ON THE ECOLOGY AND BIOGEOGRAPHY OF ALPINE TUNDRA ARACHNIDS
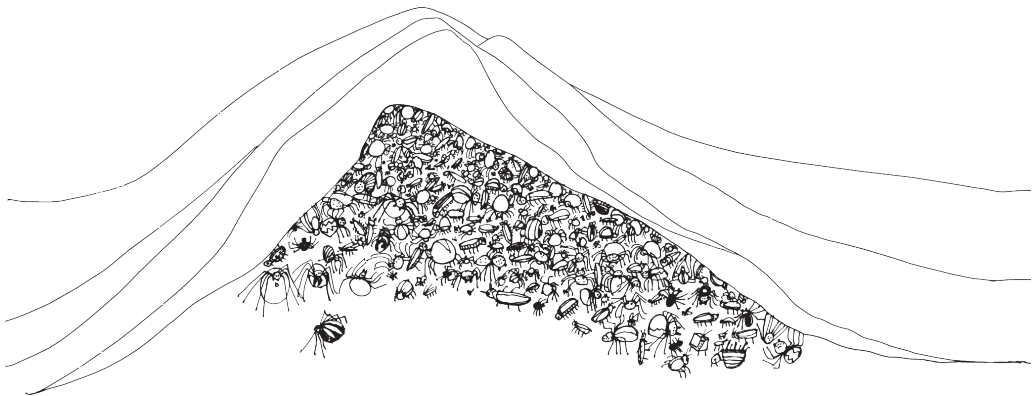
"I never thought that Spider-Man would become the world wide icon that he is. I just hoped the books would sell and I'd keep my job."

 - Stan Lee

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Acronyms and abbreviations

A	Ridge
ACIA	Arctic Climate Impact Assessment
AIC	Akaike information criterion
ANOVA	Analysis of variance
asl	Above sea level
B	Depression
C	Southern exposed slopes
D	Northern exposed slopes
EN	Egg number
ER	Elevational range
EV	Egg volume
GLM	Generalized linear model
GPS	Global positioning system
H0	Heat sums of temperatures above 0 °C
H5	Heat sums of temperatures above 5 °C
H10	Heat sums of temperatures above 10 °C
H15	Heat sums of temperatures above 15 °C
IBP	International Biological programm
IPCC	Intergovernmental Panel on Climate Change
Isopam	Ordination space partitioning
LA	Low alpine
LTAER	Long-Term Alpine Ecosystem Research in the Norwegian Scandes
MA	Middle alpine
MASS	Functions and datasets to support Venables and Ripley, 'Modern Applied Statistics with S'
MRI	Magentic resonance imaging
Mt.	Mountain
P	Precipitation
PCA	Principle Component Analysis
PC	Principal Component
pscl	Political Science Computational Laboratory
PW	Prosoma width
SL	Season length
SSD	Sexual Size Dimorphism
T+100	Air temperature in 100 cm heigth

T+15	Air temperature in 15 cm heigth
T-15	Temperature in 15 cm depth
SM-15	Soil moisture in 15 cm depth
UTM	Universal Transverse Mercator
VPD	Vapor pressure deficit
W	Wilcoxon value

Zusammenfassung

Im Zuge der Diskussion um die Auswirkungen des durch den Menschen verursachten Klimawandels auf die Ökosysteme sind die Hochgebirge der Erde in den Blickpunkt gerückt. Alpine Ökosysteme gelten gemeinhin als besonders sensibel gegenüber sich veränderten Umweltbedingungen. Die Hochgebirgsforschung konzentriert sich hierbei zumeist auf die Erforschung ökosystemarer Prozesse entlang verschiedener Gradienten und auf unterschiedlichen Skalen. Dabei können ökosystemare Forschungsprojekte im Bereich der Hochgebirge aufgrund höhenwärtiger Abhängigkeiten Raum-Zeit-Substitutionen nutzen. Der Fokus der Forschung hinsichtlich der zeitlichen und räumlichen Muster in den alpinen Lebensräumen liegt zumeist auf vegetationskundlichen Aspekten. Dem hingegen sind Untersuchungen räumlicher Muster des zoologischen Artinventars unterrepräsentiert. Dabei weisen insbesondere bodenlebende Arachniden (Spinnentiere) Eigenschaften auf, die sie für die prozessorientierte ökosystemare Forschung interessant machen: zum einen treten sie in den alpinen Lebensräumen in großen Abundanzen auf, zum anderen ist ihre Sensibilität gegenüber verschiedenen abiotischen und biotischen Faktoren ein bereits häufig beschriebenes Phänomen.

Die vorliegende Arbeit setzt dort an und untersucht raum-zeitliche Muster von Arachniden in alpinen Habitaten sowie deren Anpassungsstrategien an die konkreten Umweltbedingungen. Von besonderem Interesse ist dabei der Einfluss der vermeintlich härteren Umweltbedingungen in größeren Höhen auf die Lebenszyklus- und Reproduktionsstrategien der Arachniden. Um dies zu untersuchen wurde ein Messnetz entlang eines Kontinentalitätsgradienten sowie altitudinalen und (mikro)topographischen Gradienten installiert. Im Gelände setzt sich dieses Messnetz aus Bodenfallen, Datenloggern zur Erhebung der mikroklimatischen Bedingungen sowie zusätzlicher erhobener Umweltfaktoren wie Vegetationszusammensetzung, Schneehöhen und Schneeverteilung zusammen. Dieses multiskalige Messnetz umfasst zwei Untersuchungsgebiete in Süd-Norwegen: eines im ozeanisch geprägten Teil Norwegens in der Nähe von Stranda (Møre og Romsdal) und ein weiteres im kontinental geprägten Teil in der Nähe von Vågå (Oppland).

Die Ergebnisse dieser Studie hinsichtlich der räumlichen Verbreitungsmuster der Araneae zeigen klare Einnischungen entlang des Höhengradienten und entlang des topographischen Gradienten. Überraschenderweise scheint der Einfluss der Kontinentalität oberhalb der Baumgrenze gegenüber kleinräumiger Einflüsse zurückzutreten (Kapitel 2).

Obwohl davon ausgegangen wird, dass die Spinnengröße von den vermeintlich schlechteren Umweltbedingungen in höheren Lagen beeinflusst wird, konnte bei der Wolfspinne *Pardosa palustris* kein solcher Trend festgestellt werden. Vielmehr wurde auch hier wieder der Einfluss der, durch die Topographie bedingten, Umwelteinflüsse deutlich. Allerdings waren die im kontinental geprägten Untersuchungsgebiet gefangenen Tiere signifikant größer als die im ozeanisch geprägten Teil. Dies spricht generell eher für einen verlängerten Lebenszyklus im kontinentalen Untersuchungsgebiet Vågå (Kapitel 3).

Mit dem Fokus auf die Untersuchung höhenwärtige Anpassungen in den Reproduktionsstrategien in fünf Wolfspinnen der Gattung *Pardosa*, mit teils unterschiedlichen Habitatpräferenzen, konnte ebenso keine gemeinsame Anpassungsstrategie entlang dreier Höhengradienten im kontinentalen Untersuchungsgebiet festgestellt werden. Die Annahme, dass Weibchen in größerer Höhe dazu übergehen weniger aber dafür größere Eier zu produzieren, konnte nicht bestätigt werden (Kapitel 4).

Eine der am häufigsten in den Bodenfallen gefundenen bodenlebenden Arten war die Art *Mitopus morio* aus der Ordnung der Weberknechte (Opiliones). Hier konnte gezeigt werden, dass sowohl makro- als auch mikroklimatische Bedingungen Einfluss auf die Aktivitätsmuster von *M. morio* entlang unterschiedlicher Gradienten nehmen (Kapitel 5).

Aufgrund der angefallenen großen Menge an bodenlebenden wirbellosen Tieren in den Fallen konnte eine neue Art und deren Habitat für Fennoskandinavien beschrieben werden: die Hornmilbe *Provertex kuhnelti* wurde an einem alpinen Kuppenstandort im ozeanischen Untersuchungsgebiet nachgewiesen und die Verbreitung wird nunmehr als „boreo-alpin" angesehen (Kapitel 6).

Zusammenfassend lässt sich feststellen, dass es, aufgrund des multiskaligen Ansatzes und der Messungen entlang unterschiedlicher Gradienten, möglich war, die Einflüsse verschiedener Umweltparameter hinsichtlich der Einnischung und Anpassung einzelner Spinnenarten zu identifizieren. Zusätzlich unterstreicht diese Arbeit die Notwendigkeit insbesondere kleinräumig erhobener Daten und Parameter um ein besseres Verständnis für die Funktion alpiner Ökosysteme zu erhalten.

Summary

In the course of the discussion about the effects of man-made Climate Change on ecosystems, alpine regions of the earth have become a major focus. Alpine ecosystems are generally considered to be especially sensitive towards environmental changes. Thus, alpine research concentrates on ecosystematic processes along gradients at various scales. Within this setting of gradiental dependency, alpine ecosystem research often makes use of space-time substitution. However, the research on spatial and temporal ecological patterns is mostly limited to the analysis of vegetation patterns; studies on spatial patterns of zoological species composition are underrepresented. Yet, especially epigeic arachnids show some characteristics which makes them valuable proxies in process-oriented ecosystem research: on the one hand arachnids occur in high abundances in alpine habitats, on the other hand they are often described to be sensitive towards diverse abiotic and biotic factors.

This thesis aims to tackle this research gap by investigating spatial and temporal patterns of arachnids in alpine and arctic habitats. A further focus lies on the aranchids' adaptation strategies in relation to tangible environmental conditions within their habitats. Of special interest is, whether and to what extent supposedly harsh alpine environmental factors affect the life-history and reproductive traits of arachnids at multiple scales. Therefore, a network along a continentality, an elevational and (micro-) topographic gradients has been installed. The network consists of pit-fall traps and data loggers, recording micro-climatic factors. Furthermore, vegetation composition and snow height and distribution were recorded. This multi-scale network was implemented at two research areas in Southern Norway: one is situated in the more oceanic part close to Stranda (Møre og Romsdal), while the other site near Vågå (Oppland) is characterized by a rather continental climate.

With regard to the spatial patterns of Araneae, the results of this study, show a pronounced annidation along the elevational as well as the topographic gradient. Surprisingly, the influence of continentality weakens above the tree-line in favor of small-scale environmental factors (Chapter 2).

It is generally assumed that body sizes of spider individuals decrease with elevation and the increase of adverse environmental conditions. In this study, this trend could not be verified for the wolf spider *Pardosa palustris*. In fact, the elevation-related environmental conditions were superimposed by topographic influences. However, in direct comparison of the two research sites, specimens caught at the more continental site were significantly larger than at the oceanic site. This denotes a rather prolonged life history trait in the continental part Vågå (Chapter 3).

Focussing on the elevational adaptation of reproductive strategies of five wolf spiders of the genus *Pardosa* with partly differing habitat preferences, no common adaptation patterns along three elevational gradients in the continental research area could be identified. The assumption, that females would - with increasing

elevation - decrease the number of eggs in favor of a larger egg size could not be verified (Chapter 4).

One of the most common epigeic species trapped within this study has been the Opilionid species *Mitopus morio*. Here, we could show, how macro- as well as micro-climatic conditions influence the activity pattern of *M. morio* along different environmental gradients (Chapter 5).

As a result of the great amount of trapped epigeic Artropods, it was possible to describe a new species and its habitat for Fennoscandia: the Oribatid mite *Provertex kuhnelti* could be confirmed at an alpine ridge in the oceanic research site. With this finding, the distribution of *Provertex kuhnelti* can now be described as "boreo-alpine" (Chapter 6).

In summary it can be stated that in relation to the multi-scale approach and the sampling along three environmental gradients this thesis enables for the identification of driving forces for species annidation. Moreover, some of the influences of ecological parameters on life-history and reproductive traits could be identified. This thesis underlines the importance of measuring environmental parameters on a fine scale to better understand alpine tundra ecosystems.

CHAPTER 1: Introduction

The understanding of the processes which determine the assembly of local communities is a key objective of both community ecology and biogeography (Hortal et al. 2012). The habitat use of a certain species is characterized by several phylogenetic constraints, such as anatomical, physiological and behavioral (Morin & Lechowicz 2008). Knowledge about such 'constraints' allows for proper use in analysis and in species distribution models accordingly (Cassini 2011). The environmental processes characterizing the habitat, and thus conditioning the constraints, are assumed to differ along gradients and potentials, such as elevation, continentality and due to topography (Keddy 1991; Hodkinson 2005; Löffler & Finch 2005). In particular, long-term monitoring along environmental gradients allows for the estimation of natural variability and for the identification of how and why species might or might not react to changing environments (Pimm 2009). When it comes to species-environmental interaction research it is imperative to determine species and sex specific proxies that allow for the identification of traits along environmental gradients (Fairbairn et al. 2009; Stillwell et al. 2010). In this context, Arthropods inhabit some extraordinary features that enable them to be used in ecological research.

Arthropods and arachnids

Arthropods are one of the most abundant and diverse animal groups worldwide (Minelli et al. 2013). So far, more than 1.2 million species have been described (Zhang 2011). They inhabit terrestrial, aquatic and aerial habitats all over the world, from equatorial rainforests to the cold deserts of the Arctic and Antarctic, and from the black smokers in the deep sea up to the high alpine areas of the world. Arthropods are subdivided into various subphylum; e.g. Crustacea, Hexapoda, Chelicerata and Myriapoda (Minelli et al. 2013). The subphylum Chelicerata is further differentiated into twelve orders, of which the Araneae (spiders), Opiliones (harvestmen) and Acari (mites) belong to the class Arachnida; around 100000 species have been described so far (Cracraft & Donoghue 2004). In the order of Araneae approximately 80000 species are known worldwide today (Platnick 2013), and in the order Opiliones, 6500 species (Kury 2011). Araneae, Opilionids and Mites are ancient groups that first appeared 400 million years ago during the Devonian period (Norton et al. 1988; Pinto-Da-Rocha et al. 2007; Hillyard 2011). The Arachnida share some common features; e.g. a segmented body that holds four leg pairs, which makes it easy to distinguish them from insects, which have only three leg pairs. Nevertheless, several exceptions are known where mites have reduced leg pairs. The body of spiders and opilionids is divided into two parts, an anterior part called the prosoma and a posterior part called the opisthosoma; the prosoma carries all appendages (Foelix 1996; Pinto-Da-Rocha et al. 2007) (Photo 1.1). Besides the general morphologic characteristics of the Arachnida, the speciation of mites is much more difficult and requires an understanding of the morphology of each suborder (Walter & Proctor 2013).

Photo 1.1 Male Pardosa spec. specimen active on snow at approximately 1300 m asl in the continental research area in April 2009. The two body parts are easily to distinguish and separated by the pedicel. The anterior part (prosoma) carries all appendages, including four leg pairs and the posterior part (opisthosoma). Note that one leg of the second leg pair is missing at this specimen (Photo taken by Nils Hein 2009).

Photo 1.2 Female Pardosa amentata specimen carrying an egg sac in a Sphagnum bog in the low-alpine belt of the western research area. The egg sac is attached to the spinners and thus allows for the identification of reproductive effort of a certain female Lycosid spiders (Photo taken by Nils Hein 2009).

Araneae are known to inhabit almost every habitat of the earth surface (Wise 1993; Roberts 1995), and even the air, as aerial plankton (Roberts 1995; Duffey 1998). In response to their world wide distribution Araneae had to develop some intriguing adaptation strategies concerning the specific environmental conditions in hazard prone environments. Hendrickx et al. 2003 found adaptations in the reproductive trait of a Lycosid spider along a pollution gradient towards a heavy metal deposit, resulting in smaller clutches but bigger eggs at sites featuring a higher degree of pollution. Here, a specific feature of female Lycosid spiders is of special importance. Female lycosid spiders carry their eggs in an egg sac attached to their spinners (Photo 1.2). This characteristic feature allows for the identification of species specific reproductive effort. Furthermore, it makes female Lycosid wolf spiders especially suitable for the study on how environmental conditions affect reproductive traits of these spiders. In hazard prone environments such as the alpine areas (Lencioni 2004), the most important factors that spiders have to deal with, are related to the pronounced seasonal alpine conditions (Sømme 1997; Nagy & Grabherr 2009). Especially, adaptation strategies targeting cold hardiness, supercooling, freezing tolerance, desiccation risk and short summer seasons are probably the most important ones for Araneae occuring in alpine tundra ecosystems (Marchand 1996; Sømme 1999; Willmer et al. 2005; Nagy & Grabherr 2009). In this context, supercooling points below -10 °C were described for several Araneae species (e.g. Hågvar 1973; Kirchner 1973; Murphy et al. 2008). Various Araneae species are known to be active on snow during winter at temperatures below 0 °C (Huhta & Viramo 1979; Bayram & Varol 2000; personal observations, see Photo 1.1). A prolonged life cycle was observed and identified to be a direct response to the environmental conditions at higher elevations (Edgar 1971a; Steigen 1975).

Furthermore, the adaptation in body size was identified to be a consequence of the worsening conditions at higher elevations. Otto and Svensson (1982) found a decrease in body size in several Araneae species with increasing elevation, assuming that it is advantageous to be of smaller size at higher elevations.

The search for singular adaptive and nonadaptive theories regarding the size and reproductive traits of ectotherms became of greater interest with the rise of the Climate Change debate over the last decades and recent observations have shown a clear correlation between warmer and prolonged summers in the arctic and the size of arthropods (Høye et al. 2009; Høye & Hammel 2010). Furthermore, several studies showed a sex-specific reaction along elevational gradients; females of Lycosid wolf spiders reacted differently along elevational gradients than males (Høye & Hammel 2010; Bowden et al. 2013). Along a latitudinal gradient, Opell (2010) found a clear Bergmann's cline in a spider species in New Zealand, resulting in bigger body size in specimens present at higher latitude. The Bergmann's cline in Arthropods is most likely a result of a prolonged life cycle in colder environments (Angiletta et al. 2004). Such temperature-related effects are widely known for ectotherms since higher temperatures commonly lead to a faster development (Willmer et al. 2005). Even though there have been intensive studies regarding vegetation patterns of the alpine tundra in Norway (e.g. Gjærevoll 1956; Dahl 1986; Löffler 2003; Walker et al. 2005; Odland 2011) studies regarding the spatial-temporal patterns and life history of alpine tundra arachnid traits are still scarce.

Knowledge regarding these patterns and traits might finally allow for modeling the effects of Climate Change on alpine tundra ecosystems and its inherent arachnids.

Alpine tundra ecosystems

Life in alpine tundra presents a special case of low-temperature habitat, where elevation above sea level parallels the effect of latitudinal distance towards the equator (Willmer et al. 2005). Even though this general pattern is true, it excludes the influence of the ocean. Continentality is an important factor for alpine climates that should not be underestimated (Nagy & Grabherr 2009). Alpine tundra ecosystems are distinguished by severe, seasonal, unpredictable and variable environments and are thus assumed to be hazard prone (Lencioni 2004), therefore presenting a unique but highly heterogenic environment (Franz 1979). As a general pattern, these environmental conditions can be organized along pronounced toposequences (Nagy & Grabherr 2009). In accordance with topography, and thus the spatial variation of alpine tundra, this furthermore leads to a wide range of habitats under differing micro-environmental conditions within relatively small distances (Mani 1968; Franz 1979; Löffler 2003; Pape et al. 2009; Scherrer & Körner 2011). Because of the severe conditions in the Alpine areas of the world, they are regarded as especially sensitive towards a changing climate (Holten 1990; Chapin III et al. 1995; Beniston 2003; ACIA 2004; Löffler et al. 2011; IPCC 2007 a,b). Due to the assumption of sensitivity, these landscapes are of high scientific interest and a suitable object for global change research (Walther et al. 2002; Diaz et al. 2003).

In accordance with Löffler (2002), the specific snow cover dynamics in alpine tundra ecosystems in Scandinavia can be described as follows: annual variations of air and soil temperatures strongly depend on snow cover in response to the topographic exposure. Alpine ridge sites commonly feature no or only little snow cover during long periods of winter and thus often experience strong frost events penetrating far into the ground. Minimum soil temperature events below -10 °C are often measured during winter at snow-free alpine ridge sites (Photo 1.3). Such strong frost events appear more often at low-alpine ridge sites than at middle-alpine ridge sites, due to the commonly thicker snow cover with elevation. In contrast to the ridges, the alpine slopes and depressions are covered by thick snow packages isolating the ground from extreme winter temperatures; the longest-lasting snow covers are found at lee sites (Photo 1.4). The snow cover dynamics does not only show an elevational variation but is overall tightly linked to topography.

Photo 1.3 Typical alpine snow cover distribution in the eastern continental research area during April. The photo is taken from a middle-alpine site at around 1400 m asl. Alpine ridge sites are snow-free, while slopes and depressions are covered by thick snow layers (Photo taken by Nils Hein 2009).

Photo 1.4 Typical alpine snow cover distribution in the eastern continental research area at the end of May. The photo is taken at a middle-alpine site at around 1465 m asl. Sites with the longest lasting snow cover are lee slopes. Here, mainly the southern exposed slopes are still covered by thick snow cover (Photo taken by Nils Hein 2009).

Over the last decades, several observed changes in alpine environments in Norway could be identified as a direct or indirect consequence of climate warming (Ytrehus et al. 2008). Klanderud and Toland (2005) as well as Klanderud (2008) found changes in the vegetation due to simulated climate warming in alpine Dryas heath communities. Moreover, Hågvar and Klanderud (2009) found crucial changes in alpine soil-living Arthropods, due to simulated change in environmental conditions. Most apparent in this context is a loss of habitats and species due to an upward shift of ecotones towards higher elevation, resulting in a loss of biodiversity in the Alpine (Krajick 2004). Despite these variations Gjærevoll (1956) "conservative nature of snow" remains true for the Alpine.

Habitats and gradients at various scales

Research on gradients in the Alpine often focuses on changes with an increase in elevation, due to the space over time substitution (Hodkinson 2005). In this regard, three main variables can be directly related to increasing elevation: a) a decrease in temperature of 5.5 K every 1000 m of increasing elevation; b) a decrease in atmospheric pressure; and c) clear sky turbidity (Körner 2007). Other variables, such as e.g. moisture, precipitation, wind, and season length, are indirectly related to increasing elevation, yet with various exceptions of which some are directly related to topography and exposure (Löffler 2003; Körner 2004; Finch & Löffler 2005; Pape et al. 2009). This implies a fine-scaled heterogeneity of alpine tundra ecosystems as a result of the strong differences in response to the topographical and exposure specific conditions, which have a huge impact on vegetation complexity and thus habitat structure (Dahl 1986; Löffler 2003; Scherrer & Körner 2011). These fine-scaled exposure specific patterns in vegetational complexity have been widely recognized to be responsible for spider-species presence, richness and composition (Schaefer 1970; Uetz 1991; Wise 1993; Löffler & Finch 2010). Previous studies have shown the huge impact of conditions depending clearly on topography, e.g. southern exposed slopes and higher temperatures had a huge impact on the presence and specifically the life cycle of *Melanoplus frigidus* (Acrididae) in an alpine tundra ecosystem (Finch et al. 2008). The effective habitat of a species is often realized at a fine scale only (Nentwig et al. 2013), which postulates that species specific-environmental research is advantageous along defined gradients.

In Norway, the most famous studies regarding spiders and other arthropods were conducted in the frame of the International Biological Program (IBP). These studies focused on research to identify typical assemblages of arthropods in typical alpine and subalpine habitats (e.g. Hågvar & Østbye 1972; Hågvar et al. 1978; Hauge et al. 1978; Hauge & Refseth 1979). These studies provided some of the first conceptual samplings in alpine tundra ecosystems in Norway. However, the sampling design was not developed to study annidation along environmental gradients in the first place, but primarily to identify typical species in a certain habitat.

Ecological research along environmental gradients became of special interest, especially in response to recent Climate Change discussion, because climatic variables enable identification of the driving forces that are responsible for species distribution and life history adaptation towards changing environments. Assuming the interlink age of spatial and temporal processes of an ecosystem, a substitution

of observable spatial changes in favor of unapparent past or future changes in time is implied. Hence several studies have focused on assemblages along elevational gradients (e.g. Chatzaki 2005; Bowden & Buddle 2010; Nufio et al. 2010). Other studies focused on assemblages of ground living arthropods towards succession, e.g. in alpine glacier forelands (e.g. Gobbi et al. 2006; Bråten et al. 2012). In nearly all studies it was possible to identify clear spatial patterns of arthropod assemblage related to elevation or succession. For several invertebrates it has been shown that fitness-related traits, including characteristics of life cycle and reproduction, vary along latitudinal (e.g. Lencioni 2004), and along elevational gradients (e.g. Samietz et al. 2005; Duyk et al. 2010; Lee et al. 2012). However, these studies along gradients still have limitations as they commonly exclude the fine-scaled topographic environmental conditions. These fine-scaled environmental conditions might be of special importance when it comes to highly mobile groups of animal, since their ability allows for migration towards suitable environmental conditions.

Research gaps

Considering the size and the ability of arachnids to migrate towards suitable environmental conditions, fine-scaled environmental conditions might be the right scale to assess their adaptation and behavior strategies in alpine tundra ecosystems. However, these studies along gradients still inhabit a gap regarding fine-scaled topography as they commonly exclude such fine-scaled topographic environmental conditions. To address this gap in current gradient research and for the understanding and modeling of the consequences of changes in arctic tundra ecosystems, it is imperative to understand recent spatio-temporal patterns and ecosystem structures at different scales (O'Brien et al. 2004). The long-term monitoring of elevational transects allows for the estimation of natural variability and for the identification of why species might or might not react to changing environments (Pimm 2009). In this context it would be helpful to determine indicator species for certain subsets of the alpine tundra (e.g. ridges, depressions and slopes), to allow for their use in constant monitoring projects. Furthermore, the understanding of how individual species might adapt to changing environments requires detailed information and specific case studies (Hodkinson 2005; Pimm 2009).

Objectives

Based on almost 20 years of climatological and landscape ecological research in the LTAER (Long-Term Alpine Ecosystem Research) of Norway (starting with Köhler et al. 1994 and still ongoing), this thesis will present new approaches and possibilities for embedding epigeic arachnids into alpine tundra ecosystem research. Environmental gradients within the research regions have been well characterized during the last two decades (e.g. Löffler 1998; Naujok & Finch 2004; Löffler 2005, 2007; Löffler & Finch 2005; Finch et al. 2008; Finch & Löffler 2010). Therefore, this thesis focuses on investigating zoocoenoses along fine-scaled topographical, meso-scaled elevational, and broad-scaled oceanic-continental gradients.

Aranchids and especially Araneae hold an exceptional position in ecological research, because of their potential to populate a huge variety of habitats and their

dependence on local climatic preferences (Wise 1993; Foelix 1996; Frick et al. 2007; Muff et al. 2009). To what extent a species prefers a certain habitat in nature and how this matches the actual requirements of a species is a current problem in research (Nentwig et al. 2013). Furthermore, there is a huge lack of knowledge regarding the integration of animals into ecosystem analysis with special emphasis on their functions within the systems (Holtmeier 2002).

Ecosystem functioning in alpine tundra areas of Norway is determined by complex processes and different mosaics of ecosystems that cannot be explained by common approaches or by single parameters alone (Löffler et al. 2006). To account for the fine-scaled heterogeneity of the alpine tundra ecosystem a high resolution monitoring network was developed and installed (Figure 1.1). Sampling sites were located along three different gradients; a broad-scale climatic gradient expressed by continentality between western and eastern Norway, and two elevational gradients from the tree-line up to the highest peaks in the two research areas. Exposure specific sampling as a subset of the elevational gradients was expressed by four different exposures: A=ridges, B=depressions, C=southern exposed slopes and D=northern exposed slopes. At every sampling site three pitfall traps, containing saturated salt solution as a preservative and Agepon© as a detergent, were installed. The pit-fall traps used in this study correspond to those applied in Naujok and Finch (2004). They consisted of a glass with a diameter of 5.5 cm at the rim and a depth of approximately 12 cm. A PE-ring of 2.3 cm width was screwed onto the glass opening to avoid gaps between the trap and the surrounding ground. By means of this ring the glasses were hung into permanently installed plastic tubes and lowered into the ground. The ring carried a dull but transparent acrylic glass plate (13.7 cm x 13.7 cm) to protect the pit-fall trap from rainfall. The plates were installed 5 cm above the opening. (Photo 1.5). Moreover, one study (Chapter 4) regarding life history traits of Lycosid wolf spiders required intensive hand sampling along three elevational gradients in the eastern continental research area.

Photo 1.5 Installation of a pit-fall trap at a middle-alpine ridge site at around 1608 m asl in the eastern continental research area (Photo taken by Jeroen v.d. Kooij 2010).
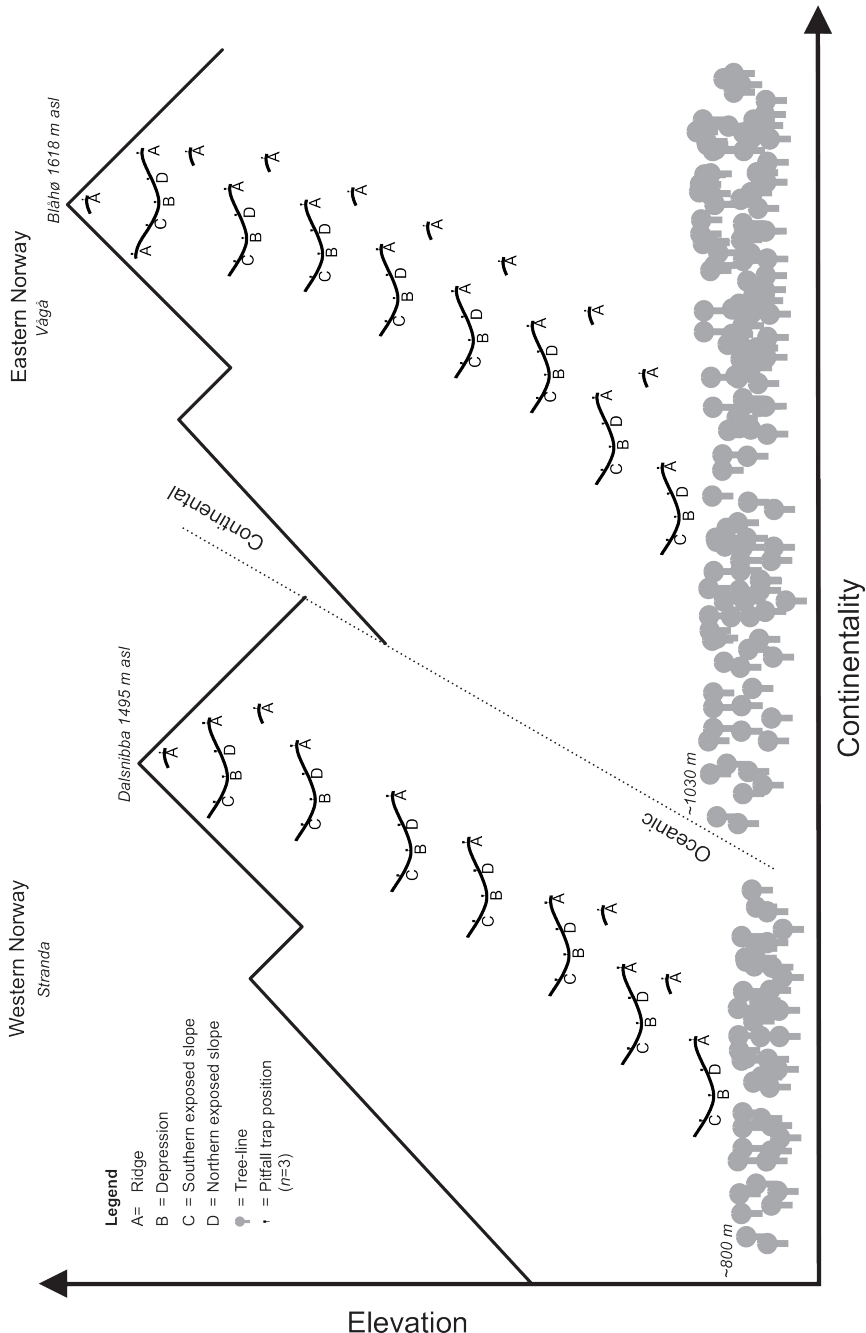
Figure 1.1 Design of the high resolution monitoring network along three different gradients. The locations of the specific sampling sites equipped with pitfall traps along the three different gradients in focus are given. The broad-scale climatic gradient is covered by two research regions, one situated in the oceanic western part of Norway (Stranda) and one in the continental eastern research area of Norway (Vågå). The elevational gradients cover sites from the tree-line up to the highest peaks in the two research areas. The fine scaled-topographic gradient covers four different exposures A=ridges, B=depressions, C=southern exposed slopes and D=northern exposed slopes, in accordance with the study of topographic dependent traits of alpine arachnids.

Pit-fall trapping has been criticized as biased towards epigeic species and males, due to their commonly higher activity during reproduction periods (Merret & Snazell 1983). Still, this method provides a reliable measure of species richness at a certain site (Uetz & Unziker 1976). Particularly when it comes to abundance, pit-fall traps are supposed to display reliable measures for most species (Topping & Sunderland 1992).

This study aims to identify spatio-temporal patterns of alpine tundra aranchids and their adaptation strategies within their populated habitats. Although the broad range of arthropod related research mentioned in subchapter *Arthropods and aranchids* shows that studies focusing on spatio-temporal patterns are not scarce, these studies often have various limitations. Such limitations often include the difficulty of identifying the abiotic and biotic factors responsible for species distribution and its annidation. Identification of these factors and the understanding of processes relying on these factors will enable the use of Arachnida for future ecosystem research with special emphasis on process oriented research along various gradients. This thesis tries to quantify actual impacts of environmental traits on arachnid assemblages and life history traits of alpine tundra arachnids. My hypothesis was that a wide range of different environmental properties are responsible for species distribution and differences in life-history traits. In particular, the influence of exposure specific traits regarding the micro-climate, mainly expressed by temperature differences and differences in season length, might be underestimated in previous research focusing on gradients. Here this thesis proposes to:

- characterize the spider assemblages and their spatial patterns in relation to multiple environmental variables;
- define the role of single environmental parameters for annidation of arachnids in an alpine tundra ecosystem;
- identify environmental traits that affect life-history traits of alpine Aranchids and thus lead to changes in phenotypic plasticity and adaptation.

Study areas

In response to the north-south extension of the Scandinavian mountain chain there is a clear differentiation of oceanic and continental climatic conditions in central Norway. Within relatively short linear distances of approximately 100 km, huge climatic differences between western oceanic and continental Norway are apparent. This thesis was implemented in two focal research areas; one located in the western oceanic (ca. 62°03' N; 7°15' E, Møre og Romsdal) and one in the eastern continental part (ca. 61°53' N; 9°15' E, Oppland) of Norway. The western oceanic research area is located in the western, inner-fjord area and is characterized by a relatively high annual precipitation of around 1500-2000 mm (Moen 1999). According to Moen (1999) this area is part of the „slightly oceanic section". In contrast, the eastern continental research area is characterized by a very low annual precipitation of approximately 300-400 mm in the valleys and up

to 600 mm in the alpine areas (Löffler et al. 2001). According to Moen (1999) this area is part of the "weak continental section".

The low-alpine belt is dominated by dwarf-shrubs and heather communities, whereas the middle-alpine belt is dominated by graminaceous vegetation. This is in agreement with Dahl's (1986) description of the alpine elevational zonation in both regions. In the western oceanic research area, the tree-line is situated at approximately 750 m asl. In the eastern continental research area it is situated at about 1030 m asl. The low-alpine belt reaches from the tree-line to approximately 1200 m asl in the western oceanic research area and from the tree-line to 1350 m asl in the eastern continental research area. The highest peaks are Mt. Dalsnibba (1495 m asl) in the oceanic research area and Mt. Blåhø (1618 m asl) in the continental research area.

Structure of this thesis

With regard to the biogeographic approach, the spatial patterns of spider assemblages in alpine tundra ecosystems have been investigated (Chapter 2). In relation to the general pattern, adaptation strategies in life history traits (Chapter 3) as well as reproductive traits (Chapter 4) have been studied. Furthermore, climate induced activity patterns of one of the most abundant species have been surveyed (Chapter 5). In Chapter 6 a species new to Fennoscandia and its habitat is described.
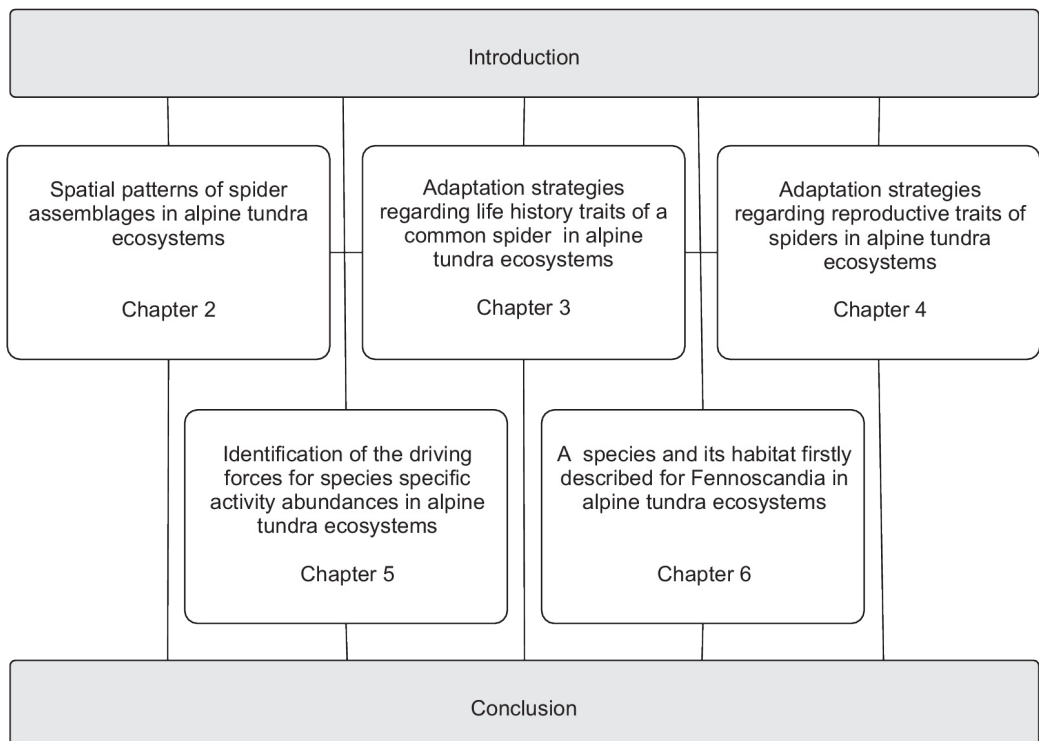

Figure 1.2 Conceptual design of this thesis and the inherent chapters.

Chapter 2 deals with spatial patterns of spider assemblages in alpine tundra ecosystems. The study was implemented in two focal research areas in southern Norway. In order to identify typical spider assemblages and in order to learn more about the impact of environmental parameters on the distribution of spider assemblages, an intensive use of pitfall traps along various gradients was implemented. Along three different environmental gradients, epigeic spiders were sampled with pitfall traps. The organization of the sampling design along a continental, an elevational and a topographic gradient allowed for the identification of certain environmental features that might be relevant for spatial patterns of spider assemblages. This study provides first findings about the annidation of spider assemblages across relatively huge climatic differences, as well as findings regarding the relationship of spider assemblages to habitats situated relatively close to each other. Furthermore, this study presents a new approach that allows for the determination of indicator species that are typical for classes of spider assemblages along various gradients.

Chapter 3 deals with adaptation strategies of a single, very common spider species of alpine tundra ecosystems, *Pardosa palustris*. This study uses a species specific subset of the data set established for the study in Chapter 2. The body size and thus fitness of the Lycosid spider *P. palustris* was measured to get a specimen specific value for fitness. Specimen specific fitness was then used at specific sampling sites as a proxy to allow for the identification of the influence of environmental features on females and males respectively along the three gradients described in *Research Gaps*.

Chapter 4 continues with hypotheses evolved from the studies in Chapter 2 and Chapter 3, even though a different data set is used. Five species of the genus *Pardosa* and their specific reproduction strategies towards changing environmental parameters were studied along three elevational gradients. The study used three different traits as proxies; female size, egg number and egg size. This was based on the assumption that maternal fitness and offspring fitness are strongly correlated. Chapter 5 assesses the spatio-temporal activity patterns of the Opilionid species *Mitopus morio*. The aim of the study was to identify the driving forces for species specific activity abundances. The sampling of *M. morio* followed a nested design in two focal research areas. One research area was situated in the oceanic part and one was situated in the continental part of Norway. Within these two research areas a low-alpine and a middle-alpine "catchment" were equipped with pitfall traps and data logging stations to measure climatic variables such as temperature, soil moisture, precipitation and humidity.

Chapter 6 evaluates findings on an Oribatid species firstly described for Fennoscandia. This section delivers a profound habitat description for *Provertex kuhnelti* and deals with the specific micro-climatic conditions an alpine species has to contend with. The distribution of *P. kuhnelti* is considered to be boreo-alpine. This section merely concentrates on species data that were randomly sampled, due to the huge amount of pitfall traps used in this study. However, this description provides important findings on the environmental conditions in alpine tundra ecosystems.

CHAPTER 2: On the ecology of spider communities in alpine tundra ecosystems

Abstract

This study addresses spider assemblages in relation to their environment along multiple environmental gradients. Two research areas representing considerable variations in climate were sampled for epigeal spiders using pit-fall traps: one area was situated in the oceanic part of Norway and one in the continental part. We aimed to identify the driving forces for spider species annidation in an alpine tundra ecosystem along specific elevation and exposure gradients. During the snow-free season in 2009, we sampled 6628 adult specimens at 73 sampling sites. These data and additional information from the literature were used to examine features of the spatial distribution of species. We analyzed the data sets using ordination space partitioning (Isopam) to identify environmental-specific results regarding species abundance and clustered the sampling sites regarding their dissimilarities. We were able to clearly identify various indicator species that showed pronounced differences and features of alpine tundra ecosystems along a continentality gradient and two elevational and inherent topographical gradients. The indicator species showed either a pronounced dependence of annidation on elevation, thus being restricted to either low- and middle-alpine sites or showed clear topographic dependent annidation towards ridges and slopes. The identified indicator species were strongly related to the fine-scaled habitat conditions which had a stronger influence on spider assemblage composition than continentality, in Scandinavian alpine tundra ecosystems.

Introduction

A main characteristic of the alpine belt is its clear organization along toposequences (Nagy & Grabherr 2009). These toposequences mainly display effects of elevation and associated environmental features (Körner 2007). Due to their presence at all latitudes and their environmental heterogeneity, high mountains are considered well-suited to a global monitoring system (e.g. Welker et al. 2001; Löffler & Finch 2005; Sergio & Pedrini 2007). Furthermore, understanding the processes that determine the assembly of local communities remains a key objective of both community ecology and biogeography (Hortal et al. 2012). In this context, Hodkinson (2005) highlighted the huge potential of using terrestrial arthropods and their distribution along spatial and temporal gradients in the alpine belt to elucidate how climate warming might affect the distribution of a certain species and thus, community structure. The interest in the environmental effects on epigeal arthropods has recently increased, due to observed changes in arctic and alpine habitats (ACIA 2004; IPCC 2007a, b; Høye et al. 2009; Høye & Hammel 2010). In this context, Araneae offer outstanding features to characterize spatio-temporal patterns and the abundance of single species, among the wide range of habitats that are occupied (Uetz 1976; Wise 1993; Finch & Löffler 2010). Furthermore, Araneae make up one of the most abundant compartments of alpine invertebrate communities and represent a huge potential with which to estimate alpine species diversity (Finch & Löffler 2010). They strongly depend on environmental factors, e.g. on the vegetation structure (Schaefer 1970; Frick et al. 2007) and they have relatively small areas of activity compared to mammals and birds. The Alpine region provides a large amount of spatial variation and potential niches and habitats (Mani 1968; Franz 1979). Communities present at different points along alpine elevational gradients are expected to show pronounced differences with respect to their species-specific niche dimensions (Otto & Svensson 1982). Araneae are assumed to be one of the most suitable groups to study and monitor species diversity in terrestrial ecosystems, especially at high latitudes (Marusik & Koponen 2002). Alpine tundra ecosystems and the diversity of their fauna have repeatedly been proposed to be good indicators of environmental change (Grabherr et al. 1995; Bowman 2001; ACIA 2004). To learn more about the driving force for the annidation of alpine epigeal invertebrates, we focused on spatial patterns of Araneae along three different gradients. Firstly, a macro-scale gradient expressed by the strong climatic differences between oceanic and continental Norway (Moen 1998; Löffler 2002). Secondly, a meso-scale gradient expressed by elevation and its inherent changes at higher elevations, e.g. a decrease in air temperature by 5.5 K for every 1 km of elevation (Barry 1981). Thirdly, a topographic gradient expressed by typical alpine habitats such as ridges, depressions, southern- and northern-exposed slopes, which display the strongest differences in alpine areas within relatively short distances (Franz 1979; Dahl 1986; Löffler & Finch 2005). Our study aims to quantitatively and qualitatively describe spider assemblages according to the climatic differences between and within the two research areas in oceanic and continental southern Norway. We researched the spatial assemblages of the Araneae fauna along these gradients in two focal research areas in typical alpine

locations in southern Norway (e.g. Löffler 2002; Löffler 2003). We assumed that alpine tundra ecosystems allow the identification of typical spider assemblages along the three gradients in focus. Moreover, we aimed to determine indicator species for alpine tundra ecosystems, with special emphasis for their use in long-term monitoring projects.

Material and methods

Research areas: Two study sites were selected for this study, to cover the broad-scaled oceanic-continental differences caused by the meridional extension of the Scandinavian mountain chain (Figure 2.1). The western, oceanic research area, Stranda (ca. 62°03' N; 7°15' E, Møre og Romsdal) is characterized by an annual precipitation of 1500–2000 mm, whereas the eastern, continental research area Vågå (ca. 61°53' N; 9°15' E, Oppland) is characterized by very low annual precipitation of approximately 300–400 mm in the valleys and up to 600 mm in the alpine areas (Löffler et al. 2001). According to the classification system of Moen (1998), the Vågå area belongs to the "weak continental section", whereas the Stranda area is part of the "slightly oceanic section". In agreement with Dahl (1986), the alpine elevational zonation is differentiated into a distinct low-alpine and a middle-alpine belt in both regions. The low-alpine belt is dominated by dwarf-shrubs and heather communities, whereas the middle-alpine belt is dominated by grassy vegetation. In Stranda, the tree-line is found at approximately 750 m asl and in Vågå at approximately 1030 m asl. The upper limit of the low-alpine belt is found at approximately 1200 m asl in Stranda and at approximately 1350 m asl in Vågå. The highest peak in the oceanic research area Stranda is Mt. Dalsnibba (1495 m asl) and in the continental research area, Vågå, is Mt. Blåhø (1618 m asl).
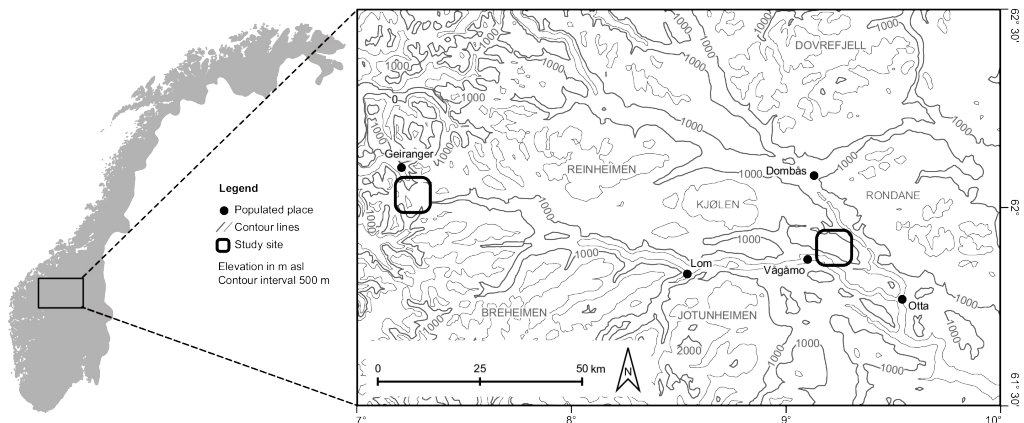
Figure 2.1 Map showing the two research areas in the western, oceanic part (Stranda) and in the eastern continental part (Vågå) of Norway.

Trapping

We collected epigeal arthropods along two elevation gradients; one situated in the oceanic part of Norway and one in the continental part. Sampling was performed during the snow-free period in 2009. Epigeal arthropods were collected from the tree-line to the highest peaks, at a total of 73 (oceanic *n*=32; continental *n*=41)

sampling sites. The elevational range of the sampling sites ranged from 767 m asl to 1488 m asl in the oceanic part of Norway and in the continental part, it ranged from 1029 m asl to 1609 m asl. The elevations (m asl) of the sampling sites were estimated using GPS. We focused our sampling along a subsystem of the elevational gradient in the four different toposequences "ridge", "southern-exposed slopes", "northern-exposed slopes" and "depression". These are assumed to display the strongest environmental differences within short distances in the alpine areas (Löffler 2005). We labeled the sampling sites of the oceanic research area with a capital W and the sites of the continental research area with a capital E. Furthermore, each sampling site was designated by its exact elevation in m asl; by its exposure, and was subsequently identified by A for ridges, B for depressions, C for southern-exposed slopes and D for northern-exposed slopes. Three pit-fall traps were installed at each sampling site, which were designed after Naujok and Finch (2004). We used a saturated salt solution as a preservative and Agepon© as a detergent. The pit-fall traps were installed at the sites as soon as they became snow-free. The collected material was emptied on a bi-weekly basis and transferred to 70% ethanol for preservation. In Stranda, 10 sampling periods from 20 May to 3 October and in Vågå, 11 sampling periods from 28 April to 29 September were implemented. The catches of pit-fall traps are assumed to be a result of the density and the abundance of a particular species. Pit-fall trapping is often criticized as being biased towards ground-living species and males, due to their routinely higher activity during periods of reproduction (Merret & Snazell 1983). However, this method provides a reliable measure of the total number of spider species present at a particular site (Uetz & Unziker 1976). Furthermore, pit-fall traps are presumed to reliably reflect the abundance of most species (Topping & Sunderland 1992). In alpine habitats, it is one of the most suitable sampling methods in rocky habitats (Finch & Löffler 2010), and has proved suitable for alpine areas in a variety of studies that have focused on epigeal fauna (Hauge et al. 1978; Hauge & Refseth 1979; Otto & Svensson 1982; Chatzaki et al. 2005; Finch et al. 2008; Hein et al. 2013). The determination of adult Araneae followed Almquist (2005, 2006), Nentwig et al. (2013) and Roberts (1987, 1995) and the nomenclature in this study follows The World Spider Catalog 14.0 (Platnick 2013).

Statistics

To balance the sampling effort for all sites, the collected material was standardized to the number of caught individuals per 100 trapnights. We used linear regression models to analyze the species-specific activity abundances along the elevation gradients for all Araneae and for the two most abundant families (Linyhpiidae and Lycosidae). To avoid the risk of Type I errors, the significances of all model fits were subjected to the Bonferroni correction (Holm 1979; Rice 1989). For the analysis of species composition at sites, species-specific activity abundances were corrected for the number of trapnights, to avoid the over- and underestimation of abundances at sites with a relatively high number of trapnights, in contrast to sites with a relatively smaller number of trapnights.

We used the classification algorithm Isopam (Schmidtlein et al. 2010) to analyze the species composition of the Araneae fauna at the alpine sampling sites. This algorithm relies on hierarchical partitioning of an ordination space and results in

classes of species that are significantly typical. The flexible and non-linear Isomap-algorithm (Tenenbaum et al. 2000) is used for ordination. Isomap is based on geodesic distances that are, in our case, derived from Bray–Curtis distances. Partitioning around medoids (PAM) (Kaufman & Rousseeuw 1990) is subsequently used to delineate classes in the ordination space. The parameterization of Isomap and subsequent classification is optimized in an iterative approach towards the determination of classes separated by a distinct set of species with maximized indicative value (phi). These indicator species are determined following classification, whereas the candidate classifications are based on the entire set of species. The choice of a number of classes resulting in a good differentiation can be included into the optimization procedure. Furthermore, it provides medoid samples representing the center or most typical sample of a class. Isopam is provided as a package for R (R Development Core Team 2011).

Results

Altogether, more than 55000 invertebrates (Araneae n=9726; Stranda n=3459 and Vågå n=6267) were sampled in 8631 trapnights in Stranda and 13065 trapnights in Vågå. Only adult spiders were identified to the species level; juveniles were excluded from this study. We sampled 2649 adult specimens in the oceanic research area and 3979 adult specimens in the continental research area. This corresponds to approximately 0.31 adult specimens per trapnight in Stranda and approximately 0.30 adult specimens per trapnight in Vågå. Linyphiid and Lycosid species were the most abundant both in the oceanic and the continental research area (Figure 2.2 a & b). In the western oceanic area, a total of 53 Linyphiid and eight Lycosid species were sampled, whereas in the eastern continental area, a total of 64 Linyphiid species and 12 Lycosid species were sampled. This corresponds in both cases to more than 75% of all species and families sampled. Notably, the number of Lycosid specimens was greater than the number of Linyphiid specimens in the continental research area; in the oceanic research area, the relationship was the opposite (Figure 2.2 c & d).
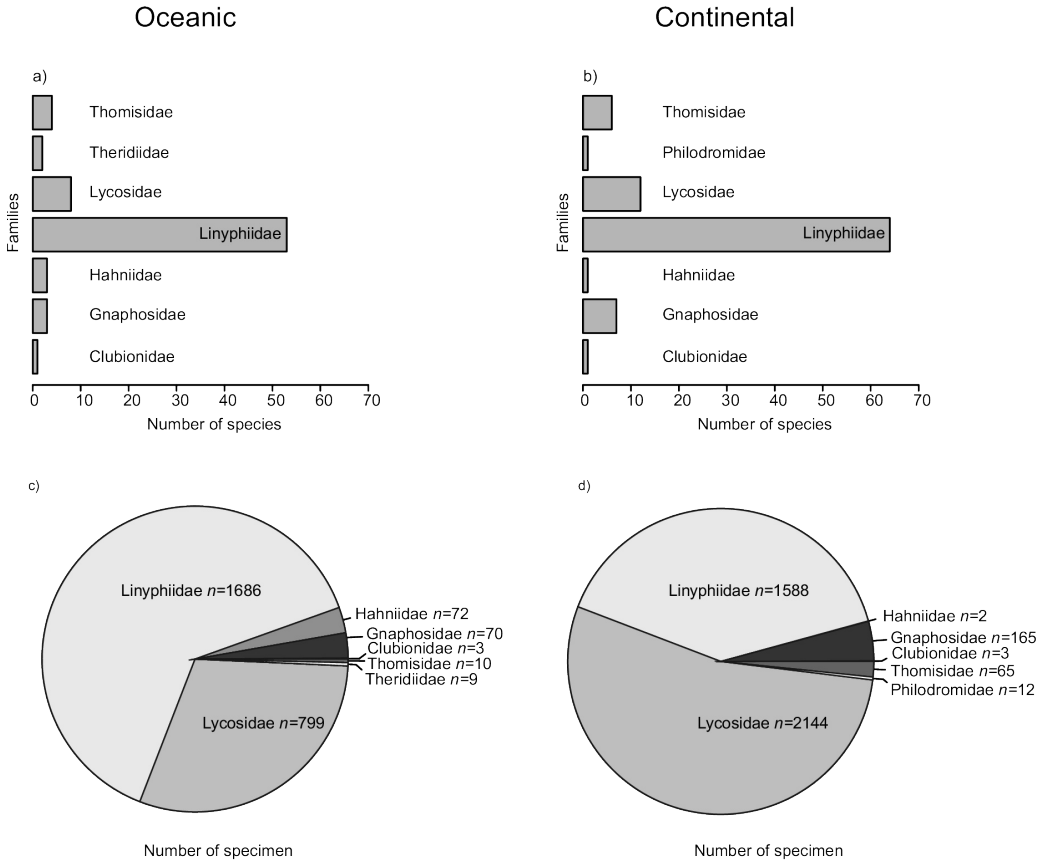
Figure 2.2 a-d Number of species and specimens in the oceanic and continental research areas. The number of family-specific species is indicated by barplots (a & b), whereas the number of family-specific specimens is displayed as a pie-chart (c & d). The figure shows only results for adults; juveniles were excluded from the analysis.

Linear regression of the abundance of species and specimens along the elevation gradient in the continental research area Vågå showed only one significant ($p<0.05$) relationship for the pooled data (all families) and for the two most common spider families, i.e., the Linyphiidae and Lycosidae, respectively. Along the elevation gradient in Vågå, the number of Lycosid species decreased significantly at higher elevations. Otherwise, we found no further significant traits in the oceanic or the continental research areas related to elevation (Figure 2.3 & 2.4). However, we found a peak of species richness at sampling sites in the oceanic research area at approximately 1100 m asl and at approximately 1300 m asl in the continental research area.

All Araneae **Lycosidae** **Linyphiidae**
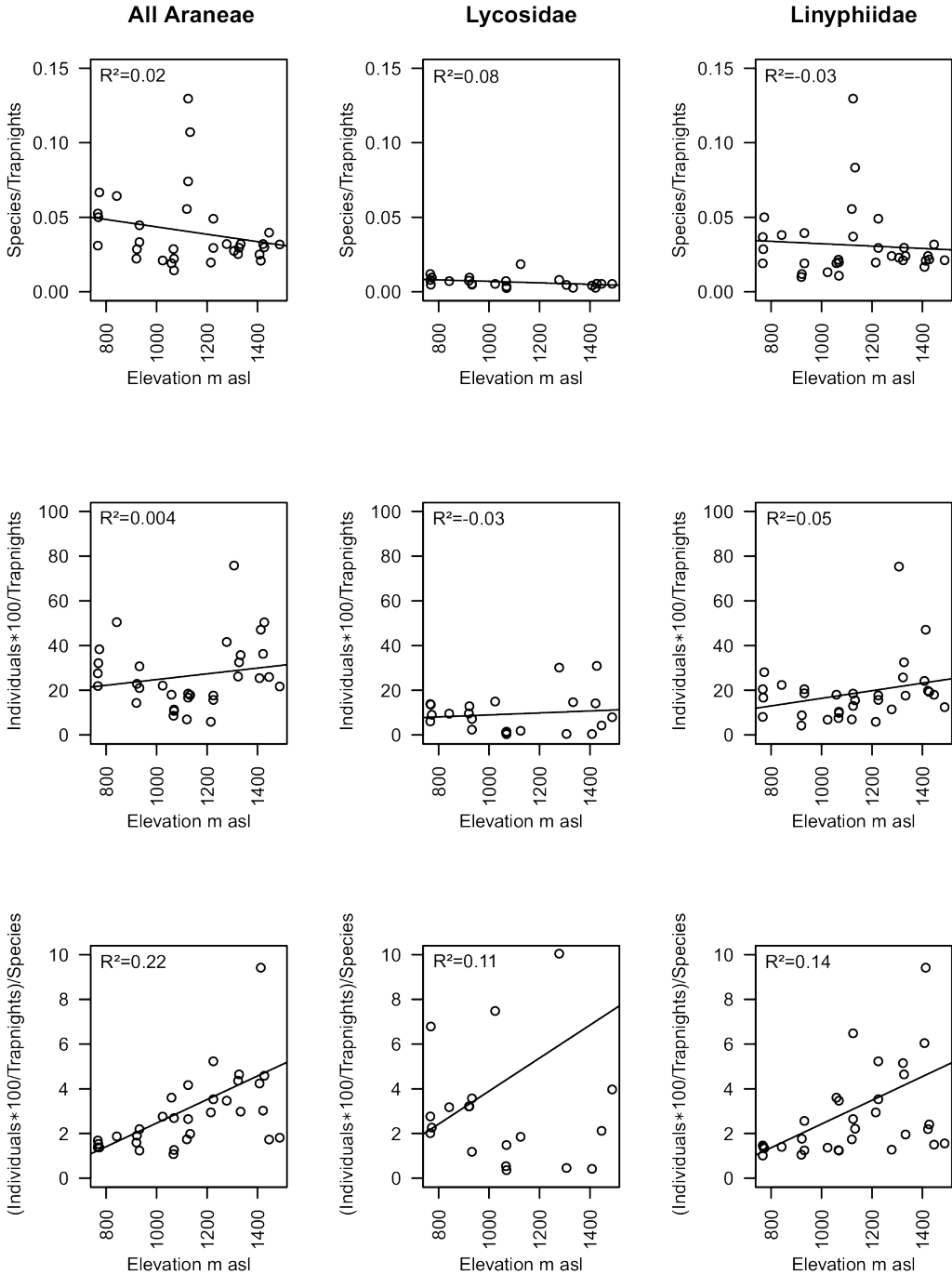
Figure 2.3 Linear regression plots showing the activity abundance of species and individuals (corrected for trapnights) along the elevational gradient in the oceanic research area. The adjusted R^2 is also provided. None of the results is significant ($p > 0.05$).
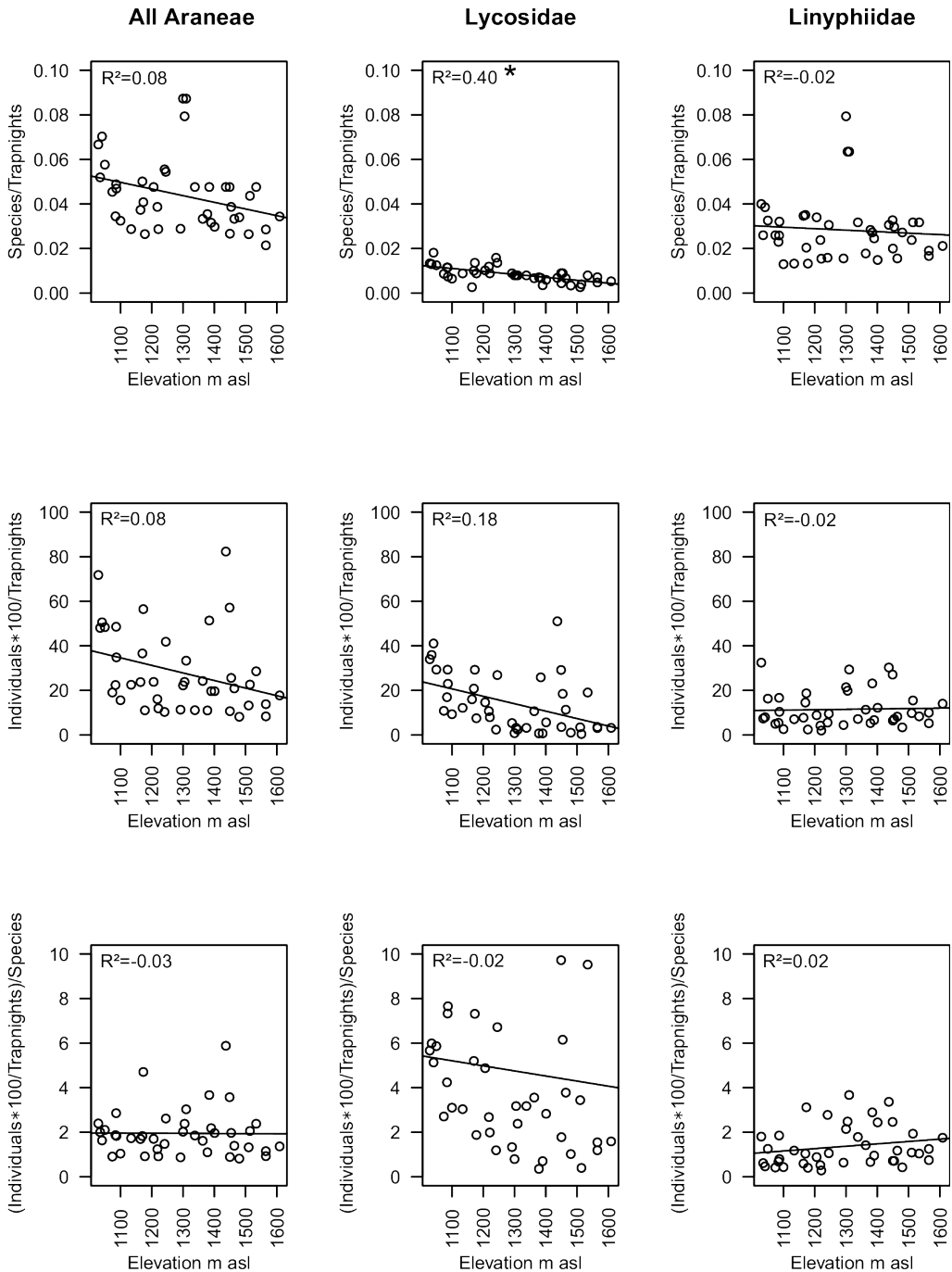
Figure 2.4 Linear regression plots showing the activity abundance of species and individuals (corrected for trapnights) along the elevational gradient, in the continental research area. Significant results (p<0.05, Bonferroni-corrected) are marked with an asterisk.
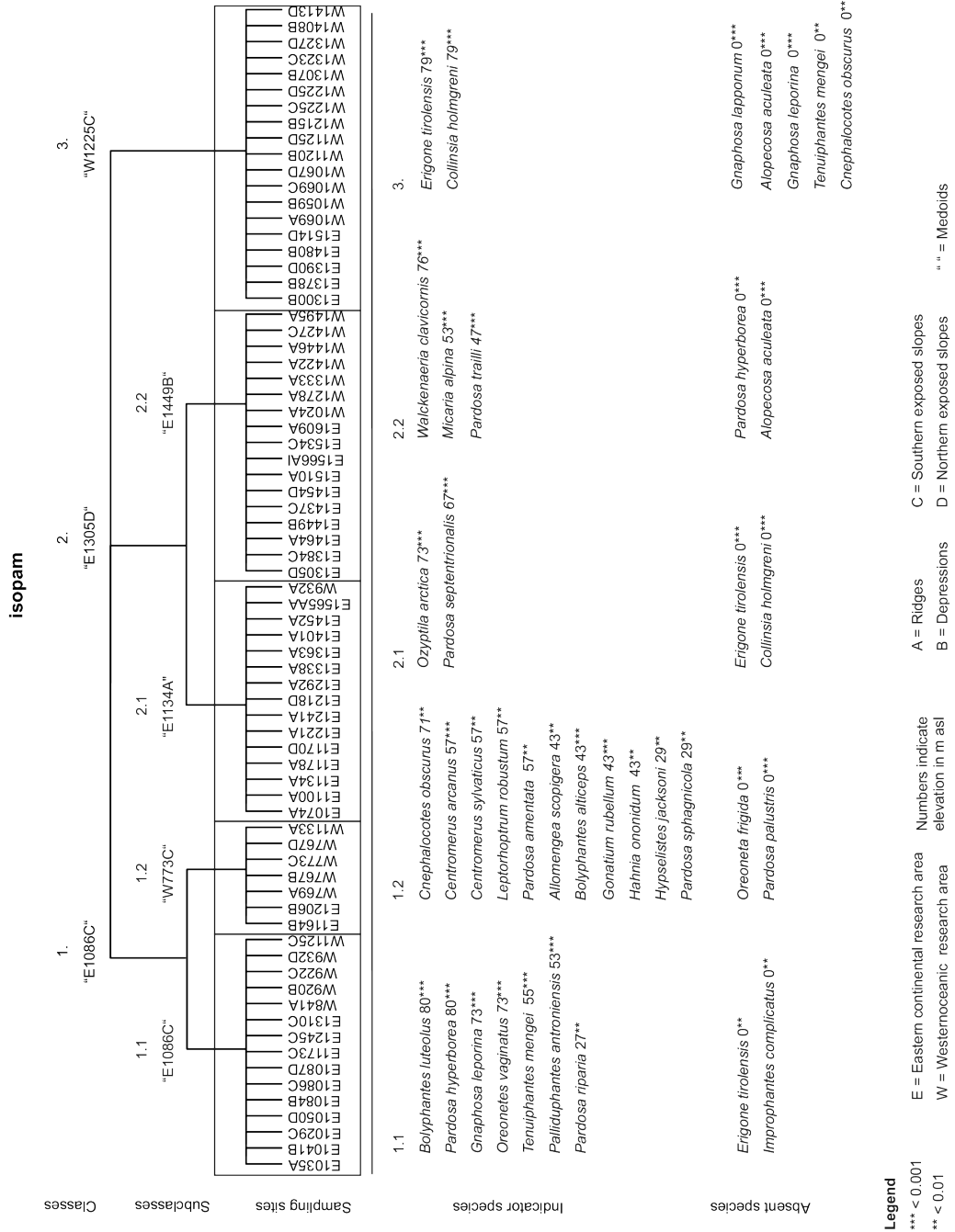
Figure 2.5 Hierarchical clustering of the sampling sites. The hierarichal clustering of the sampling sites regarding the site-specific similarities of the Araneae fauna is shown. The Isopam analysis resulted in three classes (1, 2, 3), two of which are divided into subclasses (1.1, 1.2 and 2.1, 2.2). The post-hoc defined indicator-species and absent species of the specific classes with frequency values (%) are shown. The significance is marked with asterisks: ***<0.001 and **<0.01.

Table 2.1 Total number of species for the classes defined by the Isopam algorithm (using the "isotab" function). In addition to the classes, the total number of sampled specimens, sampling-site specific number and the elevational range (m asl) in the two research areas are presented. (text continued on the following page)

Species	Isopam classes and species frequency (%)					Specimen n=			Site specific n=				Elevational range m asl	
	1.1	1.2	2.1	2.2	3.0	oceanic	continental	sum	A	B	C	D	oceanic	continental
Bolyphantes luteolus	80***	86**	13	6**	21	100	77	177	50	4	95	28	767 – 1133	1029 – 1245
Pardosa hyperborea	80***	43	53	0***	5**	41	346	387	64	6	183	134	767 – 1067	1029 – 1292
Gnaphosa leporina	73***	14	33	24	0***	23	79	102	37	3	56	6	769 – 1488	1029 – 1534
Oreonetides vaginatus	73***	0	13	18	26	8	41	49	5	5	20	19	842 – 1422	1029 – 1384
Tenuiphantes mengei	67***	57*	7	0*	0**	131	113	244	28	1	125	90	767 – 1133	1029 – 1245
Palliduphantes antroniensis	53***	14	0	6	0	6	19	25	3	1	14	7	773 – 922	1029 – 1449
Pardosa riparia	27**	0	0	0	0		152	152	36	7	89	20		1029 – 1050
Cnephalocotes obscurus	47**	71**	20	0*	0**	107	19	126	96	6	15	9	767 – 1133	1029 – 1206
Centromerus arcanus	0	57***	0	0	0	11		11	4	1	2	4	767 – 773	
Centromerus sylvaticus	20	57**	0	0	5	14	37	51	5	1	39	6	767 – 932	1029 – 1035
Hilaira nubigena	13	57**	0	0	0	2	24	26		24	2		767 – 773	1084 – 1300
Leptorhoptrum robustum	33*	57**	7	0	0	22	4	26	3	5	13	5	767 – 932	1041 – 1173
Pardosa amentata	20	57**	0	6	5	51	166	217	5	181	5	26	767 – 1307	1041 – 1206
Allomengea scopigera	13	43**	0	0	0	24		24	3	3	13	5	767 – 922	
Bolyphantes alticeps	0	43***	0	0	0	14		14	11		1	2	767 – 773	
Gonatium rubellum	0	43***	0	0	0	12		12	1		10	1	767 – 773	
Hahnia ononidum	20	43**	0	0	0	69	2	71	66		4	1	767 – 922	1029
Hypselistes jacksoni	0	29**	0	0	0	1	4	5	1	4			769	1206
Pardosa sphagnicola	0	29**	0	0	0	2		2		1	1		767 – 773	
Ozyptila arctica	27	14	73***	24	5**	7	52	59	53	1	3	2	842 – 1333	1074 – 1514
Pardosa septentrionalis	7	0	67***	47	5*		147	147	110	22	4	11		1134 – 1609
Walckenaeria clavicornis	13	0	60*	76***	5**	69	38	107	84	1	9	13	932 – 1488	1035 – 1609
Micaria alpina	7	14	0	53***	11	37	5	42	36	2	4		769 – 1488	1029 – 1609
Pardosa trailli	0	0	0	47***	0	137	103	240	75	4	106	55	1427 – 1488	1437 – 1565
Erigone tirolensis	0**	14	0**	35	79***	138	53	191	7	85	55	44	1069 – 1446	1206 – 1609
Collinsia holmgreni	7*	0	0**	35	79***	298	80	378	3	188	29	158	932 – 1427	1378 – 1609
Oreoneta frigida	33**	0***	67	94**	84	175	112	287	151	35	39	62	842 – 1488	1035 – 1609
Pardosa palustris	100***	0***	100***	82	16***	349	762	1111	607	101	341	62	842 – 1488	1029 – 1565
Gonatium rubens	67	57	100***	71	11***	101	235	336	241	18	55	22	767 – 1488	1029 – 1609
Gnaphosa lapponum	67	57	87***	29	0***	10	61	71	34	4	16	17	767 – 1133	1035 – 1437

The species-specific frequency in the classes is given in percent (%). Sampling sites with different exposures are: A = ridges, B = depressions, C = southern-exposed slopes, D = northern-exposed slopes. The indicator species for the specific classes are highlighted in gray.

Species	Isopam classes and species frequency (%) 1.1	1.2	2.1	2.2	3.0	Specimen n= oceanic	continental	sum	Site specific n= A	B	C	D	Elevational range m asl oceanic	continental
Alopecosa aculeata	67**	71	73**	0***	0***	141	276	417	113	23	168	113	769 – 932	1029 – 1363
Improphantes complicatus	0**	0	67**	65**	16	19	49	68	38	3	8	19	1422 – 1488	1074 – 1609
Zornella cultrigera	27	0	60**	35	11*		140	140	84	8	24	24		1029 – 1514
Mecynargus morulus	20	29	27	47	16	11	31	42	17	6	4	15	769 – 1446	1029 – 1510
Walckenaeria cuspidata	33	71*	13	18	26	32	33	65	25	5	18	17	767 – 1133	1029 – 1390
Tiso aestivus	13	14	40	35	16	26	52	78	23	1	46	8	1133 – 1427	1035 – 1534
Mecynargus borealis	0*	14	47*	47*	5*	21	20	41	37			4	767 – 1446	1074 – 1609
Erigone arctica	13	29	7	18	37	66	27	93	12	23	1	57	767 – 1413	1041 – 1480
Agyneta nigripes	0	0	33	35*	5	8	29	37	30	2	5		1069 – 1488	1292 – 1534
Scotinotylus evansi	7	14	7	29	21	11	10	21	6	2	11	2	842 – 1488	1074 – 1514
Thanatus formicinus	20	0	27	12	0		12	12	9		2	1		1035 – 1565
Arctosa alpigena	13	14	0	12	16	41		41	30	2	2	7	767 - 1287	
Pardosa atrata	27	29	7	0	5		143	143	1	139	3			1041 – 1300
Mecynargus sphagnicola	7	14	7	18	11	3	5	8	5	3			1278 – 1446	1035 – 1378
Ceratinella brevipes	13	0	0	6	21	8	1	9	1	3	2	3		1041
Erigone atra	7	14	7	6	16	9	10	19	2	8		9	932 – 1125	1164 – 1609
Mecynargus paetulus	13	0	7	18	5	4	3	7	5	1	1		1069 – 1446	1029 – 1074
Bathyphantes gracilis	7	14	0	12	11	4	3	7	2	3	1	1	1278 – 1333	1164 – 1310
Oryphantes angulatus	27*	29	0	0	0	1	9	10		2	8		773 – 1024	1029 – 1310
Porrhomma pallidum	7	29	0	12	5	3	3	6	2	2	1	1	773 – 1120	1050 – 1609
Erigone psychrophila	0	14	0	0	21*	37	8	45		44		1	1059 -1067	1206 – 1480
Gnaphosa muscorum	13	0	20	0	0		9	9	7		1	1		1074 – 1241
Hilaira pervicax	20	29	0	0	0	2	8	10	2	8			842	1041 – 1206
Tenuiphantes alacris	7	14	7	6	5	2	3	5	1	1	1	2	773 – 1024	1050 – 1300
Metopobactrus prominulus	0	0	27**	6	0		6	6	5	1				1074 – 1449
Mecynargus monticola	7	0	0	24**	0	6	5	11	7	1		3	1278 – 1446	1084 – 1510
Clubiona trivialis	13	14	7	0	0	3	3	6	5			1	769 – 932	1035 – 1050
Haplodrassus signifer	20*	0	7	0	0		5	5	2	1	2			1029 – 1100
Maso sundevalli	20*	0	0	0	5		5	5	2	2				1035 – 1300
Oedothorax retusus	20*	0	0	6	0	60	7	67	28	21		18	920 – 1422	1041

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Table 2.1 continued

Species	Isopam classes and species frequency (%)					Specimen n=			Site specific n=				Elevational range m asl	
	1.1	1.2	2.1	2.2	3.0	oceanic	continental	sum	A	B	C	D	oceanic	continental
Semljicola faustus	7	29*	0	6	0	3	2	5	1		2	2	767 – 773	1050 – 1510
Acantholycosa norvegica	0	0	0	12	5		8	8	7			1		1565 -1609
Agyneta cauta	13	14	0	0	0	20		20	18		1	1	773 - 932	
Agyneta decora	0	0	13	6	0	1	3	4	4				1446	1221 – 1363
Alopecosa pulverulenta	20**	0	0	0	0		12	12	5	6	1			1029 - 1035
Drassodes pubescens	20**	0	0	0	0		5	5	2	1	2			1029 – 1041
Erigone dentigera	7	14	0	0	5	2	1	3		3				1084
Flagelliphantes bergstromi	0	0	7	6	5		4	4			1	3		1170 – 1534
Tenuiphantes tenuis	0	29*	7	0	0	3	2	5	2		1	2	767 – 773	1074
Mugiphantes whymperi	0	0	0	12	5		4	4		1		3		1449 – 1514
Meioneta gulosa	7	0	13	0	0		4	4	3		1			1074 – 1245
Meioneta rurestris	13	0	0	6	0	2	1	3	2			1	842 – 1488	1087
Pardosa lugubris	20**	0	0	0	0		12	12	6		2	4		1029 – 1050
Robertus scoticus	7	29*	0	0	0	8		8	4		3	1	767 – 842	
Xysticus audax	13	0	7	0	0	1	2	3	2	1			842	1041 – 1401
Xysticus luctuosus	20**	0	0	0	0		8	8		1	5	2		1029 – 1050
Dicymbium tibiale	7	0	0	6	0		2	2		1	1			1041 – 1534
Drepanotylus uncatus	7	0	0	0	0	16	1	17		17			767	1041
Entelecara errata	0	14	0	12	0		2	2	1			1		1454 – 1609
Hilaira herniosa	0	0	7	6	0		2	2	1			1		1170 – 1565
Hypomma bituberculatum	7	14	0	0	0		5	5		5				1041 – 1206
Tenuiphantes tenebricola	13*	0	0	0	0	6		6	1			5	842 – 932	
Macrargus carpenteri	7	0	7	0	0	1	1	2	2				932	1035
Pirata piraticus	7	14	0	0	0	37	17	54		54			767	1041
Xysticus cristatus	0	14	0	6	0	1	1	2	2				769	1464
Agyneta subtilis	7	0	0	0	0	1		1				1	932	
Centromerita bicolor	7	0	0	0	0	1		1	1				842	
Diplocentria bidentata	7	0	0	0	0		2	2			2			1029
Gongylidiellum latebricola	7	0	0	0	0		4	4		4				1041
Hahnia nava	7	0	0	0	0	2		2	2				842	

Table 2.1 continued

Species	Isopam classes and species frequency (%)					Specimen n=			Site specific n=				Elevational range m asl	
	1.1	1.2	2.1	2.2	3.0	oceanic	continental	sum	A	B	C	D	oceanic	continental
Hahnia pussila	7	0	0	0	0	1		1	1				842	
Hilaira excisa	7	0	0	0	0		3	3		3				1041
Palliduphantes pallidus	7	0	0	0	0		1	1			1			1245
Micrargus herbigradus	7	0	0	0	0		1	1		1			769 – 1488	1041
Minicia marginella	7	0	0	0	0		1	1			1			1029
Ozyptila atomaria	0	0	0	6	0		1	1	1					1464
Ozyptila trux	0	14	0	0	0	1		1	1				769	
Pocadicnemis pumila	7	0	0	0	0		3	3			3			1029
Porrhomma montanum	7	0	0	0	0		1	1			1			1029
Porrhomma oblitum	0	0	0	0	5	1		1			1		1225	
Robertus lividus	0	14	0	0	0	1		1			1		773	
Semljicola lapponicus	0	14	0	0	0		9	9		9				1164
Tapinopa longidens	0	0	7	0	0	1		1	1				932	
Tapinocyba pallens	7	0	0	0	0		7	7			7			1029
Wabasso replicatus	0	14	0	0	0		1	1		1				1164
Walckenaeria capito	7	0	0	0	0		1	1			1			1245
Xysticus bifasciatus	7	0	0	0	0		1	1		1				1041

The sampling sites were grouped into five classes by the Isopam algorithm. The classes, which are exclusively based on species composition, feature clear environmental characteristics. Class 1 aggregates the sampling sites located at the lowest elevations in both research areas together. The class (medoid "E1086C") consists of 22 sampling sites and it is further divided into class 1.1 (medoid "E1086C") and 1.2 (medoid "W773C").

Class 1.1 includes typical low-alpine sites with southern-exposed slopes that reach, but do not extend further than the transition zone between the low- and middle-alpine belt. This subclass contains 15 sampling sites, with more continental sites present ($n=10$) than oceanic sites ($n=5$). The elevational distribution of the sites in this class ranged from 841 m asl to 1125 m asl in the oceanic and from 1029 m asl to 1310 m asl in the continental research area. In both research areas, the highest elevated sites of this class were southern-exposed slopes. Seven indicator species are typical for these sites: *Bolyphantes luteolus* (Blackwall 1833); *Pardosa hyperborea* (Thorell 1872); *Gnaphosa leporina* (L. Koch 1866); *Oreonetides vaginatus* (Thorell 1872); *Tenuiphantes mengei* (Kulczyński 1887); *Palliduphantes antroniensis* (Schenkel 1933) and *Pardosa riparia* (C. L. Koch 1833).

Class 1.2 is an assemblage of mainly subalpine to low-alpine sites of the oceanic research area. This subclass consists of seven sampling sites; five of which are situated in the oceanic and two in the continental research area. The elevational distribution of the specific sites ranged from 767 m asl to 1.133 m asl in the oceanic and from 1164 m asl to 1206 m asl in the continental research area. In the continental research area, only two low-alpine bogs were grouped into this class. Eleven indicator species were defined post-hoc by the Isopam algorithm: *Cnephalocotes obscurus* (Blackwall 1834); *Centromerus arcanus* (O. P.-Cambridge 1873); *Centromerus sylvaticus* (Blackwall 1841); *Leptorhoptrum robustum* (Westring 1851); *Pardosa amentata* (Clerck 1757); *Allomengea scopigera* (Grube 1859); *Bolyphantes alticeps* (Sundevall 1833); *Gonatium rubellum* (Blackwall 1841); *Hahnia ononidum* (Simon 1875); *Hypselistes jacksoni* (O. P.-Cambridge 1902) and *Pardosa sphagnicola* (Dahl 1908). In comparison, the two classes 1.1 and 1.2 are separated from each other by the absence of *Oreoneta frigida* (Thorell 1872) and *Pardosa palustris* (Linnaeus 1758) at sampling sites in class 1.2.

Class 2 (medoid "E1305D") is divided into two subclasses: 2.1 (medoid "E1134A") and 2.2 (medoid "E1449B"). The whole class contains 32 sampling sites, 22 of which are ridge sites.

Class 2.1 can easily be characterized as typical continental ridge sites covering the entire elevation gradient from the low-alpine to the pronounced middle-alpine. This subclass consists of 15 sampling sites, 13 ridge sites and two northern-exposed slopes. Only one sampling site (at 932 m asl) is situated in the oceanic research area, whereas 14 are situated in the continental research area. The sampling sites apparent in this group range from 1074 m asl to 1565 m asl in the continental research area. Two typical indicator species were identified as *Ozyptila arctica* (Kulczyński 1908) and *Pardosa septentrionalis* (Westring 1861).

Class 2.2 includes typical oceanic ridge sites from the low alpine to the middle-alpine and continental middle-alpine ridge sites and slopes. This subclass consists of 17 sampling sites, seven of which were situated in the oceanic research area.

Apart from one sampling site ("W1427C" as a mid-alpine southern exposed slope), all other sites of the oceanic research area were grouped into this class were ridges. In the continental research area, four out of ten sites in this class were middle-alpine ridge sites, three were southern-exposed slopes, two were northern-exposed slopes and one was a depression. The elevation of the sites ranged from 1024 m asl to 1.488 m asl in the oceanic research area. In the continental research area, the elevation of the sampling sites ranged from 1384 m asl to 1609 m asl. Indicator species for this class were *Walckenaeria clavicornis* (Emerton 1882), *Micaria alpina* (L. Koch 1872) and *Pardosa trailli* (O. P.-Cambridge 1873). Classes 2.1 and 2.2 are distinguished from each other by the lack of *Pardosa hyperborea* (Thorell 1872) and *Alopecosa aculeata* (Clerck 1757) in class 2.2.

Class 3 consists of sites with extraordinarily long snow coverage and a short summer season. In the continental research area, it is restricted to sites situated at the transition zone between the low- and middle-alpine belt and above. The class contains 19 sampling sites (medoid "W1225C"), five of which are situated in the continental research area and 14 in the oceanic area. This class consists of eight depression sampling sites, seven northern-exposed slope sampling sites, three southern-exposed slopes and only one ridge site. The elevational range of the sampling sites ranged from 1069 m asl to 1413 m asl in the oceanic research area. In the continental research area, the elevation of the sampling sites ranged from 1300 m asl to 1514 m asl. Indicator species for this class were *Erigone tirolensis* (L. Koch 1872) and *Collinsia holmgreni* (Thorell 1871). In comparison to the other classes, separation results also in the absence of *Gnaphosa leporina, Tenuiphantes mengei, Cnephalocotes obscures, Gnaphosa lapponum* and *Alopecosa aculeata*.

Discussion

In both research areas, the family of Linyphiidae was the most speciose spider family, followed by the Lycosidae. This is supposedly a common pattern in northern epigeal spider communities (Danks 1981; Marusik & Koponen 2002). Other families were less abundant, which corresponds to previous findings in this part of Norway (Löffler et al. 2001; Finch & Löffler 2010) and underlines additional results from arctic regions in Canada (Dondale et al. 1997; Wyant et al. 2011).

In contrast to previous findings (Gaston & Williams 1996; Brown 2001; Sergio & Pendrini 2007), we found no linear decline in species richness with increasing elevation. Only species richness in the Lycosidae decreased at higher elevations in the continental research area. This supports the findings of Marusik and Koponen (2002), who suggested that Lycosid spiders might be the only family to show a clear elevation-related decrease in northern epigeal spider communities. Furthermore, our results show a peak of species richness at medium-elevation alpine sites in both research areas. These medium-elevation sites are situated at the transition zone between the low- and middle-alpine belt in the oceanic and continental research area. This shift from low-alpine to middle-alpine obviously causes a positive ecotone effect. Such changes in spider species richness that relate to a change in habitat were previously described by Thaler (1996) in the Alps and are supported by Rahbeck (1995) and Brown (2001), who showed that species richness does not follow a linear trend and often shows humped shaped curves along elevation gradients.

Using the Isopam algorithm, several indicator species for three classes and inherent subclasses were identified (Table 2.2). The table contains previous findings on species habitat preferences and supplements our findings, concerning those preferences that might be responsible for annidation within our multi-scale approach.

Seven indicator species were defined for class 1.1: typical low-alpine sites with southern-exposed slopes reaching, but not extending beyond the transition zone; four were Linyphiids, two Lycosids and one Gnaphosid species. Two species were absent in this class: *Erigone tirolensis*, which is an indicator species for middle-alpine slopes and late-snow beds and *Improphantes complicatus*, which is found in alpine habitats on pioneer ground or dry heath (Hauge et al. 1978). For class 1.2: mainly sub-alpine to low-alpine sites of the oceanic research area, 11 indicator species were defined. The two bogs situated in the continental research area are placed in this group with a high probability, due to the absence of certain species that are typical in the lower situated bogs that were grouped into class 1.1.

Classes 1.1 and 1.2, which contained the above-mentioned indicator species, are assumed to be typical for sub-alpine and low-alpine sites, respectively, due to the absence of some typical alpine species such as *E. tirolensis* and *I. complicatus*. Furthermore, the sampling sites contain a variety of species that are typically found in woodland or forest. In comparison to class 1.1, the indicator species for class 1.2 showed a pronounced alignment towards damper habitats. These habitat preferences are expressed by higher precipitation values in the oceanic research area and the typically very moist conditions in low-alpine depressions, with constant wet conditions and vegetation dominated by sphagnum mosses (Löffler 2003). Furthermore, the absence of *P. palustris,* a species typically found in dry habitats (Nentwig et al. 2013), and the absence of *O. frigida* which is presumed to be an exclusively alpine species (Hauge et al. 1978), underline the classification of the sampling sites of class 1.2. Therefore, our results highlight the particular situation within spider assemblages at the alpine tree-line. The alpine tree-line is assumed to be one of the most heterogeneous spaces, with a high spider diversity (Thaler 1989). The heterogeneity of the physical environment at the tree-line allows for the coexistence of species with different habitat preferences at a fine scale (Muff et al. 2009; Barriga et al. 2010). We identified woodland species that were clearly bound to subalpine or low-alpine sites. In particular, the effect of the nearby-located tree-line and the influence of stand-alone trees is probably responsible for the occurrence of woodland species above the tree-line in class 1 (Frick et al. 2007). Frick et al. (2007) found that higher activity densities were shown by open-land species at the outer distance range and by forest species at the inner distance range of trees. Moreover, the differences between woodland and alpine tundra display some of the greatest contrasts in environmental conditions (Franz 1979), which is properly expressed by the indicator species and the absent species in this class.

Class 2 is divided into the subclasses 2.1 and 2.2. Class 2.1 — continental low- and middle-alpine ridge sites — contained two indicator species; one Lycosid species, *Pardosa septentrionalis,* and one Thomisid species, *Ozyptila arctica.* Class 2.1 consists only of continental ridge sites, with three exceptions: "W932A", which is an oceanic ridge site and "E1170D" and "E1218D", which are both continental north-

ern-exposed slopes. The indicator species are typical for alpine ridge sites in the continental research area and thus represent an annidation along toposequences. Class 2.2 included three indicator species, which are considered typical for low- to middle-alpine ridge sites in the oceanic and continental middle-alpine ridges and middle-alpine slopes, which are characterized by a longer season than the higher-elevation slopes that were grouped into class 3. In conclusion, class 2. contained continental as well as oceanic ridge sites along almost the entire elevational gradient, whereas the lowest-situated ridge sites were grouped into classes 1.1 and 1.2. Spider assemblages and their inherent indicator species were clearly the result of an exposure-specific annidation, whereas the elevation of these sites played a secondary role. This corresponds to previous findings of Dahl (1986) and Löffler (2003), who pointed out the special characteristics of alpine ridge sites, with respect to environmental conditions, which identify them as being the most extreme alpine sites in this part of Scandinavia. These fine-scaled environmental gradients are expressed by differences in snow coverage, thickness and snow duration. Snow coverage is a direct consequence of topography and the prevailing winds during winter (Löffler 2003). This leads to typical patterns of snow-cover distribution with snow-free ridges and snow accumulation in depressions and on slopes. Southern-exposed slopes in our research areas tend especially to have a long-lasting snow coverage in summer, due to the prevailing wind direction during winter (Löffler 2005, 2007). The typical species at ridge sites, as far as they overwinter here, have to cope with huge temperature amplitudes up to 40 K (Barry 2008; Löffler et al. 2006). Annual temperature amplitudes of 25 K have been previously described for a middle-alpine ridge site in the oceanic research area (Hein et al. 2013).

The two species, *Erigone tirolensis* and *Collinsia holmgreni*, are typical for Class 3 (medoid "W1225C"). These two species are clear indicators for middle-alpine sites that become snow-free late in the summer, which is consistent with short summer seasons. Both species are absent at sites in class 2.1, which contains mostly ridge sites that remain snow-free during winter. This underlines the strong correlation between spatial and temporal patterns of snow-coverage and annidation of ground-living spiders in alpine tundra ecosystems.

In this study, we could clearly identify indicator species for certain environmental situations in our research areas. Local environmental conditions were found to have a stronger influence on the spider assemblages than the broad climatic conditions. The climatic differences between the two research areas here, expressed by differences in continentality, had no pronounced influence on the composition of the spider assemblages. However, some species were solely in the oceanic or the continental research area, but these species were not responsible for a delineation of the classes in clear oceanic and continental assemblages. Instead, we could clearly identify indicator species that reflect clear elevation-related patterns, whereas others were more related to topographical constraints. In this context, especially the accentuated change in vegetation structure at the tree-line and sites situated in the middle-alpine belt, feature markedly different associations of indicator species. Even though the influence of elevation and its inherent changes on spider communities is perceived as a well-known phenomenon (Lomnicki 1963; Otto & Svensson 1982; Chatzaki et al. 2005; Lee et al. 2012), these changes in spider assemblages are most likely related to differences in snow coverage. Snow

cover and persistence is related to elevation, but its pattern of distribution is related to the toposequences (Löffler & Finch 2005). Differences in species assemblages at middle-alpine sites, especially on slopes and in depressions, can be explained with respect to a relatively shorter snow-free season. In this context, the unique characteristics of the alpine ridge sites are remarkable and support previous findings regarding the uniqueness of ridge sites in alpine tundra ecosystems.

Vegetation patterns that are strongly related to the topography and its inherent environmental conditions are known to be characteristic of alpine tundra ecosystems (e.g. Gjærevoll 1956; Dahl 1986; Nagy & Grabherr 2009). Snow-cover dynamics are known to be the most decisive factor concerning spatio-temporal gradients of alpine ecosystem functioning in this part of Norway (Löffler & Finch 2005). Because vegetation density and structures are assumed to be responsible for the presence, richness and composition of spider species (Schaefer 1970; Wise 1993; Muff et al. 2009), they can also be expressed by the fine-scaled exposure-specific pattern, resulting in vegetation complexity. From our results, this approach could be verified for spider fauna, at least for sites that are not influenced by close proximity to the tree-line. Thus, the Isopam algorithm is a valuable tool to detect assemblage patterns in monitoring projects that employ pit-fall traps along various gradients and scales.

In conclusion, we found topography and elevation to have a stronger influence on spider assemblage composition than continentality. This study clearly identified indicator species that are strongly related to the fine-scaled habitat conditions of alpine tundra ecosystems in Scandinavia and therefore, could serve to guide future studies that focus on environmental changes.

Acknowledgements

Table 2.2 The indicator species and their typical habitats. The indicator species are shown, together with the known habitat preferences for classes 1.1 and 1.2 from previous studies, supplemented by our findings.

Class	Species	Habitat preferences (previous studies)	Habitat preferences (this study)		
			Continentality	Elevational distribution	Toposequence
1.1	*Bolyphantes luteolus*	bogs[5]; from lowland to subalpine[12]; forests, grasslands and meadows[7]		zonation from the tree-line ecotone up to the transition zone between low- and middle alpine, thus decreasing temperatures, shorter summer seasonal length and more grassy and patchy vegetation	
1.1	*Pardosa hyperborea*	zonal and mountaineous tundra habitats[6]; alpine habitats[7]; forests[12]		zonation from the tree-line ecotone up to the transition zone between low- and middle alpine, thus decreasing temperatures, shorter summer seasonal length and more grassy and patchy vegetation	
1.1	*Gnaphosa leporina*	humid and dry heathland, raised bogs, from the lowland up to nival zone[12]		zonation from the tree-line ecotone up to middle alpine, thus decreasing temperatures, shorter summer seasonal length and more grassy and patchy vegetation	
1.1	*Oreonetides vaginatus*	submountainous and mountainous forests, up to timberline[12]; forests, grasslands meadows and similar habitats[7]		zonation from the tree-line ecotone up to the transition zone between low- and middle alpine, thus decreasing temperatures, shorter summer seasonal length and more grassy and patchy vegetation	
1.1	*Tenuiphantes mengei*	up to the subalpine[1]; in leaf litter, moss and beneath stones[12]; dominant on pastures in northern Iceland[10]		zonation from the tree-line ecotone up to middle alpine, thus decreasing temperatures, shorter summer seasonal length and more grassy and patchy vegetation	

Table 2.2 continued.

Class	Species	Habitat preferences (previous studies)	Habitat preferences (this study)		
			Continentality	Elevational distribution	Toposequence
1.1	*Palliduphantes antroniensis*	alpine habitats[7]; heath birch forests in Scandinavia[12]		zonation from the tree-line ecotone up to middle alpine, thus decreasing temperatures, shorter summer seasonal length and more grassy and patchy vegetation	
1.1	*Pardosa riparia*	fallow ground[5]; woodland edges and in pine forest[12]	continental, very low annual precipitation of 300-400 mm; most continental part of Norway	tree-line ecotone, forest and open habitats	
1.2	*Cnephalocotes obscurus*	bogs[5]; in open, damp places[12]		zonation from the tree-line ecotone up to the transition zone between low- and middle alpine, thus decreasing temperatures, shorter summer seasonal length and more grassy and patchy vegetation	
1.2	*Centromerus arcanus*	bogs[5]; humid moss of forests[12]	oceanic, annual precipitation of 1500-2000 mm	tree-line ecotone, forest and open habitats	
1.2	*Centromerus sylvaticus*	in ground litter of moderately damp woodland[12]		tree-line ecotone, forest and open habitats	
1.2	*Hilaira nubigena*	swampy localities[12]		zonation up to the transition zone between low- and middle alpine	most abundant in bogs, always wet and not frozen during winter in low-alpine
1.2	*Leptorhoptrum robustum*	in moss and leaves of damp, cool localities up to the alpine zone[12]		tree-line ecotone and low-alpine sites, moderate temperatures and longer summer season length (13-15 weeks), heather and low shrub communities	

Table 2.2 continued.

Class	Species	Habitat preferences (previous studies)	Continentality	Habitat preferences (this study) Elevational distribution	Toposequence
1.2	*Pardosa amentata*	damp habitats[12]		up to the transition zone between low- and middle-alpine	most abundant in bogs, always wet and not frozen during winter in low-alpine
1.2	*Allomengea scopigera*	forests[5]; very swampy localities[12]		tree-line ecotone, forest and open habitats and low situated low-alpine site	
1.2	*Bolyphantes alticeps*	bogs[5]; meadows and forest edges up to the subalpine zone[12]		tree-line ecotone, forest and open habitats	absent at bogs, always wet
1.2	*Gonatium rubellum*	woodland[12]		tree-line ecotone, forest and open habitats	absent at bogs, always wet
1.2	*Hahnia ononidum*	damp woodland[12]		tree-line ecotone, forest and open habitats	absent at bogs, always wet
1.2	*Hypselistes jacksoni*	swampy terrain[12]; peatlands and other wet lands[7]		tree-line ecotone, forest and open habitats	absent at bogs, always wet
1.2	*Pardosa spahgnicola*	bogs[12]; peatlands and other wet lands[7]		tree-line ecotone, forest and open habitats	absent at bogs, always wet
2.1	*Ozyptila arctica*	moist and dry tundra sites[10]		zonation from the tree-line ecotone to middle alpine	most abundant at alpine ridge sites with lichen heath, snow free conditions during winter and thus strong frost events
2.1	*Pardosa septentrionalis*	commonly in Empetrum heaths from 950 - 1200 m asl[8]	continental, very low annual precipitation of 300-400 mm; most continental part of Norway	zonation from tree-line ecotone to highest peak	most abundant at alpine ridge sites with lichen heath, snow free conditions during winter and thus strong frost events

Class	Species	Habitat preferences (previous studies)	Habitat preferences (this study)		
			Continentality	Elevational distribution	Toposequence
2.2	*Walckenaeria clavicornis*	soil crevices with high humidity[12]		zonation from tree-line ecotone to highest peak	most abundant at alpine ridge sites with lichen heath, snow free conditions during winter and thus strong frost events
2.2	*Micaria alpina*	alpine habitats[4,7]; under stones, among grass and moss usually above 750 m in Great Britain[11]		zonation from tree-line ecotone to highest peak	most abundant at alpine ridge sites with lichen heath, snow free conditions during winter and thus strong frost events
2.2	*Pardosa trailli*	mountainous areas[12]; high altitude sites[7]; in screes[2]		middle alpine, thus decreasing temperatures, shorter summer seasonal length (11-12 weeks) and more grassy and patchy vegetation	most abundant at ridges and southern exposed slopes, primarly with lichen heath, snow free conditions during winter and thus strong frost events
3	*Erigone tirolensis*	in the Alps at higher altitudes[12]; occurs under stones on mountains, usually above 900 m asl[11]		middle alpine, thus decreasing temperatures, shorter summer seasonal length (11-12 weeks) and more grassy and patchy vegetation	most abundant at slopes and depressions, protracted snow cover and very short summer seasonal length
3	*Collinsia holmgreni*	mountaines species[3]; hygrophilous[4]; in moss and litter layer[12]		middle alpine, thus decreasing temperatures, shorter summer seasonal length (11-12 weeks) and more grassy and patchy vegetation	most abundant at slopes and depressions, protracted snow cover, very short summer seasonal length

[1]Holm 1950, [2]Locket & Millidge 1953, [3]Palmgren 1976, [4]Hauge et al. 1978, [5]Hänggi et al. 1995, [6]Esynunin 1999, [7]Aakra & Hauge 2000, [8]Kronestedt 2002, [9]Gudleifsson & Bjarnadottir 2004, [10]Wyant et al. 2011, [11]British Arachnological Society 2013, [12]Nentwig et al. 2013

CHAPTER 3: Adaptation strategies of a common Lycosid spider do not follow a linear trend in alpine tundra ecosystems

Abstract

This research focuses on the influence of environmental conditions on the size and fitness of *Pardosa palustris* Linnaeus, 1758. We identify some of the driving forces for individual size in the common alpine wolf spider *P. palustris* in the southern central part of Norway. In the western oceanic research area, males and females of *P. palustris* were significantly smaller than in the continental research area. This spatial variation is most likely linked to local adaptation and a prolonged life cycle at the sampling sites in the continental research area. This phenomenon (bigger individual size due to a prolonged life cycle in ectotherms) can be referred to as a Bergmann`s cline. Along one of our two elevation gradients we found sex specific differences in relation to the environmental conditions at higher elevations. These differences are most likely related to different reproductive roles in males and females. Females of *P. palustris* showed a clear decrease in body size at southern exposed slopes at higher elevation. Most intriguing was the identification of a clear change in prosoma width along our elevation gradient in the continental research area, most likely linked to the transition zone between the low-alpine and middle-alpine belt. In conclusion, we show that alpine invertebrates are affected by macro-climatic and micro-climatic site conditions at different scales.

Introduction

It is highly probable that climate change will lead to crucial alterations in a huge variety of environments (Parmesan 2006); high mountain areas are supposed to be particularly sensitive (ACIA 2004; Parmesan 2006; IPCC 2007a,b). During the last decades, multiple changes in high mountain ecosystems have been observed (e.g. reviewed in Löffler et al. 2011). In response to the expected climate changes, species might have to cope with multiple problems within their habitats that could either lead to extinction, migration or adaptation. An extensive phenotypic plasticity might be the reason why certain species will persist in such changing environments (Scharf et al. 2010). In this context it is of special importance to comprehend the extent to which these processes are induced by environmental conditions and to ascertain how certain traits between or within populations will be affected. Both negative (e.g. limitation of habitat, greater competition) and positive (e.g broader distributional ranges) effects of climate change for certain species and their habitat breadth are expected, even though the negative effects might have stronger consequences for the ecosystem (Oliver et al. 2012).

An understanding of the underlying effects of phenotypic variation or adaptation (e.g. in body size), in ectotherms in relation to their environment is imperative for the development of climate change scenarios. In this context, body size and thus fitness can be seen as one of the key features of ecology and evolution theories (Angiletta et al. 2004). In particular, ectotherm fitness has received attention because it is assumed to influence a huge variety of factors, e.g. life cycle and reproduction traits. The body size of ectotherms is influenced by several environmental factors, often directly related to temperature. Generally, higher temperatures lead to faster development and thus earlier fertility (Willmer et al. 2000; Blanckenhorn & Demont 2004). The main indirect effect related to higher temperatures is probably prey abundance, since higher temperatures in moderate climates commonly lead to higher abundances in all ectotherms (Willmer et al. 2000). Another indirect effect related to temperature is the onset of the growing season. Changes in the onset of the growing season lead to size differences in arctic wolf spiders (Høye et al. 2009). Univoltine species in alpine climates are especially limited by season length, with respect to completion of their life cycles (Strathdee & Bale 1998).

Spiders are very suitable model organisms when focusing on individual–environment interactions (e.g. Hendrickx et al. 2003; Høye et al. 2009; Høye & Hammel 2010). Lycosid spiders became of greater interest to environmental researchers because of their commonly high abundance, the possibility of sampling them by pitfall traps and their strong relationship to micro-climate and vegetation structure (e.g. Schaefer 1970; Muff et al. 2009). In alpine areas, spiders are important predators of epigeal micro fauna (e.g. springtails), which can even affect litter decomposition and thus nutrient availability. In alpine environments where decomposition is restricted by the cold temperatures these effects can play a particularly important role in nutrient cycling (Wise 1993). We focused our research on prosoma width as a proxy for the size of the Lycosid spider *Pardosa palustris* Linnaeus, 1758. We used *P. palustris* as a model organism because of its high abundance in our research areas. The species is commonly found in open habitats

and on moist and dry meadows, and appears from the lowlands up to 2500 m asl (Heimer & Nentwig 1991). *P. palustris* is widely distributed and is present up to the northern most parts of Norway.

We expected that variations in the body size of *P. palustris* would be best explained by the onset of the growing season. Høye et al. (2009) found that longer seasons led to an increase in the size of the arctic wolf spider (*Pardosa glacialis*) in Greenland; a longer summer season length induced by the onset of the growing season led to bigger individuals. Since arctic and alpine environments usually show the same limitations when it comes to individual fitness and development (e.g. short seasons and cold temperatures) we tested our hypotheses along two alpine elevational gradients characterized by differences in continentalality in central Norway. We tried to find the main ecological drivers for body size in *P. palustris* and investigated whether adaptation strategies can be related to their spatial distribution. The study of the influence of certain environmental variables on individual body size in the field probably delivers the best answers if those variables are organized along gradients (Hodkinson 2005; Löffler & Finch 2005). We compared the spatial variation in prosoma width of *P. palustris* at different scales to explore possible future responses of the species towards a changing climate. We expected: 1) a decrease in prosoma width in *P. palustris* along alpine elevation gradients due to the shorter season length at higher elevation; 2) a sex specific difference in prosoma width in *P. palustris* along an alpine elevation gradient, due to the different life history traits of males and females; and 3) the same life history traits in both oceanic and continental Norway within the same latitudinal range.

Material and methods

Study areas

The specimens used in our study were sampled as part of "Long-Term Alpine Ecosystem Research" (LTAER) in the Norwegian Scandes (e.g. Löffler 2005, 2007). Our sampling was carried out in Vågå (Oppland, 61° N, 9° E) and Stranda (Møre og Romsdal, 61° N, 7° E) in central Norway in 2009 (Figure 3.1).

Due to the north-south extension of the Scandinavian mountain chain, Norway is divided into a western oceanic and an eastern continental climate section. In relatively short linear distances (in this study approximately 100 km), huge climatic differences are apparent. Stranda is located in the western oceanic part and Vågå is located in the eastern continental part of Norway. The annual precipitation in Stranda is around 1800 mm, while Vågå has an annual precipitation of only 300-400 mm in the valleys (Löffler 2002). Moen (1998) classifies the western research area (Stranda) as a "slightly oceanic section" and the eastern area (Vågå) as a "weak continental section". In both study areas the low-alpine vegetation is dominated by shrub and heath communities, whereas the middle alpine vegetation is dominated by graminoids (Dahl 1986). In Stranda, the tree-line is found at approximately 750 m asl, and in Vågå at approximately 1030 m asl. The upper limit of the low-alpine belt is found at approximately 1200 m asl in Stranda and at approximately 1350 m asl in Vågå. The highest peak in Stranda is Mt. Dalsnibba (1495 m asl) and in Vågå it is Mt. Blåhø (1618 m asl). Along elevation gradients from the tree-line up to the highest peaks we collected epigeal invertebrates at 73 (Stranda

32; Vågå 41) sampling sites altogether. Along topographic gradients, which are assumed to display the strongest environmental differences at short distances in the alpine areas, pit fall traps were installed at ridge sites, depressions, and southern and northern exposed slopes. During the snow-free period, three pit-fall traps with saturated salt solution as a preservative and Agepon as a detergent were installed at each site (i.e. a total of 219 traps at 73 sampling sites). Pit-fall traps were installed during 2009 at the sites as soon as they became snow-free. The pitfall traps were emptied on a biweekly basis and their contents were transferred to 70 % ethanol for preservation. In the oceanic research area, 10 sampling periods were implemented from 20th May until 3rd October 2009 and in the continental research area 11 sampling periods from 28th April until 29th September 2009.
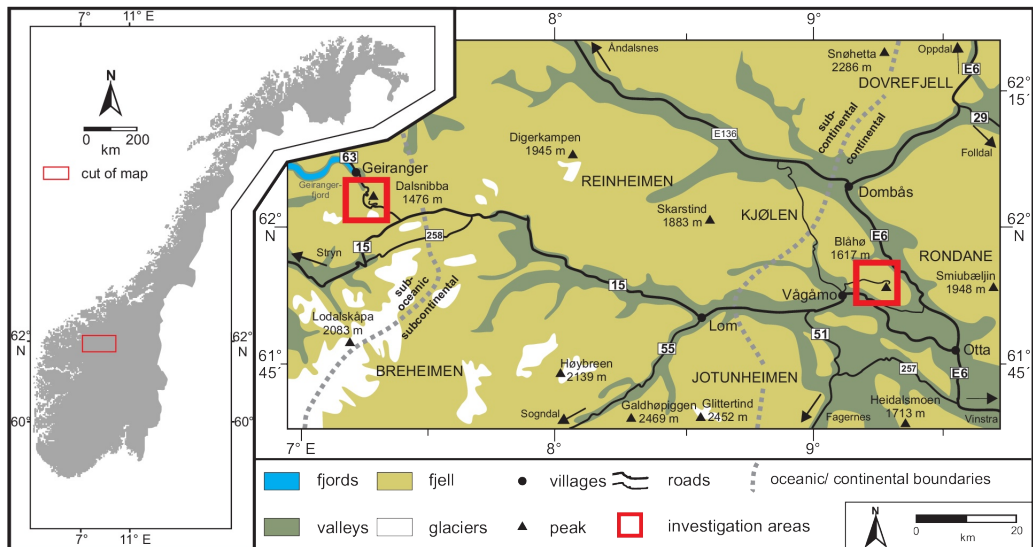

Figure 3.1. Map of Norway with focus on the two research areas in the western, oceanic part (Stranda) and in the eastern continental part (Vågå) of Norway (after Löffler & Pape 2004)

Analysis and statistics

Adult Araneae were determined to species level following Almquist (2005). Digital pictures of every adult specimen of *P. palustris* were taken through a dissecting microscope using a Canon Power Shot S70 digital camera. The measurements of the pictures were implemented using ImageJ (Rasband 2007). We used prosoma width as a proxy for body size and, thus, fitness and development, since former studies have shown a relationship between prosoma width and fitness (e.g. Hagstrum 1971; Hendrickx et al. 2003). We estimated the mean prosoma width for each sampling site with at least three specimens of *P. palustris*. The season length was estimated by simply counting the snow-free days at the specific sampling sites. First we checked for normality and homogeneity by visual inspections of plots of residual against fitted values. We used a Wilcoxon test to identify significant differences in prosoma width in males/females and between the two populations (Stranda/Vågå) in 2009. Furthermore, we tested the results for exposure specific prosoma width of females and males for ridge sites in Stranda and Vågå, and for

southern exposed slopes in Vågå. We then used linear regression models to identify relationships between prosoma width, season length, and elevation within each sex in both Stranda and Vågå, in 2009. If at least five sampling sites along the elevation gradient were of similar exposure, we used linear regression models to identify significant exposure specific relationships between prosoma width and elevation for both sexes. To avoid the possibility of Type I errors, all significances were Bonferroni corrected (Holm 1979). All data were analyzed using R (R Core Development Team 2011).

Results

Altogether, more than 55000 invertebrates of which 9726 were Araneae (Stranda n=3459 and Vågå n=6267) were sampled. Only adult spiders were identified to species level; juveniles were excluded in this study. *P. palustris* was the most common Lycosid species (n=955) appearing from the tree-line up to 1488 m asl (Stranda) and 1565 m asl (Vågå). We display results only for sites with at least three specimens of one sex of *P. palustris* (n=938 remaining). The first specimens (males and/or females) of *P. palustris* were sampled during the first sampling period from 20th May until 2nd June in Stranda. Here, the latest sampled individuals occurred during the ninth sampling period from 9th until 23rd September. In Vågå, the first males and females were sampled during the third sampling period from 26th May until 9th June. The latest males were sampled during the seventh sampling period from 21st July until 4th August, while the latest females were sampled during the eleventh sampling period from 15th until 29th September (Figure 3.2). Activity in males and females in Vågå peaked 23rd June until 7th July (Figure 3.2). Activity in males in Stranda peaked 17th June until 1st July, while female activity peaked one sampling period earlier from 5th June until 17th June. Males of *P. palustris* showed a pronounced higher activity abundance compared to the females over the entire sampling season both in Stranda and Vågå. In Stranda, a total of n=264 (male=170, female=94) and in Vågå a total of n=664 specimens (male=445, female=219) were sampled.

The results for the linear regression model on the influence of the single variables "Elevation" and "Season length" or the combination of both variables on prosoma width showed significant correlation. We analyzed the influence of the specific effects of sampling sites on prosoma width, at sampling sites with at least five similar exposures at different elevation. Thus, we analyzed only ridges in Stranda, while in Vågå, ridges and southern exposed slopes were analyzed (Figure 3.3 and 3.4).
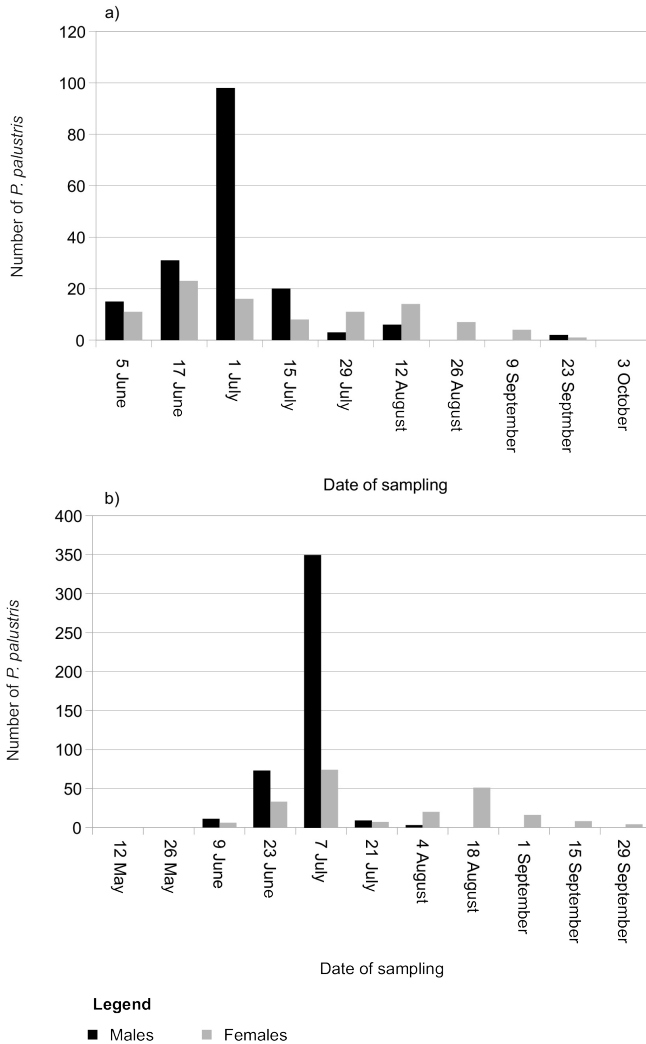
a)

b)

Legend
■ Males   ■ Females

Figure 3.2 Activity abundance of P. palustris in the oceanic two research area. The number of the trapped adult males and females during the sampling periods in 2009: a) oceanic research area, b) continental research area. Note the different scales of the x and y-axis.

Analysis of the sampling sites specifically showed significant differences along the elevation gradient at southern exposed slopes. Females showed a significant decrease in prosoma width at southern exposed slopes in Vågå, while males were not affected (Figure 3.4 e and f). At the ridge sites, no elevation related effect was visible. Remarkably in this context, prosoma width does not follow a linear trend connected to elevation. In the eastern research area Vågå females and males show a constant linear decrease in prosoma width at the ridge sites up to around approx-
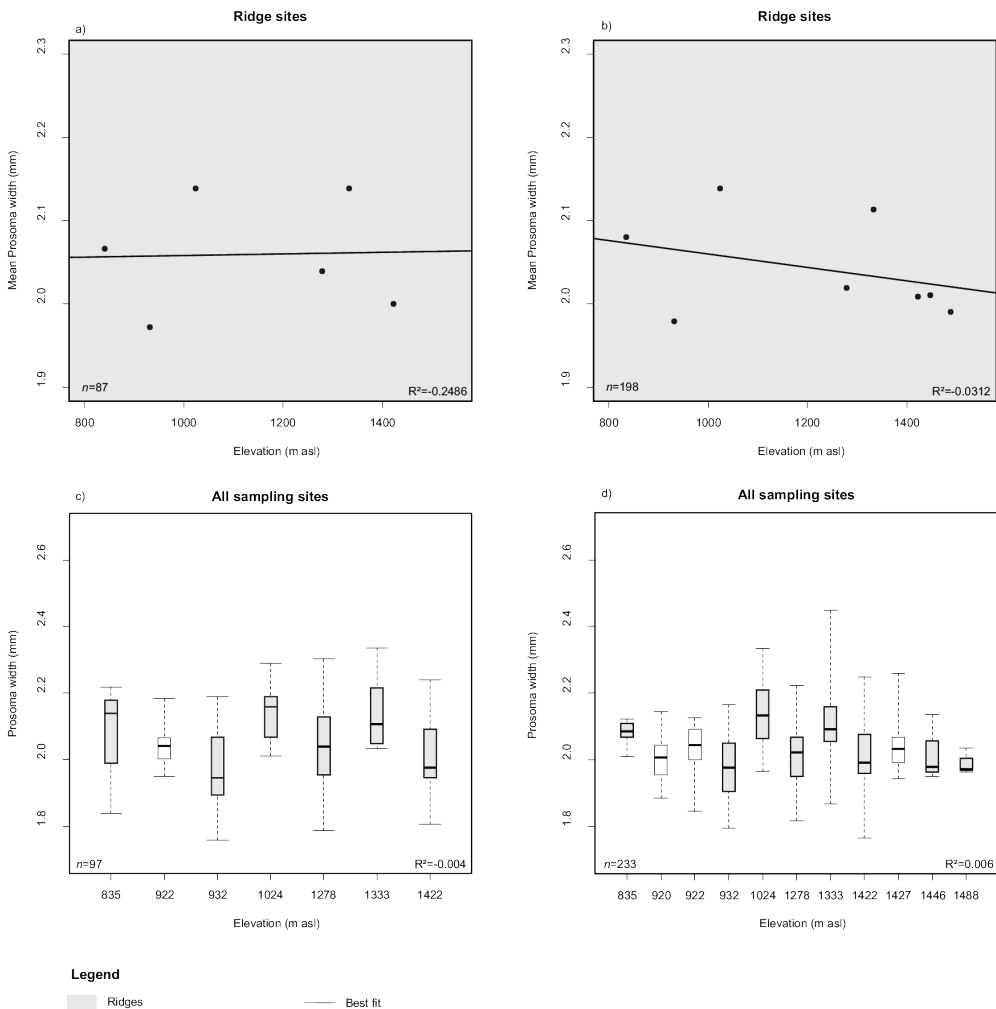
Figure 3.3 a-d Sampling site specific variation in prosoma width in females (a+c) and males (b+d) of P. palustris at the sampling sites in Stranda. The prosoma width (mm) is given at the ridges and southern exposed slopes along the elevation gradient (m asl) in oceanic Norway in 2009. In the graphs we display the line of best fit and the adjusted R². Note that none of the results was significant. Ridge sites are marked as light grey (a+b).

imately 1300 m asl. The same phenomenon is also visible in males at the southern exposed slope up to approximately 1300 m asl. Above 1300 m asl the results show no clear elevation related trend in prosoma width at these certain sites (Figure 3.4). This area around 1300 m asl corresponds well with the beginning of the transition zone between the low and middle alpine belt in Vågå.

We compared the two populations of *P. palustris* in Stranda and Vågå to see if there was a region specific difference in prosoma width. We found a significant difference between the oceanic and the continental populations in 2009 (Figure 3.5 a). The Wilcoxon test showed significant differences in prosoma width between specimens sampled in Stranda compared to those in Vågå (W=11422.5, *p*-value<0.001; female W=553, *p*-value<0.001).
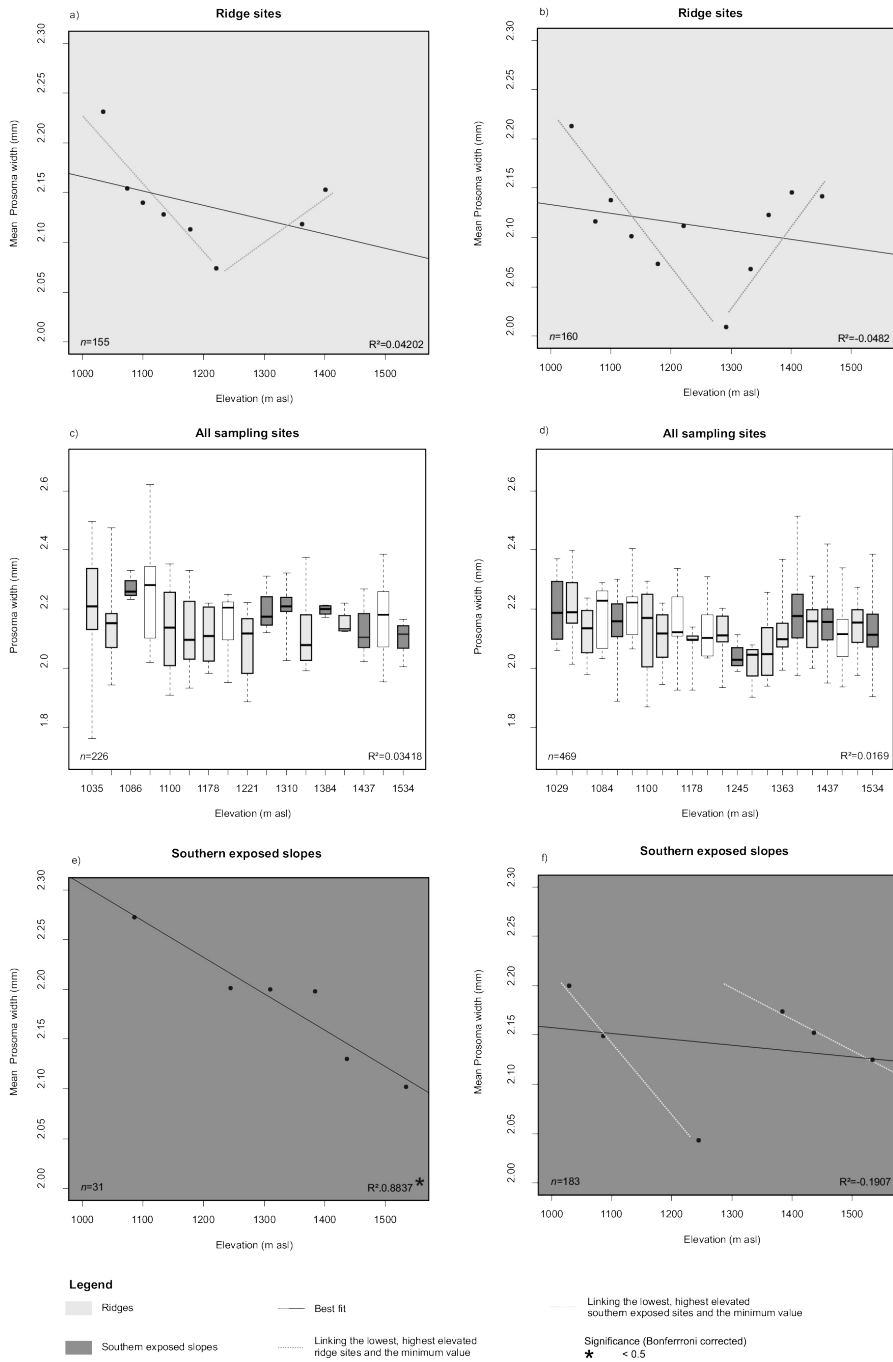
*Figure 3.4 a-f Sampling site specific variation in prosoma width in females (a+c+e) and males (b+d+f) of P. palustris at the sampling sites in Stranda. The prosoma width (mm) is given at the ridges and southern exposed slopes along the elevation gradient (m asl) in continental Norway in 2009. In the graphs we display the line of best fit and the adjusted R². Bonferroni corrected significant results are marked with an asterisk *. Ridge sites are marked as light grey (a &b) and southern exposed slopes are marked as dark grey (e & f).*
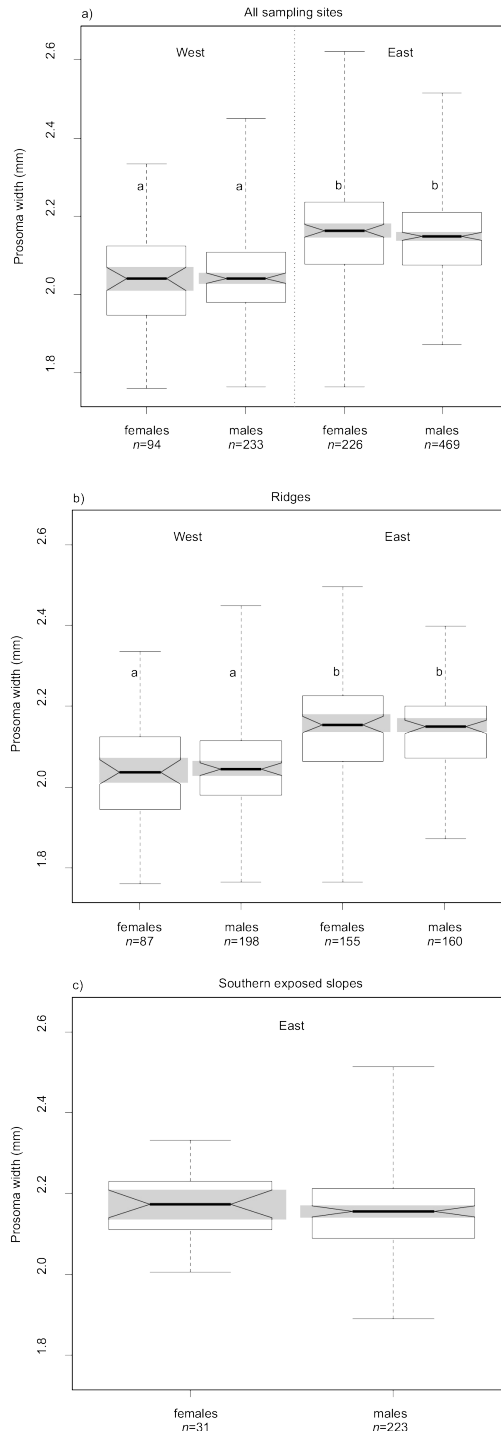
Figure 3.5 a-c Box Whisker plots displaying the prosoma width (mm) of females and males in oceanic and continental Norway in 2009. Non overlapping notches indicate significant differences between the different research areas. Different letters (a/b) indicate significant (p < 0.5) differences.

When testing for sex specific differences within the population we found no significant results indicating a SSD in *P. palustris* neither in Stranda nor in Vågå (Stranda W=10457, *p*-value=0.5236; Vågå W=3887, *p*-value=0.2619; Figure 3.5 a). Furthermore, we tested the prosoma width of females and males in dependency of habitat exposure. The comparison of the ridge sites between the oceanic and the continental region gave similar results when considering all sampling sites. Females and males at ridge sites in the oceanic research area were significantly smaller than those in the continental area (females W=3422, *p*-value<0.001; males W=8541.5, *p*-value<0.001; Figure 3.5b), while females and males showed no difference in prosoma width in the two regions (Stranda W=8077, *p*-value=0.4033; Vågå W=13411, *p*-value=0.2111). We did not find a difference in prosoma width between females and males at the southern exposed slopes in the continental region (Vågå W=3887, *p*-value=0.2619; Figure 3.5c).

Discussion

Various species-environmental interactions at different scales between and within two populations of *P. palustris* are visible along multiple scales in our research areas. Prosoma width and thus spider size and its related constraints are obviously a reliable proxy to describe species–environmental interactions. Along the elevation gradient in the continental research area we found a sex-specific response of *P. palustris* with higher elevation. These specific behavioral and physiological differences can be directly connected to the typical temporal and spatial distribution patterns in the alpine areas of Norway. The reactions of female and male *P. palustris* were noticeably different at the various exposures along the elevation gradient. The general presumption that at higher elevations the environment becomes harsher, due to the colder temperatures and shorter summer season, is not consistently true for epigeal spiders.

The results show that elevation effects on the prosoma width of *P. palustris* are strongly related to site-specific conditions and differ widely between females and males. The results for prosoma width in females of *P. palustris* at sites of similar exposure along the elevation gradient in continental Norway differed either widely (southern exposed slopes) or showed no trend in adult body size (ridges). Gjaerevoll (1956) described the characteristic snow cover distribution in the Scandinavian mountains formed by topography and the main wind direction. In our research areas this is commonly expressed by snow-free ridges (up to the middle alpine belt) and filled depressions. We found the thickest snow layers and thus the shortest seasons at the southern exposed lee-slopes, due to the main wind direction: N-NW (Löffler et al. 2006).

Males of *P. palustris* do not seem to be affected by certain site conditions in comparison to the females. Our results indicate that females of *P. palustris* are somewhat more faithful to their habitat, since we found a strong correlation between site specific environmental parameters only in females at southern exposed slopes. This might be explained by the commonly higher activity abundances in male spiders due to their more active role during phases of reproduction (Wise 1993). The pattern of elevation variation in prosoma width might be the result of sex specific growth strategies (Uhl et al. 2004; Høye & Hammel 2010), even though *P. palustris* is supposed to be one of the most active Lycosid aeronauts (Richter 1970)

and thus able to spread over long distances. Our results indicate that females of *P. palustris* are somehow more affected by the environmental conditions at a local scale than males. Therefore, our results have to be interpreted with caution, since the migration, foraging and movement behaviors of Lycosid spiders in complex ecosystems have so far received little attention, because of the great difficulties involved in following the relatively small specimens.

Concerning foraging strategies, the spatial distribution, target prey availability and nutritional content has to also be taken into consideration (Kuusk & Ekbom 2012). Our results show a clear break along the elevation gradient at the transition zone in the continental research area. Curiously, these findings are correlated to the transition zone between the low alpine and the middle alpine belt, displaying an elevational limit for *P. palustris*. The decreasing prosoma width in females (merely at ridge sites) and males (ridge sites and southern exposed slopes) along the elevation gradient up to the transition zone and the non-linear trend in prosoma width above that, corresponds with findings on microbial activity along an alpine elevation gradient in the same research area. Löffler et al. (2008) found a clear pattern of microbial activity related to the low-alpine, middle-alpine and the transition zone at their sampling sites in the continental research area. Intrinsic factors might be responsible for this change in spider response below and above the transition zone, e.g. changes in life cycle traits due to shorter season length at higher elevations, or alternately, extrinsic factors may play a part, e.g. changes in competition due to alpine species that inhabit favorable adaptation strategies.

Landscape boundaries that can be found along an elevation gradient in the alpine area are commonly controlled by climate, with a special emphasis on temperature (Nagy & Grabherr 2009). The shifting of landscape boundaries in alpine areas has been identified as a direct consequence of global change all over the world; in response to climate change an advance of the tree-line and the respective alpine zonation to a higher elevation is a world wide phenomenon (ACIA 2004; Parmesan 2006; IPCC 2007a; Löffler et al. 2011). Our results indicate that an expected upward shift of this transition zone due to global warming might affect invertebrate life cycle traits and their related features in this part of Norway with yet unpredictable effects on future community structures (e.g. Finch et al. 2008). This climate induced effect on spiders is, however, rather local and reduced to a rather narrow elevation range. Unfortunately, we could not find such a trait in the oceanic research area; this could be related to findings regarding adaptation strategies in *P. palustris* at a larger scale.

When we examine a larger scale along a longitudinal gradient we find that differences in spider size are affected by more regional conditions. Along the longitudinal oceanic-continental gradient and in a comparison of the two regions, we found a significant difference in adult body size in the two alpine populations of *P. palustris*. Individuals sampled in the continental research area showed a significantly larger body size both in females and males. Larger body size in colder environments is supposed to be a form of adaptive plasticity, where individual body size tends to be bigger because of slower growth (Atkinson & Sibly 1997; Angilletta et al. 2004). The appearance of adult males at the end of the season in Stranda could be proof of a difference in the life cycle of individuals in the western part of Norway, compared to the eastern more continental part. In both regions, adult males

of *P. palustris* showed the highest activity abundance at the beginning of July and were then absent from the pit fall traps for at least two consecutive sampling periods in August and September.

The appearance of adult males at the end of the season in Stranda might be evidence of a difference in over-wintering strategy. In the western oceanic region, males obviously overwinter in an adult stage, whereas in the continental research area the absence of adult males at the end of the season might be evidence of a prolonged life cycle here. Commonly, spiders of the genus *Pardosa* have an annual life cycle, which appears to be prolonged in some species at higher altitudes or latitudes (Edgar 1972; Buddle 2000; Pickavance 2001). Higher temperatures or other local traits at sites with *P. palustris* in Stranda might fasten the development of *P. palustris*. We expect *P. palustris* to exhibit a Bergmann`s cline along the longitudinal gradient expressed by larger individuals at the more continental sites. Opell (2010) found larger individuals of *Amaurobioides maritima* along a latitudinal cline in New Zealand, probably also as a result of Bergmann`s rule. Along our elevation gradient we could not find such a trait.

Most likely due to the high variability of micro-climatic conditions in alpine areas (e.g. Mani 1968), it is obviously possible for *P. palustris* to find suitable conditions even at higher altitudes. In this context, Scherrer and Körner (2011) showed how topographically controlled micro-climatic conditions might buffer climate warming in alpine areas. Our results indicate that not only latitudinal related changes but also longitudinal changes in relatively short distances (100 – 150 km) can affect spider size to a huge extent. Vertainen et al. (2000) found size differences related to genetically differentiated populations of *Hygrolycosa rubrofasciata* (Ohlert 1865) within a few kilometers in Finland. It is assumed that larger females have an increased fecundity and that they produce a larger egg number (Edgar 1971a; Simpson 1995; Tanaka 1995; Prenter et al. 1999; Fox & Czesak 2000), and larger eggs commonly lead to larger hatchlings and thus to a larger survivor ship (Janzen et al. 2000). Female spiders clearly benefit from larger size through augmented egg production, while male mating success is not commonly related to size (Vertainen et al. 2000).

Our results show that combined ecological and climatological data are essential to understand how species and corresponding alpine ecosystems might change in response to future climate change. Genetic research and gardening experiments should support findings regarding adaptation and life cycle strategies of invertebrates in arctic-alpine areas. This is mandatory to learn more about the underlying mechanisms that, in the end, display invertebrate adaptation stratieges in the alpine environment.

Acknowledgements

CHAPTER 4: Elevational variation of reproductive traits in five *Pardosa* (Lycosidae) species

Abstract

Differentiations in reproductive traits along climatic gradients can be substantial for a species to spread along a wide spatial range. We compared the reproductive effort allocated to first egg sacs of five species of the genus *Pardosa: P. palustris* (Linnaeus 1758), *P. amentata* (Clerck 1757), *P. lugubris* (Walckenaer 1802), *P. hyperborea* (Thorell 1872), and *P. riparia* (C.L. Koch 1833) along three elevation gradients in central Norway. We tested whether population differences are consistent among the three transects, respectively along the elevation gradient. We assumed that the harsh environments of alpine areas would lead to adaptations in reproductive traits resulting in larger eggs but smaller clutches at higher elevations. The results show that female size and egg number were positively correlated among all species. However, no clear elevation related trend was found. Other traits did not change consistently between species and along the elevation gradients. We assume that local micro-climatic impacts on spider fitness are a crucial but poorly understood factor. Without further knowledge about adaptation and phenotypic plasticity in ectotherms, modelling of possible future reproduction biology might remain flawed.

Submitted manuscript:

Introduction

Many ectotherm species that are widely distributed along elevation and latitudinal gradients have to cope with extreme differences in the environmental conditions, in particular at the upper and lower boundaries of their distribution (e.g. Hodkinson 2005). Species adaptation, e.g. in reproductive traits, along elevation gradients can help to understand how species or populations may react to environmental changes. Reproductive traits can vary between species, between populations of a certain species and between individuals of a population (Fox & Czesak 2000; Fischer et al. 2002; Moya-Laraño 2002; Høye & Hammel 2010). Variations in reproductive traits are controlled by a number of factors that include maternal fitness and environmental conditions (Simpson 1995; Hendrickx & Maelfait 2003). However, environmental factors such as temperature and food supply can also interact with intrinsic factors like maternal size (Azevedo et al. 1996; Bauerfeind & Fischer 2008). The influence of these factors on traits such as egg size is not completely understood so far (Bernardo 1996; Fox & Czesak 2000).

One of the primary challenges for ecologists today is to assess the ecological impact of global changes on physiological traits in different geographic areas (Bozinovic et al. 2011). Comparative studies of species ecology along different elevational or latitudinal gradients may provide important information on the response of populations or communities to climatic change at any point over time (Hodkinson 2005). In particular research along elevation gradients and its related environmental changes might deliver important findings in how species react to changing climatic conditions. Körner (2007) identifies four main climatic factors that change along an elevational gradient and that are relevant for organisms: a) decrease in atmospheric pressure, b) reduction of atmospheric temperature, c) increasing radiation under a cloudless sky, d) and a higher fraction of UV-B radiation. Other climatic factors are not considered relevant for unidirectional trends with elevation. Evolutionary theory suggests that harsher environments (e.g. alpine areas) can lead to a trade-off between separate life history traits (Hendrickx et al. 2003; Norry et al. 2006). For several invertebrates it has been shown that fitness-related traits, including characteristics of life cycle and reproduction, can vary along latitudinal and along elevation climatic gradients (David & Bocquet 1975; Berven & Gill 1983; Dingle et al. 1990; Ayres & Scriber 1994; Tatar et al. 1997; Telfer & Hassall 1999; Lencioni 2004; Hodkinson 2005; Samietz et al. 2005).

Lycosid spiders (i.e., wolf spiders) are well-suited model organisms for various aspects of (spider) ecology including the influence of environmental conditions on spider fitness (see, e.g. Hendrickx & Maelfait 2003; Høye et al. 2009; Høye & Hammel 2010), because they colonize a huge variety of terrestrial habitats from sea level to high alpine areas. Thus, wolf spiders have become the most intensively studied spider family to date (Wise 1993, 2006). For studies on reproductive traits, wolf spiders are exceptionally suitable model organisms, as females carry their eggs in a sac attached to the spinnerets. This makes it possible to relate reproductive traits (e.g., egg number, egg size) to each individual female. In this study we analyzed traits of Lycosid spiders of the genus Pardosa as well as the influence of elevation on these traits. Since Lycosid spiders are one of the main predators in

alpine environments (Wise 1993) we aimed to test whether climatic gradients related to elevation are driving forces for adaptation in these species. As such we aimed to learn more about how certain species might react to a possible future changing environment.

During a single reproductive period, at lower altitudes, each female spider produces up to three egg sacs which differ in clutch- and egg size. In alpine areas usually only two egg sacs are produced (e.g., Edgar 1971a; Kessler 1971; Steigen 1975; Bayram 2000; Hendrickx & Maelfait 2003). Although the duration of egg sac carrying varies with temperature (Schmoller 1970; Steigen 1975), the detailed characteristics of reproductive clines in wolf spiders along a thermal gradient remain unclear. We expected elevation dependent differences and adaptations in the reproduction traits of wolf spiders: bigger eggs but smaller clutches may occur at higher elevations, forced by the harsher environmental conditions at higher altitudes. This assumption is in line with the life history theory (Sibly & Calow 1986; Simpson 1995; Tanaka 1995; Tamate & Maekawa 2000).

Material and methods

Study area

Three transects along elevational gradients on three different mountains (Blåhø, Svarthovda, and Gråsida) were studied in the research regions Vågå and Dovre (Oppland). The study areas were located in the central southern, most continental part of Norway at about 62°N and 9°E (Figure 4.1). For a detailed description of the research areas, see, e.g. Löffler (2002). The alpine environment begins above the tree-line, which is situated at around 1000 – 1050 m asl, with a transition zone between the low alpine and middle alpine belt at about 1350 m asl. According to Dahl (1986), the vegetation in the low-alpine belt is dominated by shrub and heath communities, whereas the middle-alpine belt is dominated by graminoids.

At Mt. Blåhø, the elevation transect reached from 360 m to 1610 m asl, and included nine sampling sites below and eight above the tree-line. At Gråsida, the elevation transect covers a range from 470 m to 1440 m asl, with eight sampling sites falling below and eight sites above the tree-line. The transect at Svarthovda, ranged from 610 m to 1390 m asl. Here, the tree line was situated at around 900 m asl. Six sites were established below and six above the tree-line.

Sampling of traits

Sampling sites were chosen for their elevation range and typical aspects of Lycosid preferred habitats (Lomnicki 1963; Otto & Svensson 1982; Frick et al. 2007). Pre-examinations were implemented to assess if Lycosid spiders were present. The elevation distance between the sampling sites was around 60 - 70 m. Each sampling site was representative in its floristic composition and vegetation structure. The size of each sampling site was approximately 100 m².

In this study, we focused on the traits prosoma width, egg number, and egg size. Prosoma width is a powerful trait for determining the different development stages and the fitness of Lycosid females (Hagstrum 1971; Edgar 1971 a, b; Marshall & Gittleman 1994; Hendrickx & Maelfait 2003). Egg number is commonly closely re-

lated to female size, since a bigger female profits of the augmented egg production (Vertainen et al. 2000). Egg size is a good proxy for reproduction effort. It is species-specific and thereby suited to determine and compare offspring fitness (Anderson 1978), because bigger eggs result in bigger, healthier offspring with, for example, a higher starving resistance (Edgar 1971a; Tanaka 1995; Fox & Czesak 2000).
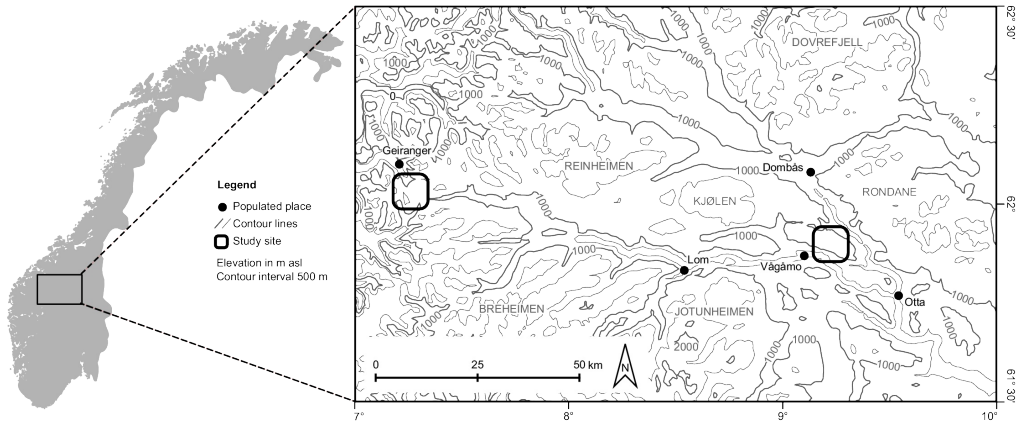

Figure 4.1 Map of the research area in southern central Norway with focus on the three mountain tops Blåhø, Gråsida, and Svarthovda.

In order to sample these traits, female wolf spiders carrying egg sacs were hand-collected from the three transects between 24th May and 26th July 2006, on warm, sunny days, when wolf spiders of the genus *Pardosa* are most active (Steigen 1975; Buddle 2000). Each site within each transect was sampled for about one hour by one person, and each transect was sampled on two consecutive days. Sites below the tree-line were sampled on one day, sites above the tree-line on the following day and vice versa to avoid the sampling of time related phenomena. As soon as the sampling sites became snow-free, they were monitored constantly at least once a week until the first females with egg sacs could be sampled. Kessler (1971) states that Lycosids usually carry their egg sac in a six week period from May until the end of June with each single female carrying the sac for not more than one or two weeks. This timing and the fact that second egg sacs contain only 50 – 60% of the number of eggs compared with first egg sacs (Kessler 1971) allowed the identification and removal of dubious clutches from our sample. Second egg sacs were assumed not to contribute to the recruitment of the population (Steigen 1975). Every female was held separately to avoid cannibalism and exchange of egg sacs. Female Lycosids and egg sacs were preserved in 70% ethanol for at least four weeks to make sure that the eggshell was able to extend to its maximum volume (Hendrickx & Maelfait 2003). Egg number was determined by counting the eggs and juveniles in the egg sac, assuming that all eggs in an egg sac would develop (Hackmann 1957; Edgar 1971a). We identified spiders following Almquist (2005). All collections were stored at the Department for Geography at the University of Bonn, Germany. We took digital photographs of all females and of 10 eggs from each female with a Nikon photo-ocular and a 100 × digital magnification. From these photographs, we

measured female prosoma width as well as egg length and width to the nearest 0.01 mm using the software "Bild'o'meter" (Mühlen 2006). Only species-specific results were used, as patterns found at an interspecific level (i.e., within a pooled analysis of all species wolf spiders) may not hold true for a single species. Based on the measured egg length (EL) and egg width (EW) we calculated egg size (EV) following Hendrickx et al. (2003, equation 1):

$$EV = \frac{\pi}{6} \times EL \times (EW)^2$$

[eq. 1]

Statistical analysis

The sampled data on prosoma width, egg size, and egg number were subjected to a Principal Component Analysis (PCA, Hotelling 1933). This technique allows to reduce the dimensionality of the trait space and to identify, quantify, and illustrate collinearities between the traits. The principal components (PC), i.e. the axes of the PCA space, represent the original variation of the data in hierarchically decreasing order. A separate PCA was used for each site and species to analyze interspecific and inter-site differences in the relation of the traits and elevation. For interpretation purposes and in order to analyze the relation between the three traits, we projected the traits as vectors into the PCA space. The direction of the vectors with respect to the PCs indicates the correlation with the respective axes; the length of the vector illustrates the strength of this correlation. The similarity of the direction of two trait-vectors describes the degree of inter-correlation between these traits. Further, co-variables such as elevation in this study can be projected and analyzed in the PCA-space. This allows to draw conclusions on possible relations between trait distributions and environmental parameters. We used permutation tests with 999 permutations of the variables to test whether the relations between the PCs and the traits as well as elevation are significant. Further, we illustrated the distribution of elevation in the PCA space using a variable symbol size of the data points. This additional illustration was used to ensure that the linear correlation as displayed in the vectors does not fail to describe a nonlinear relationship. Since the PCs are a linear combination of the original trait data, a similar representation of the trait data was not considered necessary. Although the traits were analyzed for all occurring species, the PCA was only used to analyze species specific data with an appropriate sample size of individuals with first egg sacs containing eggs.

Results

A total of 1558 female Lycosids with egg sacs of 13 species were sampled along the three transects (44 sampling sites). An overview of the sample and the variation of the measured traits is given in Table 4.1. Individuals of *P. amentata, P. lugubris*, and *P. riparia* were only found up to the transition zone between the tree-line and the alpine area. Individuals of *P. hyperborea* were only found at alpine sites and in the transition zone, while individuals of *P. palustris* were collected almost along the entire elevation gradient at sites below and above the tree-line (Figure 4.2).

Table 4.1 Morphometric and reproductive traits for the 5 Lycosid species sampled at the 44 sampling sites (EN=Egg number, PW = prosoma width in mm, EV = egg volume in mm3, ER = Elevational range, * only first egg sacs).

Species	n	EN*	Egg Volume Ø*	EV Ø range*	PW (mm)	PW range (mm)	ER (m asl)	First Sampled (Date/Elevation m asl)
Pardosa amentata	237	54.5± 11.53 (*n*=218)	0.40±0.045 (*n*=1750)	0.28 - 0.55	2.51± 0.17	2.04 - 2.92	360 - 1070	24 May 2006/ 360
Pardosa lugubris	220	37.72± 6.37 (*n*=204)	0.37±0.038 (*n*=1500)	0.29 - 0.50	2.12± 0.13	1.65 - 2.49	550 - 1010	12 June 2006/ 580
Pardosa palustris	747	45.67± 11.43 (*n*=712)	0.36 ± 0.044 (*n*=3630)	0.25 - 0.59	2.21± 0.15 (*n*=741)	1.76 - 2.70	370 - 1460	15 June 2006/ 1010
Pardosa riparia	125	37.54± 6.46 (*n*=120)	0.34 ± 0.036 (*n*=950)	0.24 - 0.43	2.04± 0.13	1.77 - 2.39	760 - 1010	15 June 2006/ 970
Pardosa hyperborea	127	32.07± 6.85 (*n*=121)	0.32 ± 0.037 (*n*=720)	0.25 - 0.41	1.84± 0.15 (*n*=126)	1.48 - 2.60	870 - 1340	23 June 2006/ 890

The PCA for the five *Pardosa* species show a strong correlation between prosoma width and egg number (Figure 4.3). This correlation is, however, the only feature that is generally applicable for the five species at the three gradients. Moreover we found partially diverging and even contradictory species-specific trends for some of the traits that were analyzed. On the one hand, *P. amentata* at Blåhø showed an increased prosoma width and thus a greater number of eggs at higher elevations, on the other hand the results at Gråsida indicated a decrease in prosoma width at higher elevations; egg number remained unaffected here. For *P. hyperborea, P. lugubris,* and *P. riparia* no clear elevation related trend in egg number or prosoma width emerged. *Pardosa palustris,* the species with the widest elevational range in our study, displayed a strong decrease in prosoma width at Gråsida and Svarthovda at higher elevations, while at Blåhø this effect was not observed at all. Elevation dependent constraints on egg size were only visible along some of the gradients. For *P. amentata* at Svarthovda, egg size decreased at higher elevations. For *P. hyperborea*, egg size increased with increasing elevation at Blåhø, while at Svarthovda the opposite effect was visible. For *P. lugubris*, a decrease in egg size at higher elevations was observed at Svarthovda. For *P. palustris* egg size increased at higher elevation at Blåhø. Along the other gradients we could not find any relationship between egg size and height of elevation. Along none of the transects relations between decreasing egg number and increasing egg size or vice versa could be observed.
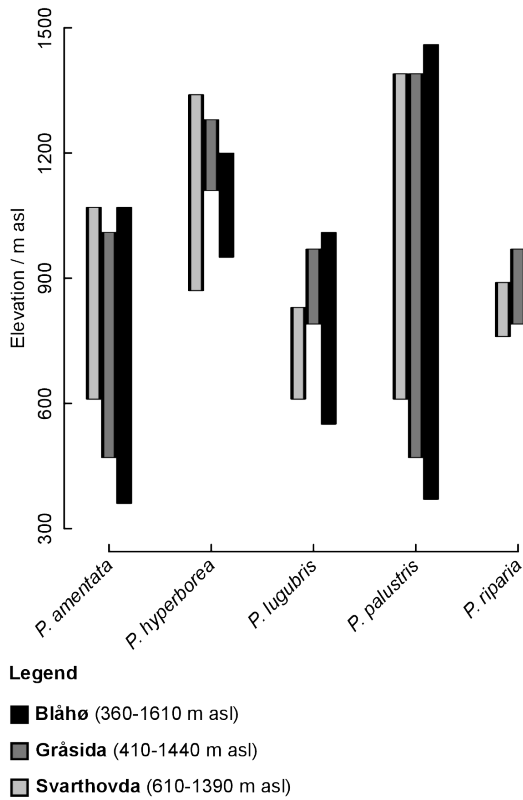
Figure 4.2 Elevation ranges of the five Pardosa species sampled along the three gradients. Pardosa amentata, P. lugubris, and P. riparia are found up to the tree-line at the three transects, while P. hyperborea was found only above and in the transition zone between tree-line and the alpine. The only species occurring along almost the entire elevation gradients was P. palustris.
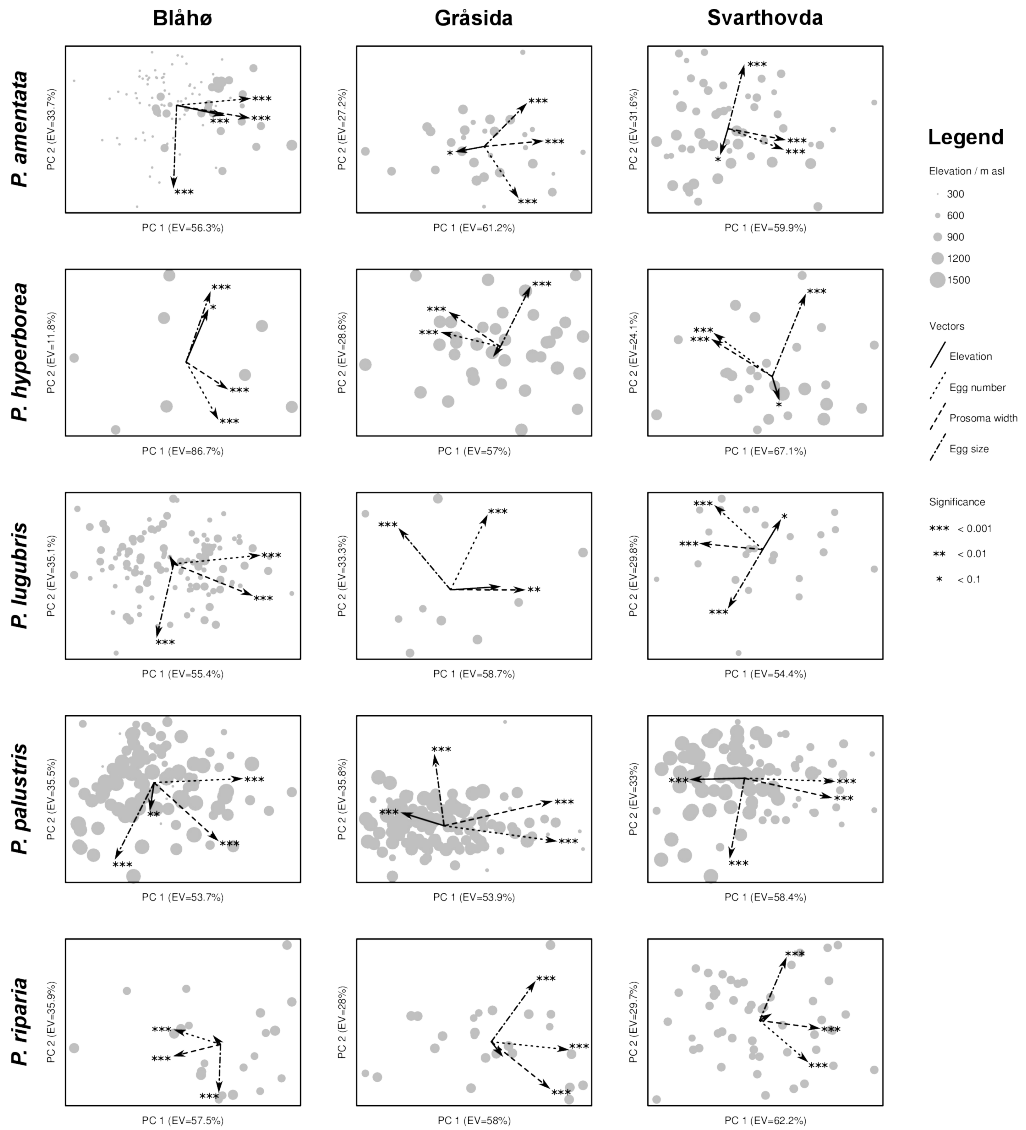
Figure 4.3 PCA for the five Pardosa species along the three elevation gradients. The axes of the PCA space represent the original variation of the data in hierarchically decreasing order. The direction of the vectors with respect to the PCs indicates the correlation with the respective axes; the length of the vector illustrates the strength of this correlation.

Discussion

Reproductive traits in Lycosid wolf spiders along elevation gradients, with focus on Pardosa differed between the different species of *Pardosa*. Our assumption that under harsh environmental conditions at higher elevation species of the genus Pardosa would tend to produce bigger eggs but smaller egg number was not confirmed. However, egg numbers were positively correlated with female size, both inter- and intra-specifically along the three elevation gradients. This relationship is in line with general rules of invertebrate ecology, including wolf spiders and other spider families (Leather 1988; Roff 1992; Stearns 1992; Kessler 1971; Brown et al. 2003). A bigger size in female spiders is beneficial due to the augmented egg production (Vertainen et al. 2000). Moreover we did not find consistent elevation related traits in reproduction of the five *Pardosa* species. In general alpine environments are associated with hazard-prone environments caused by severity, seasonality, unpredictability, and fine-scale spatio-temporal variability (Franz 1979; Otto & Svensson 1982; Lencioni 2004; Wundram et al. 2010). In accordance with life history theory, several studies showed that under extreme environmental conditions smaller clutches with bigger eggs should be produced (Sibly & Calow 1986; Simpson 1995; Tanaka 1995; Tamate & Maekawa 2000; Hendrickx & Maelfait 2003). Both traits have been assumed to compete for limited maternal resources, resulting in the phenotypic trade off "bigger but less" (Smith & Fretwell 1974; Bauerfeind & Fischer 2008), but our results did not show a general coherence between high elevations and an adaptation in reproduction traits for *Pardosa*. Thus female size and, consequently, female fitness seems to explain most of the variations in reproduction in the different species. Theoretically, interrelationships between offspring size and female size are expected to influence both offspring and parental fitness (Clutton-Brock 1991; Marshall & Gittleman 1994; Bernardo 1996). However, earlier studies concerning wolf spiders had not found correlations between female size and egg or offspring size (Kessler 1971; Brown et al. 2003; Hendrickx & Maelfait 2003). This has been assumed to be a result of the strong food limitation in many species. Females are unable to produce normal or larger sized eggs or offspring, because of this limitation (Wise 1993, 2006; Brown et al. 2003). Other selective pressures such as feeding patterns, parent-offspring conflict, and environmental conditions, may be important constraints on egg size as well (Parker & Begon 1986; Klingenberg & Spence 1997). To gain further information on the essence of elevation related effects additional, comparable studies should be provided (Körner 2007). In this context the focus should also be on factors that are not closely related to elevation like habitat type, competition, and prey availability (e.g., Buddle 2000; Hendrickx & Maelfait 2003; Høye et al. 2009; Öberg 2009).

Høye et al. (2009) as well as Høye and Hammel (2010) showed that wolf spiders in a harsh arctic environment profit from longer seasons, resulting in a larger body size, with unpredictable impacts on future community structures. Our results show that general conclusions on elevation-dependent effects on prosoma width and reproductive traits are critical. Even though we found a decrease in prosoma width in *P. palustris* at Gråsida and Svarthovda, for Blåhø we did not. Findings on

spatial patterns of spider size obviously cannot be generalised without caution, since elevation related effects may be overlain by micro-climatic site conditions. Scherrer and Körner (2011) showed that micro-climatic site conditions might buffer the effects of increasing temperatures in alpine environments. Pape et al. (2009) showed the difficulties of modelling climatic conditions at specific alpine sites, where micro-climatic conditions are inadequately known. As we found no consistent trends along elevational gradients, we suggest future research to set stronger focus on the influence of micro-climate, behavioural adaptation, and competition on physiological traits of alpine wolf spiders. This will be necessary to fill the gap in understanding reproductive traits of Lycosid wolf spiders, and supply findings on the relation between a species physiology and its distribution. Consequently, these results raise new questions about adaptation strategies in female spiders to alpine environments. A more widespread species like *P. palustris* obviously copes with the alpine environmental conditions in a more sufficient way and has a higher phenotypic plasticity than other spiders of the genus Pardosa. An extensive phenotypic plasticity is assumed to be the reason why a certain species will persist in changing environments (Scharf et al. 2010). The knowledge of phenotypic plasticity in a certain species is imperative to gain information about the structure and assemblages of future ecosystems. We showed that adaptation strategies in closely related genera can be varied even at local scales.

Acknowledgements

CHAPTER 5: Alpine activity patterns of *Mitopus morio* (Fabricius, 1779) are induced by variations in temperature and humidity at different scales in Central Norway

Abstract

Our research addresses questions about how micro-climate affects activity abundances of a common and widespread harvestman in an alpine ecosystem. Activity patterns of the Harvestman *Mitopus morio* (Fabricius, 1779) were studied along different alpine gradients in the central Norwegian Scandes. Within a nested design, we surveyed 18 alpine habitats with pitfall traps and micro-climatological equipment along oceanic-continental, two elevational, and (fine-scaled) microtopographic gradients. Sites in the oceanic region of the Scandes showed generally higher abundance of *M. morio* than sites in the continental region. Furthermore, along the elevational gradient, middle alpine sites showed higher abundances than low alpine sites. These general patterns are best explained by higher humidity in the oceanic region and in the middle alpine belt, respectively. Focusing at a finer scale, i.e. one elevational level within each region, however, revealed partly opposing activity patterns within relatively short distances: While in the western middle alpine belt these patterns were again best explained by humidity-related measures, but now with higher activity abundance during drier conditions, in the drier eastern middle alpine belt heat sums rather than humidity were found to be the best explanatory variables for the observed patterns. Hence, our results imply a pronounced different reaction of the two populations towards climatic variables that partly even contradict the previously described general pattern. Regardless whether these differences in activity abundance in *M. morio* are a form of phenotypic plasticity or adaptation, our findings stress the importance of detailed autecological knowledge combined with fine-scaled climatic measurements when aiming at predictions about possible future ecosystem structures and spatio-temporal phenomena.

Introduction

Within the ongoing debate of mountain ecosystem responses to possible future climatic change, alpine habitats are expected to react very sensitively and probably faster than other ecosystems (ACIA 2004; IPCC 2007a, b; Löffler et al. 2011). Although a broad range of changes within ecosystems might be expected, long-term predictions and the effects of non-linear feedback (e.g. changes in plant communities, and thus expected ramifications in decomposition rates) within the system are difficult to state (Rial et al. 2004; Suttle et al. 2007; Wookey et al. 2009). Predictions of future niche construction and range dynamics in alpine areas under climatic change inhabit limitations because of the huge spatial variation along alpine toposequences and the complexity of climate controlled ecological mechanisms (Buse et al. 2001; Löffler et al. 2006; Pape et al. 2009; Wundram et al. 2010; Scherrer & Körner 2011; Scherrer et al. 2012). Various studies show that possibilities for a single species under a changing climate are either to inhabit a wider range of habitats than the current one, or to become extinct (Thomas et al. 2004; Chen et al. 2011; Huntley et al. 2012). In addition, there are further constraints (e.g. barriers) that are responsible for changes in range boundaries (Thomas 2010) which are not climate driven.

M. morio is a eurytopic species (Mitov & Stoyanov 2005). It has huge potential for research into invertebrate-climate relationships, because of its wide distribution and high trapping frequency (Slagsvold 1976). As one of the most common species in the alpine areas of Scandinavia, we assumed *M. morio* to be well suited as a model organism. *M. morio* is the most common harvestman species in Norway, and occurs everywhere from the lowlands up to the alpine areas and north to Nordland (Stol 2009). Osses et al. (2008) found evidence for clear temperature-determined activity abundance in one harvestman species (*Neosadocus maximus*, Giltay 1928). In the alpine environment of the Scandes, *M. morio* occurs in all habitats along the oceanic-continental range and along the elevational transect from the tree-line up to the highest elevations. *M. morio* is usually considered to be nocturnally active, with activity being closely connected to higher air humidity (Todd 1949; Hoenen & Gnaspini 1999). Unlike spiders, harvestmen do not have a waterproof cuticula. Drought stress during the day leads to higher activity during the night and/or during humid daytime conditions (Williams 1962). *M. morio* is a generalist predator, and feeds on a large variety of prey items (Adams 1984). It feeds on other harvestmen, snails, worms, spiders and flies, and is considered to act as a scavenger for dead material (Bristowe 1949; Todd 1949). Thus, harvestmen are one of the main invertebrate predators in terrestrial environments, especially those in alpine areas. However, Adams (1984) did not find any evidence of *M. morio* feeding on vegetable matter or fungi. M. morio is an annual species, and overwinters in the egg stage. Specimens of M. morio emerge in spring and usually die at the end of autumn (Todd 1949). T. Solhøy (pers. comm.) mentioned that some individuals probably also overwinter in an adult or immature stage, resulting in adult individuals in the pitfall traps early in the season. However, Bensetad and Hågvar (2011) found no activity of Opiliones in subnivean catches during winter.

The effects of climate change, and its ramifications for Scandinavia, are part of ecological research during the last decade. Kausrud et al. (2008) showed how climate-induced changes in the snow cover during winter affect mammal life cycles, and this has consequences e.g. for alpine food webs. Selås et al. (2011) found that there have been warmer summer months in Norway during recent decades, which is having a huge impact on the grouse population and the ecological interactions of the grouse. However, research on the effects of climate change on alpine invertebrates in Scandinavia is scarce. Our focus lies on climate - invertebrate interactions in alpine landscapes. The aim of our study was to define the activity patterns of the eurytopic species *M. morio* and its adaptation to climatic conditions along multiple alpine gradients. Hodkinson (2005) pointed out the possibilities of ecological research along elevational and latitudinal gradients providing clues about the response of species or communities to climatic change. For this reason, we established a network of high resolution monitoring and measuring systems areas along certain alpine gradients in Central Norway. Alpine habitats are known to be well-developed along toposequences, where ecological conditions (e.g. wind exposure, snow cover and duration, soil moisture and disturbance regimes) vary (Nagy & Grabherr 2009).

We expected to find spatio-temporal patterns of *M. morio* representing behavioral adaptation strategies concerning the activity in alpine habitats. We wanted to find out if it is possible to determine the importance of certain climate variables for the abundance of *M. morio* in alpine habitats. We expected different abundances at higher elevations because of the lower temperatures, higher precipitation, shorter season and overall more severe conditions. Moreover, continental climatic conditions on the eastern slope of the Scandes were expected to correspond to higher activity levels during warmer and longer seasons.

Material and methods

The sampling of *M. morio* and other ground dwelling arthropods in Central Norway followed a nested design. To cover the broad-scaled oceanic-continental differences caused by the meridional extension of the Scandes, two focal research areas were chosen (cf. Figure 5.1): The eastern, continental area of Vågå (Oppland, ca. 61° 53´ N; 9° 15´ E) characterized by very low annual precipitation of approximately 300-400 mm in the valleys and up to 600 mm in the alpine areas, and the western, oceanic area of Stranda (Møre og Romsdal, ca. 62° 03´ N; 7° 15´ E) characterized by annual precipitation of 1500-2000 mm. According to the classification system of Moen (1998), the Vågå area belongs to the "weak continental section", while the Stranda area is part of the "slightly oceanic section". The alpine environment expands from tree line at around 1030 m above sea level in Vågå (Stranda: 900 m) to the highest peak Mt. Blåhø at 1617 m above sea level (Stranda: Mt. Dalsnibba at 1476 m). Within the alpine environment of each focal area, two study areas, one located in the low alpine belt and one in the middle alpine belt, were chosen to account for medium-scaled elevational differences. In Vågå (Stranda), these areas are located at 1100 m (900 m) and 1450 m (1400 m) asl. To cover also micro-scaled topographical differences, within each study area the following sites were sampled, representing the most pronounced micro-climatic differences in the alpine environment (for a detailed description of the sampling sites see Naujok and

Finch 2004): A=ridges, B=depressions, C=southern exposed slopes, D=northern exposed slopes and E=late snow beds (Finch & Löffler 2010). Sites E were present in the middle-alpine belt, only. At each of our sites three pitfall traps were installed, resulting in a total of 54 pitfall traps at 18 sites (Vågå: low alpine 12 traps, middle alpine 15 traps; Stranda: low-alpine 12 traps, middle-alpine 15 traps). However, catches from all three traps per site were pooled in order to gain representative results from each sampling site. The traps made of glass were approximately 12 cm deep and 5.5 cm in diameter, and they had roofs to minimize the risk of flooding due to heavy rain. They contained a 4% formaldehyde solution (100 ml) as preservative. The surface tension was reduced by Agepon©. The traps were installed starting at 16th May (date depended on snow melt at the different sites) and were sampled at a fixed biweekly cycle until 3rd October 2002, resulting in a maximum of 9 trapping periods to cover temporal variations. Species identification followed Stol (1999). Activity of *M. morio* was provided as count data per site a), for each trapping period and b), aggregated over the entire sampling period. To assess the environmental conditions at each site, sub-surface temperatures at -1 cm depth were recorded as hourly mean values using automatic data loggers. In addition, data on precipitation (P) and relative humidity recorded by a meteorological station at ridge position were available for each of our four study areas. These climate data were used to calculate heat sums above various thresholds, precipitation sums and sums of the vapour pressure deficit for each trapping period and site. For heat sums, we used thresholds of >0° (H0), >5° (H5), >10° (H10) and >15°C (H15). While a threshold of >5° is expected to be biologically the most justified in alpine areas, at least for vegetation analysis (Scherrer and Körner 2011), Finch et al. (2008) successfully used heat sums with thresholds of >5° and >8.8°C to assess the temperature sensitivity of a grasshopper (Acrididae: *Melanoplus frigidus*) in an alpine environment. Since precipitation was recorded only at one site per study area, we were not able to differentiate among sites but assumed spatial variation in precipitation to be negligible due to the very limited spatial extent of our study areas of about 1-2 hectares. The sum of the vapour pressure deficit (VPDsum) was calculated for each site based on the relative humidity at ridge position and actual sub-surface temperature at the specific site using the Magnus equation of Sonntag (1990).

The significance of region (oceanic vs. continental), elevation within each region (low vs. middle alpine belt) and micro-topography within each elevational belt for the activity of *M. morio* was statistically tested by sub setting the aggregated data accordingly and using the corresponding variables as predictors in generalized linear models (GLM, Dobson 1990). To account for over-dispersed count data, we applied GLMs with a quasi-poisson link function. In a second step, the significance of each environmental variable for the activity of *M. morio* (aggregated over the sampling period per site) was assessed by applying one negative-binomial GLM for each environmental variable as predictor. To identify the best predictor, we used ANOVA of the full vs. the null model to test for the significance of the predictor in conjunction with Akaikes information criterion (AIC, Sakamoto et al. 1986) for the full model and McFadden's pseudo-r-squared (Long 1997).
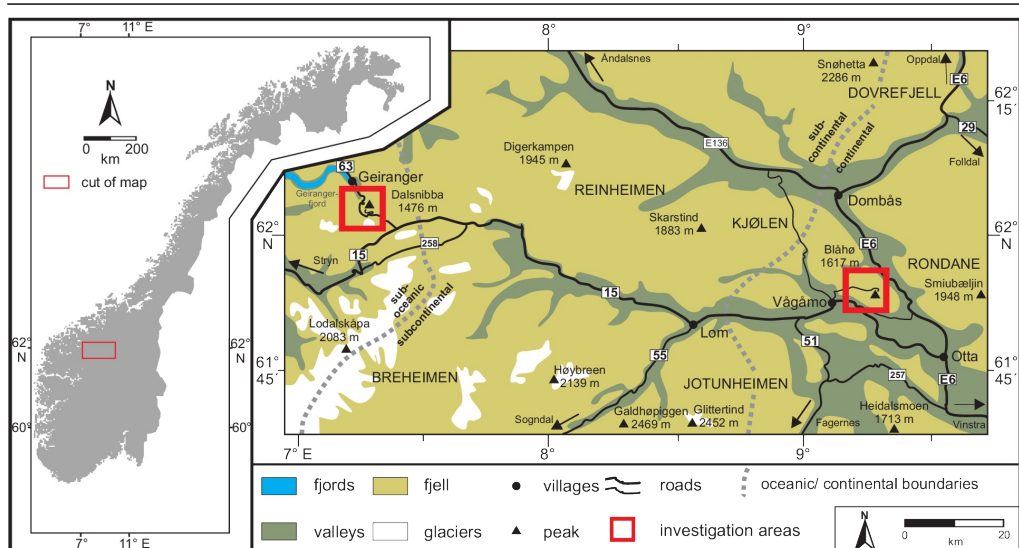
Figure 5.1 Map of Norway with focus on the two research sites Geiranger (Møre og Romsdal) and Vågå (Oppland) in central-southern Norway (after Löffler & Pape 2004).

Furthermore, the Vuong test for a goodness-of-fit-comparison between non-nested models (Vuong 1989) was applied. We used only one predictor in the GLMs due to i), a high collinearity of the environmental variables and ii), the risk of model over-fitting. In a third step, we assessed the effect of temporal variation within environmental variables on the activity of *M. morio* by setting up single-predictor GLMs with Poisson link function for each site, using each trapping period as one observation. Again, the best predictor was identified based on AIC and Vuong tests. All statistical analyses were conducted using R 3.0.0 (R Core Team 2013) with the libraries MASS (Venables & Ripley 2002) and pscl (Jackman 2012).

Results

During our sampling in 2002, a total of 4337 specimen of *M. morio* was sampled at the 18 sites. A more differentiated view (cf. Figure 5.2) revealed a significant effect of region ($p<0.001$), with much higher activity abundance in the oceanic west (3473 vs. 864 specimen), as well as elevation ($p<0.001$), with higher activities in the middle alpine belt both in the west (2634 vs. 839 specimen) and east (770 vs. 94 specimen). The effect of micro-topography was found to be significant ($p<0.05$) in the low alpine belt of both regions, only. Utilization of environmental variables as predictors for these observed general patterns identified humidity related measures, i.e. precipitation and vapour pressure deficit, to be most decisive: A GLM with VPDsum as predictor gave the best model with a pseudo-R^2 of 0.458 which proved to be significantly ($p<0.05$) better than models using heat sums as predictors. Accordingly, highest activity is to be expected at lower vapour pressure deficits (Figure 5.3). With regard to seasonal activity patterns of *M. morio* at each single site (Figure 5.2), models of activity abundance versus environmental predictors were only significant for middle alpine sites. In the west, again humidity related predictors were found to yield better models than those predictors related to temperature, but they showed the opposite effect compared to the case of general activity abundance patterns: At all sites, higher activity was correlated with drier

conditions, i.e., lower precipitation or a higher vapour pressure deficit. However, despite the lowest AIC, the Vuong test revealed these humidity related models not necessarily to be significantly better: only for site B (depression) and D (north-facing slope), the precipitation-based model was significantly better than (most) temperature-based models, whereas models were almost statistically indistinguishable at the other sites (cf. Fig. 5.2). In the east, the situation was just the opposite (cf. Fig. 5.3): Temperature-based models yielded the lowest AIC, indicating activity of *M. morio* to be more closely related to (higher) temperature than to humidity conditions. Except for site C (south-facing slope, which yielded the weakest model in terms of pseudo-R-squared), temperature-based models were even found to be statistically significantly better than their humidity-based counterparts (precipitation and/or VPDsum).
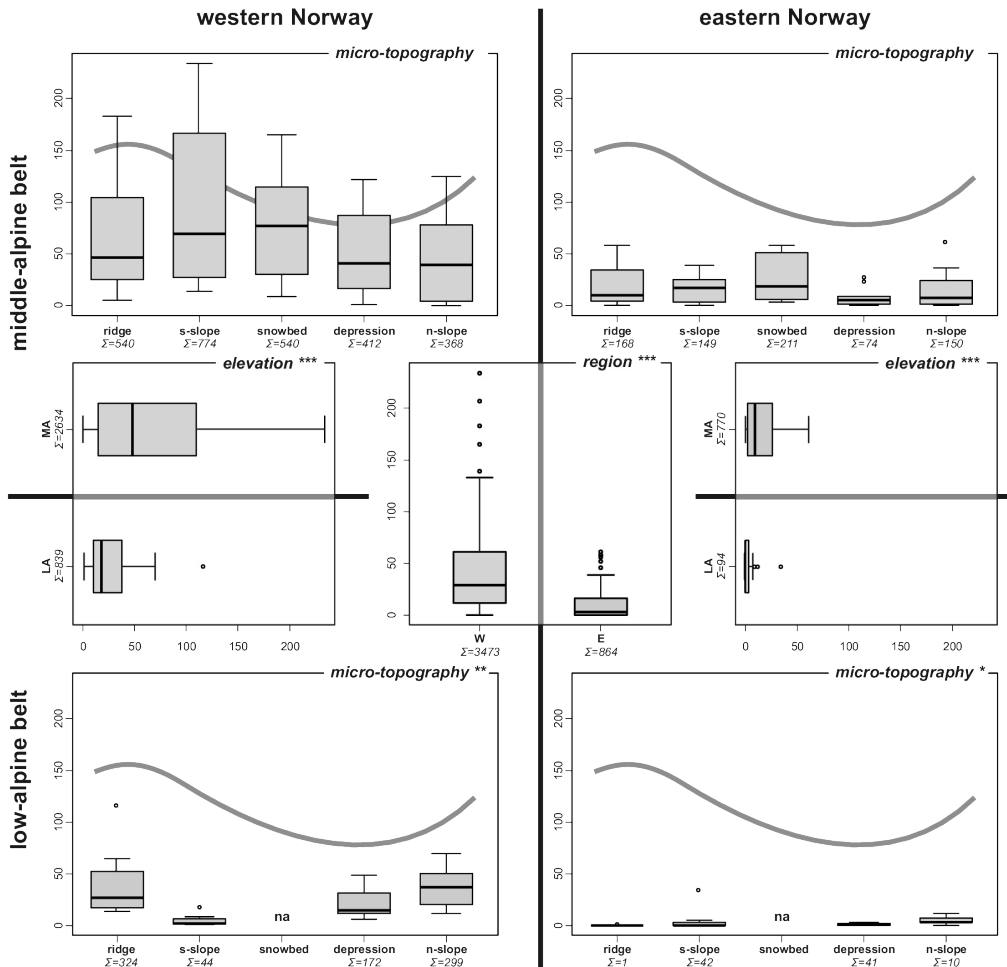

Figure 5.2 Activity abundance of M. morio in our investigation areas in central Norway, differentiated by region (oceanic vs. continental; in the center of the figure), elevation within each region (middle vs. low alpine belt; center left/right), and micro-topography within each elevational belt and region (in the corners of the figure). The total number of specimens for each level (region, elevation, micro-topography) is given, but also the variation among trapping periods is illustrated using boxplots. The statistical significance (p<0.001, p<0.05, p<0.1) of each level is illustrated using asterisks.

To summarize our findings: General activity abundance patterns of *M. morio* in Central Norway were found to be positively affected by higher humidity. However, under the generally moist conditions in the west the seasonal activity seemed to be dampened by a surplus of humidity, while activity in the drier east proved to be positively affected by higher temperatures but not at all by humidity.

Discussion

Our results show a clear climatically induced spatio-temporal pattern of *M. morio* along the gradients considered. In general (i.e. pooled over our entire data set), higher activity abundances of *M. morio* were related to the more humid sites of the oceanic west and/or the middle-alpine belt. The significantly higher activity abundance there is best explained by a low vapour pressure deficit sum (VPDsum). The overall patterns of total catches at our sites fit well with the data of Chatzaki et al. (2009), who found an increasing number of individuals at higher elevations on high mountains on Crete. They assume that species with a wide ecological range are able to reach higher elevations and build denser populations there. This pattern was also present in some Gnaphosid species along an elevation gradient on Crete (Chatzaki et al. 2005). The activity abundance of *M. morio* clearly peaked in August in our results. This activity pattern was also confirmed for seven non alpine habitats in Norway by Stol (2003), where the activity of *M. morio* also peaked in August. This might indicate that mating and egg-laying occurs during the same time period (Chatzaki et al. 2009). However, more detailed analyses at and across the different scales involved, revealed both, this general activity abundance pattern and that its driving forces are not consistent across different scales. Instead, our results imply a pronounced different reaction of the two populations towards climate variables in the oceanic and the continental research areas that partly even contradict the previously described general pattern. Even though activity abundance of *M. morio* at the oceanic middle alpine sites is again best explained by humidity-related measures, we found higher activity abundance now to be related to drier conditions. This is most likely due to the risk of being washed away during strong precipitation events. For the generally drier continental middle alpine sites, we found the activity of *M. morio* to be best explained by heat sums. Low temperatures rather than a lack of humidity seem to be the prevailing limiting factor at these sites, even though water loss is assumed to be one of the most limiting factors for species distribution in harvestmen (Hillyard & Sankey 1989; Pinto-da-Rocha et al. 2007). Our results support previous findings, but show also that at different scales (sometimes even at relatively short distances), strong climate related effects on the abundance of a single species in alpine ecosystems are visible.
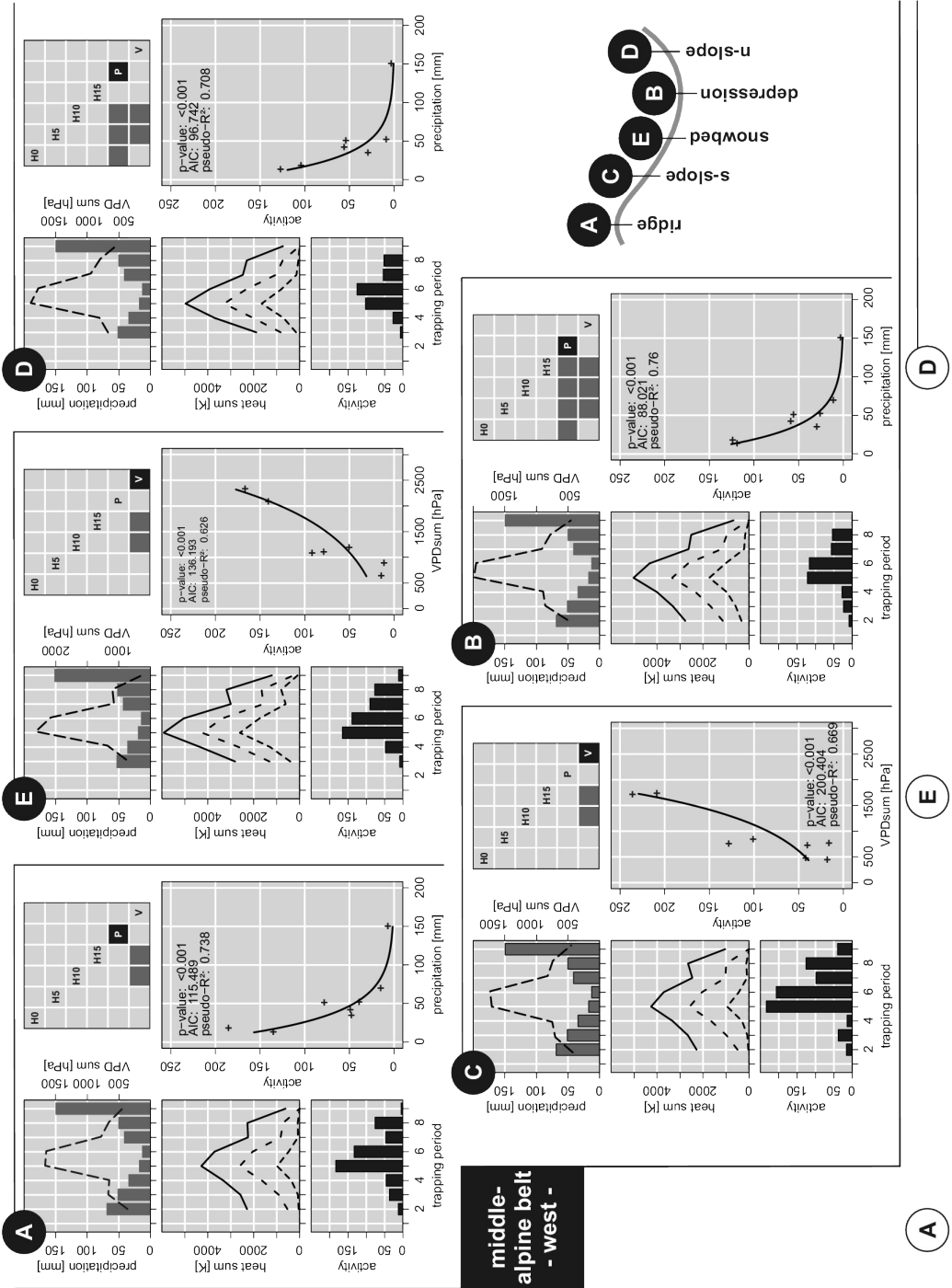
*Figure 5.3 Activity abundance of M. morio per site aggregated over the entire trapping period (lower left) compared to heat sums H0, H5, H10 (center left, top to bottom), precipitation (upper left, bars), and vapour pressure deficit sums (upper left, line). VPDsum as exploratory variable of the observed patterns yielded the best GLM with a pseudo-R² of 0.485, shown to the lower right. (text continued on following page)*
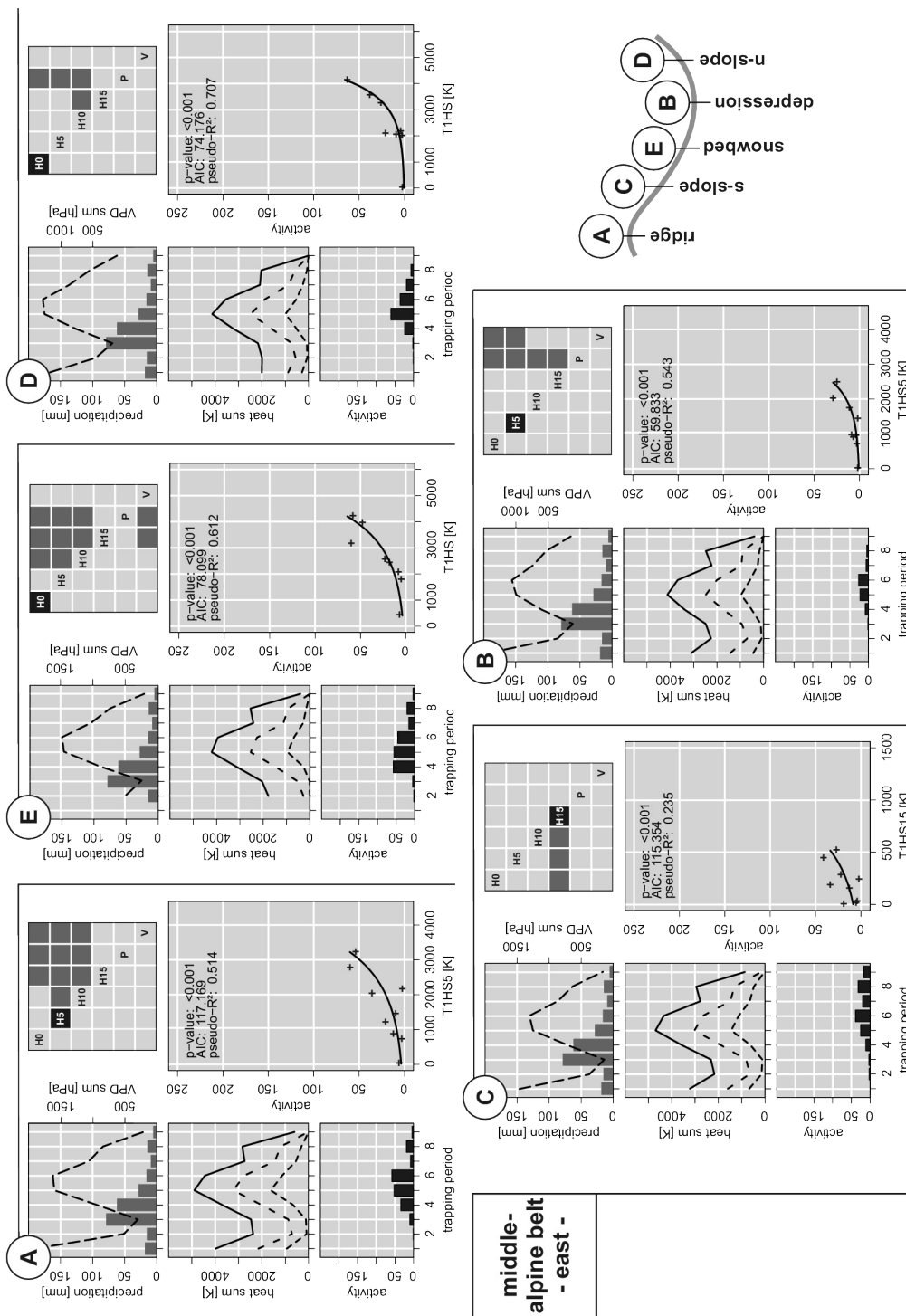
To the upper right, a model comparison matrix of all GLMs, i.e. being based on H0, H5, H10, H15, precipitation (P) and vapour pressure deficit sum (V), is shown. Dark grey shading indicates a significantly (p<0.05, based on Vuong test) better model, to be read as row versus column. The best model is indicated by a black filling.
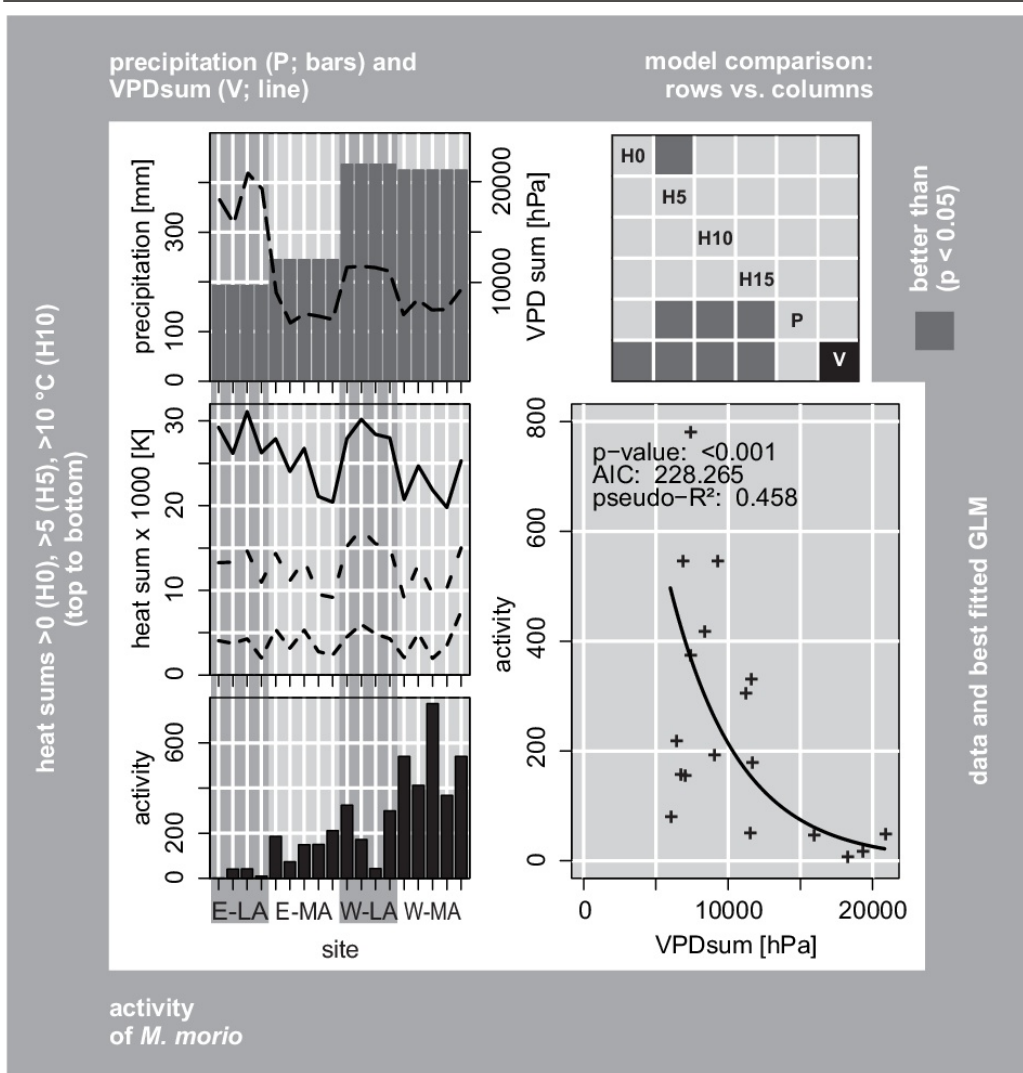
Figure 5.4 Activity abundance of M. morio in the middle alpine belt of western (top) and eastern (bottom) Norway for each site and trapping period. Graphs are arranged in the same way as in Fig. 5.3, i.e. for each site heat sums, precipitation and vapour pressure deficit sums are given and the best fitted GLM as well as the GLM comparison matrix are shown.

Our results suggest that climate change might have effects on a single species and thus on community structures in alpine areas at different scales. Changes in temperature and humidity induced by climate change will most likely effect the spatio-temporal activity patterns. Striking is that these effects might be of crucial differences within relatively short distances. Problematic is that the effects on the temporal variability of population cycles (e.g. Johnson et al. 2010) and other density-dependent population variables require constant monitoring. The estimation of extinction risk based on rising temperatures and humidity seems possible in very common species that also inhabit a wide range of habitats. However, some traits remain insufficiently displayed, since other factors (e.g. negative impacts on bene-

ficial species and positive impacts on harmful species) may affect a certain species long before its physiological tolerance is reached (reviewed in Cahill et al. 2012). Furthermore, it is not possible for us to verify whether these differences in activity abundance in *M. morio* are a form of phenotypic plasticity or adaptation. Provisional studies concerning the life history traits of *M. morio* might be beneficial in understanding how this species might react to a changing climate. Recent studies showed that it seems possible to draw conclusions about the future abundances of a species (e.g. Huntley et al. 2012). However, one problem of climate envelope modeling remains, that it has its limitations regarding the distribution of a species either because of underestimating non climate driven factors (Mustin et al. 2007) or because of the missing knowledge about the actual species range (Lawler et al. 2009). This can be of great importance when discussing the structure of alpine ecosystems under climatic change.

Temperature and humidity conditions are obviously a suitable variable to explain invertebrate abundances or distribution, even on a small scale in alpine habitats (Finch et al. 2008; Gillingham et al. 2012). Despite this fact, Pape et al. (2009) showed that there are problems with modeling near-surface temperatures in alpine habitats. The likelihood of uncertainties is quite high because of the huge number of variables involved (Wundram et al. 2010). In addition, our study implies that besides the importance of environmental data it is mandatory to gain knowledge about adaptation strategies and phenotypic plasticity of a certain species. However, the effects on ecological communities of global climatic change induced by humans are not yet well understood (Lorrilliere et al. 2012). In this context Huntley et al. (2012) recently showed that the effect of climate change on extinction risk might be underestimated in some cases. Recent observations of range boundary shifts correspond with the assumption that climate is one of the main driving forces, but it is not the sole determinant of the position of the range boundaries for the majority of terrestrial arthropods (Thomas 2010). Higher resolution data of both the biotic and the abiotic circumstances is crucial for making such predictions. Fine resolution temperature data, in particular, should be of special interest in alpine areas (Gillingham et al. 2012), since higher temperatures usually lead to higher and faster development in ectotherms (Willmer 1991; Willmer et al. 2005; Finch et al. 2008). The influence of single variables on certain organisms is possible, but the complexity of alpine habitats is difficult to represent. This leads to our conclusion that predictions about future ecosystem functioning requires constant monitoring of current autecological and environmental variables in the field.

CHAPTER 6: An oribatid species *Provertex kuehnelti* Mihelčič, 1959 (Acari, Oribatida) new to Fennoscandia

* While working on this manuscript, Torstein Solhøy passed away unexpectedly. He inspired us to undertake the present study and contributed many comments and suggestions. We dedicate this publication to the memory of this outstanding person.

Abstract

The soil living oribatid *Provertex kuehnelti* Mihelčič, 1959 was sampled for the first time in Fennoscandia in the western part of Norway at Dalsnibba (Møre og Romsdal). We found seven individuals in pit fall traps during the snow free period of 2009. The specimens were sampled on a ridge 1333.2 m asl. Between 15 July and 12 August 2009 three adults, one shell of an adult and three juveniles of *P. kuehnelti* were sampled. Up until now, the species was only known from alpine sites in Austria, Northern Italy and the Czech Republic. The distribution of *P. kuehnelti* should therefore be regarded as boreo-alpine.

Introduction

The implemented pit fall trap sampling is part of our long-term alpine ecosystem research project (LTAER) in Norway (for further information see e.g. Löffler 2003, 2005, 2007; Pape et al. 2009; Finch & Löffler 2010; Wundram et al. 2010). Here, we present our findings on *Provertex kuehnelti* Mihelčič, 1959, a species new to Fennoscandia. Altogether seven individuals of *P. kuehnelti* were found: MRI, Geiranger: Dalsnibba (UTM 32VL 409969.09 6879489.67) 15 July–12 August 2009, leg. N. Hein.

Provertex kuehnelti was originally described as *Provertex kühnelti* (regarding the correct name spelling see International Code of Zoological Nomenclature 2000: Chapter 7: Formation and treatment of names, Article 32.5.2.1.) from Eastern Tyrol, Austrian Alps (Mihelčič, 1959). A detailed re-description based on the type specimen and additional material is given by Krisper & Schuster (2009). Mihelčič (1966) describes *P. kuehnelti* as a saxicole species that prefers warm and dry habitats.

Material and methods

Due to the north-south extension of the Scandinavian Mountains Norway is divided into an oceanic and a continental part (Figure 6.1). Our research area "Geiranger" (Møre og Romsdal) is located in the western, inner-fjord area. The oceanic, western part of Norway is characterized by relatively high precipitation of around 1500–2000 mm (Moen 1999). According to Moen (1999) the area around Geiranger is part of O1 the „slightly oceanic section". Above the treeline, around 840m asl. the alpine environment covers an elevational low to middle alpine gradient up to the highest peak here: Mt. Dalsnibba, 1497 m asl. The transition zone between the low and middle alpine belt is situated around 1150 m asl.

Vegetation analysis was implemented with a frequency method. The frequency of a single species was determined by getting presence/ absence data of four single 1m² plots. Each plot was divided into 25 equally sized squares; the frequency was then determined by simply counting the squares in which a certain species occurred and consequently calculating the presence in percentages (Kratochwil & Schwabe 2001). Air and soil temperatures were measured at three different heights (+100 cm and +15 cm above, and -15 cm below ground level); while soil moisture was measured at the depth of -15 cm below ground level with the help of HOBO data loggers (Onset Corp., USA). For temperature measurements HOBO S-TMB-M002 sensors with an accuracy < ± 0.2° C were used. For soil moisture measurements, a HOBO S-SMA-M005 sensor with an accuracy of ±4% was used. The climatological results displayed in this paper are those from 1 January–31 December 2010, giving hourly mean temperatures and soil moisture values, respectively. To describe the overall habitat conditions including the minimum and maximum of a single variable during one year, we chose to discuss our findings with the climatological data from 2010. Three pitfall traps with saturated salt solution as a preservative and Agepon© as a detergent were installed at the sampling site during the snow free period from 21 May–23 September. Pitfall traps were emptied on bi-weekly basis and their content was transferred to 70% ethanol for preservation.
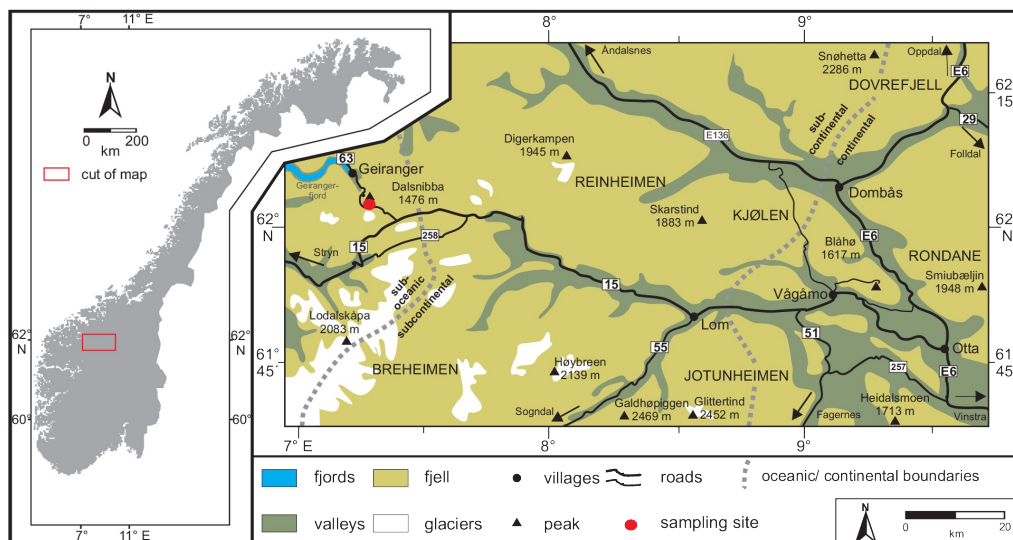
Figure 6.1 Map of Norway with focus on the research site at Dalsnibba near Geiranger (Møre og Romsdal)(after Löffler & Pape 2004). The sampling site at 62° 4′ 43′′ N, 7° 17′ 35′′ E where P. kuehnelti Mihelčič, 1959 was found is marked with a red dot.

Habitat description

The sampling site of *P. kuehnelti* is located at a ridge 1333.2 m asl. This elevation is part of the middle alpine belt in the western, oceanic part of Norway (Figure 6.1). The lichen coverage at this certain site is dense, but there is still some open ground and rocks. A lack of chionophilous species refers to little or no snow cover in winter (Table 6.1); this is supported by our near-ground climate data. Hourly means of air and soil temperatures and of soil moisture are displayed in Figure 6.2. The respective mean, minimum and maximum temperatures for 2010 are given in Table 6.2. The annual mean temperature is below -2° C. Especially the very low soil temperature of -14° C during winter indicates snow free conditions during periods of severe frosts. In addition, the annual temperature amplitudes at the three different heights are pronounced. The highest amplitude is found at +15 cm with almost 45 K. Here, the vegetation, open ground and rocks are influencing the near-ground air temperatures. At +100 cm this influence declines, which results in a lower amplitude of approximately 40 K.

The sampling site is located next to the road to the Dalsnibba peak, which is visited by a vast amount of tourists every year during summer. Reindeer grazing is also common in the area (Pape & Löffler 2012). Disturbance of the vegetation resulting in changes of the composition of species can therefore not be ruled out although not traced directly.

Table 6.1 Results of the vegetation analysis at the ridge site. Species frequency (%) is the mean of four different plots each of 25 subplots (=100) measured during 2009. The given height is the mean of the highest four individuals of a certain plant group that was present in one of the four vegetation plots.

| Species	Frequency (%)	Height (cm)
Shrubs		8
Salix herbacea	63	
Empetrum nigrum ssp. *hermaphroditum*	49	
Phyllodoce caerulea	18	
Grasses		35
Juncus trifidus	89	
Carex bigelowii	49	
Deschampsia flexuosa	10	
Festuca ovina	7	
Poa alpina ssp. *vivipara*	1	
Lichens		6
Cetraria ericetorum	100	
Cladina arbuscula	100	
Cetraria nivalis	86	
Stereocaulon spec.	80	
Cladonia spec.	71	
Cladina rangiferina	45	
Ochrolechia frigida	30	
Thamnolia vermicularis	27	
Cladina uncialis	17	
Cladina stellaris	7	
Cetraria cucculata	3	
Solorina crocea	2	
Mosses		2
Kiaeria starkei	80	
Conostomum tetragonum	39	
other Bryophytes	27	
Herbs		4
Hieracium alpinum	17	
Huperzia selago	7	
Rocks	20	
Open ground	8	
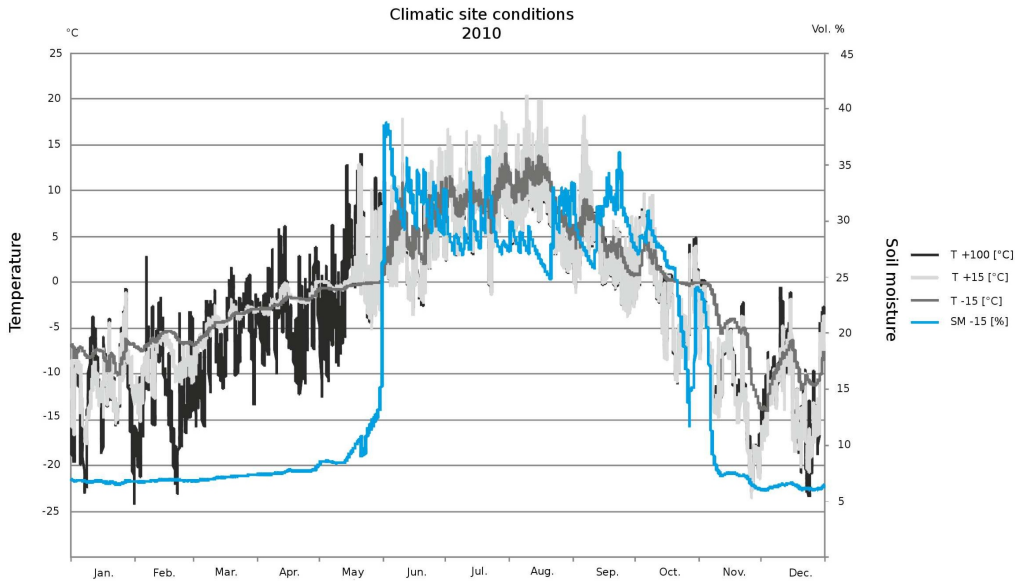
Figure 6.2. Near ground environmental conditions at the research site. Mean hourly air and soil temperatures [°C] as measured at three different heights, 100 cm above ground level (T+100), 15 cm above ground (T+15), in -15 cm depth (T-15) and soil-moisture in -15 cm depth (SM-15) [Vol.-%] are shown for the period from 1 January–31 December 2010.

Table 6.2 Annual mean temperatures for 2010 at the research site giving average annual means, minimum and maximum temperatures, as calculated from the hourly means. *Values for soil moisture were derived from those of the non-frozen period. We chose a temperature threshold of 0.5 ° C at -15 cm depth to define this period (31 May–16 October 2010).

	T+100 [°C]	T+15 [°C]	T-15 [°C]	SM-15 [Vol.%]
min	-24.0	-23.5	-14.0	17.1
mean	-2.7	-2.0	-0.4	29.7
max	16.8	20.3	14.0	38.7

Discussion

The results show that *P. kuehnelti* has to cope with periods of both relatively low/high temperatures and the risk of both desiccation and strong precipitation events. During winter, the prevailing wind speed leads to snow free ridges and snow accumulation in depressions. This can be seen in Figure 6.2, which reveals long periods (January–April and November–December) with soil temperatures below 0° C. The lack of snow cover during winter results in relatively low temperatures even at -15 cm depth. The overwintering conditions at a middle alpine ridge site in this area are severe, with a minimum temperature of -14 °C in 2010. Temperatures above 10 °C are reached several times during the summer. Temperatures at +15 cm often reach more than 15 °C. Thus, *P. kuehnelti* has to deal with high annual temperature amplitudes of around 40 K. Such amplitudes are well known phenomena in alpine environments (Barry 2008; Löffler et al. 2006). It is clear

that ridges represent one of the most extreme sites in the alpine environment (Löffler et al. 2006). *P. kuehnelti* obviously must have some remarkable adaptation strategies to cope with these severe alpine conditions. The results given here and former findings indicate that *P. kuehnelti* is euryoecious. Schuster (1997) found *P. kuehnelti* in Austria at a southern exposed slope in dry moss and lichen vegetation at the base of the Traunstein, an isolated calcareous mountain on the northern edge of the Alps in Upper Austria. In addition, this species inhabits crevices and in the Austrian Alps it has an altitudinal distribution from 480–2790 m asl (Krisper & Schuster 2001). Due to these facts, we expect *P. kuehnelti* to inhabit a wider range of alpine habitats in Fennoscandia.

According to Weigmann (2006), this species was known from Austria and the Czech Republic. Mihelčič (1966) reported additional records from xerothermous sites in the Italian Karst near Trieste and Gorizia. Recently, *P. kuehnelti* was also found in the Dolomite Alps (Prov. Bolzano, Northern Italy) on the Sciliar massiv at 2250 m asl in a cushion plant (Schatz 2008). Our new findings indicate a boreo-alpine distribution for *P. kuehnelti*. Boreo-alpine refers to a disjunctive distribution with a southern and northern areal. Species with a boreo-alpine distribution usually populate high elevation sites in the southern or middle European mountains. In the northern area these species usually populate the lowlands, even though some boreo-alpine species may occur at high elevation sites in both the southern and the northern areal (Holdhaus 1912). The statement of Subías (2004) concerning distribution of *P. kuehnelti* in Central and South Europe ("Europa centromeridional") is not correct. No records from South Europe are known; probably this statement refers to the findings in the Northern Italian Alps.

Acknowledgements

CHAPTER 7: Conclusion

The focus of this thesis has been to identify patterns of spatial and temporal variability of alpine tundra arachnids within a multi-scale approach. Thus far, alpine tundra ecological research has often described habitats for specific arachnids along a single elevational gradient or in relation to, as typically defined, alpine habitats. This thesis presents an initial approach that follows a conceptual multi-scale design developed for ecological research along various gradients in alpine tundra ecosystems. The conceptual design was introduced to cover scale-specific heterogeneity of alpine tundra ecosystems and aspired to enable further research on species preferences along environmental gradients, with special emphasis on fine-scale phenomena, the spatial and temporal scale inhabited by arachnids.

Due to the multi-scale sampling design, this study was able to define and characterize spider assemblages and their spatial patterns in relation to multiple environmental conditions. Most intriguing was the fact that the spatial patterns of spider assemblages were obviously more influenced by the local environmental conditions than by the broad scale conditions, expressed by continentality in this study. By means of the multi-scale approach, the influence of certain sets of environmental variables on alpine tundra arachnid assemblages was detectable. In regard to the fine-scaled topography of the alpine tundra, typical spider assemblages and indicator species could thus be identified. The definition of several indicator species and the typical aspects of their fine-scaled assemblage patterns will enable the use of high-resolution species-specific data in environmental change related research. However, micro-climatic conditions need to be monitored to define environmental indicators more precisely, which are most important for the assemblage habitats at these scales.

Besides the depiction of the spatial distributional pattern of *Paradosa palustris*, it was possible to identify significant differences in life history traits along various gradients within this distribution. The assumption that spider size would decrease with elevation is not true consistently. On the broad scale of our concept, the populations of *P. palustris* showed, in the oceanic as well as in the continental research area, pronounced differences in body size. This is most likely due to differences in life-cycle traits in the two populations. Specimens sampled in the eastern continental research area were significantly bigger, most likely due to slower growth. Affirmatively, this thesis found indicators for a prolonged life-cycle in the continental research area due to differences in the environmental conditions. Furthermore, the study provides findings on sex-specific variation in body size along elevational and topographic gradients. In particular, differences along the fine-scaled topographic gradient expressed by differences in season length at ridge sites and southern exposed slopes were identified to have a significant influence on spider size. Yet, females of *P. palustris* were affected by the environmental conditions along the elevational gradient only at southern exposed slopes to a significant degree, resulting in smaller specimens at higher elevation. Therefore, the prevalent assumption, that the size and thus the fitness and fecundity of spiders are conditioned by elevation cannot be fully abided. In regard to the sex-dimorphism, this is most

likely a result of different reproductive roles in females and males, assuming that males occupy a more active role during periods of mating. Furthermore, whether the differences in spider sizes along environmental gradients are a result of phenotypic plasticity or adaptation cannot be yet discerned.

Since it is a well known fact that parental fitness influences offspring fitness to a huge degree, further knowledge about the trade-off between maternal fitness and offspring fitness is imperative for the understanding of adaptation to worsening environmental conditions. In this context, this thesis provided the first approach to identifying species-specific adaptation strategies towards increasing elevation in a closely related spider genus. However, when focusing on the reproductive traits of five abundant spider species of the genus *Pardosa*, no pronounced fellow trait along the elevation gradient was found. In response to assumed harsher environmental conditions at higher elevations, no general influence on maternal size, egg number and egg size was detectable. The assumption that females would tend to produce bigger eggs but smaller clutches at higher elevations, due to the harsher environmental conditions in this area, was not confirmed. Moreover, the different species showed pronounced different strategies towards higher elevation, regarding size, egg number and egg size along the three elevational transects. Obviously, even closely related species show no consistent reproductive traits along elevational gradients. This implies that general statements on the influence of increasing elevation, and its inherent variables, on reproductive traits are difficult to validate. This highlights the importance and inclusion of environmental variables such as climate and competition in multi-scale approaches to specify species reactions along environmental gradients.

With focus on the most abundant ground dwelling arachnid captured in this study, the opilionid species *Mitopus morio*, an approach to embed fine-scaled environmental climatic conditions in the identification of activity patterns within the multi-scale design was generated. First, the activity abundances of *M. morio* were identified. Due to the measured climatic characteristics it was then possible to identify the climatic constraints on abundances of *M. morio* within our multi-scale approach. On a broad scale, higher abundances of *M. morio* were positively correlated with humidity resulting in higher abundance of *M. morio* in the western oceanic research area. However, fine-scaled specific activity abundances showed diverse reactions to micro-climate and were best explained either by heat sums or by the occurrence of precipitation events. Thus, a superimposition of climatic variables at different scales was detected due to the high resolution results of this study. The somehow contradictory result in the two populations of *M. morio* underlines the importance of measured climatic variables when focusing on species-environmental interactions.

Due to the unique sampling design and the consequential huge sampling total of epigeic arthropods, a new species could be confirmed for Fennoscandia. So far *Provertex kuhnelti* has only been detected in the alpine tundra ecosystems of southern Europe. An accurate habitat description regarding the environmental conditions is given for *Provertex kuhnelti* which has to deal with alpine tundra ecosystems. Consequently, *P. kuhnelti* is assumed to have a boreo-alpine distribution.

To conclude, this thesis provides new findings that answer questions regarding the spatial patterns of Aranchids in alpine tundra ecosystems, and reflects several theories regarding species-specific life history traits that are assumed to play an important role in habitat preferences of species. Due to the multi-scale approach and scale specific sampling along three environmental gradients it was possible to identify driving forces for species annidation and the impact of environmental parameters on life history and reproductive traits. Overall, this thesis underlines the importance of fine-scaled, measured environmental parameters for the understanding of alpine tundra ecosystems.

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Hein N, Finch OD, Löffler J (01/2009) Adaptation in Reproductive - traits of Lycosidae to High-mountain areas (poster). AK Hochgebirge annual conference, Heidelberg

Hein N, Finch OD, Löffler J (11/2008) Wolfsspinnen in Mittelnorwegen (talk). AK Norden annual conference, Bremen

Hein N, Finch OD, Löffler J (10/2008) Invertebrate Adaptation to High - mountain areas (poster). IALE-D annual conference, Bonn

Hein N, Löffler J, Finch OD (05/2008) Adaptation in Lycosid - Reproductive traits along an alpine/altitudinal gradient in Central-Norway (talk). AK Biogeographie annual conference, BfN-Akademie, Vilm

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Hein N, Solhøy T, Schatz H, Löffler J (2013) An orbatid species *Provertex kuehnelti* Mihelčič, 1959 (Acari, Orbatida) new to Fennoscandia. Norwegian Journal of Entomology 60: 163–168

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