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Broad-scale rather than fine-scale environmental variation drives body size in a wandering predator (Araneae, Lycosidae)

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ABSTRACT

Body size is one of the most important individual traits, determining various other life-history traits, including fitness. Both evolutionary and ecological factors shape the body size in arthropods, but the relative contribution of abiotic drivers acting at different spatial scales has been little investigated. We aimed to identify the importance of two broad-scale variables (study region and elevation) in shaping body size of the free-running and locally abundant wolf spider *Pardosa palustris* (Linnaeus 1758), in contrast to the fine-scaled variable topographic position. Therefore, we set up transects along environmental gradients in the arctic-alpine ecosystems of Norway, which we analyzed using a random forest approach to identify the relative importance of topographic position, elevation, and study region on body size of *P. palustris*. Our approach revealed that research region was the best explanatory variable, followed by elevation and topographic position. Differences in body size were most likely a consequence of the pronounced differences in season length and the ability of *P. palustris* to avoid local unfavorable environmental conditions due to its high mobility.

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Introduction

The identification of spatial patterns in life-history traits, as well as the mechanisms that generate and maintain them, is mandatory in ecological field studies. This will, consequently, result in a better understanding of spatio-temporal patterns of species distribution and adaptations in response to changing environments. Consequently, the driving principles of phenotypic variation in individual–environment interactions are in the focus of current research (e.g., Chevin, Lande, and Mace 2010; Ameline et al. 2018; Hein et al. 2018). However, knowledge about specific spatial and temporal variations of life history traits remains scarce in invertebrates, especially in cold environments (Homburg et al. 2013; Høye and Sikes 2013; Ameline et al. 2017). Body size is one of the key features of life history traits research in ectotherms (Angiletta et al. 2004; Chown and Gaston 2010; Høye and Hammel 2010), because it is considered a proxy for fecundity, body condition, and survival (e.g., Hodkinson 2005; Bowden, Høye, and Buddle 2013; Penell, Raub, and Höfer 2018). In general, larger individuals show higher fecundity and lower mortality rates (Smith and Fretwell 1974; Fox and Czesak 2000).

Body size is shaped by both evolutionary and ecological factors acting at different scales. Still, few studies have investigated both its fine- and broad-scale drivers (but see Lowe et al. 2014). The main local ecological drivers of body size in terrestrial arthropods are season length, the concomitant resource availability and quality, and temperature (Chown and Gaston 2010; Shelomi 2012). Univoltine alpine species are often limited by season length with respect to completion of their life cycles (Strathdee and Bale 1998). Consequently, variations of the onset of the growing season lead to an increase in the size of the arctic wolf spider *Pardosa glacialis* (Thorell 1872) in Greenland. A longer summer season length induced by the earlier onset of the growing season leads to bigger individuals (Høye et al. 2009). This finding corresponds to a converse Bergmann's cline, where warmer temperatures and prolonged summer season result in larger specimens, whereas a Bergmann's cline describes

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larger specimens in response to colder temperatures (e.g., Mousseau 1997; Blanckenhorn and Demont 2004). In this context, the characteristic snow-cover patterns and the concomitant environmental drivers in the alpine environments of the Scandes formed by topography and the dominant wind direction (Gjærevoll 1956; Löffler 2002) might also determine the life-history traits of spiders. At a local scale, we found the thickest snow layers and thus the shortest seasons on the southern exposed lee-slopes, and the least snow-cover duration on ridges with little or no snow cover during winter (Löffler 2005; Löffler and Finch 2005), resulting in specific distribution and abundance patterns of ectothermic species in arctic-alpine ecosystems (Hein et al. 2014; Beckers et al. 2018).

Commonly, higher temperatures lead to faster development and thus earlier fertility in ectothermic species (Willmer, Stone, and Johnston 2004; Blanckenhorn and Demont 2004). This results in the largest body sizes at the lowest temperatures (Chown and Gaston 2010), which is also known as the temperature-size rule (reviewed by Atkinson and Sibly 1997). Increasing body size in colder environments is assumed to be the result of prolonged life-cycles (slower growth) in response to cold temperatures (Angiletta et al. 2004). Here, the disadvantage of delayed maturation is compensated for by an increase in fecundity. Larger females have an increased fecundity and they often produce a larger number of eggs (e.g., Simpson 1995; Prenter, Elwood, and Montgomery 1999; Fox and Czesak 2000; Puzin et al. 2011). Spiders are suitable model organisms when focusing on individual–environment interactions (e.g., Wise 1993; Hendrickx et al. 2003; Renault et al. 2016), because prosoma width is fixed at each life stage and not, or only slightly, influenced by starvation (Miyashita 1968). Lycosid spiders are especially suitable for such a study for several reasons: (1) lycosid spiders are highly abundant in many ecosystems; (2) they can be easily sampled with pitfall traps; (3) they are known to show a strong relationship to micro-climate and vegetation structure. Lycosid spiders, like Araneae in general, are known to have well-defined habitat preferences (Schaefer 1970; Frick, Nentwig, and Kropf 2007; Muff et al. 2009), which are expressed at very fine scales in the heterogenous arctic-alpine ecosystems of Scandinavia (Finch and Löffler 2010; Hein et al. 2014). Prosoma width indeed proved to be a reliable proxy for body size in lycosid spiders in previous studies (e.g., Hagstrum 1971; Jakob, Marshall, and Uetz 1996; Hendrickx and Maelfait 2003; Pétillon et al. 2009).

The aim of this study was to compare the importance of broad-scaled (study region and elevation) versus fine-scaled (topographic position) environmental variables in order to decipher their respective effect on the body size of the free-running and locally abundant wolf spider *Pardosa palustris* (LINNAEUS 1758). We tested the hypothesis that the influence of these variables on body size decreases as the scale they act on increases. The local abiotic factor topographic position, acting at the fine scale, is thus expected to show a higher explanatory power on body size than the regional abiotic factors of study region and elevation, which act at the broad scale. Consequently, this hypothesis was tested using a study design from fine- to broad-scale in order to gain insights into how extent local and regional factors shape body size in the highly mobile and locally abundant spider *Pardosa palustris* (e.g., Hauge and Refseth 1979; Hein et al. 2014, 2015).

Material and methods

Study sites

The sampling was carried out in Vågå (Oppland, 61°53′ N; 9°15′ E; the highest peak here is Blåhø 1617 m.a.s.l.) and Geiranger (Møre og Romsdal, 62°03′ N; 7°15′ E; the highest peak here is Dalsnibba 1495 m.a.s.l.) in central Norway in 2009 (Figure 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 (Moen 1998). Within a relatively short linear distance (approximately 100 km in our study), considerable climatic contrasts emerge in this part of Norway. According to Moen (1998), the western study region is part of the weak oceanic section (o1), with relatively high winter temperatures, relatively low summer temperatures, and relatively high precipitation and humidity values. In contrary, the eastern study region is part of the weak continental section (c1), with relatively low winter temperatures, relatively high summer temperatures, and low precipitation values. The study region in Vågå is part of the most continental climate section in Norway and is characterized by low annual precipitation, about 300– 400 mm in the valleys. In contrast, the western study region is part of the inner fjords climate section with high annual precipitation of about 1500–2000 mm in the valleys (Löffler and Finch 2005). As such, the climatic contrasts are expressed mainly by differences in annual precipitation and the concomitant snow-cover duration, which is, on average over the last fifty years, about thirty days shorter at Vågå (Figure 2).

In both study regions, the low-alpine vegetation is dominated by shrub and heather communities, whereas the middle-alpine vegetation is dominated by graminoids (Dahl 1986). In Geiranger, the treeline is located at ~750 m.a.s.l., and in Vågå at ~1030 m.a.s.l. The upper limit of the low-alpine belt is found at ~1200 m.a.s.l. in Geiranger and at ~1350 m.a.s.l. in Vågå, respectively. The pronounced oceanity in the western oceanic section

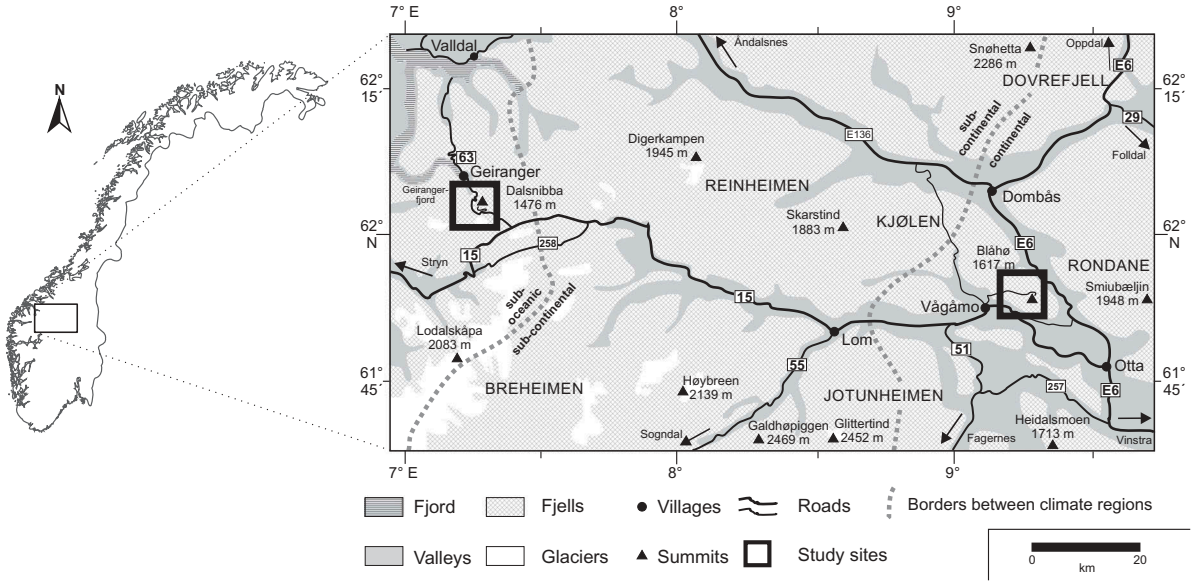

Figure 1. Map of Norway with focus on the two study regions in the western suboceanic (Geiranger) and the eastern continental (Vågå) part of Norway. According to Moen (1998), Geiranger is part of the weak oceanic section (o1) and Vågå part of the continental (c1) section.

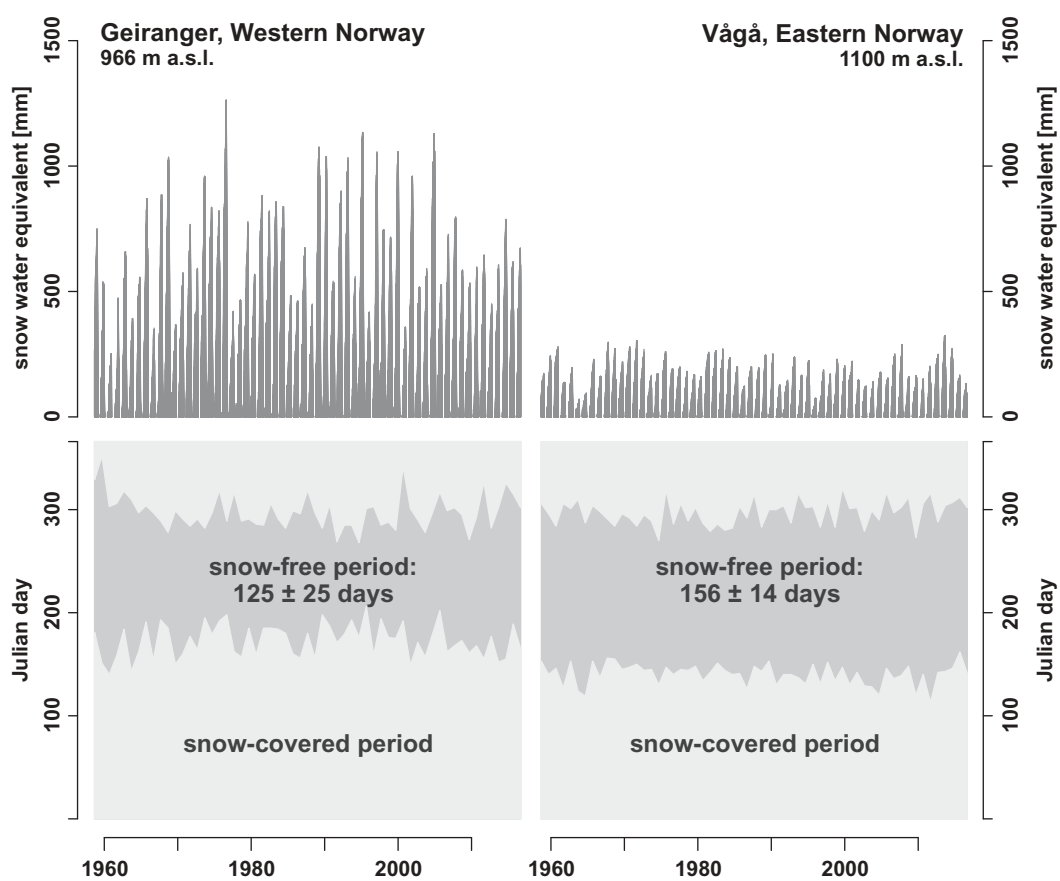

Figure 2. Long-term data on the snow water equivalent (upper) and the snow-free period (lower) in the western (left) and eastern (right) study areas. Data on the snow-free period are based on the core seasonal (i.e., continuous) snow cover, without consideration of short-term snow cover. The long-term mean is given in number of days, including the standard deviation.
Data source: MET Norway (2018).

results in a depression of the elevational belts, which leads to similar and comparable ecological settings at different elevational levels in the western oceanic and the eastern continental section (Löffler 2003; Löffler and Finch 2005; Löffler, Pape, and Wundram 2006).

Sampling design

To address the general biogeographic problem of scale (Levin 1992), we implemented a multiscale instrumental monitoring network along the regional climate gradient, the alpine elevational gradient, and the microtopographic gradient (e.g., Löffler, Pape, and Wundram 2006; Hein et al. 2014). Pitfall traps were installed at ridges, depressions, and south-/north-facing slopes to account for the pronounced differences in snow-cover duration. Ridges remain more or less snow-free during the winter, whereas snow cover lasts longest at south-facing slopes as a result of snow redistribution by the strongest winds, which occur from northern directions. Ground-dwelling arthropods were sampled at sampling sites along two elevation transects from the tree line up to the highest peaks (western oceanic Norway—Geiranger n = 32; eastern continental Norway—Vågå n = 40). The transects reached from ~ 830–1422 m.a.s.l. in Geiranger, and from 1035–1534 m.a.s.l. in Vågå, respectively. Our microtopographic gradients along the elevation gradient were assumed to display the strongest environmental differences at short distances (Nagy and Grabherr 2009; Wundram, Pape, and Löffler 2010). The snow-cover duration results in specific fine-scaled vegetation patterns, where ridge positions are dominated by lichen species (*Alectoria ochroleuca* and *Flavocetraria nivalis*), slopes by dwarf shrubs (*Betula nana, Calluna vulgaris, Vaccinium myrtillus*), and depressions by mosses and sedges (*Sphagnum* ssp. and *Carex* ssp). At higher elevations, the vegetation becomes scarcer and graminoid species increase, with *Carex bigelowii* and *Juncus trifidus* being the most abundant species. For a more detailed description of the vegetation and the respective microclimate, see Löffler (2003). The specific vegetation patterns enabled us to identify representative sites for topography-dependent snow-cover duration.

During the snow-free period, three pitfall traps with saturated salt solution as a preservative and Agepon© as a detergent were installed at each site, resulting in a total of 216 traps being used (Geiranger n = 96, Vågå n = 120). The pitfall trapping was implemented in 2009 as soon as the individual sites became snow-free. The pitfall traps consisted of a glass with a diameter of 5.5 cm at the rim and a depth of approximately 12 cm. By means of a plastic rim on top of the glass, a polycarbonate plate (13.7 cm x 13.7 cm) was fixed 5 cm above the opening as a rain shelter (e.g., Naujok and Finch 2004). The pitfall traps were emptied every two weeks and their contents were transferred to 70 percent ethanol for preservation. In order to reduce differences in phenological development in both research regions, three sampling periods were implemented after the first adult specimens of *P. palustris* were sampled in the respective study regions. Our three sampling periods reached from 20 May until 1 July (first sampling 12 June; second sampling 17 June; third sampling 1 July) in the western oceanic climate section, and from 26 May until 7 July (first sampling 9 June; second sampling 23 June; third sampling 7 July) in the eastern continental climate section, respectively. The difference in the beginning of the sampling in the respective study regions is a result of the timing of snow melt and the appearance of adult specimens in the pitfall traps.

Pitfall trapping, largely used to sample ground-active arthropods (Uetz and Unzicker 1976; Topping and Sunderland 1992; Woodcock 2005), was argued to suffer from a number of biases: (1) notably towards male specimens during times of reproduction; and (2) bigger and more mobile species and specimens (Merrett and Snazell 1983). In our study, however, we assume a limited overall bias of the sampling method, because we are focusing on one species only and we do not focus on counts per pitfall trap, but size per sampled individual. Additionally, the constraints noted earlier were systematically present at all sites, and thus should result in a comparable data set.

Pardosa palustris

Pardosa palustris is commonly found in open habitats and on both moist and dry meadows, and appears from the lowlands up to 2500 m.a.s.l. (Nentwig et al. 2019). *Pardosa palustris* has a holarctic distribution (World Spider Catalog 2017) and can be found from the northernmost parts of Scandinavia to southern Europe (Nentwig et al. 2019). In our two study regions, *P. palustris* is one of the most abundant lycosid species appearing from the tree line up to 1488 m.a.s.l. in the western oceanic climate section and up to 1534 m.a.s.l. in the eastern continental climate section (Hein et al. 2014). We took photographs of each specimen with a digital camera, by means of a 10× optical and a 100× digital magnification. From these photographs, we measured prosoma widths to the nearest 0.01 mm using ImageJ software (Rasband 2007).

Statistical analysis

Machine-learning techniques have proven to outperform more established statistical methods for many applications in ecology (Elith et al. 2006; Cutler et al. 2007; Mayr, Vanselow, and Samimi 2018).

Furthermore, relationships between biotic and abiotic factors often behave nonlinearly. Based on these facts, we decided to use a non-parametric random forest regression approach for statistical analysis. This machine-learning approach is based on an ensemble of single regression trees (Breiman 2001). It generates several random subsets from the training data set using bootstrap resampling (Efron and Tibshirani 1993; Liaw and Wiener 2002). These subsets were then used to grow a high number of single regression trees (hence forest). The trees were gradually divided into smaller binary classes, utilizing the best-fitting predictor from a randomly chosen subset of the explanatory variables. Referring to this, a threshold value was chosen that maximizes the homogeneity of the two resulting classes with regard to the response variable (Prasad, Iverson, and Liaw 2006). Then, the resulting single trees were combined to a stable final regression (Brenning 2009). A particular advantage of random forests is the out-of-bag validation (Liaw and Wiener 2002; Brenning 2009). At each bootstrap replication, the data that were excluded from the bootstrap sample (i.e., out-of-bag or OOB) are used as the test data; i.e., they were predicted on the basis of the tree grown with the bootstrap sample. The predictions for all individual trees grown with the bootstrap samples were consolidated, and the overall error rate was calculated. As such, OOB accuracy estimates were efficiently cross-validated and unbiased, providing that a sufficient number of trees were fitted (Breiman 2001). Beyond the model fit, the algorithm calculates an importance score for each explanatory variable that is based on permutation. The respective variable was permuted, while the other variables remained unchanged. The larger the increase in the prediction error due to this permutation, the higher the variable importance (Liaw and Wiener 2002). We tested the significance of the random forest models using a permutation test according to Murphy, Evans, and Storfer (2010), with 9999 permutations. In order to test for significant differences in body size (prosoma width in mm) in females and males between the two populations of *P. palustris*, we performed a two-sided Wilcoxon rank sum test. All statistics were implemented in R (R Core Team 2016) using the r-package randomForest (Liaw and Wiener 2015) for the regression analysis and the stats r-package (R Core Team 2016) for the Wilcox test.

The explanatory variables used in the sex-specific random forest approaches were topographic position, elevation, and study region. The sampling locations along the elevation gradient correspond to the typical conditions at the specific elevation and are included as a numerical variable in m.a.s.l. The four different topographical positions in focus are covering the main relief positions displaying sites with the most pronounced contrasts in snow-cover duration in arctic-alpine ecosystems. The four different topographical positions are A = ridges, B = depressions, C = south-facing slopes, and D = north-facing slopes, included as a categorical variable in the random forest model. A total number of n = 500 trees were grown in each of the respective models.

Results

In total, 163 adult female and 651 male specimens of *P. palustris* were sampled and measured during three trapping periods, corresponding to six weeks of sampling; juveniles were excluded in this study. In the western oceanic study region of Geiranger, a total of n = 50 female and n = 205 male specimens were sampled. Accordingly, in the eastern continental study region of Vågå, a total of n = 113 female and n = 446 male specimens of *P. palustris* were sampled. The largest female specimen in the western oceanic research region measured 2.335 mm, and the largest male was 2.45 mm (both sampled at 1333 m.a.s.l.). Mean prosoma width in female specimens was 2.05 mm (sd = 0.14), and 2.06 mm in males (sd = 0.10). In the eastern continental study region, the largest female specimen was 2.497 mm (sampled at 1035 m.a.s.l.), and the largest male was 2.515 mm (sampled at 1384 m.a.s.l.). Mean prosoma width in female specimens was 2.15 mm (sd = 0.13), and 2.15 mm (sd = 0.10) in males. The Wilcoxon test revealed significant differences in prosoma width between the western oceanic and the eastern continental study region in females ($W = 1727$, $p < .001$) and males ($W = 23433$, $p < .001$), respectively, with generally larger specimens in the continental region (Figure 3).

Beyond that, it is difficult to unravel clear patterns in body size in relation to elevation or topographic position. However, it is clear that there are obviously no linear trends along the elevational gradient; body size in *P. palustris* shows a somehow curvilinear pattern, probably related to the transition zones between the elevational belts.

The results from the random forest approach showed a mean of squared residuals of 0.016 with an explained variation of 17 percent ($p < .0001$) in females of *P. palustris*, and a mean of squared residuals of 0.010 with an explained variation of 20 percent ($p < .0001$) in males of *P. palustris*. In both sexes, the explanatory variables sorted by their importance in decreasing order are: (1) study region; (2) elevation; (3) topographic position (Figure 4). Here, the removal of topographic position

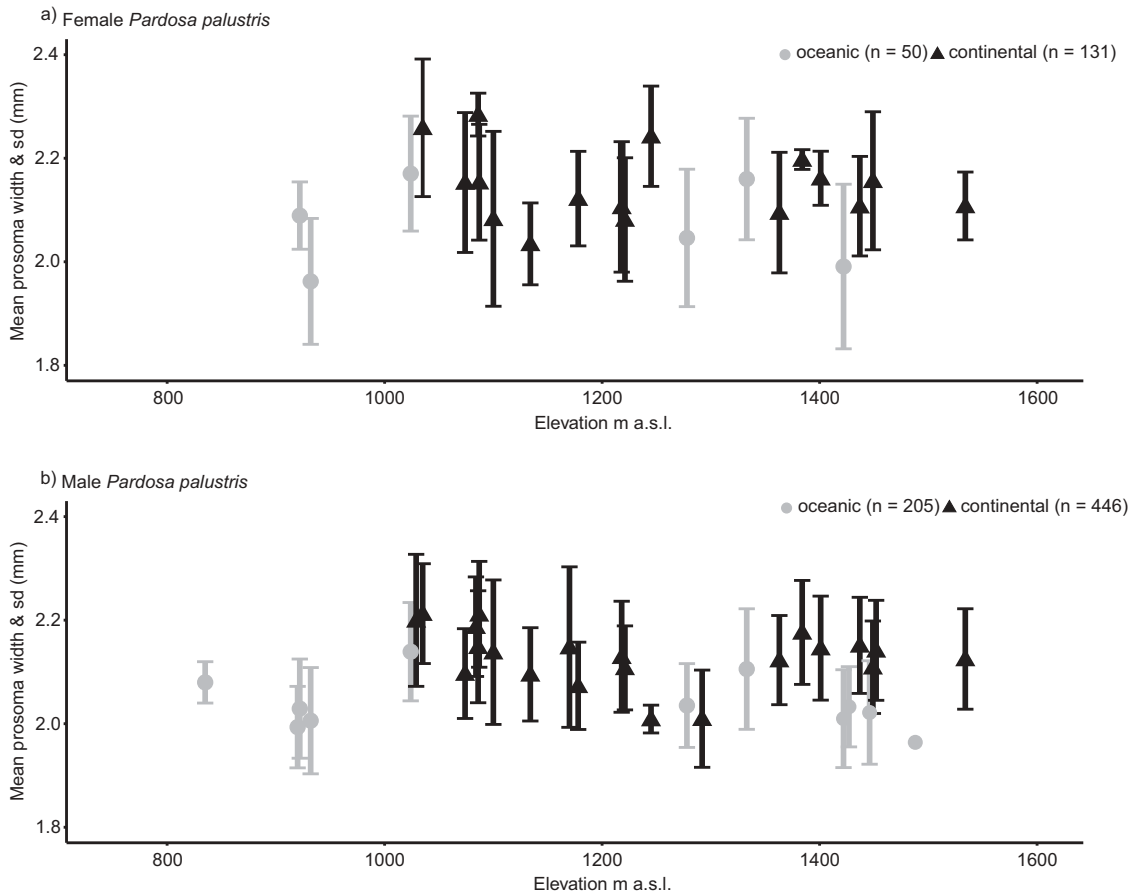

Figure 3. Body size variation of *P. palustris* along the elevational gradient. Displayed is the mean prosoma width in females (a) and males (b) of *P. palustris* along the elevational gradient in the two study regions. Given are the sampling-site specific means and the standard deviations of prosoma width (mm). The values for prosoma width for the two study regions are marked as triangles (continental) or circles (oceanic).

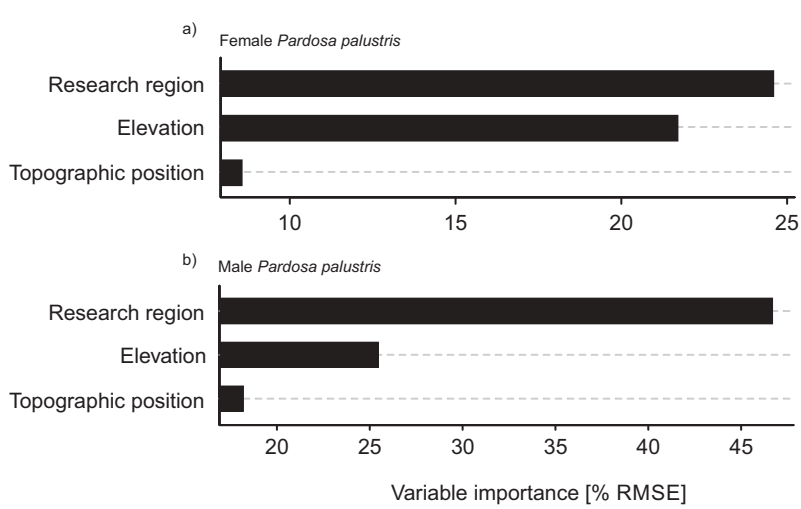

Figure 4. Importance scores of the explanatory variables used in the model. Importance is quantified as percent increase in mean square error of the random forest model when that explanatory variable is permuted. Sex-specific results for the importance of the explanatory variables are displayed for females (a) and males (b), respectively.

from the models led to almost no loss in explanatory power of the variance in body size of *P. palustris*.

Discussion

Trying to disentangle the influence of fine- vs. broad-scale ecological factors on body size of a highly mobile spider, we found that the effects of the broad-scale factors of study region and elevation were both more important than the fine-scaled factor of topographic position. This was contrary to our expectations that local factors would explain more of the variance in body size than regional factors Although a relatively large part of the variance remains unexplained, we found individuals sampled in the eastern continental climate section to be significantly larger, maybe as a result of mean annual precipitation and concomitant season length. Additionally, this effect was probably due to increased mobility of the specimens at finer spatial scales, which might have homogenized effects on body size by the ability to avoid unfavorable micro-habitat conditions. In this context, lycosids display high mobility on the ground up to hundreds of meters a day (Richter 1970; Morse 1997, 2002), whereas ballooning is supposed to be less frequent in this family (Blandenier et al. 2013), but see exceptions later in the discussion. Furthermore, ballooning is sometimes reduced in specialist species (see, e.g., Edgar 1971; Bonte et al. 2003), and often results in random (passive) displacement of individuals (Bonte, Bossuyt, and Lens 2007). In a web-building spider, Lowe et al. (2014) also found that body size was mostly influenced by broad-scale factors. Whether the differences in body size in our study were the result of direct (e.g., temperature, precipitation) or indirect climatic effects (e.g., resource availability, competition) could not be unraveled. We found indication for both direct and indirect effects, which we discuss in the following paragraphs at the scale of which they act the most.

Effects of study region

One has to keep in mind that our results regarding the effect of study region are unfortunately biased by the unbalanced sampling design, with the lack of sufficient replicates regarding the broader-scaled variables (e.g., Oksanen 2001). Comparison of the climatic conditions in the two study regions, however, revealed huge differences regarding the annual mean season length and snow-water equivalent from 1957–2017 (MET Norway 2018). Summer season length in the western oceanic research region is on average thirty days shorter. In this context, the differences in body size between our two populations could be related either to a Bergmann's cline or to a converse Bergmann's cline (e.g., Blanckenhorn and Demont 2004). Following Bergmann, a larger body size is supposed to be a form of adaptive plasticity in ectotherms to cold environments, where individual body size tends to be bigger because of slower growth (Atkinson and Sibly 1997; Angiletta et al. 2004). Consequently, this is a result of prolonged life cycles and thus of a delayed adulthood. This Bergmann trait is in concordance with some previous studies on spiders. Legault and Weis (2013) showed that a lycosid spider species would react rapidly with an increase in body size to an artificial increase in snow-cover duration. Opell (2010) found larger individuals of *Amaurobioides maritima* (O. P.-Cambridge 1883) along a latitudinal cline in New Zealand as a result of Bergmann's rule. In our study, however, the increased body size is more likely a result of a converse Bergmann's cline. Here, an increase in season length and thus in the ability to gain more resources might result in an increase in body size. This phenomenon has been described earlier for various other ectothermic species (Mousseau 1997; Ashton and Feldman 2003), including spiders (e.g., Høye et al. 2009; Puzin, Leroy, and Pétillon 2014).

Beyond that, there is also another possible explanation regarding the differences in body size. Entling et al. (2010) and Fattorini et al. (2014) found a larger body size in spiders and tenebrionid beetles in warm/dry habitats compared to cool/moist habitats. This is assumed to be most likely a result of a lower desiccation risk of bigger arthropods, and may apply to *P. palustris* in our study as well, resulting in larger specimens in our continental climate section. When looking only at the differences in precipitation between western oceanic and eastern continental climate sections, the risk of desiccation seems obvious; however, previous studies revealed continuously high soil moisture at all microtopographic sites in both study regions (Löffler 2002, 2007).

Effects of elevation

Elevation was a little less important than climate region on body size in our study. However, the elevational effect on body size in *P. palustris* was complex and difficult to unravel, due to the relatively large variation along the elevation gradient.

Even though various earlier studies have shown pronounced differences in body size of wolf spiders as a consequence of harsher conditions with elevation (e.g., Høye and Hammel 2010; Bowden, Høye, and Buddle 2013), this was not consistent for epigeal spiders in our study. Usually, spiders of the genus *Pardosa* have an annual life cycle in the lowlands that is prolonged in some species at higher elevations (Edgar 1972; Steigen 1975; Buddle 2000; Pickavance 2001). In this context,

Steigen (1975) has shown that *P. palustris* overwinters three times before reaching maturity at Hardangervidda in southern Norway. Moreover, a prolonged maturation commonly results in a larger body size in ectothermic species (Angiletta et al. 2004; Blanckenhorn and Demont 2004). However, Otto and Svensson (1982) found a decrease in body size in several Araneae species with elevation and assumed that it is advantageous to be of smaller size at higher elevations, because a smaller size makes it easier to seek shelter in open habitats if predators appear. In previous studies, we found body size in different *Pardosa* species to decrease, but also to increase with elevation in central Norway (Hein et al. 2015), and there also seems to be a pronounced inter-annual variation in body size rather than a variation along the elevational gradient (Hein et al. 2018). This corresponds with findings of Lee, Somers, and Chown (2011), who were not able to detect a linear trend in the size of the indigenous spider *Myro kerguelensis* (O.P.-CAMBRIDGE 1876) with elevational in a sub-antarctic environment. Additionally, a recent study in arctic and sub-arctic environments showed that body size and reproductive traits did not vary with elevation in a consistent manner in four different *Pardosa* species, including *P. palustris* (Ameline et al. 2018).

Toft (1979) assumed that average temperatures, in combination with prey availability, affect life-history traits and determine whether species are annual or biennial in a certain habitats. A change in foraging strategies related to prey availability of *P. palustris* along the elevational gradient might thus also be a possible explanation for our observed patterns, which might reflect related site-specific variation in body size along the elevational gradient (Figure 3).

There seems to be a curvilinear relationship between body size and elevation that might have biological relevance. The transition zone, where the low-alpine and middle-alpine belts overlap, is where the highest interspecific competition is to be expected (Marshall and Rypstra 1999). Here, the increase in competition might lead to a decrease in prosoma width due to the higher number of competitors, and would thus correspond with the *mid-elevation effect* (e.g., Rahbek 1995; Thaler 2003; Becker et al. 2007). This might be the reason for the observed decrease in male body size at approximately 1350 m.a.s.l. in our study as a consequence of the highest species numbers within the transition zones along the elevation gradient in the eastern continental study area (Hein et al. 2014).

Moreover, with elevation, less vegetation coverage and higher proportions of open ground result in higher daily maximum temperatures during summer (Löffler, Cypionka, and Löffler 2008; Wundram, Pape, and Löffler 2010). As a consequence, the conditions for *P. palustris* might be more favorable with elevation than expected. As such, the heterogeneity of microhabitat structures contrast with the overall assumption of unfavorable conditions with elevation.

Effects of topographic position

Our results show that topography-determined snow-cover distribution and its related constraints at finer scales influence body size of epigeal spiders only to a (very) limited extent. Consequently, if topographic position was removed from the model, it would explain a similar amount of variance in body size. This is most likely a result of the high variability of micro-climatic conditions within relatively short distances in arctic-alpine areas (Mani 1968; Wundram, Pape, and Löffler 2010; Scherrer and Körner 2011), and thus the ability of spiders to avoid unsuitable conditions by active selection of optimal micro-habitats (Goldsbrough, Hochuli, and Shine 2004). Wolf spiders in general are supposed to be highly mobile (Samu, Sziranyi, and Kiss 2003), and *P. palustris* is supposed to be one of the most active lycosid aeronauts (Richter 1970). Several studies have reported fine-scale differences in spider body size as a response to microhabitat conditions (e.g., Hendrickx et al. 2003; Pétillon et al. 2009; Torres–Sánchez and Gasnier 2010). Consequently, migration, foraging, and movement behaviors of lycosid spiders have so far received little attention in response to body-size variation, because of great difficulties involved in following the relatively small and highly active specimens in heterogeneous environments (Samu, Sziranyi, and Kiss 2003). The inclusion of environmental data with finer spatial resolution, especially regarding the micro-topographical gradient and the concomitant changing conditions, might result in a higher explanatory power of the variable topographic position.

Conclusions

In our model, differences in environmental factors (i.e., snow-cover duration and related season length) along broad-scaled elevational and regional gradients showed higher explanatory power as drivers of body size than the fine-scaled topographic heterogeneity. Body size variations at finer scales—here topographic position—could not be explained sufficiently. This is probably a result of interactions between elevation and topographic position-related patterns of snow-cover duration, and the concomitant variation of resource availability, predation pressure, and mobility. Accordingly, fine-scale alterations in body size related to the timing of snowmelt seem to be overruled by the broad-scale regional climatic drivers. Our

results might indicate that broad-scale patterns of the body size of *P. palustris* may be more predictable, whereas the fine-scale variation visible along the topographic and elevation gradient remains largely unclear. Consequently, further research in arthropods is needed regarding the reciprocal effects of phenotypic plasticity vs. mobility and dispersal in response to future climate variability.

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No potential conflict of interest was reported by the authors.

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