Spider Assemblages across Elevational and Latitudinal Gradients in the Yukon Territory, Canada

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ABSTRACT. Arthropod assemblages in the Arctic are set for substantial changes in response to climate change, yet we know little about the ecological structure of many groups in the North. We tested the effects of elevation and latitude on northern spider assemblages by sampling along nine mountains across three latitudes in the Yukon Territory, Canada. Spiders were collected in 216 pitfall traps placed at four elevations along each of the nine mountains, representing 36 sites sampled across three latitudes (i.e., distinct mountain ranges). We collected 1954 individuals representing 89 species, 57 genera, and 12 families of spiders. Using nested ANOVAs, we found significant main effects of latitude, elevation, and an interaction of the two factors on species richness and abundance. Using MRPP and NMS ordination, we also found significant effects of latitude and mountain on species composition, but within each of the three latitudes, only elevation produced significant effects. Our study suggests that changes along spatial gradients associated with changes in habitat can have significant effects on the structure of spider assemblages, but responses vary among mountain ranges. We show that within a given mountain range, individual mountains may be used as spatial replicates for studies about northern arthropod assemblages.

Key words: spider assemblages, elevation, latitude, Yukon Territory, diversity, species composition, terrestrial arthropods, Araneae

RÉSUMÉ. Les assemblages d'arthropodes de l'Arctique connaîtront des changements substantiels en raison du changement climatique mais malgré cela, nous en savons peu sur la structure écologique de nombreux groupes du Nord. Nous avons mis à l'épreuve les effets de l'élévation et de la latitude sur les assemblages d'araignées du Nord en prélevant des échantillons sur neuf montagnes réparties sur trois latitudes dans le territoire du Yukon, au Canada. Les araignées ont été recueillies à l'aide de 216 pièges placés à quatre élévations différentes le long de chacune des neuf montagnes, ce qui a représenté 36 emplacements échantillonnés sur trois latitudes (c'est-à-dire des chaînes de montagnes distinctes). Nous avons recueilli 1 954 individus représentant 89 espèces, 57 genres et 12 familles d'araignées. À l'aide d'analyses de variances (ANOVA), nous avons relevé d'importants effets découlant de la latitude, de l'élévation et de l'interaction de deux facteurs sur la richesse et l'abondance des espèces. Au moyen de l'ordination MRPP et NMS, nous avons également constaté que la latitude et la montagne ont des incidences considérables sur la composition des espèces, mais au sein de chacune des trois latitudes, seule l'élévation produisait des effets importants. Notre étude laisse entendre que les changements en matière de gradients spatiaux liés aux changements d'habitat peuvent avoir des effets considérables sur la structure d'assemblages d'araignées, mais les réactions varient d'une chaîne de montagne à l'autre. Nous montrons que dans une chaîne de montagne donnée, les montagnes individuelles peuvent servir de mesures spatiales en vue de l'étude d'assemblages d'arthropodes nordiques.

Mots clés : assemblages d'araignées, élévation, latitude, territoire du Yukon, diversité, composition des espèces, arthropodes terrestres, Araneae

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INTRODUCTION

The effects of spatial gradients (e.g., elevational and latitudinal) on species assemblages remain a central theme of biogeography (Willig et al., 2003; Hodkinson, 2005; Willig and Bloch, 2006). The patterns resulting from the effects of latitude and elevation have been well studied for many organisms at many spatial scales (reviewed by Willig et al., 2003 and Hodkinson, 2005). There are fundamental

ecological reasons for understanding these patterns of change across spatial gradients: specifically, understanding the effects that these gradients have on patterns of biodiversity and global distributions of species. However, spatial gradients may also serve a more applied mandate: an example is using latitudinal or elevational transects to test climate change predictions (e.g., Andrew and Hughes, 2004; Parmesan, 2006). Such studies suggest that high-latitude and high-elevation species are at greatest risk for

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range contraction and potential extinction in future climate change scenarios (Parmesan, 2006). Despite the abundance of biogeographical studies focused on tropical and temperate zones (e.g., Gotelli and Ellison, 2002; Willig et al., 2003; Andrew and Hughes, 2004; Ruggiero and Hawkins, 2008), relatively few studies have explored spatial patterns of species assemblages occurring in northern systems (but see Otto and Svensson, 1982, and meta-analyses by Cardillo, 2002; Currie et al., 2004; Kotwicki et al., 2005; Qian et al., 2009).

The patterns arising from biogeographical studies include positive, negative, hump-shaped and neutral responses of species to changes in elevation and latitude. Latitude tends to be negatively correlated with species richness (e.g., Cushman et al., 1993; Lyons and Willig, 2002; Finch et al., 2008), with some exceptions (e.g., Dixon et al., 1987; Kouki et al., 1994). Studies of elevation, which mimic environmental changes associated with latitude at a more abrupt spatiotemporal scale (Hodkinson, 2005), tend to show decreases in diversity with increasing elevation, but these responses are not often linear (Rahbek, 1995). Studies examining patterns of abundance across spatial gradients are less common. However, terrestrial arthropod community abundance has shown either a decrease or no effect with increases in elevation or latitude. For example, Otto and Svensson (1982) and McCoy (1990) show decreases in spider abundance with increases in elevation, while Chatzaki et al. (2005) found no significant effect of elevation on spider abundance (measured as activity) along an elevational gradient in Crete. Andrew and Hughes (2005) found, in an analysis of the effects of latitude on various terrestrial arthropod feeding guilds, that predators showed the only significant latitudinal trend.

At regional and continental scales, spider species richness has been correlated with latitude and mean annual temperature (Finch et al., 2008; Whitehouse et al., 2009). Spiders (Arachnida: Araneae) are a model taxon for investigating the effects of spatial gradients on species assemblages at regional scales (i.e., 200–4000 km, Waide et al., 1999). Spiders readily respond to acute changes in habitat heterogeneity (Downie et al., 1995), temperature, and humidity (DeVito et al., 2004). The fine spatial scale at which spiders partition these abiotic changes (Moring and Stewart, 1994) makes them suitable to assess species assemblage patterns across spatial gradients at regional extents. Over a broad elevational gradient, ground-dwelling spider richness has shown a hump-shaped response to changes in elevation (Chatzaki et al., 2005). Jimenez-Valverde and Lobo (2007), however, found that spider richness was more strongly correlated with habitat complexity and maximum temperature than with elevation at a regional scale of investigation.

There are other ecological reasons why spiders represent a model taxon for biogeographic research: spiders are eurytopic and thus can be collected in varying habitats encountered along spatial transects (e.g., Chatzaki et al., 2005). Spiders are important to local food web dynamics (Wise, 2004) and ecosystem processes (i.e., nutrient cycling,

Lawrence and Wise, 2000), and their taxonomy is readily accessible and relatively well known (Ubick et al., 2005). Spiders are also well represented in terms of species richness and abundance at northern latitudes (Buddle et al., 2000), and many faunal inventories illustrate this fact (Dondale et al., 1997; Marusik and Koponen, 2002; Marusik et al., 2004; Pickavance, 2006). These studies, however, have not led to quantitative regional studies of factors that determine patterns of spider assemblage structure in the far North.

Our objective was to determine the effects of elevation and latitude on spider assemblage structure. Specifically, we sought to determine the changes that occurred in species richness, activity density, and composition across elevation and latitude in the Yukon Territory, Canada. We predicted that spider species richness and activity density would be affected by both latitude (across all mountain ranges) and elevation, and that they would generally decrease with increasing elevation or latitude, or both. Because spiders are adapted to a rather narrow set of abiotic parameters (e.g., temperature, humidity, and habitat), we also predicted that composition would differ significantly among latitudes and elevations.

MATERIALS AND METHODS

Experimental Design and Sampling

Sampling was conducted in three mountain ranges in the northern Yukon Territory, Canada (Fig. 1): the Tombstone Range (64.309° N, 138.141° W), the Ogilvie Range (65.158° N, 138.148° W), and the Richardson Range (66.725° N, 136.114° W). This region of the Yukon transitions northward from boreal forest to Arctic tundra (Payette et al., 2001). In the most southern part of the study area is the valley of the Tombstone Range, a patchy matrix of black spruce (*Picea mariana* Mill.) and white spruce (*P. glauca* Moench), with non-forested areas of sphagnum, *Ledum* sp., *Vaccinium* sp., *Empetrum* sp., lichens, grasses, and patches of willow (*Salix* spp.) and dwarf birch (*Betula glandulosa* Michx.) up to 1.5 m high. This habitat transitions, with increasing elevation, into alpine tundra characterized by a thin sphagnum layer and stunted vegetation with patches of barren ground and rock. The third mountain of the Tombstone Range differs slightly and is dominated by thick willow stands approximately one meter high.

The Ogilvie Range contains thin boreal forest in the valley, which is dominated by black spruce and large willows. With increasing elevation, the forest thins to sparse black spruce and willow along the mountainside. The Ogilvie Range was the only mountain range in which trap disturbance occurred during the study period: two pitfall traps were consistently disrupted at one of the lowest-elevation sites in this range. The potential influence of this disturbance on the data is therefore discussed along with biological explanations.
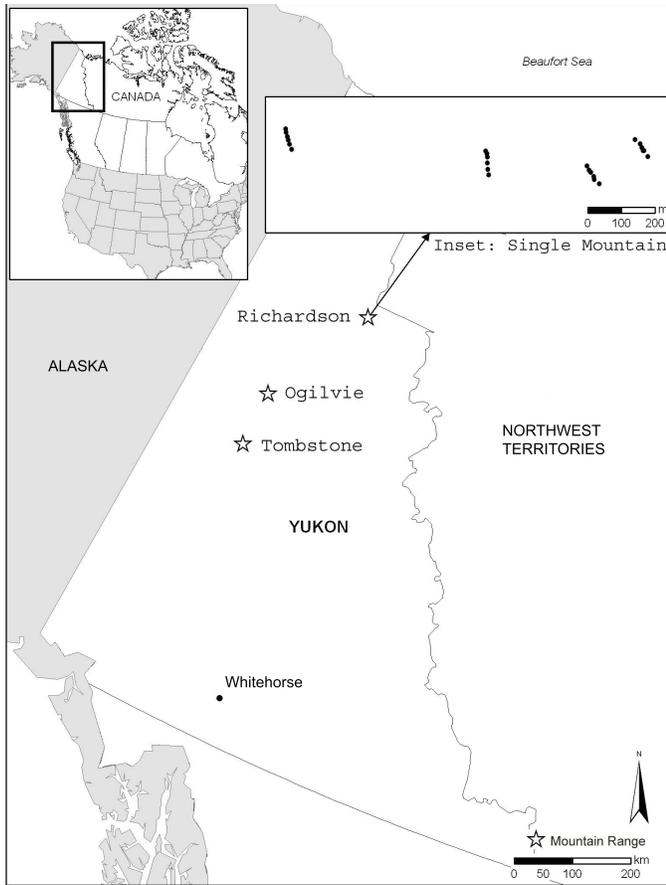
FIG. 1. Map of sampling region in Yukon Territory, Canada, showing the Tombstone, Ogilvie, and Richardson mountain ranges. Three mountains were selected in each range, and four elevational sites within each mountain transect (one transect and sites shown in inset).

In the Richardson Mountains, the northernmost range studied, open tundra dominates the valley and is characterized by a thick sphagnum layer, *Ledum* sp., *Vaccinium* sp., *Empetrum* sp., *Eriophorum* sp., lichens, and stunted *Salix* spp. and *Betula glandulosa* Michx. This valley tundra transitions through a thinning sphagnum layer to rock in the mountains.

Ground-dwelling spiders were collected using pitfall traps at each of the three mountain ranges. Pitfall trapping is useful for studying arthropod biodiversity at large spatial scales (e.g., Gotelli and Ellison, 2002; Chatzaki et al., 2005; Whitehouse et al., 2009) and allows for consistent and repeatable sampling. Each pitfall trap consisted of a transparent plastic container (6 cm in diameter, 7 cm deep) half filled with 1:1 water and propylene glycol. A cover (a 14 × 14 cm square of plastic corrugate) was placed about 2 cm above each trap and held into the ground by wire. We placed each trap into the ground so that the rim was flush with the substrate surface.

We established three transects within each mountain range (latitude). This design allowed for spatial replication, maintaining the same elevation within each range. Many altitudinal studies have chosen to maximize altitudinal variation along a single transect (e.g., Olson, 1994; Chatzaki et

al., 2005; Cardelús et al., 2006). We opted to maximize spatial replication to detect and develop generalizations about landscape and regional scale patterns in arthropod diversity (e.g., Sanders et al., 2003; Almeida-Neto et al., 2006).

We sampled sites at four different elevations along each of the three mountains within each of the three ranges. The four sites on each mountain were established every 100 m in elevation, for a total of 36 sites in the region. Each site consisted of six pitfall traps placed 10 m apart. The mountain transects were initiated in valleys and ran up the three mountains selected in each range. Elevation in the Tombstone Range began at 1060 m in the valley and ended at 1360 m. In the Ogilvies, elevation ranged from 660 m in the valley to 960 m at the top of the mountains. In the Richardson Range, pitfall trapping began at 760 m in the valley and ended at 1060 m on the mountaintops. Although actual elevation varied among latitudes, there was no difference within each range, and except as noted above, we maintained habitat among mountains within each range at a given elevation. The overall design of our study was four elevations (sites) within each mountain, three mountains within each latitude (mountain range), and three latitudes within the region.

We collected spiders with pitfall traps between 14 June and 22 July 2006. We chose this time frame because it includes the highest activity period for spiders in the North (pers. obs., Buddle and Draney, 2004). Traps were open for an average of 27.5 days ± 0.294 (mean ± SE). There was no effect of sampling effort on trap captures, so we did not standardize the data for sampling effort. Although these data represent only one year of collection, past studies from northern Alberta, Canada, suggest that arthropod community data do not change significantly from year to year (e.g., Buddle et al., 2000). All traps were emptied twice, and all arthropods were preserved in ethanol. The spiders collected were pooled by elevation per mountain, so the six pitfall traps were treated as a site. All specimens were identified to species level following nomenclature by Platnick (2009). Immature specimens were omitted from analyses and voucher specimens deposited at the Lyman Entomological Museum (Ste Anne de Bellevue, Quebec).

Statistical Analyses

We focused on three main response variables: species richness, abundance (as measured by activity density), and composition. All species data were transformed ($x' = \log(x + 1)$) to improve monotonicity and to maximize the amount of variation explained by ordination. Species richness and activity density data were transformed to a logarithmic scale (base 10) to achieve normality for parametric tests.

Two separate nested analyses of variance (ANOVA) were calculated using the transformed data for species richness and activity density. ANOVA models were calculated using latitude and elevation as random main effects and mountain as a random factor nested in latitude. We tested for the main effects of latitude and elevation, for the nested

effect of mountain, and for the interaction between latitude and elevation. We used package "lme4" (Bates and Maechler, 2009) for the R statistical software version 2.8.0 (R Development Core Team, 2008). To explore variability in species richness and activity density among elevations due to the significant interaction, we ran six one-way ANOVAs within each mountain range using SPSS version 15 (SPSS Inc., 2006).

To examine the effects of elevation and latitude on patterns of community composition, we ran a non-metric multidimensional scaling (NMS) ordination (Kruskal, 1964) with the software program PC-ORD version 4.17 (McCune and Mefford, 1999). A detrended correspondence analysis (DCA) was first completed and used as a starting configuration for the NMS ordination. To achieve the optimum NMS solution, we used step-down in dimensionality beginning at six axes. The best solution is that which minimizes stress (the relationship between the original species data and the data represented in ordination space) while maintaining the interpretability of the data by obtaining the fewest dimensions. The ordinations were run using Sørensen (Bray-Curtis) distance with 400 iterations, 20 runs with real data, 50 runs with randomized data, and an instability criterion of 0.00005. A Monte Carlo simulation using randomized data ($n = 50$) was run to determine the probability that a similar final stress could have been achieved by chance (McCune and Grace, 2002).

We used rank-transformed multi-response permutation procedures (MRPP) (Mielke and Berry, 2001) to test for differences in species composition among latitudes, elevations, and mountains. We also tested for differences among elevations within latitudes in case of variation. This nonparametric statistical procedure tests whether there are significant compositional differences (i.e., average within-group ranked distances) between two or more sample groups defined a priori. MRPP is a good complement to NMS ordinations, and it helps improve their interpretability by providing a measure of effect size given by the chance-corrected, within-group agreement statistic "A" (McCune and Grace, 2002).

To examine how individual species responded to the elevational gradient in each of the mountain ranges, we plotted the transformed activity density of the most dominant species. We also performed indicator species analyses (Dufrêne and Legendre, 1997), using PC-ORD, to determine whether a given species was abundant at a particular elevation or group of elevations (i.e., low or high) and the fidelity to that group. We chose to run two sets of indicator species analyses, using species that were both represented by more than 10 individuals and present in at least eight sites, to determine whether each species was a significant indicator of a particular elevation or elevation group.

Because different spider families use different ecological strategies (e.g., for hunting) and likely have different environmental requirements, we also examined family-level patterns in our data. We were especially interested in determining whether there were ordered changes in the

TABLE 1. Results of nested multifactor analysis of variance for spider species richness and activity density across three mountain ranges in the Yukon Territory, Canada.

Factor	df	MS	F	*p*-value
Richness:				
Latitude	2	0.06677	6.8197	0.00624
Mountain	6	0.01863	1.9026	0.13558
Elevation	3	0.0662	6.7618	0.003
Latitude-Elevation	6	0.04215	4.3048	0.00729
Activity Density:				
Latitude	2	0.83114	58.2162	1.38E-08
Mountain	6	0.03526	2.4696	0.06396
Elevation	3	0.19722	13.8139	6.43E-05
Latitude-Elevation	6	0.21689	15.1914	3.60E-06

proportions of individuals represented by the families in our data. To examine how different families of spiders respond to changes in elevation, we plotted a bar chart showing the proportional differences in relative abundance of the dominant spider families.

RESULTS

We collected and identified a total of 1954 individual spiders representing 89 species, 57 genera, and 12 families (See Appendix). Activity density averaged 54.27 ± 6.82 (mean ± SE) individuals per site (elevation/mountain), while species richness averaged 11.36 ± 0.71 species per site (range: 4–23). The four most abundant species— (*Pardosa lapponica* (Thorell), 626 individuals; *P. uintana* Gertsch, 209 individuals; *Alopecosa aculeata* (Clerck), 161 individuals; and *P. glacialis* (Thorell), 100 individuals—all belonged to the family Lycosidae and represented 56% of the total number captured. The family with the most species was Linyphiidae, which accounted for 43 species collected in the region.

Species Richness

There were significant main effects of latitude and elevation on species richness; however, there was also a significant latitude-elevation interaction (Table 1). Average richness was highest in the Tombstone Range (13.67 ± 1.42 species per site) and lowest in the Ogilvie Mountains (9.50 ± 0.58 species per site). Species richness averaged 10.92 ± 1.29 species per site in the most northern part of the study area (Richardson Mountains). The significant interaction term indicated differential responses in species richness to elevation among the mountain ranges (Fig. 2a, Table 1).

The Richardson Range displayed a decrease in species richness with increasing elevation. The Ogilvie Range did not yield any clear changes in richness with elevation; species richness did not differ between the top of the mountains and the lowest elevation. Species richness in the Tombstone Range decreased along two of the three elevational transects; however, one of the mountain transects displayed
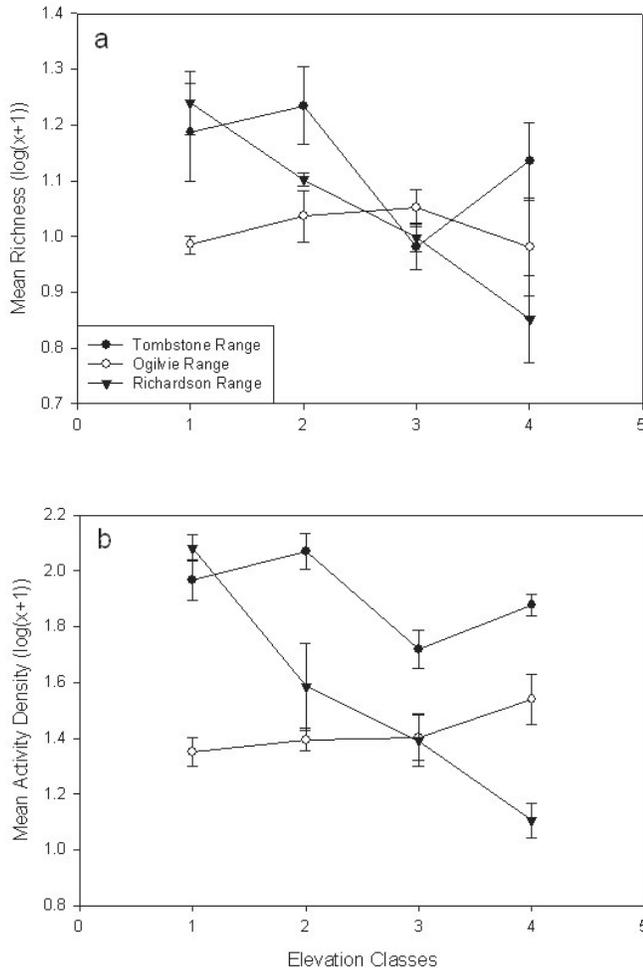
FIG. 2. Range-specific effects of elevation and its interactions with species richness and abundance (activity density) of ground-dwelling spider species in the Tombstone, Ogilvie, and Richardson ranges. Symbols indicate log-transformed means, and lines show standard error range.

highest species richness at the highest elevation, with little change among the lower elevations (Fig. 2a).

After examining a significant interaction between latitude and elevation with our species richness data, we further explored the variability within each mountain range with a one-way ANOVA. The Richardson Range was the only one to display a significant effect of elevation on species richness ($F_{3,8}$ = 10.1, p = 0.004) (Fig. 2a). There were non-significant effects of elevation on species richness in the Ogilvie Range ($F_{3,8}$ = 0.464, p = 0.715) and in the Tombstone Range ($F_{3,8}$ = 3.041, p = 0.093) (Fig. 2a).

Activity Density

Latitude and elevation had significant effects on activity density; however, as noted for the species richness data, there was also a significant latitude-elevation interaction (Table 1). The largest number of individuals per site (86.08 ± 9.37) was collected in the Tombstone range. The Ogilvie Range yielded an average of 26.50 ± 2.49 individuals per site, and the Richardson Range, 50.25 ± 13.66 individuals

per site. The mean activity densities from low to high elevation were 79.44 ± 16.10, 62.22 ± 16.29, 32.22 ± 5.66, and 41.22 ± 9.96 individuals per site.

Activity density displayed a similar pattern to species richness in yielding range-specific responses to elevation among mountain ranges (Fig. 2b). Again, the Richardson Range showed the only significant change in activity density with increasing elevation ($F_{3,8}$ = 17.62, p = 0.001; Fig. 2b). There were no significant changes in activity density across elevations within the Ogilvie Range ($F_{3,8}$ = 1.383, p = 0.316). In fact, the highest elevation in this range yielded the highest number of individuals (Fig. 2b). The Tombstone Range revealed statistically significant differences in activity density across elevations ($F_{3,8}$ = 5.73, p = 0.022), but there was no consistent pattern in response: activity density was lowest at the third-highest elevation and peaked at the lowest and highest elevations (Fig. 2b).

Analysis at species level revealed that activity density for many single species followed a pattern similar to that noted for all species in the regional data set (Fig. 3). Specifically, in the Tombstone Range some species (e.g., *P. uintana*) gradually decreased in abundance with increasing elevation, while others (e.g., *Alopecosa aculeata*) seemed to respond positively to the increase in elevation. Indicator species analysis supported these trends, as the Lycosidae *P. lapponica*, *P. moesta*, and *P. uintana* were all significant (p < 0.05) indicators of the two lower elevations in the Tombstone Range, while *A. aculeata* was a significant indicator of the two higher elevations in that range. In the Ogilvie Range, some species (e.g., *P. lapponica*) appeared to increase in abundance with increasing elevation, while others remained unchanged. In fact, *Micaria alpina* L. Koch (Gnaphosidae) was the only significant indicator in the Ogilvie Range and was an indicator of the two lower elevations. In the Richardson Range, most species responded negatively to the increase in elevation; however, a few species (e.g., *P. albomaculata* Emerton) responded positively to the gradient. *Pardosa albomaculata* and *Gnaphosa orites* Chamberlin (Gnaphosidae) were significant indicators of the two higher elevations in the Richardson Range, while *Agyneta jacksoni* Braendegaard (Linyphiidae) and *Xysticus britcheri* Gertsch (Thomisidae) significantly indicated the lowest elevation. *Pardosa sodalis* Holm was also abundantly collected at the lowest elevations in the Richardson Range, but was not included in the analysis because of its relatively low incidence.

Composition

Multi-response permutation procedures revealed significant effects of latitude and mountain, as well as an effect of elevation within each of the mountain ranges; there was no significant main effect of elevation (Table 2). These results are well supported by the final two-dimensional NMS ordination achieved (Fig. 4). The axes of the NMS ordination explained 84.9% of the variation in the species composition data (Axis 1: 20.4%; Axis 2: 64.5%). The ordination shows
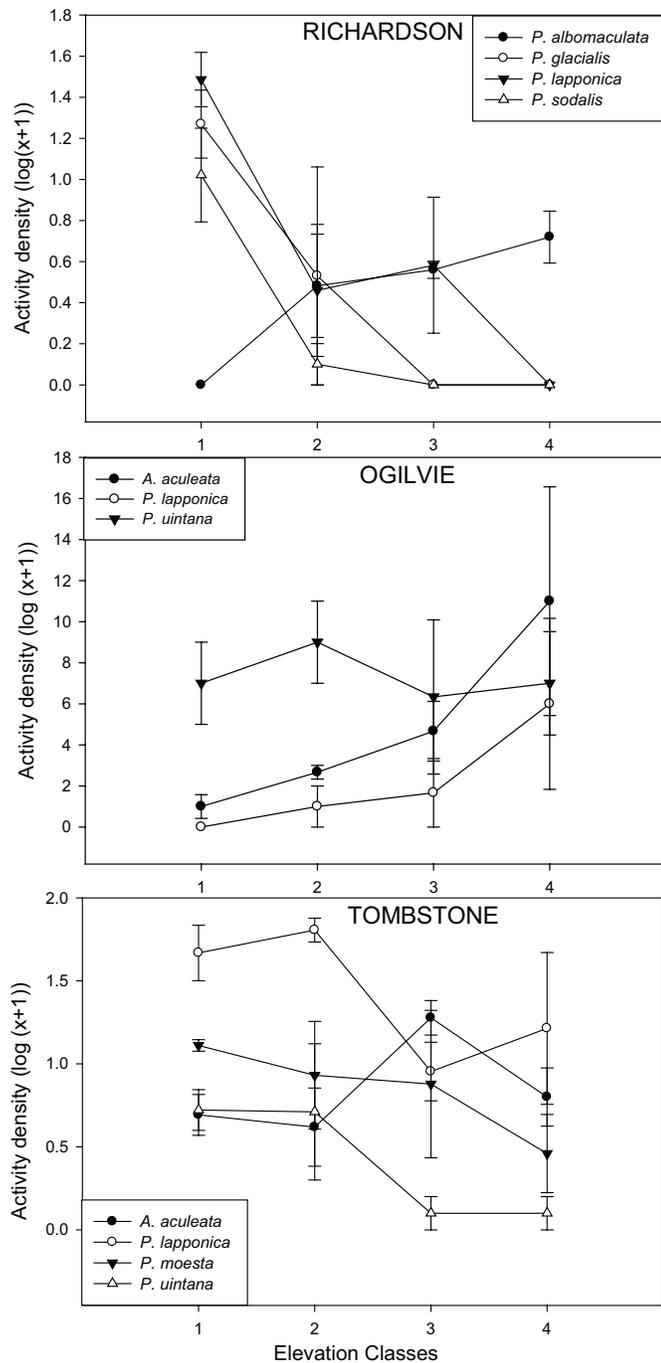
FIG. 3. Activity density in response to elevation of each of the most dominant species from the three mountain ranges studied in the northern Yukon Territory, Canada. All species belong to the family Lycosidae.

TABLE 2. Results of multi-response permutation procedures displaying main effects of latitude, elevation, and mountain, as well as effects of elevation within each mountain range, on ground-dwelling spider assemblages in the Yukon Territory, Canada.

Factor	A-Statistic	p-value
Latitude	0.36842145	0
Elevation	0.04694278	0.08902883
Mountain	0.39016795	0.00000043
Tombstone Elevation	0.36965812	0.00041355
Ogilvie Elevation	0.29059828	0.00555148
Richardson Elevation	0.3034188	0.02530073

The two lower-elevation sites yielded both a higher number of individuals and a higher number of families than the two higher-elevation sites. Other than the decrease in the proportion of Thomisidae and the lack of some other families represented at higher elevations, there were no proportional differences by family in the Tombstone Range. In the Ogilvie Range, the relative proportion of Linyphiidae decreases with increasing elevation, but there were no other obvious differences in the relative abundance of families represented. The Richardson Range displayed the largest change in activity density (also shown in Fig. 2b), but only showed a decrease in Thomisidae with increasing elevation. Overall, the Lycosidae were the most dominant family and typically accounted for 50% or more of individuals collected at each elevation, but did not change proportionally at different elevations in each range.

DISCUSSION

It is important to obtain data on species diversity patterns in the North because climate change is projected to have a disproportionate effect on the Arctic environment and Arctic biota (Callaghan et al., 2004). We used a spatially replicated regional scale design to assess the effects of elevation and latitude on spider species richness, abundance, and composition in northwestern Canada. We found significant differences in richness and abundance (activity density) among elevations and latitudes, and we detected significant interactions between latitude and elevation for both richness and abundance. Our ordination results showed that mountain range had a larger effect on assemblage structure than elevation or transect (i.e., within a mountain range) although there was evidence of elevational effects within latitude on species composition (i.e., Richardson Range, Fig. 4). The fact that spider species are typically adapted to a narrow set of abiotic factors (e.g., Moring and Stewart, 1994; DeVito et al., 2004) helps explain the changes in species composition at different latitudes and different elevations within each latitude. Local climate changes substantially with increasing elevation through adiabatic cooling, and changes across spatial gradients beget changes in habitat (Tilman and Pacala, 1993). These changes occur more abruptly across elevation than across latitude (Hodkinson, 2005). However, we found that latitude had a stronger main

a clear separation of sites by latitude and separation of the low and high elevations in the Richardson Range (Fig. 4). There was no overall clustering of high- or low-elevation sites across latitudes, which illustrates the lack of a significant main effect of elevation displayed by MRPP.

We detected very few changes in the proportion of individuals represented by each family at each elevation in each mountain range (Fig. 5). In the Tombstone Range, although there was no observable linear pattern, we did note a difference between the two low-level and the two high-level sites.
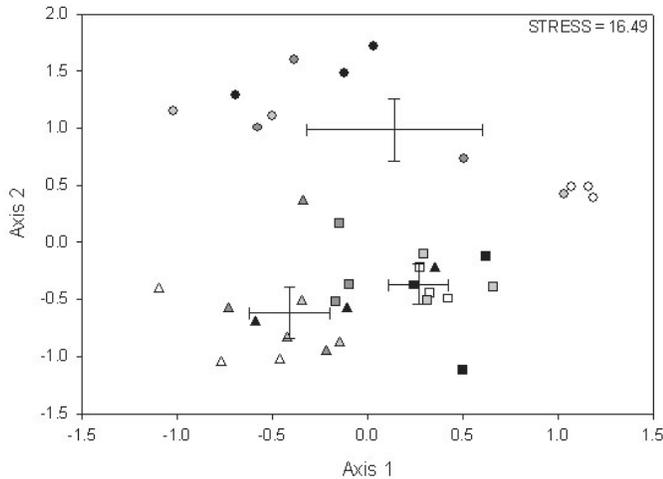
FIG. 4. Non-metric multidimensional scaling ordination of species data. Symbols indicate mountain range (latitude) (■ – Tombstone, ▲ – Ogilvie, ● – Richardson), and each point represents a site sampled. Shading indicates elevations 1 to 4 (increasing darkness indicates increasing elevation). The error bars represent 95% confidence limits for each of the three ranges sampled. We determined via Monte Carlo simulation (n = 50 runs) that the reduction in stress was significantly higher than expected by chance (*p* = 0.0196).
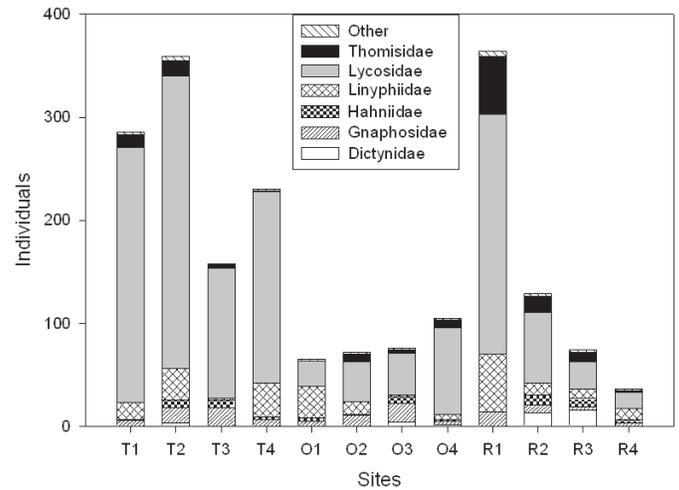
FIG. 5. Proportions of spider families collected from all mountain ranges in the northern Yukon Territory, Canada. Letter indicates the range (T = Tombstone, O = Ogilvie, R = Richardson) and number (1–4) indicates elevation from low to high. The vertical axis represents the number of individuals represented in each family. The grouping "other" includes the rare spider families collected: Araneidae, Clubionidae, Philodromidae, Salticidae, Tetragnathidae, and Titanoecidae.

effect on composition than did elevation. This finding probably reflects the differences in both current habitat and historical events (e.g., glaciations) among the three mountain ranges.

The Richardson Range, the northernmost mountains in this study, displayed the most substantial change in spider composition from low to high elevation, supported by the separation of lower- and higher-elevation sites on the NMS ordination. The significant differences observed in this mountain range may be due to changes in habitat associated with changes in elevation. For example, at a local spatial scale, Muff et al. (2009) showed significant differences in spider assemblages across a transition from alpine pasture to forest. Specifically, more species preferred an open-area habitat than a forested one, but the intermediate timberline areas yielded a positive ecotone effect. The authors pointed to the relative importance of habitat (i.e., density and structure of vegetation) than spatial variables in determining patterns of spider assemblages. Our mountain transects in the Richardson Range transitioned from tundra to talus slopes. The compositional differences in this range probably mirror changes in habitat associated with changes in elevation. Species richness and abundance also displayed the largest changes across elevations in the Richardson Range (the highest in latitude). This finding suggests a compound effect of latitude and elevation that may correspond to more extreme changes in habitat.

Spider composition in the Ogilvie Range did not exhibit strong changes with increasing elevation (Fig. 4). One explanation for the lack of change with elevation in this range is that, unlike the other ranges, it has relatively uniform (forested) habitat from low to high elevation sites. We can therefore use the Ogilvies as a control for a strict test of elevation

independent of habitat effects. We suggest that since no significant effects were detected in the Ogilvie Range, habitat is a more important determinant of spider community composition than elevation across this landscape. During a landscape scale study on a mountain in Quebec, Canada, Koponen (1987) found the highest number of species at the forest edge, supporting the positive influence of habitat transitions on spider assemblages across elevation. Trap captures were also the highest in open (mountain top) habitats and lowest at lower altitudes in forested sites (Koponen, 1987). Trap disturbance may be another explanation for the lack of change with elevation in the Ogilvie Range. The trap disturbance at one of its lower sites would have reduced the number of individuals and species caught and may help explain the pattern of no net change with elevation in this range.

At Tombstone, our most southern site, species richness, activity density, and composition yielded mixed results. The third-highest elevation had the lowest species richness and activity densities (Fig. 2), and composition did not change across elevation. We attribute these results to habitat effects: two of the three transects were similar in vegetation composition, but the third was on a steeper incline and transitioned from sparse boreal forest to talus slope with increasing elevation.

At smaller (i.e., local and landscape) spatial scales, spiders have been shown to respond strongly to habitat (Koponen, 1987; Rypstra et al., 1999; Muff et al., 2009), whereas at broad spatial scales spiders seem to follow spatial predictors (e.g., latitude) quite well (Finch et al., 2008; Whitehouse et al., 2009). However, at a regional scale, habitat complexity has been shown to be more important than spatial predictors (e.g., elevation) in determining spider

assemblages in at least one study (Jimenez-Valverde and Lobo, 2007). In our Arctic system, we show effects of elevation on spider assemblages at the landscape scale (within a range), and effects of elevation and latitude at a regional scale (all ranges). However, effects were weaker when habitat differences were weak (i.e., Ogilvie); similarly, when strong habitat differences occurred (i.e., Richardson), differences in spider assemblages across elevation were more pronounced. The results of our study may reflect spatially structured changes in habitat leading to changes in the spider assemblages.

Studies examining successional gradients have yielded much support for habitat complexity as being a key component to the development of local spider assemblages (Lowrie, 1948; Bultman et al., 1982; Buddle et al., 2000; Kaufmann, 2001). There exists a parallel between habitat successional gradient studies and our elevational study, as habitats change over spatial gradients in a manner analogous to their changing over successional gradients. For example, chronosequences of glacial retreat along an alpine transect have been used to indicate the importance of successional changes in vegetation for spider assemblages (Kaufmann, 2001; Gobbi et al., 2006). Kaufmann (2001) pointed to the importance of successional changes in soil and vegetation affecting patterns in spider fauna in an alpine glacial foreland. However, the role of biotic factors cannot be dismissed, as food availability (e.g., Halaj et al., 2000) and processes such as dispersal (e.g., Bonte et al., 2004) may also influence the dynamics and structuring of spider assemblages. For species that are adapted to high elevation, such as *Pardosa albomaculata*, the intervening lowlands likely serve as inhospitable habitat, like island habitats in an oceanic matrix. The patch-like distribution of mountains and unevenness of the ground potentially serve as effective barriers to passive dispersal of arthropods to suitable mountain habitat (Mani, 1968). In the face of climate change, these species could be greatly affected by upward elevational range expansions of lowland species now restricted by current climate conditions (Parmesan, 2006).

Aside from a decrease in Thomisidae representation with increasing elevation in two of the three mountain ranges, we detected no consistent changes in spider families along our mountain transects. Koponen (1987) found substantial differences in ground-dwelling spider composition among habitats across an altitudinal gradient in the boreal region of Quebec, Canada. Specifically, the relative proportions of Lycosidae were larger in open habitats, while the Linyphiidae were proportionately more common in forested habitats. Given this study and others investigating successional gradients (e.g., Bultman et al., 1982), the lack of change in proportions of families represented in our data is surprising. However, we did find that some species within the same family (Lycosidae) displayed very different responses to the elevational gradients. These responses contribute to the understanding of the differences in species composition and activity density detected when using the complete species data. For example, in the Tombstone Range, roughly

equal numbers of species responded positively and negatively to the increase in elevation.

Although others have found support for the effect of elevation on ground-dwelling spider assemblages (Otto and Svensson, 1982; Rushton and Eyre, 1992; Chatzaki et al., 2005), our results did not show a consistent effect of elevation on species richness, activity density, composition, or a combination, among mountain ranges (latitudes). It is possible that the elevational range sampled was not large enough to detect a consistent and significant pattern, or that patterns are range-dependent. Our design did allow us to sample many types of habitat effectively and assess the effects of spatial factors at a regional scale with good replication. These data also support previous suggestions that data collected from a single mountain transect may not be able to generalize to larger spatial scales (Sanders et al., 2003).

Climate change is projected to have strong effects on arthropod assemblages in the Arctic (Strathdee and Bale, 1998; Callaghan et al., 2004). Because these changes are predicted to occur rapidly, it will be increasingly important to understand patterns of species diversity in the North and obtain baseline data with which to compare future changes resulting from spatial shifts in climate and habitat. Our study quantifies arthropod assemblages in the Arctic and shows that spiders partition space, and probably habitat, along elevational gradients. The low numbers of individuals especially adapted to life at high latitude and high elevation (e.g., *P. albomaculata*) should be of particular concern for future studies of the effects of climate change on arthropod assemblages.

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APPENDIX: Species of spiders collected at four elevations in each of three mountain ranges in the northern Yukon Territory, Canada, between 14 June and 22 July 2006. The mountain ranges are Tombstone (64.309° N, 138.141° W), Ogilvie (65.158° N, 138.148° W), and Richardson (66.725° N, 136.114° W). An asterisk (*) indicates presence of a species.

Species	Tombstone				Ogilvie				Richardson			
	1060 m	1160 m	1260 m	1360 m	660 m	760 m	860 m	960 m	760 m	860 m	960 m	1060 m
Hypsosinga nr *groenlandica*								*				
Clubiona praematura Emerton		*							*			
Hackmania prominula (Tullgren)		*					*	*				
Lathys alberta Gertsch							*			*	*	
Gnaphosa borea Kulczynski	*	*	*	*					*	*	*	
Gnaphosa microps Holm		*		*			*					
Gnaphosa muscorum (L. Koch)			*			*				*		
Gnaphosa orites Chamberlin				*					*	*	*	*
Haplodrassus hiemalis (Emerton)									*	*		
Haplodrassus signifer (C.L. Koch)	*	*	*									
Micaria aenea Thorell						*						
Micaria alpina L. Koch	*	*	*	*	*	*	*					
Micaria constricta Emerton			*			*	*					
Micaria tripunctata Holm	*		*			*	*	*				
Zelotes sula Lowrie & Gertsch							*	*				
Hahnia cinerea Emerton		*		*			*					
Hahnia glacialis Sorensen	*	*	*		*	*	*	*		*	*	*
Agyneta jacksoni (Braendegaard)				*					*	*	*	*
Agyneta olivacea (Emerton)	*			*								
Agyneta simplex (Emerton)			*							*	*	*
Agyneta sp. 2	*											
Bathyphantes simillimus (L. Koch)	*	*			*				*	*		
Ceraticelus sp.					*	*	*		*			
Ceratinella nr *alaskae*	*											
Ceratinopsis labradorensis Emerton		*			*	*						
Cnephalocotes obscurus (Blackwall)				*								
Diplocentria bidentata (Emerton)	*			*				*				
Erigoninae sp. 1									*			
Gonatium crassipalpum Bryant	*	*		*	*	*			*			
Hilaira vexatrix (O.P.-Cambridge)									*			
Hilaria herniosa (Thorell)		*		*								
Hybauchenidium aquilonare (L. Koch)									*	*		*
Hybauchenidium gibbosum (Sorensen)		*			*							
Hypselistes semiflavus (L. Koch)	*	*		*					*			
Improphantes complicatus (Emerton)	*									*		
Incestophantes washingtoni (Zorsch)				*		*						
Islandiana cristatus Eskov					*							
Islandiana sp.	*											
Lepthyphantes alpinus (Emerton)					*	*			*			
Linyphiinae sp. 1	*	*			*	*			*		*	
Linyphiinae sp. 2									*			
Linyphiinae sp. 4											*	
Macrargus multesimus (O.P.-Cambridge)				*					*		*	
Mecynargus monticola (Holm)				*								
Mecynargus sphagnicola (Holm)				*								
Metopobactrus prominulus (O.P.-Cambridge)	*											
Pelecopsis mengei (Simon)				*	*							
Procerocymbium sibiricum Eskov									*			
Satilatlas gertschi Millidge									*	*	*	*
Scotinotylus alpinus (Banks)										*	*	
Silometopoides pampia (Chamberlin)		*		*								
Sisicottus montanus (Emerton)				*								
Sisis rotundus (Emerton)				*				*				
Sitticus ranieri (Peckham & Peckham)								*				
Tapinocyba bicarinata (Emerton)		*			*							
Tarsiphantes latithorax Strand												*
Tunagyna debilis (Banks)						*						
Walckenaeria castanea (Emerton)											*	
Walckenaeria karpinskii (O.P.-Cambridge)	*		*		*							
Zornella cultrigera (L. Koch)	*	*			*							
Alopecosa aculeata (Clerck)	*	*	*	*	*	*	*	*				
Alopecosa pictilis (Emerton)									*		*	
Arctosa alpigena (Doleschall)	*	*		*	*	*		*				
Pardosa albomaculata Emerton							*			*	*	*
Pardosa beringiana Dondale & Redner										*	*	
Pardosa furcifera (Thorell)	*			*				*				
Pardosa fuscula (Thorell)									*			

APPENDIX: Species of spiders collected at four elevations in each of three mountain ranges in the northern Yukon Territory, Canada, between 14 June and 22 July 2006. The mountain ranges are Tombstone (64.309° N, 138.141° W), Ogilvie (65.158° N, 138.148° W), and Richardson (66.725° N, 136.114° W). An asterisk (*) indicates presence of a species – continued:

Species	Tombstone				Ogilvie				Richardson			
	1060 m	1160 m	1260 m	1360 m	660 m	760 m	860 m	960 m	760 m	860 m	960 m	1060 m
Pardosa glacialis (Thorell)									*	*		
Pardosa hyperborea (Thorell)	*	*		*				*		*	*	
Pardosa lapponica (Thorell)	*	*	*	*		*	*	*	*	*	*	
Pardosa moesta Banks	*	*	*	*			*	*	*	*		*
Pardosa podhorskii (Kulczynski)									*	*		
Pardosa sodalis Holm									*	*		
Pardosa uintana Gertsch	*	*	*	*	*	*	*	*				
Pardosa xerampelina (Keyserling)										*		
Pirata bryantae Kurata		*										
Thanatus arcticus Thorell	*	*		*					*	*	*	
Chalcoscirtus alpicola Emerton					*	*	*			*		
Chalcoscirtus carbonarius Emerton										*		
Tetragnatha extensa (Linnaeus)												*
Ozyptila arctica Kulczynsk			*			*	*	*			*	
Xysticus britcheri Gertsch	*	*		*		*	*	*	*	*	*	
Xysticus emertoni Keyserling									*			
Xysticus labradorensis Keyserling										*	*	*
Xysticus luctuosus (Blackwall)	*	*						*				
Xysticus nr *alboniger*												*
Xysticus nr *durus*	*	*	*				*	*				
Xysticus obscurus Collett	*											
Titanoeca nivalis Simon							*					