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ORIBATID MITES (ACARI: ORIBATIDA) IN SUB-ARCTIC PEATLANDS

A Multidisciplinary investigation into
climate change, permafrost dynamics
and indicator values of subfossils

Inkeri Markkula



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*To my parents,
who first introduced to me the land of white fells,
northern lights, and frost that never melts.*

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ABSTRACT

Sub-Arctic peatland ecosystems are undergoing rapid changes due to climate warming. Palsa and peat plateau mires, northern peatlands with permafrost as a definitive character, are degrading particularly rapidly. Rising temperatures are causing permafrost thaw, leading to alterations in hydrology, vegetation structure and microhabitat diversity. At the same time, the microinvertebrate fauna, such as oribatid mites (Acari: Oribatida), of these mires remain poorly known. Oribatid mites are microscopic (0.1–1 mm), mainly soil-dwelling arachnids, found in all terrestrial ecosystems, where they function as decomposers of organic matter. With 11 000 species described worldwide, and densities reaching 200 000 individuals per square meter, oribatids are one of the most species-rich and abundant soil-living animal taxa. Despite this, oribatids are considered a poorly known animal group. Oribatid mites have been shown to be good bioindicators of natural and anthropogenic environmental change, but they are rarely included in studies detecting ecosystem dynamics in the sub-Arctic region.

The aims of this thesis were to study the impacts of climate change on oribatid mite communities living in sub-Arctic peatlands, and to investigate if oribatid mites can be used as bioindicators in studies detecting historical permafrost dynamics. Data was collected from peatlands in Northern Fennoscandia, Siberia and Canada, and the studies included investigations of contemporary and past oribatid mite communities, covering a timescale 6000 years, as well as warming experiments.

The results of this thesis show that permafrost thaw in peatlands leads to alterations in the species composition and dominance structure of oribatid communities. The direct impacts of warming on peatland-dwelling oribatid mites are season-dependent: findings revealed that summer warming had a positive and winter warming a negative impact on oribatid densities. Small-bodied oribatid mites belonging to the genus *Suctobelba* significantly increased in abundance under summertime warming. The taxon richness of oribatid mites was negatively affected by year-round warming. The results also reveal that oribatid mites are valuable indicators of past permafrost conditions in sub-Arctic peatlands. Three permafrost-indicator species, *Carabodes labyrinthicus*, *Neoribates aurantiacus* and *Chamobates borealis*, were recorded.

This thesis provides novel information about the impacts of climate change on sub-Arctic oribatid mite communities. The studies highlight the conservational importance of palsa mires, and the importance of seasonal effects to be included in climate change studies. Moreover, findings of this thesis can help to understand the history of permafrost aggradation and degradation in peatlands, as oribatid mites can contribute to multi-proxy approaches aiming to reconstruct past environmental conditions. The results are significant, because understanding of past permafrost dynamics will help to predict future climate feedbacks and associated ecosystem shifts in changing sub-Arctic peatlands.

KEYWORDS: oribatid mites, climate change, sub-Arctic peatlands, permafrost dynamics, subfossils

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TIIVISTELMÄ

Ilmaston lämpeneminen aiheuttaa nopeita muutoksia subarktisisa suoekosysteemeissä. Erityisen herkkiä lämpenemisen vaikutuksille ovat pohjoiset palsasuot, joille on tunnusomaista turpeesta muodostuneiden palsojen sisältämä ikirouta. Ilmaston lämpeneminen sulattaa palsasoiden ikiroutaa, mikä aiheuttaa muutoksia kosteusoloissa, kasvillisuuden rakenteissa ja mikroelinympäristöjen monimuotoisuudessa. Toisaalta palsasoiden mikroselkärangattomien, kuten sammalpunkkien (Acari: Oribatida), lajisto tunnetaan puutteellisesti. Sammalpunkit ovat mikroskooppisia (0.1–1 mm), pääasiassa maaperässä eläviä selkärangattomia, jotka toimivat hajottajina erilaisissa ekosysteemeissä. Sammalpunkkilajeja tunnetaan maailmasta noin 11 000, ja yhdellä neliömetrillä niitä voi elää 200 000 yksilöä. Runsaudesta ja monimuotoisuudesta huolimatta sammalpunkit luokitellaan puutteellisesti tunnetuksi eläinryhmäksi. Sammalpunkit ovat aiemmissa tutkimuksissa osoittautuneet hyviksi indikaattorilajeiksi, jotka voivat ilmentää ekosysteemeissä tapahtuvia muutoksia. Toistaiseksi sammalpunkkeja on kuitenkin käytetty subarktisten ekosysteemien muutosten tutkimisessa varsin vähän.

Tämän työn tavoitteina oli tutkia, miten ilmaston lämpeneminen vaikuttaa subarktisisa soilla elävien sammalpunkkien yhteisöihin, sekä selvittää, voiko sammalpunkkeja käyttää bioindikaattorilajeina historiallisen ikiroutadynamiikan tutkimisessa. Tutkimuksen aineisto kerättiin Pohjois-Fennoskandian, Siperian ja Kanadan ikiroutasoilta. Tutkimuksissa kartoitettiin soiden tämänhetkistä sekä historiallista sammalpunkkilajistoa 6000 vuoden aikajänteellä. Ilmastonmuutoksen vaikutuksia sammalpunkkien yhteisöihin tutkittiin lisäksi lämmityskokeita käyttäen.

Tutkimukset osoittivat, että ikiroudalla on tärkeä merkitys sammalpunkkien lajikoostumuksen muokkaajana, ja ikiroudan sulaminen johtaa muutoksin sammalpunkkien eliöyhteisöissä. Ilmaston lämpenemisen vaikutukset soilla eläviin sammalpunkkeihin riippuvat vuodenajasta: sammalpunkkien tiheydet kasvoivat, kun kesäaikainen lämpötila oli korkeampi, mutta vähenivät silloin kun vain talven lämpötilat nousivat. Erityisesti pienikokoiset, *Suctobelba* -sukuun kuuluvat punkit hyötyivät kesäaikaisesta lämpenemisestä. Ympärivuotinen lämpeneminen vaikutti negatiivisesti sammalpunkkien lajiston monimuotoisuuteen. Sammalpunkit osoittautuivat hyviksi ikiroudan indikaattoreiksi. Tutkimuksessa löydettiin kolme lajia, *Carabodes labyrinthicus*, *Neoribates aurantiacus* sekä *Chamobates borealis*, jotka ilmentävät vahvasti ikiroudan esiintymistä.

Tämä väitöskirja tuo uutta tietoa ilmaston lämpenemisen vaikutuksista sammalpunkkien eliöyhteisöihin. Tutkimustulokset painottavat palsasoiden luonnonsuojelullista merkitystä sekä sitä, että ilmaston lämpenemisen vaikutuksia maaperän eliöyhteisöissä tutkittaessa tulisi vuodenaikojen vaikutus ottaa paremmin huomioon. Lisäksi, tämän tutkimuksen tulokset voivat auttaa ymmärtämään paremmin historiallista ikiroutadynamiikkaa subarktisisa soilla, sillä sammalpunkit tuovat niiden tutkimiseen yhden indikaattorin lisää. Menneiden ilmastonmuutosten ja niihin liittyvän ikiroutadynamiikan tutkiminen on ensisijaisen tärkeää, sillä se auttaa ennustamaan tulevia muutoksia subarktisisa ekosysteemeissä.

ASIASANAT: sammalpunkit, ilmastonmuutos, subarktiset suot, ikiroutadynamiikka, subfossiilit

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List of Original Publications

This dissertation is based on the following original publications, which are referred to in the text by their Roman numerals:

- I Markkula, I. Permafrost dynamics structure species compositions of oribatid mite (Acari: Oribatida) communities in sub-Arctic palsa mires. *Polar research*, 2014; 33: 22926.
- II Markkula, I., Oksanen, P. & Kuhry, P. Indicator value of oribatid mites in determining past permafrost dynamics in northern European sub-Arctic peatlands. *Boreas*, 2018; 47: 884–896.
- III Markkula, I., Cornelissen, J.H.C. & Aerts, R. Sixteen years of simulated summer and winter warming have contrasting effects on soil mite communities in a sub-Arctic peat bog. *Polar Biology*, 2019; 42: 581–591.
- IV Markkula, I. & Kuhry, P. Subfossil oribatid mite communities indicate Holocene permafrost dynamics in Canadian mires. Accepted manuscript, *Boreas* 2020.

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	I	II	III	IV
Original idea	IM	IM, PK, PO	IM, HC, RA	IM, PK
Literature review	IM	IM	IM	IM
Fieldwork	IM	PO, PK, IM	IM	PK
Material sorting	IM	IM	IM	IM
Species identification	IM	IM	IM	IM
Data analyses	IM	IM	IM	IM
Writing	IM	IM, PK, PO	IM, HC, RA	IM, PK

IM: Inkeri Markkula; PK: Peter Kuhry; PO: Pirita Oksanen; HC: Hans Cornelissen; RA: Rien Aerts

1 Introduction

1.1 Changing sub-Arctic peatlands

Terrestrial Arctic and sub-Arctic environments are characterized by long, cold winters, short summers and permanently frozen grounds: approximately 24% of the ice-free land in the northern Hemisphere is underlain by permafrost (Zhang 2003). In this era of climate warming, these cold environments are going through rapid changes. Globally, mean annual temperatures have increased by 0.85 °C, over the period from 1880 to 2012 (IPCC 2014). In Arctic and sub-Arctic regions climate warming is more severe: For several decades already, the surface air temperatures have been warming at a rate more than twice the global rate (AMAP 2017).

Permafrost thaw is one of the most worrying consequences of climatic warming in Arctic and sub-Arctic regions (IPCC 2019). Permafrost is defined as ground, including rock or soil, which remains frozen (temperature below the freezing point of water 0 °C) for more than two years. In the Arctic permafrost is continuous, covering more than 90% of the ice-free land area. In the sub-Arctic permafrost is usually discontinuous (covering 50-90% of the land area) or sporadic (covering 0-50%), and it occurs mostly in peatlands in the form of permanently frozen peat hummocks or peat plateaus (International Permafrost Association 2019). These peatland complexes are often called *palsa mires*, and are found in Northern Fennoscandia, Siberia, Canada and Alaska. Located at the outer limit of the permafrost zone, *palsa mires* represent a marginal permafrost feature (Luoto et al. 2004), and thus, are very sensitive to climatic fluctuations (Aalto et al. 2017).

The occurrence of permafrost in *palsa mires* depends on several climatic factors, including low annual mean temperature (<0.0°C), low precipitation (<500 mm/year) and relatively thin snow cover (Seppälä 1988, 1990, 2011). Permafrost hummocks, also called *palsas*, are formed by frost upheaval and contain a frozen core of peat and/or silt, with small ice crystals and thin layers of isolated ice, which remain frozen throughout the summer (Seppälä 1986). The formation and preservation of permanently frozen *palsas* is dependent on the different thermal conductivity of dry and wet peat, the latter being a ten times more effective conductor of heat, while dry peat is a good insulator (Seppälä 1994). *Palsa mires* are considered a sub-type or eco-climatic variant of *aapa mires*, minerotrophic mire complexes

common to northern regions (Seppä 2002; Laitinen et al. 2007). Palsa and aapa mires share many similarities in vegetation, and the main difference between the two mire types is the presence of permafrost in palsa mires.

At present, palsa mires are degrading throughout Northern Fennoscandia and North America (e.g. Karlgård 2008; Thibault et al. 2009; Borge et al. 2017). Degradation of permafrost causes alterations in vegetation structure, microhabitat diversity, hydrological conditions, nutrient availability and carbon cycling in peatland ecosystems, and can lead to increased release of methane and carbon dioxide to the atmosphere (Camill et al. 2009; Bosiö 2012; Christensen et al. 2012; Voigt et al. 2019). Studies conducted in various locations have revealed via aerial images and ground surveys of plant communities that the vegetation in palsa mires is changing: palsa hummocks and hummock vegetation such as mosses and evergreen dwarf shrubs are decreasing, and wet sites and minerotrophic vegetation such as tall graminoids are increasing (e.g. Malmer et al. 2005; Karlgård 2008; Bosiö 2012).

Palsa mires are listed as a priority habitat type in the European Union Habitat Annex (European Commission 2013), and are important ecosystems in terms of nature conservation (Luoto et al. 2004). Permafrost contributes to biodiversity in palsa mires by creating a diverse set of microhabitats which are formed in a cyclic process of permafrost aggradation and thaw (Luoto et al. 2004). First, permafrost hummocks (palsas) are formed by frost heaving. Palsa hummocks rise to a height of 0.5–10 m above the peatland surface, and create dry nutrient-poor peat islands within a minerotrophic fen ecosystem (Fig.1). In the degradation process of permafrost, palsa hummocks collapse and consequently form remnants such as peat ridges, thermokarst pools, depressions and smaller hummocks (Zuidhoff and Kolstrup 2005; Fig. 2). Dynamics of palsa formation and collapse create minerotrophic-ombrotrophic gradients and water table gradients: in contrast to wet minerotrophic habitats, ombrotrophic permafrost hummocks receive water only from precipitation (Charman 2002; Luoto et al. 2004). Consequently, microhabitats with several different degrees of moisture are formed. However, climate warming has impacted the natural cycling processes of permafrost hummock formation and collapse: more and more hummocks are collapsing and very few new ones are formed. Changes in permafrost dynamics have been reported in number of studies. For example, Fronzek (2013) predicted that dry permafrost hummock microhabitats will disappear from palsa mires if average temperatures rise by 4°C from the years 1961–1990. Also, Borge et al. (2017) predicted that in some areas in Northern Norway, palsas and permafrost peat plateaus will be lost by 2030. Moreover, Bosiö et al. (2012) predicted 97 % reduction in dry hummock areas in palsa mires in Northern Fennoscandia by 2041–2060, compared to the 1961–1990 coverage. Microhabitat heterogeneity is known to be an important factor for maintaining invertebrate

diversity in peatlands and other ecosystems through increase in niche differentiation and resource availability (e.g. Hansen 2000; Verberk 2006). Thus, climate warming may lead to changes in invertebrate species composition in northern peatlands, through the decrease in microhabitat diversity.



Figure 1. Palsa hummocks rise 1–10 m above the fen surface. Picture: Reijo Nenonen/Vastavalo.



Figure 2. Collapsing palsa hummocks create thermokarst pools. Picture: Eero Vilmi/Vastavalo.

1.2 Oribatid mites of peatlands

Oribatid mites (Acari:Oribatida), commonly called moss mites, are microscopic (0.1–1mm), mainly soil-dwelling arachnids, and are one of the most abundant and diverse groups of microinvertebrates inhabiting peatlands (Behan-Pelletier and Bissett 1994). In general, oribatids are an abundant and species-rich animal group: 11 000 species are described, and up to 200 000 individuals and 50 species can be found per one square meter of forest soil (Schatz and Behan-Pelletier 2008; Subías 2018). The oribatid fauna of northern peatlands is still poorly documented, but some studies have shown that their diversity and abundance might be as high in peatland as in forest habitats (Behan-Pelletier and Bissett 1994; Seniczak et al. 2019).

In peatlands, oribatids inhabit both terrestrial and aquatic microhabitats, including dry hummocks, water-saturated hollows, and water bodies such as ponds and pools (Behan-Pelletier and Bissett 1994). Oribatids are detritivorous and fungivorous decomposers and due to their abundance, are also one of the central decomposer groups of organic matter in peatlands (Murvanidze and Kvavadze 2010). Consequently, oribatids also contribute to nutrient cycling, soil formation, litter chemistry and the distribution of fungal spores in soil and peat (Renker et al. 2005; Schneider et al. 2005; Wickings and Grandy 2011).

While the main habitat of oribatid mites is the moist soil surface covered with mosses, lichens and decaying vegetation litter, they are also found abundantly in a variety of other microhabitats such as tree hollows and canopies (Taylor and Ranius 2014; Salvatulin 2019), decaying wood (Siira-Pietikäinen et al. 2008) and ant nest mounds (Elo 2016). They also occur in aquatic and semi-aquatic habitats and on submerged plants (Schatz and Behan-Pelletier 2008), in bird nests (Lebedeva et al. 2006), and even inside spruce needles (Hågvar 1998). Because of their vast abundance in soils, oribatid mites are also often called “soil mites”, however, the soils are in fact inhabited not only by oribatid mites, but also by other mite groups from the suborders Mesostigmata, Prostigmata and Astigmata (Walter and Proctor 2013). The group of mesostigmatid mites include many predator species, which feed on oribatids (Schneider and Maraun 2009), and are frequently found in sub-Arctic peatlands, but do not reach as high densities as oribatid mites.

Oribatid mites have many names. Because of their morphological appearance, oribatids are also commonly called “beetle mites”, “armored mites” or “shell mites”. Oribatids have a polished and rounded body shape and hard, shell-like cuticle, characteristics that separate them from other mite groups. The hard shells of oribatids are well preserved in sediments and peat as fossils and subfossils (partially fossilized remains). The oldest recorded oribatid fossil is from the Devonian period, 450 mya (Norton et al. 1988), and oribatid mites are known to be one of the oldest animal groups on Earth (Schaefer et al. 2010).

1.3 Oribatid mites in studies of permafrost dynamics in palsa mires

Even though soil mites, including oribatids, are important contributors to decomposition processes and nutrient cycling in soils throughout the Earth, in high latitudes their role is particularly important (Ruess et al. 1999). This is because in high-latitude soil systems, the biomass and diversity of macrofauna such as earthworms is usually low (Ruess et al. 1999), and thus mites, together with springtails (Collembola), enchytraeids (Enchytraeidae) and nematodes (Nematoda), dominate the soil fauna. Consequently, they also dominate the decomposition and soil formation processes (Heal 1997; Sohlenius et al. 1997).

While the impacts of climate warming on oribatid mites in the Arctic and sub-Arctic regions have been a focus in a number of research covering, for example, direct impacts of warming (Coulson et al. 1996; Dollery et al. 2006; Hågvar and Klanderud 2009; Alatalo 2017), alterations in freeze-thaw cycles (Sulkava and Huhta 2003; Sjurksen et al. 2005), and winter ice encapsulation (Coulson et al. 2000), these studies have mainly been conducted in tundra and forest ecosystems (except the study of Alatalo 2017, which also included peatlands). Currently, there is still a lack of knowledge about the effects of permafrost thaw on oribatid mites inhabiting sub-Arctic peatlands, and the seasonality of impacts of climate warming on peatland oribatid fauna.

In general, oribatid mites have proven to be good bioindicators of natural and anthropogenic changes in ecosystems (Gergócs and Hufnagel 2009; Lehmitz 2014; Dirilgen et al. 2016; Lehmitz et al. 2020). Unlike many other members of the soil fauna, oribatid mites are often K-strategists, with low reproductive capacity and long life cycles (Behan-Pelletier 1999), which makes them particularly suitable bioindicators (Gergócs and Hufnagel 2009). The distribution of oribatid species is generally associated with moisture, vegetation and food sources (Gao et al. 2016), and in peatlands, important environmental factors that impact oribatid distribution include water table depth, local plant diversity, and the phosphorus content in *Sphagnum* tissues (Minor et al. 2019). Thus, the species compositions of oribatid mite communities reflect prevailing environmental conditions, and alterations in their community assemblages can indicate environmental change. These factors make oribatid mites a particularly interesting and important group to study in sub-Arctic ecosystems, which are undergoing rapid changes due to climatic change.

1.4 Peatland archives and oribatid mite subfossils as indicators of past environmental change

Peatlands are important ecosystems due to their rich biodiversity, but also as ecological archives storing information about vegetation, landscape, climate and

human history. Peatlands form particularly useful palaeoenvironmental records because of their sensitivity to climatic and hydrological changes, good preservation of organic matter in the waterlogged conditions, and due to the stratigraphy of the peat deposits providing chronology (Lamarre et al. 2012; Greiser and Joosten 2018). Peatland archives contain a wide collection of organic material, which stores information about the past species assemblages and form a multi-proxy record of the development of the peatland ecosystem and its surroundings (Greiser and Joosten 2018). These proxies include both plant and animal macro- and microfossils, archaeological artefacts, minerals, charcoal, volcanic ash, biochemicals, stable isotopes, and other natural or anthropogenic matter that has ended up in the peatland (Greiser and Joosten 2018).

In this era of climatic change, peatland archives are perhaps more important than ever, because reconstructions of past environmental conditions in mires help to understand how these ecosystems will react to future temperature increases and the resulting ecological shifts (e.g. Treat et al. 2016). In particular, in the Arctic and sub-Arctic regions, the concern about melting of permafrost calls for more investigations of past ecosystem dynamics and change. Historical permafrost dynamics can be reconstructed by combining analyses of plant macrofossil assemblages and succession with radiocarbon dating (e.g. Oksanen 2005; Kuhry 2008; Routh et al. 2014; Treat et al. 2016; Sannel et al. 2018). Plant macrofossil analyses used to detect historical permafrost dynamics are based on plant community succession, particularly during rapid shifts of plant and moss assemblages (Oksanen 2005). In addition, the absence of certain plant species which do not occur on permafrost can indicate permafrost aggradation; however, positive permafrost-specific indicator plant species have not been found. Some studies have shown that there are mosses that are characteristic for dry palusa hummock habitats, for example *Dicranum* spp., but these do not grow exclusively on permafrost (e.g. Oksanen 2005; Kuhry 2008). Thus, it can be difficult to determine the exact timing of permafrost aggradation within peatlands based on plant macrofossils (Oksanen and Väliranta, 2006; Treat et al. 2016).

Previous studies have pointed out that there is a need to develop and test new proxy methods, which could be used in studying past and present changes in sub-Arctic peatlands (Swindles et al. 2015; Gałka et al. 2018). Together with plant macrofossils, diatoms, rhizopods, Chironomidae and testate amoeba have been used as indicators of past environmental changes and permafrost dynamics in northern peatlands (Wetterich et al. 2011; Lamarre et al. 2012, 2013; Gałka et al. 2017; Zhang 2018). Previously, oribatid mite subfossils from lake sediments (e.g. Solhøy and Solhøy 2000; Presthus Heggen et al. 2010; Słowiński et al. 2018), peatlands (Markkula 1986) and river floodplains (Krivolutskii and Sidorchuk 2003; Sidorchuk 2004) have been used to reconstruct past ecosystems. However, the value of oribatid

mites as indicators of historical permafrost dynamics has not been investigated before.

1.5 Aims of the thesis

The general aims of this thesis were to provide novel information about 1) the impacts of climate change on oribatid mites and oribatid mite communities, 2) the bioindicator values of oribatid mites in studying past climatic changes and permafrost dynamics, in sub-Arctic peatlands, in particular in palsa and peat plateau mires.

More specifically, the following were investigated:

1. In order to estimate the impacts of permafrost thaw on oribatid mite communities in sub-Arctic palsa mires, two different field studies were conducted. First, the differences of oribatid mite communities in different microhabitats in two palsa mires in northern Finland and Norway, one well preserved and one degrading, were examined (Paper I). Second, oribatid species compositions between palsa mires and non-permafrost peat mires were compared (Paper II).
2. By using long-term (16 years) experimental warming conducted in a peatland in Northern Sweden, the effects of higher year-round, summer, and winter temperatures on oribatid mite communities were tested. The impacts of higher temperatures on densities, taxon diversity, community composition and the composition of morphological, ecological and life-history traits of oribatid mites were investigated. In addition, the impacts of climate manipulation on densities of Mesostigmata, predatory mites that feed on oribatids, were investigated. (Paper III).
3. One aim of this pioneer study was to find indicator oribatid species that could serve as new proxies in palaeoecological studies detecting historical permafrost dynamics. This was investigated by comparing subfossils extracted from peat profiles (covering a time period of approx. 6000 years), collected from palsa mires in northern Europe (Paper II) and Canada (Paper IV), with the present-day oribatid fauna of the same locations. Based on literature and findings from study I, permafrost dynamics were expected to be reflected in subfossil oribatid mite assemblages as changes in species compositions, and their communities were expected to include specific permafrost indicator species.

2 Materials and Methods

2.1 Study area

The research sites consisted of a total of 16 peatland areas, situated in the northern parts of Finland, Norway, Sweden, Canada and Russia (Fig. 3). The Fennoscandian study areas are located on sporadic or discontinuous permafrost, and the main study sites in Canada and Russia lie at the border of discontinuous and continuous permafrost zones (Fig. 4, 5).

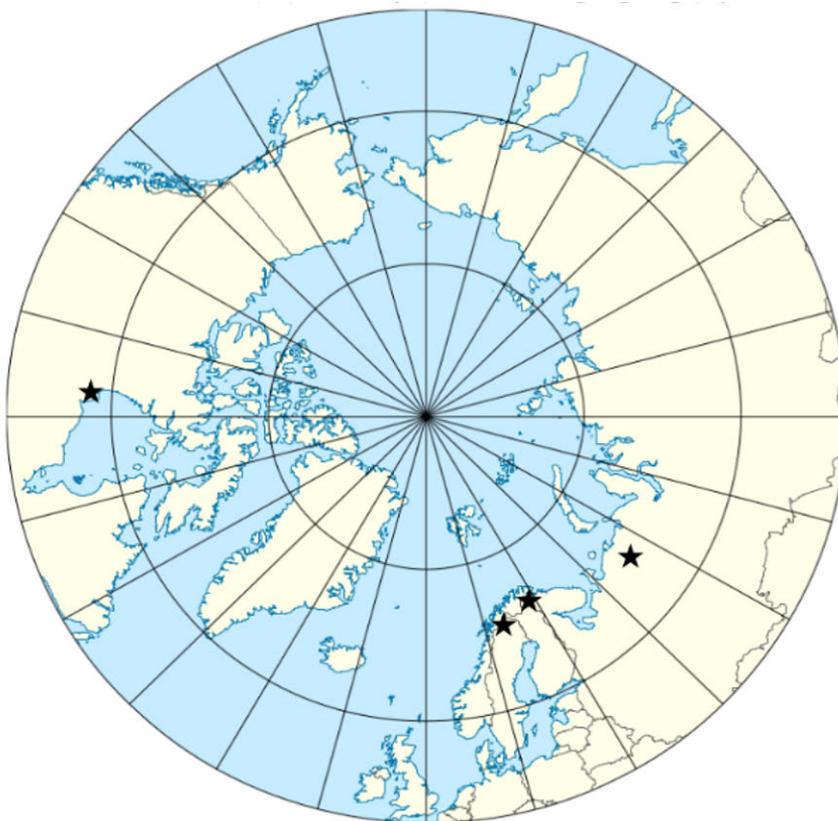


Figure 3. Locations of research sites in Finland/Norway, Sweden, Russia and Canada. Map source: Wikipedia.

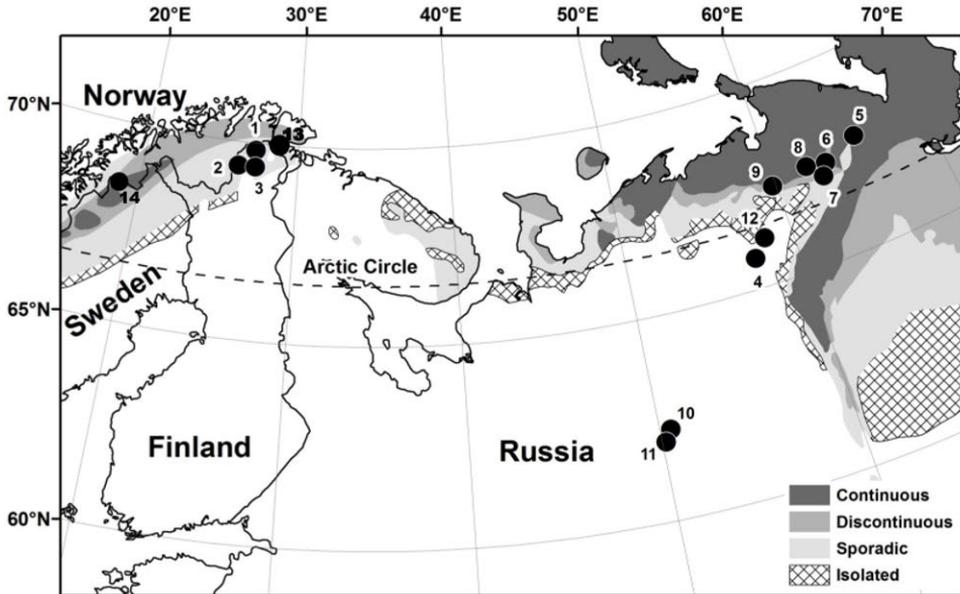


Figure 4. Locations of research sites in Northern Europe. The main research sites were: Vaisjeäggi (1), Per Bihtos jeäggi (2), Kuumpijeäggi (3), Usinsk (4), Ferdesmyra (13) and Abisko (14). Original map: Vesa Nivala.

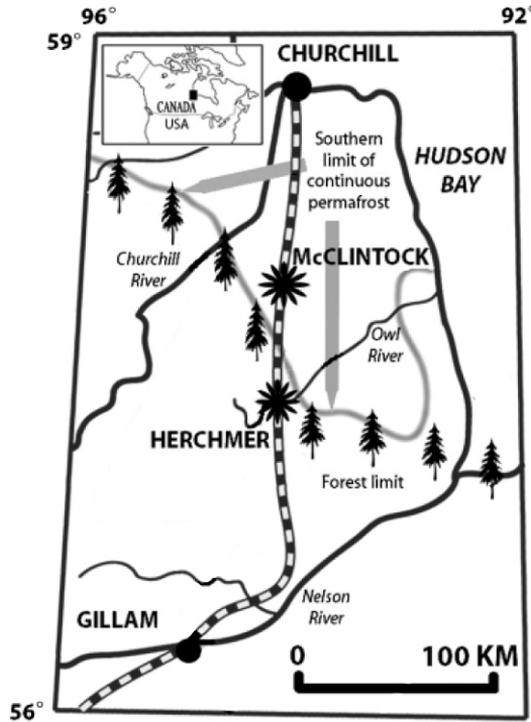


Figure 5. Location of the Herchmer palsa and McClintock peat plateau sites along the railroad between Gillam and Churchill in the Hudson Bay area in Canada. Map modified from Kuhry 2008.

Study I was conducted in two palsa mires, located in Utsjoki in Finland (Vaisjeäggi) and East Varanger (Ferdesmyra) in Norway. Vaisjeäggi in Finland (69°48'N; 27°14'E), is a relatively well preserved palsa mire, where plenty of palsa hummocks were found at the time of sampling. In this area, the mean annual temperature recorded at the Kevo Subarctic Research Station (12 km south-west from the mire) is -1.6°C, and the mean annual rainfall is 415 mm (average for years 1981–2010, Finnish meteorological institute). The Ferdesmyra mire (69°44'N; 29°16'E) in Norway, has undergone a major thawing of permafrost, and decrease in size and height of palsa hummocks, documented between 1970–2008 (Hofgaard 2009). The mean annual temperature for the area is -1°C, and the mean annual rainfall is 470 mm (Norwegian Meteorological Institute).

Samples analyzed in study II were collected from peatland sites in Northern Finland and Russia. In Finland study sites included Vaisjeäggi, and samples for faunal comparisons were also collected from Kuumpijeäggi (69°23'N; 27°13'E) and Per-Bihtos jeäggi (69°23'N; 26°07'E), two aapa mires located in Inari. Mean annual temperature in Inari is 0.6°C and mean total annual precipitation 500 mm (average for years 1981–2010, Finnish meteorological institute). In Russia, the main study site was Usinsk mire (65°45'N; 57°30'E), located in the extreme northern taiga subzone. In Usinsk, permafrost occurs as isolated patches in the form of small peat plateaus, palsa hummocks and palsa strings. The mean annual temperature in the nearest town, Ust'-Usa is -1.7 °C, and the mean total annual precipitation is 409 mm (average for years 2005–2016, Russian weather archive). In addition, reference data was analyzed from eight peatland areas in different parts of Northern Russia (Fig 4).

Study III was conducted on an experimental site in a mire adjacent to Lake Torneträsk in Abisko, Sweden (68°21'N; 18°49'E), where long-term heating of *Sphagnum* dominated mire habitats has been ongoing since 2000. At this site, mean annual temperature is -0.1 °C and mean annual precipitation 332 mm (1981–2010, National Network Sweden). Permafrost in the site is sporadic, and present only in small palsa remnants. Most of the site is permafrost-free.

Peat profiles analyzed for study IV were collected in Canada from two mires, called Herchmer and McClintock, situated in the Hudson Bay Lowlands of northeastern Manitoba, along a railway between the towns of Gillam and Churchill (Fig. 5). Mean annual temperatures at Churchill Airport and Gillam Airport are -6.5°C and -3.7°C, respectively (Average for 1981–2010, Canadian climate stations data). Annual precipitation is 452.5 mm for Churchill and 496.4 mm for Gillam. In the Herchmer mire site (57°23'N; 94°11'W) palsa bogs with trees, permafrost-free fens and ponds are found, forming a mosaic of habitats. Palsas are raised about 1.5 m above the fen surface. The McClintock mire (57°50'N; 94°12'W) is an extensive peat plateau with scattered thermokarst lakes, and at the site the permafrost peat plateau is elevated by about 1 m relative to the lake surfaces.

2.2 Study design and oribatid sampling

2.2.1 Sampling of contemporary oribatid fauna

In study I, three types of microhabitats in two palsa mires were sampled for oribatid mites. The sampled microhabitats were selected according to field observations of dominant vegetation and presence/absence of permafrost. The presence of permafrost was confirmed by a vegetation survey and by detection with an iron probe. Microhabitats were: (1) permafrost-underlain palsa hummocks dominated by evergreen dwarf shrubs; (2) non-permafrost hummocks dominated by herbs; and (3) adjacent wet microhabitats dominated by graminoids. Wet microhabitats included minerotrophic internal meadows, and thermokarst ponds, which are formed by thawing permafrost. Five replicated samples were taken from each microhabitat, 30 samples in total. The percentage of vegetation coverage around the sampling plots was measured by using vegetation quadrats of 0.5 m². Moisture content was measured from a soil/peat sample taken from each study plot by drying the samples at 35°C: the moisture content was calculated as the difference in sample weight before and after drying (fresh weight minus dry weight). The sample pH was measured in the laboratory using dried and sieved soil (one sample per sampling plot) mixed with distilled water (100 ml water, 10 ml dried soil).

In study II, four study sites were sampled, two in palsa and two in aapa mires. At each study site, three separate study plots were set, at least 80 m from each other. At each plot, soil samples were taken under five types of vegetation: 1. Lichen (*Cladina* spp.); 2. Crowberry (*Empetrum hermaphroditum*); 3. Cloudberry (*Rubus chamaemorus*); 4. *Sphagnum* mosses (*Sphagnum* spp., hollow type); 5. Sedge (*Carex* spp.). Next to each sample, a core was taken in order to analyze the soil moisture content (measured similarly to study I, except the samples were dried at 70 °C).

2.2.2 Subfossil sampling

Oribatid mite subfossils were analyzed from peat profiles collected from Northern Finland and Russia (study II) and Canada (study IV). These profiles were originally collected for studies discussing Holocene peatland succession, permafrost dynamics and peat accumulation, based on plant macrofossil and physio-chemical analysis (Kuhry 1998; Oksanen et al. 2003; Oksanen 2006; Kuhry 2008). As part of these studies, the profiles had been dated with the AMS (accelerator mass spectrometry) radiocarbon dating method. The peat profiles were excavated from the cleaned edges of palsa hummocks and peat plateaus. At the McClintock mire site in Canada, the material was also collected from a fen site near the peat plateau using peat samplers.

All material was stored at $-18\text{ }^{\circ}\text{C}$, and the remaining peat material which had not been used for plant macrofossil studies was subsampled for the oribatid subfossil analyses conducted here.

In study II, two drilled peat profile samples were checked at 5–10 cm intervals for oribatid mite subfossils; a total of 51 samples were checked (10 cm^3 in size). The peat profiles were 130 and 250 cm long, the oldest (lowermost) layers being approximately 4500 years old (calibrated years BP). In study IV, two peat profiles were checked at 2 cm intervals and one profile at 5–10 cm intervals (peat profiles 154, 162 and 194 cm long); a total of 51 samples (25 cm^3 in size) were checked for oribatids. The oldest age was approximately 6000 years (calibrated years BP). Subfossil data was compared with previously published reconstructions of permafrost history based on plant macrofossil analyses from the same locations.

2.2.3 Experimental design

Study III was conducted on a climate manipulation experiment (Fig. 6). The experiment started in June 2000, when six different treatments, simulating possible future climate scenarios with higher summer, spring and winter temperatures and increase in winter precipitation, were established (Aerts et al. 2004; Dorrepaal et al. 2004). The experimental set up used in this study consisted of a control treatment and three climate change manipulations: summer warming (June–September), winter warming (October–late May) with snow accumulation, and year-round warming. Each treatment was replicated five times, so the total number of sampling plots was 20.

In the treatments, artificial climate change was imposed by passive warming using a modified version of the open-top chambers (OTCs) developed in the International Tundra Experiment (Marion et al. 1997). The OTC's raise air temperatures at approximately 5 cm above the soil by $0.5\text{--}2.8\text{ }^{\circ}\text{C}$ in winter, $0.7\text{--}1.2\text{ }^{\circ}\text{C}$ in spring and by $0.9\text{ }^{\circ}\text{C}$ in summer. The soil temperatures (at 5 cm depth) were raised in spring by about $1\text{ }^{\circ}\text{C}$, in summer by $0.6\text{--}0.9\text{ }^{\circ}\text{C}$ and in winter by $0.5\text{--}2.2\text{ }^{\circ}\text{C}$ (Aerts et al. 2009). Increased winter snow accumulation was accomplished as the OTCs serve as passive snow traps, when strong winds blow snow into them at the exposed site. Winter treatment increased the snow thickness two or threefold. During December–January, the average snow depths were 7.9 cm in the control and 25.5 cm in the winter warming treatment. During February–April, the snow depths were 15.7 and 30.5 cm, respectively.



Figure 6. Abisko experimental site. Picture: Inkeri Markkula.

2.3 Oribatid extraction and species identification

Oribatid mites were extracted from the fresh soil samples (studies I, II, III) by using Tullgren-Berlese -type funnels (Berlese 1905; Tullgren 1918). Extraction started within 48 hours from sampling, and funnels were run until all samples were dry, 4–8 days depending on the sample size used. In the subfossil studies (II, IV), frozen peat samples were thawed at room temperature and mixed with water. Oribatid mite subfossils were hand-picked from the solution by using a pipet or pincers within 3 days of thawing. All oribatid mites were stored in 75 % ethanol.

Oribatid mites were identified to species or genera, or in some cases to higher taxonomic levels, based on Weigmann (2006). In study IV, additional information was gained from the Canadian Biodiversity Information Facility (<https://www.cbif.gc.ca>) and Behan-Pelletier and Lindo (2019). All materials are stored at the Zoological Museum of the University of Turku.

2.4 Statistical analyses

In studies I, II and III, generalized linear mixed models (the Glimmix procedure in SAS, with Tukey-Kramer post-hoc multiple comparisons) were used to test

differences in oribatid mite abundances: I. In different microhabitats within palsa mires; II. Between palsa and aapa mires and III. Between climate manipulation treatments.

Because normality could not be achieved even after data transformations in any of the oribatid mite species datasets, negative binomial distribution were used in the analyses in studies II and III. In study I, the sample size was different in the two study areas, and thus standardized abundance data (number of individuals per 100 cm²+0.01), and the gamma distribution were used in the analyses. A small number (0.01) was added to the original values to omit zero abundance values.

In study III, Shannon biodiversity indices were calculated to investigate how climate manipulations affect oribatid species richness and diversity. Differences in biodiversity indices and the mean number of oribatid taxa between climate manipulation treatments were tested using Analyses of Variance (ANOVA) with Dunn's post-hoc tests. The same tests were used to test the differences in mesostigmatid mite densities between the treatments. Homogeneity of variances was tested prior to analyses, and the data was log-transformed to conform to normality.

To illustrate the differences/similarities in oribatid mite community composition between microhabitats in palsa mires (study I) and between climate manipulation treatments (study III), Non-Metric Multidimensional Scaling (NMDS) with the Bray-Curtis similarity index were conducted. To analyze microhabitat and vegetation preferences of oribatid mites in palsa and aapa mires (study II), Canonical Correspondence Analyses (CCA) were carried out. In CCA analyses, presence/absence of lichen and plant species/genera (binary 0/1) and soil humidity (continuous, from 0.57 to 0.86), measured at the sampling plots, were used as environmental variables.

Statistical analyses were carried out using the PAST software (<http://folk.uio.no/ohammer/past/>), and the SAS software version 6.1.

2.5 Trait analyses

In study III, both a taxonomic approach and analyses of morphological, ecological and life-history traits were used to test the effects of climate manipulation on oribatid mite communities. Three morphological, life-history and ecological traits were used: feeding guild, reproductive mode and body size. Information regarding feeding guild and reproductive mode was gained from previous studies and literature (e.g. Fischer 2010, 2014; Farska et al. 2014a, 2014b; Bluhm et al. 2016, for more information see Paper III). Information regarding body size was taken from Weigmann (2006), and the maximum values of the body length range were used.

To study the effects of warming treatments on trait compositions of oribatid mite communities, differences in mean trait values ($N=5$) between treatments were tested with ANOVA and Dunn's post hoc test. Community Weighted Mean (CWM) values were calculated prior to analyses by using equations from Garnier et al. (2004):

$$\text{CWM} = \sum_i p_i X_i$$

where X is the trait value of the i -th species, and p is the relative abundance of the i -th species.

3 Results

3.1 Impacts of permafrost thaw on oribatid mite communities (I, II)

To investigate the impacts of permafrost thaw on oribatid mite communities, the species compositions were compared: 1) between different microhabitats within palsa mire ecosystems and 2) between two mire types: palsa mires and non-permafrost aapa mires. These comparisons were based on the assumption that impacts of permafrost thaw on oribatid mite communities will occur through alterations in vegetation and microhabitat composition and hydrological conditions, all which have been reported in previous studies conducted in palsa mires (eg. Malmer et al. 2005; Bosiö et al. 2012). Moreover, previous studies have predicted a total loss of permafrost in mires, if average yearly temperatures rise by 4°C from the average temperatures of years 1961–1990 (Fronzek 2013; Aalto 2017).

In study I, the microhabitat preferences of oribatid mites were tested in three microhabitats (permafrost hummock, non-permafrost hummock, and wet microhabitats) in two palsa mires in Finland and Norway. Based on a dataset that consisted of 8101 specimens, identified to 28 species and 6 genera, the community compositions of oribatid mites differed significantly between the microhabitats. A total of 65 % of the oribatid taxa were characterized as having microhabitat preferences, but most of the differences were found between wet microhabitats and hummock microhabitats. Because the area covered by dry palsa hummock microhabitats is predicted to decrease remarkably during the coming decades in palsa mires (Bosiö 2012; Fronzek 2013), particular interest was paid to species which were associated with permafrost-underlain microhabitats. Of the identified oribatids 18 % showed a preference for palsa hummock microhabitats. The main differences in community composition between permafrost-underlain and non-permafrost hummocks were caused by the high numbers of one species, *Carabodes labyrinthicus*, in palsa microhabitats (Fig. 7).

In study II, the data consisted of 3141 oribatid specimens, which were identified to 24 species and 6 genera. Most of the oribatid taxa were indifferent to mire type, but three species (*Carabodes labyrinthicus*, *Chamobates borealis* and *Melanozetes mollicomus*) were significantly more abundant in palsa mires and three species

(*Carabodes subarcticus*, *Ceratozetes thienemanni* and *Conchogneta traegardhi*) more abundant in aapa mires. When the vegetation preferences of oribatids were further tested, it was revealed that species associated with the palsa mire type showed preferences for hummock vegetation including lichen, crowberry and cloudberry. Oribatid mite communities under lichen stands differed significantly between the mire types: in palsa mires *Carabodes labyrinthicus* was four times more abundant, and *Chamobates borealis* eight times more abundant under *Cladina* spp. stands than in aapa mires. There was no difference in mean humidity in *Cladina* stands between aapa and palsa mires.



Figure 7. *Carabodes labyrinthicus* on lichen. Picture: Riikka Elo/Zoological Museum, University of Turku.

3.2 Impacts of simulated climate warming on oribatid mite communities (III)

In study III, the direct impacts of climate warming on oribatid communities were examined in a long-term (16 years) warming experiment conducted at a peatland site in Northern Sweden. The study was based on findings from previous research, reporting that oribatid mite communities are resistant to modest changes in mean air and soil temperatures (e.g. Hågvar and Klanderud 2009; Alatalo et al. 2017) but

benefit from earlier snow melt, longer growing season and lower soil temperatures during winter (Sjursen et al. 2005; Dollery et al. 2006), and on the assumption that the impacts of climate warming on organisms may display differently in different seasons of the year, an aspect that has not been covered by previous studies.

Based on 2401 oribatid specimens collected in this study, the results revealed that the impacts of warming on oribatid mite communities are season-dependent. The results showed that summer and winter warming had contrasting effects on oribatid mite communities: densities of oribatid mites were 50 % higher in the summer warming treatment plots, than in the winter warming treatment plots. Here the small-bodied oribatid mites belonging to genus *Suctobelba* were significantly affected by warming: mean densities of *Suctobelba* spp. were 65% higher in summer warming treatment plots compared to control plots, and 70% higher compared to winter warming treatments. Year-round warming had a negative effect on the species richness of oribatid taxa, and on the mean densities of mesostigmatid specimens.

The relative dominance structure of the oribatid communities was similar in all experiments, and, in contrast to expectations, warming treatments had no significant effect on the ecological and life-history trait composition of oribatid mite communities.

3.3 Oribatid mites as indicators of past permafrost dynamics (II, IV)

In studies II and IV conducted in Finland, Russia and Canada, subfossils of oribatids from four mire sites were analyzed, and the results were compared with previously published reconstructions of permafrost history based on plant macrofossil analyses from the same locations (Kuhry 1998, 2008; Oksanen et al. 2003; Oksanen 2006). Based on a dataset consisting of 914 subfossil oribatid mites from Northern Finland, 987 from Northern Russia and 1909 from Canada, the studies demonstrated that oribatid mites are valuable indicators of past permafrost conditions in peatlands. Permafrost dynamics were reflected as changes in species compositions in oribatid mite subfossil assemblages. In particular, at mire sites where permafrost conditions were stable, a shift from a community dominated by hygrophilous and aquatic taxa to a community consisting of taxa associated with drier habitats was clearly visible. At mire sites where repeated aggradation and thaw of permafrost was recorded based on plant macrofossil analyses, oribatid taxa associated with drier habitats occurred together with hygrophilous taxa in peat layers, which had permafrost in the past. Moreover, the results suggest that subfossil oribatid mite remains can reveal periods of permafrost, which cannot be determined with certainty based on plant macrofossils alone.

Three permafrost indicator species were identified from Northern European mire sites (Fig. 8). Two of these, *Carabodes labyrinthicus* and *Chamobates borealis* dominated the oribatid communities in peat layers with permafrost. Of these, *C. labyrinthicus* was also found in two studied mires in the Hudson Bay lowlands in Canada. In addition, *Neoribates aurantiacus* occurred in low numbers in subfossil data both in Canada and Northern Europe, where it was associated with permafrost. These findings were supported by the present-day datasets. *C. labyrinthicus* and *C. borealis* were significantly more abundant in palsa mires than in non-permafrost aapa mires, and showed preference for dry hummock vegetation. *N. aurantiacus* was clearly associated with the presence of lichens, and because lichen remains are rarely preserved in peat deposits, this finding is significant for future investigations.

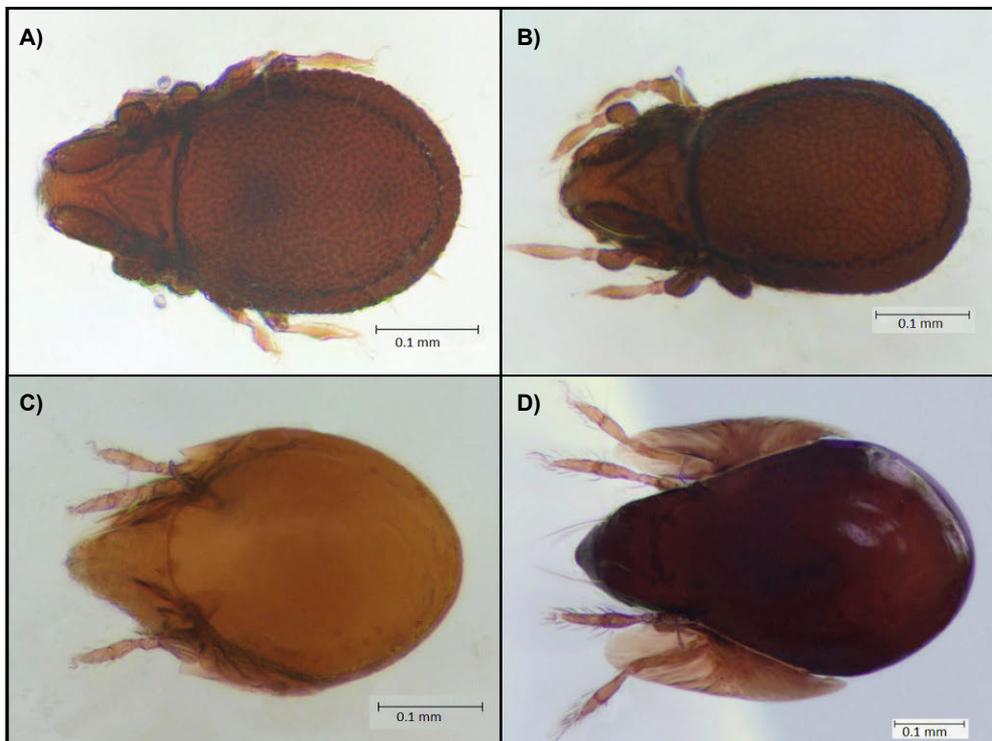


Figure 8. Indicator oribatid species: A) *Carabodes labyrinthicus*, B) *Carabodes subarcticus*, C) *Chamobates borealis*, D) *Neoribates aurantiacus*. *Carabodes subarcticus* (B) is abundant in aapa mires. Picture: Riikka Elo/Zoological Museum, University of Turku.

4 Discussion

4.1 Peatland oribatid communities and the current climatic change

The effects of climate change on soil communities may occur through direct and indirect pathways. Direct pathways are driven by alterations in soil physical properties, for example in microclimate and soil structure, and indirect pathways are mediated by changes in below-ground resource availability, following from the plants' responses to warming (Mori et al. 2014). In sub-Arctic peatlands, changes in plant communities, hydrology and soil carbon dynamics, resulting from climatic warming and permafrost thaw, are currently occurring. Consequently, changes in microinvertebrate communities can be expected to take place, and in turn, changes in microarthropod communities can impact vegetation and carbon dynamics, as microarthropods contribute to decomposition processes and nutrient cycling. In addition, alterations in densities of predators (e.g. mesostigmatid mites) and species interactions resulting from changes in resource availability may further impact microarthropod communities.

The results from the studies I and II suggest that permafrost thaw will alter species compositions and dominance structures of oribatid mite communities in sub-Arctic mires, and lead to a decrease in abundance of species associated with permafrost. This particularly applies to one species, *Carabodes labyrinthicus*, which was clearly associated with permafrost and dry hummock vegetation including lichen, which it feeds on (Ermilov 2011; Hågvar et al. 2014). Interestingly, another species in the *Carabodes* genus also known to feed on lichen, *C. subarcticus*, was abundant among *Cladina* spp. in aapa mires, but not in palsa mires, where *C. labyrinthicus* prevailed. As the geographic distributions of the two species overlap, this finding may be a result of interspecies competition. This is in line with previous research by Mumladze et al. (2013) reporting that interspecific interactions, in particular food-niche differentiation, play a significant role in structuring species compositions of oribatid communities in Holarctic peat bogs. It has been shown that *C. labyrinthicus* can endure both low humidity and very low temperatures (Sømme 1981), which probably explains its dominance in palsa hummocks, which are barren and cold microhabitats, especially in winter. Moreover, palsa hummocks seem to be

one of the main habitats of *C. labyrinthicus* in the mountain birch area in Northern Finland: According to my records, it occurs only in low numbers in the birch forests surrounding palsa mires (Markkula, unpublished data).

Previous studies have shown that litter and resource heterogeneity resulting from diverse plant communities are important factors structuring the species compositions and diversity of oribatid communities (e.g. Hansen and Coleman 1998; Hansen 2000; Nielsen et al. 2010). In peatlands, vegetation diversity, especially of mosses, seems to be important for the diversity of oribatid mites (Minor et al. 2016; Seniczak et al. 2019). In study I, 65 % of the oribatid taxa showed microhabitat preferences, most of these between wet graminoid-dominated, and dry, dwarf shrub-dominated hummock microhabitats. Even though none of the identified oribatid species occurred strictly in permafrost underlain habitats, the results showed distinct communities in different microhabitats. Thus, the predicted reduction in dry hummock areas and increase in graminoid and carpet moss vegetation as a result of permafrost thaw (Bosiö et al. 2012), can be expected to lead to alterations in oribatid communities in palsa mires.

In general, in Arctic and sub-Arctic areas, there are great seasonal changes in temperature and the light regime, to which all living organisms need to adapt. Soil-dwelling organisms also have to cope with seasonal environmental variability, including shifts from frozen soil in winter to very wet and cold soil during spring when the snow melts, then to warmer and drier soil in summer, and again back to frozen soil in winter. Given this, seasonality of the effects of climate warming may be of great importance for soil-dwelling organisms. However, this aspect has not been covered in previous experimental studies addressing the impacts of climate warming on oribatid mites. Here, study III revealed that the effects of simulated summer and winter warming on oribatid mite communities contrast; the densities of oribatids increased when summer temperatures were higher, but decreased under winter-time warming. The results are partly in line with previous studies reporting that oribatid mites benefit from earlier snow melt and a longer growing season associated with climatic warming (Dollery et al. 2006), but also from lower soil temperatures during winter (Sjursen et al. 2005). Moreover, the results suggest that the overall impacts of warming on oribatid mite communities in sub-Arctic peatlands are likely to depend on season-specific changes rather than on the increase in average yearly temperatures. As for the diversity of oribatid taxa, there was no difference between the seasons, but year-round warming had a negative effect on the taxon richness.

Based on earlier findings, species responses to climate manipulations were predicted to be dependent on body size and feeding mode, and consequently, the trait composition of oribatid mite communities were expected to be altered by warming. These predictions were based on studies reporting that small-bodied oribatid mites

benefit from higher temperatures (Lindo 2015), and that increased temperatures cause changes in the relative proportions of fungi and bacteria in soil, which may affect fungivoric and bacterivoric oribatid mites (Blankinship et al. 2011; Garcia-Palacios et al. 2015; Asemaninejad et al. 2018). However, the results did not support the expectations that the responses of oribatid species to warming will depend on their body size and feeding mode, as neither species nor trait composition of oribatid communities were altered by warming. However, even though the composition of traits were not affected, the higher abundances of oribatid mites under summer warming treatment was related to body size, which is in accordance with previous findings of Lindo (2015).

The responses of soil invertebrate communities to warming are assumed to be habitat-specific, for example, a recent study from Greenland reported that climate warming impacts on arthropod communities are much more pronounced in dry than in wet habitats (Koltz et al. 2018). Moreover, drought is known to have negative effects on soil microarthropods (Blankinship et al. 2011; Lindo et al. 2012), but, microarthropods living in peatland ecosystems can benefit from reductions in soil moisture due to changes in aerobic conditions and increase in habitable pore spaces (Turnbull and Lindo 2015). It is noteworthy that the warming experiment used here was in relatively wet microhabitat dominated by *Sphagnum* spp. The results could have been different if the study would have been conducted in the palsa hummock microhabitat, which differs from fen sites in terms of oribatid species composition and moisture levels. Moreover, because summer-time precipitation may play an important role in oribatid responses to warming, it would be beneficial if studies investigating warming impacts would be repeated for at least two consequent years.

Microarthropods' responses to warming can also depend on other factors such as predation and interspecific competition. For example, Koltz et al. (2018) reported an increase in numbers of herbivores and parasitoids and decrease in numbers of springtails and mites under higher seasonal temperatures. Laboratory experiments have shown that predation by mesostigmatid mites has a strong negative effect on small-bodied oribatid mites (Schneider and Maraun 2009). In this study, densities of mesostigmatid mites decreased under year-round warming, however, the changes were not concomitant with those of oribatid mites, suggesting a minor role for predation in the studied system.

4.2 Oribatid mites as indicators of ecosystem changes in the past

Sensitivity to climate changes makes peatlands valuable with their palaeoenvironmental records. Historical permafrost dynamics in sub-Arctic peatlands can be reconstructed by combining analyses of plant macrofossil

assemblages and vegetation succession together with radiocarbon dating (e.g. Routh et al. 2014; Treat et al. 2016; Sannel et al. 2018). However, the lack of positive permafrost indicator plant species causes challenges, such as difficulties in the exact timing of permafrost aggradation. At the same time, the need to understand past climate events, permafrost dynamics and associated ecological shifts in Arctic and sub-Arctic ecosystems is perhaps greater than ever, as this kind of understanding helps predict future climate feedbacks. For this reason, studies II and IV aimed to find permafrost-specific oribatid species, which could be used as indicators in palaeoecological studies detecting historical permafrost dynamics in peatlands across the circumpolar sub-Arctic.

In my studies three indicator species, *Carabodes labyrinthicus*, *Neoribates aurantiacus* and *Chamobates borealis* were found. Of these, *C. labyrinthicus* and *N. aurantiacus* were recorded in research sites both in Northern Europe and Canada. According to the results of the two studies, the identified oribatid indicator species have a good potential to be used as proxies in palaeoecological studies and can help in the timing of historical permafrost aggradation events. In addition, based on the data analyzed from a fen site in Canada in Hudson Bay lowlands, it was found that oribatid mite subfossils can reveal past permafrost events, which could not be otherwise determined with certainty based only on plant macrofossil analyses alone (see paper IV).

Results from these two studies are in accordance with earlier studies showing that oribatid mites are useful indicators of past environmental change (e.g. Solhøy and Solhøy 2000; Presthus Heggen et al. 2010; Słowiński et al. 2018). However, palaeoecological peatland studies, which use oribatid mites as bioindicators, are few in number (but see Markkula 1986 for a study in peatland oribatid subfossils, and Krivolutskii & Sidorchuk 2003 and Sidorchuk 2004 for river flood plains). One of the limitations in oribatid mite subfossil studies is the taxonomic difficulty. It is common that important body parts that are used in identification of specimens are lacking in fossils (Luoto 2009). This caused problems with one of the indicator species identified in this study, *N. aurantiacus*, which easily loses parts of its pteromorph as subfossil, making definite identifications impossible. For this reason, the numbers of *N. aurantiacus* were probably too low in the subfossil record. On the other hand, oribatid mites belonging to the genus *Carabodes* are less difficult to identify to species level, because the distinctive features of these species, such as characteristics of the notogaster and the surface sculpture, are usually visible in subfossil specimens. Interestingly, new DNA based species identification methods, such as DNA barcoding, have the potential to complement species identification with more accuracy, and are already being used for the identification of current soil mite communities (Young et al. 2012). Hence, these methods, together with methodological improvements in preserving ancient DNA (aDNA), could in future also be applied to oribatid subfossils, which would then enhance studies of past permafrost dynamics.

5 Conclusions

This thesis provided novel information about the impacts of climate change on oribatid mites, a relatively poorly known soil animal group, in sub-Arctic peatlands (I, II, III). Three oribatid mite species, which could serve as permafrost-specific bioindicators in studies reconstructing past climate changes and permafrost dynamics, were presented (II, IV).

While simulated higher temperatures had no impact on species compositions of oribatid mite communities, permafrost dynamics were found to be an important factor in structuring oribatid species compositions. Even though climate warming will impact oribatid mite communities in sub-Arctic peatlands both directly (higher air and soil temperatures) and indirectly (permafrost thaw leading to changes in hydrology, vegetation and microhabitat compositions), the indirect effects have received less attention. This thesis is among the pioneer studies investigating the impacts of permafrost thaw on soil invertebrate communities. The findings of this thesis also highlight the importance of seasonal effects to be included in studies investigating the effects of climate warming on soil faunal communities.

Palsa mires are vulnerable ecosystems listed as a priority habitat in the European Union (European Commission 2013). Permafrost, which is currently melting rapidly, is the definitive character of palsa mires, and known to play an important role in different ecosystem functions. The findings of this thesis are in line with earlier studies (e.g. Luoto et al. 2004) reporting that permafrost dynamics are an important factor supporting biodiversity in palsa mires.

In general, sub-Arctic ecosystems are relatively simple in terms of biodiversity. However, in areas of low species diversity, loss or gain of even a single species can have strong impacts on ecosystem functions (Chapin and Körner 1995; Heemsbergen et al. 2004; Roscher et al. 2004). Changes in species compositions of oribatid mite communities caused by permafrost thaw, and the possible reductions in oribatid richness caused by higher temperatures, may impact ecosystem functions in northern peatlands through alterations in the decomposition, nutrient and carbon cycles. However, the overall consequences of climate warming on belowground ecosystem functions in sub-Arctic ecosystems are still unclear, and more studies addressing this topic are needed.

In the upcoming decades, temperatures will continue to rise in sub-Arctic and Arctic areas. Therefore, it is now more important than ever to study how different organisms and communities, in different habitats, at all ecosystem levels and in different seasons, respond to the changes that are about to take place during climate warming. Palaeoecological studies reconstructing past environmental conditions have an important role in this, as knowledge on past ecosystem changes helps to estimate future shifts (e.g. Swindles et al. 2015; Gałka et al. 2018). Multi-proxy analyses, in which different indicators, such as plant macrofossils and testate amoebae and invertebrates, are analyzed in parallel, make these palaeoecological interpretations more accurate (Loisel and Garneau 2010). Here, another group, the soil-dwelling oribatid mites, were shown to be similarly valuable permafrost indicators providing a new proxy for palaeoecological studies. Moreover, oribatid mite subfossils should in future be included in analyses of past environmental changes as they can help to detect past permafrost dynamics in tundra and peat plateau mires and can reveal areas that had permanently frozen peat layers in the past. Currently, permafrost covers 24% of the exposed land in the Northern Hemisphere and vast amounts of it lie under tundra. As in tundra mires, the permafrost under tundra is melting, and as impacts of permafrost thaw on soil invertebrate communities in tundra ecosystems remain poorly known, these changes should be addressed in future studies with a multidisciplinary approach including the ubiquitous oribatid mites.

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