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

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Abstract—A comparison is made between a three-year structured-sampling study that compared spider faunas of two tundra habitats and a single-year unstructured-sampling study, both within the Arctic Long-Term Experimental Research (LTER) field station at Toolik Lake, Alaska, United States of America. The three-year study documented 51 species and predicted a total of 60 species for the area. Our one season study documented 39 species, of which 24, or 62%, are not shared by the three-year study, raising the total count for the LTER to 75 species. These findings emphasise limitations of species richness estimation methods and help dispel the perception that Arctic tundras are homogeneous and species poor.

Résumé—Nous comparons une étude de trois ans sur les faunes d'araignées de deux habitats de toundra basée sur une échantillonnage structuré à une autre étude d'un an basée sur un échantillonnage non structuré; les deux études ont été réalisées dans le cadre de l'Arctic LTER (Long Term Experimental Research – recherche expérimentale à long terme) station de recherche au lac Toolik, Alaska, États-Unis d'Amérique. L'étude de trois ans a découvert 51 espèces et a prédit un total de 60 espèces dans la région. Notre étude d'une saison a découvert 39 espèces dont 24, soit 62%, ne sont pas partagées par l'étude de trois ans, ce qui amène le décompte total pour le LTER à 75 espèces. Ces résultats soulignent les limites des méthodes d'estimation de la richesse spécifique et aident à corriger l'impression que les toundras arctiques sont homogènes et pauvres en espèces.

Introduction

The spider fauna of the Alaskan Arctic has been sparsely sampled with few publications documenting the fauna. Early reports from Chamberlin and Ivie (1947), Weber (1949, 1950), Holm (1960, 1970), Watson *et al.* (1966), and MacLean (1975) brought the total to 50 spider species known for the Alaskan Arctic as of 1975. These and additional records from various publications and collections were summarised in Danks (1981) who listed a total of 92 species for Arctic Canada west of the Mackenzie River and Alaska, United States of America.

Perhaps the most intensive spider sampling to be undertaken in the region was that performed by Wyant *et al.* (2011). They trapped a total of 6980 spiders representing 51 putative species over three field seasons (2004–2006) at the Arctic Long-Term Experimental Research (LTER) site at Toolik Lake, Alaska. Their study was the first to document spiders from the Toolik Lake LTER and, in addition to finding eight new state records, showed that the spider faunas of two tundra types were significantly different. Given their quantitative sampling approach and large sample sizes, they were able to estimate an upper confidence interval for the total species richness of spiders for the LTER at 60 species. They wrote: "We attribute our high species richness to persistence in trapping effort over time (3 years) and efforts made to trap over the

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growing season (June–August) when spiders are most active. Our collection efforts yielded a species richness estimate in the upper 95% confidence limit of a rarefaction curve, which leads us to conclude that our collection of fauna captured by pitfall trap is fairly complete and our sampling methods are justified…". We also sampled spiders at the Toolik Lake field station and herein compare our findings with those of Wyant *et al*. (2011).

Materials and methods

Between 1 June and 30 July 2008 the first author, via the use of pitfall traps, Berlese funnels, sweep net, and visual searching collection methods, sampled spiders as part of a general arthropod survey at the Toolik Lake LTER field station at sites ~1.5 km or less from those sampled by Wyant *et al*. (Table 1, Fig. 1). The study site (68.626137°N, 149.593705°W ± 2 km; Fig. 1) is adequately described in Wyant *et al*. (2011). Three pitfall traps (10.5 cm diameter, 13 cm deep), half filled with 100% propylene glycol as preservative, with rain roofs, were set within a 36 m radius area (68.62860°N, 149.59772°W; Table 1) in moist nonacidic graminoid tundra on 2 June 2008 and emptied 58 days later on 30 July 2008 for a total of 174 trap days. Three BioQuip (Rancho Dominguez, California, United States of America) collapsible Berlese funnels were used (40 W bulbs, 24-hour runs) to extract arthropods from each of three collection events of sifted *Betula* Linnaeus (Betulaceae) and *Salix* Linnaeus (Salicaceae) leaf litter (68.62813°N, 149.59828°W; 68.62722°N, 149.59860°W; 68.62945°N, 149.59227°W; Table 1) between 1 and 4 June 2008. One visual searching collection event, which involved ~2 hours of rolling rocks along the Toolik lakeshore, was conducted on 1 June 2008 (68.62945°N, 149.59227°W; Table 1). One sweep net collection event was conducted in erect-shrub tundra on 30 July 2008 (68.62551°N, 149.59657°W; Table 1). All specimens are vouchered in the University of Alaska Museum Insect Collection, Alaska, United States of America and the data are available online via the Arctos database (http://arctos.database.museum/saved/Toolik_Spiders_2008). Adult specimens (juveniles were discarded) were identified by the second and third authors, and Jozef Slowik, University of Alaska Museum, Fairbanks, United States of America, using appropriate keys (Dondale and Redner 1978, 1990; Platnick and Dondale 1992; Buckle *et al*. 2001; Dondale *et al*. 2003; Ubick *et al*. 2005); the classification follows that of Paquin *et al*. (2010).

Results

The total spider count was 165 adult specimens representing 39 putative species (in 54 lots) of seven families (Table 2). Surprisingly, over half, 24 (61.5%), of these 39 species are not shared with the Wyant *et al*. (2011) list, thereby increasing the total count from 51 to 75 putative spider species for the LTER and exceeding Wyant *et al*.'s 95% upper confidence interval estimate of 60 species. Two of our species, *Agyneta maritima* (Emerton) (Araneae: Linyphiidae) and *Oreoneta magaputo* Saaristo and Marusik (Araneae: Linyphiidae) are new state records.

Discussion

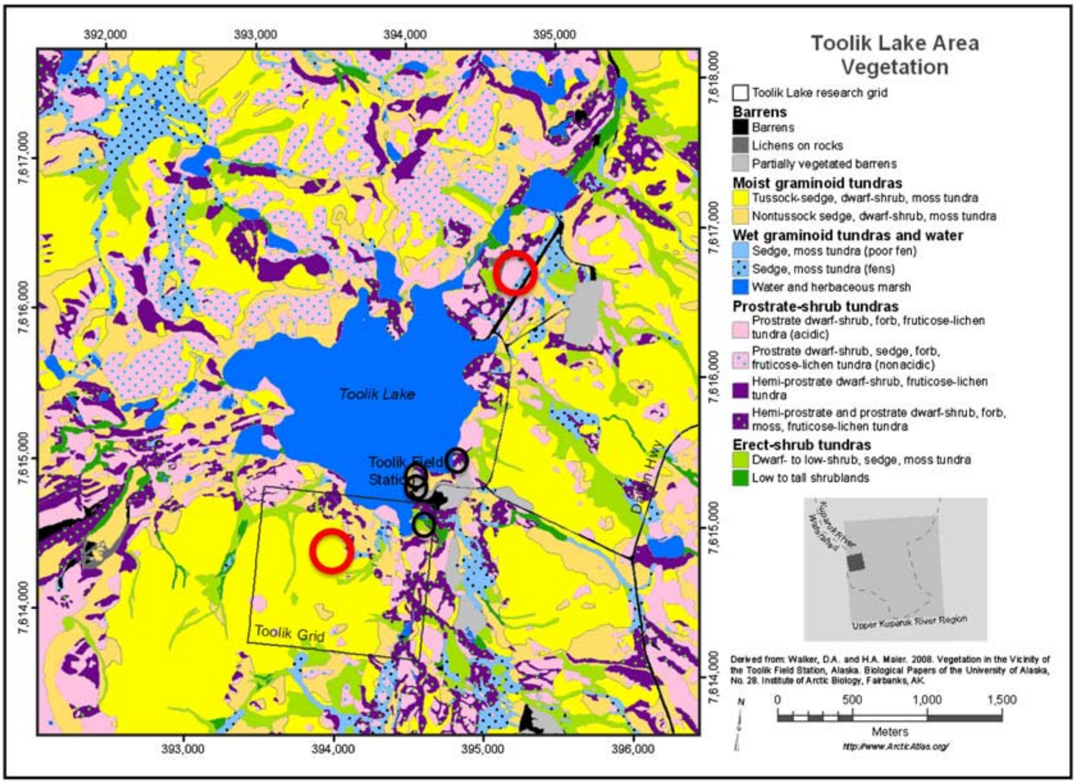
Wyant *et al*. (2011) sampled two sites intensively over three field seasons during June–August,

Table 1. Five sites from which the 2008 spider samples were taken on the Toolik Lake LTER, Alaska, United States of America.

Habitat	Microhabitat	Geocoordinates	Error (m)	Species/specimens
MNT	Tundra, under rocks	68.62860°N, 149.59772°W	±36	30/43
MNT	*Betula*/*Salix*/tundra	68.62813°N, 149.59828°W	±14	3/3
MNT	*Betula nana* litter	68.62722°N, 149.59860°W	±4	1/1
PST	Lakeshore rocks, *Salix*	68.62945°N, 149.59227°W	±36	2/4
EST	Stream side shrubs	68.62551°N, 149.59657°W	±8	4/4

Notes: Error = radius of circle centred on the listed geocoordinates in which collections were made (WGS84 datum).
LTER, Long-Term Experimental Research; MNT, moist nonacidic graminoid tundra: nontussock sedge, dwarf-shrub, moss tundra; PST, hemi-prostrate and prostrate dwarf-shrub, forb, moss, fruticose-lichen tundra EST, low to tall erect-shrub tundra (Walker and Maier 2007).

Fig. 1. Toolik Lake Field Station of the Arctic Long-Term Experimental Research (LTER) site, Alaska, United States of America, vegetation map by Walker and Maier (2007) showing the sites sampled for spiders by Wyant *et al*. (2011) during the summers of 2004, 2005, and 2006 (red circles) and the sites we sampled for spiders during the summer of 2008 (black circles).



accumulating 3642 trap days, so it is entirely reasonable to expect that this resulted in a "fairly complete" sampling of at least the ground-active spider fauna at Toolik Lake LTER. However, our short-term (174 trap day, June/July), nonintensive study using a few collection methods resulted in the addition of many undetected species with comparatively little collection effort, including some obtained via pitfall traps. So, what are plausible explanations for our surprising results?

First, there were habitat differences between collection sites for the two studies. Although both studies took place in the LTER, Wyant *et al*. (2011) ran pitfall traps in dry heath (DH) and moist acidic tundra (MAT) sites some distance from the field station (Fig. 1), while our 2008 samples were all taken adjacent to Toolik Lake itself, most within the boundaries of the field station (Fig. 1) in a variety of microhabitats, including anthropogenic/disturbed habitats and rocky lake and stream shorelines (Table 1). According to the Toolik LTER vegetation mapping of Walker and Maier (2007), our 2008 sites were in three main habitat types (Table 1): (1) moist nonacidic graminoid tundra: nontussock sedge, dwarf-shrub, moss tundra; (2) hemi-prostrate and prostrate dwarf-shrub (*e.g.*, *Betula nana* Linnaeus (Betulaceae)), forb, moss, fruticose-lichen tundra; and (3) low to tall erect-shrub tundra (*e.g.*, *Salix pulchra* Chamisso (Salicaceae)). Most ($n = 30$) of our 39 species were found in the moist nonacidic tundra (Table 1). The Wyant *et al.* (2011) DH site was ~1500 m NNE from our sites and their MAT site was ~500 m SW from our sites. To one unacquainted with Arctic tundras these distances and habitat differences may seem minor, yet Wyant *et al.* (2011) found their DH and MAT samples were

Table 2. Spider species ($n = 39$) based on 165 specimens collected at Toolik Lake Field Station, Alaska, United States of America, during 2008.

n, Family	Species	Wyant *et al.*	Method	Microhabitat
Araneidae				
1	*Larinioides cornutus* (Clerck, 1757)		S	Stream side shrubs
Dictynidae				
1	*Dictyna major* Menge, 1869		S	Stream side shrubs
Gnaphosidae				
2	*Gnaphosa orites* Chamberlin, 1922	+	P	Tundra/under rocks
1	*Haplodrassus hiemalis* (Emerton, 1909)	+	P	Tundra/under rocks
Linyphiidae				
2	*Agyneta maritima* Eskov, 1994		V	Tundra/under rocks
1	*Agyneta simplex* (Emerton, 1926)	+	P	Tundra/under rocks
1	*Bathyphantes canadensis* (Emerton, 1882)		S	Stream side shrubs
1	*Bathyphantes simillimus* (Koch, 1879)	+	P	Tundra/under rocks
1	*Bathyphantes yukon* Ivie 1969		V	Tundra/under rocks
2	*Erigone arctica* (White, 1852)		V	Tundra/under rocks
13	*Gnathonarium taczanowskii* (Cambridge, 1873)		V,B	Tundra/under rocks, lake shore rocks
2	*Halorates holmgrenii* (Thorell, 1871)		V	Tundra/under rocks
2	*Horcotes strandi* (Sytshevskaja, 1935)	+	V	*Betula*/*Salix*/tundra
3	*Islandiana cristata* Eskov, 1987	+	P,V	Tundra/under rocks
8	*Islandiana falsifica* (Keyserling, 1886)		P,V	Tundra/under rocks
2	*Kaestneria pullata* (Cambridge, 1863)		S	Stream side shrubs
1	*Lepthyphantes alpinus* (Emerton, 1882)		P	Tundra/under rocks
1	*Macrargus multesimus* (Cambridge, 1875)		V	Tundra/under rocks
1	*Mecynargus tungusicus* (Eskov, 1981)	+	P	Tundra/under rocks
1	*Oreoneta magaputo* Saaristo and Marusik, 2004		B	Lakeshore rocks
2	*Semljicola obtusus* (Emerton, 1915)		B	Lakeshore rocks
1	*Tapinocyba matanuskae* Chamberlin and Ivie, 1947		P	Tundra/under rocks
2	*Walckenaeria karpinskii* (Cambridge, 1873)	+	P	Tundra/under rocks
1	*Oreoneta* sp.		P	Tundra/under rocks
1	*Tapinocyba* new species? (male)		V	*Betula*/*Salix*/tundra
2	*Tapinocyba* sp. (females)		B	*Betula nana* litter
1	Linyphiidae (unknown genus, female)		P	Tundra/under rocks
1	Linyphiidae (near *Zygottus corvallis*, female)		V	Tundra/under rocks
Lycosidae				
1	*Alopecosa hirtipes* (Kulczynski, 1907)	+	P	Tundra/under rocks
7	*Arctosa insignita* (Thorell, 1872)	+	P,V	*Betula*/*Salix*/tundra/ under rocks
1	*Pardosa fuscula* (Thorell, 1875)		P	Tundra/under rocks
21	*Pardosa lapponica* (Thorell, 1872)	+	P	Tundra/under rocks
60	*Pardosa podhorskii* (Kulczynski, 1907)	+	P,V	Tundra/under rocks
2	*Pardosa prosaica* Chamberlin and Ivie, 1947		V	Tundra/under rocks
10	*Pardosa tesquorum* (Odenwall, 1901)		P,V	Tundra/under rocks
Philodromidae				
2	*Thanatus formicinus* (Clerck, 1757)		P	Tundra/under rocks
Thomisidae				
1	*Ozyptila arctica* Kulczynski, 1908	+	P	Tundra/under rocks
1	*Xysticus britcheri* Gertsch, 1934	+	P	Tundra/under rocks
1	*Xysticus deichmanni* Sorensen, 1898	+	P	Tundra/under rocks

Notes: Wyant *et al.* (+) = present in Wyant *et al.* (2011) list.
Microhabitat corresponds with site descriptions in Table 1.
S, sweep net; P, pitfall traps; V, visual searching; B, Berlese funnel.

quite different in sharing only ~45% of their total spider species. It remains surprising, however, that samples taken between Wyant *et al*.'s sites would show equally significant differences between their total sample and ours. The patchy local occurrence of species observed between ours and Wyant *et al*.'s (2011) studies is not what one would expect given the circumpolar distribution of many of these species (Paquin *et al*. 2010) and the relative lack of vegetative structural heterogeneity of Arctic tundras, at least relative to boreal forest habitats. This points to the critical importance of seemingly subtle microhabitat differences in Arctic ecosystems. Arctic spiders may be highly vagile and widely distributed, but only thrive in one or a few appropriate habitat/microhabitat types.

Second, collection methods differed between our studies. Wyant *et al*. (2011) used pitfall traps almost exclusively. To address the fact that sit-and-wait and nonground active species are less likely to be trapped in pitfalls they made some effort to sweep net spiders from vegetation near traps but they report this yielded no arboreal or stem/trunk dwelling spiders that were not also captured by pitfall trap. Although we used pitfall traps, we also performed visual searching under rocks and some limited sweep sampling and Berlese funnel leaf litter extraction. Of our 39 species, 22 were found in pitfalls, 15 were found via visual searching, four were found via Berlese funnels, and four via sweeping (Table 2). Six species were found using multiple methods. As expected, of the 15 species shared between Wyant *et al*.'s list and ours, 14 were caught in pitfall traps by us. None of the Berlese funnel or sweep net species were shared with the Wyant *et al*. (2011) list. Of the 24 species not shared with the Wyant *et al*. (2011) list, seven were found via pitfalls, four by sweeping, 11 by visual searching, and four by Berlese funnels. Among the sweep net captures are shrub-dwelling species that were not found by Wyant *et al*. (2011) such as the orb-weaver *Larinioides cornutus* (Clerck) (Araneae: Araneidae).

The total area sampled also differed between our studies, and it is well known that larger areas hold more species than smaller areas (Rosenzweig 1995). Wyant *et al*. (2011) had a total of 28 pitfall trap plots of 5 m^2 each for a total sample area of 700 m^2. The estimated area covered by our sampling was 9008 m^2 (Table 1), which included three pitfall traps.

Additionally relevant to collection method differences is that the species richness rarefaction procedure used by Wyant *et al*. (2011) to predict an upper limit of species richness of 60 is limited to extrapolation based on the collection methods used to generate the data (Longino and Colwell 1997) and to the specific location and habitat sampled. Furthermore, their rarefaction curve does not appear to be levelling off, but continues to increase. Therefore, despite the fact that long-term intensive collecting was conducted, their data actually suggest that there may be significantly more species that have yet to be detected. It would be interesting to see what their data would yield for an estimate of total species richness (*i.e.*, the actual number of species in an area, based on the number of rare species, including those so rare they were not collected), using a species richness estimator such as Chao 1 or Jacknife, *etc.* (Colwell *et al*. 2004; Chao 2005). It is possible that the number would be quite a bit higher. However, contrary to the wishes of biologists everywhere, even these estimators cannot predict the actual species richness of a site unless the methods used can reliably capture all species of the site, which for spiders, pitfall traps cannot (Uetz and Unzicker 1976; Melbourne 1999). If we had limited our methods to pitfall traps this would have reduced our list from 39 species with 24 new Toolik records to 22 species with eight new Toolik records bringing the Wyant *et al*. (2011) count of 51 species to 59 species – almost identical with their predicted 60 species for the region. This is probably coincidence, however, given the restrictions of estimating species richness by rarefaction. The Wyant *et al*. (2011) prediction of 60 species, therefore, should be interpreted as a low estimate of ground-active spider richness expected in MAT and DH habitats of the LTER. This emphasises the importance of proper interpretation of these estimators based on collection methods and habitat types sampled.

A few final points may be made. It is unknown how much year-to-year variation occurs in these spider communities. Perceived among-habitat diversity may have been increased by ecological or climatic changes that occurred between the end of Wyant *et al*.'s study in 2006 and the start of ours in 2008. However, it would be surprising if even half of the 24 nonoverlapping species owed their detections to ecological or climatic changes between 2006 and 2008. Given the potentially dramatic changes anticipated for Arctic ecosystems (Stone *et al*. 2002; Lawrence and Slater 2005; Sturm *et al*. 2005; McGuire *et al*. 2009; Beck *et al*. 2011), long-term arthropod sampling that quantifies annual variability and that can detect departures from baseline values would be necessary to assess this factor.

Taxonomic issues were encountered in both studies. Five species in each study could not be identified. These animals could be undescribed species, members of poorly known species, or represent large range extensions of known species. These taxonomic uncertainties notwithstanding, the second author in both studies performed the identifications, and material from both studies was compared. Accordingly, we are confident that the five incompletely identified linyphiid species are not conspecific with any other species in either study.

Another important factor is that the goals of Wyant *et al*. (2011) and our study differed. Wyant *et al*. (2011) performed a structured sampling to allow statistical comparison of spider faunas between two habitat types while our study was to establish a baseline inventory of species performed by maximising the number of species found per unit effort expended. This explains the large efficiency differences of our study (1 species/4.23 adult specimens) to theirs (1 species/99 adult specimens).

The notion that tundra habitats are species poor and homogenous is a reasonable hypothesis, which Wyant *et al*.'s and our data have falsified, at least for spiders in the Arctic LTER. Why such high among-habitat diversity occurs is not well understood. It is possible that a critical survival advantage is gained by specialising in particular microhabitats in harsh Arctic environments and that the benefit of specialisation outweighs the risk of not finding the appropriate habitat for animals with superior dispersal abilities. This would seem to be supported by the fact that the dominant spider family in Arctic habitats is the Linyphiidae – tiny spiders that maintain the ability to balloon as adults (disperse by being lifted on warm air currents) and are thus capable of wide dispersal throughout their lifecycle. Not only is this family often numerically dominant in these habitats, but it also accounts for much of the species richness in Arctic spider communities. Other spiders are also highly capable of ballooning, but most are limited to dispersal during juvenile stages. Another family that is extremely abundant and relatively species rich in the Arctic, the Lycosidae, tend to have several overlapping cohorts of offspring throughout the summer, and thus can be found dispersing by ballooning throughout most of the season.

Northern habitats, in general, are species poor if you compare the number of spider species per unit land area to locations at lower latitudes (Koponen 1993). However, the reason for the latitudinal species trend is much debated in the scientific literature (*e.g.*, Pianka 1966; Rohde 1992; Hillebrand 2004), and the pattern may vary for different spider taxa (Koponen 1993; and our own observations).

Finally, we expect the inventory is not yet complete. There are a few families that are likely present but were not found such as the Clubionidae, the Theridiidae, and the Tetragnathidae. Given these results, future efforts to improve the baseline inventory should continue with all four methods, but extend the collecting effort over greater habitat diversity, samples, and time. This study may be of value in the interpretation of the much-anticipated 30-year pitfall datasets to be generated by the National Ecological Observatory Network (NEON) (Hopkin 2006), which will have a station at the Arctic LTER.

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References

Beck, P.S.A., Juday, G.P., Alix, C., Barber, V.A., Winslow, S.E., Sousa, E.E., *et al*. 2011. Changes in forest productivity across Alaska consistent with biome shift. Ecology Letters, **2011**: 1–7. doi:10.1111/j.1461-0248.2011.01598.x.

Buckle, D.J., Carroll, D., Crawford, R.L., and Roth, V.D. 2001. Linyphiidae and Pimoidae of America north of Mexico: checklist, synonymy, and literature. Part 2. *In* Contributions à la connaissance des Araignées (Araneae) d'Amérique du Nord. Supplément 10, *Edited by* P. Paquin and D.J. Buckle. Fabreries, Supplément, Association des entomologists amateurs du Québec, Quebec, Canada, **10**: 89–191.

Chamberlin, R.V. and Ivie, W. 1947. The spiders of Alaska. Bulletin of the University of Utah, **37**: 1–103.

Chao, A. 2005. Species richness estimation. *In* Encyclopedia of statistical sciences. *Edited by* N. Balakrishnan, C.B. Read and B. Vidakovic. Wiley, New York, United States of America. Pp. 7909–7916.

Colwell, R.K., Mao, C.X., and Chang, J. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology, **85**: 2717–2727.

Danks, H.V. 1981. Arctic arthropods: a review of systematics and ecology with particular reference to the North American fauna. Entomological Society of Canada, Ottawa, Canada.

Dondale, C.D. and Redner, J.H. 1978. The insects and arachnids of Canada. Part 5. The crab spiders of Canada and Alaska: Araneae: Philodromidae and Thomisidae. NRC Research Press, Ottawa, Ontario, Canada.

Dondale, C.D. and Redner, J.H. 1990. The insects and arachnids of Canada. Part 17. The wolf spiders, nursery web spiders, and lynx spiders of Canada and Alaska: Araneae: Lycosidae, Pisauridae, and Oxyopidae. NRC Research Press, Ottawa, Ontario, Canada.

Dondale, C.D., Redner, J.H., Paquin, P., and Levi, H.W. 2003. The insects and arachnids of Canada. Part 23. The orb weaving spiders of Canada and Alaska (Araneae: Uloboridae, Tetragnathidae, Araneidae, Theridiosomatidae). NRC Research Press, Ottawa, Ontario, Canada.

Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. The American Naturalist, **163**: 192–211.

Holm, A. 1960. On a collection of spiders from Alaska. Zoologiska Bidrag fran Uppsala, **33**: 109–134.

Holm, A. 1970. Notes on spiders collected by the "Vega" expedition I878-I880. Insect Systematics and Evolution, **1**: 188–208.

Hopkin, M. 2006. Spying on nature. Nature, **444**: 420–421.

Koponen, S. 1993. On the biogeography and faunistics of European spiders: latitude, altitude and insularity. Bulletin de la Société Neuchâteloise des Sciences Naturelles, **116**: 141–152.

Lawrence, D.M. and Slater, A.G. 2005. A projection of severe near-surface permafrost degradation during the 21st century. Geophysical Research Letters, **32**: L24401. doi:24410.21029/22005GL025080.

Longino, J.T. and Colwell, R.K. 1997. Biodiversity assessment using structured inventory: capturing the ant fauna of a tropical rain forest. Ecological Applications, **7**: 1263–1277.

MacLean, S.F., Jr. 1975. Ecology of tundra invertebrates at Prudhoe Bay, Alaska. *In* Ecological investigations of the tundra biome in the Prudhoe Bay Region, Alaska. *Edited by* J. Brown. Biological Papers of the University of Alaska. Special Report, **2**: 115–123.

McGuire, A.D., Anderson, L.G., Christensen, T.R., Dallimore, S., Guo, L., Hayes, D.J., *et al*. 2009. Sensitivity of the carbon cycle in the Arctic to climate change. Ecological Monographs, **79**: 523–555.

Melbourne, B.A. 1999. Bias in the effect of habitat structure on pitfall traps: an experimental evaluation. Australian Journal of Ecology, **24**: 228–239.

Paquin, P., Buckle, D.J., Dupérré, N., and Dondale, C.D. 2010. Checklist of the spiders (Araneae) of Canada and Alaska. Zootaxa, **2461**: 1–170.

Pianka, E.R. 1966. Latitudinal gradients in species diversity: a review of concepts. The American Naturalist, **100**: 33–46.

Platnick, N.I. and Dondale, C.D. 1992. The insects and arachnids of Canada. Part 19. The ground spiders of Canada and Alaska: Araneae: Gnaphosidae. NRC Research, Ottawa, Ontario, Canada.

Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. Oikos, **65**: 514–527.

Rosenzweig, M.L. 1995. Species diversity in space and time. Cambridge University Press, New York, United States of America.

Stone, R.S., Dutton, E.G., Harris, J.M., and Longenecker, D. 2002. Earlier spring snowmelt in northern Alaska as an indicator of climate change. Journal of Geophysical Research, **107**: 10-1–10-13. D10. doi:10.1029/2000JD000286.

Sturm, M., Schimel, J., Mechaelson, G., Welker, J.M., Oberbauer, S.F., Liston, L.E., *et al*. 2005. Winter biological processes could help convert Arctic tundra to shrubland. BioScience, **55**: 17–26.

Ubick, D., Paquin, P., Cushing, P.E., and Roth, V. 2005. Spiders of North America: an identification manual. American Arachnological Society, Poughkeepsie, New York, United States of America.

Uetz, G.W. and Unzicker, J.D. 1976. Pitfall trapping in ecological studies of wandering spiders. Journal of Arachnology, **3**: 101–111.

Walker, D.A. and Maier, H.A. 2007. Geobotanical maps in the vicinity of the Toolik Lake Field Station, Alaska [online]. Institute of Arctic Biology, Biological Papers of the University of Alaska, No. 27. Available from http://www.arcticatlas.org/maps/themes/tl5k/tl5kvg [accessed 6 July 2012].

Watson, D.G., Davis, J.J., and Hanson, W.C. 1966. Terrestrial invertebrates. *In* Environment of the Cape Thompson region, Alaska. *Edited by* N.J. Wilimovsky and J.N. Wolfe. Division of Technical Information, United States Atomic Energy Commission. Springfield, Virginia, United States of America. Pp. 565–584.

Weber, N.A. 1949. Late summer invertebrates, mostly insects, of the Alaska Arctic Slope. Entomological News, **60**: 118–128.

Weber, N.A. 1950. A survey of the insects and related arthropods of Arctic Alaska. Part 1.Transactions of the American Entomological Society, **76**: 147–206.

Wyant, K.A., Draney, M.L., and Moore, J.C. 2011. Epigeal spider (Araneae) communities in moist acidic and dry heath tundra at Toolik Lake, Alaska. Arctic, Antarctic, and Alpine Research, **43**: 301–312. doi:10.1657/1938-4246-43.2.301.