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Assessing changes in arthropod predator–prey interactions through DNA-based gut content analysis—variable environment, stable diet

Bernhard Eitzinger[1,2] | Nerea Abrego[1] | Dominique Gravel[3] | Tea Huotari[1] | Eero J Vesterinen[1,4] | Tomas Roslin[1,5]

[1]Faculty of Agriculture and Forestry, University of Helsinki, Helsinki, Finland

[2]Nature Conservation and Landscape Ecology, University of Freiburg, Freiburg, Germany

[3]Département de biologie, Université de Sherbrooke, Sherbrooke, Quebec, Canada

[4]Biodiversity Unit, University of Turku, Turku, Finland

[5]Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

Correspondence
Bernhard Eitzinger, Faculty of Agriculture and Forestry, University of Helsinki, Helsinki, Finland.
Email: nanuuto@gmail.com

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Abstract

Analysing the structure and dynamics of biotic interaction networks and the processes shaping them is currently one of the key fields in ecology. In this paper, we develop a novel approach to gut content analysis, thereby deriving a new perspective on community interactions and their responses to environment. For this, we use an elevational gradient in the High Arctic, asking how the environment and species traits interact in shaping predator–prey interactions involving the wolf spider *Pardosa glacialis*. To characterize the community of potential prey available to this predator, we used pitfall trapping and vacuum sampling. To characterize the prey actually consumed, we applied molecular gut content analysis. Using joint species distribution models, we found elevation and vegetation mass to explain the most variance in the composition of the prey community locally available. However, such environmental variables had only a small effect on the prey community found in the spider's gut. These observations indicate that *Pardosa* exerts selective feeding on particular taxa irrespective of environmental constraints. By directly modelling the probability of predation based on gut content data, we found that neither trait matching in terms of predator and prey body size nor phylogenetic or environmental constraints modified interaction probability. Our results indicate that taxonomic identity may be more important for predator–prey interactions than environmental constraints or prey traits. The impact of environmental change on predator–prey interactions thus appears to be indirect and mediated by its imprint on the community of available prey.

KEYWORDS
altitudinal gradient, body mass, interaction probability, lycosidae, metabarcoding, predator–prey interaction

1 | INTRODUCTION

Ecological communities can be represented as networks, where species are represented as nodes connected by interactions. Analysing the structure and dynamics of biotic interaction networks and understanding the elements and processes shaping them are currently one of the key fields in ecology. In fact, biotic interactions are considered some of the main drivers of species distributions (Morales-Castilla, Matias, Gravel, & Araújo, 2015; Wisz et al., 2013) However, while earlier descriptions of interaction networks were based

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on the assumption of static structure (Memmott, Godfrey, & Gauld, 1994; Morris, Lewis, & Godfray, 2004; Summerhayes & Elton, 1923; Van Veen, Müller, Pell, & Godfray, 2008), recent research emphasizes the dynamic nature of interactions along environmental and spatial gradients (Desjardins-Proulx, Laigle, Poisot, & Gravel, 2017; Gravel, Poisot, Albouy, Velez, & Mouillot, 2013; Pellissier et al., 2017).

Importantly, the abiotic environment may have a crucial impact on the structure of local biotic interaction networks as well as on the strength of the interactions (Pellissier et al., 2017; Poisot, Stouffer, & Gravel, 2015). The way in which environment shapes these interactions is a complex topic, as interactions are a sum of often diverging responses of species to their environment. For instance, increasing temperature in freshwater systems affects feeding interaction strength and number of trophic links through changes in body size distributions, prey abundances and changed metabolic demands of the predator (O'Gorman et al., 2012). Current global environmental changes emphasize the need to understand such environmental effects on biotic interactions, but empirical knowledge is still scarce (Gilman, Urban, Tewksbury, Gilchrist, & Holt, 2010; Tylianakis, 2009; Tylianakis, Didham, Bascompte, & Wardle, 2008; Van der Putten, Macel, & Visser, 2010).

On top of environmental constraints, species' traits also influence interspecific interactions (Bolker, Holyoak, Krivan, Rowe, & Schmitz, 2003; Rossberg, Brännström, & Dieckmann, 2010). Approaches based on how traits affect the outcomes of interspecific interactions provide more mechanistic perspectives on network structure than approaches focusing solely on species identities. In pollination networks, for example, studies have suggested that it will be essential to know the match between plant and pollinator traits in order to understand how the interaction network works, as well as for predicting changes in their structure (Garibaldi et al., 2015; Maglianesi, Blüthgen, Böhning-Gaese, & Schleuning, 2014), but see Bartomeus, Cariveau, Harrison, and Winfree (2018); CaraDonna et al. (2017). Likewise, results from experiments have shown that body mass can largely influence biotic interactions, in particular predator–prey links (Brose, 2010; Brousseau, Gravel, & Handa, 2018; Gravel et al., 2013).

Predation is among the most important biotic interactions, connecting species over different trophic levels and affecting their distribution, abundance and behaviour (Begon, Townsend, & Harper, 2005). Recent developments in molecular tools have revolutionized the methods for describing food web structures (Roslin & Majaneva, 2016), especially for species for which the direct observation of the interactions is difficult or even impossible (Traugott, Kamenova, Ruess, Seeber, & Plantegenest, 2013; Valentini, Pompanon, & Taberlet, 2009). This applies particularly to invertebrate food webs involving myriads of species, which in themselves are often difficult to identify visually. Moreover, molecular diet analysis allows tracking of predator–prey interactions in situations where soft prey remains in gut or faeces contain no identifiable morphological structures—or when a predator digests its prey extra-orally, as is the case for centipedes or spiders (Eitzinger, Rall, Traugott, & Scheu, 2018; Wirta, Weingartner, Hambäck, & Roslin, 2015). Molecular tools have thus made it possible to track the multitude of invertebrate trophic interactions of predators by screening gut contents by DNA barcoding (Nielsen, Clare, Hayden, Brett, & Kratina, 2018; Traugott et al., 2013). The resultant molecular data offer unique insights into ecological network structure, by improving node and link resolution.

How interaction structure might be described and compared along gradients is currently a field of active research (Pellissier et al., 2017; Sundqvist, Sanders, & Wardle, 2013). Rather than measuring interaction changes in controlled experiments, environmental gradients offer a wider perspective on biotic processes under varying conditions (Sundqvist et al., 2013). In particular, gradients can be used as a more integrative proxy for complex environments, where the use of single environmental variables would only inadequately describe variation in microclimate and habitat structure. This is because in nature, several abiotic conditions tend to vary in concert —just as multiple climatic characteristics are predicted to change together in climatic predictions for the future (IPCC, 2013). Where environmental gradients encompass suites of abiotic variables projected to change in future, they can be used as "space-for-time" substitutes (Körner, 2007). Observed changes in biotic interaction structure along current, spatial gradients in abiotic and biotic variables can be studied as proxies of future, temporal shifts. While sometimes criticized (e.g., Chuine, 2010), such assumptions form the basis for a wide set of species distribution models, and for most predictions combining future scenarios of climate change with current knowledge of species' ranges (Araújo & New, 2007; Pereira et al., 2010; Thuiller, Lavorel, Araújo, Sykes, & Prentice, 2005). Adopting the same rationale for representing species interaction distribution is a natural step forward.

In this paper, we draw on molecular analysis of predator gut content to derive a new take on feeding interactions and its responses to environment. For this, we use an altitudinal gradient in the High Arctic and examine how the environment, species traits and phylogenetic relationships shape trophic interactions. In the arctic biome, recent research has revealed an increase in temperature and humidity (Bintanja & Andry, 2017; IPCC, 2013), increased plant biomass and extension of shrubs and subsequent changes in arthropod abundances and community composition (Bowden, Hansen, Olsen, Schmidt, & Høye, 2018; Høye, Post, Schmidt, Trøjelsgaard, & Forchhammer, 2013; Koltz, Schmidt, & Høye, 2018; Loboda, Savage, Buddle, Schmidt, & Høye, 2018). Importantly, the very same parameters vary along our elevational gradient, emphasizing the space-for-time connection (IPCC, 2013). Our target predator species is the wolf spider *Pardosa glacialis*, an abundant top arthropod predator in the study area. We determined the composition of the available prey community using pitfall traps and suction sampling along the altitudinal gradient. We applied high-throughput sequencing to analyse predator gut contents. These data allow us to (a) assess how the availability of prey changes along environmental gradients; (b) determine whether predators exert active prey choice by examining the extent to which the consumed prey communities reflect available prey communities; (c) model the interaction distribution as a function

of the predator and prey functional traits as well as environmental conditions. A priori, we expect (a) the richness and abundance of available arthropod prey to decline with increasing elevation, (b) this decline to be reflected in matching trends in the diversity and composition of prey found in the gut of *P. glacialis*; and (c) prey choice to reflect trait matching, with the predator predominantly feeding on abundant prey groups with an optimal predator–prey body size ratio.

We used a set of different approaches to tackle each of these questions. Using joint species distribution models (JSDM), we first relate the prey community available to the environmental parameters defining our altitudinal gradient. In a second step, we use JSDM to assess the match between the available prey community with the consumed prey community detected in predator gut contents, and thus test the level of selectivity in prey choice. In a third step, we assess how predation probability changes with respect to the match between predator and prey body size, prey phylogeny and environmental conditions.

2 | MATERIAL AND METHODS

2.1 | Study system, study area and study design

The High Arctic is currently facing rapid transformation, making this region an ideal system in which to explore the effects of environmental change. Higher temperatures in combination with increasing precipitation are shifting the flowering phenology (Høye et al., 2013; Schmidt et al., 2016) and converting a predominantly graminoid vegetation into one dominated by shrubs (Myers-Smith et al., 2011), altering the timing, diversity and abundances of arthropods (Høye et al., 2013; Nielsen & Wall, 2013). In the absence of ants and beetles, wolf spider *Pardosa glacialis* (Araneae, Lycosidae) is at the top of the arthropod food web, feeding on a wide range of prey (Wirta et al., 2014; Wirta, Weingartner, et al., 2015). *Pardosa* itself is experiencing a shift in body size distribution with warming, reflected by an increase in female spider size over the last two decades (Høye, Hammel, Fuchs, & Toft, 2009). These changes may also be coupled with changes in female fecundity resulting in changes of spider abundance and population structure (Bowden, Høye, & Buddle, 2013; but see Bowden et al., 2018).

The Zackenberg valley (74°28′N, 20°34′W) is situated in the Northeast Greenland National Park (for detailed description, see Meltofte & Rasch, 2008). The area is characterized by a high-arctic tundra adapted to very cold and snow-rich winters and cool summers with a mean summer temperature (June–August) of 4.7°C and 29 mm of precipitation. Time without snow cover lasts from July to September (Kankaanpää et al., 2018). The tundra at Zackenberg hosts a limited arthropod fauna of over 330 species, dominated by Diptera and Hymenoptera (Wirta, Várkonyi, et al., 2015). As a specific asset for the current study, previous work has yielded a comprehensive reference library of DNA barcodes for almost all taxa recorded in the area (Wirta, Várkonyi, et al., 2015).

To record elevation-dependent changes in arthropod community and interaction processes, we defined three parallel altitudinal gradients on the south-facing slopes of the Aucella mountain, spanning from 19 to 586 m above sea level (asl) (Figure 1). In each altitudinal gradient, we placed six plots of *c*. 50 m × 50 m. We selected plots according to the presence of *Pardosa*, thereby excluding very wet sites (i.e., fen in low elevations) and high-elevation sites without vegetation (over 600 m asl). The vegetation in most of the study plots is dominated by mountain aven *Dryas octopetala* × *integrifolia* (Rosaceae). Beyond this species, *Cassiope tetragona* and *Vaccinium uliginosum* (both Ericaceae) are also abundant at lower elevations up to 200 m asl, whereas *Salix arctica* (Salicaceae), lichens and mosses are abundant at higher elevations starting from 300 m asl. In each study plot (except three: DX, IX and LX in Figure 1), we measured temperature and humidity. Given a general decline in temperature with increasing elevation (generally 0.4°C per 100 m in this geographical region; Marshall, Sharp, Burgess, & Anslow, 2007), elevation was used as a catch-all metric of the main gradients in the environment, with a direct link to projected future climate change (see above).

2.2 | Data collection

We sampled terrestrial invertebrates every fifth day (i.e., on four occasions) on each of the 18 plots through July 2015, the period of maximum invertebrate activity. *Pardosa glacialis* individuals were collected by hand, transferred individually to 2-mL microcentrifuge tubes and stored at −20°C on the same day. On average, we collected ten *Pardosa* individuals per plot on each sampling day. In total, we collected 670 spiders, which were determined for sex, developmental stage and body length. Additionally, we used a mass–length regression to infer *Pardosa* body mass from body length (see Supporting Information).

We used two different collection methods to record the composition and abundance of the available prey community. Large flying insects and running arthropods (e.g., butterflies, muscid flies, spiders) were collected using two yellow pitfall traps per plot, which were emptied every fifth day (i.e., three sampling time intervals). Yellow pitfall traps (10 cm diameter; filled with water and a single drop of Tween-20 detergent (Sigma-Aldrich, Munich, Germany) combine the advantages of yellow pan traps with standard pitfall traps (Buchholz, Jess, Hertenstein, & Schirmel, 2010). Litter-dwelling and vegetation-associated arthropods (e.g., aphids, mites, sciarid flies) were sampled using a suction sampling device (Stihl SH 56, Andreas Stihl AG & Co. KG, Waiblingen, Germany) on two randomly chosen areas of 0.5 × 0.5 m per plot every fifth day on four occasions. While any collection method will come with certain biases towards particular taxa, we expected this combination of collection techniques to offer a wholesale description of the arthropod community available to predatory spiders. All specimens were stored in 75% ethanol and identified to family level using the identification keys by Böcher, Kristensen, Pape, and Vilhelmsen (2015). The complexity of the local vegetation was described by vegetation mass, measured as the dry weight of the organic layer sampled in two soil cores (5 cm diameter) per site. This metric will specifically reflect the vertical dimension

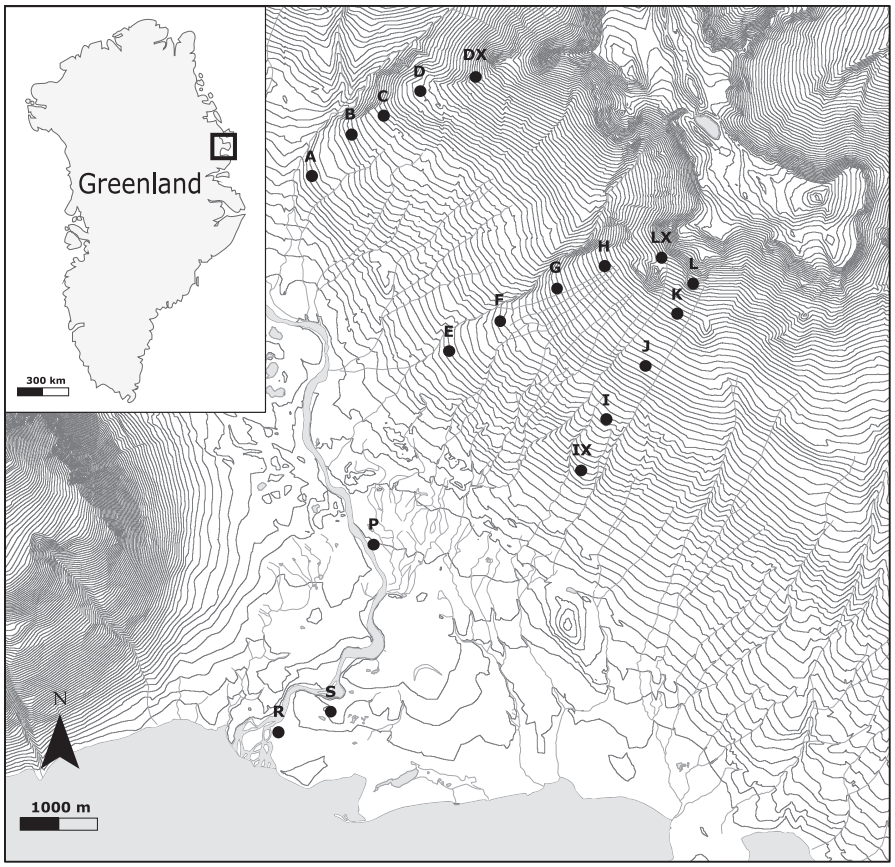

FIGURE 1 Map of the Zackenberg valley (74°28′N, 20°34′W) in the Northeast Greenland National Park. Dots indicate 18 study plots along altitudinal gradients from 19 to 586 m asl

(i.e., topographical complexity) of the very short and essentially two-dimensional high-arctic tundra vegetation.

2.3 | DNA extraction, PCR and library preparation

We extracted DNA of whole *Pardosa* individuals including prey DNA using a salt-based extraction protocol (Aljanabi & Martinez, 1997), adopting the modifications proposed by Vesterinen et al. (2016). DNA extracts were purified using a SPRI bead solution at a ratio of 1:2 (Vesterinen et al., 2016). A blank control was included within each batch of 47 individuals to test for DNA carry-over contamination. No contamination was detected when analysing PCR products of these blank controls on agarose gel.

All *Pardosa* samples were analysed for arthropod prey DNA using primers ZBJ-ArtF1c and ZBJ-ArtR2c (Zeale, Butlin, Barker, Lees, & Jones, 2011), which amplify a 157-bp-long target fragment *cytochrome c oxidase subunit I* (COI) region (Folmer, Black, Hoeh, Lutz, & Vrijenhoek, 1994). In silico testing of these primers showed their efficiency in detecting most insect prey present in Zackenberg, as also empirically corroborated by recent studies (Schmidt, Mosbacher, Eitzinger, Vesterinen, & Roslin, 2018; Wirta, Vesterinen, et al., 2015) for further justification of primer choice, see Supporting Information). However, primers ZBJ-ArtF1c and ZBJ-ArtR2c perform poorly in amplifying soil-living prey such as Collembola and mites, whereas they do amplify DNA of *Pardosa* spiders. This amplification of the quantitatively dominant source of DNA, that is, the predator itself, risks masking small amounts of prey DNA, resulting in high detectability thresholds. We therefore screened all *Pardosa* samples with additional primers ARCF3 and ARCR6 (Schmidt et al., 2018), which amplify a 69-bp-long target fragment within the mitochondrial *cytochrome c oxidase subunit I* (COI) region (Folmer et al., 1994). This primer pair (ARCF3/ARCR6) does not amplify wolf spider DNA, whereas it does efficiently amplify DNA of Collembola and Acari in the spider gut content. A comparison of the efficiency of the two primer sets to amplify local arthropod taxa is provided in Supporting Information Table S4.

Each 10 μl PCR contained 5 μl MyTaq Red Mix PCR mastermix (Bioline, London, UK), 0.5 μl bovine serum albumin (BSA, 3%; Roth, Karlsruhe, Germany), 0.5 μl sterile water, 0.5 μM of each primer and 3 μl of DNA extract. PCR cycling conditions for primers ZBJ-ArtF1c/ZBJ-ArtR2c followed the protocol in Zeale et al. (2011), while primers ARCF3/ARCR6 followed the protocol offered in Schmidt et al. (2018). Each PCR was carried out as two separate replicates. After the first, locus-specific PCR round, the second-step PCR followed directly including Illumina-specific adapters with a unique dual-index combination for each single reaction, that is, also PCR replicates were tagged with unique indexes. Indexed PCR products were purified using a SPRI bead protocol (Vesterinen et al., 2016). Sequencing was performed by the Functional Genomics Unit of the University of Helsinki, Finland, using v2 chemistry with 300 cycles and 2*150 bp paired-end read length on an Illumina MiSeq platform.

2.4 | Bioinformatics

The sequencing run yielded 5806962 (Zeale fragment) and 2455031 (ARC fragment) paired-end raw reads pre-processed through Q20 filter by MISEQ software. The reads were uploaded to CSC servers (IT Center for Science, www.csc.fi) for trimming and further analysis following the bioinformatics pipeline as described in Kaunisto, Roslin, Sääksjärvi, and Vesterinen (2017). We first merged and trimmed paired-end reads using USEARCH version 9 (Edgar, 2010). We then removed primers using CUTADAPT version 1.11 (Martin, 2011). The reads were then collapsed into unique sequences (singletons removed), chimaeras were removed, and reads were clustered into zero-radius OTUs (ZOTU; Edgar, 2016) and mapped back to the original trimmed reads to establish the total number of reads in each sample using USEARCH version 9. Our final data set consisted of 3087049 (*COI*) reads for Zeale sequences and 1143355 (*COI*) for ARC sequences, respectively. Zeale products were assigned to a taxonomic level using BLAST (Altschul, Gish, Miller, Myers, & Lipman, 1990) and the PYTHON script package "bold-retriever," version 1.0.0 (Vesterinen et al., 2016), while ARC products were assigned to a local database build on Greenlandic arthropod species (unpublished). About 90% of all reads could be identified to at least order level (98% similarity threshold) and were thus retained for further analyses, whereas the rest of the reads (10%) were discarded.

2.5 | Statistical analyses

We first analysed the prey family × plots matrix, where we pooled the data of all captured *Pardosa* individuals for each plot, as well as the data from different trapping methods for each plot. For gut content analyses, we pooled data derived by primer pairs ZBJ-ArtF1c/ZBJ-ArtR2c and ARCF3/ARCR6, respectively, into prey family × plot matrix, where each entry denotes a joint observation of presence and interaction. The abundance of specific prey families in the gut was calculated as the sum of *Pardosa* individuals containing DNA from specific prey families. The abundance of prey families per plot was calculated as prey individuals caught per trap-day and number of prey individuals per m^2, for pitfall traps and for suction sampling, respectively.

2.5.1 | Modelling variation in available prey community

We used a three-step approach to assess changes in prey availability along the altitudinal gradient. First, we fitted two versions of joint species distribution models (JSDM) using Hierarchical Model of Species Communities (HMSC) R package (Ovaskainen et al., 2017; R Core Team, 2018). We fitted one JSDM to the presence–absence data matrix using a probit link function and another one to the abundance data matrix using a log-normal link function. As explanatory variables, we used elevation and (log-transformed) vegetation mass, both treated as continuous variables. The visit time and plot identity were included as random effects. We also included a phylogenetic tree of prey species to assess whether relatedness of prey families influences their occurrences along the altitudinal gradient (details about how the phylogenetic tree of prey taxa was constructed are provided in the Supplementary Information) and calculated phylogenetic signal as explained in Ovaskainen et al. (2017). We used the variance partitioning described in Ovaskainen et al. (2017) to characterize the effect of each of the explanatory variables as well as how much the species' responses were influenced by the insect feeding type (i.e., whether they are carnivores, herbivores, detritivores or parasitoids). Second, we modelled the total available prey species richness (i.e., family count per plot) by fitting a Poisson model with lme4 (Bates, Mächler, Bolker, & Walker, 2014) in R software. Third, we modelled the total available prey abundance (i.e., sum of the abundances per plot) by fitting a log-normal model with lme4.

2.5.2 | Comparing consumed vs. available prey communities

As the next step, we examined what prey was consumed out of the prey available. We first compared the differences in species (family) richness between the consumed vs. available prey communities. For this, we computed species richness for each sample as the number of distinct families identified. We then examined how the consumed community composition differed from the available prey community composition, by applying non-metric multidimensional scaling analysis (NMDS) with Bray–Curtis dissimilarity distance using the vegan R package (Oksanen et al., 2018). We assessed the differences in community composition both for the presence–absence data and for (square root transformed) abundance data. We used the betapart R package (Baselga & Orme, 2012) to assess whether the differences in community composition originated from changes in species identities (i.e., species turnover) or differences in species richness (i.e., nestedness).

We analysed whether and how the consumed prey community composition depends on the available prey community composition. We used the data matrix where the consumed (i.e., families found in spider gut) and available (i.e., families found in the study plots) prey were combined. We fitted one JSDM to the presence–absence data of this data table (using a probit link function) and another one to the abundance data (using a log-normal link function), in both cases using the HMSC R package (Ovaskainen et al., 2017). In both models, we included information on whether the families were identified in the spider gut or in the field as a categorical explanatory variable, and the elevation of the plots and the local vegetation mass as continuous explanatory variables. To control for the non-independence of data collected during individual visits to individual plots, we included the visit time and plot identity as random effects. We also included the combination of plot and time as a random effect to examine whether the composition of the available prey community matched that of the prey community consumed. As in the previous analyses, we also included a phylogenetic tree and prey feeding type into the models.

2.5.3 | Modelling prey consumption

We examined which variables determined prey consumption by fitting two alternative mixed-effects logistic regression models to the binary data indicating whether the insect families were consumed or not. The first alternative model included prey family as a categorical explanatory variable, and the second alternative model included log-transformed prey body mass (measured at the family level) as a continuous explanatory variable. In both alternative models, we included elevation and vegetation as continuous explanatory variables. To account for the structure of the study design, we included the plot and sampling time as random effects. We selected the most parsimonious model following a backward variable selection procedure based on Akaike information criterion (AIC) (Burnham & Anderson, 2004). The models were fitted using the lme4 R package (Bates et al., 2014).

2.5.4 | Modelling predation probability

We examined how occurrence of predatory interaction depends on predator traits, prey traits, prey phylogeny and the environment by applying a model based on the matching-centrality formalism (Brousseau et al., 2018; Rohr, Naisbit, Mazza, & Bersier, 2016). In this modelling approach, the interaction probability, that is, the encounter probability between the predator and prey, is hypothesized to be constrained by the match of the predator and prey traits given environmental conditions. The explanatory part of the model includes both "matching" and "centrality" components (Rohr et al., 2016). In our fitted model, the matching component included the matching between predator and prey body mass, whereas the centrality components included non-matching traits (prey feeding type), prey phylogeny (i.e., the first and second PCoA axes applied to the phylogenetic correlation matrix; Brousseau et al., 2018) and environment (elevation and vegetation mass). The mathematical details of the fitted model are provided as Supplementary Information. We selected the most parsimonious model following forward variable selection and comparing model's performance based on AIC (Burnham & Anderson, 2004).

3 | RESULTS

3.1 | Prey community composition and interactions

The available prey community was composed of 26 arthropod families representing five different orders: Araneae, Diptera, Hemiptera, Hymenoptera and Lepidoptera. Specimens of four other arthropod orders (Collembola, Mesostigmata, Oribatida and Prostigmata) were not identified to a lower taxonomic level. Pitfall traps and suction sampling yielded complementary information on the available prey community composition. Catches from pitfall traps were dominated by relatively large flying and cursorial taxa, whereas suction samples consisted mostly of small, litter-associated prey. In pitfall traps, most individuals belonged to Diptera in families Muscidae (20.3%), Chironomidae (12.1%) and Phoridae (9.9%) and mites in Prostigmata (14.2%) and Mesostigmata (10.9%) (Supporting Information Figure S2). Suction sampling showed a dominance of mites in Oribatida (38.8%) and Mesostigmata (28.9%), followed by Diptera in family Chironomidae (16.6%), and Collembola (10.5%) (Supporting Information Figure S3).

Of 670 collected *Pardosa* individuals, 668 were found to contain DNA of 172 different prey species representing 51 families and 13 arthropod orders. Most *Pardosa* individuals contained DNA of Dipteran families Chironomidae (95.7%), Sciaridae (78.1%), Culicidae (59.3%), Empididae (54.3%) and Ceratopogonidae (51.2%) (Supporting Information Figure S4).

To allow comparison of available prey community with community found in predator gut, we pooled soil arthropod prey families in higher level taxa: Isotomidae, Hypogastruridae and Katiannidae in "Collembola"; Anystidae, Bdellidae, Diptilomiopidae, Erythraeidae, Eupodidae, Penthaleidae, Rhagidiidae, Stigmaeidae and Tetranychidae in "Prostigmata"; Linyphiidae and Dictinydae in "other Araneae."

3.2 | Factors influencing available prey community composition

The JSDM fitted to data on the available prey community explained 26% of total variance in both presence–absence and abundance. Elevation was by far the most important factor influencing prey presence–absence and abundances, accounting for 61% and 56% of explained variance, respectively (Figure 2a and Supporting Information Figure S5A). Vegetation mass explained 18% and 16% of the variance explained for presence–absence and for abundance data. On the other hand, feeding type of prey explained very little, 2% and 8% of the variance explained for presence–absence and for abundance data, respectively. Phylogenetically related species tended to respond to altitude and vegetation mass in a similar way, as revealed by the parameter value measuring the phylogenetic signal: On a scale from 0 to 1 (from total independence to perfect correlation), the phylogenetic signal was 0.22 for prey presence–absence and 0.55 for prey abundance.

In general, the abundance of all taxa tended to decrease (although non-significantly) with elevation and vegetation mass. Collembola and spiders in family Thomisidae showed the most negative response to higher elevations, whereas flies in Tachinidae showed the most positive response (posterior probability >0.95). In addition, Tachinidae showed a negative response to vegetation mass (posterior probability >0.95). Yet, neither the species richness nor total abundance of available prey varied significantly with elevation or vegetation mass ($p > 0.05$).

3.3 | A comparison between consumed vs. available prey communities

The mean number of prey families identified in *Pardosa* gut contents did not differ from the mean number of prey families identified in the sampling plots (14.4 vs. 13, $p = 0.4801$). Yet, the

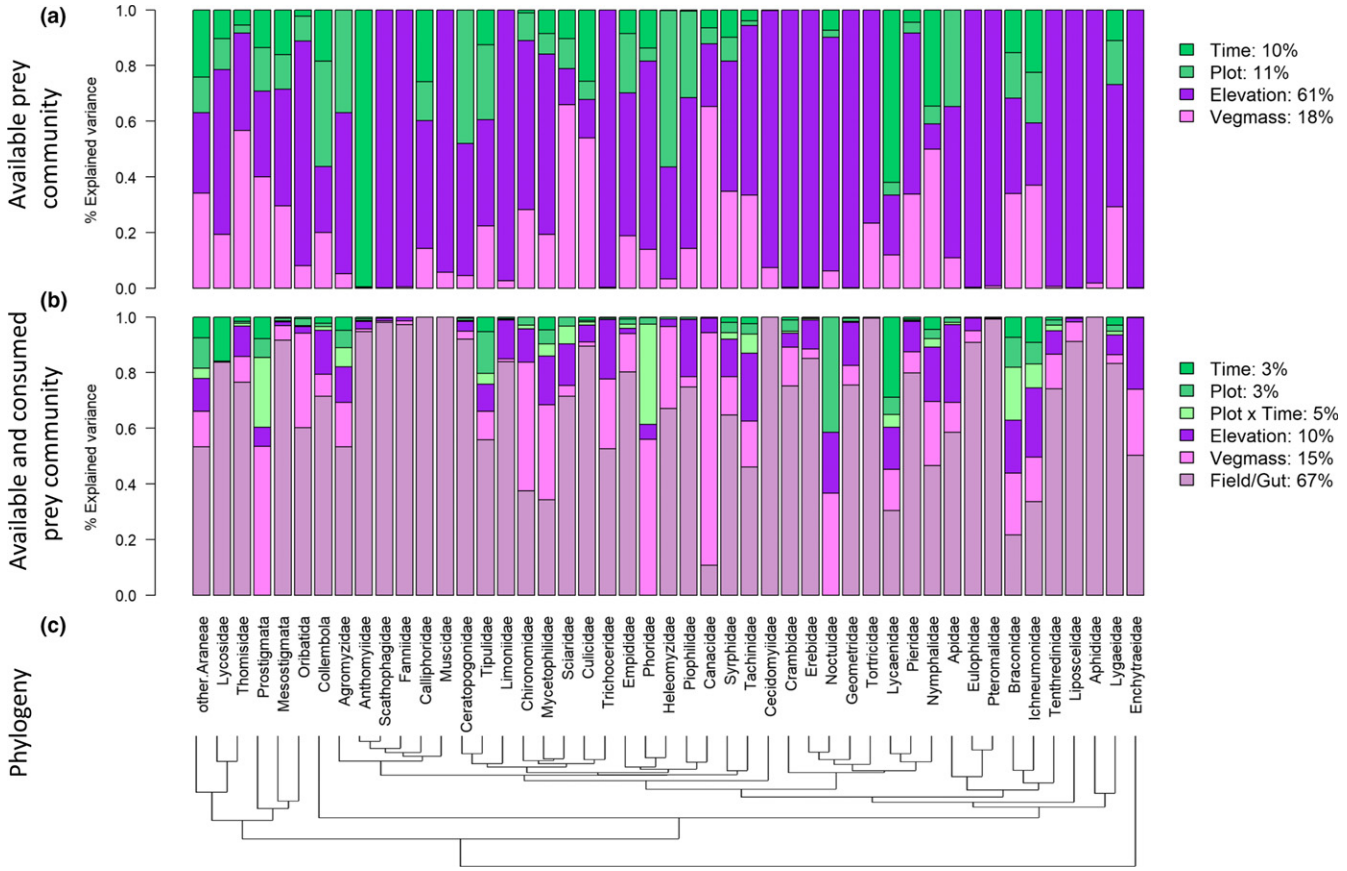

FIGURE 2 Relative proportions of variance attributed to different descriptors of prey community composition: visit time, plot identity, their interaction, whether the families were identified in the spider gut or in the field (Field/Gut), vegetation mass (Vegmass) and elevation. Panel a shows the results from the JSDM fitted to the available prey community data and, Panel b to the data containing both consumed and available community data. Panel c shows the phylogenetic tree of the prey species. The variance attributed to the fixed effects is indicated in shades of purple, and the variance attributed to the random effects is indicated in shades of green. Each bar represents a prey family. The results are drawn from the probit models fitted to presence–absence data. The same plot but for the model fitted to the abundance data is provided as Supporting Information Figure S5

composition of prey families consumed differed strongly from the composition of prey families available (Figures 3 and 4). This difference in community composition was mostly driven by differences in family identity; that is, there was high turnover in the set of families encountered in available vs. consumed prey (Supporting Information Table S2).

The JSDM fitted to the data matrix including both the consumed and available prey communities explained 38% of the total variance in presence–absence and 37% of variance in abundance. The composition of prey encountered in *Pardosa* gut differed considerably from the composition of the prey community available in the field: Whether the communities were found in guts or in the field explained most of the variance for both the presence–absence model and the abundance model (67% vs. 72%, Figure 2b and Supporting Information Figure S5B). More than half of all families in the data set were positively selected by *Pardosa* spiders (with 26 out of 46 taxa showing a positive estimate value to being found in spider gut with posterior probability >95%), whereas the rest of families showed no statistically strong results. In comparison, the combination of plot identity and visit time explained little variation (5%). Elevation and vegetation mass explained the most prey presence–absences, whereas the rest explained less than 10% of variation in both prey presence–absences and abundances. The feeding type of the prey families explained only 2% of the responses to environmental conditions. The responses of the species to whether they were found in the spider gut or in the field were quite randomly distributed across prey phylogeny (phylogenetic signal for presence–absence model was 0.05 and 0.40 for abundance model).

3.4 | Factors influencing prey consumption

Pardosa spiders used specific prey families regardless of the altitudinal zone where they were found, or the surrounding vegetation. Likewise, what *Pardosa* consumed did not depend on prey size, but on prey identity (i.e., family). The mixed-effects regression model revealed the five most positively selected prey families to be flies Chironomidae (estimate = 9.10, $p < 0.001$), Sciaridae (estimate = 7.70, $p < 0.001$), Culicidae (estimate = 6.82, $p < 0.001$), Empididae (estimate = 6.63, $p < 0.001$) and Ceratopogonidae

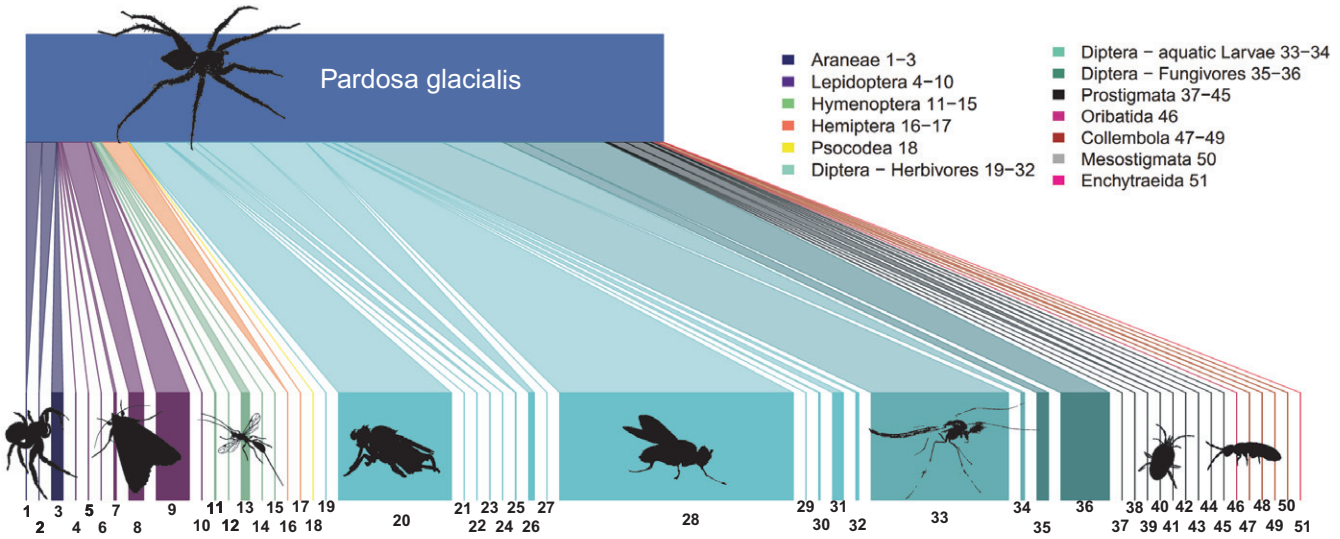

FIGURE 3 Trophic link structure between *Pardosa glacialis* (upper bar; $n = 668$ and its prey (lower bars; identified to the family level) at Zackenberg, Northeast Greenland. Trapezoids connecting the upper and lower bars show the frequency of prey taxa in the gut contents of *Pardosa* (upper end of connector) and in the field (lower end of connector). Thus, non-parallel sides in a trapezoid suggest some selectivity in spider predation on the focal taxa, with an upward tapering trapezoid suggesting an underrepresentation of this item in the diet of *Pardosa*, and an upward widening trapezoid showing the opposite. For soil-living prey (mites and Collembola, lower right), this interpretation is lacking, since these taxa were sampled by a separate method (suction sampling) and thus assigned uniform width in the graph (see text for details). Each arthropod order is identified by a specific colour. Note that this metaweb combines data from all 18 plots and sampling dates, and hence does not account for variation in prey availability realized between sites. Numbers refer to following prey families. 1 Dictynidae, 2 Linyphiidae, 3 Thomisidae, 4 Crambidae, 5 Erebidae, 6 Geometridae, 7 Lycaenidae, 8 Noctuidae, 9 Nymphalidae, 10 Tortricidae, 11 Braconidae, 12 Eulophidae, 13 Ichneumonidae, 14 Pteromalidae, 15 Tenthredinidae, 16 Aphididae, 17 Lygaeidae, 18 Liposcelidae, 19 Limoniidae, 20 Phoridae, 21 Trichoceridae, 22 Agromyzidae, 23 Anthomyiidae, 24 Cecidomyiidae, 25 Ceratopogonidae, 26 Empididae, 27 Fanniidae, 28 Muscidae, 29 Scathophagidae, 30 Syrphidae, 31 Tachinidae, 32 Tipulidae, 33 Chironomidae, 34 Culicidae, 35 Mycetophilidae, 36 Sciaridae, 37 Anystidae, 38 Bdellidae, 39 Diptilomiopidae, 40 Erythraeidae, 41 Eupodidae, 42 Penthaleidae, 43 Rhagidiidae, 44 Stigmaeidae, 45 Tetranychidae, 46 Achipteriidae, 47 Isotomidae, 48 Katiannidae, 49 Hypogastruridae, 50 Zerconidae and 51 Enchytraeidae

(estimate = 6.53, $p < 0.001$) (Supporting Information Table S3). For example, *Pardosa* spiders did not consume more Tachinidae or Phoridae flies along the elevational gradient even if they were increasingly available and did not consume less Thomisidae spiders even if their availability decreased (Supporting Information Figure S6).

3.5 | The influence of trait matching on predation probability

We found the most parsimonious model (Table 1) relates the occurrence of an interaction to predator and prey body mass, including their quadratic terms, and their interaction, elevation and square of elevation, a binary variable indicating whether prey is a detritivore feeding type or not, and prey phylogeny. This model was significantly better than the previous-best model (delta AIC = 1019.85) and explained 12% of the variation in predation probability (Table 1).

The parameterized model suggested that predation probability is highest for small and large prey (Figure 5). This specific relation was affected by elevation, in particular for large prey and predators. At the lowest elevation, the probability of predation decreased with increasing prey body size and predator body size; that is, at lowest elevation large predators fed less on large prey. In contrast, at the highest elevation, the probability of predation increased with increasing prey body size and predator body size—large predators fed more on large prey.

4 | DISCUSSION

In this study, we have shown how molecular data can be used for a novel purpose: to address interaction change and its drivers along environmental gradients. The composition of available arthropod prey changed significantly along with elevation but not the gut content of a dominant predator. Rather than being modified by environmental constraint, such as elevation or vegetation complexity, this predator tended to always select similar prey. Below, we will examine each finding in turn.

4.1 | Prey community available vs. prey community used

Consistent with our expectations, elevation and vegetation had significant effects on the presence and abundance of single arthropod families. However, these imprints did not translate into significant changes in emergent community properties such as species richness

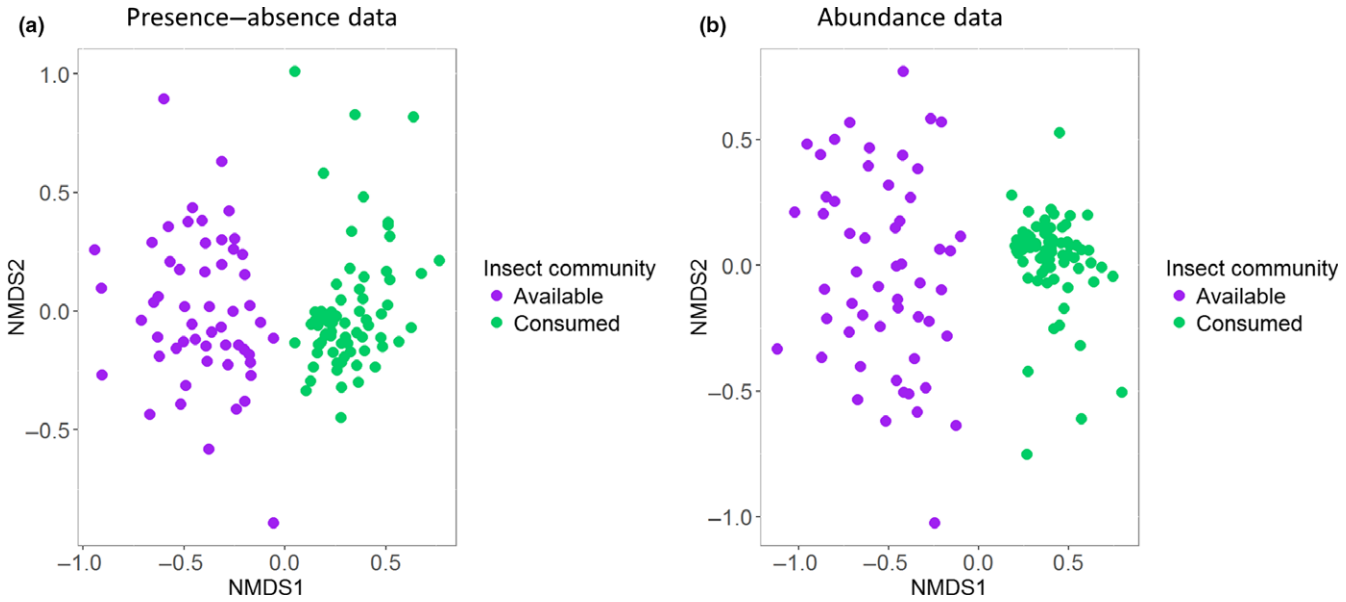

FIGURE 4 Available vs. consumed prey community composition displayed in the ordination space of a non-metric multidimensional scaling analysis (NMDS). Panel a is based on Bray–Curtis dissimilarity distances calculated from the presence–absence data, and Panel b is based on Bray–Curtis dissimilarity distances calculated from the square root transformed abundance data

TABLE 1 Model comparison explaining predation probability-based environmental variables 'Elevation' (m asl; continuous) and 'Vegetation mass' (g, continuous), species traits 'Prey feeding mode' (detritivore; categorical 1/0), trait match of predator and prey body masses (BM, mg, continuous) and prey phylogeny (first two PCoA axes of the phylogenetic correlation matrix, continuous), as well as their interaction terms. MacFadden pseudo R^2 was calculated by comparing model-specific maximum likelihood (ML) with a null model (including intercept only). The last row shows the best model selected based on AIC

Model	Variables included	ML	Pseudo R^2	AIC
m1	Prey abundance, Elevation	−6972.18	0.016	13950.36
m2	m1 + Vegetation mass	−6970.75	0.016	13947.5
m3	Prey abundance, Pred BM, Prey BM, Pred BM*Prey BM	−6927.35	0.022	13864.71
m4	m1 + Pred BM, Prey BM, Pred BM*Prey BM	−6925.74	0.02	13863.49
m5	m4 + Pred BM^2, Prey BM^2	−6743.63	0.05	13503.26
m6	m5 + Pred BM*Prey BM*Elevation	−6752.80	0.05	13521.6
m7	m6 + $Elevation^2$	−6750.39	0.05	13518.79
m8	m7 + Vegetation mass	−6750.21	0.05	13520.41
m9	m5 + $Elevation^2$	−6741.48	0.05	13500.95
m10	m9 + Feeding mode	−6737.54	0.05	13495.08
m11	m10 + Phylogeny	−7082.40	0.12	12475.23

or overall abundance with elevation. Thus, the overall availability and local diversity of arthropod prey remained more or less constant across the gradient.

Changes in arthropod community composition along the elevation and vegetation gradient will likely reflect adaptation to dominant environmental conditions, such as ambient temperature and humidity. These observations are consistent with those described in tundra communities of plants, microbes and invertebrate communities (e.g., Bowden & Buddle, 2010; Høye et al., 2017; Rich, Gough, & Boelman, 2013; Sundqvist et al., 2011). In plots at low elevation, which are characterized by high humidity, we found many small taxa associated with soil, such as Collembola, as well as mesostigmatid and oribatid mites. Such mesofauna, but also fungivore groups including sciarid flies, are predominantly decomposers and thus dependent on the litter and microbial resources—the availability of which is linked to humid conditions (Hansen et al., 2016; Hodkinson, 2005). Decreases in their abundance with increasing elevation may therefore be explained by a decline of available resources, while herbivorous, predacious and pollinating arthropods are less affected.

At higher elevation and plots with low vegetation mass, however, the community is increasingly dominated by flower visitors such as muscid flies and chironomid midges. Diptera in general, and muscid flies in particular, are increasingly dominant northwards along a latitudinal gradient in the Arctic (Böcher et al., 2015)—and have declined with warming conditions over time (Høye et al., 2013; Loboda et al., 2018). These parallel observations support the interpretation that spatial clines in prey availability seen along our local environmental gradient at Zackenberg may be similar to temporal changes associated with ongoing climate change. With spatiotemporal changes in abiotic conditions, we then see changes in the community of available prey—and the question is how it reflects into prey use by predators.

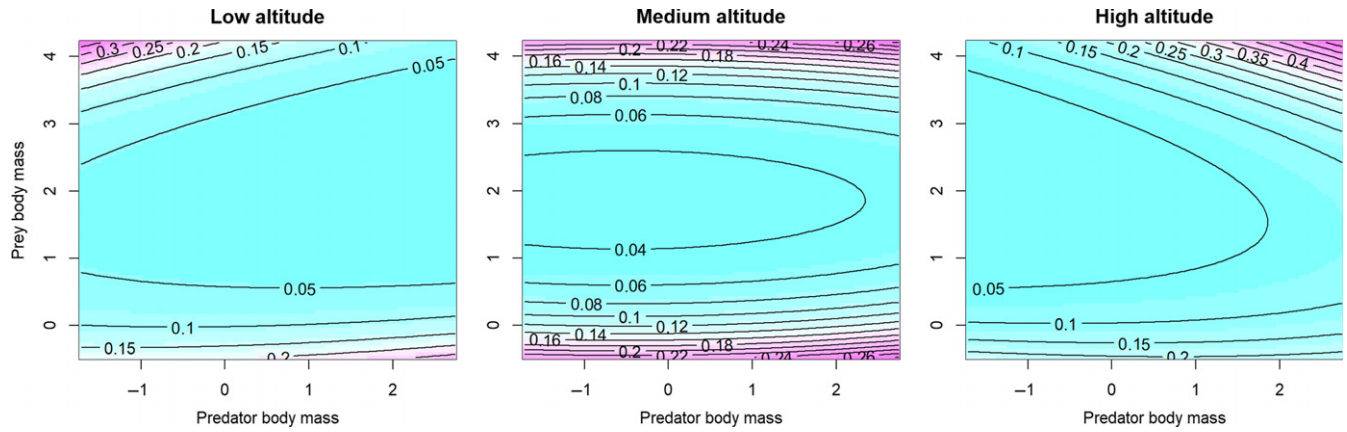

FIGURE 5 Predicted changes in predation probability in relation to log-transformed prey and predator body mass match along the altitudinal gradient. The isoclines depict the predation probabilities, with the lowest probabilities coloured in blue and the and highest probabilities in purple. The three panels show (from left to right) the predation probabilities predicted for the lowest elevation in the data set, for the mean elevation, and for the highest elevation

Contrary to our expectations, the community found in *Pardosa* gut contents was similar across elevation and did not change in response to local shifts in the abundances of prey families (for important caveats regarding gut content analysis, see Supplementary Information). Moreover, the ingested prey community included prey taxa which were relatively rarely recorded in our environmental traps, for example, aphids. The consumed prey community consists mostly of small to medium-sized Diptera such as chironomid and sciarid midges, which were found in more than 90% of all analysed predator individuals. In addition, many other Diptera families, such as Anthomyidae, Cecidomyidae and Culicidae, are proportionally overrepresented in the gut content samples as compared to field samples, again indicating a preference independent of prey abundance in the environment. However, in contrast to the diet of wolf spiders in high alpine glacier forelands (Ingimarsdóttir, Michelsen, Ripa, & Hedlund, 2014; Raso et al., 2014), springtails and intraguild prey (i.e., other spider species) proved relatively unimportant prey for *Pardosa glacialis*. The present results demonstrate highly selective feeding by *Pardosa* spiders. This selectivity occurs in the face of variation in the environment and in the prey community, and is not well explained by prey size or phylogeny as such (yet, for other traits, see below).

4.2 | Environmental conditions vs. trait matching as determinants of trophic interactions

The observed mismatch between consumed and available prey groups may be explained by preferred feeding on certain prey families. *Pardosa*, like other species within the wolf spider family, employs a generalist feeding style, preying on a wide spectrum of arthropod groups. In our study, we found *Pardosa* to be feeding on up to 51 arthropod families, corroborating previous studies suggesting a wide prey spectrum for wolf spiders in general (Nentwig, 1986; Nyffeler & Breene, 1990) and of arctic spiders in particular (Wirta, Vesterinen, et al., 2015; Wirta, Weingartner et al., 2015).

While *Pardosa* may be a generalist predator, this does not imply that it chooses its prey at random or opportunistically. From the ten most important prey groups found in *Pardosa* guts, which account for 74% of all diet, eight belong to Diptera, the largest and most diverse prey group found at Zackenberg (Wirta, Vesterinen, et al., 2015). Adult Diptera are predominantly found in aboveground vegetation strata and are often active during daytime, both factors of which facilitate encounter rates with the diurnal predator. Wolf spiders have also been observed to sit on open *Dryas* flowers, probably ambushing flower-visiting insects (M. Tiusanen, personal communication).

Diptera are prey of relative high nutritional value and do not show anti-predator behaviour besides flight (Rickers, Langel, & Scheu, 2006). Indeed, wolf spider will select for such prey in order to maximize energy uptake for metabolic and catabolic expenditures, such as reproduction (e.g., Schmidt, Sebastian, Wilder, & Rypstra, 2012). Interestingly, however, the high local abundance of specific Diptera, like muscid and tachinid flies (Figure 3; see also Loboda et al., 2018; Tiusanen, Hebert, Schmidt, & Roslin, 2016; Wirta, Vesterinen, et al., 2015), is not reflected in the gut content. Thus, their behaviour or morphology seems to include traits (e.g., large body size) making them either hard to catch or difficult to handle by wolf spiders.

Aphididae (Hemiptera) and Noctuidae (Lepidoptera) emerged as the most important non-dipteran prey of *Pardosa* predators. Aphids have already been reported to be important prey in agricultural sites (Kuusk, Cassel-Lundhagen, Kvarnheden, & Ekbom, 2008), and share many characteristics with chironomid and sciarid midges, such as small size, which makes them a likely prey. High feeding rates on noctuid moths, in particular on *Sympistis nigrita*, are likely due to predation on their larvae, which are abundant feeders on *Dryas octopetala*, the dominant dwarf shrub in our study plots. Interestingly, more than half of all prey families had been fed on by less than 5% of all *Pardosa* individuals examined, thus emphasizing the predator's focus on a few prey groups only while still being able to feed on a wide range of other prey.

4.3 | Modelling interactions based on trait matching

The importance of trait matching between predator and prey has been repeatedly highlighted in recent literature (Bartomeus et al., 2016; Gravel, Albouy, & Thuiller, 2016). Here, even the best trait-based model explained relatively little (12%) of the overall variance in the occurrence of interactions. Interpretation of parameters suggests that predators of all sizes will be likely to attack small prey regardless of elevation, but that the probability of larger predators feeding on large prey changes with elevation, from being low at low elevation to being high at high elevation. Including prey phylogeny significantly improved the model, indicating that some phylogenetic conserved traits may override the impact of the focal trait (body size). The different effects of body size at different elevation will simply reflect elevational differences in the availability of (constantly) preferred prey.

Importantly, limited explanatory power attributed to trait matching in terms of body size does in no way rule out an importance of trait matching in terms of other, unmeasured attributes. Rather, a strong effect of phylogeny is fully consistent with an importance of other, as-yet-unmeasured traits, since so many traits will covary among related species. Thus, an imprint of evolutionary history can essentially be seen as a catch-all for the imprint of one or several unmeasured traits (e.g., cuticular toughness; Brousseau et al., 2018). Furthermore, we note that our inference about trait matching might also be limited by the fact that prey size was measured at the family level, masking substantial variation among species and consumed individuals. Ideally, for assessing trait matching, traits should be measured at the individual level, but in our case, this was not possible since those individuals were already consumed. In our case, we chose to focus on the family level, to be able to describe the range of available vs. used prey at the same taxonomic resolution. This solution was essentially dictated by constraints on time and effort for identifying a massive material of available prey as sampled by multiple techniques (see below). Yet, we note that identification to this level is a good compromise between effort and biological information. While species will differ in exact biology within families, family identity still encapsulates a lot of information on size, life cycle, development, trophic position, etc., as also revealed by the phylogenetic signal detected in prey responses to the environment. Body mass also ranged greatly among prey families, and thus, we argue that our family-level trait data involved most variation that could be found at the species level.

4.4 | Comparing communities in the field and in the gut

Comparing community data sets collected by field sampling and gut content analysis calls for special attention. We used two standard methods, pitfall traps and suction sampling, to assess abundance and diversity of the arthropod community in the field sites, while molecular gut content analysis allowed us to define prey community found in *Pardosa* predators. Both field approaches come with restriction: Pitfall traps have been criticized for catching mainly large, running arthropods, and for characterizing activity densities rather than real abundances (e.g., Spence & Niemelä, 1994; Topping & Sunderland, 1992). The efficiency of suction sampling on the other hand may vary with the height of the vegetation and with the relative dryness of conditions during sampling (Brook, Woodcock, Sinka, & Vanbergen, 2008). In addition, the identification of samples may be problematic due to damaged morphological characteristics (personal observation). What we argue is that the combination of both methods, as we did in this study, offers realistic estimates of the natural diversity and abundances of animal groups present in the study area, in particular at the family level adopted.

In terms of characterizing the prey community present in gut contents, high-throughput sequencing of predator gut contents has revolutionized the field. Yet, its validity relies on methodological constraints, such as efficiency of primers to detect a maximum of prey taxa in the predator's gut (e.g., Pompanon et al., 2012). In this context, we believe that a combination of multiple primer pairs—just as we combined different sampling methods to characterize the community of available prey (above)—will offer the best way forward. The use of two primer sets and uniquely indexed PCR replicates in the present study proved successful to circumvent potential primer bias towards specific groups (Alberdi, Aizpurua, Gilbert, & Bohmann, 2018) and revealed the broad prey spectrum of *Pardosa*, including soil arthropods and intraguild prey (for in-depth considerations, see Supporting Information).

4.5 | Implications: predator–prey interactions in a future Arctic—and beyond

Overall, our results suggest that environmental factors have an only small impact on *Pardosa* prey choice—but a major effect on the community of available prey. Assuming that the spatial clines in prey community composition seen along our local environmental gradient at Zackenberg will translate into temporal changes driven by climate change (see above), our findings evoke a clear-cut scenario: In a rapidly warming Arctic, trophic interactions involving wolf spiders are due to change—not because of changes in prey selection or use, but because of changes in the availability of preferred prey. In contrast to other areas of high-arctic tundra, vegetation structure at our study area of Zackenberg has been relatively stable so far (IPCC, 2013; Schmidt, Kristensen, Michelsen, & Bay, 2012). Yet, the area has experienced changes in flower phenology, soil moisture and air temperature in the last 19 years, leading to a decline in muscid flies and Collembola but to an increase in Hemiptera and parasitoid wasps (Høye et al., 2013; Koltz et al., 2018; Loboda et al., 2018). The availability of the most important prey of *Pardosa*—chironomid and culicid midges—may perhaps be less affected by climate change due to the buffered, aquatic habitat of their larvae. In addition, future changes in the abundance of *P. glacialis* are unlikely to result in density-dependent changes in

predation rates—since where sought for, direct top-down regulation of arctic prey communities has not been found (Visakorpi, Wirta, Ek, Schmidt, & Roslin, 2015).

Our study casts light on the mechanisms dictating trophic link structure and suggests that for *the focal predator species*, species distribution modelling may offer a good proxy of future interaction structure, with little additional insight added by separate interaction distribution modelling. Here, we emphasize that while the current findings are contingent on the predator taxon examined, the analytic machinery adopted is general. It offers a pathway for identifying selective feeding from molecular gut content analysis combined with estimates of available prey, and to thereby establish the impact of trait matching, prey phylogeny, environment and their interaction on trophic linkage structure. Most importantly, it can be readily transferred to other systems, for example, generalist predators along gradients of agricultural management intensity. A similar comparison along other environmental clines may then offer other results, and most certainly added insights.

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DATA ACCESSIBILITY

Data of arthropod communities collected in the field and in the spider gut content, along with sequence data including ZOTU reads, have been deposited in the Dryad digital repository (https://doi.org/10.5061/dryad.k6gf1tf).

AUTHOR CONTRIBUTIONS

B.E. and T.R. conceived the study and planned its design. B.E. did the fieldwork in Greenland. B.E. and E.J.V. did the molecular work and bioinformatics. N.A. and T.H. performed the analysis of community data, D.G. developed the statistical framework for the interaction distribution modelling and together with B.E. and N.A. performed the analysis of predator–prey interaction probability. All authors wrote and reviewed the final draft of the manuscript.

ORCID

Bernhard Eitzinger http://orcid.org/0000-0001-5903-4887
Nerea Abrego http://orcid.org/0000-0001-6347-6127

Eero J Vesterinen http://orcid.org/0000-0003-3665-5802

REFERENCES

Alberdi, A., Aizpurua, O., Gilbert, M. T. P., & Bohmann, K. (2018). Scrutinizing key steps for reliable metabarcoding of environmental samples. *Methods in Ecology and Evolution*, *9*(1), 134–147. https://doi.org/10.1111/2041-210X.12849

Aljanabi, S. M., & Martinez, I. (1997). Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. *Nucleic Acids Research*, *25*(22), 4692–4693. https://doi.org/10.1093/nar/25.22.4692

Altschul, S. F., Gish, W., Miller, W., Myers, E. W., & Lipman, D. J. (1990). Basic local alignment search tool. *Journal of Molecular Biology*, *215*(3), 403–410. https://doi.org/10.1016/S0022-2836(05)80360-2

Araújo, M. B., & New, M. (2007). Ensemble forecasting of species distributions. *Trends in Ecology and Evolution*, *22*(1), 42–47. https://doi.org/10.1016/j.tree.2006.09.010

Bartomeus, I., Cariveau, D. P., Harrison, T., & Winfree, R. (2018). On the inconsistency of pollinator species traits for predicting either response to land-use change or functional contribution. *Oikos*, *127*, 306–315. https://doi.org/10.1111/oik.04507

Bartomeus, I., Gravel, D., Tylianakis, J. M., Aizen, M. A., Dickie, I. A., & Bernard-Verdier, M. (2016). A common framework for identifying linkage rules across different types of interactions. *Functional Ecology*, *30*(12), 1894–1903. https://doi.org/10.1111/1365-2435.12666

Baselga, A., & Orme, C. D. L. (2012). Betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution*, *3*(5), 808–812. https://doi.org/10.1111/j.2041-210X.2012.00224.x

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), https://doi.org/10.18637/jss.v067.i01

Begon, M., Townsend, C. R., & Harper, J. L. (2005). *Ecology: From individuals to ecosystems*, 4th ed. Wiley-Blackwell. Retrieved from https://www.wiley.com/en-us/Ecology%3A+From+Individuals+to+Ecosystems%2C+4th+Edition-p-9781405111171

Bintanja, R., & Andry, O. (2017). Towards a rain-dominated Arctic. *Nature Climate Change*, *7*(4), 263–267. https://doi.org/10.1038/nclimate3240

Böcher, J., Kristensen, N., Pape, T., & Vilhelmsen, L. (Eds.) (2015). *The Greenland Entomofauna: An Identification Manual of Insects, Spiders and Their Allies*, Vol. *44*. Fauna Entomologica Scandinavica, Leiden, the Netherlands: Brill.

Bolker, B., Holyoak, M., Krivan, V., Rowe, L., & Schmitz, O. J. (2003). Connecting theoretical ad empirical studies of trait-mediated interactions. *Ecology*, *84*(5), 1101–1114. https://doi.org/10.1890/0012-9658(2003)084[1101:CTAESO]2.0.CO;2

Bowden, J. J., & Buddle, C. M. (2010). Spider assemblages across elevational and latitudinal gradients in the Yukon Territory, Canada. *Arctic*, *63*(3), 261–272.

Bowden, J. J., Hansen, O. L. P., Olsen, K., Schmidt, N. M., & Høye, T. T. (2018). Drivers of inter-annual variation and long-term change in High-Arctic spider species abundances. *Polar Biology*, *1*, 1–15. https://doi.org/10.1007/s00300-018-2351-0

Bowden, J. J., Høye, T. T., & Buddle, C. M. (2013). Fecundity and sexual size dimorphism of wolf spiders (Araneae: Lycosidae) along an elevational gradient in the Arctic. *Polar Biology*, *36*(6), 831–836. https://doi.org/10.1007/s00300-013-1308-6

Brook, A. J., Woodcock, B. A., Sinka, M., & Vanbergen, A. J. (2008). Experimental verification of suction sampler capture efficiency in grasslands of differing vegetation height and structure. *Journal of Applied Ecology*, *45*(5), 1357–1363. https://doi.org/10.1111/j.1365-2664.2008.01530.x

Brose, U. (2010). Body-mass constraints on foraging behaviour determine population and food-web dynamics. *Functional Ecology*, *24*(1), 28–34. https://doi.org/10.1111/j.1365-2435.2009.01618.x

Brousseau, P. M., Gravel, D., & Handa, I. T. (2018). Trait matching and phylogeny as predictors of predator–prey interactions involving ground beetles. *Functional Ecology*, *32*(1), 192–202. https://doi.org/10.1111/1365-2435.12943

Buchholz, S., Jess, A. M., Hertenstein, F., & Schirmel, J. (2010). Effect of the colour of pitfall traps on their capture efficiency of carabid beetles (Coleoptera: Carabidae), spiders (Araneae) and other arthropods. *European Journal of Entomology*, *107*(2), 277–280. https://doi.org/10.14411/eje.2010.036

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods and Research*, *33*(2), 261–304. https://doi.org/10.1177/0049124104268644

CaraDonna, P. J., Petry, W. K., Brennan, R. M., Cunningham, J. L., Bronstein, J. L., Waser, N. M., & Sanders, N. J. (2017). Interaction rewiring and the rapid turnover of plant-pollinator networks. *Ecology Letters*, *20*, 385–394. https://doi.org/10.1111/ele.12740

Chuine, I. (2010). Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1555), 3149–3160. https://doi.org/10.1098/rstb.2010.0142

Desjardins-Proulx, P., Laigle, I., Poisot, T., & Gravel, D. (2017). Ecological interactions and the Netflix problem. *PeerJ*, *5*(2000), e3644. https://doi.org/10.7717/peerj.3644

Edgar, R. C. (2010). Search and clustering orders of magnitude faster than BLAST. *Bioinformatics (Oxford, England)*, *26*(19), 2460–2461. https://doi.org/10.1093/bioinformatics/btq461

Edgar, R. C. (2016). *UNOISE2: Improved error-correction for Illumina 16S and ITS amplicon sequencing*. *bioRxiv*. doi:/10.1101/081257

Eitzinger, B., Rall, B. C., Traugott, M., & Scheu, S. (2018). Testing the validity of functional response models using molecular gut content analysis for prey choice in soil predators. *Oikos*, *127*, 915–926. https://doi.org/10.1111/oik.04885

Folmer, O., Black, M., Hoeh, W., Lutz, R., & Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, *3*(5), 294–299.

Garibaldi, L. A., Bartomeus, I., Bommarco, R., Klein, A. M., Cunningham, S. A., Aizen, M. A., … Woyciechowski, M. (2015). Trait matching of flower visitors and crops predicts fruit set better than trait diversity. *Journal of Applied Ecology*, *52*(6), 1436–1444. https://doi.org/10.1111/1365-2664.12530

Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W., & Holt, R. D. (2010). A framework for community interactions under climate change. *Trends in Ecology and Evolution*, *25*(6), 325–331. https://doi.org/10.1016/j.tree.2010.03.002

Gravel, D., Albouy, C., & Thuiller, W. (2016). The meaning of functional trait composition of food webs for ecosystem functioning. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*, 20150268. https://doi.org/10.1098/rstb.2015.0268

Gravel, D., Poisot, T., Albouy, C., Velez, L., & Mouillot, D. (2013). Inferring food web structure from predator-prey body size relationships. *Methods in Ecology and Evolution*, *4*(11), 1083–1090. https://doi.org/10.1111/2041-210X.12103

Hansen, R. R., Liset, O., Hansen, P., Bowden, J. J., Treier, U. A., & Normand, S. (2016). Meter scale variation in shrub dominance and soil moisture structure Arctic arthropod communities. *PeerJ*, *1–18*, https://doi.org/10.7717/peerj.2224

Hodkinson, I. D. (2005). Terrestrial insects along elevation gradients: Species and community responses to altitude. *Biological Reviews of the Cambridge Philosophical Society*, *80*(03), 489–513. https://doi.org/10.1017/S1464793105006767

Høye, T. T., Bowden, J. J., Hansen, O. L. P., Hansen, R. R., Niebuhr, A., & Skytte, M. G. (2017). Elevation modulates how Arctic arthropod communities are structured along local environmental gradients. *Polar Biology*, *41*, 1555–1565. https://doi.org/10.1007/s00300-017-2204-2

Høye, T. T., Hammel, J. U., Fuchs, T., & Toft, S. (2009). Climate change and sexual size dimorphism in an Arctic spider. *Biology Letters*, *5*(4), 542–544. https://doi.org/10.1098/rsbl.2009.0169

Høye, T. T., Post, E., Schmidt, N. M., Trøjelsgaard, K., & Forchhammer, M. C. (2013). Shorter flowering seasons and declining abundance of flower visitors in a warmer Arctic. *Nature Climate Change*, *3*(8), 759–763. https://doi.org/10.1038/nclimate1909

Ingimarsdóttir, M., Michelsen, A., Ripa, J., & Hedlund, K. (2014). Food sources of early colonising arthropods: The importance of allochthonous input. *Pedobiologia*, *57*(1), 21–26. https://doi.org/10.1016/j.pedobi.2013.09.004

IPCC. (2013). *Climate change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: IPCC.

Kankaanpää, T., Skov, K., Abrego, N., Lund, M., Schmidt, N. M., & Roslin, T. (2018). Spatiotemporal snowmelt patterns within a high Arctic landscape – with implications for flora and fauna. *Arctic, Antarctic, and Alpine Research*, *In Press*(1), 1–17. https://doi.org/10.1080/15230430.2017.1415624

Kaunisto, K. M., Roslin, T., Sääksjärvi, I. E., & Vesterinen, E. J. (2017). Pellets of proof: First glimpse of the dietary composition of adult odonates as revealed by metabarcoding of feces. *Ecology and Evolution*, *7*(20), 8588–8598. https://doi.org/10.1002/ece3.3404

Koltz, A. M., Schmidt, N. M., & Høye, T. T. (2018). Differential arthropod responses to warming are altering the structure of Arctic communities. *Royal Society Open Science*, *5*, 171503. https://doi.org/10.1098/rsos.171503

Körner, C. (2007). The use of "altitude" in ecological research. *Trends in Ecology and Evolution*, *22*(11), 569–574. https://doi.org/10.1016/j.tree.2007.09.006

Kuusk, A.-K., Cassel-Lundhagen, A., Kvarnheden, A., & Ekbom, B. (2008). Tracking aphid predation by lycosid spiders in spring-sown cereals using PCR-based gut-content analysis. *Basic and Applied Ecology*, *9*(6), 718–725. https://doi.org/10.1016/j.baae.2007.08.012

Loboda, S., Savage, J., Buddle, C. M., Schmidt, N. M., & Høye, T. T. (2018). Declining diversity and abundance of High Arctic fly assemblages over two decades of rapid climate warming. *Ecography*, *41*(2), 265–277. https://doi.org/10.1111/ecog.02747

Maglianesi, M. A., Blüthgen, N., Böhning-Gaese, K., & Schleuning, M. (2014). Morphological traits determine specialization and resource use in plant-hummingbird networks in the neotropics. *Ecology*, *95*(12), 3325–3334. https://doi.org/10.1890/13-2261.1.sm

Marshall, S. J., Sharp, M. J., Burgess, D. O., & Anslow, F. S. (2007). Near-surface-temperature lapse rates on the Prince of Wales Icefield, Ellesmere Island, Canada: Implications for regional downscaling of temperature. *International Journal of Climatology*, *27*(3), 385–398. https://doi.org/10.1002/joc.1396

Martin, M. (2011). Cutadapt removes adapter sequences from high-throughput sequencing reads. *EMBnet.journal*, *17*(1), 10–12. https://doi.org/10.14806/ej.17.1.200

Meltofte, H., & Rasch, M. (2008). The study area at Zackenberg. *Advances in Ecological Research*, *40*, 101–110. https://doi.org/10.1016/s0065-2504(07)00005-0

Memmott, J., Godfrey, H. C. J., & Gauld, I. D. (1994). The structure of a tropical host-parasitoid community. *Journal of Animal Ecology*, *63*(3), 521–540. https://doi.org/10.2307/5219

Morales-Castilla, I., Matias, M., Gravel, D., & Araújo, M. (2015). Inferring biotic interactions from proxies. *Trends in Ecology and Evolution*, *30*, 347–356. https://doi.org/10.1016/j.tree.2015.03.014

Morris, R. J., Lewis, O. T., & Godfray, H. C. J. (2004). Experimental evidence for apparent competition in a tropical forest food web. *Nature*, *428*(6980), 310–313. https://doi.org/10.1038/nature02394

Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., … Hik, D. S. (2011). Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. *Environmental Research Letters*, *6*(4), 045509. https://doi.org/10.1088/1748-9326/6/4/045509

Nentwig, W. (1986). Non-webbuilding spiders: Prey specialists or generalists? *Oecologia*, *69*(4), 571–576. https://doi.org/10.1007/BF00410365

Nielsen, J. M., Clare, E. L., Hayden, B., Brett, M. T., & Kratina, P. (2018). Diet tracing in ecology: Method comparison and selection. *Methods in Ecology and Evolution*, *9*(2), 278–291. https://doi.org/10.1111/2041-210X.12869

Nielsen, U. N., & Wall, D. H. (2013). The future of soil invertebrate communities in polar regions: Different climate change responses in the Arctic and Antarctic? *Ecology Letters*, *16*(3), 409–419. https://doi.org/10.1111/ele.12058

Nyffeler, M., & Breene, R. G. (1990). Evidence of low daily food consumption by wolf spiders in meadowland and comparison with other cursorial hunters. *Journal of Applied Entomology*, *110*(1–5), 73–81. https://doi.org/10.1111/j.1439-0418.1990.tb00097.x

O'Gorman, E. J., Pichler, D. E., Adams, G., Benstead, J. P., Cohen, H., Craig, N., … Woodward, G. (2012). *Impacts of warming on the structure and functioning of aquatic communities. Individual- to ecosystem-level responses. Advances in ecological research* (Vol. 47). Burlington, NJ: Academic Press. https://doi.org/10.1016/b978-0-12-398315-2.00002-8

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., … Wagner, H. (2018). *vegan: Community Ecology Package*.

Ovaskainen, O., Tikhonov, G., Norberg, A., Blanchet, F. G., Duan, L., Dunson, D., … Abrego, N. (2017). How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters*, *20*(5), 561–576. https://doi.org/10.1111/ele.12757

Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M., … Gravel, D. (2017). Comparing species interaction networks along environmental gradients. *Biological Reviews*, *93*(2), 785–800. https://doi.org/10.1111/brv.12366

Pereira, H. M., Leadley, P. W., Proença, V., Alkemade, R., Scharlemann, J. P. W., Fernandez-Manjarrés, J. F., … Walpole, M. (2010). Scenarios for global biodiversity in the 21st century. *Science*, *330*(6010), 1496–1501. https://doi.org/10.1126/science.1196624

Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary through space and time. *Oikos*, *124*(3), 243–251. https://doi.org/10.1111/oik.01719

Pompanon, F., Deagle, B. E., Symondson, W. O. C., Brown, D. S., Jarman, S. N., & Taberlet, P. (2012). Who is eating what: Diet assessment using next generation sequencing. *Molecular Ecology*, *21*(8), 1931–1950. https://doi.org/10.1111/j.1365-294X.2011.05403.x

R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Raso, L., Sint, D., Mayer, R., Plangg, S., Recheis, T., Brunner, S., … Traugott, M. (2014). Intraguild predation in pioneer predator communities of alpine glacier forelands. *Molecular Ecology*, *23*, 3744–3754. https://doi.org/10.1111/mec.12649

Rich, M. E., Gough, L., & Boelman, N. T. (2013). Arctic arthropod assemblages in habitats of differing shrub dominance. *Ecography*, *36*(9), 994–1003. https://doi.org/10.1111/j.1600-0587.2012.00078.x

Rickers, S., Langel, R., & Scheu, S. (2006). Dietary routing of nutrients from prey to offspring in a generalist predator: Effects of prey quality. *Functional Ecology*, *20*(1), 124–131. https://doi.org/10.1111/j.1365-2435.2006.01077.x

Rohr, R. P., Naisbit, R. E., Mazza, C., & Bersier, L.-F. (2016). Matching-centrality decomposition and the forecasting of new links in networks. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1824), 20152702. https://doi.org/10.1098/rspb.2015.2702

Roslin, T., & Majaneva, S. (2016). The use of DNA barcodes in food web construction—terrestrial and aquatic ecologists unite!. *Genome*, *59*(9), 603–628. https://doi.org/10.1139/gen-2015-0229

Rossberg, A. G., Brännström, Å., & Dieckmann, U. (2010). How trophic interaction strength depends on traits. *Theoretical Ecology*, *3*(1), 13–24. https://doi.org/10.1007/s12080-009-0049-1

Schmidt, N. M., Kristensen, D. K., Michelsen, A., & Bay, C. (2012). High Arctic plant community responses to a decade of ambient warming. *Biodiversity*, *13*(3–4), 191–199. https://doi.org/10.1080/14888386.2012.712093

Schmidt, N. M., Mosbacher, J. B., Eitzinger, B., Vesterinen, E. J., & Roslin, T. (2018). High resistance towards herbivore-induced habitat change in a high Arctic arthropod community. *Biology Letters*, *14*(5), 20180054. https://doi.org/10.1098/rsbl.2018.0054

Schmidt, N. M., Mosbacher, J. B., Nielsen, P. S., Rasmussen, C., Høye, T. T., & Roslin, T. (2016). An ecological function in crisis? The temporal overlap between plant flowering and pollinator function shrinks as the Arctic warms. *Ecography*, *39*(12), 1250–1252. https://doi.org/10.1111/ecog.02261

Schmidt, J. M., Sebastian, P., Wilder, S. M., & Rypstra, A. L. (2012). The nutritional content of prey affects the foraging of a generalist arthropod predator. *PLoS ONE*, *7*(11), e49223. https://doi.org/10.1371/journal.pone.0049223

Spence, J. R., & Niemelä, J. K. (1994). Sampling carabid assemblages with pitfall traps: The madness and the method. *The Canadian Entomologist*, *126*(3), 881–894. https://doi.org/10.4039/Ent126881-3

Summerhayes, V. S., & Elton, C. S. (1923). Contributions to the ecology of Spitsbergen and Bear Island. *Journal of Ecology*, *11*(2), 214–286. https://doi.org/10.2307/2255863

Sundqvist, M. K., Giesler, R., Graae, B. J., Wallander, H., Fogelberg, E., & Wardle, D. A. (2011). Interactive effects of vegetation type and elevation on aboveground and belowground properties in a subarctic tundra. *Oikos*, *120*(1), 128–142. https://doi.org/10.1111/j.1600-0706.2010.18811.x

Sundqvist, M. K., Sanders, N. J., & Wardle, D. A. (2013). Community and ecosystem responses to elevational gradients: Processes, mechanisms, and insights for global change. *Annual Review of Ecology, Evolution, and Systematics*, *44*(1), 261–280. https://doi.org/10.1146/annurev-ecolsys-110512-135750

Thuiller, W., Lavorel, S., Araújo, M. B., Sykes, M. T., & Prentice, I. C. (2005). Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(23), 8245–8250. https://doi.org/10.1073/pnas.0409902102

Tiusanen, M., Hebert, P. D. N., Schmidt, N. M., & Roslin, T. (2016). One fly to rule them all — muscid flies are the key pollinators in the Arctic. *Proceedings of the Royal Society B*, *283*, 20161271. https://doi.org/10.1098/rspb.2016.1271

Topping, C. J., & Sunderland, K. D. (1992). Limitations to the Use of Pitfall Traps in Ecological Studies Exemplified by a Study of Spiders in a Field of Winter Wheat. *The Journal of Applied Ecology*, *29*, 485–491. https://doi.org/10.2307/2404516

Traugott, M., Kamenova, S., Ruess, L., Seeber, J., & Plantegenest, M. (2013). Empirically characterising trophic networks: What emerging DNA- based methods, stable isotope and fatty acid analyses can offer. In *Advances in ecological research*. Amsterdam: Academic Press.

Tylianakis, J. M. (2009). Warming up food webs. *Science*, *323*(5919), 1300–1301. https://doi.org/10.1126/science.1170909

Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, *11*(12), 1351–1363. https://doi.org/10.1111/j.1461-0248.2008.01250.x

Valentini, A., Pompanon, F., & Taberlet, P. (2009). DNA barcoding for ecologists. *Trends in Ecology & Evolution*, *24*(2), 110–117. https://doi.org/10.1016/j.tree.2008.09.011

Van der Putten, W. H., Macel, M., & Visser, M. E. (2010). Predicting species distribution and abundance responses to climate change: Why it

is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365* (1549), 2025–2034. https://doi.org/10.1098/rstb.2010.0037

Van Veen, F. J. F., Müller, C. B., Pell, J. K., & Godfray, H. C. J. (2008). Food web structure of three guilds of natural enemies: Predators, parasitoids and pathogens of aphids. *Journal of Animal Ecology*, *77*(1), 191–200. https://doi.org/10.1111/j.1365-2656.2007.01325.x

Vesterinen, E. J., Ruokolainen, L., Wahlberg, N., Peña, C., Roslin, T., Laine, V. N., … Lilley, T. M. (2016). What you need is what you eat? *Prey selection by the bat Myotis daubentonii*. *Molecular Ecology*, *25*(7), 1581–1594. https://doi.org/10.1111/mec.13564

Visakorpi, K., Wirta, H. K., Ek, M., Schmidt, N. M., & Roslin, T. (2015). No detectable trophic cascade in a high-Arctic arthropod food web. *Basic and Applied Ecology*, *16*(7), 652–660. https://doi.org/10.1016/j.baae.2015.06.003

Wirta, H. K., Hebert, P. D. N., Kaartinen, R. R., Prosser, S. W., Varkonyi, G., Roslin, T., … Roslin, T. (2014). Complementary molecular information changes our perception of food web structure. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(5), 1885–1890. https://doi.org/10.1073/pnas.1316990111

Wirta, H. K., Várkonyi, G., Rasmussen, C., Kaartinen, R., Schmidt, N. M., Hebert, P. D. N., … Roslin, T. (2015). Establishing a community-wide DNA barcode library as a new tool for arctic research. *Molecular Ecology Resources*, *16*(3), 809–822. https://doi.org/10.1111/1755-0998.12489

Wirta, H. K., Vesterinen, E. J., Hambäck, P. A., Weingartner, E., Rasmussen, C., Reneerkens, J., … Roslin, T. (2015). Exposing the structure of an Arctic food web. *Ecology and Evolution*, *5*(17), 3842–3856. https://doi.org/10.1002/ece3.1647

Wirta, H. K., Weingartner, E., Hambäck, P. A., & Roslin, T. (2015). Extensive niche overlap among the dominant arthropod predators of the High Arctic. *Basic and Applied Ecology*, *16*(1), 86–92. https://doi.org/10.1016/j.baae.2014.11.003

Wisz, M. S., Pottier, J., Kissling, W. D., Pellissier, L., Lenoir, J., Damgaard, C. F., … Svenning, J. C. (2013). The role of biotic interactions in shaping distributions and realised assemblages of species: Implications for species distribution modelling. *Biological Reviews*, *88*(1), 15–30. https://doi.org/10.1111/j.1469-185x.2012.00235.x

Zeale, M. R. K., Butlin, R. K., Barker, G. L. A., Lees, D. C., & Jones, G. (2011). Taxon-specific PCR for DNA barcoding arthropod prey in bat faeces. *Molecular Ecology Resources*, *11*(2), 236–244. https://doi.org/10.1111/j.1755-0998.2010.02920.x

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