

Synchronous seasonal dynamics in composition, richness and turnover of arthropod assemblages across the Arctic

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Abstract

Tracking changes in community composition in response to environmental change, requires knowledge on species distributions in space and time. For Arctic Arthropods this knowledge is accumulating slowly due to the prohibitive costs of field work and species identification. Accordingly, it is important to determine to which extent the timing and duration of sampling affects detectability of species. With a solid base in a monitoring scheme incorporating nearly 20 years of consecutive weekly arthropod sampling in North-Greenland, we studied how sampling time and duration of sampling, affected the distribution patterns of Arctic arthropods at family and species level resolutions. Through multivariate models, turnover measures, and species richness, we assessed the seasonal window where arthropod diversity was stable and compared the results to similar data from three other sites in the Arctic, spanning a large geographic and climatic. To further document how this seasonal window could be expected to deviate in response to climate change, we used environmental fitting analysis to correlate findings with environmental variables. Arthropod compositions displayed a similar multivariate pattern across sites, habitats taxonomic resolution and years. However, compositions differed significantly between habitats as well as sampling dates, and there was an interaction between sampling dates and habitats for most sites. Increasing temperatures and advancement in timing of snowmelt extended the seasonal window where richness peaked, and this also varied slightly among sites. The recommendations made here are a useful tool for accruing large scale data on distributional patterns.

Introduction

Global biodiversity loss is occurring at an alarming rate, due to global change and increasing human influence (Butchart et al. 2010). Monitoring of biodiversity, as well as, gaining a full comprehension of the spatial and temporal distribution of species are among the top priorities in ecology (Heller & Zavaleta 2009). Recent accelerating climate change, which alters habitats and compromises species living conditions, increases relevance further (Elmendorf et al. 2012). In spite of increasing focus, sufficient information about the distribution of species richness in large regions, such as the Arctic, remains sparse for many biological groups (CAFF 2013; Hodkinson 2013). Many ecological studies seek to track changes in species diversity and composition throughout the season and over multiple years (Høye & Forchhammer 2008; Spitzer & Jaroš

2009; Bowden et al. 2015), in order to adequately describe the changes in communities brought on by environmental disturbances, such as climate change (Magurran et al. 2010). Although sampling all taxa at multiple sites through a full season of activity is preferable, it may be a daunting task, due to logistical constraints and limited resources available. This predicament, however, raises an interesting question. What fraction of the community is ignored by not covering full seasons?

Numerous studies on species-area relationships have shown strong positive relationships between species richness and turnover and the area or the heterogeneity of the habitat sampled (Connor & McCoy 1979; Lomolino 2000; Hansen et al. 2016a; Hansen et al. 2016b; Vandvik et al. 2016). The temporal pendant of species area relationship, the species–time relationship (Adler & Lauenroth 2003; White & Gilchrist 2007; McGlenn & Palmer 2009), describes the similarly positive relationship between species richness and the length of time a site is studied (Preston 1960), but has not yet been studied as intensively. Temporal species accumulation operates at multiple time scales. Firstly species accumulates intraannually as seasons and conditions shifts. Secondly, variability in weather patterns between years accumulates species over decades or even centuries. Thirdly, there is the evolutionary change in extinction and speciation rates, operating over centuries and millennia (Preston 1960; Magurran et al. 2010; Boggs 2016). Therefore the seasonal development of species is expected to change across years. Moreover, changes over time in a community may occur as the observed accumulation of richness as more species are added throughout the time frame, but also from turnover events where one species replaces another, making both community composition and richness important measures (Yen et al. 2016). Most past and contemporary studies of species-time relationships refer to the interannual variation of species aggregating over the course of multiple years.

A few studies have indicated that lowering the temporal extent and resolution of sampling may have limited impact on species compositions and diversity (Nally et al. 2004; Xu et al. 2015). It is, however, unknown to what spatial and taxonomic extent the generality of these patterns can be inferred. Furthermore, when combining spatial and temporal patterns, the influence of increasing the spatial extent exceeds that of temporal increments on species richness (Erös & Schmera 2010). One way of capturing the seasonal window where local colonization and extinction patterns are low, is to look for statistical regularity and aggregation in the

observed compositional patterns (White & Gilchrist 2007). Considering this, the rate of species accumulation might not be constant over the span of a season, and specific subsets in time may capture significant proportions of the community.

Multiple studies of Arctic distributional patterns have disputed the common conception of the Arctic as a rather homogenous landscape and that heterogeneity between habitats cause great diversification (Bowden & Buddle 2010; Normand et al. 2013; Sikes et al. 2013; Ernst et al. 2016; Hansen et al. 2016a), yet little focus has been given to the temporal variation in arthropod compositions across the active season in Arctic regions. While species in the Arctic are under strong seasonal impacts, the region offers a powerful model system for studying changes over time. Hence temporal studies of Arctic communities can prove useful for overcoming the challenges brought on by sampling large or multiple areas. Moreover, the Arctic region spans large climatic gradients, rendering results of temporal studies applicable at the global scale.

Invertebrates have long been recognized as good indicators of changing communities due to their small body sizes, relatively short generation time and ectothermic lifestyle. Terrestrial arthropods furthermore play an important role in the Arctic food webs as they represent more than one third of all terrestrial organisms, including plants and fungi (CAFF 2013). Since timing of snowmelt and increasing summer temperatures have been identified as important drivers of the active season length of Arctic arthropods (Høye & Forchhammer 2008), they are likely to be important factors in controlling seasonal dynamics of Arctic arthropod communities.

In this study, we evaluate the effect of sampling time and duration on arthropod diversity, turnover and composition. More specifically, we study the seasonal development across multiple sites, taxa and habitats. By including both family- and species level data, we verify whether the patterns are replicated at lower taxonomic resolutions. We investigate the difference in species composition and diversity between habitats and discuss this in relation to temporal variation in species composition and species richness. We propose an optimal timeframe where communities are stable and furthermore suggest a tradeoff between sampling more habitats and shorter timeframes for answering questions regarding compositional changes. An optimal sampling window (a) maximizes community diversity; (b) is characteristic of whole-season community composition; and (c) is robust to effects of inter-annual weather variability and long-term climate

change. The goal of this study was to determine the “optimal” sampling window (date and duration of sampling) for arthropod communities across a wide array of terrestrial arctic locations and habitat types. We divided this goal into two objectives:

Objective 1: We describe seasonal dynamics in community composition and compare indices of arthropod community composition, stability and species richness for sampling windows that vary in date and duration across multiple Arctic sites and habitat types;

Objective 2: We evaluate the effects of inter-annual weather variability and long-term climate trends on community assembly and community indices for each sampling window within sites and habitat types.

Methods

Data

We compiled datasets entailing three different regions within the Arctic (Svalbard, Greenland and Alaska). The Greenland datasets are comprised of two datasets collected as part of Greenland ecosystem Monitoring (GEM). One consists of 18 consecutive years (1996 – 2014) (samples from 2010 were lost in transit from Greenland) of weekly pitfall trap samples from Zackenberg valley, North-east Greenland (74°28' N, 20°34' W). The Nuuk dataset, consists of weekly pitfall trap samples (2008 – 2010) in Kobbefjord, South-west Greenland (64°07'N / 51°21'W). Both datasets have been identified to family level and furthermore butterflies, spiders and muscid flies have been identified to the species level for Zackenberg. The Alaskan dataset, sampled at Toolik lake at (68°38' N, 149°35' W) holds two consecutive years (2010 and 2011) of weekly pitfall trap sampling, and has been identified to family level (Rich et al. 2013). From Svalbard (78°55' N, 11°55' W), pitfall sampling occurred from 2009 to 2011 and has been identified to the lowest possible taxonomic level (Table 1). For each dataset, we selected the weeks where all habitats had been equally sampled across all years and standardized to counts per trap per week. The week numbers were calculated from day of year.

Analysis of site characteristics

We examined the distribution of the four regions in relation to climatic gradients within the Arctic using Principal Component Analysis (PCA). Data for five climatic variables were extracted from the worldclim data set (Hijmans et al. 2005): annual mean temperature, mean temperature of the warmest quarter, precipitation of the warmest quarter, precipitation of the coldest quarter, and minimum temperature of the coldest month. PCA was conducted with climate data within the sub- to high Arctic and the most common climate (75-percentile) within Greenland, subarctic, low arctic, and high arctic was delineated. The four regions were plotted according to their climatic conditions with the multidimensional climate space.

Arthropod community composition and seasonal assembly

To visually identify the time frame of the season where arthropod species composition was most stable, we first modeled each dataset through latent variable modelling. Latent variable modelling is a Bayesian model-based approach that explains community composition through a set of underlying latent variables to account for residual correlation, for example due to biotic interaction. This method offers the possibility to adjust the distribution family to account for over-dispersion- in count data via negative binomial distribution. Thus, it also accounts for the increasing mean-variance relationship without confounding location with dispersion (Hui et al. 2015). Three “types” of models may be fitted: 1) With covariates and no latent variables, boral fits independent response GLMs such that the columns of y are assumed to be independent; 2) With no covariates, boral fits a pure latent variable model (Rabe-Hesketh et al. 2004) to perform model-based unconstrained ordination (Hui et al. 2015); 3) With covariates and latent variables, boral fits correlated response GLMs, with latent variables.

We created latent variable models at site levels for each dataset with two latent variables. to visualize how the arthropod communities were distributed. This method is comparable to a two dimensional non metric multidimensional scaling (NMDS) plot. From the latent variable model, we extracted the posterior median values of the latent variables which we used as coordinates on ordination axes to represent family level composition at plot level (Hui et al. 2015). We drew convex ellipses around posterior median values belonging to each habitat for each dataset based on 95 percent confidence limits of the yearly averages. For this purpose, we used the function ‘ordiellipse’ in the r package ‘Vegan’ (Oksanen et al. 2016). We repeated this analysis at species level for the Zackenberg dataset.

We then tested whether the seasonal development in arthropod composition differed significantly between habitats through a multivariate extension of General Linear Models (GLMs), using the function ‘manyglm’ in the package ‘mvabund’ (Wang et al. 2012). This recently developed method offers the possibility to model distributions based on count data by assuming a negative binomial distribution. We tested for main effects of week and habitats and for an interaction between the two terms. We then repeated the latent variable modeling at habitat level for all datasets with a significant interaction term, and calculated convex ellipsoids around posterior median values belonging to each week based on the standard error of the yearly averages. We extracted the centroid of each ellipsoid, which we plotted on top of the latent variable plot. At habitat level, we tested if the seasonal development differed significantly between years, by testing for an interaction between time of season (week) and year.

Sampling window – based arthropod species richness and turnover

Multivariate methods for measuring beta diversity have been shown robust compared to classical methods. This is due to the dependency upon gamma diversity in classical methods, such that when sampling effort increases, so does beta diversity along with gamma diversity (Bennett & Gilbert 2016). We used the centroids extracted from the latent variable models for each habitat from the Zackenberg family level dataset. While the distance to the group centroid is a common way of measuring spatial beta diversity (Anderson et al. 2006), it describes the yearly variations in beta diversity within the weeks and not the unidirectional, temporal drift in multivariate space from one week to the next. We used the distance between week to week centroids as a measure of temporal turnover, and used the average area of the two ellipsoids as error bars to represent the interannual variation. We calculated species richness for each week and each habitat across all years. To identify the timeframe and length of timeframe in which the highest number of species were represented, we calculated species richness for each combination of timing and duration; four week sampling at nine different points, three week sampling at ten different points, two week sampling at eleven different points of the season and one week sampling at 12 different points. We explored how what proportion of total season species richness was captured for each of the sampling strategies.

Climatic variability and the effect on seasonal development

We used the Zackenberg family level dataset to analyze the sensitivity of diversity to climatic variables. This dataset is the only one, where environmental variables were measured every year. Timing of snowmelt has been shown to occur significantly earlier, as well as average may-august temperatures to become significantly warmer (Bowden et al. 2015). Timing of snowmelt has furthermore proven a significant predictor of season length for arthropods (Høye et al. 2014). To identify if the different seasonal development between years was climate related, we ran a multivariate correlation analysis with the function 'envfit' in the 'vegan' package. We used the posterior median values of the latent variables as response variables and timing of snowmelt, average may-august temperature, year and week as predictor variables. We examined how the changing climate has affected seasonal development of arthropod assemblages by dividing the Zackenberg family level dataset into years of early and late snowmelt, as well as, warm and cold years. Early snowmelt years were categorized as years where the average day of year for snowmelt lay below the average day of year for all years. Similarly, warm years were categorized as years where the average summer (may august) temperature lay above the average across years. Following these divisions, we calculated species richness for each category.

Results

Analysis of site characteristics

The investigated sites were distributed across the climatic space of the PCA. Two sites were distributed within the high Arctic climate (Ny Aalesund and Zackenberg) and two sites in the low Arctic (Nuuk and Toolik) (Fig. 1). The first two axis of the PCA explained 87% of the variation and was mainly correlated with precipitation of the warmest quarter (1. Axis) and temperature of the warmest quarter (2. axis). Toolik have warmer summers than the other sites and Nuuk, Ny Aalesund and Zackenberg is distributed along a gradient from wet to dryer conditions.

Arthropod community composition and seasonal assembly

Arthropod compositions differed significantly between all of the investigated habitats at each site and there was a significant effect of week (Table 2). The moisture gradient was a driving component across sites. At Zackenberg, there was a clear distinction between arthropod communities, in the wet habitats and arthropod communities in the dry and mesic habitats. For

Nuuk habitats, the biggest distinction was found between the shrub covered habitat and the wet, with the dry habitat as an intermediate (Fig. 2). However, the interaction between seasonal development and habitat was not significant for Toolik and Ny Aalesund, even though arthropod compositions differed significantly between both habitats and week (Table 2).

The weekly development through the season, displayed a characteristic u-shaped pattern for all the habitats at all the sites. The arthropod compositions were more similar towards the beginning and the end of the season. There was a change in multivariate space from week to week throughout the season, yet, the communities seemed to stabilize during mid-season with less distance between the weekly centroids (Fig. 3).

Sampling window – based on arthropod species richness and turnover

At Zackenberg, the weeks of significantly (non-overlapping error bands) highest richness were between week 29 until week 33 for the dry habitat. The mesic habitat varied from week to week and richness never reached a plateau. In the wet habitat, richness increased until week 29 and stabilized before dropping in week 32. Turnover patterns were opposite to richness and stabilized at the lowest point between week 29 and 30, until increasing again between week 32 and 33. Turnover in the mesic habitat did not reach a stable low point until between week 32 and 33. In Nuuk, there was inter annual variability both in species richness and turnover, but species richness in the shrubs and the dry habitat peaked from week 29 to 32. The wet habitat had significantly higher species richness in week 32 and it was overall lower than in the shrub and dry habitat. Turnover did not differ significantly in any of the habitats between any of the weeks for Nuuk. Species richness at Toolik was significantly highest in week 25 to 30 and declined drastically in week 31. Turnover was lowest between weeks 26 to 28. In Svalbard, species richness was significantly highest in week 29 with a maximum of 13 taxa present, and turnover did not change significantly between any of the weeks (Fig. 4).

Analysis of sampling strategy in Zackenberg mirrored the weeks of highest richness and turnover and revealed that sampling either week in a one-week sampling strategy between weeks 28-32, yielded 69-72 percent of the taxa present when sampling a full season. Four weeks of sampling that time frame yielded 79-81 percent of the full season taxa detected. The optimal timespan for one week sampling strategy in Nuuk was starting week 28 and 29 which detected

55-57 percent of the full season taxonomic richness, whereas four weeks of sampling with the same starting weeks presented 64-69 percent. In Toolik, the optimal starting week was between week 26 and 28 for one week sampling duration, which detected 59-61 percent of the taxa present throughout a full season and four week in with the same starting weeks yielded 75-77 percent. In Ny-Aalesund, there was no significant difference between sampling duration (Fig. 5).

The effect of climatic variability on seasonal development

Temperatures had a significant effect on arthropod compositions in the dry and mesic habitat at Zackenberg and year was highly correlated with temperature. In the wet habitat, there was no significant effect of snowmelt, temperature and year (Fig. 6). The average day of year for snowmelt across all years was day 152. For six years (2004, 2005, 2009, 2010, 2011 and 2013) the average snowmelt date lay below this threshold, and these were categorized as early snowmelt years. Average may-august temperature was 2.23 °C and the years 1996 – 2002 and 2014 had an average may-august temperature below this threshold. Taxonomic richness was higher and peaked earlier for the warm and early snowmelt years (Fig. 7).

Discussion

Across sites, habitats, and taxonomic levels, arthropod compositions displayed similar trends in seasonal development with less seasonal drift during the peak season weeks (i.e. weeks with low turnover). In present study one week of carefully planned sampling at Zackenberg research station, represented up to 72 percent of richness detected through a full season of sampling.

Zackenberg monitoring program presents us with a unique chance of studying temporal trends as it has been operating for 20 years and has collected data on arthropods with weekly intervals throughout the active season. A long term monitoring program at ecosystem level is quite unique and can answer questions entailing interaction dynamics through trophic mismatch and cascades (Mortensen et al. 2014). Additional short term sampling schemes with high spatial resolution across multiple sites could help fill gaps in our knowledge of species distributions and add information to the model predictions of climate change effects on biodiversity. This could be partly accomplished through citizen science schemes as well as cross disciplinary cooperation among researches, where full seasonal commitments may not be an option, but simultaneous

multiple year and site collections are. With a strong standardized sampling design available, people without scientific training can carry out fieldwork and will be capable of generating data, which will help biologists answer questions regarding species distributions. Utilizing local communities is a valuable way of accruing large amounts of data otherwise unattainable. It is important to note that we are not trying to limit the temporal extent, nor resolution of long term monitoring schemes. These recommendations are solely for studies of distributional patterns and inferences on life history traits, species interactions and other species specific responses, require longer timeframes to answer. We are still dependent on long term sampling strategies spanning full seasons with higher detailed resolution levels. However, these findings have merits in addition to the high resolution monitoring schemes.

Climate changes are altering habitats (Myers-Smith et al. 2011; Elmendorf et al. 2012) and expanding the active season for arthropods (Høye & Forchhammer 2008), affecting arthropod compositions across the Arctic (Bowden & Buddle 2010; Hansen et al. 2016b). Time and duration of peak richness may therefore change with a changing climate. Our results show that increasing temperatures does not cause shifts in timing of peak richness, but increases species richness and extends the time frame, where species richness is significantly highest. Sampling strategies have previously been studied in other ecosystems and for other groups of organisms with the intent of describing effect of lower sampling extent and intensity on diversity patterns. For instance temporal aggregation of species had a substantial effect on the species-time relationship of rodent populations in Arizona (White & Gilchrist 2007). A study of ciliated protozoa in the Yellow sea, north China, a sampling regime with one third the amount of original sampling, recovered > 75% information of the total seasonal variability and > 90 percent of protozoan ciliate species present (Xu et al. 2015). Compared to our findings of little effect of changing climates on timing of optimal sampling window, as well as, the similar u-shaped pattern across a large climatic gradient, super generalizations to other ecosystems and regions is possible.

The study indicates that short term sampling procedures comes with some considerations. The peak in species richness varies between sites with earlier seasonal peaks at the lower latitudes. As a consequence, sampling one week requires careful consideration of the geographic location of the study. Interaction between seasonal development and habitat coupled with

different temporal development in species richness underlines not only a need to sample multiple habitats, but also a detailed consideration towards habitat characteristics, such as soil moisture and vegetation structures. For instance, wet and mesic habitats display the lowest and latest peaks in species richness. These results mirror a previous study from the Godthåbsfjord area in Nuuk, where diversity and species richness were overall lowest in the fens (Hansen et al. 2016b). The year to year variation in turnover for some sites (Nuuk and Ny Aalesund), which is less pronounced for species richness, indicates that abundances vary substantially between years. However, multiple inter annual short term samplings will help counterbalance the year-to-year variability. Shorter sampling windows are more sensitive to stochastic events, such as less optimal weather and it is therefore always desirable to sample the longest term possible.

This study is to our knowledge the first to answer questions regarding sampling time and duration of Arctic arthropods, and may prove valuable in the planning of logistically challenging field work (Post & Høye 2013). In conclusion, should compromises be made between spatial and temporal sampling resolution and extent, we believe that an increase of spatial, at the cost of temporal intra annual extent and resolution, is preferable. In combination with the long term monitoring programs, these recommendations will go a long way in mapping species distributions, as well as, responses to climate change.

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Adler PB, and Lauenroth WK. 2003. The power of time: spatiotemporal scaling of species diversity. *Ecology Letters* 6:749-756 DOI: 10.1046/j.1461-0248.2003.00497.x.

Anderson MJ, Ellingsen KE, and McArdle BH. 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* 9:683-693 DOI: 10.1111/j.1461-0248.2006.00926.x.

Bennett JR, and Gilbert B. 2016. Contrasting beta diversity among regions: how do classical and multivariate approaches compare? *Global Ecology and Biogeography* 25:368-377 DOI: 10.1111/geb.12413.

Boggs CL. 2016. The fingerprints of global climate change on insect populations. *Current Opinion in Insect Science* 17:69-73 DOI: <http://dx.doi.org/10.1016/j.cois.2016.07.004>.

Bowden JJ, and Buddle CM. 2010. Determinants of ground-dwelling spider assemblages at a regional scale in the Yukon Territory, Canada. *Ecoscience* 17:287-297 DOI: 10.2980/17-3-3308.

- Bowden JJ, Eskildsen A, Hansen RR, Olsen K, Kurle CM, and Høye TT. 2015. High-Arctic butterflies become smaller with rising temperatures. *Biology Letters* 11 DOI: 10.1098/rsbl.2015.0574.
- Butchart SHM, Walpole M, Collen B, van Strien A, Scharlemann JPW, Almond REA, Baillie JEM, Bomhard B, Brown C, Bruno J, Carpenter KE, Carr GM, Chanson J, Chenery AM, Csirke J, Davidson NC, Dentener F, Foster M, Galli A, Galloway JN, Genovesi P, Gregory RD, Hockings M, Kapos V, Lamarque J-F, Leverington F, Loh J, McGeoch MA, McRae L, Minasyan A, Morcillo MH, Oldfield TEE, Pauly D, Quader S, Revenga C, Sauer JR, Skolnik B, Spear D, Stanwell-Smith D, Stuart SN, Symes A, Tierney M, Tyrrell TD, Vié J-C, and Watson R. 2010. Global Biodiversity: Indicators of Recent Declines. *Science* 328:1164-1168 DOI: 10.1126/science.1187512.
- CAFF. 2013. *Arctic Biodiversity Assessment. Status and trends in Arctic biodiversity*. Akureyri.
- Connor EF, and McCoy ED. 1979. The Statistics and Biology of the Species-Area Relationship. *The American Naturalist* 113:791-833
- Elmendorf SC, Henry GHR, Hollister RD, Bjork RG, Boulanger-Lapointe N, Cooper EJ, Cornelissen JHC, Day TA, Dorrepaal E, Elumeeva TG, Gill M, Gould WA, Harte J, Hik DS, Hofgaard A, Johnson DR, Johnstone JF, Jonsdottir IS, Jorgenson JC, Klanderud K, Klein JA, Koh S, Kudo G, Lara M, Levesque E, Magnusson B, May JL, Mercado-Diaz JA, Michelsen A, Molau U, Myers-Smith IH, Oberbauer SF, Onipchenko VG, Rixen C, Schmidt NM, Shaver GR, Spasojevic MJ, Porhallsdottir PE, Tolvanen A, Troxler T, Tweedie CE, Villareal S, Wahren CH, Walker X, Webber PJ, Welker JM, and Wipf S. 2012. Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change* 2:453-457 DOI: 10.1038/Nclimate1465.
- Ernst CM, Loboda S, and Buddle CM. 2016. Capturing northern biodiversity: diversity of arctic, subarctic and north boreal beetles and spiders are affected by trap type and habitat. *Insect Conservation and Diversity* 9:63-73 DOI: 10.1111/icad.12143.
- Erös T, and Schmera D. 2010. Spatio-temporal scaling of biodiversity and the species–time relationship in a stream fish assemblage. *Freshwater Biology* 55:2391-2400 DOI: 10.1111/j.1365-2427.2010.02438.x.
- Hansen RR, Hansen OLP, Bowden JJ, Normand S, Bay C, Sørensen JG, and Høye TT. 2016a. High spatial variation in terrestrial arthropod species diversity and composition near the Greenland ice cap. *Polar Biology*:1-10 DOI: 10.1007/s00300-016-1893-2.
- Hansen RR, Hansen OLP, Bowden JJ, Treier UA, Normand S, and Høye T. 2016b. Meter scale variation in shrub dominance and soil moisture structure Arctic arthropod communities. *PeerJ* 4:e2224 DOI: 10.7717/peerj.2224.
- Heller NE, and Zavaleta ES. 2009. Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation* 142:14-32 DOI: <http://dx.doi.org/10.1016/j.biocon.2008.10.006>.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, and Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25:1965-1978 DOI: 10.1002/joc.1276.
- Hodkinson ID. 2013. Terrestrial and Freshwater Invertebrates. In: Meltofte H, ed. *Arctic Biodiversity Assessment Status and trends in Arctic biodiversity*. Akureyri, 195-219.
- Høye TT, Eskildsen A, Hansen RR, Bowden JJ, Schmidt NM, and Kissling WD. 2014. Phenology of high-arctic butterflies and their floral resources: Species-specific responses to climate change. *Current Zoology* 60:243-251
- Høye TT, and Forchhammer MC. 2008. Phenology of High-Arctic Arthropods: Effects of Climate on Spatial, Seasonal, and Inter-Annual Variation. In: Hans Meltofte TRCBEMCF, and Morten R, eds. *Advances in Ecological Research*: Academic Press, 299-324.

- Hui FKC, Taskinen S, Pledger S, Foster SD, and Warton DI. 2015. Model-based approaches to unconstrained ordination. *Methods in Ecology and Evolution* 6:399-411 DOI: 10.1111/2041-210X.12236.
- Lomolino MV. 2000. Ecology's most general, yet protean pattern: the species-area relationship. *Journal of Biogeography* 27:17-26 DOI: 10.1046/j.1365-2699.2000.00377.x. 1
- Magurran AE, Baillie SR, Buckland ST, Dick JM, Elston DA, Scott EM, Smith RI, Somerfield PJ, and Watt AD. 2010. Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. *Trends in Ecology & Evolution* 25:574-582 DOI: <http://dx.doi.org/10.1016/j.tree.2010.06.016>.
- McGlinn DJ, and Palmer MW. 2009. Modeling the sampling effect in the species–time–area relationship. *Ecology* 90:836-846 DOI: 10.1890/08-0377.1.
- Mortensen LO, Jeppesen E, Schmidt NM, Christoffersen KS, Tamstorf MP, and Forchhammer MC. 2014. Temporal trends and variability in a high-arctic ecosystem in Greenland: multidimensional analyses of limnic and terrestrial ecosystems. *Polar Biology* 37:1073-1082 DOI: 10.1007/s00300-014-1501-2.
- Myers-Smith IH, Forbes BC, Wilmsking M, Hallinger M, Lantz T, Blok D, Tape KD, Macias-Fauria M, Sass-Klaassen U, Levesque E, Boudreau S, Ropars P, Hermanutz L, Trant A, Collier LS, Weijers S, Rozema J, Rayback SA, Schmidt NM, Schaepman-Strub G, Wipf S, Rixen C, Menard CB, Venn S, Goetz S, Andreu-Hayles L, Elmendorf S, Ravolainen V, Welker J, Grogan P, Epstein HE, and Hik DS. 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters* 6 DOI: 10.1088/1748-9326/6/4/045509.
- Nally RM, Fleishman E, and Murphy DD. 2004. Influence of Temporal Scale of Sampling on Detection of Relationships between Invasive Plants and the Diversity Patterns of Plants and Butterflies. *Conservation Biology* 18:1525-1532 DOI: 10.1111/j.1523-1739.2004.00399.x.
- Normand S, Randin C, Ohlemuller R, Bay C, Høye TT, Kjaer ED, Korner C, Lischke H, Maiorano L, Paulsen J, Pearman PB, Psomas A, Treier UA, Zimmermann NE, and Svenning JC. 2013. A greener Greenland? Climatic potential and long-term constraints on future expansions of trees and shrubs. *Philosophical Transactions of the Royal Society B-Biological Sciences* 368 DOI: 10.1098/Rstb.2012.0479.
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, and Wagner H. 2016. *vegan: community ecology package*. 2.0-10 ed.
- Post E, and Høye TT. 2013. Advancing the long view of ecological change in tundra systems. *Philosophical Transactions of the Royal Society B-Biological Sciences* 368 DOI: 10.1098/Rstb.2012.0477.
- Preston FW. 1960. Time and Space and the Variation of Species. *Ecology* 41:612-627 DOI: 10.2307/1931793.
- Rabe-Hesketh S, Skrondal A, and Pickles A. 2004. Generalized multilevel structural equation modeling. *Psychometrika* 69:167-190 DOI: 10.1007/bf02295939.
- Rich ME, Gough L, and Boelman NT. 2013. Arctic arthropod assemblages in habitats of differing shrub dominance. *Ecography* 36:994-1003 DOI: 10.1111/j.1600-0587.2012.00078.x.
- Sikes DS, Draney ML, and Fleshman B. 2013. Unexpectedly high among-habitat spider (Araneae) faunal diversity from the Arctic Long-Term Experimental Research (LTER) field station at Toolik Lake, Alaska, United States of America. *Canadian Entomologist* 145:219-226 DOI: 10.4039/tce.2013.5.
- Spitzer K, and Jaroš J. 2009. Long-term monitoring of moth populations (Lepidoptera) associated with a natural wetland forest: synthesis after 25 years. *Terrestrial Arthropod Reviews* 1:155-163

- Vandvik V, Klanderud K, Meineri E, Måren IE, and Töpper J. 2016. Seed banks are biodiversity reservoirs: species–area relationships above versus below ground. *Oikos* 125:218-228 DOI: 10.1111/oik.02022.
- Wang Y, Naumann U, Wright ST, and Warton DI. 2012. mvabund– an R package for model-based analysis of multivariate abundance data. *Methods in Ecology and Evolution* 3:471-474 DOI: 10.1111/j.2041-210X.2012.00190.x.
- White EP, and Gilchrist MA. 2007. Effects of population-level aggregation, autocorrelation, and interspecific association on the species-time relationship in two desert communities. *Evolutionary Ecology Research* 9:1329-1347
- Xu H, Yong J, and Xu G. 2015. Sampling frequency of ciliated protozoan microfauna for seasonal distribution research in marine ecosystems. *Marine Pollution Bulletin* 101:653-659 DOI: <http://dx.doi.org/10.1016/j.marpolbul.2015.10.034>.
- Yen JDL, Thomson JR, Keith JM, Paganin DM, and Nally RM. 2016. How do different aspects of biodiversity change through time? A case study on an Australian bird community. *Ecography*:n/a-n/a DOI: 10.1111/ecog.02306.

1 Table 1

2 Overview of sites: The asterisk indicates that the dataset is used for supportive analyses and the
3 results can be found in supplement material

Dataset	Position	Years	Selected sampling period (weeks)	Sampling intensity	Taxonomic resolution	Habitats
Zackenberg (Greenland)	74°28' N, 20°34' W	1996 – 2014	24:35	Weekly	Family level	Dry, mesic and wet
Nuuk (Greenland)	64°07' N / 51°21' W	2008 – 2014	25:39	Weekly	Family level	Dry, wet and shrub
Ny Aalesund (Svalbard)	78°55' N, 11°55' W	2009 – 2011	27:33	Two-day interval	Family, super family and order	Mesic and dry
Toolik lake	68°38' N, 149°35' W	2010 – 2011	21:30	Weekly	Family level	Open and shrub
Zackenberg*	74°28' N, 20°34' W	1996 – 2014	24:35	Weekly	Species level (butterflies, spiders and muscid flies)	Dry, mesic and wet

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14 Table 2

15 Table of deviance. Table showing results of the multivariate GLM, testing the difference
16 between habitat and weeks, as well as the interaction between them at family and species level.
17 The Zackenberg family level interaction between year and week at habitat level is also shown.

Dataset	Variable	Degrees of freedom	Deviance	P
Zackenberg	Week	1	753	<0.001
	Habitat	2	2848.1	<0.001
	Week:Habitat	2	554.7	<0.001
Nuuk	Week	1	493.2	<0.001
	Habitat	2	761.7	<0.001
	Week:Habitat	2	186.1	<0.001
Ny Aalesund	Week	1	133.6	<0.001
	Habitat	1	130.8	<0.001
	Week:Habitat	1	23.9	0.190
Toolik lake	Week	1	508.1	0.010
	Habitat	1	244.8	<0.001
	Week:Habitat	1	91.6	0.265
Zackenberg species level	Week	1	511.2	<0.001
	Habitat	2	2194.7	<0.001
	Week:Habitat	2	97.5	<0.001
Zackenberg wet	Year	1	198	<0.001
	Week	1	382.2	<0.001
	Year:Week	1	65.9	0.020
Zackenberg mesic	Year	1	233.5	<0.001
	Week	1	640.9	<0.001
	Year:Week	1	93.2	0.010
Zackenberg dry	Year	1	406	<0.001
	Week	1	321.3	<0.001
	Year:Week	1	130.3	0.010

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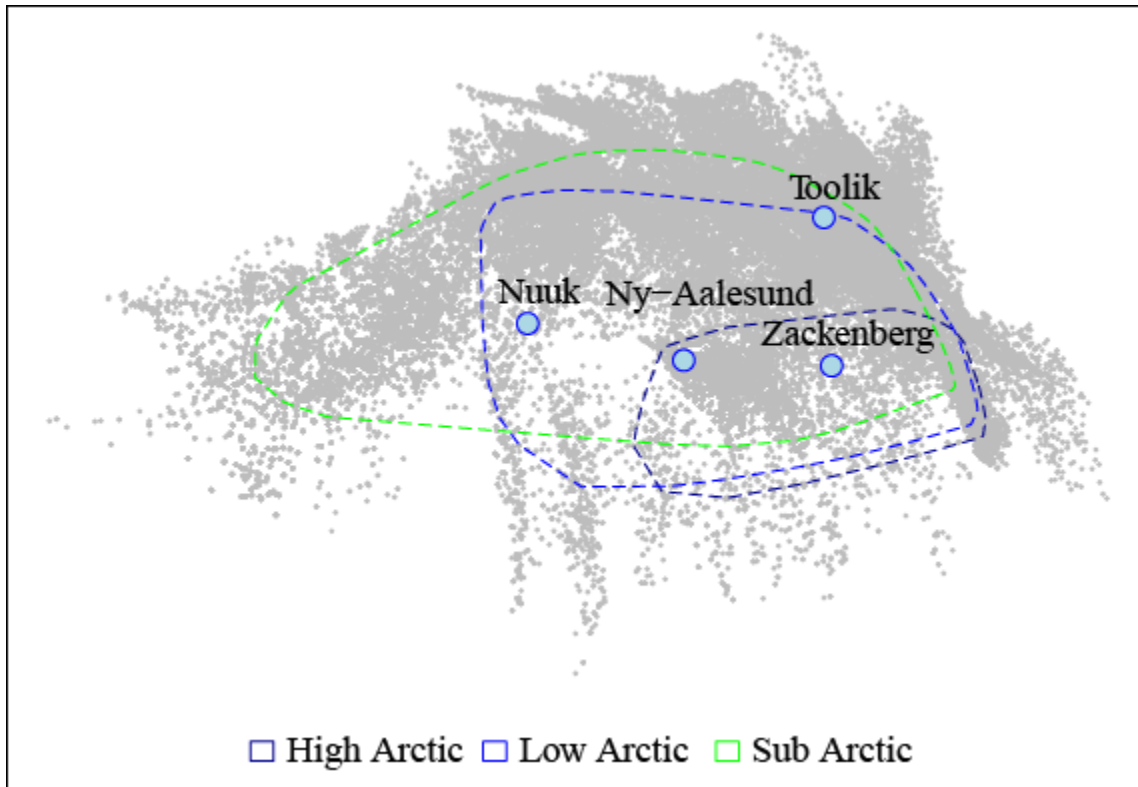
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24 Figure 1

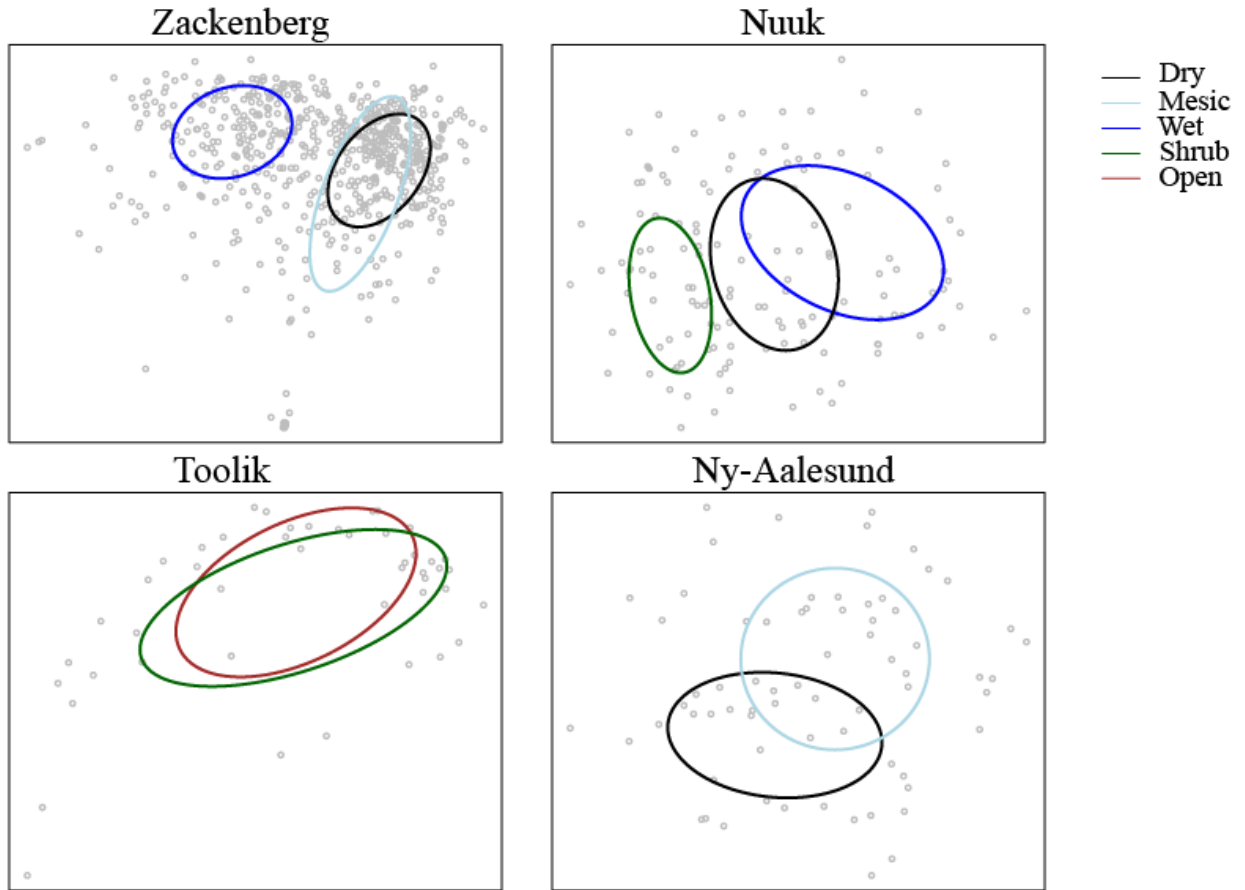
25 Climate space. Plot of the principal component analyses with the following variables
26 downloaded from <http://www.worldclim.org/bioclim>: annual mean temperature, minimum
27 temperature of the coldest month, mean temperature of the warmest quarter, precipitation of the
28 warmest quarter and precipitation of the coldest quarter. Climate data is plotted with grey colors
29 and the sites in blue. Dashed lines delineate the 75-percentile of the climatic conditions within
30 high-, low- and sub-Arctic, respectively.



34 Figure 2

35 Site level latent variable plots. Latent variable plots displaying how arthropod communities are
36 distributed along two latent variables. Ellipsoids show the 95 percent confidence bands around
37 habitats.

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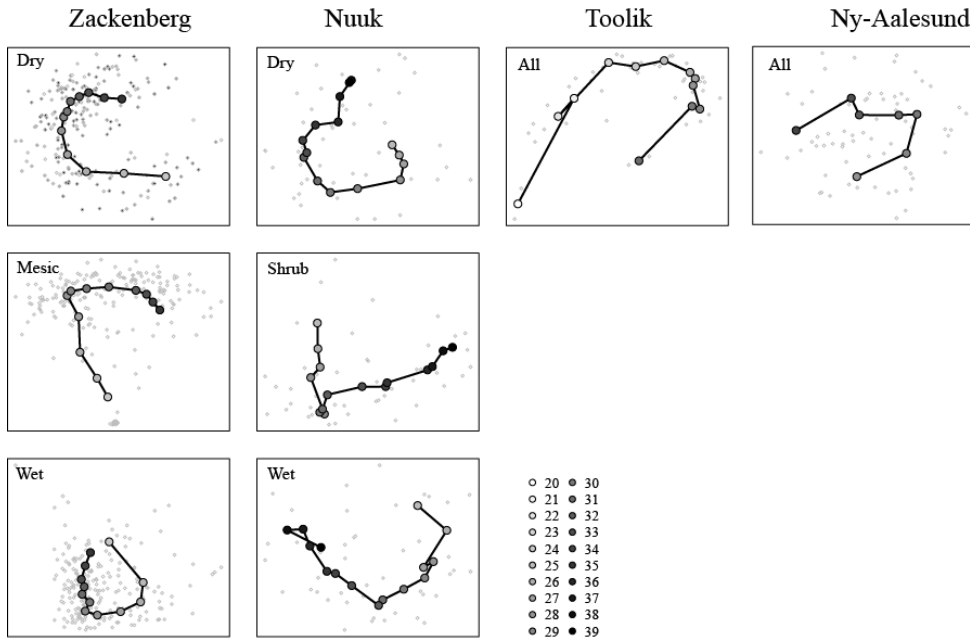
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42 Figure 3

43 Seasonal variation in arthropod community composition. Latent variable plots showing the latent
44 variable models divided onto habitats. The division was only made if there was a significant
45 interaction between habitat and week. The points below are centroids of the standard error of the
46 weekly centroids.



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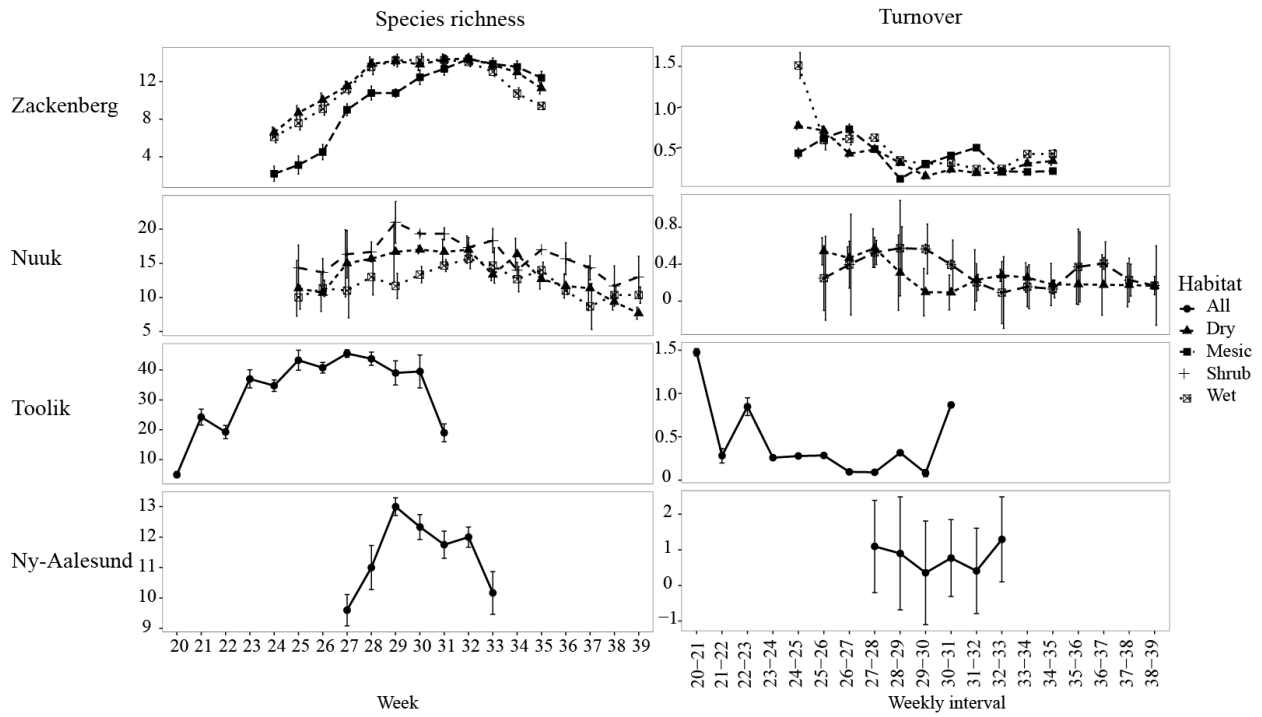
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51 Figure 4

52 Richness and turnover plots. Family level richness and turnover plots showing species richness,
53 as well as, distance between centroids for the weekly average of across years. Both indices are
54 shown with standard errors of interannual variation.



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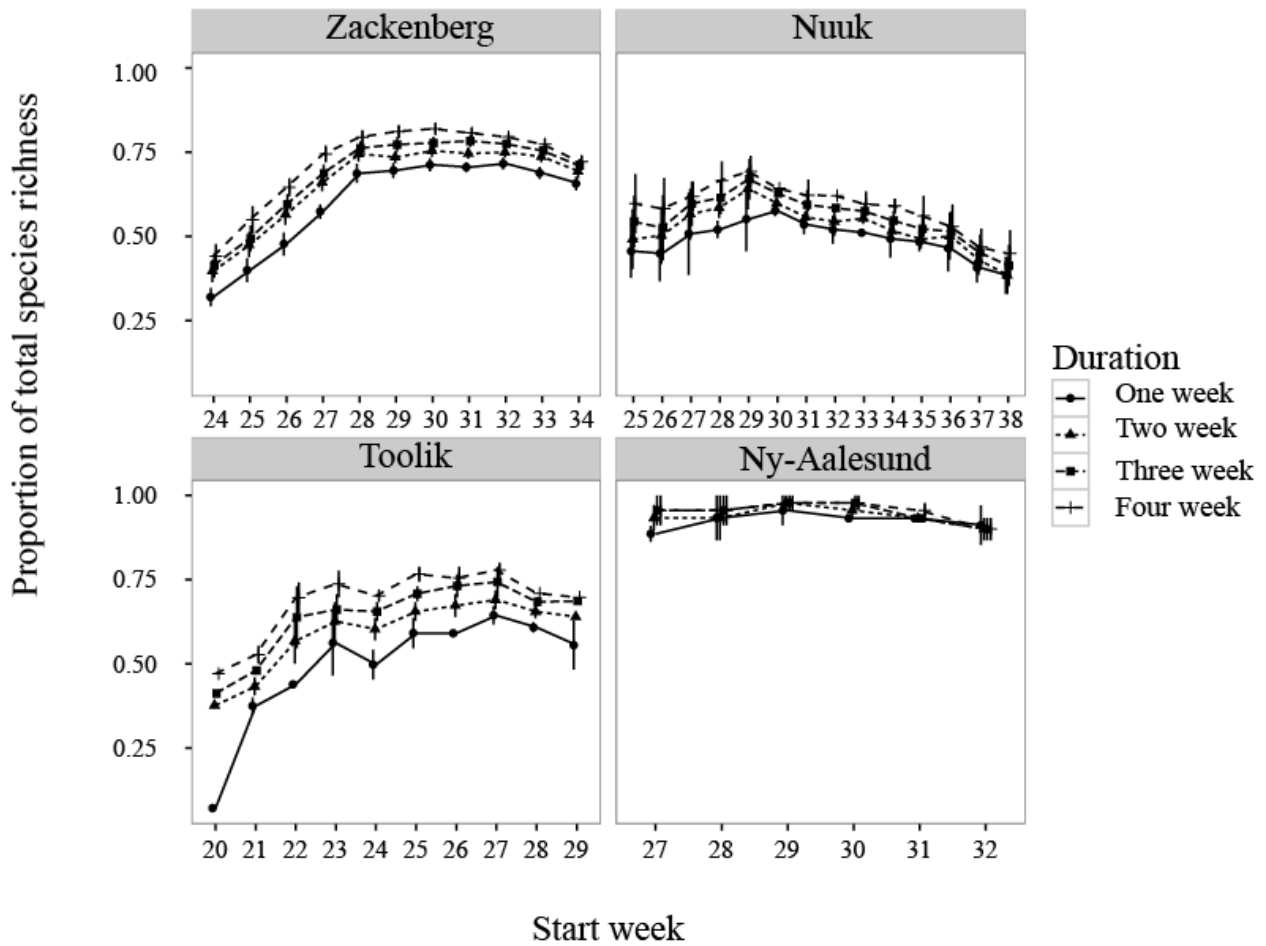
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66 Figure 5

67 Proportion of total species richness. Line graph showing how much of the total species richness
68 is detected with four different sampling durations (one week, two week, three week and four
69 week). The week number on the x-axis shows starting week and the y-axis shows the proportion
70 of the total species richness detected within a year. Error bars are standard error of the
71 interannual variation.



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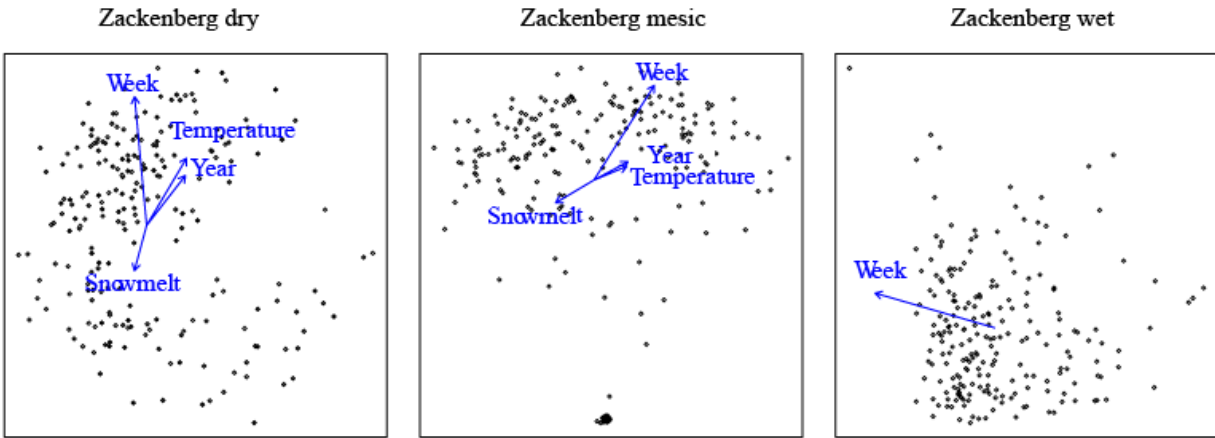
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79 Figure 6

80 Correlation with environmental variables. Biplots showing only significant ($p < 0.05$) variables
81 from the environmental fitting analysis



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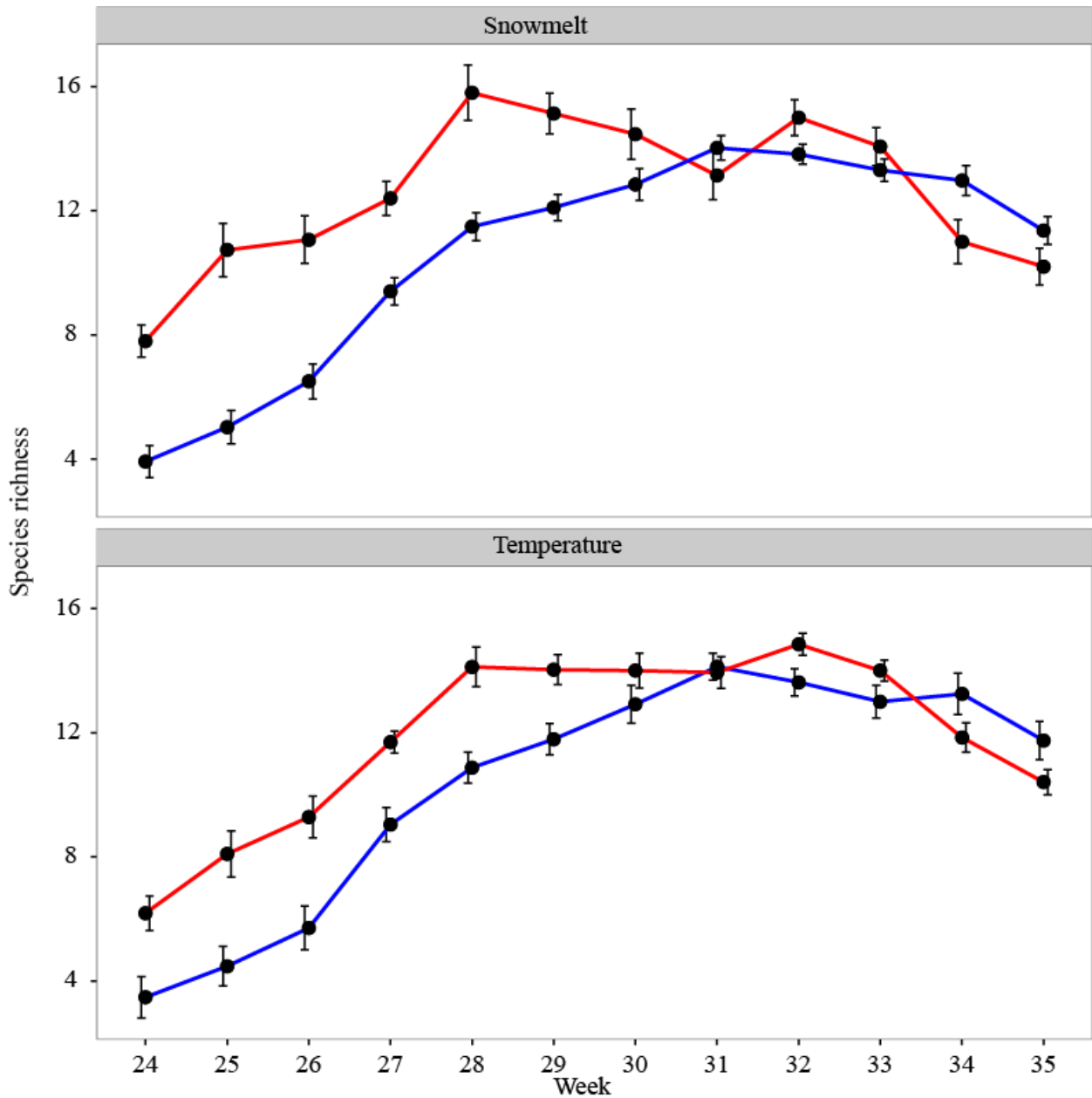
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95 Figure 7

96 A) Climatic variability and effect on species richness. Seasonal development of species richness
97 divided into years with late (blue colors) versus early (red colors) snowmelt and cold (blue
98 colors) versus warm (red colors) years. Error bars represents standard error of the weekly
99 average across years.



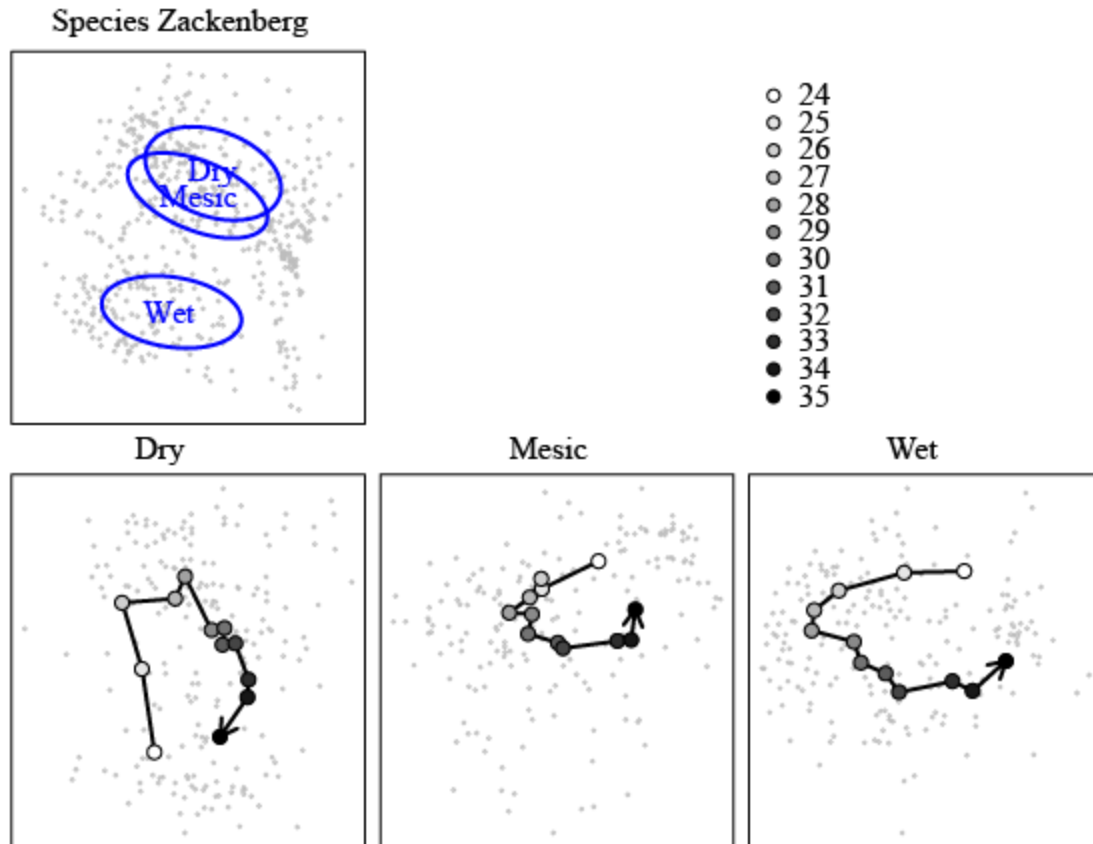
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103 Supplements

104 Fig S1: Species level latent variable models for Zackenberg data. The top figure shows all
105 habitats and the three figures below shows the seasonal weekly development divided onto
106 habitats



107

Effects of climate change on Arctic arthropod assemblages and distribution

PhD thesis

Rikke Reisner Hansen



Academic advisors: Main supervisor Toke Thomas Høye and co-supervisor Signe Normand

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Data sheet

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