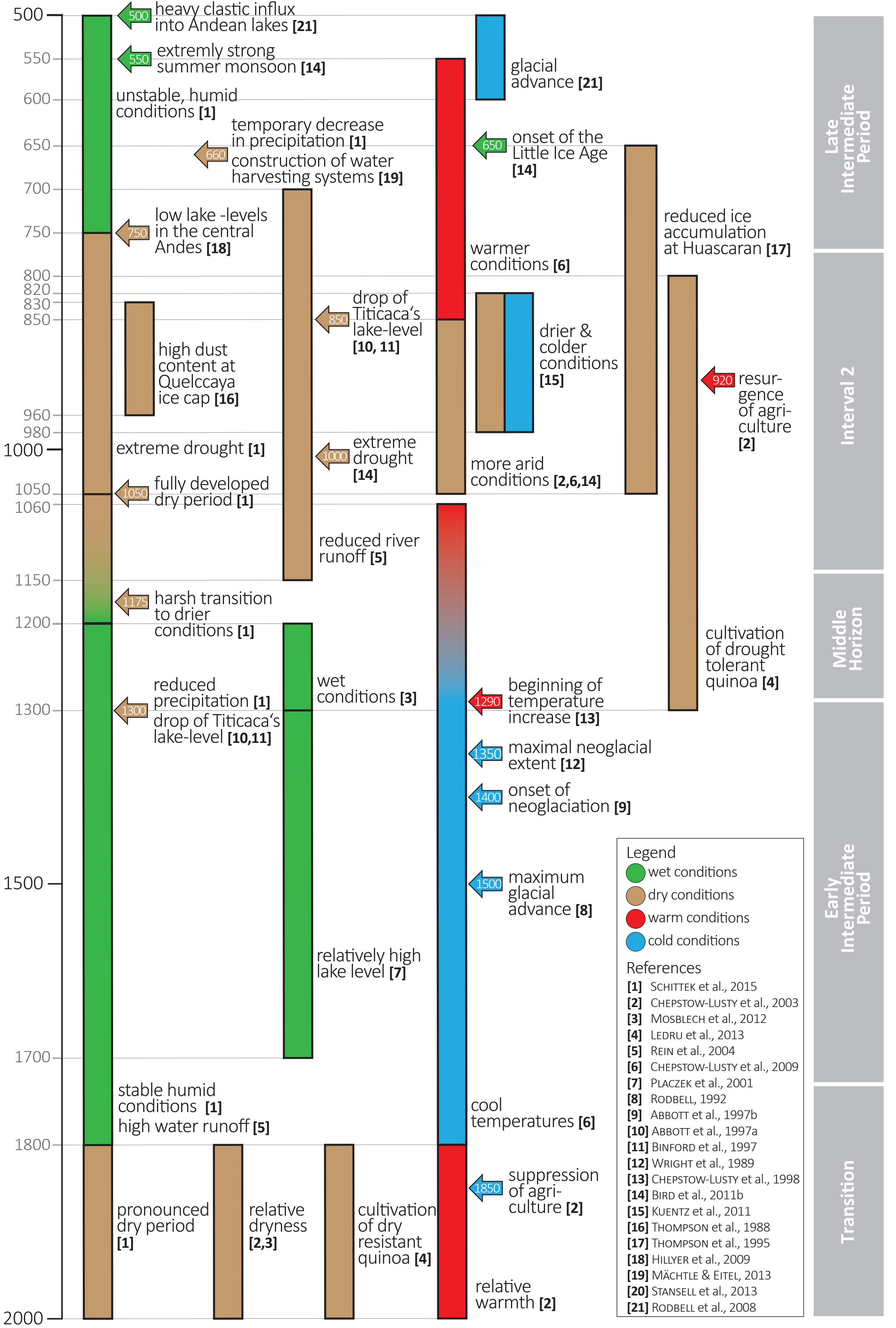

Figure 6.4 | Schematic overview of relevant palaeoclimatic evidence from the Central Andes for the 2000-500 yr BP period investigated. All ages are given as cal. yr BP. The archaeological cultural chronology for the western slope and coastal regions of southern Peru follows Unkel et al. (2012).

temperature decrease (Bird et al., 2011b), which is interpreted as the onset of the "Little Ice Age", referring to the climate anomaly better known from the Northern Hemisphere (Ljungqvist, 2010).
An overview of the different sources of evidence for the described climatic fluctuations is given in Figure 6.4.

6.1.5 | Local archaeological setting

A chronology of pre-Columbian cultures in the Nasca region and adjacent Andean areas has been proposed by Unkel et al. (2012). This is based on precise dating of cultural transitions and the limits of pre-Columbian periods. An excerpt of this chronology, spanning the interval of ca. 2250-400 yr BP, is shown in Figure 6.5. From this interval, four cultures are known: Initial Nasca (2280-1840 yr BP), Nasca (1910-1290 yr BP) – subdivided into three phases (Early Nasca: 1910-1610 yr BP, Middle Nasca: 1680-1480 yr BP, Late Nasca: 1540-1290 yr BP), Wari (1330-1100 yr BP) and Ica (820-390 yr BP). These can be assigned broadly to four corresponding archaeological periods: Initial Nasca to the Transition Period (2210-1870 yr BP), Nasca to the Early Intermediate Period (1870-1310 yr BP), Wari to the Middle Horizon (1310-1160 yr BP) and Ica to the Late Intermediate Period (770-415 yr BP). The period of no archaeological evidence in the region from 1160-770 yr BP is referred to as Interval 2.

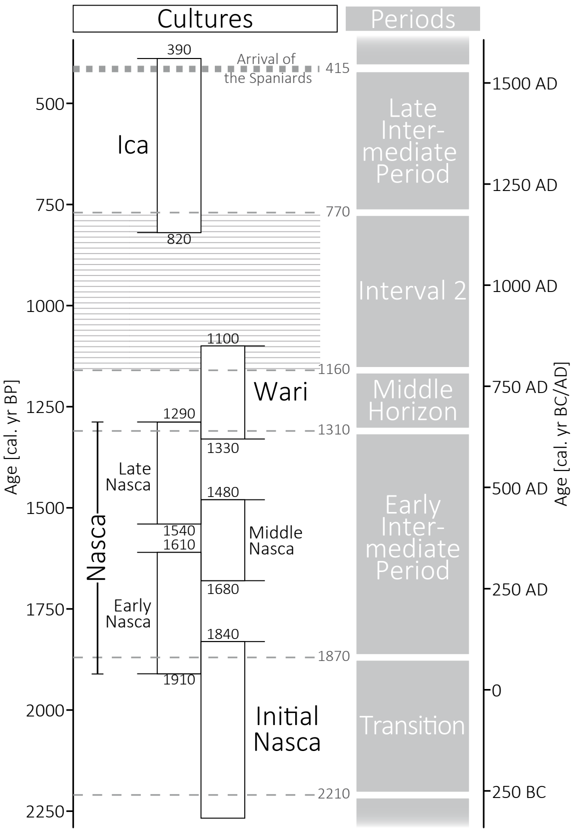

Figure 6.5 | Chronology of Pre-Columbian cultures in the Nasca region and archeological periods proposed by Unkel et al. (2012) focussing on the 2250-400 yr BP time interval. The white ribbons indicate the temporal span of individual cultures, whereas black solid lines and dates mark the age of each culture by its 1σ probability interval of ^{14}C dating. Boundaries of periods (grey dashed lines and grey dates) are defined by the median age of two overlapping cultural phases. The archaeological periods are shown as grey boxes. The period of archaeological silence with so far no archaeological findings (Interval 2) is hatched. An additional thick dashed line marks the arrival of the Spaniards in the region. All ages are given in cal. yr BP. For easier conversion, the cal. yr AD/BC timescale was added on the right side of the diagram.

6.1.6 | Hypotheses

Two main hypotheses are tested in this investigation:

- The preserved Oribatid mite and Chironomid assemblages in the peat deposits of the CLP show significant changes in time.
- A combined use of the Oribatid mite and Chironomid proxies and indicator functions quantitatively reveals environmental changes in time.

6.2 | Material & Methods

6.2.1 | Material

In total, 23 palaeosamples between 623-471 cm depth were analysed from the core Pe852, retrieved in 2009 (Schittek et al., 2012, 2015). The sample treatment and subfossil preparations are identical to the procedures applied to the modern peatland samples (see Chapter 3.2.2).

6.2.2 | Identification

The Oribatid mites and Chironomids were identified according to the literature listed in Chapter 3.2.5. For the identification of other faunal subfossils, additional references such as Domínguez & Fernández (2009), McAlpine et al. (1981) and Szadziewski et al. (1997) were used.

6.2.3 | Chronology

The chronology was established by ^{14}C dating of peat samples from the retrieved cores. Dating was carried out at the Klaus Tchira Centre for Archaeometry and Heidelberg Academy of Sciences, and calibrated with the CALIB 6.0.1 software using the IntCal09 data set (Reimer et al., 2009). For further methodological procedure and full information on the used dates, see Schittek et al. (2015).

6.2.4 | Numerical analysis

With the help of the rioja package ver. 0.9-5 (Juggins, 2015), stratigraphical clustering was obtained with a constrained incremental sum of squares (CONISS) method (Grimm, 1987). For the prediction of environmental values from biological assemblages for the investigated time interval, different analysis methods such as a Weighted Averaging regression and calibration (WA), the Maximum Likelihood Response Surfaces analysis (MLRC), a Modern Analogue Technique (MAT) based on chord distances, and the Imbrie & Kipp Factor Analysis (IKFA) were used, which are all implemented in the rioja package (Juggins, 2015). All derived models were cross-validated running 1000 bootstrap routines. For the selection of an adequate environmental reconstruction model for all datasets, the root mean squared error (RMSE), maximal bias and determination coefficient (R^2) were compared following the procedure by Juggins & Birks (2012). For a better visualisation of the geochemical data, the 'Gaussmooth' function by Rehfeld et al. (2011) was used, which smoothes irregularly sampled time series with gaussian weights.

6.3 | Results

6.3.1 | Stratigraphy and chronology of core Pe852

The stratigraphy and age-depth model of core Pe852 has been published by Schittek et al. (2015). In general, the substrate consisted of peat more or less intermixed with silt, clay and sand. These peat layers of varying thickness were interrupted by debris material consisting of pure fine or medium sand, or coarse sand and gravel. These kinds of substrate, resulting from the interplay of

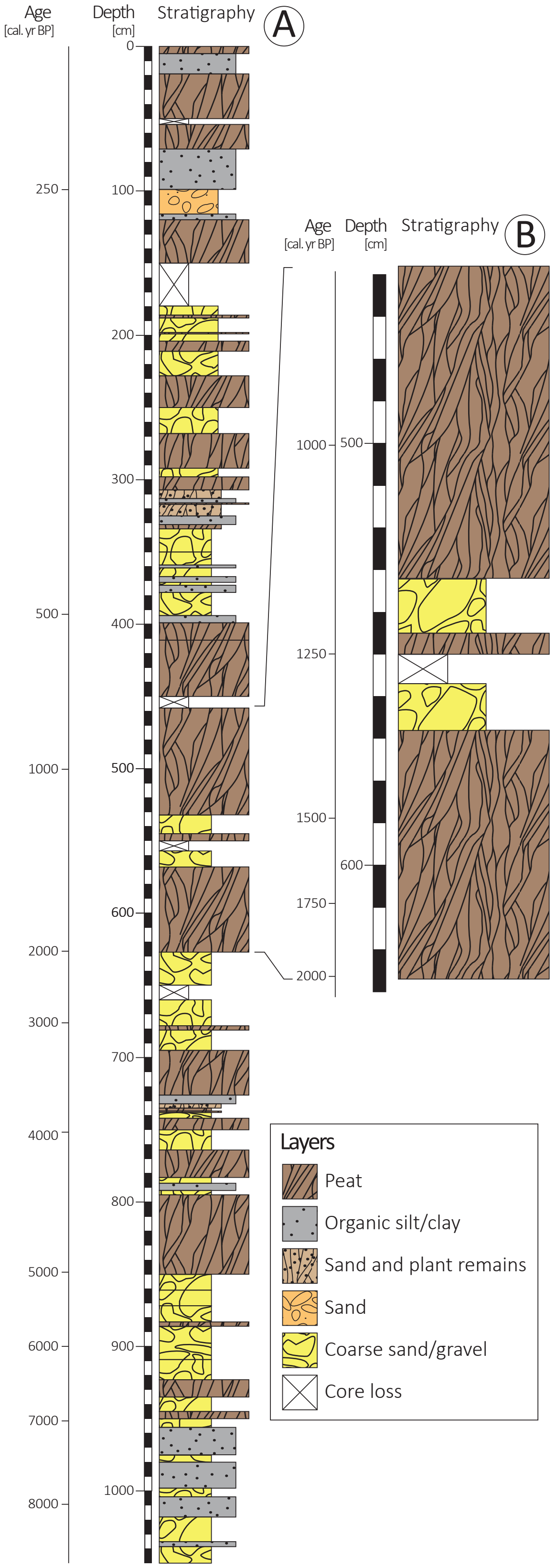

Figure 6.6 | Stratigraphy of the complete core Pe852 (A) by Schittek et al. (2015). The subsection (625-450 cm) investigated in this study is shown in detail (B). The age of the sediment is marked in an additional non-symmetric axis in both diagrams.

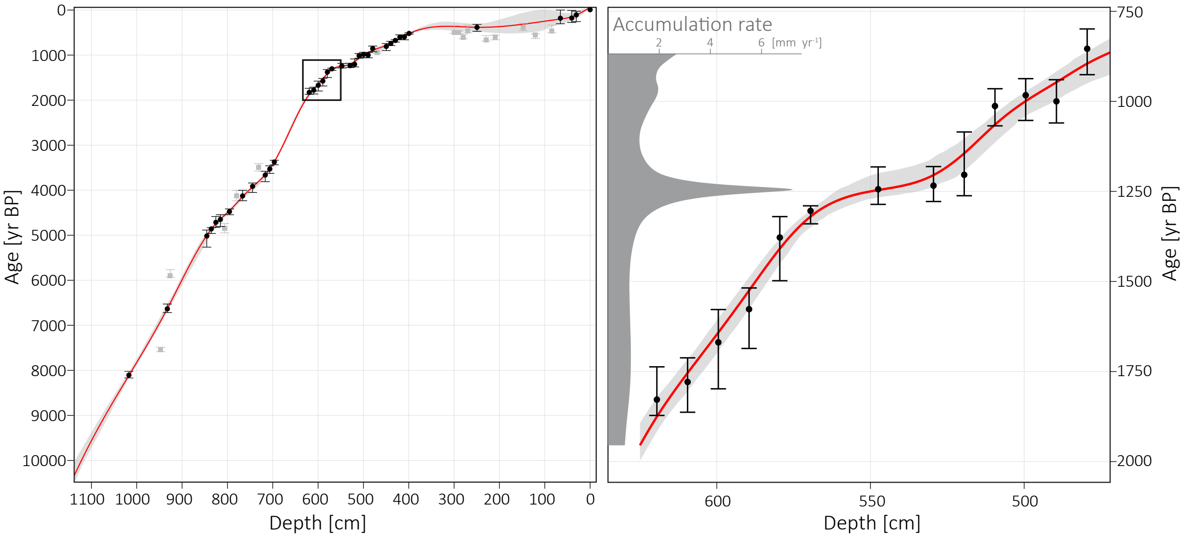

Figure 6.7 | The age-depth model of core Pe852 (left) (Schittek et al., 2015) and the section 625-470 cm in detail (right). The red line indicates the median of 800 Monte Carlo simulations, which was also used to calculate the confidence interval (grey area) of the probabilistic age-depth model. Each calibrated (IntCal09) radiocarbon date is shown with its specific confidence interval. In the left diagram, grey symbols indicate omitted dates before age-depth-modelling. In the right diagram, the accumulation rate is depicted additionally.

alluvial and aeolian sediment influx, debris deposition and peat growth, are typical for high-altitude cushion peatlands (Schittek et al., 2012).

This study focused on a subdivision of the core from 623-471 cm (see Figure 6.6). The deepest part was characterised by a thick pure peat layer from 625-568 cm before a coarse sand/gravel layer appeared from 568-533 cm. Within this sand/gravel section, the sediment from 557-550 cm was lost during coring. A thinner peat layer was enclosed from 550-544 cm. Subsequently, the upper part of the subsection was again characterised by a thick peat layer from 533-471 cm.

The age-depth model of core Pe852 is based on 50 radiocarbon dates, of which, due to presumably re-deposition, 15 were excluded from modelling (Schittek et al., 2012). For the core section between 623-471 cm, used in this study, 13 ^{14}C dates determine the age-depth model (see Figure 6.7) suggesting an age of 1924 yr (95% CI: 1866-1968) to 860 yr (95% CI: 821-922). The accumulation rate was stable around 0.8 mm per year from 1924 yr BP to about 1300 yr BP, before it rapidly increased to >6 mm per year at 1250 yr BP. From then, until circa 1200 yr BP, the accumulation rate decreased again to 1.2 mm per year, whereas after 1060 yr BP, the rate started to evenly decrease to 2.6 mm per year at the upper end of the core section at 870 yr BP.

6.3.2 | The subfossil Oribatid mite community

In total, 123 oribatid specimens were found, belonging to 16 taxa (15 species and one genus type). 6% of all the specimens found could not be identified. Nine taxa could still be found in modern samples from the peatland (see Chapter 3.3.2), but seven taxa occurred only in the archive samples. The subfossil community consisted of nine families, of which the Ceratozetidae and Scheloribatidae were represented most by four members each. A full overview of the subfossil Oribatid mite fauna is given in Table 6.3.

6.3.2.1 | Taxonomy, zoogeography and autecology

The majority of the identified subfossil taxa are also present in modern surface samples. The description for these is presented in Chapter 3.3.2. Taxonomic remarks and information on the zoogeography and autecology for the exclusively subfossil taxa are given here:

1. *Anderemaeus* cf. *monticola* Hammer, 1958

Taxonomy: the protuberances on the lamellae, the presence of well developed sublamellae, a chitinous triangular behind the origin of the interlamellar hairs and a sternal ridge between epimera I and II referred to *Anderemaeus monticola*. In contrast to

Table 6.3 | Systematic overview of the subfossil Oribatid mite community identified from the CLP

Family *Species*	Author
Nanhermannidae	
1. *Nanhermannia* cf. *elegantissima*	Hammer, 1958
Caleremaeidae	
3. *Anderemaeus* cf. *monticola*	Hammer, 1958
Oxyoppiinae	
3. *Oxyoppia suramericana*	Hammer, 1958
4. *Neoamerioppia* cf. *notata*	Hammer, 1958
Phenopelopidae	
5. *Eupelops apicalis*	Hammer, 1962
Oribatellidae	
6. *Oribatella illuminata*	Hammer, 1961
Ceratozetidae	
7. Ceratozetes nigrisetosus	Hammer, 1958
8. *Jugatala armata* *Syn. Edwardzetes armatus*	Hammer, 1958
9. *Jugatala montana* *Syn. Trichoribates hammerae*	Hammer, 1961 Subías, 2010
10. *Zetomimus furcatus*	Warburton & Pearce, 1905
Liebstadiidae	
11. *Areozetes altimontanus*	Hammer, 1961
Scheloribatidae	
12. *Scheloribates confundatus*	sensu Hammer, 1961; non sensu Berlese, 1908
13. *Scheloribates* cf. *elegantulus*	Hammer, 1961
14. *Scheloribates huancayensis*	Hammer, 1961
15. *Scheloribates laticlava*	Hammer, 1961
16. *Scheloribates pallidulus*	sensu Hammer, 1958; non sensu Koch, 1841

the original description of the species by Hammer (1958), the rostrum was pointed as was indicated for *A. chilensis* and *A. magellanis* (Hammer, 1962a). The description was based on 17 specimens.

Zoogeography & autecology: *A. monticola* is known from the Neotropics and south-eastern China (Subìas, 2004) and prefers moist habitats, inhabiting bryophytes and cushions of various other plants (Balogh & Balogh, 1988).

2. *Eupelops apicalis* Hammer, 1962

Taxonomy: the genus *Eupelops* could be identified by a sclerotised bridge on the anterior part of the notogaster between the pteromorphae (Balogh & Balogh, 1990). The three found specimens of

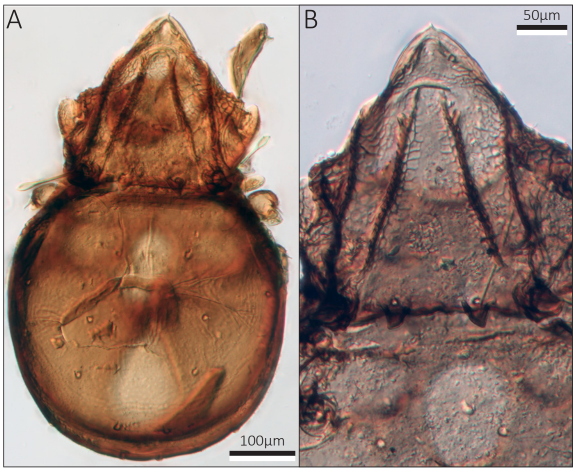

Figure 6.8 | *Anderemaeus* cf. *monticola:* dorsal view (A) and details of the prodorsum (B)

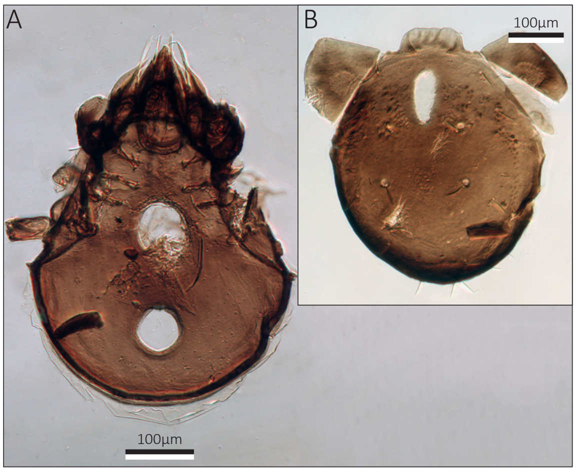

Figure 6.9 | *Eupelops apicalis:* dorsal view on the ventral plate (A), and details of the notogaster (B)

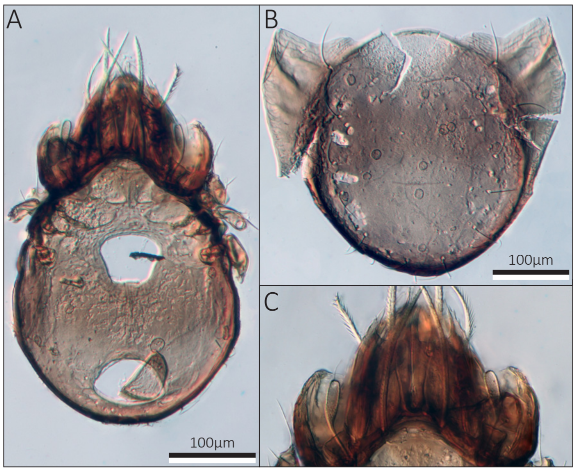

Figure 6.10 | *Oribatella illuminata:* dorsal view on the ventral plate (A), and details of the notogaster (B) and the prodorsum (C)

Eupelops apicalis resembled the description given by Hammer (1962b)
Zoogeography & autecology: *E. apicalis* is known from parts of the Neotropics, namely from Argentina, where it was associated with mosses and other plants on wet soils (Hammer, 1962b), as wells as from high altitudes in southern Ecuador (Illig et al., 2007). Members of the genus Eupelops are characterised as secondary decomposers, feeding on fungi and in part on litter (Schneider et al., 2004). The ecology of the genus is described as mesohygrophilous, being associated with peatlands, springs and wet forests in Europe (Wild et al., 2008).

3. *Oribatella illuminata* Hammer, 1961

Taxonomy: the morphological characteristics of the four specimens of *Oribatella illuminata* found in this study concurred with the descriptions provided by Hammer (1961). The most important features for identification of this species within the genus *Oribatella* were the large and pointed pteromorphae and the distinctly long sensillus, which consisted of a clavate and ciliated head, and a long stalk (Balogh & Balogh, 1990).
Zoogeography & autecology: the species *Oribatella illuminata* is only known from Peru and Chile (Subìas, 2004) and was found in thick moist mosses at high altitude (Hammer, 1961). Members of the genus *Oribatella* are known to be primary decomposers, feeding mostly on litter and partly on fungi (Schneider et al., 2004). However, the genus is rich in species, comprising more than 100 species (Behan-Pelletier & Paoletti, 1993), which impedes the generalisation of ecological traits.

4. *Areozetes altimontanus* Hammer, 1961

Taxonomy: the morphological characteristics of the three specimens found resembled the descriptions by Hammer (1961). The most important features for identification were the very broad ribbon-like lamellae, the big pteromorphae, and the large areae porosae on the notogaster, distinctly surrounded by a ring (Balogh & Balogh, 1990).
Zoogeography & autecology: *A. altimontanus* has only been identified from Peru and the Canary Islands (Subìas, 2004). In Peru, the species was found in mosses on wet soils at altitudes >4000 m (Hammer, 1961).

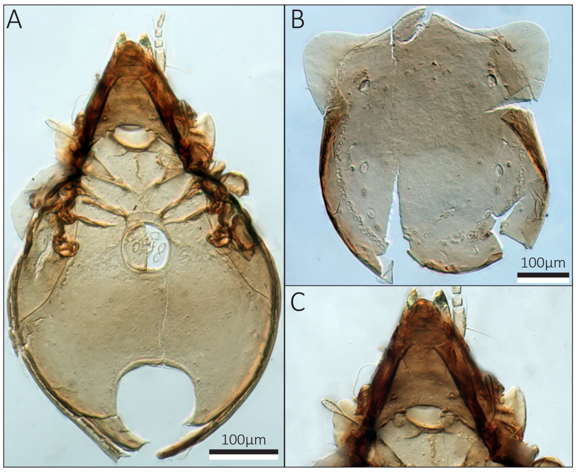

Figure 6.11 | *Aerozetes altimontanus:* dorsal view on the ventral plate (A), and details of the notogaster (B) and the prodorsum (C)

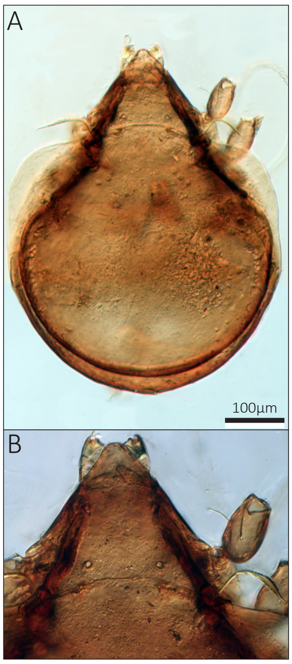

Figure 6.12 | *Scheloribates huancayensis*: dorsal view (A) and details of the prodorsum (B)

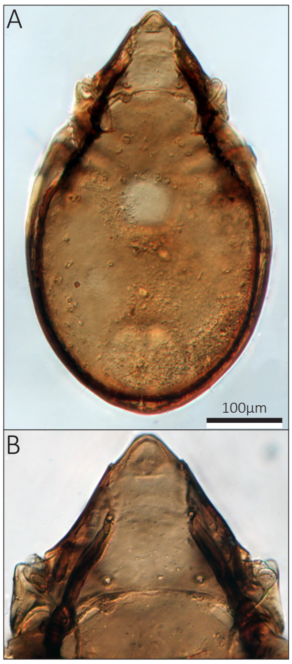

Figure 6.13 | *Scheloribates laticlava*: dorsal view (A) and details of the prodorsum (B)

5. *Scheloribates huancayensis* Hammer, 1961

Taxonomy: *Scheloribates huancayensis* was characterised by a hysterosoma that shows a semi-circular posterior part and an almost rectangular anterior part, derived from very broad and nearly right-angled pteromorphae. Additionally, the pseudostigmatic organs were very long as a result of a long stalk in combination with an elongated, very narrow and bristly head, running out in a fine tip (Hammer, 1961). However, in contrast to the descriptions and drawings provided by Hammer (1961), the four specimens examined showed clearly visible maculae anterior on the notogaster, which seem to be typical for neotropical Scheloribatid taxa (see Chapter 3.3.2).

Zoogeography & autecology: *S. huancayensis* has been identified from the Neotropics and India (Subìas, 2004). In the Andes, the species was found in wet mosses at 3500 m a.s.l (Hammer, 1961). The species reproduces sexually (Maraun et al., 2013).

6. Scheloribates laticlava Hammer, 1961

Taxonomy: the best recognisable characteristics of *Scheloribates laticlava* in comparison to other species of the same genus were a pseudostigmatic organ that shows a broad, flat and rounded head with a distinctly short stalk, and the elongated rather than truly rounded shape of the hysterosoma, with rounded shoulders of the pteromorphae (Hammer, 1961). Recent studies verify the taxonomic position of *S. laticlava* (Ermilov & Anichkin, 2014). As it was the case for all Scheloribatid species in this study, all ten specimens examined of *S. laticlava* featured maculae on the notogaster.

Zoogeography & autecology: *Scheloribates laticlava* shows a pantropic distribution (Illig et al., 2007), occurring in the Neotropics and the Himalaya (Subìas, 2004), and inhabits mosses at high altitude (Hammer, 1961; Iglesias et al., 2008).

6.3.3 | The subfossil Chironomid community

1199 specimens were investigated, which, after consideration of separated head capsules, comprised a minimum number of 761 individuals, including 15.6% not identifiable. In total, 12 taxa were identified belonging to four subfamilies. Of these, ten taxa could also be identified in modern surface peatland samples (see Chapter 3.3.3). The subfamily Orthocladiinae was the most diverse in the subfossil Chironomid assemblage, comprising nine taxa. A systematic overview on the subfossil Chironomid fauna is given in Table 6.4.

6.3.3.1 | Taxonomy & autecology

Most of the identified taxa were also present in modern surface samples. The description for these is given in Chapter 3.3.3. In the following, taxonomic and ecological remarks for the exclusively subfossil taxa represented are denoted:

1. *Podonomus*

Taxonomy: in accordance to the description by Prat & Rieradevall (2011), the mentum showed five median teeth and 5-6 lateral teeth. The median

Table 6.4 | Systematic overview of the subfossil Chironomid community identified from the CLP

Sub-family *Species*	Author	Taxonomic description
Tanypodinae		
1. *Apsectrotanypus/Alotanypus*	Johannsen-Roback	Williams et al., 2012; Prat & Rieradevall, 2011
Podonominae		
2. *Parochlus*	Enderlin	Prat & Rieradevall, 2011; Brooks et al., 2007
3. *Parochlus*	Enderlin	Prat & Rieradevall, 2011; Brooks et al., 2007
Diamesinae		
4. *Diamesinae-type*	Kieffer	Prat & Rieradevall, 2011
Orthocladiinae		
5. *Limnophyes/Paralimnophyes*	Eaton	Williams et al., 2012; Brooks et al., 2007
6. *Smittia/Parasmittia*	Holmgren	Brooks et al., 2007
7. *Cricotopus/Paratrichocladius* type I	van der Wulp	Matthews-Bird et al., 2016; Williams et al., 2012
8. *Cricotopus/Paratrichocladius* type II	van der Wulp	Matthews-Bird et al., 2016; Williams et al., 2012
9. *Paracricotopus*	Thienemann & Harnisch	Brooks et al., 2007
10. *Pseudosmittia*	Goetghebuer	Brooks et al., 2007
11. *Pseudorthocladius*	Goetghebuer	Brooks et al., 2007
12. *Parametriocnemus/Paraphaenocladius*	Goetghebuer-Thienemann	Prat & Rieradevall, 2011; Brooks et al., 2007

teeth were of similar size and form an even apex. The lateral teeth overlaid each other with the result that the lateral dentation was hardly visible. Even in fossil specimens, the premento-hypopharyngeal complex was often visibly well preserved. The description was based on five specimens.

Ecology: The Podonominae in general are cold-tolerant and rheophilic taxa, depending on high oxygen conditions (Ashe et al., 1987).

2. Diamesinae-type

Taxonomy: in accordance to the description by Prat & Rieradevall (2011), the mentum featured more than 12 teeth which is in accordance with the subfamily Diamesinae. The arrangement of the teeth with slightly recessed median teeth suggested an affiliation with *Paraheptagyia*. However, due to poor preservation of the only two specimens found, further determination was not possible.

3. *Smittia/Parasmittia*

Taxonomy: in accordance tothe description by Brooks et al. (2007), the mentum had a single median tooth and five lateral teeth. The median tooth was broad and showed a distinct hump in the centre with shoulders to the lateral sides of the median tooth. The lateral teeth decreased in size from the first to the fifth. The sockets of the SSm were positioned close to an imaginary line between the bases of the fifth lateral teeth on each side. The description was based on seven specimens.

Ecology: Most species in the *Smittia/Parasmittia* genera are terrestrial (Cranston et al., 1983;

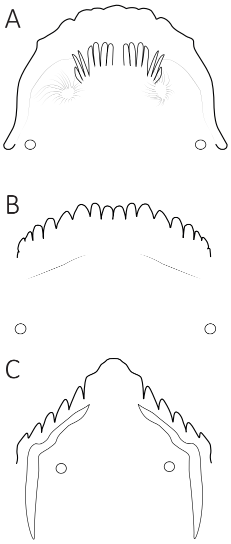

Figure 6.14 | Characteristic features of the Chironomid taxa exclusively found as subfossils, summarised as schematic drawings: **A)** mentum of *Podonoms;* **B)** mentum of *Diamesinae*-type; **C)** mentum of *Smittia/Parasmittia.* The taxa, which were also found in the modern community, are schematically drawn in Figure 3.31

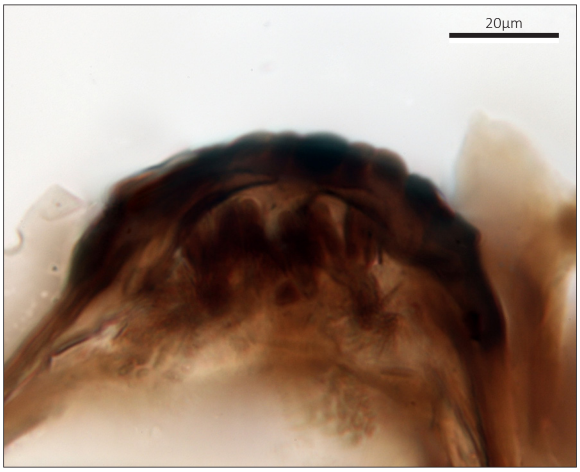

Figure 6.15 | *Podonomus:* details of the mentum

Figure 6.16 | *Diamesinae*-type*:* ventral view on a headcapsule

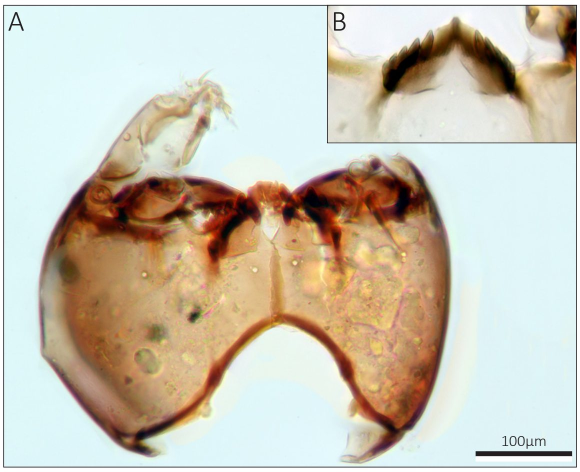

Figure 6.17 | *Smittia/Parasmittia:* ventral view on a headcapsule (A) and details of the mentum (B)

Epler, 2001), but some authors assume that the taxon occurs in the littoral zone of lakes and link their presence in lake sediments to erosion (Brooks et al., 2007). Members of the genus *Parasmittia* are known from the soils of meadows and woodlands (Ashe et al., 1987).

6.3.4 | Other subfossil remains

Besides Chironomids, some other dipteran taxa could be identified from the palaeosamples:

In total, 67 subfossil remains of the family Ceratopogenidae, the “biting midges”, were identified. The Ceratopogenidae were the most abundant of the non-chironomid taxa (mean of all samples= 1.3 specimens cm^{-3}). When present, the density of deposited Ceratopogenids ranged from 0.4-5.8 specimens cm^{-3}. The head capsules of this taxon can be identified by the conspicuous two-armed pharyngeal apparatus. This apparatus is located inside the head capsule and shows a semi-circular row of teeth in the central part (McAlpine et al., 1981) (see Figure 6.18 and Figure 6.19). The ecology of the Ceratopogenidae is highly varied; however, all species need moist environments for egg and larval development (Borkent & Spinelli, 2007; Brooks et al., 2007).

Six head capsules were found which belong to the family Simuliidae, the “black flies”. The Simuliid head capsules can easily be distinguished from other dipterans by the large size and the prolonged feeding apparatus, the hypostoma, which features heavily sclerotised teeth at the anterior margin (see Figure 6.20-A,B). These teeth are often distinctly grouped in a central group with one lateral group on each side (McAlpine et al., 1981). The abundance of Simuliid remains in the peat sediments was low (mean of all samples = 0.06 specimens cm^{-3}), with a range of 0.5-0.7 specimens cm^{-3} in the samples in which this taxon was found. Simuliid taxa occur in highly variable environments, in relation to factors such as temperature or salinity. However, as all Simuliids filter water to obtain food and oxygen, the only distinct environmental consideration within the entire family is their dependence on continuously running water (Brooks et al., 2007; Coscarón & Arias, 2007).

Five head capsules derived from the palaeosamples can most probably be assigned to the family Thaumaleidae. This represented a mean abundance of 0.11 specimens cm^{-3} in all samples, ranging from 0.5-1.3 specimens cm^{-3} in the sediment layers in which Thaumaleids were present. The larval head capsules are characterised by an elongated and distinctly bent hypostoma (McAlpine et al., 1981; Brooks et al., 2007) (see Figure 6.20-C). Thaumaleid larvae are found on vertical structures such as rocks, which are washed gently by a water film (i.e. hygropetricous), that has to be thin enough not to submerge the larvae (Smith, 1989). In general, the biology of this dipteran family remains largely unknown (McAlpine et al., 1981).

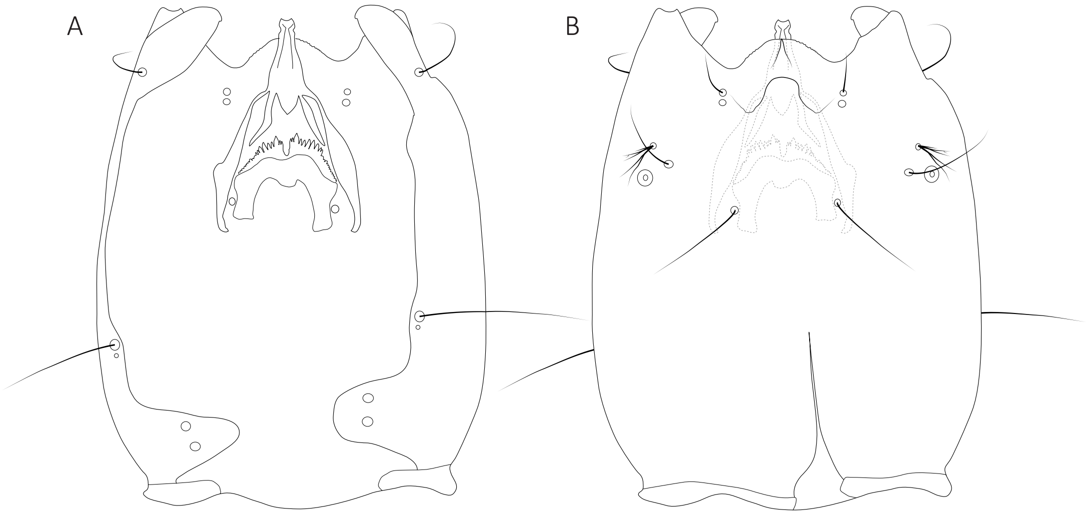

Figure 6.18 | Schematic drawing of a *Ceratopogenidae* headcapsule: (A) shows on the ventral side with the details of the feeding apparatus, and (B) the dorsal setation

Figure 6.19 | *Ceratopogenidae:* ventral view (A) and dorsal view (B) on a headcapsule

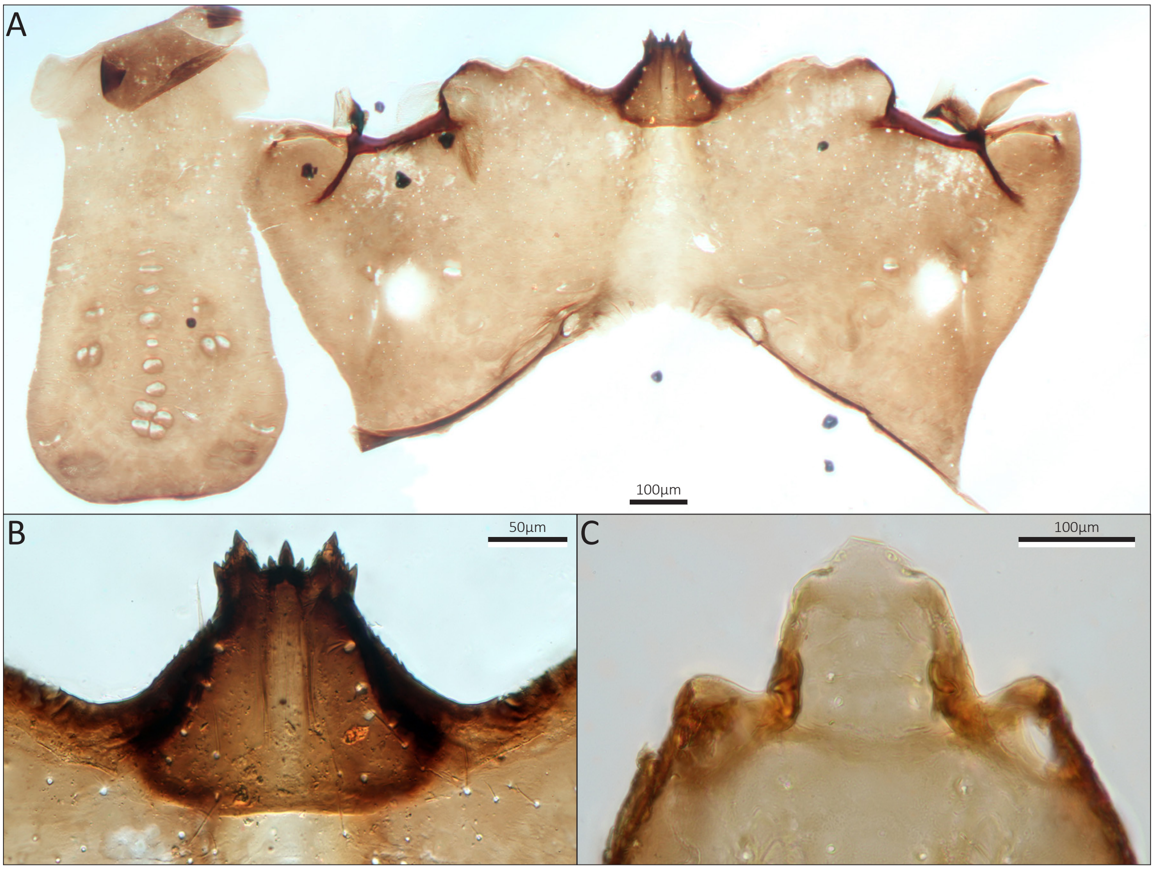

Figure 6.20 | Other dipteran subfossil remains: A) overview of a unfurled Simuliidae-headcapsule and B) details of the corresponding hysterosoma; C) anterior part of a Thaumaleidae-headcapsule

6.3.5 | Stratigraphic distribution of subfossil Oribatid mites

The most abundant taxa derived from the palaeosamples were *Neoamerioppia notata* (mean number = 0.82 specimens cm^{-3}), *Oxyoppia suramericana* (mean number = 0.46 specimens cm^{-3}) and *Anderemaeus monticola* (mean number = 0.40 specimens cm^{-3}). All other 13 taxa showed lower mean densities with <0.3 specimens cm^{-3}. The densities of Oribatid mites ranged from 0.4-4.8 specimens cm^{-3} in the investigated samples which contained any subfossil remains.

Based on the changes in abundance of subfossil Oribatid mites, the investigated core section could be subdivided into three stratigraphic zones by significant CONISS clustering solutions (see Figure 6.21). These zones ranged from: **I**) 1924 to 1903±7 yr BP; **II**) 1903±7 to 1426±22 yr BP, and; **III**) 1426±22 to 861 yr BP.

The Oribatid community of **zone I** was characterised by the highest observed overall density, with 22.7 specimens cm^{-3} at 1910 yr BP and the highest diversity with nine species in this time interval. Four species, *Scheloribates laticlava*, *S. huancayensis*, *S. confundatus* and *Areozetes altimontanus* occurred only in this part of the record. During this short occurrence, some species showed high abundances, e.g *S. laticlava*, *Neoamerioppia notata* and *Anderemaeus monticola* with 4.7 specimens cm^{-3} each or *S. huancayensis* with 2.7 specimens cm^{-3}. Rare species of zone I were *Scheloribates pallidulus*, *Zetomimus furcatus*, and *Jugatala montana* with abundances of 0.7 specimens cm^{-3}.

In **zone II**, the overall density of Oribatid mites decreased to average values of 5.7 specimens cm^{-3} with a distinct peak of 12.7 specimens cm^{-3}. The diversity was lower compared to zone I and fluctuated from five species at 1896 yr BP to two species from 1771-1692 yr BP before it increased again to five species at 1448 yr BP. The most abundant species in this zone was *Neoamerioppia notata*, with a mean abundance of 1.73 specimens cm^{-3} and two clear peaks at 1692 and 1519 yr BP. In between, at 1566 yr BP, the species was absent in the record. A similar occurrence pattern showed *Oxyoppia suramericana*, which exclusively was found in zone II, where it was quite common with a mean abundance of 1.5 specimens cm^{-3} (with peaks at 1692 and 1519 yr BP) with a period of absence at 1636 yr BP. Additionally, two other species could be found solely in this zone, with abundances of 0.7-1.0 specimens cm^{-3} from 1519-1448 yr BP for *Eupelops apicalis* and 0.7 specimens cm^{-3} at 1636 yr

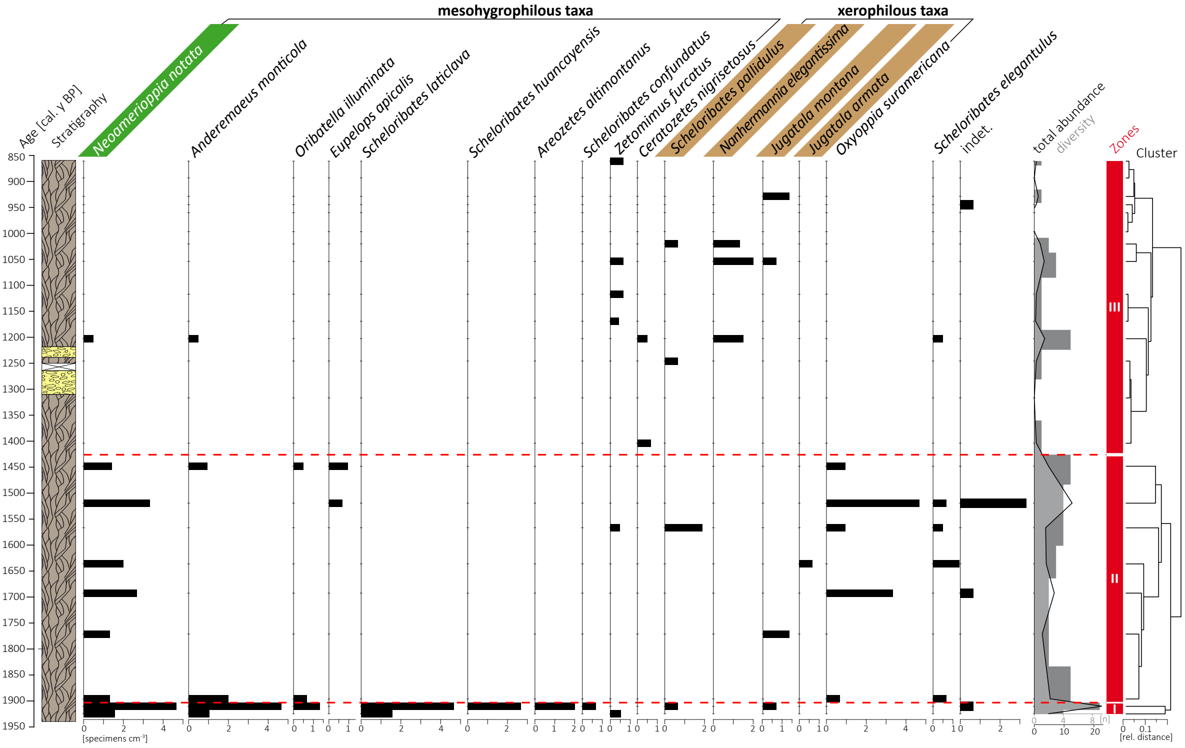

Figure 6.21 | Stratigraphic distribution of subfossil Oribatid mites between 1924-860 yr BP. The significant indicator species for soil wetness conditions >73% is marked in green, and the indicators for conditions <57% in brown. The depth zonation was achieved using the CONISS method. Significant zones are marked by the red dotted lines. Additionally, the stratigraphy of the core, the total abundance of Oribatd mite subfossils and the corresponding taxa diversity are depicted.

BP for *Jugatala armata*. Two species, *Anderemaeus monticola* and *Oribatella illuminata*, with highest abundances in zone I, disappeared around 1896 yr BP and re-appeared briefly at 1448 yr BP with low densities of 1.0 and 0.5 specimens cm^{-3} respectively. *Scheloribates elegantulus* first occurred at 1896 yr BP in the record, before re-appearing at 1636 yr BP with 1.3 specimens cm^{-3} until 1519 yr BP with mean densities of 0.6 specimens cm^{-3}.

The revealed Oribatid mite community of **zone III** was less divers with a mean of 1.1 species per sample. The overall abundance of Oribatid mites was also lower, attaining a mean of 1 specimens cm^{-3}. The dominant species of the older zones I and II, *Neoamerioppia notata*, almost completely vanished with only a single occurrence at 1203 yr BP which equated to 0.5 specimens cm^{-3}. Similarly, *Anderemaeus monticola* and *Scheloribates elegantulus*, both found repeatedly and with higher densities in zone II, was only found at 1203 yr BP with an average density of 0.5 specimens cm^{-3}. The most abundant species of zone III became *Nanhermannia elegantissima*, which first occurred at 1203 yr BP with 1.5 specimens cm^{-3} and again at 1054 and 1020 yr BP with 2.0 and 1.3 specimens cm^{-3}, respectively. All other species in this zone showed low abundances and singular occurrences: *Ceratozetes nigrisetosus* occurred at 1404 and 1203 yr BP with 0.7 and 0.5 specimens cm^{-3}, respectively; *Scheloribates pallidulus* at 1245 and 1020 yr BP both with 0.7 specimens cm^{-3}; and *Jugatala montana* at 1054 and 929 yr BP with 0.7 and 1.3 specimens cm^{-3}, respectively. The only species for which a relatively constant occurrence over a long time period in zone II was revealed is *Zetomimus furcatus*. It was found continuously from 1317-1054 yr BP with mean densities of 0.6 specimens cm^{-3} in mean.

6.3.6 | Stratigraphic distribution of subfossil Chironomids

The most abundant taxa in the palaeosamples were *Limnophyes/Paralimnophyes* with a mean of 8.3 specimens cm^{-3} and *Parochlus* with a mean of 3.2 specimens cm^{-3}. All the other 12 taxa showed mean abundances of <0.7 specimens cm^{-3}. *Limnophyes/Paralimnophyes* was the only taxon that could be identified from every sample. The overall density of Chironomids in the investigated core section ranged between 0.7-71.3 specimens cm^{-3} and with a mean of 20.0 specimens cm^{-3}.

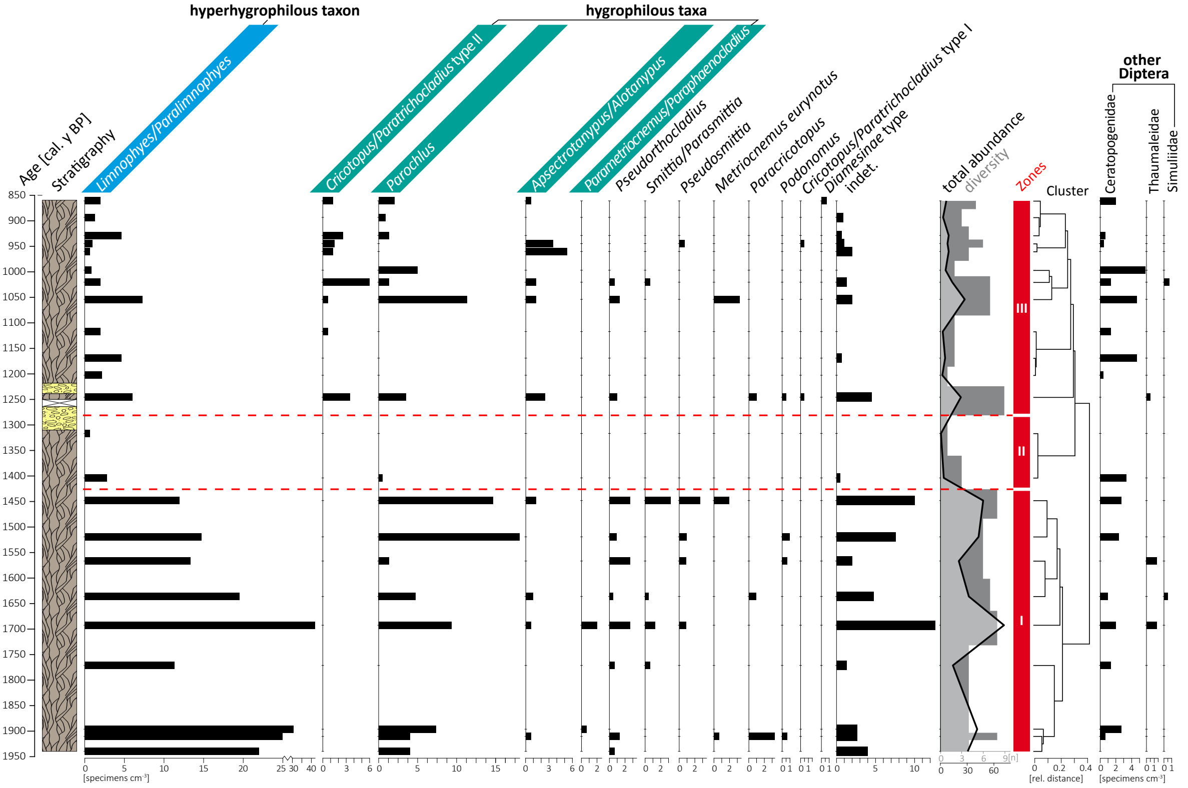

Figure 6.22 | Stratigraphic distribution of subfossil Chironomids between 1924-860 yr BP. The significant indicator taxon for soil wetness conditions of >81% is marked in blue, and the indicators for conditions of 80-81% in blue-green. The depth zonation was achieved using the CONISS method. Significant zones are marked by the red dotted lines. Additionally, the stratigraphy of the core, the total abundance of Chironomid subfossils and the corresponding taxa diversity are depicted.

Using the CONISS clustering method, the changes in Chironomid abundances subdivided the palaeorecord into three zones (see Figure 6.22). These zones ranged from: **I**) 1924 to 1426±22 yr BP; **II**) 1426±22 to 1287±35 yr BP; and **III**) 1287±35 to 861 yr BP.

The Chironomid community of **zone I** was characterised by a high diversity with a mean of 5.1 taxa and a high overall density of Chironomid remains, with a mean abundance of 37.6 specimens cm^{-3}. The most common taxon in this zone (with a mean of 21.1 specimens cm^{-3}), *Limnophyes/Paralimnophyes*, showed a distinct abundance pattern with a first peak of 30.7 specimens cm^{-3} at 1896 yr BP, followed by a decrease to 11.3 specimens cm^{-3} at 1771 yr BP, and once again an increase to an overall maximum of 42.0 specimens cm^{-3} at 1692 yr BP. Subsequently, the densities of this taxon decreased to 12.0 specimens cm^{-3} until the end of the zone at 1448 yr BP.

Another very abundant taxon in **zone I** was *Parochlus*, the occurrence of which showed three distinct peaks with 7.3 specimens cm^{-3} at 1896 yr BP, 9.3 specimens cm^{-3} at 1692 yr BP and 18.1 specimens cm^{-3} at 1519 yr BP. In between these marked peaks, *Parochlus* was absent at 1771 yr BP and showed an abundance of only 1.3 specimens cm^{-3} at 1566 yr BP.

All other taxa in **zone I** were much less abundant than *Limnophyes/Paralimnophes* and *Parochlus*. Three taxa mainly occurred towards the end of the zone: i) *Pseudorthocladius* with a brief spell at 1924-1903 yr BP with an abundance of 0.7-1.3 specimens cm^{-3}, before disappearing and re-appearing between 1771-1448 yr BP with slightly variable mean abundances of 1.7 specimens cm^{-3}; ii) *Smittia/Parasmittia* showed a low abundance from 1771-1636 yr BP before disappearing. It reoccured at the end of zone I at 1448 yr BP with 3.3 specimens cm^{-3}; iii) *Pseudosmittia* was present in the samples from 1692 yr BP with densities of 0.7 specimens cm^{-3}, with the exception of 1636 yr BP, and a peak at 1448 yr BP with 2.0 specimens cm^{-3}. Specimens of *Parametriocnemus/Paraphaenocladius* were exclusively identified from zone I with two occurrences at 1896 yr BP of 0.7 specimens cm^{-3} and at 1692 yr BP with 2.0 specimens cm^{-3}. All other taxa featured only sporadic occurrences in the palaeosamples; *Apsectrotanypus/Alotanypus* was present only at 1903, 1636 and 1448 yr BP with 0.7-1.3 specimens cm^{-3}; *Metriocnemus eurynotus* at 1903 and 1448 yr BP with 0.7 and 2.0 specimens cm^{-3}; *Paracricotopus* at 1903 and 1636 yr BP with 3.3 and 1.0 specimens cm^{-3}; and *Podonomus* at 1903 and 1566-1519 yr BP with 0.7 and 0.7-1.0 specimens cm^{-3}, respectively.

The subsequent **zone II**, ranging from 1426±22 to 1287±35 yr BP, was characterised by distinctly low abundances of Chironomids with a mean of 2.2 specimens cm^{-3}. Furthermore, the mean diversity was low with only 1.5 taxa. The previously highly abundant taxa, *Limnophyes/Paralimnophyes* and *Parochlus* declined at the beginning of zone II to 2.9 specimens cm^{-3} and 0.5 specimens cm^{-3} at 1404 yr BP, respectively. Subsequently, *Parochlus* disappeared completely and the abundance of *Limnophyes/Paralimnophyes* decreases to only 0.7 specimens cm^{-3} at 1317 yr BP. No other taxa were present in zone II.

In **zone III**, the overall abundance of Chironomids increased again and reaches a mean of 9.7 specimens cm^{-3}. The mean diversity was higher compared to zone II and comprises 3.7 taxa. Particularly at the beginning of this zone, at 1246 yr BP, the diversity increased to the maximum of eight taxa in the investigated core section. Three taxa, *Cricotopustopus/Paratrichocladius* type I and II, and one *Diamesinae* type occurred exclusively in this zone. Of these, *Cricotopustopus/Paratrichocladius* type II showed relatively high mean abundances of 2.2 specimens cm^{-3} with distinct peaks of 3.5 specimens cm^{-3} at 1246 yr BP and of 6.0 specimens cm^{-3} at 1020 yr BP, though it was not observed between 1203-1169 yr BP and at 997 and 893 yr BP. The other taxa exclusively found in zone III, occurred sporadically with *Cricotopustopus/Paratrichocladius* type I at 1246 and 960 yr BP with 0.5 specimens cm^{-3} and the *Diamesinae* type at 860 yr BP with 0.7 specimens cm^{-3}.

Comparable sporadic occurrences were shown by six other taxa: i) *Pseudorthocladius* with 1.0 and 0.7-1.3 specimens cm^{-3} at 1246 and 1054-1020 yr BP; ii) *Smittia/Parasmittia* with 0.7 specimens cm^{-3} at 1020 yr BP; iii) *Pseudosmittia* with 0.5 specimens cm^{-3} at 945 yr BP; iv) *Metriocnemus eurynotus* with 3.3 specimens cm^{-3} at 1054 yr BP; v) *Paracricotopus* with 1.0 specimens cm^{-3} at 1246 yr BP; vi) *Podonomus* with 0.5 specimens cm^{-3} at 1246 yr BP. The abundance of the most dominant taxon of zone I and the only taxon of zone II, *Limnophyes/Paralimnophyes,* increased to a mean of 2.9 specimens cm^{-3} in zone III.

Parochlus re-appeared at 1246 yr BP with 3.5 specimens cm^{-3}, and although absent from 1203-1117 yr BP and 960-945 yr BP showed high abundances of up to 11.3 specimens cm^{-3} from 1054-997 yr BP. After 929 yr BP and until the end of the core section at 860 yr BP, *Parochlus* was present in only low mean densities of 1.4 specimens cm^{-3}. A similar distribution pattern showed *Apsectrotanypus/Alotanypus* with its highest abundance in this zone of up to 5.3 specimens cm^{-3}. This taxon briefly occurred at 1246 yr BP with 2.5 specimens cm^{-3}, and again from 1054-945 yr BP, and apart from one exception at 997 yr BP, showed a mean abundance of 2.3 specimens cm^{-3}.

6.3.7 | Distribution of other subfossils

In addition to the subfossils of the family Chironomidae, insect remains of the dipteran families Ceratopogenidae, Thaumaleidae and Simuliidae were found. When present in samples, the Ceratopogenid subfossils reached a mean abundance of 2.2 specimens cm^{-3} and ranged between 0.4-5.8 specimens cm^{-3}. This taxon occurred nearly throughout the entire investigated core section, but reached higher mean abundances of 1.8 specimens cm^{-3} in the younger part, corresponding to cluster III of the Chironomid community. In this part of the core, remains of Ceratopogenids could constantly be found between 1203-997 yr BP, with the highest densities at 1169, 1054 and 997 yr BP. In the older part of the core, corresponding to zone I, the Ceratopogenidae showed relatively stable abundances of around 2.0 specimens cm^{-3}. Only at 1566 yr BP, this taxon was absent. Additionally, a high abundance occurred at the beginning of zone II, at 1404 yr BP. During this time interval, the Ceratopogenidae reached higher densities than the most abundant Chironomid taxon *Limnophyes/Paralimnophyes*. However, between 1317-1246 yr BP, no Ceratopogenidae were observed. Subfossil remains of the Thaumaleidae occurred sporadically at 1692, 1566 and 1246 yr BP with a mean of 1.1 specimens cm^{-3} and of the Simuliidae at 1636 and 1020 yr BP with a mean of 0.6 specimens cm^{-3}.

6.3.8 | Reconstruction of soil wetness

The palaeo-reconstructions of soil wetness were exclusively based on five indicator taxa from both the Oribatid mites (*Neoamerioppia notata*, *Scheloribates pallidulus*, *Nanhermannia elegantissima*, *Jugatala armata* and *J. montana*) and from the Chironomids (*Limnophyes/Paralimnophyes*, *Cricotopus/Paratrichocladius* type II, *Parochlus*, *Apsectrotanypus/Alotanypus* and *Parametriocnemus/Paraphaenocladius*), which were identified as significant indicators of the different conditions for soil wetness (see Chapter 5.4.4).

In the comparison of palaeoenvironmental reconstruction models, the IKFA models showed large bootstrapping errors at several data points for all tested datasets and were therefore excluded from further analysis.

For the reconstruction based on the Oribatid mite data, a WA model was given priority over the MLRC and MAT methods, because it showed the second lowest root mean squared error (RMSE= 13.9) and the second lowest maximum bias of 34.0 in combination with a high determination coefficient (R^2= 0.49). The MLRC model revealed lower RMSE and higher R^2, but the maximum bias was higher with 40.3. All determining values of the MAT model were worse with the exception of a very low maximum bias with 17.7.

The final WA-model predicted high soil wetness from 1925-1448 yr BP with a mean of 86% wetness and maximum values of 93%. However, distinct fluctuations were reconstructed for this period with distinct dry spells at 1910 (86%), 1771 (76%) and 1567 yr BP (64%) and humid periods with values >90% at 1896 and 1692 yr BP. From 1519-1448 yr BP, the soil wetness was constantly high with 93%. After this stable period, the soil conditions shifted to drier conditions and from 1246-929 yr BP, a mean value of 60% with very small maximal fluctuations of ±4% was predicted. For the last part of the sequence, from 893-861 yr BP, no data could be predicted due to limitations of the WA method.

The reconstruction based on the Chironomid data was performed with a MAT model, which revealed the lowest RMSE of 19.3 combined with the second lowest maximum bias of 40.1. However, the reconstruction based on the Chironomid data in general was less precise with very low R^2 in all models in comparison to the Oribatid mite models. The preferred MAT model featured the second lowest determination coefficient of 0.17.

The model reconstructed stable wet soil conditions from 1925-1567 yr BP with 81%, with maximal ±0.8% fluctuations. Between 1519-1448 yr BP, the model predicted a wetter period with a mean of 84% before the soil wetness decreased to a mean of 78% for the period 1404-861 yr BP. Additionally, this slightly drier period was characterised by more variable conditions with dry spells at 1317, 1117, 1020 and 945 yr BP (driest conditions at 1117 yr BP with 70%) in combination with wet phases at 1246, 1169, 1057 and 893 yr BP (wettest conditions at 1054 yr BP with 84%).

Comprising all available data in a combined dataset, a MAT model was also used to reconstruct soil wetness. This model was given priority over the MLRC model because it showed a lower RMSE with 15.8, although the MLRC featured a slightly higher determination coefficient and lower maximum bias.

The chosen MAT-model, which was used to predict soil wetness changes from the combined dataset, revealed a variable wet period with 76% water content in mean from 1925-1448 yr BP with distinct wet peaks at 1910 (84%), 1692 (82%) and 1519 yr BP (84%). In between, at 1567 yr BP the model showed a pronounced dry spell of 57% soil wetness. After 1448 yr BP, the soil wetness was predicted to decrease significantly to a mean of 54% for the period 1404-860 yr BP. Only minor increases in soil wetness were suggested for 1203 (59%) and 1054-1020 yr BP (57%).

All model characteristics are denoted in Appendix 10.

6.4 | Discussion

In general, the deposition conditions for mesofaunistic subfossils appear favourable in the peat deposits of the CLP. For example in the Oribatid mites, most morphological structures, which are important for determination, e.g. sensilli and lamellae on the prodorsum, or the porose areas and the setation sockets on the notogaster, are unimpaired. Many taxa (28 taxa from the Oribatida and Chironomidae) were retrieved with high mean abundances of 3.3 Oribatid mite remains per cm^3, which is 6-10 x higher in comparison to other studies (Drouk, 1997; Solhøy & Solhøy, 2000), and 20.0 Chironomid remains per cm^3.

However, in the case of the subfossil Oribatid mites, only heavily sclerotised taxa seem to be preserved over time in the peat deposits. For example *Tyrphonothrus maior*, a weakly sclerotised species that showed densities of up to 1.4 specimens cm^{-3} in the modern peatland was not found in the palaeosamples. Though, this could also be accounted for by the absence of the species in the investigated time interval and a clear connection between absence in the record and absence in the ecosystem can not be established.

Nevertheless, the absence of *Tectocepheus* sp., despite being heavily sclerotised is remarkable, because this taxon is the most abundant taxon (mean of 1.8 specimens cm^{-3}) in the modern peatland samples, one of the most common worldwide (Hajmová & Smrž, 2001) and has been identified from many sites in the high Andes (see Chapter 3.3.2) for more detailed information on this taxon). The first occurrence of this taxon at CLP remains unknown, although analyses of palaeosamples, which were not included in this study, indicate an arrival of the taxon later than 362 yr BP (1588 AD).

Additionally, the conditions in the sediments seem to be suitable for the preservation of sclerotised structures of other dipteran taxa as revealed by this study. The usage of Ceratopogenid head capsules as a palaeo-proxy is a promising approach for future palaeoenvironmental investigations (Luoto, 2009). If identification to genus level could be achieved in subfossil specimens, the abundance of the genus *Culicoides* in palaeo-archives could reveal a signal, e.g. for the presence of large herbivores at the study site, as all adult females need to suck blood for egg production (Szadziewski et al., 1997; Borkent & Spinelli, 2007). In future studies, this signal could reveal the presence of pastoral activities, and potentially large herbivores densities. For this aim, however, more research on the Ceratopogenidae and their deposition in palaeo-archives is needed to derive a useful palaeoproxy. Additionally, in future research, the usage of Simuliidae and Thaumaleidae as palaeoproxies could provide moisture signals for shallow water ecosystems, e.g. for archives from lake margins or peatlands. For this purpose, therefore, focussed taxonomic and ecological research on these taxa is obligatory.

6.4.1 | Palaeoenvironmental interpretation

To interpret the Oribatid mite community fluctuations, the available autecological data have to be considered. The results of the ecological investigations (see Chapter 5.4.3) suggest *Neoamerioppia notata* as a significant indicator for wet soil conditions with a water content >73%. Other species, such as *Anderemaeus monticola*, *Oribatella illuminata*, *Eupelops apicalis*, *Areozetes altimontanus*, *Zetomimus furcatus*, *Ceratozetes nigrisetosus*, *Scheloribates laticlava*, *S. huancayensis* and *S. confundatus* are regarded to be hygrophilous. On the other hand, *Scheloribates pallidulus*, *Nanhermannia* *elegantissima*, *Jugatala montana* and *J. armata* significantly indicate soil wetness <58%, while *Oxyoppia suramericana* is suggested to be rather xerophilous. The ecology of *Scheloribates elegantulus* remains unknown. For a full overview of the autecology and indicator properties of the given taxa, see Chapters 3.3.2 and 6.3.2.

Using this information to characterise the zones revealed by the cluster analysis, **zone I** (from 1924-1903±7 yr BP) is dominated by hygrophilous taxa and indicator species for high water content >73%, which together indicate stable wet conditions. In the subsequent **zone II** (1903±7-1426±22 yr BP), an interplay of both wetness and dryness indicators suggest rapidly changing phases of wet and dry conditions. The peaks in abundance of *Neoamerioppia notata* at 1692 and 1519 yr BP could hint at rapid wet spells, whereas distinct declines of this taxon accompanied by sporadic occurrences of *Scheloribates pallidulus* and *Jugatala montana* at 1771 and 1566 yr BP could represent dry spells. In this context, the fluctuations in abundance of *Oxyoppia suramericana*, which is regarded as a xerophilous species in different references (see Chapter 3.3.2), appear counter-intuitive and seem more likely in response to wet phases. Accordingly, *Oxyoppia suramericana* was not considered to be a significant dryness indicator in the ecological investigations. In the youngest period of the investigation, **zone III** (1426±22-861 yr BP), the wetness indicator species and hygrophilous taxa are nearly completely absent, while the xerophilous and dryness indicating taxa dominate. At 1245-1203, 1054-1020 and 929 yr BP *Scheloribates pallidulus*, *Nanhermannia elegantissima* and *Jugatala armata* occur together with high abundances. Based on their indicator qualities, these phases would have been dominated by pronounced dry conditions, especially from 1054-1020 yr BP when these three taxa occur together in high abundances.

Similar to the interpretation of the Oribatid mite community changes, the available autecological data for the Chironomidae have to be considered. The results of the ecological investigations (see Chapter 3.3.3) suggest that *Cricotopus/Paratrichocladius* type II, *Parochlus*, *Apsectrotanypus/Alotanypus* and *Parametriocnemus/Paraphaenocladius* are significant indicators for soil conditions dominated by water content between 80-81%. Additionally, the taxon *Limnophyes/Paralimnophyes* is suggested to be a significant indicator for soil wetness conditions of >81%. However, the ecology of all other taxa identified from the palaeosamples remains unknown. Considering these ecological data, the soil conditions of the time **zone I** (1924-1426±22 yr BP) can be regarded as distinctly wetter in comparison to the other zones. Within this period, abundance peaks especially of *Limnophyes/Paralimnophyes* and *Parochlus* could indicate spells of pronounced wetter conditions around 1896, 1692 and 1519 yr BP before the soils significantly shifted to drier conditions starting at 1448 yr BP. The subsequent **zone II** (1426±22-1287±35 yr BP) could be interpreted as a transitional period between different environmental conditions in zones I and III. The distinctly lower abundances of *Limnophyes/Paralimnophyes* and *Parochlus*, and the new occurrence of *Cricotopus/Paratrichocladius* type II, suggest the youngest **zone III** (1287±35-861 yr BP) to be drier in comparison to zone I. However, within this overall drier period, some small-scale wet spells derived by the abundance peaks of *Limnophyes/Paralimnophyes* and *Parochlus* at 1246 and 1054 yr BP could be implied.

6.4.2 | Comparison

Schittek et al. (2015) pioneered the use of arsenic (As) and the ratio between manganese and iron content (Mn/Fe) and between iron and titanium content (Fe/Ti) as indicators of water fluctuations in the palaeo-archives of Cerro Llamoca peatland. The changing solution ability of Mn-ions in different environmental conditions is responsible for its indicator function. Under saturated conditions and low pH, the Mn content will increase due to the reduction of mineral Mn-oxides to soluble Mn^{2+} (Blume et al., 2002), leading to high Mn/Fe ratios under wet conditions. Conversely, Fe^{2+}-ions are oxidised to non-soluble Fe^{3+} in aerated conditions. By this mechanism, Fe precipitates in drying soils and the Mn/Fe ratio is decreased. The Titanium content can be used to normalise fluctuations of higher soluble elements in geochemical stratigraphical analyses, as it is regarded to be immobile in peat (Thomson et al., 2006). Thus, the Fe/Ti ratios can be used to detect periods of pronounced water table fluctuations of the peatland. Furthermore, high As content is regarded as either indicating dry conditions or rewetting conditions, subsequent to the drying out of the peat. A full overview on the usage of the mentioned elements as geochemical palaeoproxies is presented by Schittek et al. (2015, 2016). The geochemical proxies revealed from the CLP are shown in Figure 6.23-F.

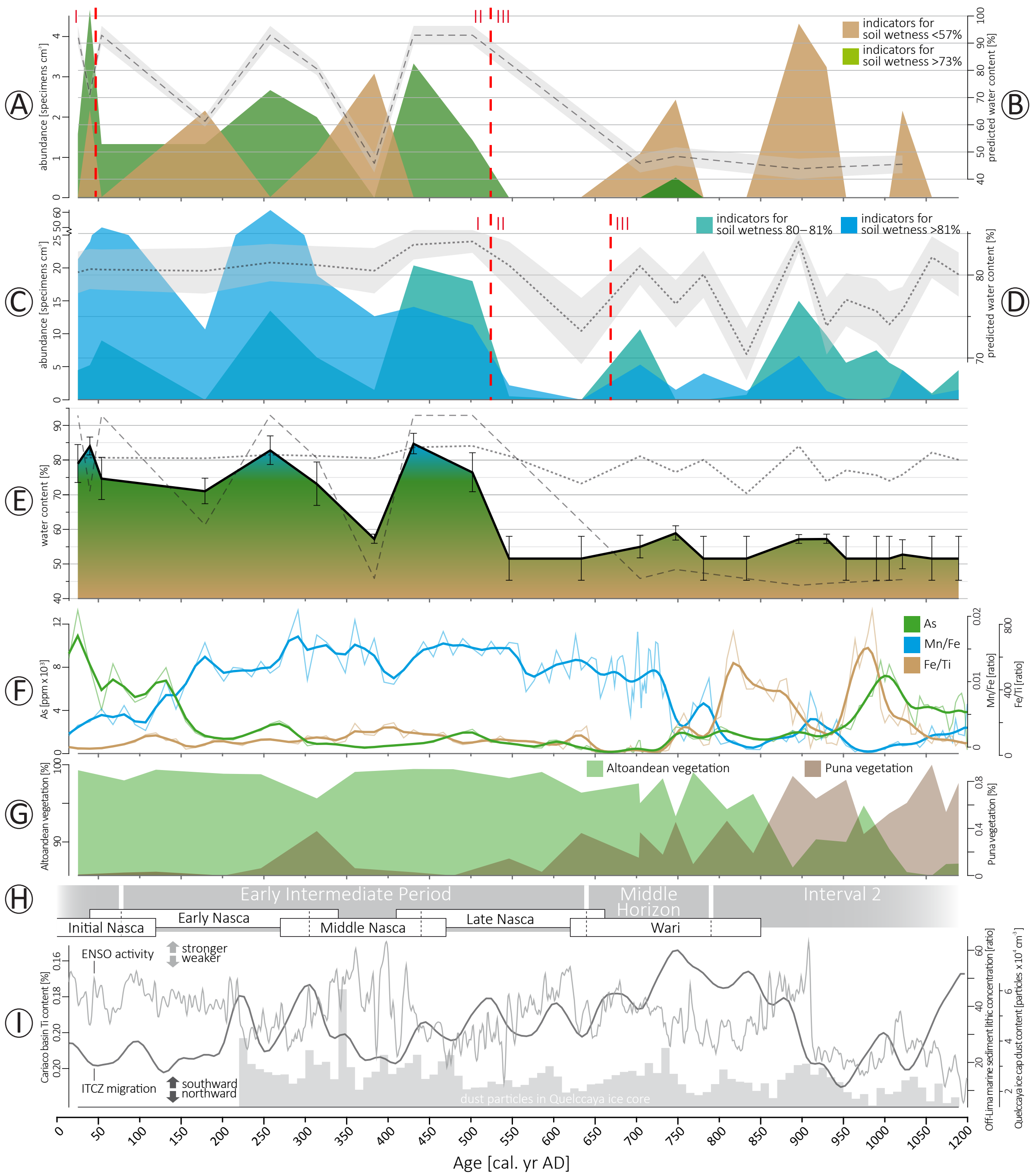

Figure 6.23 | Palaeoenvironmental reconstruction of soil wetness for the CLP between 1924-860 yr BP. The following diagrams are compared: **A)** shows the abundance changes of Oribatid mite indicator species with indicators for soil wetness conditions <57% (brown) and >73% (green). The red lines indicate depth zones derived by CONISS clustering; **B)** shows the corresponding WA-reconstruction (dashed line) of soil wetness based. The grey area states the 95% CI; **C)** shows the abundance changes of significant soil wetness indicators from the Chironomids with indicators for conditions 80-81% (green-blue) and >81% (blue). The red lines indicate depth zones derived by CONISS clustering; **D)** gives the corresponding MAT-reconstruction (dotted line) of soil wetness. The grey area states the 95% CI; **E)** shows a MAT-model for the reconstruction of soil wetness based on a combination of the Oribatid mite and Chironomid data (solid black line with errorbars indicating the 95% CI). For comparison, the WA-model shown in (A) and the MAT-model shown in (B) are plotted as well; **F)** shows element content fluctuations in the core (Schittek et al., 2015) with the As content (brown), and the Mn/Fe (blue) and Fe/Ti ratios (green). The original data are shown as thin lines, whereas the thick lines show the same data smoothed by Gaussian weights; **G)** shows the results of the pollen analysis by Schittek et al. (2015) plotted as summed percentages of pollen originating from the Altoandean vegetation (green) and from Puna vegetation (brown); **H)** defines the archaeological chronology for the study area (Unkel et al., 2012). See Figure 6.5for further description; **I)** shows different supra-regional palaeoclimatic records: Ti content in sediments retrieved from the Cariaco Basin (Haug et al., 2001); the lithic content of marine sediment off the Peruvian coast (Rein et al., 2005). Both datasets were smoothed by Gaussian weights for plotting; lastly, the dust content in the ice cores retrieved from the Quelccaya ice cap in southern Peru is plotted as shown as decadal averages (Thompson et al., 2013).

As a biological proxy to reconstruct wet and dry phases for the study area, Schittek et al. (2015) used the amount of different pollen assemblages deposited in the CLP. Periods showing a nearly exclusive occurrence of Poaceae pollen were interpreted as wet phases, dominated by dense grass steppes, typical of the Altoandean vegetation. Conversely, phases with a higher influence of Puna vegetation elements, indicated by Asteraceae-, Brassicaceae-, Malvaceae- and *Alnus* pollen, were regarded as characterising drier conditions. The results of the pollen analysis are shown in Figure 6.23-G.

For further comparison, the results of other important palaeoclimatic investigations are compared. The titanium content record of the sediments derived from the Cariaco Basin in Venezuela has been interpreted to reflect changes in the position of the Inter-Tropical Convergence Zone (ITCZ) (Haug et al., 2001), which is of significance for understanding precipitation intensity in the study area (see Chapter 2.2). High titanium content can therefore be inferred to indicate a more northward position of the ITCZ and hence, theoretically, a reduced amount of precipitation at CLP. Conversely, low values may indicate a more southward position and result in intensified precipitation in the study area.

In addition, the lithic content, assessed from a marine sediment core, retrieved off the Peruvian coast by Rein et al. (2005), is suggested to reflect the intensity of the El Niño-Southern Oscillation (ENSO). During the wet El-Niño conditions along the Peruvian coast, run-off from Pacific-draining rivers is strengthened, intensifying erosion, fluvial transport and ultimately off-shore deposition of fine-grained lithics. From this study, periods of stronger ENSO activity are characterised by a higher lithic content, while low values indicate weaker ENSO activity. However, the effect of ENSO events on the amount of precipitation remains unclear as the distribution of intensified precipitation can be extremely heterogenous (Rein et al., 2004, 2005).

Furthermore, the amount of dust particles in the ice-cores retrieved from the Quelccaya ice cap by Thompson et al. (2013) is shown. The dust content is suggested to represent phases of drier conditions, as these are characterised by a reduction of vegetation cover in the Altoandean belt (Schittek et al., 2015), which facilitates aeolian transport of small eroded soil particles. In the time interval examined, no major volcanic eruptions are known from the region (Beal et al., 2014), which can also be contributors to the dust influx.

Comparing the independent studies above with the soil wetness indications recorded by the subfossil Oribatid mite and Chironomids data in the CLP core, the stable humid period from 1924-1426±22 yr BP is evident in regional and supra-regional records. The predicted occurrence of a dry spell from 1601±35-1543±24 yr BP and a significant shift to an environment dominated by drier conditions at 1426±22 yr BP are supported by lagged signals in other proxies from the CLP and by distinct fluctuations in supra-regional records:

At the beginning of the period investigated, from 1924 yr BP, Schittek et al. (2015) suggest dry conditions until 1800 yr BP, indicated by elevated arsenic content in the sediment (see Figure 6.23-F). However, it is also considered by the authors and others (e.g. Blodau et al., 2008; Rothwell et al., 2010), that increased As content could be linked to peatland rewetting after a dry period. The latter hypothesis is supported by this study as high water content >70% is indicated for this time period. Additionally, a comparative analysis of water and arsenic content from 15 modern peat samples (eight from degraded and dry peat, and seven from un-decomposed and wet peat) from the study site (see Chapter 5.3.2) reveals a strong positive correlation between soil wetness and arsenic content ($F(1, 13)= 18.0$, $p<0.001$, $R^2= 0.58$), which reinforces the rewetting hypothesis.

Hence, a distinct arsenic peak at 1896 yr BP, interpreted as rewetting of the peatland, is followed by an abundance peak of mesohygrophilous Oribatid mites and a predicted increase of soil wetness at 1910 yr BP, which represents a lag of 14 years.

Schittek et al. (2015) characterise the period beginning at **1800 yr BP** as dominated by stable wet conditions leading to a continuous water saturation of the peatland, indicated by elevated and stable Mn/Fe ratios and low As content. Additionally, the vicinity of the peatland is dominated by a dense grass steppe, as inferred from the high percentage of Poaceae pollen, summed as Altoandean vegetation in Figure 6.23-G, which also indicates wet conditions. However, the reconstruction based on the Oribatid mite and Chironomid data, suggests a dry spell during the interval 1601±35-1543±24 yr BP (fully established by 1567 yr BP), which questions the stability of environmental conditions in this period. Hence, a minor decrease in the Mn/Fe ratios at 1557 yr BP could be interpreted as the corresponding geochemical signal for the predicted lowering of the water table, though lagging by 10 years.

A comparison with other palaeoclimate investigations reveals remarkably similar features. The Ti content curve by HAUG et al. (2001) suggests a retreat of the ITCZ to a more northward position starting from 1655 yr BP. The most northward position is maintained between ca. 1580-1540 yr BP, before the ITCZ migrates again to a more southward position. The ENSO record by REIN et al. (2005) indicates strongly fluctuations of climatic conditions with pronounced El Niño conditions, followed by short spells of severely weakened river run-off between 1589-1529 yr BP. Also, the dust concentrations in the ice layers from Quelccaya, peak between 1610-1600 yr BP, indicating a pronounced dry episode in the region (THOMPSON et al., 2013).

Although this interspersed dry episode had a direct impact on the peatland soil mesofauna, the effect appeared to be temporary. Shortly after the dry incursion, from 1519 yr BP on, a hygrophilous soil community re-established. SCHITTEK et al. (2015) estimate the end of the wet period to about 1200 yr BP when the Mn/Fe ratios rapidly decreases and the Fe/Ti ratios rise, which could indicate a harsh transition to drier conditions. Nevertheless, the first evidence of reduced precipitation is recognisable from 1300 yr BP by a reduction of Mn/Fe ratios in combination with fluctuating and slightly decreasing percentages of Poaceae pollen, as well as the rising influence of dryness indicating Puna vegetation at CLP (SCHITTEK et al., 2015). Other supra-regional archives also suggest drier conditions, e.g. a drop in Titicaca's lake-level (ABBOTT et al., 1997a; BINFORD et al., 1997).

According to this study, faunal evidence indicates that drier conditions at the peatland itself have to be preponed to 1426±22 yr BP, when both indicator groups, the Oribatid mites and Chironomids, show significant changes in their community compositions. This most severe change in the investigated time interval is well reflected in the corresponding reconstruction, which suggests a drop of soil wetness from 76% to 52%, reached at 1404 yr BP, followed by sustained drier conditions of around 54% soil wetness. For the same time interval, the Mn/Fe ratios by SCHITTEK et al. (2015) show a minor decrease with a short-lived minimum at 1384 yr BP, which represents a lag of 20 years after the inferred establishment of low soil wetness. Similarly, the record by REIN et al. (2005) shows a rapid decrease of lithic deposition at 1410 yr BP to a remarkably low value, which, however, is indicated only for a limited episode of circa five years.

The fully established dry conditions, at 1050 yr BP, indicated by low percentages of Altoandean pollen reflecting a high influence of Puna vegetation at the study site, low Mn/Fe and high Fe/Ti ratios as revealed by SCHITTEK et al. (2015), and by other compared investigations (HAUG et al., 2001; REIN et al., 2005), coincide with the highest abundance of Oribatid mite indicators for <57% soil wetness, although are not reflected by the reconstruction model. This divergence indicates a reduced indicator value for pronounced dry conditions for both palaeoproxies of this study. These possible constraints for the usage of these proxies requires further research effort.

6.4.3 | Archaeological implications

The impact of environmental changes on pre-Columbian cultures in the Nasca region has been revealed by many studies (EITEL et al., 2005; MÄCHTLE, 2007; BERESFORD-JONES et al., 2009; MÄCHTLE & EITEL, 2013; FEHREN-SCHMITZ et al., 2014; SCHITTEK et al., 2015). As the CLP is situated in the Nasca drainage area, the role of climatic variation and its effect on human populations is evident from such palaeo-archives (FEHREN-SCHMITZ et al., 2014; SCHITTEK et al., 2015). In particular, the amount of water supplied by rivers from the Andean highlands was vital for agriculture in the arid environment of the foothills. Therefore, migrations of the human populations between the highlands and the coast must be interpreted as cultural adaptions to unfavourable dry conditions.

In this context, FEHREN-SCHMITZ et al. (2014) note a decrease of settlement density in the adjacent foothill areas starting at ~1510 yr BP, which remained unexplainable from the results of palaeoclimate investigations. The analysis of the CLP archive by SCHITTEK et al. (2015) revealed only a minor deflection of the Mn/Fe ratios at 1557 yr BP. However, the major changes in the Oribatid mite and Chironomid communities in this study indicate a marked impact on the peatland environment and predict a significant dry spell from 1601±35-1543±24 yr BP, which is fully established at 1567 yr BP. This dry spell almost certainly resulted in reduced water supply towards the foothill areas, thus initiating migration. Subsequent to this short but marked shift to drier conditions, the transition between the Middle Nasca and the Late Nasca cultures is dated at 1540-1480 yr BP (Unkel et al., 2012). At the beginning of the Late Nasca cultural period, from 1519-1448 yr BP, the reconstruction suggests high and relatively stable soil wetness, before it declined again between 1448-1404 yr BP and changed into conditions with lower water availability. The repeated shift towards unfavourable conditions in this time interval could corroborate the hypothesis of climate triggered emigration, fragmentation and ultimately the disappearance of the Nasca culture at the end of the Late Intermediate Period/Middle Horizon transition (Beresford-Jones et al., 2009; Fehren-Schmitz et al., 2014).

6.5 | Conclusion

This study revealed for the first time conclusive evidence for a short but pronounced spell toward arid climatic conditions in the Middle Nasca prevalence, with full established dry conditions at the beginning of the Middle Nasca to Late Nasca cultural transition. This evidence for short-term changes in water availability provides first hints for the interpretation of observed cultural changes and migratory movements in the coastal area of southern Peru in the Early Intermediate Period.

Through these significant results, the study shows the potential of Oribatid mites and Chironomids as proxies for palaeoenvironmental research on high-Andean peatland ecosystems and concomitant on cultural transitions of human populations. The combined indicator system detects fine-scale changes in soil wetness, which appear to be crucial for understanding the history of the local peatland environment. The developed palaeo-proxies with their distinct local validity, achieved high temporal resolution when corroborated by independent regional and supra-regional proxy records. The assessment did benefit by the two different indicator groups which contrast in abundance, possible systematic precision, and in ecological traits. The addition of novel local proxies to a more regional set of proxies revealed new information on environmental drivers and provided innovative ideas for the interpretation of already established proxies.

This study shows the advantages of high-resolution palaeoenvironmental studies focussing on a short time interval. The results show that minor changes in the proxy data, can be of high ecological importance and be relevant for understanding the human-environment interactions.

7 | Conclusion

To conclude all the different aspects presented in this thesis, the earlier hypotheses are compared with the results as revealed by the different investigations:

- **The ecosystem of a high-Andean cushion peatland is characterised by a subset of different ecotopes, which can be connected and ranked according to successional processes.**

This hypothesis could partly be verified. In the field, five different ecotopes were identified, e.g. by botanical composition and soil type. These ecotopes were ranked and connected in a theoretical succession order. The geochemical classification of all the ecotopes indicated homogenous soil conditions within each ecotope, though significantly different conditions between the ecotopes. As such, the proposed two extremes and the one out-grouped successional stage could be verified. However, the classification didn't show a significant separation between the two medium successional stages and reveals rather a transition in soil conditions. The initially proposed succession model had to be altered due to the results of the geochemical analysis, albeit on the basis of a more fine-scaled and focussed sampling scheme; a separation of mid-successional stages nevertheless may become evident in future research approaches.

- **The ecotopes of a high-Andean cushion peatland are inhabited by distinct Oribatid mite and Chironomid communities.**

This hypothesis could be verified by the results of this study. However, while some ecotopes were inhabited by richer and more abundant Oribatid mite and Chironomid communities, others were distinctly poorer and sparsely inhabited. Degraded, organic rich ecotopes showed the highest abundance of Oribatid mites. Most of the Oribatid mite species revealed could be characterised as specialists, occurring mainly in a single ecotope, though a few dwelled in different parts of the peatland. Among the Chironomids, a few taxa dominated the community and occurred in all ecotopes, though with significant abundances variations. In contrast, the majority of taxa inhabited a distinct ecotope. Overall, Chironomids predominantly inhabited wet pioneer soils in the peatland.

- **The Oribatid mite and Chironomid communities are associated with specific microhabitats, defined by geochemical soil parameters.**

This hypothesis needs to be altered as revealed by this investigation. Community responses to different soil condition parameters were revealed, but, though only a few distinct impacts became obvious. Due to high collinearity of the data and indications of pronounced ecological shaping of the communities, the geochemical dataset had to be reduced and instead of using the entire communities, ecological specifications could only be assessed for single taxa in the following analyses.

- **Oribatid mite and Chironomid taxa can be used as significant soil condition indicators.**

This hypothesis should be respecified in the way, that Oribatid mites and Chironomid taxa can be used as significant indicators for soil wetness conditions. All other tested environmental factors did not reveal a significant indicator functionality. Additionally, as indicated in the previous hypothesis, an indicator function could only be ascribed to single taxa. However, if enhanced geochemical and faunal sampling were applied, more indicator taxa and functionality may be revealed from the Oribatid mite and Chironomid peatland communities.

- **The preserved Oribatid mite and Chironomid assemblages in peat deposits show significant changes in time.**

This hypothesis can fully be accepted as both subfossil assemblages are diverse, abundant and show distinct fluctuations within the investigated archive. Furthermore, it was possible to achieve a high taxonomical accuracy as the assemblages of Oribatid mites could be identified to species level in comparison to genera level in the case of the Chironomids. Besides Oribatid mites and Chironomids, other dipteran remains were obtained and identified from the deposits, which also show abundance changes in the investigated time interval.

- **Oribatid mite and Chironomid proxies and their indicator functions combined quantitatively reveal environmental changes in time.**

This hypothesis is verified by this thesis, but should be restricted to soil wetness conditions. A set of five indicator taxa from both the Oribatid mites and Chironomids was used successfully to quantitatively predict wetness changes. However, the precision of the developed indicators should be retested and maybe increased in additional investigations of different peatland sequences and with enhanced modern sampling.

Perspectives

Obligatory for establishing the future use of these newly presented palaeo-proxies from this environmental context is their repeated application in peatland ecosystems of the high Andes.

Based on the available dataset, the importance of high taxonomic accuracy on the precision of palaeoenvironmental reconstructions should be highlighted in future investigations. Such an approach may provide guidance in choosing adequate proxies for the future questions of palaeo-studies and contribute to evaluate a “cost-benefit-ratio”, in which the increased preparation and identification effort of using a highly accurate proxy is contrasted with enhanced reconstruction precision.

Final Conclusion

This research has revealed that the high-Andean cushion peatlands are inhabited by a distinct fauna adapted to highly variable and, in parts, extreme soil conditions. Some ideas on the mechanisms shaping these specific soil dwelling communities have been formulated, and although the majority of interactions and impacts remain unknown, this study provides a firm foundation for future work.

The role of high-Andean cushion peatlands as archives for palaeoenvironmental investigations, as indicated by other studies, has been reinforced by this thesis. In particular, the potential of Oribatid mites and Chironomids as palaeo-proxies in high-Andean cushion peatlands has been demonstrated for the first time. In the context of the proposed “multiscale” approach (see Chapter 1), the Oribatid mite and Chironomid proxies can be characterised as:

- having a very local signal validity;
- reacting dynamically in comparison to other proxies, and;
- being directly influenced by at least some local environmental fluctuations.

These characteristics are advantageous for developing a palaeo-proxy, though could cause problems in interpretation. As a consequence, the Oribatid mite and Chironomid indicator system should be used in combination with more regional, indirectly and idly proxies. Nevertheless, the new proxies presented in this thesis, can provide valuable information in future investigations.

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Abstract – Zusammenfassung

The edaphic Oribatid mites and Chironomid larvae of five different successional stages of a high-Andean cushion peatland in southern Peru (14°S) were investigated. In total, 17 Oribatid mite taxa, belonging to eight families could be identified. Taxonomic remarks for the species found and an analysis of community structures are provided. The investigation shows significantly higher Oribatid mite densities in the early and medium successional stages in comparison to the successional climax ecotope. From the Chironomids, 11 taxa belonging to three subfamilies could be identified. For the taxa found, taxonomic descriptions and an analysis of community structures are also provided. Within the successional rank order of the peatland, the abundance of Chironomids is highest in pioneer soils, followed by mid-successional and degraded soils.

Subsequently, a biogeographical investigation is presented of the Oribatid mite fauna from the high Andes is. Only 39 sampling sites, ranging from 3000-5200 m altitude from southern Ecuador (4°S) to mid-Argentina (34°S), have been sampled before. Only seven of these sampling sites can be assigned to cushion peatlands. For all available sampling sites, a diversity analysis was carried out, which revealed 219 species from 116 genera, comprising 51 families from the high Andes >3000 m a.s.l.. For cushion peatlands, 48 species from 34 genera, comprising 18 families were identified, of which only nine species were found in two or more sampling sites. In the high Andes, the γ-diversity of Oribatid mites shows evident fluctuations with latitude. At low latitudes <10°S, species richness is high with >30 species. With increasing latitude, the richness declines to seven species at 19°S before it increases again to 14 species at >30°S. This fluctuation is probably associated with changes in precipitation. The analysis reveals that the high Andean Oribatid mite community is highly nested at both the genus- and species-level, and shows a zonal character for the community in contrast to the azonal occurrence of cushion peatlands; a significant change in the taxonomic composition of the community is indicated at about 4-7°S.

In a subsequent geochemical investigation, the soil conditions (water content, C/N ratios, conductivity, pH and element content) of 38 samples from five ecotopes of the selected peatland in southern Peru were analysed. The data reveal the ecological heterogeneity of the peatland with strong variations in nutrient availability (very poorly oligotrophic - strongly mesotrophic), soil wetness (dry - saturated) and element content (e.g. in As, Cr, Cu, Fe, K, Pb and Rb). On the basis of these results, an advanced succession model is proposed for the different peatland ecotopes. Furthermore, the geochemical data were used to reveal microhabitat descriptions, community responses and the soil condition indicator potential of the Oribatid mite and Chironomid communities. From the Oribatid mites, seven indicators were assessed, with six species indicating low soil wetness <58%, and a single species indicating high soil wetness >73%. From the Chironomids, five indicator taxa were revealed, with four taxa indicating soil wetness of 80-81%, and a single taxon indicating soil wetness >81%.

Finally, to apply the autecological data to the palaeoecological record, the Oribatid mite and Chironomid subfossil assemblages were investigated in a 152 cm-long core, retrieved from the cushion peatland, which represents a record covering 1064 years (1924-860 cal yr BP; 26-1090 AD). 16 Oribatid mite species and 12 Chironomid taxa were identified, with five significant indicator taxa from each being used to reconstruct soil wetness quantitatively, by employing a modern analogue technique (MAT) model. The model predicts a humid period from 1924-1426±22 yr BP (26-524±22 AD) with a significant dry spell occurring from 1601±35-1543±24 yr BP (349±35-407±24 AD), and which was fully established by 1567 yr BP (383 AD). After 1426±22 yr BP (524±22 AD), the soil wetness shifted to drier conditions and remained stable until 860 yr BP (1090 AD). The reconstructed soil wetness fluctuations are supported by supra-regional signals revealed by other studies and coincide with migration movements and cultural changes of the Nasca people in the Peruvian costal area.

This investigation confirms the sensitivity of the high-Andean cushion peatlands for climate fluctuations and highlights the strong dependency of the foothill region and the local population on the water supply from the high Andes. The water supply is essentially controlled by the peatlands in the headwaters, which basically act as water storages and drainage controllers. The results emphasise the need for a sustained conservation effort to protect the high-Andean cushion peatlands, which are nowadays endangered by mining activities and overgrazing.

Die edaphischen Oribatiden und Chironomiden-Larven aus fünf verschiedenen Sukzessionsstadien eines hochandinen Hartpolstermoores in Süd-Peru (14°S) wurden untersucht. Insgesamt konnten 17 Oribatiden Arten aus acht Familien identifiziert werden. Zu den nachgewiesenen Arten wurden taxonomische Hinweise zusammengestellt und eine Strukturanalyse der nachgewiesenen Gemeinschaft erstellt. Die Untersuchung zeigt, dass im frühen und mittleren Sukzessionsstadium des Moores signifikant mehr Oribatiden nachweisbar sind als im Klimaxstadium. Bei den Chironomiden konnten 11 Taxa aus drei verschiedenen Unterfamilien identifiziert werden. Für die nachgewiesenen Arten wurden taxonomische Hinweise verfasst und eine Analyse der Gemeinschaftsstruktur durchgeführt. In dem Moorbereich, der erste Pionierbesiedlung von polsterbildenden Pflanzen aufwies, konnten am meisten Chironomiden nachgewiesen werden, gefolgt vom mittleren Sukzessionsstadium und vom degradierten Moorbereich.

Anschließend erfolgte eine biogeographische Analyse der Oribatiden-Gemeinschaft der Hochanden. Bis jetzt sind zwischen Süd-Ecuador (4°S) und Zentral-Argentinien (34°S) nur 39 Probeflächen in der Höhenstufe zwischen 3000-5200 m NN untersucht worden, von denen sieben als Polstermoor klassifiziert werden konnten. Insgesamt wurden 219 Arten aus 116 Gattungen und 51 Familien in den Hochanden >3000 m NN nachgewiesen. Aus Hartpolstermooren sind 48 Arten aus 34 Gattungen und 18 Familien bekannt. Neun dieser Arten konnten in zwei oder mehr Mooren nachgewiesen werden. Die γ-Diversität innerhalb der Hochanden ändert sich mit zunehmender geographischer Breite: bei <10°S ist die Diversität mit >30 Arten pro Probefläche hoch, verringert sich dann auf sieben Arten bei ca. 19°S und nimmt anschließend mit mehr als 14 Arten pro Probefläche bei >30°S wieder zu. Diese Schwankung der Diversität kann statistisch mit Änderungen der Niederschlagsmenge in den Hochanden assoziiert werden. Die Analyse der Artgemeinschaft der Hochanden zeigt, dass diese sowohl auf Art- wie auch auf Gattungsebene aus vielen unabhängigen Untergruppierungen besteht. Außerdem deutet die Analyse einen signifikanten Wechsel der Oribatiden-Artengemeinschaft der Anden im Hinblick auf ihre systematische Zusammensetzung bei 4-7°S hin. Für die Artengemeinschaft der Moore konnte ein eher zonaler Einfluss auf die Zusammensetzung festgestellt werden, wohingegen das Vorkommen der typischen Polsterpflanzen, die die Vegetation der Moore bestimmen, azonal ist.

Im Anschluss werden die Ergebnisse einer geochemischen Analyse verschiedener Bodenparameter (Bodenfeuchte, C/N Verhältnis, Leitfähigkeit, pH-Wert und Elementgehalte) der unterschiedlichen Sukzessionsstadien des Moores in Süd-Peru vorgestellt. Die Daten zeigen heterogene Umweltbedingungen in den Böden mit starken Schwankungen der Nährstoffverfügbarkeit (oligotroph bis mesotroph), der Bodenfeuchte (trocken bis gesättigt) und der Elementgehalte (z.B. von As, Cr, Cu, Fe, K, Pb und Rb). Auf der Basis dieser Ergebnisse wurde ein erweitertes Sukzessionsmodell für das Moor erstellt. Außerdem wurden die Mikrohabitate der nachgewiesenen Oribatiden- und Chironomidengemeinschaften herausgearbeitet, die Einflüsse der Bodenparameter auf die Abundanz der Gemeinschaften modelliert und das Potential einzelner Taxa als Indikatoren für verschiedene Bodenbedingungen getestet. Dabei konnten sechs Arten der Oribatiden als signifikante Indikatoren für trockene Böden <58% und eine Art als Indikator für Bodenfeuchte >73% identifiziert werden. Von den nachgewiesenen Chironomiden konnten vier Indikatoren für Bodenfeuchte zwischen 80-81% und ein Indikator für Bodenfeuchte >81% herausgestellt werden.

Abschließend wurde auf Basis der vorhergehenden Untersuchungen ein 152 cm langer Torfbohrkern aus dem Moor paläoökologisch untersucht, der einen Zeitraum von 1064 Jahren von 1924-860 kal. a BP (26-1090 n. Chr.) abdeckt. In diesem Zeitfenster wurden die subfossil abgelagerten Oribatiden und Chironomiden analysiert. 16 Oribatiden-Arten und 12 Chironomiden-Taxa konnten identifiziert werden, von denen jeweils fünf in der vorhergehenden Untersuchung als signifikante Indikatoren für die Bodenfeuchte definiert worden waren. Auf dieser Grundlage wurde der Wassergehalt des Bodens mit Hilfe der Modern Analogue Technik (MAT) quantitativ rekonstruiert. Die rekonstruierten Werte zeigt stabil feuchte Bedingungen zwischen 1924-1426±22 a BP (26-524±22 n. Chr.) mit einer kurzen Unterbrechung mit trockeneren Bedingungen zwischen 1601±35-1543±24 a BP (349±35-407±24 n. Chr.), die um 1567 a BP (383 n. Chr.) voll ausgeprägt waren. Nach 1426±22 a BP (524±22 n. Chr.) ändern sich die Bedingungen dauerhaft hin zu trockeneren Bedingungen, die bis zum Ende des Untersuchungszeitraums um 860 a BP (1090 n.

Chr.) andauern. Vergleiche mit den Ergebnissen anderer über-regionaler Paläoklimauntersuchungen bestätigen die rekonstruierten Schwankungen der Umweltbedingungen. Außerdem überscheiden sich die festgestellten Änderungen der Wasserversorgung des Moores zeitlich mit Wanderungsbewegungen und kulturellen Veränderungen innerhalb des Volkes der Nasca in der Küstenregion Südperus.

Diese Untersuchung zeigt die hohe Sensibilität der Hartpolstermoore der Hochanden für Klimaschwankungen und betont die starke Abhängigkeit der Bereiche des Andenvorlandes und damit auch der dort lebenden Bevölkerung von der Wasserversorgung aus den Bergen. Die Versorgung wird maßgeblich von den Hartpolstermooren im Hochland beeinflusst, die Wasser speichern und den Wasserabfluss regulieren. Dadurch wird auch die Dringlichkeit des Schutzes dieses so wichtigen Ökosystems, das heutzutage durch Bergbau und durch starke Überbeweidung bedroht ist, verdeutlicht.

Appendix

Appendix 1 | Oribatid mite species: results of the indicator species analysis for the ecotopes and ecotope combinations. Only significant species are shown. ***= p<0,001; **= p<0,01; *= p<0,05; p was tested with 999 random permutations; [1]coverage is the proportion of the ecotope to which one or more indicators were found; [2]specificity is the probability that the surveyed sample belong to the targeted ecotope if the regarding species has been found; [3]sensitivity is the probability of finding the species in the sample belonging to the ecotope.

Ecotope (or ecotope combinations)	Coverage[1]	Taxon	Indicator value	Specificity[2]	Sensitivity[3]	p
Degraded ecotope	1.0	Juga_mont***	0.94	0.88	1.00	0.001
		Juga_arma***	0.94	0.88	1.00	0.001
		Nanh_eleg***	0.87	1.00	0.75	0.001
		Sche_pall*	0.66	0.87	0.50	0.024
Succession ecotope	0.875	Neoa_nota***	0.92	0.96	0.88	0.001
		Sche_eleg**	0.71	1.00	0.50	0.006
		Sche_conf*	0.68	0.74	0.63	0.014
(degraded + succession) ecotope	0.875	Tect_sp***	0.92	0.97	0.88	0.001
(degraded + succession + pioneer) ecotope	0.45	Mala_mono*	0.67	1.00	0.45	0.042

Appendix 2 | Chironomid taxa: results of the indicator species analysis for the ecotopes and ecotope combinations. Only significant species are shown. ***= p<0,001; **= p<0,01; *= p<0,05; p was tested with 999 random permutations; [1]coverage is the proportion of the ecotope to which one or more indicators were found; [2]specificity is the probability that the surveyed sample belong to the targeted ecotope if the regarding species has been found; [3]sensitivity is the probability of finding the species in the sample belonging to the ecotope.

Ecotope (or ecotope combinations)	Coverage[1]	Taxon	Indicator value	Specificity[2]	Sensitivity[3]	p
Pioneer ecotope	1.0	Cric/Para_II***	0.95	0.90	1.00	0.001
		Apse/Alot***	0.90	0.81	1.00	0.001
		Paro***	0.86	0.74	1.00	0.001
		Para/Phae**	0.71	1.00	0.50	0.009
		Para**	0.70	0.65	0.75	0.007
(degraded+ pioneer + succession) ecotope	0.85	Limn/Para***	0.91	0.97	0.85	0.001

Appendix 3 | Oribatid mite sampling sites from the high Andes >3000 m a.s.l., sorted from North to South. The classification of the ecoregion refers to Olson et al., 2001.

Abbreviation	Name	Latitude	Longitude	Country	Author	Altitude [m a.s.l.]	Precipitation [mm / yr]	Mean annual Temperature [°C]	Mean diurnal amplitude [°C]	Ecoregion	Habitat	Diversity [no. of species]
CJA	Cajanuma	3°58'S	79°04'W	Ecuador	Illig et al., 2008	3100	1505	17.7	10.6	Eastern Cordillera Real Montane Forests	Cloud Forest	26
CMA	Cajamarca	7°09'S	78°27'W	Peru	Hammer, 1961	3000	733	13.4	15.7	Peruvian Yungas		37
HZ	Huaraz	9°31'S	77°31'W	Peru	Hammer, 1961	4400	666	13.0	15.8	Sechura Desert		35
HO	Huancayo	12°03'S	75°10'W	Peru	Hammer, 1961	3500	751	11.0	14.7	Peruvian Yungas		19
CU	Cusco	13°30'S	71°55'W	Peru	Hammer, 1961	3625	707	9.9	15.9	Central Andean Wet Puna		45
MA	Marcona	13°30'S	73°44'W	Peru	Hammer, 1961	3000	860	13.3	16.5	Peruvian Yungas		7
IV	Sierra (IV)	14°01'S	72°00'W	Peru	Beck, 1962	3256	847	8.3	17.0	Peruvian Yungas	Sierra	10
LL	Llamoca	14°10'S	74°44'W	Peru	this study	4200	729	4.7	15.8	Sechura Desert	Cushion peatland	14
V	Puna (V)	14°21'S	70°29'W	Peru	Beck, 1962	4088	763	2.1	17.9	Central Andean Wet Puna	Puna	14
PO	Puno	15°49'S	70°00'W	Peru	Hammer, 1961	3900	709	8.1	14.0	Central Andean Wet Puna		5
SI	Sillustani	15°50'S	70°02'W	Peru	Hammer, 1961	3900	720	7.5	14.1	Central Andean Wet Puna		5
CH	Chacaltaya	16°21'S	68°07'W	Bolivia	Hammer, 1958	4734	601	0.7	14.9	Central Andean Wet Puna	Cushion peatland	21
EOC	East of Cumbre	16°21'S	68°01'W	Bolivia	Hammer, 1958	4632	611	2.6	14.7	Central Andean Wet Puna		18
C	Cumbre	16°22'S	68°01'W	Bolivia	Hammer, 1958	4827	611	2.6	14.7	Central Andean Wet Puna		20
VI	dry Puna (VI)	16°28'S	71°23'W	Peru	Beck, 1962	3000	7	18.3	13.7	Sechura Desert	Tola heath	4
UI	Unduavi	16°29'S	68°07'W	Bolivia	Hammer, 1958	3690	566	9.6	15.9	Central Andean Wet Puna		10
LP	La Paz	16°29'S	68°09'W	Bolivia	Hammer, 1958	3796	579	8.9	15.7	Central Andean Wet Puna		2
TA	Lomas del cerro Taapacà	18°06'S	69°30'W	Chile	Covarrubias, 2009	5200	344	-2.7	18.3	Central Andean Dry Puna	Llaretal	6
P	Putre	18°11'S	69°33'W	Chile	Covarrubias, 2009	3500	210	7.4	18.1	Central Andean Dry Puna	Plantation of alfalfa	1
CH-B	Chungara (Bofedal)	18°19'S	69°08'W	Chile	Covarrubias, 2009	4580	311	1.6	18.6	Central Andean Dry Puna	Cushion peatland	7
CH-Q	Chungara (Quenoal)	18°19'S	69°08'W	Chile	Covarrubias, 2009	4580	311	1.6	18.6	Central Andean Dry Puna	Queñoal	6
LS	Lago Surire	18°50'S	69°06'W	Chile	Covarrubias. 2009	4245	251	3.8	18.3	Central Andean Dry Puna	Tolar	4
PA	Parinacota	19°03'S	69°15'W	Chile	Covarrubias. 2009	3700	170	6.6	17.7	Central Andean Dry Puna	Yaretilla	8
ME	Mucomucone	19°03'S	68°56'W	Chile	Covarrubias, 2009	4272	227	3.8	18.2	Central Andean Dry Puna	Pajonal	8
COS	Cosapilla	17°46'S	69°25'W	Chile	Covarrubias, 2009	3250	144	6.8	17.5	Central Andean Dry Puna	Quenoal	2
CO-T	Colchane & Enquelca (Tolar)	19°17'S	68°38'W	Chile	Covarrubias, 2004	3800	191	7.3	17.6	Central Andean Dry Puna	Tolar	4
CO-P	Colchane & Enquelca (Pajonales)	19°17'S	68°38'W	Chile	Covarrubias, 2004	3800	191	7.3	17.6	Central Andean Dry Puna	Pajonales	5
CO-B	Colchane & Enquelca (Bofedal)	19°17'S	68°38'W	Chile	Covarrubias, 2004	3800	187	7.3	17.6	Central Andean Dry Puna	Cushion peatland	13
PU-L	Puchuldiza (Llaretal)	19°24'S	69°02'W	Chile	Covarrubias, 2004	4100	165	5.3	17.8	Central Andean Dry Puna	Llaretal	6
PU-Q	Puchuldiza (Quenoales)	19°24'S	69°02'W	Chile	Covarrubias, 2004	4100	165	5.3	17.8	Central Andean Dry Puna	Queñoal	5
CQA	Cariquima	19°38'S	68°28'W	Chile	Covarrubias, 2004	3765	164	5.2	17.7	Central Andean Dry Puna	Cardonal	7

Appendix 3 | … continued

Abbreviation	Name	Latitude	Longitude	Country	Author	Altitude [m a.s.l.]	Precipitation [mm / yr]	Mean annual Temperature [°C]	Mean diurnal amplitude [°C]	Ecoregion	Habitat	Diversity [no. of species]
SC	San Antonio de los Cobres	24°16'S	66°20'W	Argentina	Hammer, 1958	3857	114	7.1	17.1	Southern Andean Steppe	Cushion peatland	12
VN	Valle Nevado	33°18'S	70°14'W	Chile	Figueroa & Covarrubias, 2005	3200	464	13.7	13.7	Southern Andean Steppe	Cushion peatland	18
AC	Arroyo de la Cruz	34°10'S	69°39'W	Argentina	Hammer, 1958	3600	504	14.5	14.5	Southern Andean Steppe		23
EO	El Obscuro	34°31'S	70°03'W	Argentina	Hammer, 1958	3354	619	14.5	14.5	Southern Andean Steppe		10
LA	Laguna Atuel	34°33'S	70°05'W	Argentina	Hammer, 1958	3083	647	14.5	14.5	Southern Andean Steppe		10
EAV	El Angulo - Vulcan Overo	34°35'S	70°02W	Argentina	Hammer, 1958	3763	594	14.5	14.5	Southern Andean Steppe		2
EA	El Angulo	34°36'S	70°04'W	Argentina	Hammer, 1958	3089	647	14.6	14.6	Southern Andean Steppe		11
AS	Arroyo de Los Pajaritos	34°45'S	70°04'W	Argentina	Hammer, 1958	2179	708	15.0	15.0	Southern Andean Steppe	Cushion peatland	20

Appendix 4 | Test statistics of multiple regression models for the influence of environmental factors (precipitation, mean diurnal temperature and mean annual temperature) on the number of Oribatid mite species in the high Andes (>3000m a.s.l.).

	ΔR^2	B	SE B	β	p
Regression model 1	0.25				
Constant		3.87	2.79		0.17
Precipitation**		0.02	0	0.5	<0.01
Regression model 2	0.003				
Constant		4.81	26.06		0.85
Precipitation*		0.02	0.01	0.46	<0.05
Mean diurnal temperature range		-0.1	1.36	-0.02	0.94
Mean annual temperature		0.16	0.39	0.08	0.69
ANOVA F(model 1, 2)= 0.16, p= 0.85					

Appendix 5 | Jonckheere-Terpstra tests statistics to reveal significant trends in the geochemical data.

Environmental factor	p	JT	Trend in succession
C/N ratio ***	<0.001	234	enrichment
Ca ***	<0.001	232	enrichment
Cr ***	<0.001	224	enrichment
Water con. ***	<0.001	203	enrichment
C ***	<0.001	195	enrichment
Ti ***	<0.001	38	depletion
K ***	<0.001	29	depletion
Rb ***	<0.001	19	depletion
Ba **	0.002	58	depletion
Cond. **	0.002	57	enrichment
Sr **	0.003	61	depletion
Pb **	0.005	64	depletion
Zr **	0.006	65	depletion
pH *	0.013	179	enrichment
N	0.066	165	no significant trend
As	0.185	154	no significant trend
Mn	0.190	153	no significant trend
Fe	0.274	149	no significant trend

Appendix 6 | Statistics of the response analysis for the Oribatid mite community assessed for various environmental factors. The assessment and classification of response types follows Huismann et al. (1993), Oksanen & Minchin (2002) and Jansen & Oksanen (2013). Significant factors are marked with *: p<0.05, **: p<0.01, ***: p<0.001. For each factor, the p-value, the adjusted R^2 is and the F-value are denoted.

Environ-mental factor	Deviance	R^2	p	F	Assosciated HOF-model	Response type
N* **	57.1	0.54	<0.001	15.53	II	monotonouse
Fe**	55.7	0.47	0.001	4.86	VII	bimodal
Ca**	26.8	0.25	0.002	11.36	VII	bimodal
Rb**	49.8	0.40	0.007	3.85	V	skewed unimodal
Cu**	55.3	0.42	0.007	3.58	V	skewed unimodal
Zn*	39.8	0.32	0.012	3.85	VII	bimodal
As*	47.7	0.37	0.012	3.35	VII	bimodal
Ti*	47.5	0.37	0.013	3.32	V	skewed unimodal
Water con.*	39.8	0.30	0.023	3.10	VII	bimodal
Pb*	23.5	0.19	0.026	4.06	VI	bimodal
Zr*	50.3	0.35	0.030	2.64	II	monotonouse
pH*	17.0	0.14	0.044	2.00	VII	bimodal
Cr	35.8	0.25	0.059	2.40		
C	45.2	0.26	0.060	2.21		
Sr	10.7	0.06	0.273	1.35		
Ba	1.9	-0.01	0.444	0.60		
Cond.	33.3	0.08	0.460	1.01		
P	0.0	-0.03	0.776	0.08		
Mn	insufficient data					

Appendix 7 | Statistics of the response analysis for the Chironomid community assessed for various environmental factors. The assessment and classification of response types follows Huismann et al. (1993), Oksanen & Minchin (2002) and Jansen & Oksanen (2013). Significant factors are marked with *: p<0.05, **: p<0.01, ***: p<0.001. For each factor, the p-value, the adjusted R^2 is and the F-value are denoted.

Environ-mental factor	Deviance	R^2	p	F	Assosciated HOF-model	Response type
C***	85.8	0.80	<0.001	15.41	VII	bimodal
Cu***	80.3	0.77	<0.001	19.28	VII	bimodal
N***	77.1	0.69	<0.001	8.60	VII	bimodal
pH***	67.6	0.58	<0.001	5.71	VII	bimodal
As***	58.5	0.51	<0.001	6.24	VII	bimodal
Rb***	63.6	0.54	<0.001	5.59	IV	symmetric unimodal
Zn**	44.1	0.38	0.002	3.66	VII	bimodal
Cond.**	60.0	0.46	0.004	3.87	VI	bimodal
Pb*	48.7	0.34	0.028	2.68	VII	bimodal
Fe*	16.1	0.13	0.032	4.32	II	monotonous
Ba	10.9	0.08	0.060	3.81		
Zr	20.5	0.14	0.149	1.90		
Ti	15.6	0.10	0.157	1.89		
Water con.	31.3	0.14	0.231	1.44		
Sr	26.5	0.14	0.293	1.29		
Cr	10.1	0.04	0.528	0.71		
Ca	4.1	0.00	0.679	0.315		
P	0.0	-0.03	0.776	0.08		
Mn	insufficient data					

Appendix 8 | XRF measurement accuracy, limitations and post-collection data calibration referring to Knight et al. (2013)

Category	Elements	Precision (%RSD)	Linearity (R^2)	Calibration slope	Measured with	Advice for data usage	Post-collection data calibration	Summary of least square regression	Adjusted R^2
1	Sr	<5%	>0,97	0,95≤m≤1,05	high precision and high linearity				
	Zn	<5%	>0,97	0,95≤m≤1,05	high precision and high linearity				
2	Ca	<5%	>0,97	m≤0,95 or m≥1,05	high precision and high linearity	should be corrected with a post-collection data calibration	$x_{cal}=1.082x-233$	F(1, 2)= 540, p=0.002	0.9934
	Fe	<5%	>0,97	m≤0,95 or m≥1,05	high precision and high linearity	should be corrected with a post-collection data calibration	$x_{cal}=0.90x+6730$	F(1, 2)= 13160, p<0.001	0.9998
	K	<5%	>0,97	m≤0,95 or m≥1,05	high precision and high linearity	should be corrected with a post-collection data calibration	$x_{cal}=0.9545x+1334$	F(1, 2)=142, p=0.007	0.9792
	Mn	<5%	>0,97	m≤0,95 or m≥1,05	high precision and high linearity	should be corrected with a post-collection data calibration	$x_{cal}=0.9534x+75$	F(1, 2)= 1109, p<0.001	0.9973
	Rb	<5%	>0,97	m≤0,95 or m≥1,05	high precision and high linearity	should be corrected with a post-collection data calibration	$x_{cal}=1.116x-0.7$	F(1, 2)=1265, p<0.001	0.9976
	Zr	<5%	>0,97	m≤0,95 or m≥1,05	high precision and high linearity	should be corrected with a post-collection data calibration	$x_{cal}=0.937x-2.5$	F(1, 2)= 894, p=0.001	0.9967
3	As	<5%	>0,97	m≤0,95 or m≥1,05	lower precision but high linearity	calibration improves accuracy of data, but still less precise than Cat1&2. RSD much greater than 5% = repeat measurement			
	Cu	<5%	>0,97	m≤0,95 or m≥1,05	lower precision but high linearity	calibration improves accuracy of data, but still less precise than Cat1&2. RSD much greater than 5% = repeat measurement			
4	Ba			0,95≤m≤1,05	less linear result	calibration can only provide minor improvements (however, the element can effectively analysed but with minor precautions)			
	Ti				less linear result	calibration can only provide minor improvements (however, the element can effectively analysed but with minor precautions)			
	Cr				less linear result & less precise	calibration can only provide minor improvements (however, the element can effectively analysed but with minor precautions)			
	Pb				less precise	calibration can only provide minor improvements (however, the element can effectively analysed but with minor precautions)			
5	Cs	>5%	<0,97	m≤0,95 or m≥1,05	not any linearity near the determination limit				
	Th	>5%	<0,97	m≤0,95 or m≥1,05	not any linearity near the determination limit				
	Ni	>5%	<0,97	m≤0,95 or m≥1,05	not any linearity near the determination limit				
	V	>5%	<0,97	m≤0,95 or m≥1,05	not any linearity near the determination limit				

Appendix 9 | Palaeostudies from the Central Andes with details on archive resolution and analysed proxies

								Analysed palaeoproxies																			
								Biological proxies								Geophysical and chemical proxies											
Nr	Latitude	Longitude	Name	Altitude	Archive	Length [cal. yr]	Resolution [cal.yr sample^{-1}]	Pollen	Charcoal	Diatoms	Chironomids	Oribatid mites	Macrofossils	Spores	Phytoliths	Magnetic Susceptibility	Spectral analysis	Bulk density	Isotope analysis	Ammonium content	Element analysis (XRF)	Loss on ignition (LOI)	Carbon content (TIC&TOC)	Nitrogen content	Biogenic silica	Clastic influx	References
1	-7,50	-78,60	La Compuerta	3950	Lake sediment	47900	1597	●	●							●		●									Weng et al., 2006
2	-7,63	-77,47	L. de Chochos	3285	Lake sediment	12340	263	●	●							●		●									Bush et al., 2005
3	-7,70	-77,53	L. Baja	3575	Lake sediment	12100	126	●																			Hansen & Rodbell, 1995
4	-9,10	-77,60	Nev. Huascaran	6048	Ice core	20000	N.A.												●								Thompson et al., 1995, 2000, 2006
5	-9,80	-77,30	Lower Queshquecocha	4260	Lake sediment	13130	N.A.									●					●		●		●	●	Stansell et al., 2013
6	-9,82	-77,30	Upper Queshquecocha	4275	Lake sediment	18440	N.A.									●		●					●			●	Rodbell et al., 2008
7	-10,23	-76,93	Jahuacocha	4076	Lake sediment	7520	N.A.									●					●		●		●	●	Stansell et al., 2013
8	-10,43	-76,83	Huarmicocha	4670	Lake sediment	17350	N.A.									●		●					●			●	Rodbell et al., 2008
9	-10,55	-76,67	Lutacocha	4320	Lake sediment	8330	N.A.									●					●		●		●	●	Stansell et al., 2013
10	-10,68	-76,05	Pumacocha	4300	Lake sediment	11560	N.A.												●								Bird et al., 2011a, b
11	-10,78	-76,58	Huatacocha	4500	Lake sediment	10050	245	●																			Hansen et al., 1984
12	-10,83	-75,33	R. Blanco	4270	Lake sediment	11945	385	●																			Hansen et al., 1984
13	-11,00	-76,17	L. Junin	4100	Lake sediment	39020	411	●								●			●				●				Hansen et al., 1984; Seltzer et al., 2000
14	-11,23	-75,82	Pacupahuain Cave	3800	Speleothem	48830	N.A.												●								Kanner et al., 2012
15	-11,27	-75,78	Huagapo Cave	3850	Speleothem	7111	N.A.												●								Kanner et al., 2013
16	-11,57	-76,35	L. Milloc	4320	Peat	10465	654	●																			Graf, 1992
17	-11,57	-76,35	L. Milloc	4325	Lake sediment	10970	645	●																			Graf, 1992
18	-11,67	-75,00	L. Tuctua	4250	Lake sediment	11360	299	●																			Hansen et al., 1994
19	-11,72	-75,50	L. Paca	3600	Lake sediment	5305	133	●																			Hansen et al., 1994
20	-11,75	-75,25	Pomacocha	4450	Lake sediment	9820	546	●																			Hansen et al., 1994
21	-11,78	-75,22	L. Jeronimo	4450	Lake sediment	10960	322	●																			Hansen et al., 1994
22	-12,05	-77,66	106KL	0	Marine sediment	20000	N.A.										●										Rein et al., 2004, 2005
23	-13,22	-72,20	Marcacocha	3355	Lake sediment	1055	26			●																	Sterken et al., 2006
24	-13,22	-72,20	Marcacocha	3355	Lake sediment	1200	6					●												●			Chepstow-Lusty et al., 2007
25	-13,22	-72,20	Marcacocha	3355	Lake sediment	3650	130	●															●				Chepstow-Lusty et al., 2003
26	-13,42	-72,13	L. Huaypo	3500	Lake sediment	3930	54	●															●				Mosblech et al., 2012
27	-13,60	-73,50	L. Pacucha	3095	Lake sediment	24773	157	●	●																		Valencia et al., 2010
28	-13,60	-73,50	L. Pacucha	3095	Lake sediment	24773	221			●												●					Hillyer et al., 2009
29	-13,67	-71,28	Caserococha	3975	Lake sediment	26270	N.A.									●		●					●			●	Rodbell et al., 2008
30	-13,93	-70,83	Quelccaya	5670	Ice core	1800	N.A.											●									Thompson et al., 1995, 2013
31	-13,95	-70,88	Pacococha	4925	Lake sediment	14440	N.A.									●		●					●			●	Rodbell et al., 2008

Appendix 9 |...continued

								Analysed palaeoproxies Biological proxies								Geophysical and chemical proxies											
Nr	**Latitude**	**Longitude**	**Name**	**Altitude**	**Archive**	**Length [cal. yr]**	**Resolution [cal.yr sample^{-1}]**	**Pollen**	**Charcoal**	**Diatoms**	**Chironomids**	**Oribatid mites**	**Macrofossils**	**Spores**	**Phytoliths**	**Magnetic Susceptibility**	**Spectral analysis**	**Bulk density**	**Isotope analysis**	**Ammonium content**	**Element analysis (XRF)**	**Loss on ignition (LOI)**	**Carbon content (TIC&TOC)**	**Nitrogen content**	**Biogenic silica**	**Clastic influx**	**References**
32	-13,95	-68,98	L. Consuelo	1360	Lake sediment	41800	N.A.	●																			Bush et al., 2004
33	-13,95	-68,98	L. Consuelo	1360	Lake sediment	46300	400	●		●												●					Urrego et al., 2010
34	-14,17	-74,73	Cerro Llamoca	4450	Peat	8092	95	●						●							●						Schittek, 2014; Schittek et al., 2015
X	-14,17	-74,73	Cerro Llamoca	4450	Peat	1563	56				●	●											●	●			this study
35	-14,81	-69,18	Kantatica	4820	Peat	7490	357	●																			Graf, 1981
36	-15,22	-69,11	Cotapampa	4450	Peat	9560	503	●																			Graf, 1981
37	-15,24	-69,00	Amarete	4000	Peat	7290	521	●																			Graf, 1992
38	-15,48	-71,70	Q. Carhuasanta	4809	Peat	3771	N.A.												●		●						Engel et al., 2014
39	-15,50	-72,67	Nev. Coropuna	6377	Ice core	20000	annual												●								Herreros et al., 2009
40	-15,55	-72,68	Nev. Coropuna	4400	Peat	9608	69	●																			Kuentz et al., 2011
41	-15,83	-71,80	R. Sallalli	4400	Peat	9650	689	●																			Graf, 1999
42	-16,14	-71,83	Q. Chilcane	2750	Rodent middens	8560	535						●														Holmgren et al., 2001
43	-16,17	-68,37	Hichu Kkota	4800	Peat	4240	96	●																			Ostria, 1987
44	-16,17	-68,37	Hichu Kkota	4800	Peat	4240	112			●																	Roux et al., 1987
45	-16,20	-68,35	L. Taypi Chaka Khota	4300	Lake sediment	13550	N.A.									●		●					●			●	Rodbell et al., 2008
46	-16,20	-68,07	Tiquimani	3760	Peat	6070	169	●		●					●				●								Ledru et al., 2013
47	-16,26	-68,50	Cerro Calvario	3950	River terrace	23290	970	●																			Graf, 1992
48	-16,35	-68,04	Cumbre Unduavi	4620	Peat	9240	264	●																			Graf, 1979
49	-16,37	-68,15	Chacaltaya I	4750	Peat	9800	245	●																			Graf, 1979
50	-16,40	-71,15	L. de Salinas	4300	Peat	4990	624	●																			Graf, 1999
51	-16,43	-68,15	Chacaltaya II	4350	Peat	7310	159	●																			Graf, 1979
52	-16,43	-68,13	Rio Kaluyo	4070	Lake terrace	9645	804	●																			Graf, 1979
53	-16,62	-67,77	Nev. Illimani	6300	Ice core	18000	annual												●	●							Ramirez et al., 2003; Kellerhals et al., 2010
54	-17,03	-67,35	Monte Blanco	4780	Peat	8135	232	●																			Graf, 1979
55	-17,28	-65,73	L. Khomer Kocha Upper	4153	Lake sediment	14112	362	●	●					●			●						●				Williams et al., 2011a
56	-17,37	-70,30	L. Aricota	2800	Lacustrine sediment	6150	N.A.																				Placzek et al., 2001
57	-17,53	-65,82	Wasa Mayu	2720	Lake terrace	80000	4444	●																			Graf, 1992
58	-17,55	-65,57	L. Challacaba	3400	Lake sediment	4471	140	●	●		●					●	●						●				Williams et al., 2011b, 2012
59	-17,57	-65,94	Cala Conto	2700	Lake terrace	70000	2500	●																			Graf, 1992
60	-18,02	-70,83	Q. de los Burros	150	Peat	8730	N.A.																				Fontugne et al., 1999
61	-18,10	-68,88	Nev. Sajama	6542	Ice core	25000	annual												●								Thompson et al., 1998
62	-18,12	-68,97	Sajama	4250	Debris & Cushion plants	4500	321	●																			Graf, 1992
63	-18,18	-69,25	L. Seca	4500	Lake sediment	11155	446	●																			Baied & Wheeler, 1993

Appendix 10 | Statistics of the tested models for the reconstruction of soil wetness based on the Oribatid mite, Chironomid and the combined datasets. WA: Weighted Averaging regression and calibration; MLRC: Maximum Likelihood Response Surface analysis; MAT: Modern Analogue Technique; IKFA: Imbrie & Kipp Factor Analysis

		Datasets		
Model	**Statistics**	**Oribatid mites**	**Chironomids**	**combined**
WA (inverse)	Root mean squared error (RMSE)	13.94	20.56	17.09
	Determination coefficient (R^2)	0.49	0.01	0.33
	Maximum bias	34.04	43.9	38.7
MLRC	Root mean squared error (RMSE)	13.85	28.32	16.33
	Determination coefficient (R^2)	0.52	0.19	0.54
	Maximum bias	40.32	37.35	23.34
MAT	Root mean squared error (RMSE)	17.72	19.29	15.83
	Determination coefficient (R^2)	0.21	0.17	0.43
	Model components	5	6	5
	Maximum bias	17.72	40.06	29.09
IKFA	Root mean squared error (RMSE)	13.15	15.16	17.28
	Determination coefficient (R^2)	0.54	0.45	0.31
	Significance	<0.001	>0.05	<0.001
	Model components	2	3	5
	Maximum bias	32.55	20.17	35.48
	Bootstrapping	large bootstrap errors		

Erklärung

Ich versichere, dass die von mir vorgelegte Dissertation selbstständig angefertigt, die benutzten Quellen und Hilfsmittel vollständig angegeben und die Stellen der Arbeit – einschließlich Tabellen, Karten und Abbildungen –, die anderen Werken im Wortlaut oder dem Sinn nach entnommen sind, in jedem Einzelfall als Entlehnung kenntlich gemacht habe; dass diese Dissertation noch keiner anderen Fakultät oder Universität zur Prüfung vorgelegen hat; dass sie – abgesehen von unten angegebenen Teilpublikationen – noch nicht veröffentlicht worden ist, sowie, dass ich eine solche Veröffentlichung vor Abschluss des Promotionsverfahrens nicht vornehmen werde.

Die Bestimmungen der Promotionsordnung sind mir bekannt. Die von mir vorgelegte Dissertation ist von Prof. Dr. Michael Bonkowski betreut worden.

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