SNOW COVER DETERMINES THE ECOLOGY AND BIOGEOGRAPHY OF SPIDERS (ARANEAE) IN ALPINE TUNDRA ECOSYSTEMS

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With 5 figures, 2 photos, 1 appendix and 1 supplement
Received 29. December 2013 · Accepted 06. May 2014

Summary: This study addresses the spatial distribution of spiders (Araneae) in relation to their environment along multiple ecological and biogeographical gradients. Two study regions representing considerable variation in the alpine climate were sampled for epigeal spiders using pitfall traps: one in the oceanic region and one in the continental region of Norway. We aimed to identify the driving forces for spider species annidation in an alpine tundra ecosystem using a multi-scale approach. During the snow-free season in 2009, we sampled 6,628 adult specimens at 73 sampling locations. These data and additional information from previous studies on spider habitat preferences were used to examine the features of the species' spatial distribution. We analysed our data set using ordination space partitioning (Isopam), which relies on hierarchical partitioning of the ordination space. This method is based on a hierarchical classification of the sampling locations according to their species composition and results in classes that can be distinguished by indicator species. The aggregated classes and their spatial patterns could be linked to snow cover. Local climatic conditions had a stronger influence on spider biogeography than did broad-scale climatic conditions. We identified various indicator species for typical alpine tundra habitats that could be described as either 'chionophobous' or 'chionophilous', depending on the topography-related snow cover at the sites where they occurred. Through this multi-scale approach, this study is the first to demonstrate the importance of snow-cover patterns on the ecology and biogeography of spiders in alpine tundra ecosystems.

Zusammenfassung: Diese Studie untersucht Webspinnen (Araneae) und ihre räumlichen Verteilungsmuster in Bezug zu ihrer Umwelt entlang verschiedener ökologischer und biogeographischer Gradienten. Die epigäische Webspinnenfauna zweier alpiner Untersuchungsgebiete, die sich aufgrund ihrer klimatischen Bedingungen erheblich voneinander unterscheiden, wurde mit Hilfe von Bodenfallen untersucht. Eines der Untersuchungsgebiete befand sich im westlichen, ozeanisch geprägten Teil Norwegens, ein weiteres im östlichen, kontinental geprägten Teil Norwegens. Unser Ziel war es, die Kontrollfaktoren für die Einnischung einzelner Webspinnenarten in alpinen Tundraökosystemen unter Verwendung eines multiskaligen Ansatzes zu identifizieren. Während der schneefreien Periode im Jahr 2009 wurden insgesamt 6,628 adulte Individuen an 73 Standorten gefangen. Diese Daten sowie Erkenntnisse früherer Studien wurden verwendet, um Charakteristika der räumlichen Verteilung der vorhandenen Webspinnenarten zu untersuchen. Zur Analyse des Datensatzes wurde der Ordinationsraum der Standorte mit Hilfe des Isopam-Algorithmus unterteilt. Diese Methode basiert auf einer hierarchischen Einteilung der Standorte anhand ihrer Artenzusammensetzung und ergibt Klassen, die über Indikatorarten abgegrenzt werden können. Die aggregierten Klassen und ihre räumliche Verteilung konnten als direkte Folge der Schneebedeckung identifiziert werden. Die lokalen klimatischen Bedingungen erklärten die Zusammensetzung der Webspinnen-Gemeinschaften besser als die großräumigen klimatischen Bedingungen. Weiterhin konnten mit der Isopam-Methode verschiedene Indikatorarten für die kleinräumigen alpinen Tundrahabitate bestimmt werden. Diese Indikatorarten können entsprechend ihres Vorkommens als ‚chionophob' oder ‚chionophil' beschrieben werden. Auf Basis unseres multiskaligen Ansatzes konnten wir erstmals zeigen, dass auch die Ökologie und Biogeographie von Webspinnen einem übergeordneten Schneedeckengradienten folgt.

Keywords: High mountain research, arctic-alpine environment, snow ecology, multi-scale approach, Norway

1 Introduction

A main characteristic of the alpine belt is its clear organization along toposequences (Nagy and Grabherr 2009) that display the 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 for a global monitoring system (e.g. Welker et al. 2001; Löffler and Finch 2005; Sergio and Pedrini 2007). Furthermore, understanding the processes that determine the assembly of local communities remains a key objective of both community ecol-

DOI: 10.3112/erdkunde.2014.03.01 ISSN 0014-0015 http://www.erdkunde.uni-bonn.de

ogy and biogeography (Hortal et al. 2012). In this context, Hodkinson (2005) highlighted the great potential of using terrestrial arthropods and their distribution along spatial and temporal gradients in the alpine belt to reveal how climate warming might affect the distribution of certain species and the community structure. Interest in environmental effects on epigeal arthropods has recently increased due to the observed changes in arctic and alpine habitats (ACIA 2004; IPCC 2007a, b; Høye et al. 2009; Høye and Hammel 2010; CAFF 2013). Spiders (Araneae) offer outstanding features to characterise the spatio-temporal patterns and abundance of single species among the wide range of habitats that are occupied (Uetz 1976; Wise 1993; Finch and Löffler 2010; Legault and Weis 2013). Furthermore, spiders constitute one of the most abundant compartments of alpine invertebrate communities and represent a huge potential for estimating alpine species diversity (Finch and Löffler 2010). They strongly depend on environmental factors (Schaefer 1970; Frick et al. 2007) and have relatively small areas of activity in comparison to mammals and birds.

The alpine region provides considerable spatial variation and a large number of potential niches and habitats for invertebrates (Mani 1968; Franz 1979). Communities present at certain locations along alpine elevational gradients are expected to show pronounced differences with respect to their species-specific niche dimensions (Otto and Svensson 1982), and spiders are assumed to be one of the most suitable groups to study and monitor species diversity in terrestrial ecosystems, especially at high latitudes (Marusik and Koponen 2002). In addition, alpine tundra ecosystems and the diversity of their fauna have repeatedly been proposed as good indicators of environmental change (Grabherr et al. 1995; Bowman 2001; ACIA 2004).

To learn more about the driving force behind the annidation of alpine epigeal invertebrates, we used a multi-scale approach to focus on the spatial patterns of spiders along three different gradients (Löffler et al. 2006): (1) a macro-scale gradient, represented by the strong climatic differences between oceanic and continental Norway (Moen 1998); (2) a meso-scale gradient, represented by elevation and its inherent environmental changes at higher elevations, e.g. a 5.5 K decrease in air temperature for every 1 km of elevation (Barry 1981); and (3) a topographic gradient, represented by four typical alpine habitats (ridges, depressions, and southern- and northern-exposed slopes). Together, these habitats display the strongest differences in alpine environments within relatively short distances (Franz 1979; Dahl 1986; Löffler and Finch 2005).

Our main study aim was to analyse the spatial distribution of spiders based on climatic differences along gradients between and within the two study regions in oceanic and continental Central Norway under the assumption that alpine tundra ecosystems would allow for the identification of typical spider assemblages along the three gradients of our focus. We also aimed to determine indicator species typical for the habitats in alpine tundra ecosystems, with a special emphasis on their potential use for long-term monitoring.

2 Methods and materials

2.1 Study sites

Two regions were selected for this study to cover the broad-scaled oceanic-continental differences caused by the meridional extension of the Scandinavian mountain chain (Fig. 1). The western oceanic study region (Stranda; ca. 62°03' N, 7°15' E; Møre og Romsdal) is characterised by an annual precipitation of 1,500–2,000 mm, whereas the eastern continental study region (Vågå; ca. 61°53' N, 9°15' E; Oppland), is characterised by a very low annual precipitation of only 300–400 mm (Moen 1998). The Vågå region belongs to the 'weak continental section', and the Stranda region is part of the 'slightly oceanic section'. As described by Dahl (1986), the alpine elevational zonation is differentiated into distinct low-alpine and middle-alpine belts in both regions. The low-alpine belt is dominated by dwarf-shrubs and heathers such as *Betula nana*, *Empetrum hermaphroditum*, and *Vaccinium myrtillus*, whereas the middle-alpine belt is dominated by graminoids such as *Juncus trifidus*, *Carex bigelowii*, and *Luzula confusa*. In Stranda, the treeline is at approximately 750 m a.s.l., while it is at approximately 1,030 m a.s.l. in Vågå. The upper limit of the low-alpine belt is found at approximately 1,200 m a.s.l. in Stranda and at approximately 1,350 m a.s.l. in Vågå. The highest peak in the Stranda oceanic study region is Mt. Dalsnibba (1,495 m a.s.l.), and in the Vågå continental study region, it is Mt. Blåhø (1,618 m a.s.l).

In accordance with Löffler (2002), the specific snow-cover dynamics in alpine tundra ecosystems in Scandinavia can be described as annual variations of air and soil temperatures strongly dependent on snow cover in response to the topographic position. Alpine

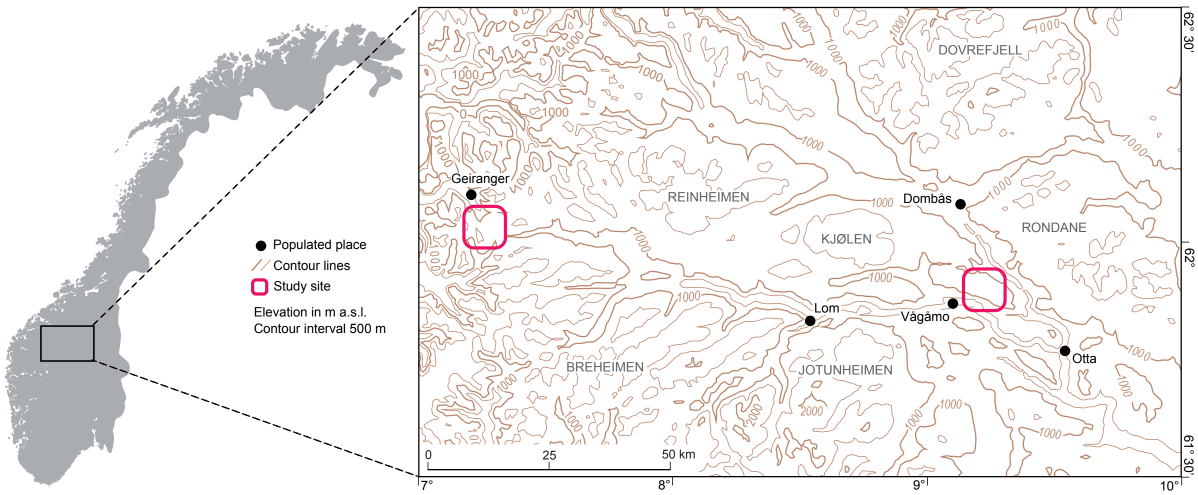

Fig. 1: Map showing the two study areas in the western, oceanic region (Stranda) and in the eastern, continental region (Vågå) of Norway

ridge sites commonly feature no or only minimal snow cover during long periods of the winter, and thus they often experience strong frost events penetrating deep into the ground. Minimum soil temperatures below -10 °C are often measured during the winter at snow-free alpine ridge sites (Photo 1). Such strong frosts appear more often at low-alpine ridge sites than at middle-alpine ridge sites due to the commonly thicker snow cover at the higher elevations (Löffler 2003). In contrast to the ridges, the alpine slopes and depressions are covered by thick snowpack, isolating the ground from extreme winter temperatures; the longest lasting snow cover is found at the leeward sites (Photo 2). The snow-cover dynamics not only show elevational variation, but are also tightly linked to the overall topography.

2.2 Trapping

We collected epigeal arthropods during the snow-free period of 2009 along two elevation gradients; one in the oceanic region of Norway, and one in the continental region. Epigeal arthropods were collected from the treeline to the highest peaks from a total of 73 (oceanic, *n* = 32; continental, *n* = 41) sampling locations. The range in elevation of the sampling locations extended from 767 m a.s.l. to 1,488 m a.s.l. in the oceanic region, and from 1,029 m a.s.l. to 1,609 m a.s.l in the continental region. Each sampling location was described by its exact elevation in m a.s.l. and by its topographic position. The elevation (m a.s.l.) of the sampling locations was measured using differential GPS equipment. We conducted our sampling along a

Photo 1: Typical alpine snow-cover pattern in the eastern continental study region during April. The photo is taken from a middle-alpine site at around 1,400 m a.s.l. Alpine ridge sites are snow-free, while slopes and depressions are covered by thick snowpack (Hein 2013).

Photo 2: Typical alpine snow-cover pattern in the eastern continental study region at the end of May. The photo is taken at a middle-alpine site at around 1,465 m a.s.l. Sites with the longest lasting snow cover are the lee slopes. Here, it is mainly the southern-exposed slopes that are still covered by thick snowpack (Hein 2013).

subsystem of the elevational gradient in the four different toposequences ('ridge', 'southern-exposed slopes', 'northern-exposed slopes', and 'depression') displaying the strongest environmental differences within short distances in alpine environments (Löffler 2005). We labelled the sampling locations (Fig. 2) of the oceanic study site with a W and the sites of the continental study site with an E, with each sampling location identified by an A (ridges,) B (depressions), C (southern-exposed slopes) or D (northern-exposed slopes). As soon as they became snow-free, three pitfall traps were installed as described by Naujok and Finch (2004) at each sampling location using a saturated salt solution as the preservative and Agepon as the detergent. The collected material was emptied on a bi-weekly basis and transferred to 70% ethanol for preservation. There were ten sampling periods from 20 May to 3 October 2009 in Stranda and eleven sampling periods from 28 April to 29 September 2009 in Vågå. Pitfall trap catches are assumed to indicate the density and abundance of the particular species. Although pitfall trapping is often criticised as being biased towards ground-living species and males due to their higher activity during reproductive periods (Merrett and Snazell 1983), the method provides a reliable measure of the total number of spider species present at a particular site (Uetz and Unziker 1976). Furthermore, pitfall traps are believed to reliably reflect the abundance of most species (Topping and Sunderland 1992). It is also one of the most suitable sampling methods in rocky environments (Finch and Löffler 2010), especially in alpine habitats, and has proven suitable for alpine regions in a variety of epigeal fauna studies (e.g. Hauge et al. 1978; Hauge and Refseth 1979; Otto and Svensson 1982; Chatzaki et al. 2005; Hein et al. 2013). Adult spiders were determined as described by Almquist (2005, 2006), Nentwig et al. (2013) and Roberts (1987, 1995), and the nomenclature used is that of The World Spider Catalog v14.0 (Platnick 2013).

2.3 Statistical analysis

To balance the sampling effort for the sites, the collected material was standardised to the number of individuals caught per 100 trapnights. We used linear regression models to analyse the species-specific

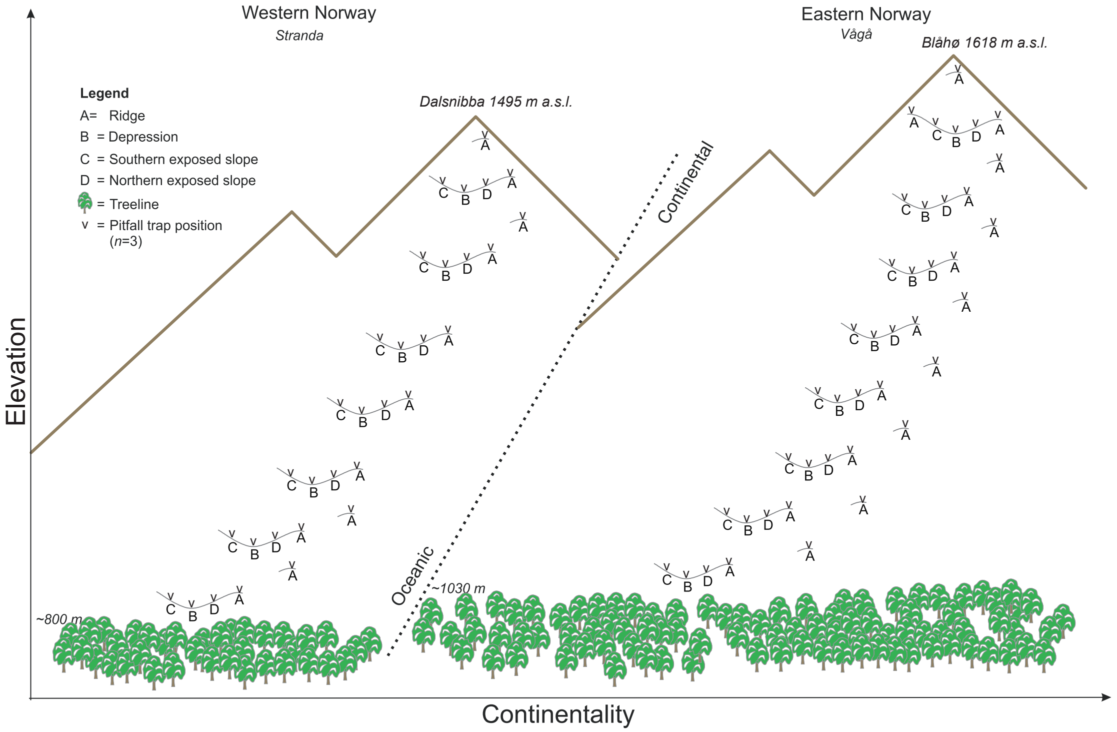

Fig. 2: Design of the high resolution monitoring network used along three different gradients. The specific sampling locations equipped with pitfall traps along these gradients are shown. The broad-scale climatic gradient is covered by two research regions, one situated in the oceanic western portion of Norway (W, Stranda) and one in the continental eastern portion of Norway (E, Vågå). The elevational gradients cover sites from the treeline up to the highest peaks. The fine-scaled topographic gradient covers four different positions: A, ridges; B, depressions; C, southern exposed slopes; and D, northern exposed slopes (Hein 2013).

abundance along the elevation gradients for all spiders (Araneae) and for the two most abundant families (Linyphiidae and Lycosidae). To avoid the risk of Type I errors, the significance of all model fits were Bonferroni corrected (Holm 1979; Rice 1989). For the analysis of the species composition at the sampling locations, the species-specific abundances were corrected for the number of trapnights to avoid over- or underestimating the abundances.

We used the Isopam classification algorithm (Schmidtlein et al. 2010) to analyse the species composition of the spider fauna at the alpine sampling locations. This algorithm relies on the hierarchical partitioning of an ordination space and results in species classes that are significantly typical for a certain location. The flexible and non-linear Isomap algorithm (Tenenbaum et al. 2000) was used for the ordination. Isomap is based on geodesic distances that are, in our case, derived from Bray-Curtis distances. Partitioning around medoids (PAM) (Kaufman and Rousseeuw 1990) subsequently delineates the classes in the ordination space. The parameterisation of Isomap and the subsequent classifications are optimised in an iterative approach to determine classes that are separated by a distinct set of species with a maximised indicative value (*phi*). These indicator species are determined based on the classification, whereas the candidate classifications are based on the entire set of species. The choice of a number of classes to ensure good differentiation can be included in the optimisation procedure. Furthermore, medoid samples are provided that represent the centre or most typical sample of a class. Isopam is provided as a package for R (R Development Core Team 2011).

3 Results

Altogether, more than 55,000 invertebrates (Araneae $n = 9{,}726$; Stranda $n = 3{,}459$ and Vågå $n = 6{,}267$) were sampled during 8,631 trapnights in Stranda and 13,065 trapnights in Vågå. Only adult spiders were identified to the species level (juveniles were excluded), leaving 2,649 adult specimens in the oceanic study region (Stranda) and 3,979 adult specimens in the continental study region (Vågå). 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 in both the oceanic and continental study regions (Fig. 3a, b). In the western oceanic region, 53 linyphiid and 8 lycosid species were sampled, whereas in the eastern continental region, 64 linyphiid and 12 lycosid species were sampled. In both cases, they corresponded to more than 75% of all species sampled. Notably, the number of lycosid specimens was greater than the number of linyphiid specimens in the continental study region, a relationship that was reversed in the oceanic study region (Fig. 3c, d).

The linear regression between the abundance of species and specimens and the elevational gradient in the continental study sites showed only one significant ($p < 0.05$) relationship; in Vågå, the number of lycosid species decreased significantly with increasing elevation. No other traits were significantly correlated with elevation (Figs. 4 and 5). However, we found peaks of species richness at approximately 1,100 m a.s.l. and 1,300 m a.s.l. in the oceanic and continental study regions, respectively.

The sampling locations and the representative spider species were grouped into three classes and four subclasses by the Isopam algorithm (Appendix 1). The classes, which are exclusively based on species composition, featured clear environmental characteristics (Supplement I).

Class 1 aggregated subalpine and low-alpine sites in both study regions. The class (medoid E1086C) consisted of 22 sampling locations and was further divided into Subclasses 1.1 (medoid E1086C) and 1.2 (medoid W773C).

Subclass 1.1 included subalpine and low-alpine sites with southern exposed slopes that reached, but did not extend above, the transition zone between the low-alpine and middle-alpine belts. This subclass contained 15 sampling locations, with more continental sites ($n = 10$) than oceanic sites ($n = 5$). The elevational distribution of the sites in this class ranged from 841 m a.s.l. to 1,125 m a.s.l. in the oceanic study region and from 1,029 m a.s.l. to 1,310 m a.s.l. in the continental region. In both study regions, the highest elevations for the subclass were on southern-exposed slopes. Seven indicator species were typical for these sites (defined *post-hoc* by the Isopam algorithm): *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).

Subclass 1.2 included typical subalpine and low-alpine sites in the two study regions. This subclass consisted of seven sampling locations, five oceanic sites and two continental sites. The elevational distribution of these specific sites ranged from 767 m a.s.l.

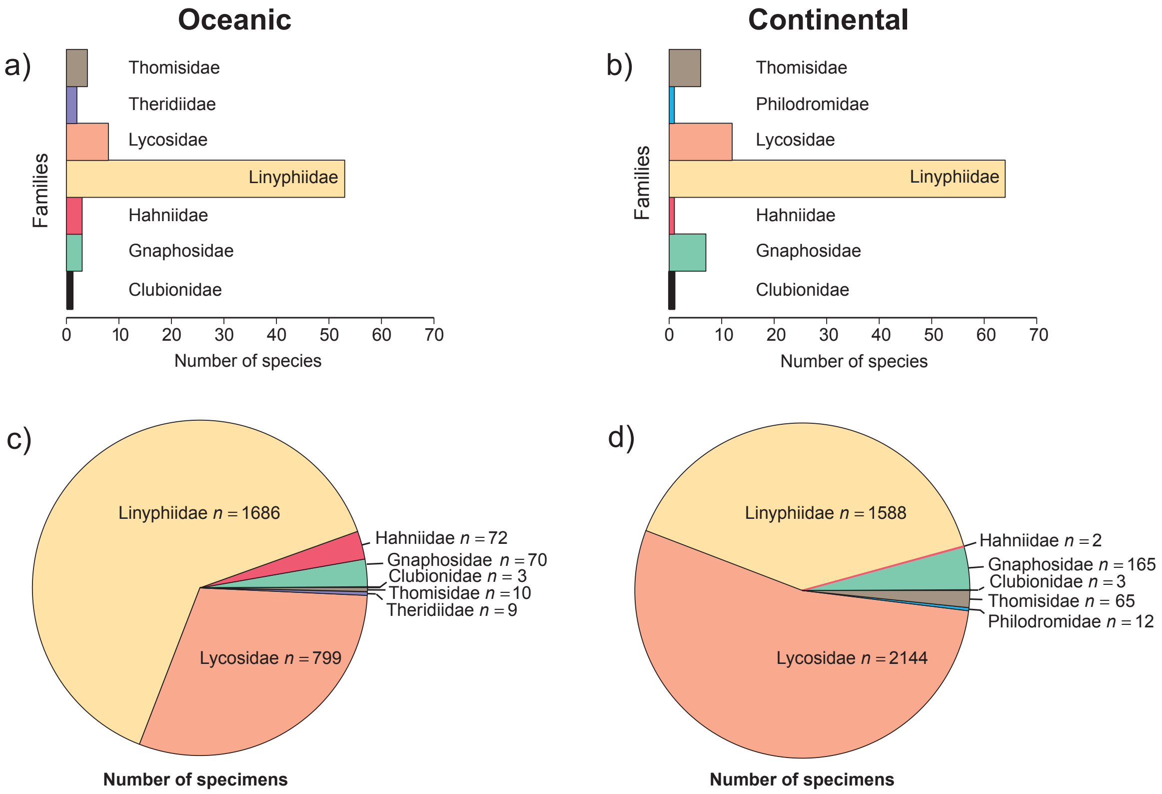

Fig. 3 a)-d): Total number of adult species and specimens in the oceanic (a and c) and continental (b and d) study regions. The number of family-specific species is indicated in barplots (a and b), and the number of family-specific specimens is displayed in pie-charts (c and d).

to 1,133 m a.s.l. in the oceanic region and from 1,164 m a.s.l. to 1,206 m a.s.l. in the continental region. The two continental sites grouped into this class were low-alpine bogs. 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 comparing all the Class 1 species, it was found that Subclasses 1.1 and 1.2 were separated from each other by the absence of *Oreoneta frigida* (Thorell, 1872) and *Pardosa palustris* (Linnaeus, 1758) at the sampling locations in Subclass 1.2.

Class 2 (medoid E1305D) aggregated low-alpine and middle-alpine sites with early and long summers, and it was also divided into two subclasses: 2.1 (medoid E1134A) and 2.2 (medoid E1449B). The entire class contained 32 sampling locations, 22 of which were ridge sites.

Subclass 2.1 was dominated by ridge sites in the continental study region covering the entire elevational gradient, from the low-alpine to the pronounced middle-alpine (1,074–1,565 m a.s.l.). This subclass consisted of 15 sampling locations: 13 ridge sites and two northern-exposed and windward slopes. Only one sampling location (932 m a.s.l.) was in the oceanic study region, while 14 were in the continental region. Two typical indicator species were identified *post-hoc*: *Ozyptila arctica* Kulczyński, 1908 and *Pardosa septentrionalis* (Westring, 1861).

Subclass 2.2 included oceanic ridge sites from the low-alpine to the middle-alpine and continental middle-alpine ridge sites and slopes. This subclass consisted of 17 sampling locations, seven of which were in the oceanic study region. Apart from one sampling location (W1427C, a middle-alpine southern-exposed slope), all of the oceanic study region sites grouped into this class were ridges. In the continental study region, four out of ten sites were middle-alpine ridge sites, three were southern-exposed slopes, two were northern-exposed and windward slopes, and one was a depression (E1449B which is characterised by minimum snowpack). The elevation of the sampling locations ranged from 1,024 m a.s.l. to 1,488 m a.s.l. in the oceanic study region and from 1,384 m a.s.l. to 1,609 m a.s.l. in the continental study region. The indicator species (defined *post hoc*) for this class were *Walckenaeria clavicornis* (Emerton, 1882); *Micaria alpina* L. Koch, 1872; and *Pardosa trailli* (O. P.-Cambridge, 1873). Subclasses 2.1 and 2.2 were distinguished from each other by the lack of *Pardosa hyperborea* (Thorell, 1872) and *Alopecosa aculeata* (Clerck, 1757) in Subclass 2.2.

Class 3 consisted of low-alpine and middle-alpine sites with late and short summers. In the continental study region, the class was restricted to sites in the transition zone between the low- and middle-alpine belts and higher. The class contained 19 sampling locations (medoid W1225C), 5 in the continental study region and 14 in the oceanic region. This class consisted of eight depressions, seven northern-exposed slopes, three southern-exposed slopes, and one ridge sampling location. The elevations ranged from 1,069 m a.s.l. to 1,413 m a.s.l. in the oceanic study region and from 1,300 m a.s.l. to 1,514 m a.s.l. in the continental region. The indicator species (defined *post-hoc*) for this class were *Erigone tirolensis* L. Koch, 1872 and *Collinsia holmgreni* (Thorell, 1871). In comparison to the other classes, this class was characterised by the absence of *Gnaphosa leporina*, *Tenuiphantes mengei*, *Cnephalocotes obscurus*, *Gnaphosa lapponum*, and *Alopecosa aculeata*.

4 Discussion

The family Linyphiidae was the most speciose spider family in both study regions, followed by family Lycosidae. This is a commonly reported pattern in northern epigeal spider communities (Danks 1981; Marusik and Koponen 2002). Other families were less abundant, which agrees with previous findings in this part of Norway (Löffler et al. 2001; Finch and Löffler 2010) and additional results from arctic regions in Canada (Dondale et al. 1997; Wyant et al. 2011).

In contrast to previous findings (Gaston and Williams 1996; Brown 2001; Sergio and Pendrini 2007), we found no linear decline in species richness with elevation. Species richness decreased only in the family Lycosidae at the higher elevations in the continental study region. This supports the suggestion by Marusik and Koponen (2002) that lycosid spiders might be the only family to show a clear elevation-related decrease in species number within northern epigeal spider communities. Furthermore, our results showed a peak of species richness at the medium-elevation alpine sites in both regions. These medium-elevation locations are situated at the transition zone between the low-alpine and middle-alpine belts in both the oceanic and continental study regions. This shift from low-alpine to middle-alpine habitat apparently causes a positive ecotone effect. Such changes in spider species richness in relation to changes in habitat were previously described for the Alps by Thaler (1996) and are supported by Rahbek (1995) and Brown (2001), who showed that species richness does not necessarily follow a linear trend, but often displays hump-shaped curves along the elevation gradients.

Using the Isopam algorithm, several indicator species for three classes and their integral subclasses were identified (Supplement I, lower left). Previous knowledge and our findings on the habitat preferences of the indicator species (Supplement I, right) point to what might be responsible for the annidation and spatial distribution of spiders in alpine tundra ecosystems. Based on these species habitat preferences, interesting west-east contrasts can be detected (Supplement I, upper left). By way of illustration, the contrasts in the spatial expansion of the Isopam classes are shown (upper left figure) in proportion to their spatial presence in the field. The steeper topographic relief in the western oceanic study region results in thicker and longer lasting snow cover in comparison to the eastern continental study region. Thus, the chionophilous elements sit lower in the western study region than in the eastern study region and show more spatial expansion relative to the chionophobous elements. Therefore, the spatial expansion of Class 3 is proportionally more in the western study region than in the eastern study region. Conversely, the chionophobous elements show a more areal expansion in the eastern continental study region due to less winter snowpack. Beyond that, the subalpine elements range higher in the eastern study region than in the western study region. Low-alpine southern exposed slopes in the continental study region, in particular, are characterised by early snow cover, but still have relatively long and warm summers. Early snow cover provides protection from strong frosts, while the overall lower amounts of snow (relative to the oceanic study region) and greater insulation result in an extended summer season.

Class 1 contained subalpine and low-alpine sampling locations from both study regions and was divided into Subclasses 1.1 and 1.2. Seven indicator species (four linyphiids, two lycosids, and one gnaphosid) were defined for Subclass 1.1, which was composed of

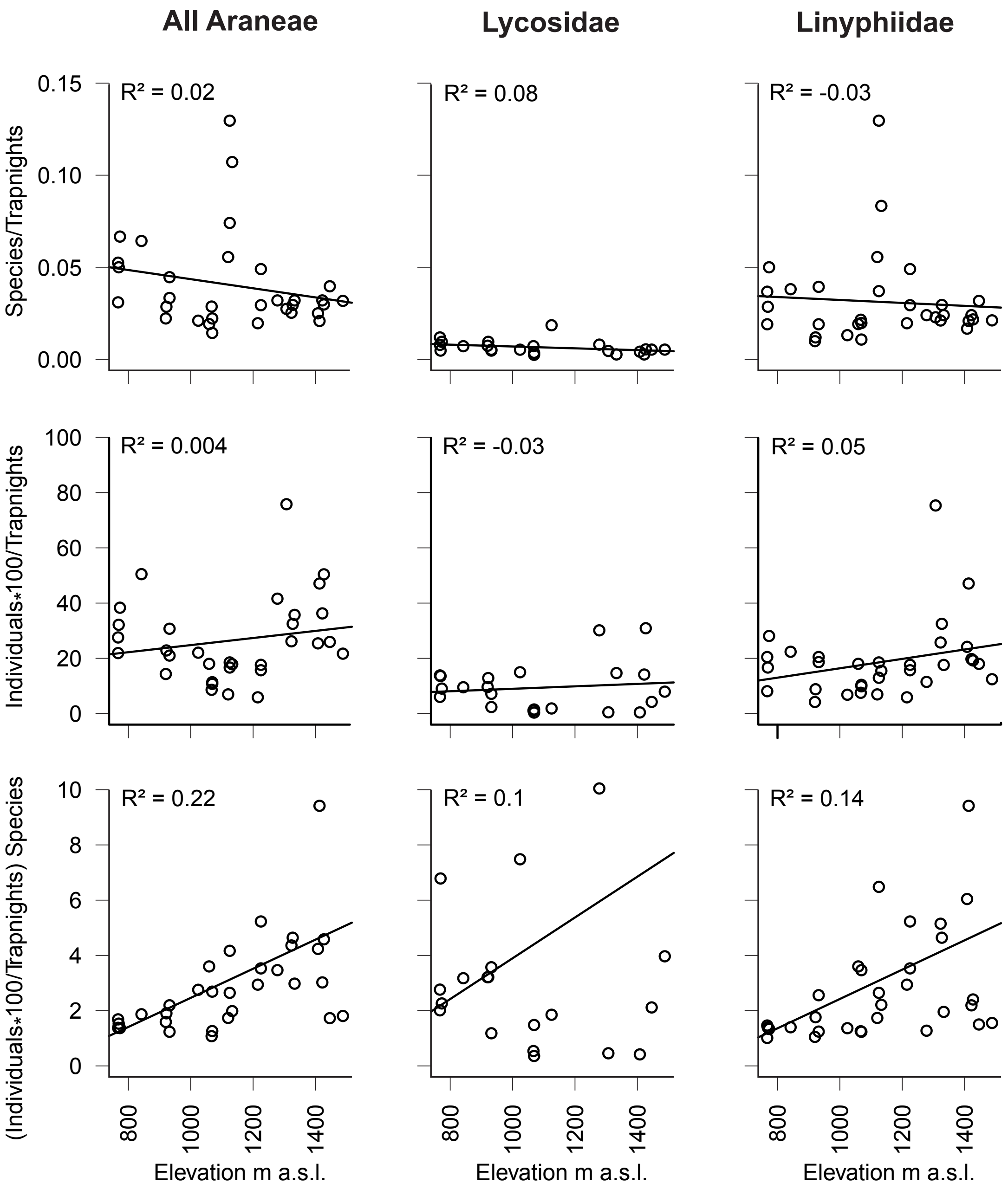

Fig. 4: Linear regression plots showing the abundance of species and individuals (corrected for trapnights) along the elevational gradient in the oceanic study region. The adjusted R^2 is provided. None of the results were significant ($p < 0.05$, Bonferroni-corrected).

subalpine and low-alpine sites with southern-exposed slopes reaching, but not extending beyond, the transition zone between the low- and middle-alpine belts (Supplement I). Three species were absent in this class: (1) *Erigone tirolensis*, an indicator species (Class 3) for low- and middle-alpine sites with late and short summers, based on our results; (2) *Erigone tirolensis*, which is considered a typical nival species in the Alps (Thaler 1988); and (3) *Improphantes complicatus*, which is found in alpine habitats on pioneer ground or dry heath in the Scandes (Hauge et al. 1978).

For Subclass 1.2, subalpine to low-alpine sites in the oceanic study region, 11 indicator species were defined (Supplement I). The two bogs in the continental study region were in this group, most likely due to the absence of species that are typical for the

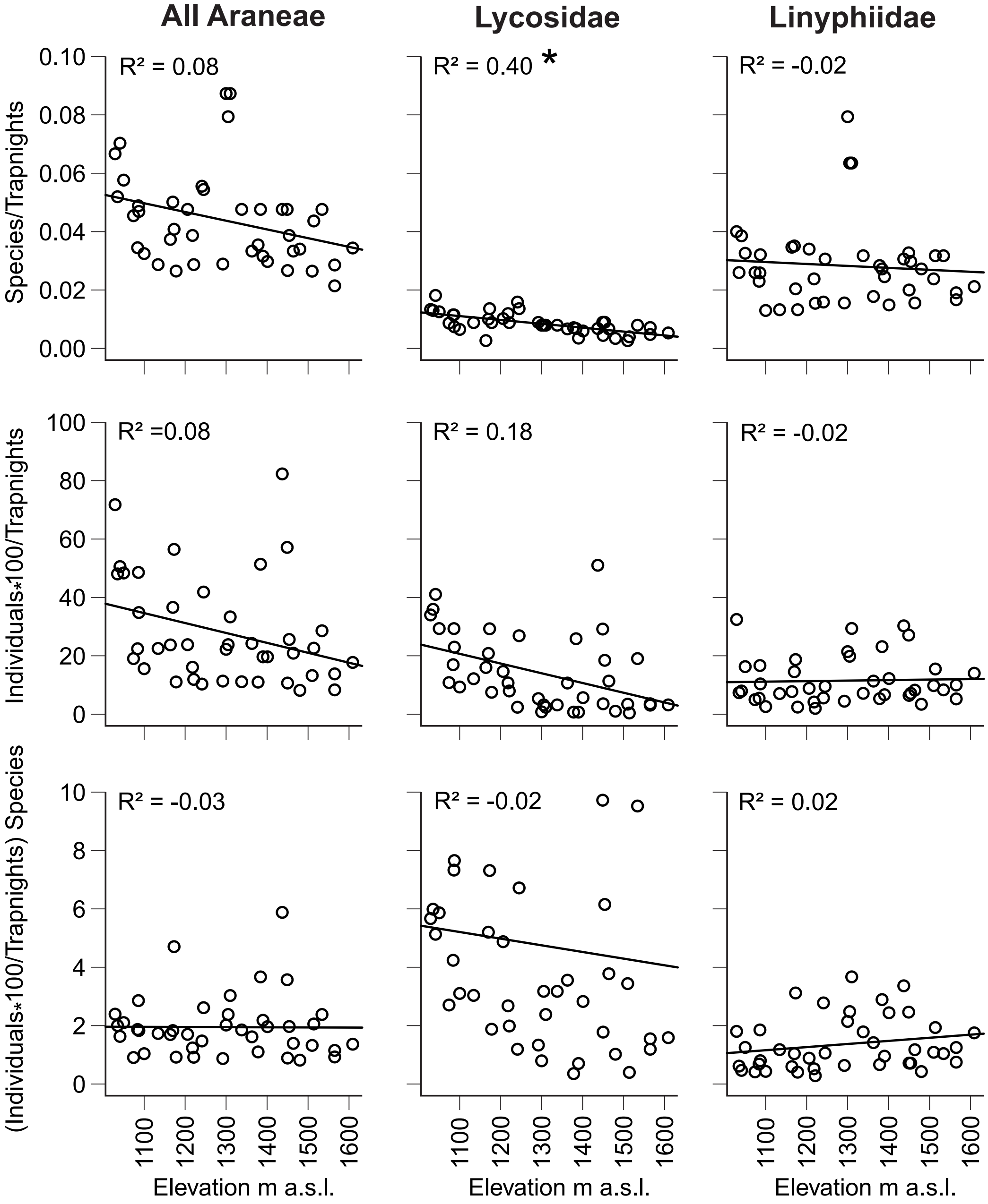

Fig. 5: Linear regression plots showing the abundance of species and individuals (corrected for trapnights) along the elevational gradient in the continental study region. Significant results ($p < 0.05$, Bonferroni-corrected) are marked with an asterisk.

lower-situated bogs, which were assigned to Subclass 1.1. The sampling locations contained a variety of species that are typically found in woodlands or forests (Supplement I). In comparison to Subclass 1.1, the indicator species for Subclass 1.2 showed a pronounced alignment in favour of damper habitats. These habitat preferences are reflected by the higher precipitation in the oceanic study region and the typically very moist conditions in low-alpine depressions, which have constant wet conditions and vegetation dominated by Sphagnum mosses (Löffler 2003). Furthermore, the absence of *Pardosa palustris*, a species typically found in dry habitats (Nentwig et al. 2013), and *Oreoneta frigida*, which is presumed to be an exclusively alpine species (Hauge et al. 1978), reinforces the classification of the Subclass 1.2 sampling locations. Our results are related to the specific characteristics of the alpine treeline, which is known to be one of the most heterogeneous ecosystems, with high spider diversity (Thaler 1989; Frick et al. 2007). This heterogeneity of the physical environment at the treeline allows for the coexistence of species with different habitat preferences at a fine-scale (Muff et al. 2009; Barriga et al. 2010). We identified indicator species that were clearly bound to subalpine or low-alpine sites. In particular, the effect of the treeline located nearby and the influence of stand-alone trees are probably responsible for the occurrence of woodland species above the treeline in Class 1 (Frick et al. 2007). Frick et al. (2007) also found the higher species densities typical of open habitats further away from the trees in comparison to the forest species, which had higher densities near the trees. Moreover, the differences between woodland and alpine tundras display some of the greatest contrasts in environmental conditions (Franz 1979), which is exhibited by the indicator species known typically for forests and woodlands and by the absence of alpine species in this class (Supplement I).

Class 2 contained low-alpine and middle-alpine sites with early and long summers, and it was divided into Subclasses 2.1 and 2.2. The indicator species for Subclass 2.1 can be described as 'extremely chionophobous', whereas the indicator species for Subclass 2.2 can be described as 'slightly chionophilous'. Subclass 2.1 contained continental low-alpine and middle-alpine ridge sites and two 'extremely chionophobous' indicator species: one lycosid, *Pardosa septentrionalis*, and one thomisid, *Ozyptila arctica* (Supplement I). Subclass 2.1 was composed almost exclusively of continental ridge sites, with only three exceptions: 'W932A', which is an oceanic ridge site, and 'E1170D' and 'E1218D', which are continental northern-exposed and windward slopes. The indicator species can be regarded as typical for alpine ridge sites in the continental study region, and they therefore represent an annidation along toposequences.

Two species, *Erigone tirolensis* and *Collinsia holmgreni*, were absent in Subclass 2.1. Both of these species were indicator species for Class 3 and can be regarded as 'extremely chionophilous'. The absence of these two species underscores the effect of snow cover on annidation for the spider fauna in alpine-tundra environments.

Subclass 2.2 included three 'slightly chionophilous' indicator species (in comparison to Subclass 2.1), and the sampling locations were characterised by a shorter and later summer than the sites aggregated into Subclass 2.1. The three indicator species were *Walckenaeria clavicornis*, *Micaria alpina*, and *Pardosa trailli* (Supplement I). The absence of *Pardosa hyperborea*, an indicator species for Subclass 1.1 (subalpine and low-alpine sites), and *Alopecosa aculeata*, a species found in damp but sunny forests up to the timberline (Nentwig et al. 2013), demonstrates the pronounced alpine character of the sampling locations aggregated into Subclass 2.2.

As a whole, Class 2 contained continental and oceanic ridge sites along almost the entire elevational gradient, while the lowest ridge sites were grouped into Class 1. The spatial distribution of the spiders, and in particular, the spatial distribution of the indicator species, showed a topography-dependent annidation closely related to the prevalent snow cover. The elevation gradient along these ridge sites played a secondary role. This corresponds to ecological and biogeographical findings that the alpine vegetation at ridges is the most extreme type of alpine site in the Scandes (Dahl 1956; Löffler 2003; Wundram et al. 2010). These fine-scale environmental gradients can be seen as spatial patterns of snow thickness and duration. Snow cover as a direct consequence of the topography and prevailing winds during the winter lead to typical patterns of snow-free ridges, but thick snowpack in the depressions and on the lee slopes (Löffler 2003; Nagy and Grabherr 2009). In our study regions, the southern-exposed slopes, especially, tended to have long-lasting snow cover lasting into the summer due to the prevailing wind direction during the winter (Löffler 2005, 2007). To the extent that they overwinter there, the typical species at ridge sites have to cope with huge temperature amplitudes of up to 40 K (Barry 1992; Löffler et al. 2006). In the oceanic study region, annual temperature amplitudes of 25 K have been previously described for one middle-alpine ridge site (Hein et al. 2013).

Class 3 contained low-alpine and middle-alpine sites with late and short summers, and *Erigone tirolensis* and *Collinsia holmgreni* were identified as indicator species (medoid 'W1225C'). These two species are clear indicators for low-alpine and middle-alpine sites that become snow-free very late (related to short summer seasons) and can be regarded as 'extremely chionophilous' (Supplement I). Both species are absent at sites in Subclass 2.1, which primarily contains ridge sites that remain snow-free during the winter. This reflects the strong correlation between the spatial and temporal patterns of snow coverage and the annidation of ground-living spiders in alpine tundra ecosystems. For the sites aggregated into Class 3, the pronounced alpine characteristics with late and short summers were evidenced by the absence of the following species: *Gnaphosa leporina*; *Tenuiphantes mengei*, an indicator species for Subclass 1.1 (subalpine and low-alpine sites); *Gnaphosa lapponum* (L. Koch, 1866), typically found in alpine and subalpine regions (Nentwig et al. 2013); *Alopecosa aculeata*, found in damp but sunny forests up to the timberline (Nentwig et al. 2013); and *Cnephalocotes obscurus* (Blackwall, 1834), a species found in open and damp environments (Urak and Samu 2008; Nentwig et al. 2013).

Overall, our study indicates that local environmental conditions have a stronger influence on the ecology and biogeography of alpine spiders than the broad-scale climatic conditions. As such, the climatic differences between the two study regions, resulting from the pronounced differences in continentality, had little or no influence on the spatial distribution of spiders. The identified indicator species reflect elevation-related patterns and are associated with topographical constraints. Although the influence of elevation on alpine spider communities is perceived as a well-known phenomenon (Lomnicki 1963; Otto and Svensson 1982; Chatzaki et al. 2005; Lee et al. 2012), our results emphasize the importance of snow cover on their ecology and biogeography.

5 Conclusion

Vegetation density and structure are assumed to be responsible for the species presence, richness, and composition in spider communities (e.g. Schaefer 1970; Wise 1993; Muff et al. 2009). The vegetation patterns, themselves, are strongly related to the topography and its inherent environmental conditions, which is a known characteristic of alpine tundra ecosystems (e.g. Gjærevoll 1956; Dahl 1986; Nagy and Grabherr 2009). As such, the environmental condition of snow cover is the most decisive factor concerning the spatio-temporal patterns within these ecosystems (Löffler and Finch 2005; Odland and Munkejord 2008). The spatial patterns of alpine vegetation are therefore an expression of the fine-scale topography-dependent snow-cover dynamics (e.g. Gjærevoll 1956; Dahl 1986; Löffler 2003). From this perspective, our results indicate that the influence of snow cover on the spatial distribution of alpine spiders is pronounced.

Moreover, our results indicate that snow-cover thickness and duration have a direct influence on the spatial distribution of spiders (Araneae). Using a multi-scale approach, our study has demonstrated the importance of fine-scale topography-related environmental conditions on the ecology and biogeography of alpine spiders.

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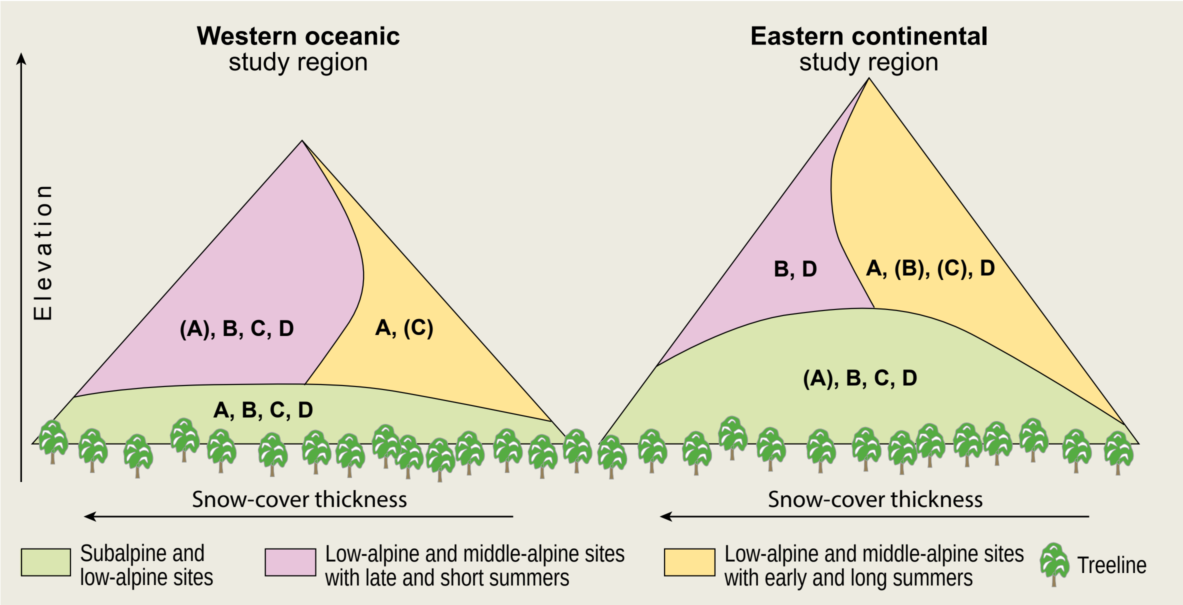
Appendix 1: Total number of species for the classes defined by the Isopam algorithm (using the isotab function). In addition to the classes, the total number of sampled specimens, sampling-site specific numbers, and elevational ranges (m a.s.l.) at the two study sites are shown. The species-specific frequency in the classes is shown as a percentage (%). Sampling locations with different topographic positions: A, ridges; B, depressions; C, southern-exposed slopes; D, northern-exposed slopes. The indicator species for the specific classes are highlighted in grey.

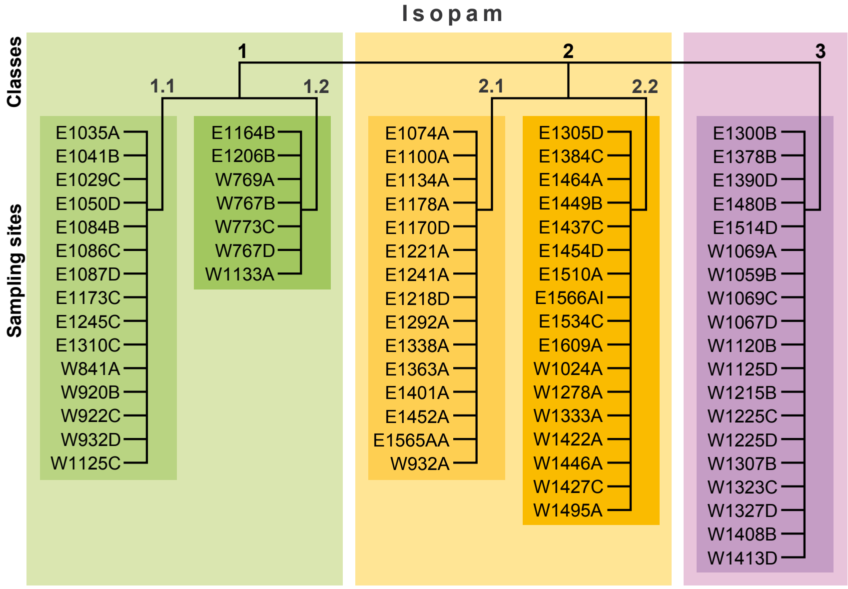
Species	Isopam classes and species frequency (%)					Specimens *n*=			Site specific *n*=				Elevational range m asl	
	1.1	1.2	2.1	2.2	3.0	ocea.	cont.	sum	A	B	C	D	oceanic	continental
Bolyphantes luteolus	80***	86**	13	6**	21	100	77	177	50	4	95	28	767–1133	1029–1245
Pardosa hyperborea	80***	43	53	0***	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	0	14	37	51	5	1	39	6	767–932	1029–1035
Hilaira nubigena	13	57**	0	0	5	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
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

Species	Isopam classes and species frequency (%)					Specimens *n*=			Site specific *n*=				Elevational range m asl	
	1.1	1.2	2.1	2.2	3.0	ocea.	cont.	sum	A	B	C	D	oceanic	continental
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		1		1035–1300
Oedothorax retusus	20*	0	0	6	0	60	7	67	28	21		18	920–1422	1041
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	14	0	0	0	16	1	17		17			767	1041
Entelecara errata	0	0	0	12	0		2	2	1			1		1454 – 1609
Hilaira herniosa	0	0	7	6	0		2	2	1			1		1170 – 1565
Hypomma bitubercultaum	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	
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

Snow cover determines the ecology and biogeography of spider (Araneae) in alpine tundra ecosystems



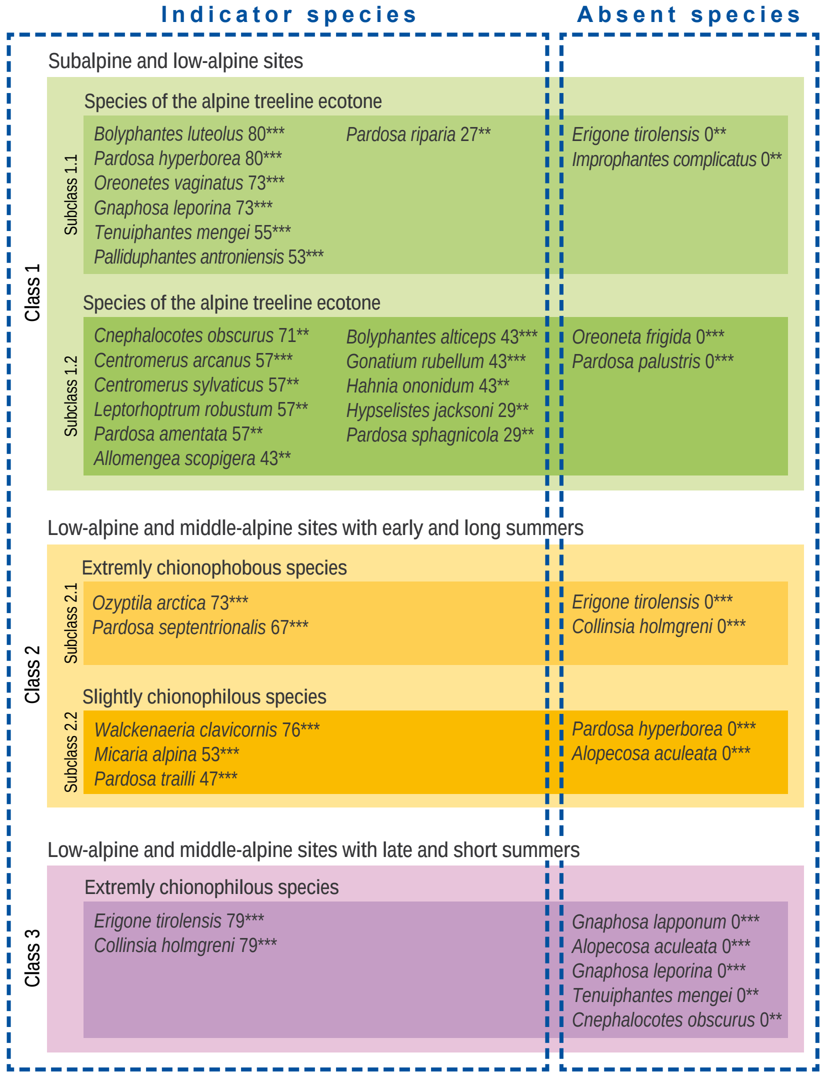
Schematic diagramm showing the distribution of the three classes in the two study regions. Class 1 (green) contains subalpine and low-alpine sites of both study regions. In the eastern study region, the subalpine elements range relatively higher than in the western study region. Class 2 (yellow) contains low-alpine and middle-alpine sites with early and long summers. In the eastern study region, the chionophobous elements range relatively deeper than in the western study region. Class 3 (purple) contains low-alpine and middle-alpine sites with late and short summers. The chionophile range sets deeper in the western study region than in the eastern study region.



E = Eastern continental research area
W = Western oceanic research area
A = Ridges
B = Depressions
C = Southern-exposed slopes
D = Northern-exposed slopes

Numbers indicate elevation in m asl

Hierarchal clustering of the sampling sites. The hierarchal clustering of the sampling sites regarding the site-specific similarities of the spider assemblages is shown above. 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 on the right. The significance is marked with asterisks: ***p < 0.001 and **p < 0.01.



Indicator species | **Absent species**

Subalpine and low-alpine sites

Species of the alpine treeline ecotone

Bolyphantes luteolus 80***
Pardosa hyperborea 80***
Oreonetes vaginatus 73***
Gnaphosa leporina 73***
Tenuiphantes mengei 55***
Palliduphantes antroniensis 53***
Pardosa riparia 27**

Absent: *Erigone tirolensis* 0**
Improphantes complicatus 0**

Species of the alpine treeline ecotone

Cnephalocotes obscurus 71**
Centromerus arcanus 57***
Centromerus sylvaticus 57**
Leptorhoptrum robustum 57**
Pardosa amentata 57**
Allomengea scopigera 43**
Bolyphantes alticeps 43***
Gonatium rubellum 43***
Hahnia ononidum 43**
Hypselistes jacksoni 29**
Pardosa sphagnicola 29**

Oreoneta frigida 0***
Pardosa palustris 0***

Low-alpine and middle-alpine sites with early and long summers

Extremly chionophobous species

Ozyptila arctica 73***
Pardosa septentrionalis 67***

Erigone tirolensis 0***
Collinsia holmgreni 0***

Slightly chionophilous species

Walckenaeria clavicornis 76***
Micaria alpina 53***
Pardosa trailli 47***

Pardosa hyperborea 0***
Alopecosa aculeata 0***

Low-alpine and middle-alpine sites with late and short summers

Extremly chionophilous species

Erigone tirolensis 79***
Collinsia holmgreni 79***

Gnaphosa lapponum 0***
Alopecosa aculeata 0***
Gnaphosa leporina 0***
Tenuiphantes mengei 0**
Cnephalocotes obscurus 0**

The indicator species and their typical habitats. Given are the indicator species for the three classes and inherent subclasses with habitat preferences known from previous studies, supplemented by our findings.

Class	Species (Platnick 2013)	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 treeline ecotone up to the transition zone between low-alpine 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 treeline ecotone up to the transition zone between low-alpine 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 treeline 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 treeline ecotone up to the transition zone between low-alpine 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 treeline ecotone up to middle-alpine, thus decreasing temperatures, shorter summer seasonal length and more grassy and patchy vegetation	
1.1	*Palliduphantes antroniensis*	alpine habitats[7], heath birch forests in Scandinavia[12]		zonation from the treeline 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 edgesand in pine forest[12]	continental, very low annual precipitation of 300-400 mm; most continental part of Norway	treeline ecotone, forest and open habitats	
1.2	*Cnephalocotes obscurus*	bogs[5], in open, damp places[12]		zonation from the treeline ecotone up to the transition zone between low-alpine 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	treeline ecotone, forest and open habitats	
1.2	*Centromerus sylvaticus*	in ground litter of moderately damp woodland[12]		treeline ecotone, forest and open habitats	
1.2	*Hilaira nubigena*	swampy localities[12]		zonation up to the transition zone between low-alpine 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]		treeline ecotone and low-alpine sites, moderate temperatures and longer summer season length (13-15 weeks), heather and low shrub communities	
1.2	*Pardosa amentata*	damp habitats[12]		up to the transition zone between low-alpine 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]		treeline ecotone, forest and open habitats and low situated low-alpine sites	
1.2	*Bolyphantes alticeps*	bogs[5], meadows and forest[12] edges up to the subalpine zone[12]		treeline ecotone, forest and open habitats	absent at bogs, always wet
1.2	*Gonatium rubellum*	woodland[12]		treeline ecotone, forest and open habitats	absent at bogs, always wet
1.2	*Hahnia ononidum*	damp woodland[12]		treeline ecotone, forest and open habitats	absent at bogs, always wet
1.2	*Hypselistes jacksoni*	swampy terrain[12], peatlands and other wet lands[7]		treeline ecotone, forest and open habitats	absent at bogs, always wet
1.2	*Pardosa sphagnicola*	bogs[12], peatlands and other wet lands[7]		treeline ecotone, forest and open habitats	absent at bogs, always wet
2.1	*Ozyptila arctica*	moist and dry tundra sites[10]		zonation from the treeline 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 treeline 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	*Walckenaeria clavicornis*	soil crevices with high humidity[12]		zonation from treeline 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 treeline 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, 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

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[1]Holm 1950 · [2]Locket and Millidge 1953 · [3]Palmgren 1976 · [4]Hauge et al. 1978 · [5]Hänggi et al. 1995 · [6]Esyunin 1999 · [7]Aakra and Hauge 2000
[8]Kronestedt 2002 · [9]Gudleifsson and Bjarnadottir 2004 · [10]Wyant et al. 2011 · [11]BRITISH ARACHNOLOGICAL SOCIETY 2013 · [12]Nentwig et al. 2013