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Meter scale variation in shrub dominance and soil moisture structure Arctic arthropod communities

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The Arctic is warming at twice the rate of the rest of the world. This impacts Arctic species both directly, through increased temperatures, and indirectly, through structural changes in their habitats. Species are expected to exhibit idiosyncratic responses to structural change, which calls for detailed investigations at the species and community level. Here, we investigate how arthropod assemblages of spiders and beetles respond to variation in habitat structure at small spatial scales. We sampled transitions in shrub dominance and soil moisture between three different habitats (fen, dwarf shrub heath, and tall shrub tundra) at three different sites along a fjord gradient in southwest Greenland, using yellow pitfall cups. We identified 2547 individuals belonging to 47 species. We used species richness estimation, indicator species analysis and latent variable modeling to examine differences in arthropod community structure in response to habitat variation at local (within site) and regional scales (between sites). We estimated species responses to the environment by fitting species-specific generalized linear models with environmental covariates. Species assemblages were segregated at the habitat and site level. Each habitat hosted significant indicator species, and species richness and diversity were significantly lower in fen habitats. Assemblage patterns were significantly linked to changes in soil moisture and vegetation height, as well as geographic location. We show that meter-scale variation among habitats affects arthropod community structure, supporting the notion that the Arctic tundra is a heterogenous environment. To gain sufficient insight into temporal biodiversity change, we require studies of species distributions detailing species habitat preferences.

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25 Abstract

26 The Arctic is warming at twice the rate of the rest of the world. This impacts Arctic species both
27 directly, through increased temperatures, and indirectly, through structural changes in their habitats.
28 Species are expected to exhibit idiosyncratic responses to structural change, which calls for detailed
29 investigations at the species and community level. Here, we investigate how arthropod assemblages
30 of spiders and beetles respond to variation in habitat structure at small spatial scales. We sampled
31 transitions in shrub dominance and soil moisture between three different habitats (fen, dwarf shrub
32 heath, and tall shrub tundra) at three different sites along a fjord gradient in southwest Greenland,
33 using yellow pitfall cups. We identified 2547 individuals belonging to 47 species. We used species
34 richness estimation, indicator species analysis and latent variable modeling to examine differences
35 in arthropod community structure in response to habitat variation at local (within site) and regional
36 scales (between sites). We estimated species responses to the environment by fitting species-
37 specific generalized linear models with environmental covariates. Species assemblages were
38 segregated at the habitat and site level. Each habitat hosted significant indicator species, and species
39 richness and diversity were significantly lower in fen habitats. Assemblage patterns were
40 significantly linked to changes in soil moisture and vegetation height, as well as geographic
41 location. We show that meter-scale variation among habitats affects arthropod community structure,
42 supporting the notion that the Arctic tundra is a heterogenous environment. To gain sufficient
43 insight into temporal biodiversity change, we require studies of species distributions detailing
44 species habitat preferences.

45 Introduction

46 Understanding the factors that structure ecological communities on continental, regional and local
47 scales provides the basis for understanding how global changes might affect species composition
48 and biodiversity (Vellend et al. 2013; Dornelas et al. 2014). Climate change is happening at an
49 accelerated pace in the Arctic (Callaghan et al. 2004; IPCC 2014), and altered moisture regimes and
50 shrub expansion are two of the most prominent habitat-altering phenomena caused by these changes
51 (Rouse et al. 1997; Tape et al. 2006; Myers-Smith et al. 2011; Elmendorf et al. 2012). Shrub
52 expansion and altered moisture regimes represent considerable consequences of climate change to
53 the Arctic tundra; altering unique habitats such as open heath, wetlands and grasslands (ACIA
54 2004). Firstly, warming in the Arctic has led to accelerated plant growth, particular for woody
55 plants, causing a shift towards greater shrub cover, and a northward migration of the tree line
56 (Callaghan et al. 2011), increased biomass (Epstein et al. 2012), and changes in plant species

57 composition (Walker et al. 2012). These trends are expected to continue during future climate
58 change (Normand et al. 2013; Pearson et al. 2013). Secondly, a changing Arctic climate with
59 changes in precipitation, glacial melt, and permafrost degradation may alter the spatial extent of
60 wetlands (Avis et al. 2011). In areas with continuous permafrost, top soils become wetter due to the
61 impermeable strata that prevent infiltration and percolation (Woo & Young 2006). Some areas with
62 discontinuous permafrost, however, become drier, due to increased net evapotranspiration and
63 increased drainage due to permafrost thaw (Zona et al. 2009; Perreault et al. 2015). The long term
64 persistence of Arctic wetlands is debated, but climate change projections and field studies indicate
65 deterioration and ultimate destruction of Arctic wetlands (Woo & Young 2006). These habitat
66 changes, both shrubification and wetland deterioration, will trigger several feedback loops within
67 the climate system (Chapin et al. 2005) and may have profound effects on ecosystems (Post et al.
68 2009). In order to understand how these habitat changes affect Arctic biodiversity, we need to
69 adequately describe how Arctic species composition responds to environmental changes.

70 The alteration of habitats, due to e.g., shrub expansion into open tundra and changing
71 wetland hydrology, are likely to affect habitat availability for many organisms, through changes in
72 species' distributions, diversity, and composition. Terrestrial arthropods (e.g. insects and spiders) in
73 particular, are associated with specific habitat types and likely respond strongly to habitat changes
74 in the Arctic (Bowden & Buddle 2010; Rich et al. 2013). Arthropods have long been recognized as
75 valuable indicators of changing environments because of their relatively short lifecycles and their
76 physiology being directly driven by the external environment (ectothermic). Studies of the impacts
77 of habitat changes upon Arctic arthropod communities are, however, only beginning to emerge
78 (Bowden & Buddle 2010; Rich et al. 2013; Sikes et al. 2013; Sweet et al. 2014; Hansen et al. 2016).
79 In spite of the common conception of the Arctic as a species-poor and relatively homogenous
80 environment, studies have shown that arthropod assemblages vary substantially over short distances
81 (Hansen et al. 2016), with species responding to local and regional climatic gradients (OLP.
82 Hansen, unpublished work). Arthropod communities are expected to change in response to the
83 direct effects of increasing temperatures and prolonged growing seasons (Høye et al. 2013; Høye et
84 al. 2014), but also indirectly through changes in soil moisture and vegetation structure (Bowden &
85 Buddle 2010; Hansen et al. 2016), changes to snowmelt dynamics (Høye et al. 2009; Bowden et al.
86 2015b), and shrub expansion (Rich et al. 2013). Several studies indicate direct effects of
87 temperature change on arthropods (Post et al. 2009; Høye et al. 2013; Bowden et al. 2015a), but we
88 do not yet fully comprehend the distribution of, or habitat requirements for, the majority of Arctic
89 arthropod species.

90 Arctic and alpine tundra areas are vast, and the knowledge of geographical variation
91 associated with recent environmental and ecosystem change is limited. In this study, we explore the
92 influence of moisture regime and habitat structure on the composition and diversity of Arctic
93 arthropod communities, and investigate the site specific effects of the drivers of change. We
94 propose the following hypothesis: Arctic arthropod assemblages and diversity vary with soil
95 moisture and vegetation height at very small spatial scales (10 - 20 meters). Specifically, we
96 compare beetle and spider communities sampled in different habitats (fen, dwarf shrub heath, and
97 tall shrub tundra) at three sites along a large scale gradient. We expect to find distinct arthropod
98 communities in each habitat, and that abundances of groups like wolf spiders, and other active
99 hunters, will be lower in the tall shrub tundra compared to open habitats.

100 Methods

101 *Study area and sampling design*

102 Arthropods were sampled with uncovered pitfall traps from the 29th of June to the 23rd of July 2013
103 at three sites (1, 2, and 3) along the Godthaabsfjord in West Greenland (Fig 1). Site 1 was situated
104 at the mouth of the fjord and thus characterized by a coastal climate with relatively high
105 precipitation, narrow annual temperature range, and topographic variation (app. 0 - 300 m.a.s.l.).
106 The shrub community at site 1 was dominated by dwarf shrubs and a very sparse cover of tall shrub
107 species such as *Salix glauca* (Lange [family: Salicidae]). Site 2 was low lying and flat, and
108 characterized by a mosaic of low shrub vegetation (<50 cm), dominated by *S. glauca*, mixed with
109 *Betula nana* (Lange [family: Betulaceae]), *Vaccinium uliginosum* (L., [family: Ericaceae]),
110 *Rhododendron groenlandicum* (Oeder [family: Ericaceae]), and *Empetrum nigrum* (Lange [family:
111 Ericaceae]). Site 3 was characterized by a continental climate and pronounced topographic variation
112 (app. 0 – 600 m.a.s.l.) with well-defined tall shrub patches dominated by high growth of *S. glauca*
113 and *Alnus crispa* (Aiton [family: Betulaceae]) (>50cm). These patches were mainly located at south
114 facing slopes below 100 m.a.s.l. All dwarf shrub species at site 2 were also present at site 3.

115 Moisture transitions (fen-heath) were sampled at sites 1 and 2, while transitions in
116 vegetation height and cover of tall shrubs (heath-shrub) were sampled at sites 2 and 3. Four fen-
117 heath plots were established, two at site 1 and two at site 2. Each fen-heath plot consisted of two
118 sub-plots placed ten meters apart. Each sub-plot was situated exactly five meters from a distinct fen-
119 heath transition zone (Fig. 2). Twelve heath-shrub plots were established at site 2 and site 3 (six at
120 each site). Each heath-shrub plot consisted of two sub-plots 20 meters apart; one located at the
121 center of a patch of tall shrubs and one in the adjacent open dwarf shrub heath. Each sub-plot was

122 delineated by a circle with a five meter radius. At the center of each sub-plot, two yellow pitfall
123 traps (nine cm diameter) were placed 50 centimeters apart (Fig 2). The traps were dug down such
124 that the rim was flush with the surface and filled one third with a soap water solution. There was no
125 overflow due to rainwater accumulation during sampling. The color of the pitfalls was chosen to
126 catch flying as well as surface-active arthropods (Høye et al. 2014). Pitfall traps were emptied
127 twice, once halfway through and once at the end of the sampling period. Samples were stored
128 separately.

129 The following structural and environmental parameters were measured in each sub-plot: (i)
130 percent cover of shrubs, herbs, graminoids and bare ground in six categories: 0%, 1–20%, 21–40%,
131 41–60%, 61–80%, and 81–100%, (ii) height (to the nearest 5 cm) of the vegetation height with the
132 highest coverage in the sub-plot. (iii) presence of plant species, (iv) slope in vertical meters between
133 the highest and lowest point of the sub-plot, (v) aspect, recorded using a handheld GPS and
134 classified to nearest cardinal direction (North, South, East, and West), (vi) pH, measured directly
135 with a soil pH measurement kit, model HI 99121, (vii) soil type at 15 cm. depth was recorded as
136 humus or sand.

137 *Specimens and data*

138 All spiders and beetles were sorted from the samples and the adult specimens were identified (by
139 RRH) to species based on morphological characters using a Wild® M5A stereo microscope. Not all
140 juveniles could be assigned to species, so only adult specimens were included in the analysis.
141 Spiders were identified using the available literature through The World Spider Catalog (World
142 Spider Catalog 2016) and Spiders of North America (Paquin & Dupérré 2003). Beetles were
143 identified using both Scandinavian and North American literature (Lindroth 1985; Lindroth 1986;
144 Böcher 1988) and by consulting the collection at the Natural History Museum Aarhus, Denmark.
145 Specimens are preserved in 75% ethanol at the Natural History Museum Aarhus. The dataset is
146 available through the Global Biodiversity Information Facility (<http://doi.org/10.15468/li6jkm>).

147 *Data analysis*

148 The mean and standard error were calculated for significant environmental variables across
149 all habitats at each site. We ran a correlation analysis of all potential variables, based on Pearson's
150 correlation coefficient, and tested whether the uncorrelated variables differed significantly between
151 sites and habitats with a MANOVA. To counteract effects of potential-under sampling, all analyses
152 were carried out excluding singletons. All analyses were carried out in R version 3.2.2.

153 *Species diversity*

154 Species diversity was rarefied and extrapolated for investigation across habitats based on Hill
155 numbers ($q=0$; species richness, $q=1$; Shannon diversity, $q=2$; Simpson diversity) and standardized
156 by sample coverage (Chao & Jost 2012; Chao et al. 2014) using the iNEXT R-package (Hsieh et al.
157 2014). We extrapolated to double the reference sample of the habitat with the smallest sample
158 coverage (shrub). Samples were compared at base-coverage, estimated as a minimum of C_a and C_b ,
159 where C_a is maximum coverage at reference sample size and C_b is minimum coverage at two times
160 reference sample size. iNEXT computes bootstrap confidence bands around the sampling curves,
161 facilitating the comparisons of diversity across multiple assemblages. We then visually assessed if
162 diversity measures differed significantly between habitats.

163 We ran a species indicator analysis to assess the strength and statistical significance of the
164 relationship between species abundances and the specific habitats. We used the function ‘multipatt’
165 in the R package ‘indicspecies’ (De Cáceres et al. 2010). This analysis provides a specificity value
166 ‘A’(0-1), which indicates the probability of a certain species occurring in a certain habitat as well as
167 a sensitivity value ‘B’(0-1), which indicates how many of the plots belonging to a certain habitat the
168 target species is located in. Significance ($p < 0.05$) is assessed based on the A and B values (De
169 Cáceres & Legendre 2009). In addition to significance testing, we opted to describe habitat
170 preferences more broadly by assigning all species with an A value for a given habitat larger than 0.8
171 and a B value larger than 0.1 to that specific habitat. In this way, the importance of the sensitivity
172 value is down weighted.

173 *Species composition*

174 Traditional methods to visually investigate how arthropod species composition varies between
175 habitats, such as non-metric multidimensional scaling (NMDS), have been shown to confound
176 trends in location with changes in dispersion, leading to potentially misleading results (Warton et al.
177 2012). To avoid these issues while still enabling visualization, we employed latent variable
178 modelling through the R package ‘boral’ (Hui 2016). Latent variable modelling is a Bayesian
179 model-based approach that explains community composition through a set of underlying latent
180 variables to account for residual correlation, for example due to biotic interaction. This method
181 offers the possibility to adjust the distribution family to e.g. negative binomial distribution which
182 better accounts for over-dispersion in count data. Thus, it accounts for the increasing mean-variance
183 relationship without confounding location with dispersion (Hui et al. 2015). Three “types” of
184 models may be fitted: 1) With covariates and no latent variables, boral fits independent response

185 GLMs such that the columns of y are assumed to be independent; 2) With no covariates, boral fits a
186 pure latent variable model (Rabe-Hesketh et al. 2004) to perform model-based unconstrained
187 ordination (Hui et al. 2015); 3) With covariates and latent variables, boral fits correlated response
188 GLMs, with latent variables.

189 Sub-plots placed in dwarf shrub heath could potentially differ depending on the transition
190 examined (fen-heath or shrub-heath). Therefore, we created latent variable plots for both plants and
191 arthropods to visually assess if the heath sub-plots in the fen-heath and shrub-heath plots groups
192 were distinguishable. In the latent variable plot for plant species composition, heath sub-plots were
193 not segregated (Fig. S1) and all heath plots were hereafter treated as one category.

194 We modelled arthropod species' distributions with two latent variables to enable
195 visualization comparable to a two dimensional NMDS. From the latent variable model, we
196 extracted the posterior median values of the latent variables which we used as coordinates on
197 ordination axes to represent species composition at plot level (Hui et al. 2015). We then tested the
198 difference in local species composition based on these coordinates between the paired samples (fen-
199 heath or shrub-heath) for each transect using paired t-tests.

200 To test the significance of and, interactions between, the environmental variables and site,
201 we used a multivariate extension of General Linear Models (GLMs) using the function 'manyglm'
202 in the package 'mvabund' (Wang et al. 2012). This recently developed method offers the possibility
203 to model distributions based on count data by assuming a negative binomial distribution. Vegetation
204 height and graminoid cover have higher resolutions compared to the classifications 'fen' and
205 'shrub' as these are measured on a continuous scale. We used vegetation height as a proxy for shrub
206 treatment effects and cover of graminoids as a proxy for soil moisture. The gradients in these
207 variables are representative of the moisture transition of fen-heath plot groups and the shrub
208 dominance transition of the shrub-heath plot groups (Fig S2). We tested for main effects of all the
209 un-correlated variables, selected by the Pearson correlation analyses, and for an interaction between
210 the variables and site. The model assumptions of mean-variance and log-linearity were examined
211 with residual vs. fit plots and a normal quantile plot, and no transformations were needed.

212 Results

213 A total of 2547 individuals, constituting 45 species and 13 families were identified within the two
214 orders: Araneae (2223 individuals, 7 families, 37 species) and Coleoptera (324 individuals, 6
215 families, 8 species). We found a species of sheet web spider [*Wabasso cacuminatus* (Millidge,

216 1984)] not previously known from Greenland, represented by one individual. One species
217 [*Pelecopsis mengei*, (Simon, 1884)], represented in our samples by three individuals, remained
218 unknown from Greenland until recently (Marusik 2015; Hansen et al. 2016) (Table 1).

219 Extrapolated species richness ($q = 0$) did not differ significantly between habitats due to
220 overlapping confidence intervals but there was a trend towards higher species richness in heath sub-
221 plots, lower in shrub sub-plots, and lowest in fen sub-plots (Fig. 3). The same pattern was observed
222 for Shannon diversity ($q = 1$) as well as for Simpson diversity ($q = 2$), however both these indices
223 differed significantly between habitats, with the highest diversity in the shrub sub-plots,
224 intermediate in the heath sub-plots, and lowest in the fen sub-plots (Fig. 3).

225 The three species significantly ($p < 0.05$) associated with fen habitats were all sheet web
226 spiders. *Erigone whymeri* (O.P. Cambridge, 1877), *Mecynargus paetulus* (O.P. Cambridge, 1875),
227 and *Wabasso quaestio* (Chamberlin, 1948). Just one species, the ladybird *Coccinella*
228 *transversoguttata* (Faldermann, 1835), was significantly associated with heath habitats. Shrub
229 habitats housed six significantly associated species: the comb-footed spider *Ohlertidion lundbecki*
230 (Sørensen, 1894), and five species of sheet web spiders: *Dismodicus decemoculatus* (Emerton,
231 1852), *Improphantes complicates* (Emerton, 1882), *Pocadicnemis americana* (Millidge, 1984),
232 *Semljicola obtusus* (Emerton, 1914), *Sisicus apertus* (Holm, 1939) (Table 1).

233 The latent variable plots showed that the plant species composition of the shrub sub-plots
234 overlapped with the composition of the heath plots (Fig. S1), but vegetation height was significantly
235 different (Table 2). The plant species composition of the fen plots was different from both the heath
236 and shrub sub-plots (Fig. S1). Arthropod species composition was segregated both at site and
237 habitat level, but the distribution of sub-plots in the latent variable arthropod plot indicated
238 interaction between site and treatment (Fig. 4).

239 Vegetation height in the shrub sub-plots at site 2 was significantly lower than that at site 3
240 ($F_{1,21} = 13.46$, $p = 0.001$), and the overall cover of graminoids was significantly lower at the fen
241 sub-plots at site 1, compared to the fen sub-plots at site 2 ($F_{1,29} = 0.21$, $p = 0.049$). The pH levels
242 were nearly significantly different between the shrub sub-plots from site 2 to site 3 ($F_{1,21} = 4.17$, $p =$
243 0.054) and highly significantly different between the fen sub-plots from site 1 to site 2 ($F_{1,29} = 66.01$,
244 $p < 0.0001$). pH did not differ between fen and heath ($F_{1,29} = 0.69$, $p = 0.41$) or shrub and heath ($F_{1,21}$
245 $= 0.50$, $P = 0.49$). Cover of graminoids was significantly lower for heath sub-plots compared to fen
246 sub-plots ($F_{1,29} = 74.54$, $p < 0.0001$). Vegetation height differed significantly between shrub and

247 heath habitats ($F_{1,21} = 26.04$, $p < 0.0001$), with lower vegetation height in the heath sub-plots
248 compared to shrub sub-plots. (Table 2 and Fig. S2).

249 Arthropod species composition differed significantly due to different moisture regimes and
250 different height classes. pH levels were not a significant driver of arthropod communities, nor was
251 there a significant interaction between site and the levels of pH. There was a significant interaction
252 between cover of graminoid species and site, but no significant interaction was detected between
253 height class and site (Table 3). Arthropod species composition differed significantly between the
254 local fen-heath transitions, but for site 2 only; one latent variable axis differed significantly between
255 fen-heath transitions. The local shrub-heath transects differed significantly for both axes and both
256 sites (Table 4).

257 Discussion

258 Although Arctic tundra is often perceived as a relative homogenous biome, it consists of a wide
259 range of habitat types due to strong environmental transitions occurring over short spatial scales. In
260 this study, we have demonstrated clear effects of vegetation height and soil moisture on diversity
261 and composition of spiders and beetles in low Arctic Greenland. This effect is evident across
262 distances of 10 - 20 meters. Fen, heath, and shrub vegetation hosted distinct arthropod communities
263 differing in both composition and diversity. While previous studies have emphasized the
264 importance of vegetation structure as predictors of Arctic arthropod communities (Bowden &
265 Buddle 2010; Rich et al. 2013; Sweet et al. 2014), it has not been demonstrated that such effects are
266 visible at the scale of meters.

267 Existing literature generally agrees with the habitat classifications we have assigned the
268 species in this study. According to existing descriptions of habitat preferences, the wetland species
269 we find in this study are found strictly in wet open habitats, whereas both shrub and heathland
270 species mostly have a more general distribution (Leech et al. 1966; Böcher 2015; Marusik 2015),
271 indicating a higher degree of habitat specialization in the fens. The sheet web spider, *Erigone*
272 *arctica*, was significantly linked to wet fen habitats in an alpine study site in West Greenland
273 (Hansen et al. 2016), and in this study, *E. arctica* was also linked to fen plots, further suggesting
274 habitat specialization. We found the lowest diversity in the fens, which are spatially limited,
275 compared to much more wide spread heathland habitats. Both tall shrub tundra and dwarf shrub
276 heath are comprised of different habitats with open patches, moist areas, and varying vegetation
277 structure. Such variation in habitat structure likely leads to higher diversity compared to the fen
278 habitats, which are rather homogenous.

279 This particular study area is characterized as low Arctic with discontinuous permafrost
280 unaffected by glacial meltwater. Models predict that this area will experience increased
281 evapotranspiration and precipitation (Rawlins et al. 2010). Increased drainage due to permafrost
282 melt coupled with evapotranspiration is likely to lead to wetland deterioration. Shrubification has
283 been forecasted to be most pronounced at the boundary between high and low Arctic where
284 permafrost is melting and in areas where soil moisture is greatest (Myers-Smith et al. 2015). In the
285 Godthåbsfjord, it is therefore likely that shrub expansion will be most notable in the fens and snow-
286 beds. With shrubification (Myers-Smith et al. 2011; Elmendorf et al. 2012), as well as, increased
287 land use such as forestry and agriculture (ACIA 2004), wetland habitats are at risk (CAFF 2013).
288 Our results suggest that wetland deterioration and shrubification will strongly affect arthropod
289 communities, and may compromise the living conditions of individual specialized species.

290 We found an interaction between site and graminoid cover, suggesting that the fens differ
291 between sites. Wetlands with coastal proximity are known to be impacted by salt influx from the
292 sea (Woo & Young 2006). This is supported by the slightly higher pH at site 1 compared to site 2,
293 but does not explain differences in arthropod composition in the fens between the coastal (site 1)
294 and intermediate site (site 2), as pH was not significant in the multivariate GLM. Even though plant
295 species composition showed clear segregation of wet and dry plots, conditions may be drier at the
296 intermediate site than at the coastal site, where summer precipitation is higher. Plant species
297 composition reflects an integration of seasonal variation in soil moisture conditions (Daniels et al.
298 2011) such that they may not reflect sudden soil moisture changes. The variation in moisture regime
299 only partially explained arthropod species composition at the intermediate site and supports the idea
300 of drier conditions at the intermediate site affecting arthropod species composition differently.

301 We expected the effect of vegetation height to be less pronounced at the intermediate site
302 due to the patchy structure of the shrubs and overall lower vegetation; yet, we did not find an
303 interaction between site and treatment. We studied mostly mobile predatory species. The few
304 herbivores like the weevils: *Otiorynchus arcticus* (O. Fabricius, 1780) and *Otiorynchus nodosus*
305 (Müller, 1764) are mostly found in open heath plots with low vegetation. It is conceivable that even
306 a small change in vegetation height has an effect on the surface active predatory species, because
307 vegetation height may also affect the composition and abundance of prey items. The web builders,
308 like sheet web spiders, require some amount of vegetation structure to form webs, but even low
309 shrubs provide structure and shelter. Rich et al. (2013) found that overall arthropod abundance and
310 species richness increased in shrub plots in Arctic Alaska, but suggested that for groups like wolf

311 spiders and other active hunters, full shrub encroachment of open habitats could be detrimental. Our
312 results show that abundances of these groups are lower in shrub sub-plots and support this notion.

313 Conclusion

314 We have established a baseline of species occurrence in relation to transition in soil moisture and
315 shrub dominance which will facilitate future assessment of changes in Arctic arthropod
316 communities, where these transitions in habitat structure are likely to change. The variation in
317 community composition at the scale of meters was surprising and suggests drastic changes in
318 arthropod species composition given continued shrubification and wetland deterioration. We found
319 that the strength of the environmental predictor variables varied among sites. Understanding the
320 sources of such site variation is an important topic for future studies. Two important steps are
321 needed to further the knowledge of arthropod responses to changing habitats. Primarily, we need
322 information on species occurrence across multiple taxa and multiple environmental gradients.
323 Habitat preferences of species are needed to determine the effects that climate change will have in
324 Arctic ecosystems. Spiders and butterflies have proven useful for detection of rapid environmental
325 change due to climate change (Høye et al. 2014; Bowden et al. 2015a; Bowden et al. 2015b) and
326 may serve as important indicator taxa in future studies. Secondly, we need further studies of spatial
327 variability and change in environmental gradients like soil moisture.

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496 Tables

497 Table 1: List of arthropod species sampled and their abundance in three habitats; fen, dwarf shrub
 498 heath, and tall shrub tundra at three sites along the Nuuk fiord in Western Greenland. The last
 499 column shows the results of a species indicator analysis (for details see main text). Species were
 500 assigned to one of the three habitats if A (specificity value) > 0.8 and B (sensitivity value) > 0.1.
 501 Significance ($p < 0.05$) is indicated with an *. The table is sorted by order, family, and species,
 502 respectively.

Order	Family	Species	Abundance			Habitat	
			Fen	Heath	Shrub		
Araneae	Dictynidae	<i>Dictyna major</i> (Menge, 1869)			1	No classification	
	Gnaphosidae	<i>Haplodrassus signifer</i> (C.L. Koch, 1839)		1		No classification	
	Hahniidae	<i>Hahnia glacialis</i> (Sørensen, 1898)	1	7	1	No classification	
	Linyphiidae		<i>Agyneta jacksoni</i> (Simon, 1884)	3	8	1	No classification
			<i>Agyneta nigripes</i> (Brændegård, 1937)	2	3		Fen and heath
			<i>Bathyphantes simillimus</i> (L. Koch, 1879)			1	No classification
			<i>Dismodicus decemoculatus</i> (Emerton, 1852)	1	2	10	Shrub*
			<i>Erigone arctica</i> (White, 1852)	6			Fen
			<i>Erigone psycrophila</i> (Thorell, 1871)	1			No classification
			<i>Erigone whymperi</i> (O.P. Cambridge, 1877)	8			Fen*
			<i>Hilaira herniosa</i> (Thorell, 1875)		1		No classification
			<i>Hybauchenidium gibbosum</i> (Sørensen, 1898)		5	3	Heath and shrub
			<i>Hyposinga groenlandica</i> (Simon, 1889)	2	2	4	Heath and shrub
			<i>Improphantes complicatus</i> (Emerton, 1882)		2	8	Shrub*
			<i>Lepthyphantes turbatrix</i> (O.P. Cambridge, 1877)			1	No classification
			<i>Mecynargus borealis</i> (Jackson, 1930)		4		Heath
			<i>Mecynargus morulus</i> (O.P. Cambridge, 1873)		2	1	Heath and shrub
			<i>Mecynargus paetulus</i> (O.P. Cambridge, 1875)	33			Fen*
			<i>Oreonetides vaginatus</i> (Thorell, 1872)			1	No classification
			<i>Pelecopsis mengei</i> (Simon, 1884)		2	1	Heath and shrub
			<i>Pocadicnemis americana</i> (Millidge, 1976)		6	18	Shrub*
			<i>Sciastes extremus</i> (Holm, 1967)		1		No classification
			<i>Scotinotylus sacer</i> (Crosby, 1929)			5	Shrub
			<i>Semljicola obtusus</i> (Emerton, 1914)	3	6	15	Shrub*
			<i>Sisicus apertus</i> (Holm, 1939)		1	3	Shrub*
			<i>Tiso aestivus</i> (L. Koch, 1872)	1	31	1	Heath
		<i>Wabasso cacuminatus</i> (Millidge, 1984)		1		No classification	
		<i>Wabasso quaestio</i> (Chamberlin, 1948)	12			Fen*	
		<i>Walckenaeria karpinskii</i> (O.P. Cambridge, 1873)	6	21		Fen and heath*	
		Thomisidae	<i>Xysticus durus</i> (Sørensen, 1898)		17		Heath
	Lycosidae		<i>Arctosa insignita</i> (Thorell, 1872)	17	29	2	Fen and heath*
			<i>Pardosa furcifera</i> (Thorell, 1875)	524	552	257	No classification
			<i>Pardosa groenlandica</i> (Thorell, 1872)	17	23	8	No classification
		<i>Pardosa hyperborea</i> (Thorell, 1872)	6	347	140	Heath and shrub*	
Philodromidae		<i>Thanatus arcticus</i> (Thorell, 1872)	2	10		Fen and heath	
Theridiidae		<i>Robertus fuscus</i> (Emerton, 1894)			1	No classification	
		<i>Ohlertidion lundbecki</i> (Sørensen, 1898)			2	Shrub	
Coleoptera	Byrrhidae	<i>Byrrhus fasciatus</i> (Forster, 1771)	1	11		Heath	
	Carabidae	<i>Patrobus septentrionis</i> (Dejean, 1821)	50	17	23	Fen and shrub*	
	Coccinellidae	<i>Coccinella transversoguttata</i> (Falderman, 1835)		51	2	Heath*	
	Cryptophagidae	<i>Caenoscelis ferruginea</i> (Sahlberg, 1820)		38	2	Heath and shrub	
	Curculionidae		<i>Otiorynchus arcticus</i> (O. Fabricius, 1780)	1	20	1	Heath
			<i>Otiorynchus nodosus</i> (Müller, 1764)	18	66	19	No classification
	Staphylinidae		<i>Mycetoporus nigrans</i> (Mäklin, 1853)		2		No classification
			<i>Quedius fellmanni</i> (Zetterstedt, 1838)		2		No classification

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508 Table 2: Mean (\pm S.E) of the environmental variables included in GLM's and latent variable models,
 509 showing the difference between sites and treatments. Graminoid cover was measured in six
 510 categories: 0%, 1–20%, 21–40%, 41–60%, 61–80%, and 81–100%. Vegetation height was
 511 measured (classified to the nearest 5 cm) of the vegetation height with the highest coverage in the
 512 sub-plot.

Site	Habitat	Vegetation height (height classes)	Graminoid (% cover)	pH
Site 1	Heath	2.6 (0.2)	15 (5)	5.8 (0.1)
	Fen	2.5 (0.2)	55 (6.3)	5.5 (0.2)
Site 2	Heath	2.4 (0.2)	18.6 (3.7)	6.4 (0.1)
	Fen	2.3 (0.3)	75 (6.3)	6.5 (0.04)
	Shrub	7.5 (1.2)	10.3 (3.5)	6.2 (0.3)
Site 3	Heath	3.2 (0.4)	12.7 (11.4)	6.2 (0.2)
	Shrub	28.5 (4.1)	4 (1.9)	6.5 (0.04)

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531 Table 3: Deviance table showing the results of the multivariate generalized linear model, including
 532 all variables tested, along with residual degrees of freedom, degrees of freedom, deviance and P-
 533 value.

Parameter	Residual degrees of freedom	Degrees of freedom	Deviance	<i>p</i> -value
Intercept	55			
Vegetation height (heightclass)	54	1	117.9	0.001
Graminoid cover (% cover)	53	1	93.2	0.001
pH	52	1	43.0	0.389
Site	50	2	296.2	0.001
Vegetation height:Site	48	2	35.0	0.639
Graminoid cover:Site	46	2	103.8	0.003
pH:Site	44	2	40.8	0.568

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548 Table 4: Paired t-test of the local transitions in soil moisture and shrub dominance. LV1 and LV2
 549 represent the first and second coordinate of the latent variable.

Model	Residual degrees of freedom	Estimates	<i>t</i>	<i>p</i>
Fen transect site 1 LV1	7	- 0.86	- 5.32	0.001
Fen transect site 1 LV2	7	- 0.43	- 4.78	0.002
Fen transect site 2 LV1	7	- 1.70	- 0.26	0.13
Fen transect site 2 LV2	7	- 0.37	- 3.21	0.02
Shrub transect site 2 LV1	5	- 0.72	- 3.90	0.01
Shrub transect site 2 LV2	5	- 0.35	- 3.10	0.03
Shrub transect site 3 LV1	5	- 1.16	- 5.50	0.003
Shrub transect site 3 LV2	5	- 0.62	- 3.28	0.02

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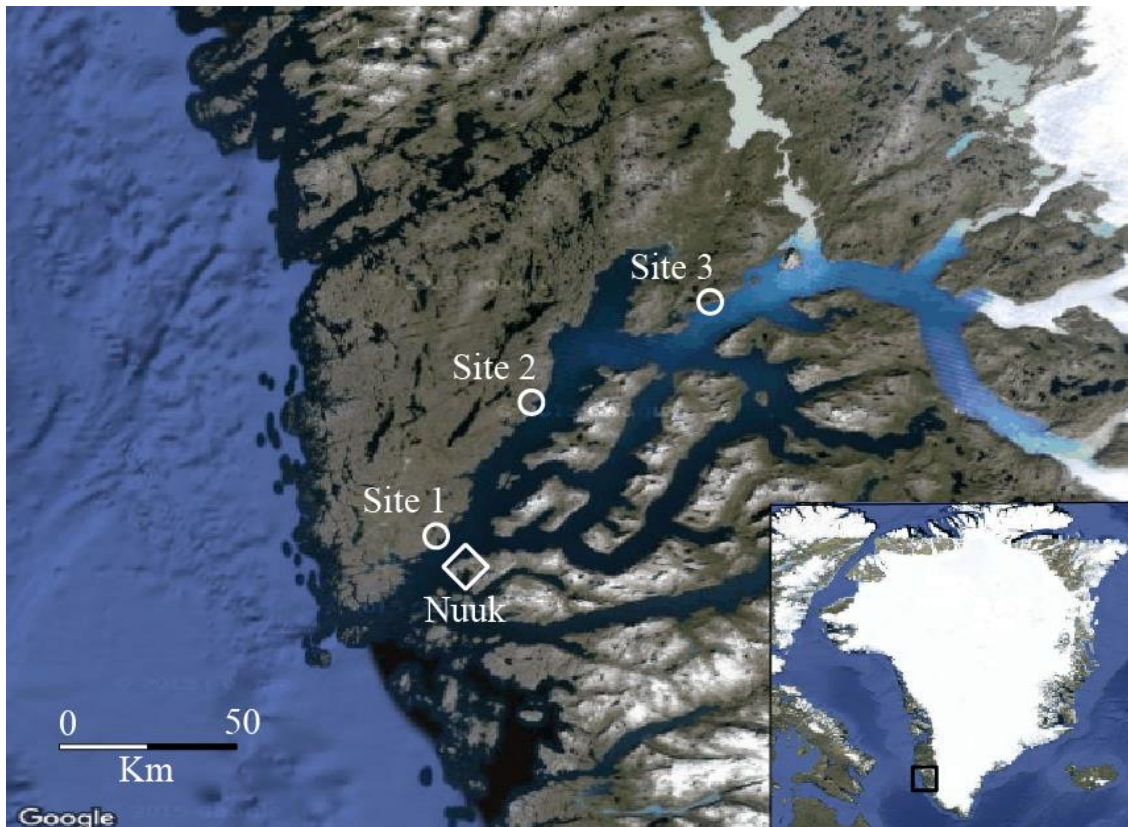
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567 Figures

568 Fig. 1: Map of the Godthåbsfjord area, South-West Greenland (64° 11' N, 51° 44' W), showing the
569 three study sites (1, 2, and 3) depicted with a circle and the capital Nuuk depicted with a diamond.
570 The inset figure in the lower right corner shows Greenland with the study area framed in a square.
571 The map was created with the R package 'RgoogleMaps' (Loecher & Ropkins 2015). Mapdata: ©
572 Google 2016



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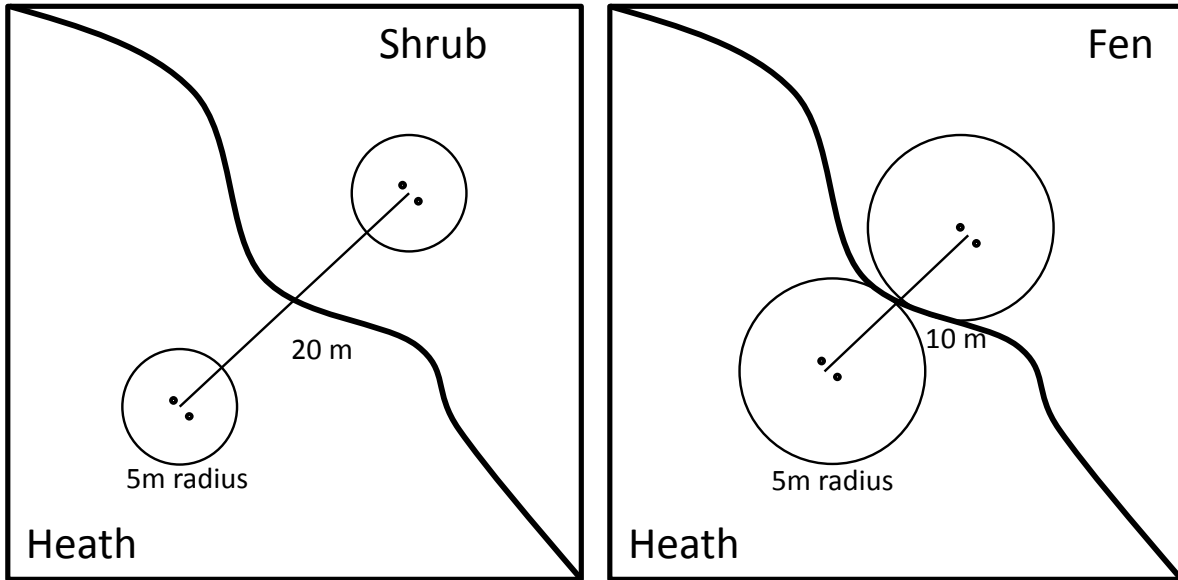
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584 Fig. 2: Conceptual figure of the sampling design showing fen transects in the right panel and shrub
585 transects in the left panel.

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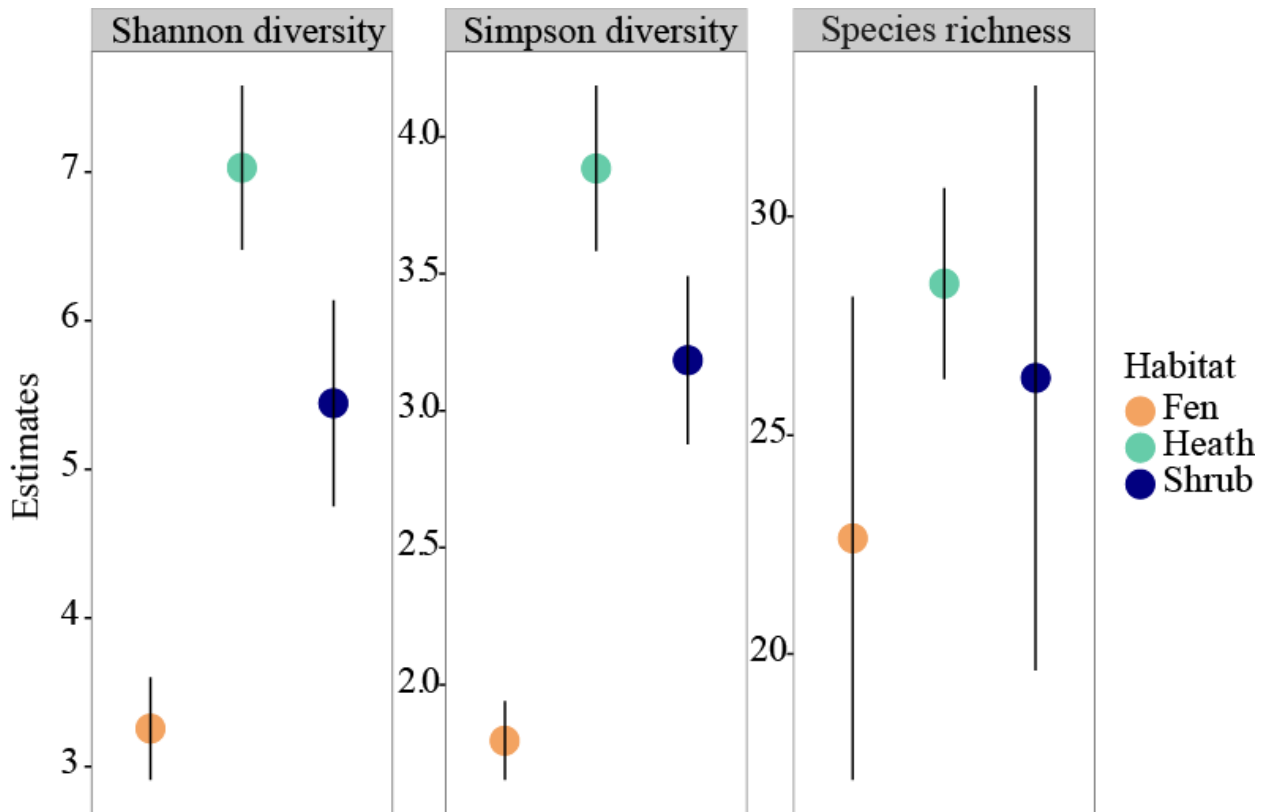
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603 Fig. 3: Diversity profiles for species richness, Shannon diversity, and Simpson diversity coloured
604 by habitat. Error bars represent 95 percent confidence intervals.



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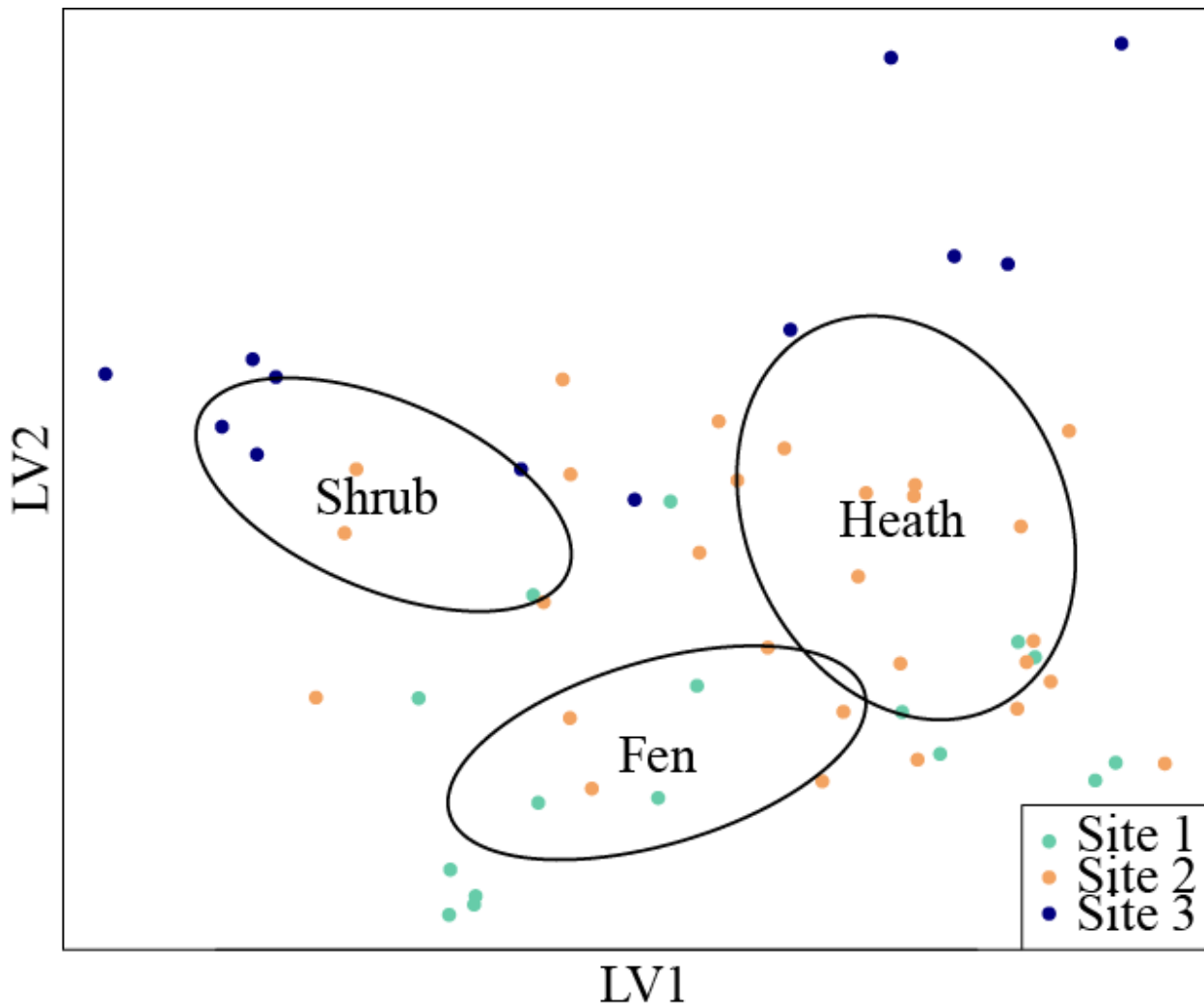
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619 Fig. 4: Species distribution plot of the best fitted latent variable model showing the mean of the
620 latent variable with a negative binomial distribution. Ellipses represent 95 percent confidence
621 intervals around the centroids of each habitat.



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