Seasonal change and microhabitat association of Arctic spider assemblages (Arachnida: Araneae) on Victoria Island (Nunavut, Canada)

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Abstract—Arctic ecosystems are characterised by a mosaic of distinct microhabitats, which play a key role in structuring biodiversity. Understanding species diversity in relation to these microhabitats, and how communities are structured seasonally, is imperative to properly conserve, monitor, and manage northern biodiversity. Spiders (Arachnida: Araneae) are dominant arthropod predators in the Arctic, yet the seasonal change in their communities in relation to microhabitat variation is relatively unknown. This research quantified how spider assemblages are structured seasonally and by microhabitat, near Cambridge Bay, Nunavut, Canada. In 2014, spiders were collected in 240 pan and pitfall traps placed in common microhabitat types (two wet and two dry) from 3 July to 11 August, the active season in the high Arctic. In total, 10 353 spiders from 22 species and four families were collected. Non-metric multidimensional scaling ordinations revealed that spider assemblages from wet habitats were distinct from those occurring in drier habitats, but that differences within each of those habitats were not evident. Abundance and diversity was highest in wet habitats and differed significantly from dry habitats; both these variables decreased seasonally. Spider assemblages in the north are structured strongly along moisture gradients, and such data informs planning for future ecological monitoring in the Arctic.

Introduction

Microhabitats are delimited from one another by mere metres, allowing for fine scale examination of an ecosystem. In the Arctic, terrestrial landscapes are not delineated by abrupt transition zones such as forests to fields, or canopies to forest floors. Instead, all microhabitats experience harsh open conditions, and vegetation structure is limited and ranges from mosses and lichens to grasses and small shrubs, seldom more than knee-height. Moreover, it is thought that communities within microhabitats operate at fine spatial scales (Hansen *et al*. 2016). The few studies that have been done in the Arctic suggest that even these slight differences between Arctic habitats can produce distinct arthropod communities; at least between more broadly defined wet and dry habitat types (Koponen 1992; Marusik and Koponen 2002; Wyant *et al*. 2011; Rich *et al*. 2013).

Biodiversity in the north is dominated by arthropods (Danks 1992), and among terrestrial species, spiders are the dominant apex predators at the "micro" scale of the insect world. Predators have been observed to not only alter herbivore density, which sustains a diverse and beneficial plant community (Schmitz 2003; Estes *et al*. 2011) but to also alter herbivore behaviour by displacing them and therefore minimising herbivory stress on local plants (Beckerman *et al*. 1997). Loss or change in top predator communities can have ripple effects down through the food chain leading to a loss of plant life and lowered diversity (Schmitz 2003; Estes *et al*. 2011). This reduction in plant biomass could lead to a drop in suitable nesting grounds for migrating birds and a loss of food resources for mammals (Ims and Henden 2012). Conserving Arctic systems begins from the producers up, adding more support for the need to understand basic spider distribution across the tundra as they control much of the insect-specific herbivory.

Historically, research with Arctic spiders has focussed on distributional data and overall biodiversity checklists or inventories (Marusik and Koponen 2000). With climate change occurring at

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accelerated rates in the Arctic (Parmesan 2006; Høye *et al*. 2007), present research must shift focus to better understand the factors that govern northern biodiversity, including how spider communities are structured across space and time. Recent research predicts that the habitat mosaics found in the Arctic will respond at different rates and in different ways to climate change (Bowden *et al*. 2015). As such, the Arctic we see today will not have the same microhabitat distribution, proportions, and characteristics as the Arctic of the coming decades. Shrub encroachment, as well as changes in snowmelt timing, permafrost melt, and disturbance regimes (Arctic Climate Impact Assessment 2004; Myers-Smith *et al*. 2011; Naito and Cairns 2011) are already being observed in the north and will continue to progress. To be able to accurately predict how spider assemblages may respond to these habitat changes requires knowledge of the determinants of community structure.

Current research shows that habitat complexity and type govern spider community composition (Greenstone 1984; Uetz 1991; Halaj *et al*. 2000; Weeks and Holtzer 2000; Schaffers *et al*. 2008; Bowden and Buddle 2010a). Though abiotic (Willis and Whittaker 2002; DeVito *et al*. 2004; Bowden *et al*. 2015) and landscape (Willis and Whittaker 2002; Finch *et al*. 2008; Schaffers *et al*. 2008; Bowden and Buddle 2010a) factors can also shape spider assemblages, they are often considered to be of lesser importance than habitat complexity (Bowden and Buddle 2010a), notably changes in plant community structure, complexity, and diversity (Greenstone 1984; Uetz 1991; Rypstra *et al*. 1999; Weeks and Holtzer 2000; Beals 2006).

Spider communities differ between biomes (Willis and Whittaker 2002; Bowden and Buddle 2010b) and altitudinal gradients (Greenstone 1984; Willis and Whittaker 2002; Bowden and Buddle 2010b; Cardoso *et al*. 2011), between different forest types in the same region (Pearce *et al*. 2004; Ziesche and Roth 2008), and between different forest (Pinzon *et al*. 2012) and agricultural (Rypstra *et al*. 1999) management strategies. These variations can even be perceived at various microhabitat levels, whereby canopy versus ground assemblages in a single stand (Larrivée and Buddle 2009) or the relative decay of deadwood (Varady-Szabo and Buddle 2006) can support different spider communities. However, specific knowledge about the factors structuring spiders in the high Arctic remains limited.

In addition to habitat complexity, seasonal turnover can influence Arctic arthropod assemblages. Tulp and Schekkerman (2008) showed that arthropod abundance, including spiders, strongly correlated with seasonal markers (date, temperature, precipitation). Due to the accelerated growing season in Arctic systems, seasonal constraints may also influence spider communities and diversity, though this is not well studied. In other ecosystems, spiders can respond to plant succession and seasonal change (Usher 1992; Ziesche and Roth 2008). In contrast, some studies have found no relationship between spider communities and seasonal change (Mallis and Hurd 2005; Ziesche and Roth 2008) Therefore, to understand the assemblage patterns of northern spiders, the influence of seasonal change requires attention.

The objective of this study is to quantify the relationship between Arctic spider assemblages and microhabitats, and to assess how spider assemblages change over the short Arctic growing season. Doing so will not only allow us to enhance our knowledge of Arctic spider communities as a whole, but also identify any between-habitat differences that may occur at the microhabitat level.

Methods

Experimental design and sampling

We sampled spiders in Cambridge Bay, Nunavut, Canada (69.1172°N, 105.0531°W) in 2014. Cambridge Bay is a hamlet on Victoria Island and experiences a polar climate with summer averages for temperature and precipitation of 7.9 °C and 24.9 mm, respectively. We determined the sampling sites based in part on existing environmental data. Specifically, the Canadian High Arctic Research Station, run by Polar Knowledge Canada (POLAR), has produced an Arctic microhabitat classification system (each microhabitat unit is called an ecosite (ES), analogous to microhabitats), which relates the biotic plant components with local abiotic components to describe the ecosystem at a fine scale (McLennan *et al*. 2013). We sampled the four most abundant ecosites of the Cambridge Bay region

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(ES01, ES03, ES07, ES08 – descriptions in Table 1), herein referred to as Dry1, Dry2, Wet1, and Wet2 (Table 1).

We selected four locations (*i.e.*, replicates) all within 12 km of the hamlet of Cambridge Bay. Each replicate needed to contain the four above mention habitats in large, uniform, representative patches and in proximity to one another (Table 2). The size of the microhabitat patches varied (from about 50 m^2 to over 100 m^2). In each microhabitat, we established a grid of nine yellow pan traps and six pitfall traps (Fig. 1). As much as possible, the grid plots were placed in the centre of each microhabitat, needing a minimum distance of 1 m from the edge on all sides. Each trap was ~ 10 m from each other (for a total approximate grid area of 50 m by 30 m), and the trap type order was randomly determined. For a few grids, the design was altered from a 5 × 3 trap design to a 15 × 1 trap design to better reflect habitat shape and keep the plot in the centre of the microhabitat. The use of both trap types ensured we were sampling the complete spider assemblage, and helped reduce trap bias (Ernst *et al*. 2015). This design was repeated in each of the four microhabitats and at all four locations, leading to a total of 16 grids and 240 traps.

We installed both pan and pitfall traps with ~ 3 cm (depth) of glycol mixture (50:50 water and propylene glycol with a drop of dish soap) in each. The traps were open between 3 July (vii) 2014 and 11 August (viii) 2014 inclusively, and were separated into seven sampling periods (1 = 3–8.vii, 2 = 8–14.vii, 3 = 14–19.vii, 4 = 19–26.vii, 5 = 26–30.vii, 6 = 26.vii–5.viii, 7 = 5–11.viii). This spanned nearly the entire active season in Cambridge Bay (late June to mid-August), though ideally trapping would have begun at first snowmelt about five to seven days earlier. Data from periods 1, 2, 4, 5, and 7 are included in the analyses. Periods 3 and 6 were omitted due to logistical and time constraints. Upon servicing a trap, we rinsed all samples with water, then placed them in a whirl pak (eNasco, Fort Atkinson, Wisconsin, United States of America) and immersed them with 70% ethanol. All samples were taken back to the laboratory for processing.

Spider identification keys and guides were used to determine the species identity of adult specimens, including the *Insects and Arachnids of Canada* series (Dondale *et al*. 2003) and the *Guide d'indentification des Araignées (Araneae) du Quebec* (Paquin and Duperre 2003). Juveniles were only identified to family. Vouchers were made for both male and female adult specimens of each species, and are deposited at the Lyman Entomological Museum of McGill University (Sainte-Anne-de-Bellevue, Québec, Canada).

Data analyses

To test the overall effects of microhabitats and seasonal change on spider assemblages, we considered measures of relative abundance and diversity. Spider community matrices were log transformed and plotted in ordination space using the *metaMDS* function in the vegan package (Oksanen *et al*. 2015) of R 3.1.1 (R Core Team 2014). The matrix was a species abundance by site construct whereby the "site" values differed in their habitat, replicate (site), time period, and trap type (*e.g.*, Dry1, replicate 3, period 2, pan 4). An ordination gives a visual representation of community similarity with each point in the ordination space representing a spider assemblage at a given time, replicate, trap type, and microhabitat. Environmental variables (maximum temperature, minimum temperature, mean temperature, total precipitation, maximum wind gust, trap type, site, microhabitat, and period) were then plotted on the ordination as vectors, using the *envfit* function in vegan (Oksanen *et al*. 2015), to determine their relative influence on community composition. Trap type, site (replicate), microhabitat, and period data was recorded on site while sampling, but the remaining environmental data was taken from the historical climate data on the Environment Canada website (climate.weather.gc.ca). Microhabitat centroids (*ordispider* function in vegan) and 68% confidence intervals (*ordiellipse* function in vegan) were included on the ordination to obtain statistically testable values and delimit the ecosite boundaries.

Using multivariate analysis of covariances (MANCOVA), we determined the influence of habitat and time on spider total relative abundance. Tukey's honest significant difference tests determined the differences between microhabitat pairings. Time was considered as a continuous variable because we were interested in whether or not communities changed over time, and were less interested in determining whether individual time

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Table 1. Description of the four common ecosites used in this study.

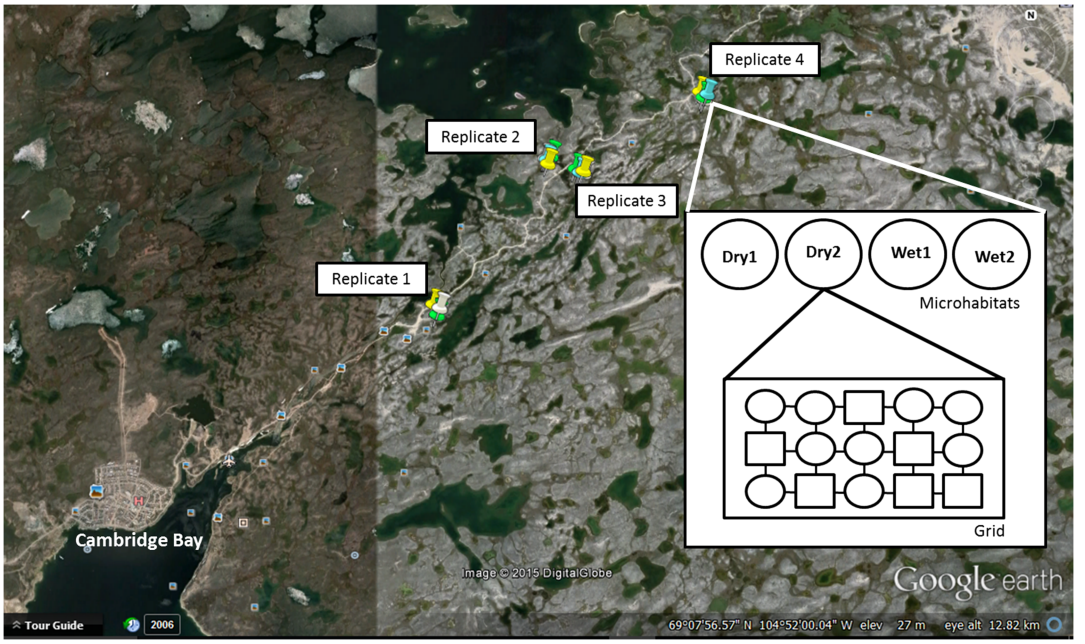
Classification	Characteristics	Vegetation	Moisture and Soil	Snow Depth/Melt
Dry1 (ES01)	Flat and rocky, often located on the tops of hills. Highly exposed to the elements and often located in winter exposed areas	Characterised by a discontinuous mat of *Dryas integrifolia* Vahl (Rosaceae), *Saxifraga oppositifolia* Linnaeus (Saxifragaceae), and *Carex rupestris* Allioni (Cyperaceae). Also contains high percentage of unvegetated or crustose lichen cover	Driest of the four habitats – located atop well-drained calcareous soils	Least snow accumulation (often areas with exposure all winter) and earliest snowmelt
Dry2 (ES03)	Located on leeward slope sides, in areas with a larger snow accumulation and subsequently more moist soil (often between Dry1 and Wet1)	A more diverse and well-vegetated system, which often occurs in hummocky areas. Common plants include *Dryas integrifolia*, *Arctagrostis latifolia* (Brown) Grisebach (Poaceae), *Cassiope tetragona* (Linnaeus) Don (Ericaceae), *Vaccinium uliginosum* Linnaeus (Ericaceae), *Pedicularis capitata* Adams (Orobanchaceae), and several species of lichen	Located on moderately well-drained Turbic Cryosols. Higher snow accumulation also leads to a moister soil moisture regime than Dry1	Occurs only in areas with higher snow accumulation and later snowmelt than Dry1 due to the protected position on leeward slopes
Wet1 (ES07)	Flat habitat with waterlogged soil, located in close proximity to water bodies. Often sheltered by valleys – less exposed	Characterised by the dominance of *Carex aquatilis* Wahlenberg (Cyperaceae) with some cover of *Salix arctica* Pallas (Salicaceae). Several other species of sedge and polargrass and saxifrage are also common and a well-developed moss cover is typical (lichens mostly absent)	Occurs in poorly drained, wetter sites and prone to short-term seasonal flooding. Wet1 is a wetland association distributed on wet gradual slopes, below snowbeds, drainage channels, and pond margins. Soils are Fibric Organic Cryosols or Gleysolic Static Cryosols with an active layer of 10–30 cm	Mid accumulation and mid to late snowmelt
Wet2 (ES08)	Flat and slightly rocky, with highest vegetation complexity (shrub height ranging from 15 cm to 1.2 m. Located along edges of water bodies	Characterised by the dominant presence of *Salix richardsonii* Hooker (Salicaceae). Common vegetation also includes: *Carex aquatilis*, *Eriophorum angustifolium* Honckeny (Cyperaceae), *Salix arctica*, *Equisetum arvense* Linnaeus (Equisetaceae), and *Campylium stellatum* (Hedwig) Jensen (Amblystegiaceae)	Soils are very poorly drained a loamy to sandy texture, and can be Gleysolic Static Cryosols. Active layer depth of 25 cm with seepage at 16–18 cm. Sites commonly flooded for part of the year	Highest accumulation and latest snowmelt

Note: For the classifications, the ecosite codes in bracket refer back to the Cambridge Bay classifications.

Table 2. Global positioning system (GPS) coordinates for all sampled locations (samples and replicates) used in this study.

Location	GPS coordinates	Locations	GPS coordinates
Replicate 1 – Dry1	69.1398°N, 104.9517°W	Replicate 3 – Dry1	69.1564°N, 104.8990°W
Replicate 1 – Dry2	69.1396°N, 104.9510°W	Replicate 3 – Dry2	69.1562°N, 104.9004°W
Replicate 1 – Wet1	69.1394°N, 104.9494°W	Replicate 3 – Wet1	69.1561°N, 104.8980°W
Replicate 1 – Wet 2	69.1385°N, 104.9504°W	Replicate 3 – Wet 2	69.1597°N, 104.9017°W
Replicate 2 – Dry1	69.1574°N, 104.9115°W	Replicate 4 – Dry1	69.1664°N, 104.8576°W
Replicate 2 – Dry2	69.1579°N, 104.9120°W	Replicate 4 – Dry2	69.1661°N, 104.8550°W
Replicate 2 – Wet1	69.1581°N, 104.9126°W	Replicate 4 – Wet1	69.1654°N, 104.8560°W
Replicate 2 – Wet 2	69.1586°N, 104.9093°W	Replicate 4 – Wet 2	69.1657°N, 104.8563°W

Fig. 1. Map showing the relation of sampling locations to the hamlet of Cambridge Bay. Each pin represents the location of a microhabitat; the cluster therefore being one sampling site (replicate). A zoom in view at any replicate shows there are four microhabitats, and within each microhabitat a grid of nine pan (circles) and six pitfall (squares) was randomly established. The distance between each trap is ~ 10 m, for a total grid measurement of ~ 50 m by 30 m.



periods differed from each other. Data for all MANCOVAs were pooled to include all trap types and replicates for this analysis and the data was log transformed in order for the residuals to be normally distributed. Trap types were treated the same for these analyses as no significant differences to the community where detected for trap type in our study – despite other studies having found otherwise (Ernst *et al.* 2015).

We examined species diversity by first constructing rarefaction curves to determine if adequate sampling had been conducted (Buddle *et al.* 2005). These were created using the *rarefy* function (Oksanen *et al.* 2015) in R 3.1.1 (R Core Team 2014). Our rarefaction curves of our sampled communities did approach an asymptote (Fig. 4), so species richness was used as a metric of diversity along with other measures

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of species diversity: Shannon, Simpson, Pielou's evenness, and Fisher's α. To infer about statistical significance, we again performed MANCOVAs and Tukey's honest significant difference tests. As with the abundance data, all trap types and replicates were pooled.

Results

Project-wide, 10 353 spiders were collected representing four families and 22 species (Table 3). Lycosidae (wolf spiders) were the most commonly collected spiders (7523 individuals, 73% of the total sample) and represented only two species. The Linyphiidae (micro sheet web spiders) were the most diverse family – with 18 species; Linyphiids were also the second most commonly collected spiders (2020 individuals, 20% of the total sample). A complete list of species, and their associated species code and abundance values, can be found in Table 3.

This study identified three new territory records for Nunavut: a long-jawed orb weaver *Pachygnatha clercki* Sundevall (Tetragnathidae: Araneae), and two species from the Linyphiidae (Araneae): *Agyneta allosubtilis* Loksa and *Bathyphantes simillimus* Koch.

Spider assemblages were oriented along a moisture-driven microhabitat gradient, where dry ecosites differed from wet ecosites but there was no discernable difference within them (Fig. 2). Microhabitat identity was the most important variable in determining where communities fall within the ordination space (Fig. 2; $P = 0.001$). Site location also seemed to influence spider communities but to a lesser degree (Fig. 2; $P = 0.034$).

Table 3. List of spider species collected in each of the four ecosite types, collected in Cambridge Bay, Nunavut in 2014.

Family/species	Species code	#Per ecosite	#Per ecosite	#Per ecosite	#Per ecosite	Total collected
Microhabitat		Dry1	Dry2	Wet1	Wet2	
Lycosidae						**4913**
Pardosa algens (Kulczynski)	PAAL	6	15	2088	1166	3275
Alopecosa hirtipes (Kulczynski)	ALHI	330	633	258	417	1638
Dictynidae						**115**
Emblyna borealis (Pickard-Cambridge)	EMBO	27	85	1	2	115
Tetragnathidae						**352**
Pachygnatha clercki (Sundevall)*	PACL	3	37	289	23	352
Linyphiidae						**1406**
Erigone arctica (White)	ERAR	3	54	196	291	544
Erigone psychrophila (Thorell)	ERPS	0	0	117	66	183
Semljicola beringianus (Eskov)	SEBE	0	0	71	107	178
Baryphyma groenlandium (Holm)	BAGR	0	0	98	32	130
Hybauchenidium aquilonare (Koch)	HYAQ	1	4	33	56	94
Masikia indistincta (Kulczynski)	MAIN	0	0	44	34	78
Hilaria proletaria (Koch)	HIPR	1	0	67	6	74
Hilaria vexatrix (Pickard-Cambridge)	HIVE	1	6	8	13	28
Agyneta maritima (Emerton)	AGMA	4	14	5	1	24
Diplocephalus barbiger (Roewer)	DIBA	5	11	0	0	16
Tarsiphantes latithorax (Strand)	TALA	0	0	6	8	14
Walckenaeria karpinskii (Pickard-Cambridge)	WAKA	4	4	1	4	13
Halorates holmgrenii (Thorell)	HAHO	0	0	4	6	10
Silometopoides pampia (Chambelin)	SIPA	0	2	4	3	9
Bathyphantes simillimus (Koch)*	BASI	2	3	0	0	5
Oreonata eskimopoint (Saaristo and Marusik)	ORES	2	0	1	0	3
Agyneta allosubtilis (Loksa)*	AGAL	0	0	2	0	2
Halorates thulensis (Jackson)	HATH	0	1	0	0	1
Total		**389**	**869**	**3293**	**2235**	**6786**

Notes: Ecosite descriptions are in Table 1. Abundance values per ecosite represent the pooled totals from all sampling periods, replicates, and trap types. New territory records are denoted by an asterisk. Note the juveniles are not included in these totals. Bolded values denote family level or habitat level totals.

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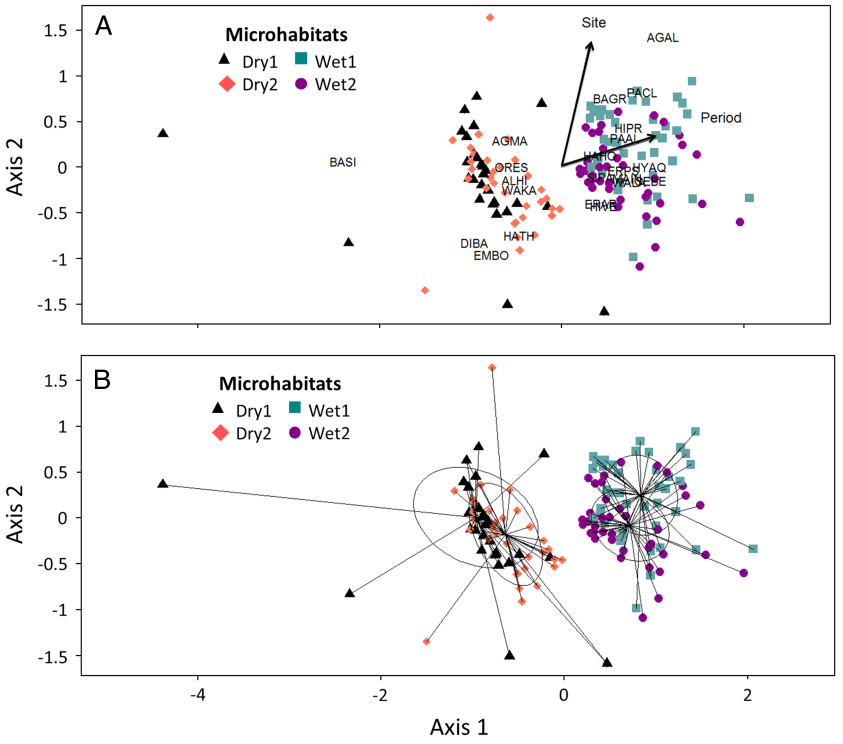
Fig. 2. Non-metric multidimensional scaling ordination of spider community across all replicates and time periods using the log values of species relative abundance. Each point indicates the location of a sampled microhabitat: where every microhabitat type is distinguished by a unique shape and colour. Each habitat contains four replicates (sites) at a given sampling period, over five sampling periods, for a total of 20 points/habitat. Points that are located more closely together have more similar communities than points located further away from one another. (A) The text represents the individual species codes (two first letters of genus and two first letters of species names (see Table 3)) and shows the location of each species within the ordination space; where a strong association of a species to a particular habitat type can be observed. The centroid variable of the plot is the microhabitat type ($P < 0.001$), making it the determining factor for point location in the ordination space. Of all environmental variables tested, "Site" ($P = 0.014$) and "Period" ($P = 0.103$) had the strongest vector effects. (B) The location of each habitat centroid along with the 68% confidence areas is shown. There are significant differences between wet and dry habitat pairings but no differences between the communities of Dry1 and Dry2 or Wet1 and Wet2.



All other tested environmental variables (temperature, precipitation, wind, *etc.*) had no effect on overall spider assemblages.

Spider abundance and diversity varied significantly by microhabitat. Total abundance trends over time remained consistent across all four ecosites, but relative values differed between them (Fig. 3). Wet habitats contain significantly more individuals than dry habitats (Fig. 3, Tables 4–5) though differences between similar microhabitats were non-significant (Table 5).

Rarefaction curves illustrated an adequate sampling of microhabitats (Fig. 4) and therefore, species richness could be used as a measure of diversity, along with a suite of common biodiversity indices. However, results did differ depending on the metric used. Simpson's diversity index, Pielou's evenness, and Shannon's diversity index all revealed a significant effect of microhabitat on diversity, though Fisher's α diversity index did not (Table 4). For diversity measures that had a significant effect on the community, both Wet1 and Wet2 ecosites consistently differed with Dry1 (Table 5). However, the wet ecosites did not significantly differ from Dry 2 (Table 5). There was no difference between

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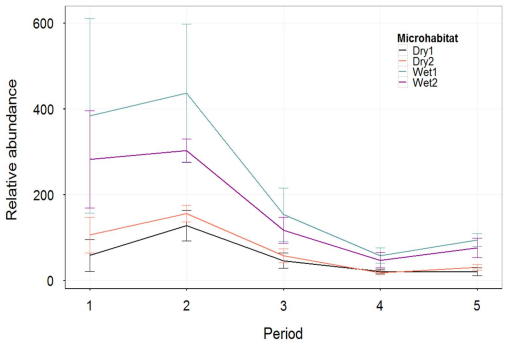
Fig. 3. Spider total relative abundance across the five sampling periods in each of the four microhabitats. Abundance values include both adult and juvenile specimens and represent the pooled total of all replicates and trap types. Sampling periods spanned the entire 2014 summer season, and break down as follows: 1 = 3–8 July, 2 = 8–14 July, 3 = 19–26 July, 4 = 26–30 July, 5 = 5–11 August. See Table 1 for ecosite descriptions. Differences between the microhabitats can be observed, but the overall pattern of spider peak abundance seems to remain consistent. Associated *P*-values for the effect of time (period) and habitat (ecosite) can be found in Table 4. Error bars represent one standard deviation.



the two wet and the two dry ecosites. Again, we concluded that wet ecosites supported different communities than dry ecosites, but that finer habitat divisions (*i.e.*, distinct communities between different wet or different dry microhabitats) were not apparent.

At a species level, many specialists (defined here as a species for which 70% or more of the captured individuals were found in a single habitat type (dry or wet)) and very few generalists (defined as a species with a more even distribution between both habitat types) were present (Fig. 6). Species tended to be more specialised for either a wet or a dry microhabitat type, and were rarely found with a similar relative abundance in both. This observation did not hold true at the family level (Fig. 7). No apparent ecosite preference existed for Lycosidae or Linyphiidae, the two dominant families.

In the ordination, sampling period was insignificant and did not seem to affect the community composition (Fig. 2; $P = 0.129$). Other environmental variables, such as mean temperature ($P = 0.554$), total precipitation ($P = 0.422$) and maximum wind gust ($P = 0.672$), had no effect. However, when the

Table 4. Multivariate analysis of covariances *P*-values for the effect of time (period) and microhabitat on the total abundance, richness, and diversity of spiders in Cambridge Bay.

Response	Factor	df	Sum squared	Mean squared	*F* value	*P* value
Abundance	Period	1	30.9253	30.9253	99.4402	3.325e-15*
	Microhabitat	3	26.9514	8.9838	28.8874	2.267e-12*
	Period:Microhabitat	3	0.1536	0.0512	0.1646	0.9198
Species richness	Period	1	104.0	104.01	41.655	1.100e-08*
	Microhabitat	3	471.4	157.13	62.932	2.000e-16*
	Period:Microhabitat	3	16.8	5.61	2.245	0.0903
Simpson	Period	1	0.1099	0.10992	6.891	0.0222*
	Microhabitat	3	0.4173	0.13910	8.721	0.0024*
	Period:Microhabitat	3	0.1914	0.01595	0.288	0.8334
Pielou's evenness	Period	1	0.05342	0.05342	22.044	0.0005*
	Microhabitat	3	0.02612	0.00871	3.592	0.0464*
	Period:Microhabitat	3	0.02908	0.00055	0.226	0.8765
Fisher's α	Period	1	1.386	1.386	2.543	0.1370
	Microhabitat	3	1.724	0.5748	1.054	0.4040
	Period:Microhabitat	3	0.911	0.3036	0.557	0.6530
Shannon	Period	1	0.6016	0.6016	8.326	0.0137*
	Microhabitat	3	2.3899	0.7966	11.026	0.0009*
	Period:Microhabitat	3	0.0950	0.0317	0.438	0.7299

Notes: Here, abundance values are taken from the log total abundance. Significant values are denoted with an asterisk. Additional Tukey's honest significant difference tests were conducted for "Microhabitat" and those *P*-values can be found in Table 5.

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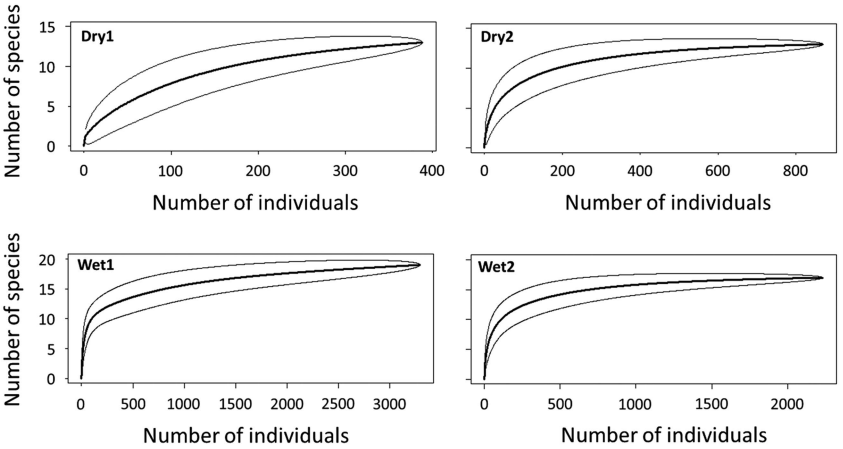
Table 5. Tukey's honest significant difference test *P*-values for the factor "Microhabitat".

	Dry2-Dry1	Wet1-Dry1	Wet2-Dry1	Wet1-Dry2	Wet2-Dry2	Wet2-Wet1
Abundance	0.3104	0.0000*	0.0000*	0.0000*	0.0000*	0.4780*
Species richness	0.0382*	0.0000*	0.0000*	0.0000*	0.0000*	0.2151
Simpson	0.2175	0.0103*	0.0025*	0.3178	0.0882	0.8390
Pielou's evenness	0.2446	0.1479	0.0356*	0.9871	0.6535	0.8322
Fisher's α	0.9101	0.4935	0.4459	0.8565	0.8150	0.9997
Shannon	0.2999	0.0031*	0.0016*	0.0762	0.0389*	0.9787

Note: Abundance values are taken from the log total abundance. Significant values are denoted by an asterisk.

Fig. 4. Rarefaction curves of species richness per microhabitat. See Table 1 for ecosite descriptions. Only when sampling has reached asymptotic can species richness be used as a measure of biodiversity – as is the case here. Rarefied species richness values are: Dry1 = 7.854, Dry2 = 8.330, Wet1 = 9.992, Wet2 = 9.753.



community was considered at the species level, the effect of time told a more complex story (Fig. 5). Here, we observed variability in the emergence time and abundance peak patterns of different species. Early emergence was observed by most species but not all of these species abundances decreased in the same manner. *Pachygnatha clercki* had its peak abundance in the first sampling period and then tapered off consistently until the fourth period whereas *Erigone arctica* White (Linyphiidae: Araneae) maintained a high abundance for the first two periods and then declined quickly by the third time period (Fig. 5). In contrast, *Semljicola beringianus* Eskov (Linyphiidae: Araneae) had its peak abundance in the middle of the sampling period and species such as *Hilaria vexatrix* Pickard-Cambridge (Linyphiidae: Araneae) and *Hybauchenidium aquilonare* Koch (Linyphiidae: Araneae) peaked at the end (Fig. 5). This suggested that the community was dynamic over time, and the relative proportions of different species were not static even if the species presence/absence (as was measured by the ordination) did not change.

Seasonality had a significant effect on overall community abundance and diversity (Table 4). The relative abundance of species changed over the course of the season. Community abundance peaked around the second sampling period (8–14 July) and subsequently declined over the remainder of the season, with a slight increase in the final sampling period (Fig. 3). Spider diversity also proved to be influenced by sampling period, according to the significant values of Simpson's diversity index, Pielou's evenness, and Shannon's diversity index (Table 2). As with microhabitats, Fisher's α diversity index showed no significant effect.

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Fig. 5. Individual species abundance peaks across the five sampling periods. Species codes are given as the *y*-axis (associated species names can be found in Table 3). Plotted values are the total abundance of a given species at each time period (microhabitats, trap types, and replicates are pooled). The figure only includes 20 of the 22 species collected as the singleton and doubleton were excluded.

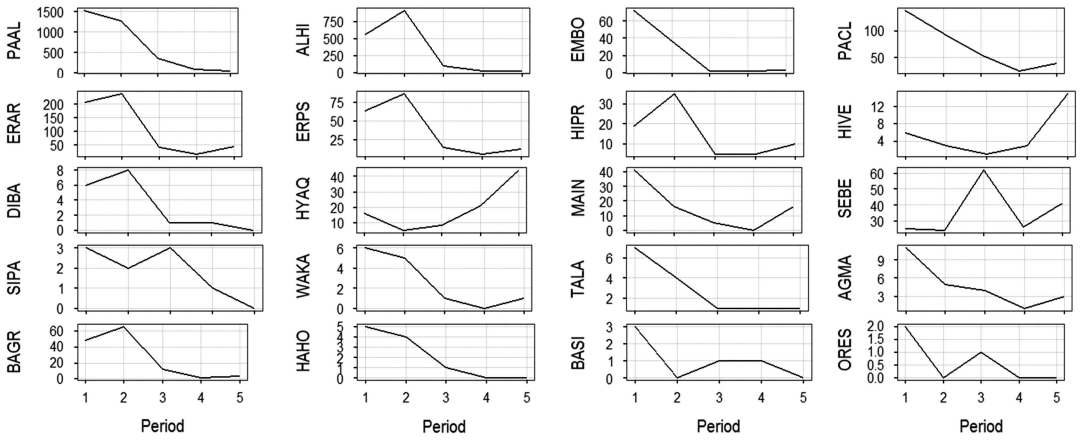
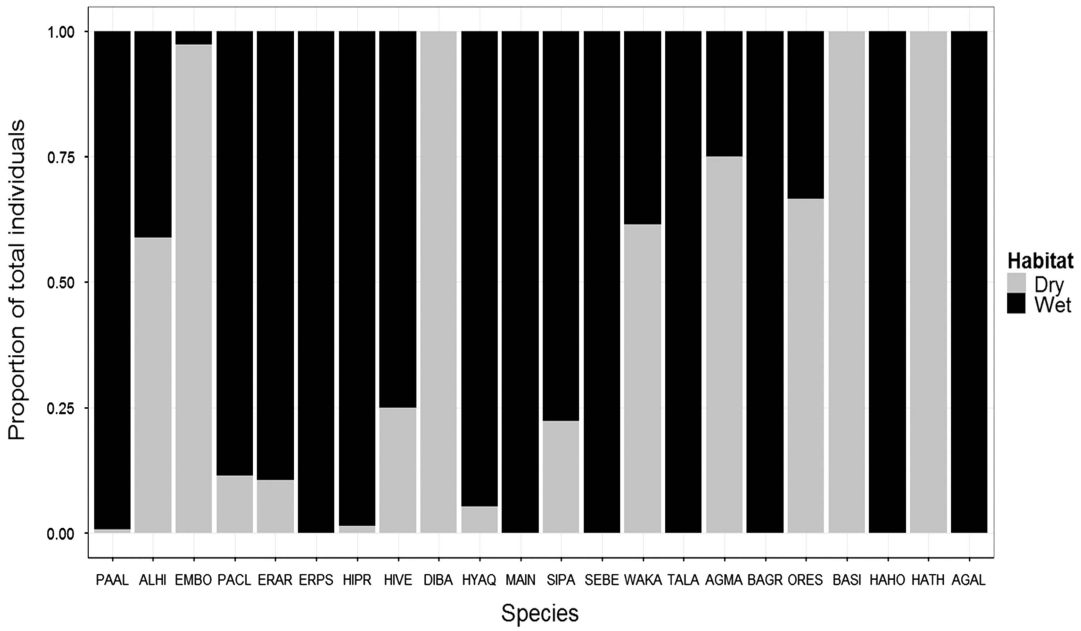


Fig. 6. Proportion of total individuals of each species found in dry and wet habitats. Ecosites have been combined into the dry or wet categories to better show the pattern. No significant differences have been observed between the two dry or the two wet ecostites (Fig. 2 and Table 1). Species identity is portrayed on the *x*-axis by its code (species names can be found in Table 3). The bolded values above the bar denote the total number of individuals collected for that species, across all time periods, replicates, and habitats.



Discussion

The objective of this research was to characterise Arctic spider assemblages in relation to microhabitats and seasonal change, near Cambridge Bay, Nunavut. Our main results show that Arctic microhabitats are non-uniform, and spiders are structured along a moisture

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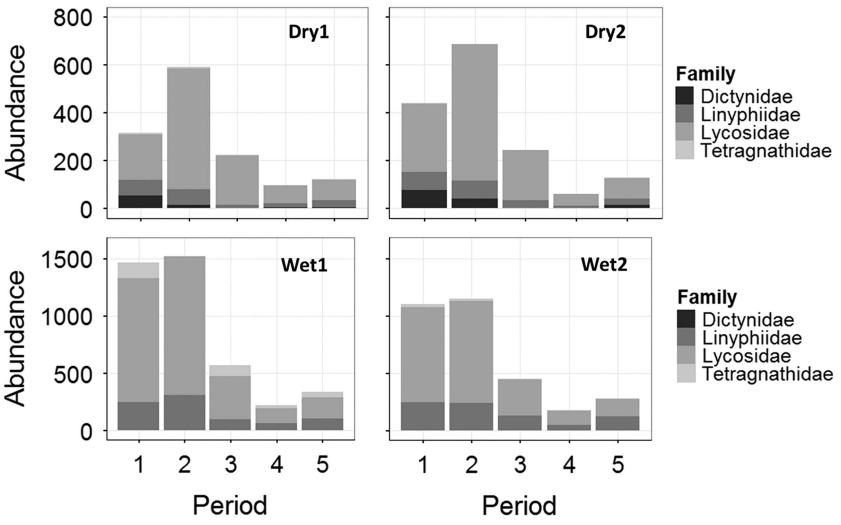
Fig. 7. Relative dominance of the four spider families in each microhabitat and through time. Total abundance numbers come from pooled replicates and trap types. Abundance values include both adult and juvenile specimens. Periods represent the following dates: 1 = 3–8 July, 2 = 8–14 July, 3 = 19–26 July, 4 = 26–30 July, 5 = 5–11 August.



gradient; assemblages from dry habitat types differ significantly from those collected from wet habitat types. We also documented a shift in spider assemblages in relation to seasonal change: a pattern that was most evident at the species level. The spider assemblages were dynamic, with different species showing higher catch rates at specific times of the short growing season.

Microhabitats

Spider communities respond to small-scale habitat differences within the tundra as distinct assemblages were observed in dry and wet habitats. A high degree of overlap was observed between the two dry microhabitat types and the two wet microhabitat types, suggesting there is redundancy in dividing microhabitats further than "wet" and "dry" (Fig. 2). This distinction between wet and dry communities has also been found for Arctic beetles (Ernst and Buddle 2013), Arctic arthropods as a whole (Hansen *et al.* 2016), and in similar studies of Arctic spiders (Koponen 1992; Usher 1992; Pickavance 2006; Wyant *et al.* 2011). Finer differences within the same ecosite were not apparent. Legault and Weis (2013) found that snowmelt timing (the main distinction between the two wet habitats in this study) of different wet habitat types had no effect on spider assemblage structure or emergence timing. In contrast, one study on Arctic spiders in Alaska demonstrated that communities of two different wet habitat types were significantly distinct (Rich *et al.* 2013). So at finer scales there is still conflicting evidence of effects on spiders, although on Victoria Island, spider assemblages are mostly structured by broad habitat categories.

Microhabitats support a high degree of species specificity (Fig. 6). Only two species could be classified as generalists, *Alopecosa hirtipes* Kulczynski (Araneae: Lycosidae) and *Walckenaeria karpinskii* Pickard-Cambridge (Araneae: Linyphiidae), as they are found just over 50% of the time in dry ecosites and the rest of the time in wet habitats. The remaining species can be defined as specialists, with more than 70% of the individuals having been caught in a single microhabitat type (Fig. 6). The idea that spiders can be specialists has been reported indirectly in other studies (Rypstra *et al.* 1999; Mallis and Hurd 2005). This habitat specialisation could be explained by the guild or hunting strategy (Uetz 1991), abiotic restrictions (DeVito *et al.* 2004; Bowden and Buddle 2010b), or habitat complexity requirements (Schaffers *et al.* 2008; Bowden

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and Buddle 2010a) of a species. Further research is needed in order to determine the influence of abiotic components in shaping spider communities in the high Arctic, and if those communities are driven directly by the abiotic conditions in that habitat (wet or dry) or indirectly by the subsequent plant community and prey type under those abiotic conditions.

In Cambridge Bay, dry habitats are characterised by relatively flat, low lying vegetation and differ dramatically from the taller, more structurally complex vegetation at the wet habitats (see Table 1). The variance in the plant species dominance, vegetation complexity and overall habitat architecture between these habitats most likely explains the majority of the observed differences in spider assemblages and species preferences (Uetz 1991; Rypstra *et al*. 1999; Halaj *et al*. 2000; Weeks and Holtzer 2000; Willis and Whittaker 2002; Larrivée and Buddle 2009). Given the importance of habitat type and complexity, it can be expected that as Arctic habitats continue to undergo changes that affect the timing of snowmelt (Legault and Weis 2013), the vegetation dominance, and the habitat complexity, the abundance and diversity of the spider community will also likely change.

One study found that a net change of lichen/moss dominated habitats to graminoid dominated habitats triggered an overall loss in plant species diversity (Walker *et al*. 2006), which would most likely have cascading effects to the spider community. Halaj *et al*. (2000) also observed a decrease in overall abundance and diversity of arthropods when habitats were made less complex and more uniform. As the prediction for the Arctic is increased shrubification at the expense of other microhabitats (Myers-Smith *et al*. 2011), one could argue that there will be an increase in habitat uniformity but also an increase in overall complexity. In contrast, increased shrub cover may simply change the Arctic landscape and ecosystems types without impacting uniformity, making the impact of habitat change on spider communities uncertain to predict.

The uniformity caused by shrub expansion is currently the greatest threat to microhabitat mosaics in the Arctic (Eldridge *et al*. 2011; Myers-Smith *et al*. 2011; Naito and Cairns 2011). In Cambridge Bay, this may lead to neighbouring Dry2 and Wet1 habitats being overtaken by the Wet2 willow type habitat. This could have important implications to local diversity, as the species *Pachygnatha clerckii* is found almost exclusively in Wet1 and *Emblyna borealis* Pickard-Cambridge (Araneae: Dictynidae) is most commonly found in Dry2 (Fig. 7). Increase in shrub cover also leads to changes in local abiotic factors, nutrient cycling, disturbance regimes, and decomposition, all of which could affect spider communities and their prey in unpredictable ways (Walker *et al*. 2006; Eldridge *et al*. 2011; Myers-Smith *et al*. 2011; Naito and Cairns 2011).

Seasonal change

Arctic spider assemblages exhibited seasonal change patterns, though this change cannot be defined specifically as species turnover. A similar study by Ernst and Buddle (2013) found that beetle communities exhibited strong species turnover and that communities were very different at the start and end of the season. With our work, most species were present throughout the entire sampling season, leading to an insignificant effect of sampling period in the ordination (Fig. 2). However, sampling period did have a significant effect on overall spider abundance and diversity (Table 1), and differences in abundance peaks of individual species were observed (Fig. 5).

With climate change altering the timing of snowmelt and accelerating the warming process (Parmesan 2006; Høye *et al*. 2007), these abundance curves may shift with time – potentially leading to new community dynamics based upon how quickly individual species will react or adapt to these temperature changes. As we know that ecologically similar species are often restricted by different temperature profiles (DeVito *et al*. 2004), climate change may give certain species a competitive edge over others. Also, although all communities change over time, they may not always change at a similar rate within each habitat type – restricted by different conditions associated with those habitats. Weeks and Holtzer (2000), for example, observed a distinct seasonal effect in steppe grass systems, where communities from different habitats changed in different ways throughout the season. The reason we did not concretely observe this in our study may stem from differences in growing season length and ecoclimatic zones.

In the Arctic, presence or absence of a species seems less important than the relative dominance

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of a species in the community as a function of time. In this way, spider communities are not static throughout the season but do not exhibit a true turnover (Fig. 5). The explanation behind this observed pattern is still unclear. It may help decrease competition with species of similar guilds without sacrificing emergence time in the short growing season (Uetz and Uetz 1977; Uetz 1991; Uetz *et al*. 1999; Halaj *et al*. 2000; Weeks and Holtzer 2000; DeVito *et al*. 2004), or it may be a function of timing with favourite prey sources. Another possible explanation is differential movement, whereby some species may move more or less and therefore have different catch rates. Further research would be needed to make definitive conclusions.

Conclusion

In the Arctic, both microhabitat type and seasonal change play a role in structuring spider communities. Of the four tested ecosites, distinct communities emerge when comparing wet microhabitats to dry microhabitats but the differences between more similar microhabitats were insignificant. This distinction is most likely explained by the dramatic differences in the habitat complexity of the ecosites: something spiders are known to respond strongly to in other ecosystems, even at finer scales. Still, it would be ideal to test all 11 microhabitat types in Cambridge Bay for community differences before making concrete statements about the uniformity of all wet or dry microhabitat types. Though the effect of time is not as clear cut as the effect of microhabitats, communities are not static; their abundance, diversity, and species dominance all change throughout the season. This research has therefore shown that fine scale microhabitat level sampling is necessary to capture the full complement of Arctic spiders. This knowledge will aid in the development of future ecological monitoring programmes as well as more accurate and meaningful sampling designs.

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