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The Effect of Road Proximity on Arthropod Communities in Yukon, Canada

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ABSTRACT. Roads affect the ecosystems they traverse: road construction and maintenance constitute substantial disturbance, while roads and vehicles have hydrological, thermal, and other abiotic effects. Arthropod communities respond to these abiotic effects of roads, as well as to the indirect effects of vegetation changes. The Dempster Highway is a year-round gravel highway that travels 737 km through the Subarctic and Arctic ecosystems of Yukon and the Northwest Territories, Canada. In July 2016, in a Subarctic region of Yukon, we established nine transects spaced at 4–12 km intervals along a 56 km segment of the Dempster Highway and sampled arthropods at 1, 10, and 100 m from the highway on each transect. Our objective was to determine the effect of road proximity on the diversity, abundance, and composition of arthropod communities, with a special focus on the functionally and phylogenetically diverse group, Hymenoptera. We found that total arthropod abundance was lowest at the intermediate distance from the road, a pattern driven by high Diptera abundance close to the road and high Collembola abundance far from the road. We suggest that Diptera may be responding to increased moisture and plant biomass near the road, while Collembola may be responding to changes in soil characteristics. Hymenoptera abundance was greater close to the road than farther away, a pattern that may be driven by high Diptera parasitoid abundance near the road. Our results suggest that arthropods are good indicators of ecosystem function and that roads may have important effects on Subarctic ecosystem services (e.g., pollination, pest control). As infrastructural development continues in the Canadian North, it is of vital importance to anticipate and predict the effects of this development on the unique and diverse fauna of the Subarctic ecosystem.

Key words: roads; arthropods; entomology; northern; Subarctic; tundra; disturbance; insects; Hymenoptera; diversity; abundance

RÉSUMÉ. Les routes ont des effets sur les écosystèmes qu'elles traversent. La construction et l'entretien des routes sont une source importante de perturbation, et en soi, les routes et les véhicules ont des incidences de nature hydrologique et thermique ainsi que d'autres effets abiotiques. Les populations d'arthropodes réagissent aux effets abiotiques des routes de même qu'aux effets indirects des changements de la végétation. La route Dempster est une route de gravier utilisée à l'année. Elle s'étend sur 737 km dans les écosystèmes subarctiques et arctiques du Yukon et des Territoires du Nord-Ouest, au Canada. En juillet 2016, dans une région subarctique du Yukon, nous avons établi neuf transects à intervalles de quatre à 12 km sur un segment de 56 km de la route Dempster, ce qui nous a permis de prélever des échantillons d'arthropodes à des distances de un, dix et 100 m de la route sur chacun des transects. Notre objectif consistait à déterminer l'effet de la proximité de la route sur la diversité, l'abondance et la composition des populations d'arthropodes, en portant une attention particulière au groupe fonctionnellement et phylogénétiquement divers des hyménoptères. Cette étude nous a permis de constater que l'abondance d'arthropodes était à son niveau le plus bas à distance intermédiaire de la route, tendance attribuable à la forte abondance de diptères à proximité de la route et à la forte abondance de collemboles loin de la route. Nous suggérons que les diptères répondent peut-être au degré d'humidité plus élevé et à la biomasse végétale plus grande le long de la route, tandis que les collemboles répondent peut-être aux changements des caractéristiques du sol. L'abondance d'hyménoptères était plus grande à proximité de la route que loin de celle-ci, une tendance susceptible de découler de la forte abondance de diptères parasitoïdes près de la route. Nos résultats suggèrent que les arthropodes sont de bons indicateurs de la fonction de l'écosystème et que les routes peuvent avoir des effets importants sur les services écosystémiques subarctiques (c'est-à-dire la pollinisation, la lutte antiparasitaire). Au fur et à mesure que la mise en place d'infrastructures se poursuit dans le Nord canadien, il est d'une importance capitale de pouvoir prévoir et prédire les effets de ces infrastructures sur la faune unique et diverse de l'écosystème subarctique.

Mots clés : routes; arthropodes; entomologie; nord; subarctique; toundra; perturbation; insectes; hyménoptères; diversité; abondance

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INTRODUCTION

Roads are found across most of the world and are indisputably integral to modern society. The area that they cover is relatively small, but their density and length mean that their effect on natural communities can be substantial (Trombulak and Frissell, 2000; Coffin, 2007; Muñoz et al., 2015). The effects of a given road on the surrounding landscape will depend on many variables, including the climate, the road usage, and the material composition of the road. In this study, we investigate the effects of a remote, northern road on adjacent arthropod assemblages. For remote communities, roads serve as important supply lines for goods and services, as well as access routes for traditional foods and activities. These roads, however, have unintended effects on the surrounding landscape. Anthropogenic disturbances are already having noticeable effects on Subarctic ecosystems, and these effects are likely to become more severe as climate change worsens (Sanderson et al., 2012).

Northern roads are often gravel because gravel roads are easier to construct and maintain in areas underlain by permafrost (Gill et al., 2014). The Dalton Highway in Alaska, USA, and the Dempster Highway in Yukon, Canada, are two such highways. Dust from these roads strongly affects the soil characteristics up to 300 m away (Walker and Everett, 1987; Myers-Smith et al., 2006), by increasing soil pH and altering nutrient availability (Auerbach et al., 1997; Gill et al., 2014). The dust also decreases snow albedo, leading to an earlier melt date (Auerbach et al., 1997). The permafrost that underlies northern roads is vulnerable to thaw because of changes in the thermal regime induced by the road. Permafrost can thaw several meters deep below the road, causing embankment and subsidence (Gill et al., 2014), an effect observed along the Dempster Highway (Idrees et al., 2015; O'Neill and Burn, 2015). Roads can also affect hydrology by the construction of culverts, obstruction of water flow, and the removal of vegetation (Gill et al., 2014). Lastly, the construction and maintenance of gravel roads, including the extraction of fill and the use of heavy machinery, constitute a major disturbance to soil and vegetation (Kershaw and Kershaw, 1987).

These abiotic effects of roads on the hydrological, thermal, nutritional, and other physical properties of the surrounding area then affect the adjacent vegetation in turn. Shrubs, especially willow (*Salix* spp.; Kershaw and Kershaw, 1987) and alder (*Alnus* spp.; Gill et al., 2014), are found in higher density close to the Dempster Highway than farther away (Cameron and Lantz, 2016). Both monocots (Kershaw and Kershaw, 1987) and graminoids (Auerbach et al., 1997; Myers-Smith et al., 2006) have also been positively associated with the Dempster and Dalton Highways, while moss, lichen, and forbs have been negatively associated with them (Farmer, 1993; Forbes, 1995; Auerhach et al., 1997; Myers-Smith et al., 2006). Where subsidence due to permafrost thaw has occurred, the resulting saturation of the ground with water can lead to a shift in vegetation towards moisture tolerance (O'Neill and Burn, 2015). Finally, several non-native plants have been introduced, some deliberately, some inadvertently, along the Dempster and other Yukon highways (Bennett and Mulder, 2009). These invaders include species such as tansy (*Tanacetum vulgare*) and sweetclover (*Melilotis albans*) that are pollinated by many insect groups, including Diptera, Hymenoptera, and Lepidoptera (LeCain and Sheley, 2006; Bennett and Mulder, 2009).

In general, animal abundance and diversity tend to decrease near roads (Przybylski, 1979; Haskell, 2000; Carpio et al., 2009; Muñoz et al., 2015), largely because of increased mortality (roadkill) or behavioural effects (avoidance of road-adjacent habitat; Muñoz et al., 2015). Whether this general pattern holds true for a given plant or animal group will depend on the characteristics of that group and of the road (Melis et al., 2010; Knapp et al., 2013). Arthropod populations (insects, spiders, and their relatives) are affected directly by the abiotic effects of roads, as well as indirectly, through road-associated changes in vegetation. For example, the species richness and abundance of soil invertebrates is lower immediately adjacent to roads, because the soil is underdeveloped and compacted, with less organic matter (Haskell, 2000). Overall, however, arthropods near northern roads may be positively affected by road proximity. Habitat generalists, including many arthropods, may benefit from roads because of their ability to colonize disturbed habitat, whereas habitat specialists are often disadvantaged by the altered habitats, unless they specialize in open and disturbed habitats themselves (Koivula, 2005; Knapp et al., 2013). In northern Canada, the warmth generated by road surfaces may provide a hospitable environment to organisms such as arthropods with low tolerance to cold. Temperature tends to be higher within the first 10 m of a road's edge, so in cold climates, ectotherms may be attracted to the warmth of the road (Gilbert and Raworth, 1996; Delgado et al., 2007).

Beta diversity relates to the amount of variation in communities across a landscape. It is as fundamental a measure of diversity as alpha diversity, and yet the effect of roads on beta diversity is much less known (Przybylski, 1979; Haskell, 2000; Muñoz et al., 2015). The homogenization of the habitats bordering roads may reduce the beta diversity of the communities in those habitats (Forbes, 1995; Tscharntke and Brandl, 2004).

In July of 2016, we sampled arthropod taxa at 1, 10, and 100 m from the Dempster Highway in Yukon, Canada. The Yukon arthropod assemblages are very diverse, with many species endemic to the territory (Danks et al., 1997). Arthropods carry out important functions and services in the Subarctic ecosystem, in their roles as decomposers, parasites, and pollinators, and as a food source for vertebrates. The objective of this research was to investigate how the Dempster Highway affects the adjacent Subarctic arthropod community, in terms of abundance and diversity (at a coarse scale, for both alpha and beta diversity). We focus particularly on the Order Hymenoptera (wasps, ants, bees, and their relatives) because of their abundance in the region, as well as their high functional and phylogenetic diversity. Overall, we hypothesized that total arthropod abundance and diversity, as well as Hymenoptera abundance and diversity, would increase with road proximity because of low road traffic mortality and conditions that could be beneficial to generalists (Koivula, 2005), pollinators (Kevan, 1972; Debinski and Holt, 2000), organisms with aquatic lifecycle stages (O'Neill and Burn, 2015), and ectotherms (Gilbert and Raworth, 1996; Delgado et al., 2007). We also hypothesized that community composition would change with road proximity, because taxa would differ in their response to the road.

METHODS

The Dempster Highway

The Dempster Highway is a gravel road that travels 737 km through Yukon and the Northwest Territories. This highway began its construction in 1959 and by 1979 had reached its northern limit in Inuvik (Environment Yukon, 2014). It is of vital importance for the delivery of goods and services to several communities. Twice yearly, large trucks are used to apply additional gravel to the highway to fill holes created by weather and vehicles (Department of Highways and Public Works Yukon, pers. comm. 2017). Overall, our study spanned a 56 km segment of the Dempster Highway, beginning at the northern boundary of Tombstone Territorial Park (64˚N) and continuing northward (Fig. 1). This segment of the highway passed through a typical Subarctic landscape, with some areas covered by tundra, and others by small trees and tall shrubs, typically spruce and poplar (Table 1). Average temperatures in Dawson City, the closest station to our study area (64.0609˚ N, 139.1267˚ W), were 16.4˚C in July 2016, with a total of 54.7 mm of precipitation, and −15.8˚C in January 2015, with a total of 17.9 mm of precipitation (Environment Canada, 2017).

Data Collection

To obtain samples of the arthropod communities at different distances from the Dempster Highway, we set up 27 pan traps (yellow, 20 cm in diameter) at 1 m, 10 m, and 100 m from the road. These triplets of pan traps formed nine transects adjacent to the road at intervals of 4 to 12 km (Fig. 1). All transects were on the western side of the highway. We chose yellow pans because of their proven effectiveness at sampling arthropods, especially in the North (Blades and Marshall, 1994; Gollan et al., 2011; Ernst et al., 2016). Pan traps are known to attract certain taxa more than others (Ernst et al. 2016): for example, they are more efficient at capturing flying insects than many ground-dwelling groups like spiders (Ernst et al., 2016),

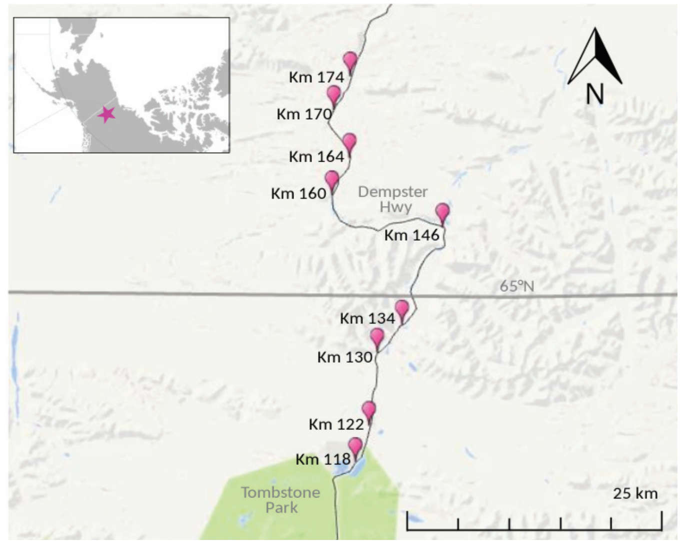

FIG. 1. The locations of the nine pan-trap transects set out adjacent to the Dempster Highway on 19 and 25 July 2016 in Yukon, Canada. At each transect, the pan traps were set out on the western side of the road, at 1 m, 10 m, and 100 m from the road's edge, for a total of 27 samples.

but this is likely not a major issue in our study since we are focusing on the patterns of change within groups and not the absolute abundances. We installed the pans flush with the ground and filled them with trap liquid to a depth of approximately 2 cm. The liquid consisted of equal parts water and RV plumber's antifreeze, with a small amount of dish detergent (Thomas, 2008).

We carried out two rounds of sampling: the five more southern transects were sampled on 19 July 2016, and the four more northern transects on 25 July 2016 (trap set dates; Table 1). For the first round of sampling, we allowed the pan traps to collect arthropods for 48 h. For the second round, because of logistical issues, we allowed the pan traps to collect arthropods for 72 h. We preserved the arthropods in 70% ethanol.

We identified all arthropods to the level of order. We further identified the Hymenoptera to subfamily or family (whichever was the lowest level identified by Goulet and Huber, 1993). We categorized Hymenoptera families or subfamilies into functional groups (online Appendix 1: Table S1). Some families or subfamilies were categorized as "diverse parasitoid" because the host order differed between taxa within the family or subfamily. Hymenoptera voucher specimens were deposited in the Lyman Museum (Sainte-Anne-de-Bellevue, Quebec, Canada).

Statistical Analyses

We carried out all statistical tests using the R software environment (R Development Core Team, 2016).

We tested for differences in total arthropod abundance with road proximity, treating road proximity as a factor variable. First, we applied a Poisson-family generalized linear model (GLM), with abundance as the response variable and road proximity as the only explanatory

TABLE 1. Characteristics of the nine transects, with pan traps set out at 1 m, 10 m, and 100 m from the edge of the Dempster Highway, for a total of 27 samples. Each transect is named for the Dempster kilometre marker next to which it was placed. Also shown are the geographic coordinates and elevation of the 1 m sample for each transect. (None of our sites had major changes in elevation within the 100 m transect.) The traps were set on two dates (19 and 25 July 2016) in three habitat types: tundra, forest or tall shrub, and mixed (mix of tundra and forest or tall shrub).

Transect (Dempster km)	Trap set date	Habitat type	Latitude	Longitude	Elevation (m asl)
118	July 19	Tundra	64.844	−138.324	984
122	July 19	Tundra	64.885	−138.285	949
130	July 19	Mixed	64.953	−138.270	944
134	July 19	Forest or tall shrub	64.979	−138.218	896
146	July 19	Mixed	65.067	−138.131	853
160	July 25	Forest or tall shrub	65.096	−138.364	859
164	July 25	Mixed	65.129	−138.326	813
170	July 25	Mixed	65.174	−138.360	754
174	July 25	Mixed	65.206	−138.326	711

variable. We then tested the model for overdispersion (function dispersiontest from the package AER; Kleiber and Zeileis, 2008). In the case of overdispersion, we applied a negative binomial generalized linear model instead of a Poisson (function glm.nb from the package MASS; Venables and Ripley, 2002). Next, we applied an ANOVA to the Poisson or negative binomial GLM to detect whether significant differences in abundance were present between the three distances. Finally, if the ANOVA detected a significant difference ($\alpha = 0.05$), we performed a Tukey honest significant difference test (function glht from the package multcomp; Hothorn et al., 2008).

To test for effects of road proximity on several arthropod taxa, we followed the same procedure as above. We tested the effect of road proximity first on the five most abundant arthropod orders, then on the five most abundant Hymenoptera families or subfamilies, and finally on the five most abundant Hymenoptera functional groups (excluding "diverse parasitoid").

We then tested for changes in diversity with road proximity by using three measures of diversity: richness (function specnumber from the package vegan; Oksanen et al., 2016), Shannon diversity (function diversity from the package vegan), and local contribution to beta diversity (LCBD; function beta.div from the package adespatial; Dray et al., 2017). LCBD is the contribution of each sample (pan trap) to the total variance of the full community (all 27 pan traps). It represents the uniqueness of each sample in terms of species composition. To calculate the LCBD, we first $\log(x + 1)$ transformed the community matrix, then applied the LCBD function using Euclidian distance.

In all cases, the distributions of the biodiversity measures were strongly non-normal, and so we used Kruskal-Wallis rank sum tests. First, we tested two models: the effect of road proximity on Shannon diversity and on LCBD of arthropod orders. Next, we tested three additional models: effect of road proximity on the family or subfamily richness, Shannon diversity, and LCBD of Hymenoptera families or subfamilies. We then tested three final models: effect of road proximity on functional richness, Shannon diversity, and LCBD of Hymenoptera functional groups.

Last, we tested the effect of road proximity on arthropod and Hymenoptera community composition. We computed a distance matrix of the arthropod orders using the Bray dissimilarity index (function vegdist from the package vegan). We then applied a PERMANOVA to the distance matrix, with road proximity as the only explanatory variable. PERMANOVA tests for differences in the centroids of groups within the space defined by the dissimilarity index, which we interpret as a test of difference in community composition between groups. We followed the same procedure for the Hymenoptera families and subfamilies and the Hymenoptera functional groups (excluding "diverse parasitoid").

RESULTS

Specimens

We collected 10 081 arthropods from 11 orders (Fig. 2). The majority of these were Diptera (43.9%) and Collembola (42.9%). Hymenoptera (4.7%), Hemiptera (2.9%), and Araneae (2.9%) were the next most abundant, followed by Acarina (1.3%) and Coleoptera (1.0%). Lepidoptera (20), unidentified larvae (17), Plecoptera (7), Thysanoptera (7), and Orthoptera (1), together made up less than 1% of the sample (online Appendix 1: Table S2).

We identified 471 Hymenoptera belonging to 21 families and at least 34 subfamilies (Fig. 2). The most abundant of these taxonomic groups was Diapriidae (19.1%), followed by Platygastridae (16.3%), Mymaridae (8.7%), Ceraphronidae (7.2%), Phygadeuontinae (Ichneumonidae) (6.6%), and Myrmicinae (Formicidae) (5.9%). All other groups each made up less than 5% of the sampled Hymenoptera (online Appendix 1: Table S3).

We identified 10 functional groups amongst the Hymenoptera. Two subfamilies (Alysiinae and Vespinae) each belonged to two functional groups, while all other families or subfamilies belonged to only one each. The most abundant of these functional groups was Diptera parasitoids (46.3% of Hymenoptera), followed by diverse parasitoids

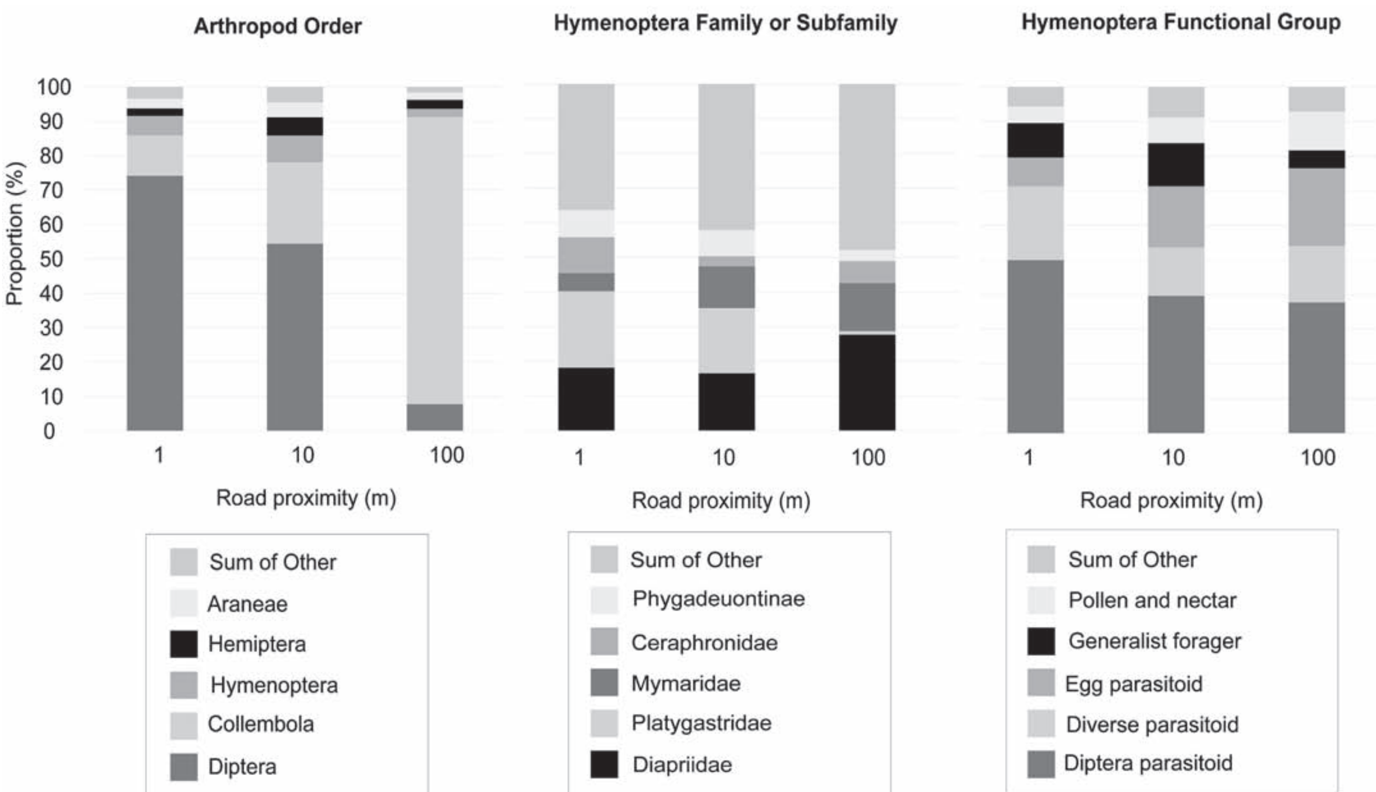

FIG. 2. Relative proportions of arthropod orders (left panel), Hymenoptera families or subfamilies (middle panel), and Hymenoptera functional groups (right panel) collected from pan traps at three distances (1 m, 10 m, and 100 m) from the Dempster Highway, Yukon, Canada, in July 2016. The groups are stacked in each bar in the same order as in the legend below the bar chart. Only the five most abundant groups are shown specifically; the "Sum of Other" category encompasses all other groups sampled.

(17.2%), egg parasitoids (13.8%), generalist foragers (9.5%), and pollinators (6.8%). All other groups together made up less than 5% of the sampled Hymenoptera.

Abundance and Road Proximity

Significant differences in total arthropod abundance were related to road proximity: total arthropod abundance at 10 m was significantly lower than at 1 m and 100 m (Fig. 3; GLM (poisson) ANOVA; χ^2 (2, n = 27) = 1275.9; $p < 0.0001$).

Of the five most abundant arthropod orders, the three most abundant (Diptera, Collembola, and Hymenoptera) differed significantly in abundance with road proximity. Diptera abundance was significantly greater at 1 m than at 100 m (Fig. 3; GLM (neg. binom.) ANOVA; $\chi^2 = 16.1$; $p = 0.0003$). Collembola abundance was greater at 100 m than at 1 m or 10 m (Fig. 3; GLM (Poisson) ANOVA; $\chi^2 = 2757.3$; $p < 0.0001$). Additionally, Collembola abundance was slightly, yet significantly greater at 1 m than at 10 m. Hymenoptera abundance was greater at 1 m than at 100 m (Fig. 4; GLM (neg. binom.) ANOVA; $\chi^2 = 6.5617$; $p = 0.0376$). The two next most abundant orders did not change in abundance with road proximity. These were Hemiptera (GLM (neg. binom.) ANOVA; $\chi^2 = 0.0514$; $p = 0.9746$) and Araneae (GLM (neg. binom.) ANOVA; $\chi^2 = 0.4546$; $p = 0.7967$).

Of the five most abundant Hymenoptera families or subfamilies, three differed significantly in abundance with road proximity. Platygastridae abundance was significantly less at 100 m than at 1 m or 10 m (GLM (neg. binom.) ANOVA; $\chi^2 = 17.863$; $p = 0.00013$). Ceraphronidae abundance was significantly greater at 1 m than at 100 m (GLM (neg. binom.) ANOVA; $\chi^2 = 10.189$; $p = 0.0061$). Phygadeuontinae abundance was significantly greater at 1 m than at 100 m (GLM (Poisson) ANOVA; $\chi^2 = 11.903$; $p = 0.0026$). The remaining two families, Diapriidae (GLM (neg. binom.) ANOVA; $\chi^2 = 1.0714$; $p = 0.5853$) and Mymaridae (GLM (Poisson) ANOVA; $\chi^2 = 0.6226$; $p = 0.7325$), did not change significantly in abundance with road proximity.

For the most abundant Hymenoptera functional group, Diptera parasitoids, abundance was significantly greater at 1 m than at 100 m (Fig. 4; GLM (neg. binom.) ANOVA; $\chi^2 = 6.892$; $p = 0.0318$). Abundance did not change significantly with road proximity for the three next most abundant functional groups, egg parasitoids (GLM (Poisson) ANOVA; $\chi^2 = 0.59039$; $p = 0.7444$), generalist foragers (GLM (neg. binom.) ANOVA; $\chi^2 = 1.9787$; $p = 0.3718$), and pollinators (GLM (Poisson) ANOVA; $\chi^2 = 0.06318$; $p = 0.9689$). For the fifth most abundant functional group, Lepidoptera parasitoids, the ANOVA detected a significant difference in abundance with road proximity (GLM (Poisson) ANOVA; $\chi^2 = 7.1328$;

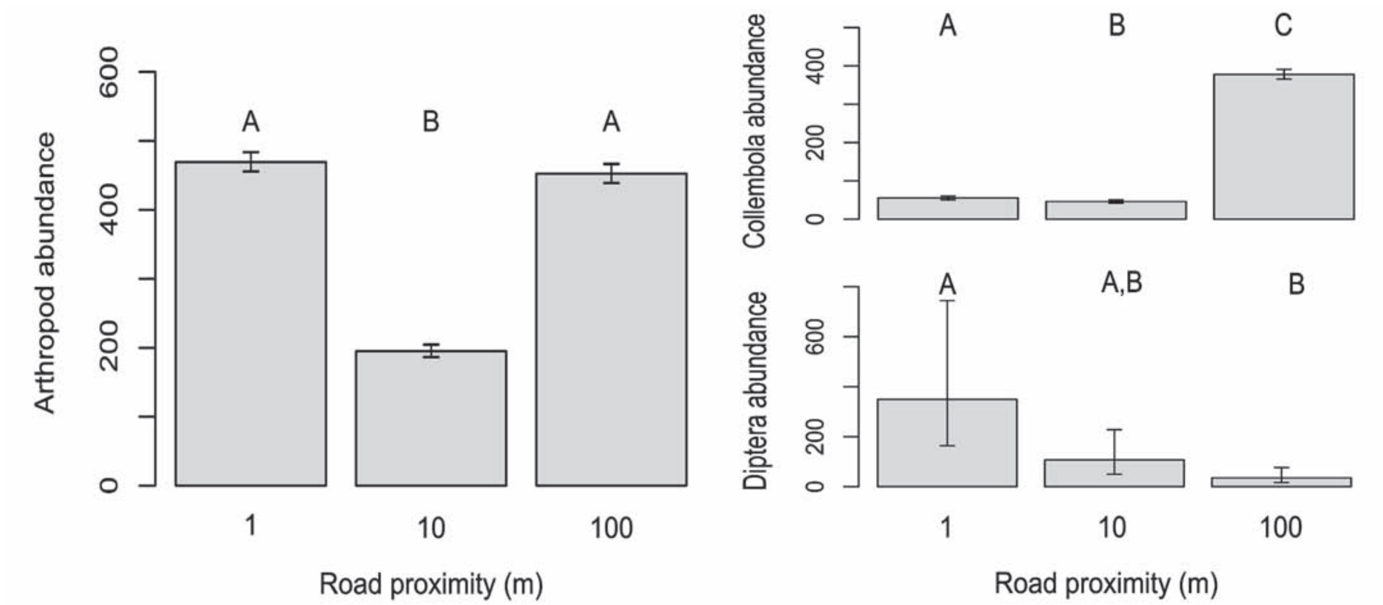

FIG. 3. The abundance of arthropods (left panel), Diptera (top right panel), and Collembola (bottom right panel) collected by pan traps at three distances (1 m, 10 m, and 100 m) from the Dempster Highway in Yukon, Canada, in July 2016. Bars that do not share the same letter (A, B, or C) are significantly different ($\alpha = 0.05$), while the error bars indicate 95% confidence intervals taken from the corresponding models.

p = 0.02826). However, the Tukey HSD, which is a more conservative test, did not detect any difference in Lepidoptera parasitoid abundance between road distances.

Diversity and Road Proximity

No measure of diversity differed significantly with road proximity. Shannon diversity of the arthropod orders did not change with road proximity (Kruskal-Wallis; $\chi^2 = 2.5079$; $p = 0.2854$), nor did LCBD of the arthropod order change with road proximity (Kruskal-Wallis; $\chi^2 = 0.067019$; $p = 0.967$). Hymenoptera family or subfamily richness did not change with road proximity (Kruskal-Wallis; $\chi^2 = 3.9959$; $p = 0.1356$), nor did the Shannon diversity (Kruskal-Wallis; $\chi^2 = 3.9452$; $p = 0.1391$) or the LCBD (Kruskal-Wallis; $\chi^2 = 3.6226$; $p = 0.1634$) of the Hymenoptera families or subfamilies. Finally, Hymenoptera functional richness did not change with road proximity (Kruskall-Wallis; $\chi^2 = 2.455$; $p = 0.3254$), nor did the Shannon diversity (Kruskal-Wallis; $\chi^2 = 0.00353$; $p = 0.9982$) or the LCBD (Kruskal-Wallis; $\chi^2 = 3.4392$; $p = 0.1791$) of the Hymenoptera functional groups.

Community Composition and Road Proximity

The arthropod order community composition did not differ significantly with road proximity (PERMANOVA; $F_{2,26} = 1.0677$; $p = 0.361$; $R^2 = 0.0817$). However, the Hymenoptera family or subfamily community composition did differ significantly with road proximity (PERMANOVA; $F_{2,26} = 1.0802$; $p = 0.014$; $R^2 = 0.12954$). The Hymenoptera functional composition did not differ significantly with road proximity (PERMANOVA; $F_{2,26} = 1.1148$; $p = 0.35$; $R^2 = 0.08837$).

DISCUSSION

The Dempster Highway strongly influenced the arthropod communities collected next to the road. Road proximity affected abundance for several taxonomic and functional groups, and the nature of the effect differed between groups. Some groups, such as Diptera and Hymenoptera, were more abundant close to the road than farther away, while the abundant order, Collembola, was less abundant next to the road. As a result, the total abundance of arthropods and Hymenoptera, as well as the community composition of Hymenoptera, differed strongly with road proximity. Given the known impact of the Dempster Highway on abiotic and vegetation characteristics, as well as the characteristics of the affected arthropod groups, we can speculate about the mechanistic relationship between the highway and each group's abundance. Further study is required to test these speculations.

Abundance

Arthropod abundance displayed a non-linear relationship with road proximity: mean total abundance at 10 m was less than half of that at 1 m or 100 m (Fig. 3). Other authors have observed a decrease in abundance of arthropod groups with road proximity (Haskell, 2000; Muñoz et al., 2015), largely attributed to roadkill mortality and avoidance behaviour (Muñoz et al., 2015). We predicted that total arthropod abundance would increase with road proximity because road traffic, and therefore vehicle-caused mortality, are minimal for the Dempster Highway and because the area bordering the road would present an ideal habitat for many groups, including generalists, pollinators, organisms with aquatic lifecycle stages, and ectotherms.

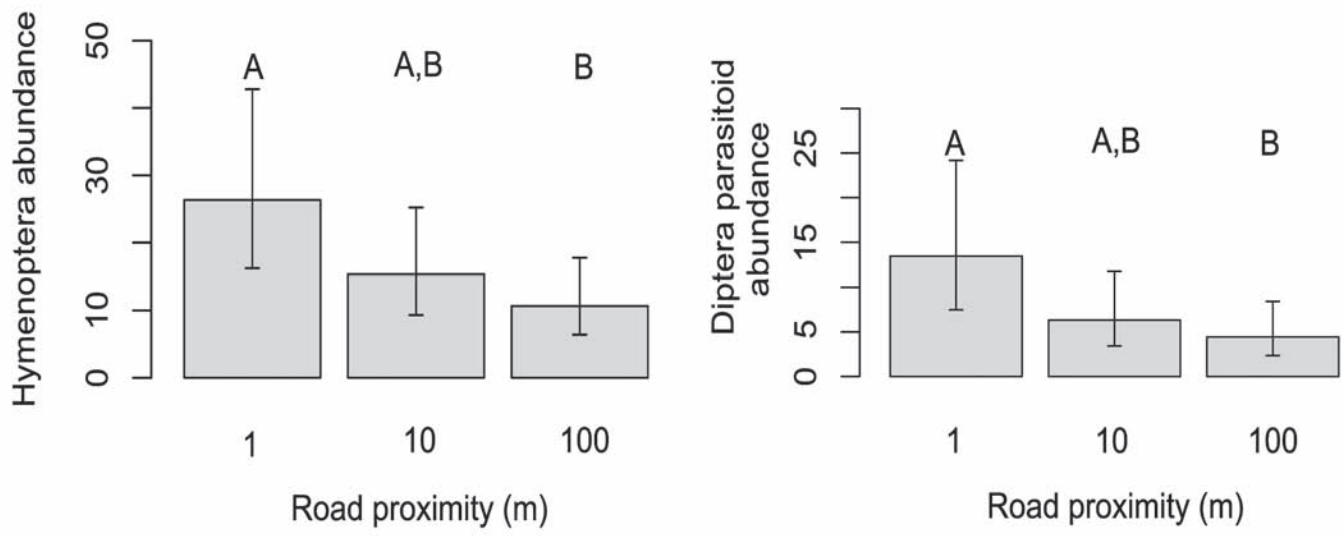

FIG. 4. The abundance of Hymenoptera (left panel) and Diptera parasitoids (right panel) collected by pan traps at three distances (1 m, 10 m, and 100 m) from the Dempster Highway, Yukon, Canada, in July 2016. Bars that do not share the same letter (A or B) are significantly different ($\alpha = 0.05$), while the error bars indicate 95% confidence intervals taken from the corresponding models.

Our findings suggest that elements of these two alternative hypotheses (negative versus positive relationship of arthropod abundance with road proximity) are both correct. The abundances of some arthropod groups are positively affected by the presence of the Dempster Highway, while the abundances of other arthropod groups are negatively affected (Fig. 3). The net effect is a non-monotonic relationship between total arthropod abundance and road proximity, in which abundance is greatest both closest to and farthest from the road. In other words, our results suggest that the road decreases arthropod abundance, but the decrease is displaced several meters from the road edge. This U-shaped relationship between abundance and distance from the Dempster Highway was driven largely by two groups: Diptera and Collembola. Diptera were more abundant close to the road than farther away, while Collembola were more abundant far from the road than close to it (Fig. 3). Together, these orders made up 86.8% of the total abundance, so changes in their abundance account for changes in total arthropod abundance.

Collembola abundance was much less at 1 m and 10 m than at 100 m (Fig. 3). Collembola are small, soil-dwelling arthropods, closely related to insects. Their negative relationship with road proximity is likely the result of reduced soil suitability near the highway. Road dust induces changes in adjacent soil, including increased soil pH and higher albedo (Auerbach et al., 1997; Gill et al., 2014). Dust from the road and the addition of new inorganic sediment twice a year for road maintenance makes it difficult for mosses and lichens to establish themselves and makes the soil bordering the road underdeveloped and compacted (Farmer, 1993; Forbes, 1995; Department of Highways and Public Works Yukon, pers. comm. 2017). Subarctic collembolans have strong associations with mosses and lichens and are sensitive to changes in moisture and climate (Babenko, 2000). Our findings strongly suggest that the altered soil and vegetation adjacent to the Dempster Highway render the area unsuitable for Collembola.

In contrast with Collembola, Diptera were most abundant at 1 m from the road, a pattern that might be associated with changes in hydrology close to the Dempster Highway (Gill et al., 2014; Idrees et al., 2015; O'Neill and Burn, 2015). Many Diptera are aquatic at some stage of their lifecycle and therefore require moist environments or environments close to open water. If permafrost thaw, which is a growing problem in northern regions (Schuur et al., 2015), has led to subsidence and increased soil moisture adjacent to the studied stretch of highway, these changes could account for the increased Diptera abundance.

The relationship of Hymenoptera abundance to road proximity mirrors closely that of Diptera. Hymenoptera were, on average, approximately twice as abundant at 1 m from the road as at 100 m (Fig. 4). In another study, Luce and Crow (2001) found no effect of roads on Hymenoptera communities, but they sampled only the first 15 m from the road's edge. This distance may have been insufficient and could explain why that study did not detect any spatial patterns, while our study did. This comparison emphasizes the importance of scale when observing ecological phenomena.

Three of the five most abundant Hymenoptera families or subfamilies changed in abundance with road proximity: Platygastridae, Ceraphronidae, and Phygadeuontinae were all more abundant at 1 m than at 100 m from the Dempster Highway. Platygastridae are parasitoids of gall midges (Diptera), and Ceraphronidae and Phygadeuontinae parasitize several groups, including Diptera. Indeed, the only functional group to change in abundance with road proximity was the Diptera parasitoid group (Fig. 4). Nearly half (46.3%) of the sampled Hymenoptera belonged to this group. Diptera parasitoids were, on average, approximately twice as abundant at 1 m from the road as they were at

100 m. Given that we would expect to see more Diptera parasitoids where there are more Diptera to parasitize, the positive relationship observed between Diptera abundance and road proximity accounts well for the positive relationship between Hymenoptera abundance and road proximity. In other words, the positive relationship between Dempster Highway proximity and Hymenoptera is indirect and mediated by the parasitoid-host relationship between Hymenoptera and Diptera.

The relationship between Diptera and Hymenoptera abundance and road proximity may also be due to direct physical effects of the road or to indirect effects of the road via changes in vegetation. Many Diptera are herbivorous, pollinators, gall-forming, or otherwise have a direct relationship with plants. Many Hymenoptera are pollinators or parasitoids of herbivorous insects. Therefore, the indirect effects of the Dempster Highway, via the highway's effects on vegetation (Kershaw and Kershaw, 1987; Farmer, 1993; Forbes, 1995; Auerbach et al., 1997; Myers-Smith et al., 2006; Bennett and Mulder, 2009; Gill et al., 2014; O'Neill and Burn, 2015), may also play an important role in the observed relationship between Diptera and Hymenoptera abundance and road proximity. Finally, the warmer conditions along the road could also be partly responsible for the higher abundances observed there (Gilbert and Raworth, 1996; Delgado et al., 2007).

Community Composition and Diversity

Arthropod taxa differed in their response to road proximity. The two most abundant orders (Diptera and Collembola) contrasted strongly: Diptera was the dominant order close to the road, but far from the road it was Collembola. Despite the different response of these important orders, proximity to the Dempster Highway did not significantly affect the overall arthropod community composition. This fact suggests that the abundance of most arthropod orders did not change with road proximity. Within the order Hymenoptera, community composition changed with road proximity. Although three of the most abundant families or subfamilies (Platygastridae, Ceraphronidae, and Phygadeuontinae) were all more abundant at 1 m than at 100 m from the road, not all families or subfamilies responded in the same way. We observed no universal effect of the Dempster Highway on arthropod taxa: some groups increased, others decreased, and yet others displayed a non-linear response or no response. As a result, the dominant taxa and community composition differed with road proximity.

We did not observe any relationship between arthropod diversity (at the ordinal level) and road proximity, measured as Shannon diversity and beta diversity. If the number of taxa that thrive near the road is approximately equal to the number that thrive far from the road, we would not observe a relationship between diversity and road proximity. Alternatively, if a relationship were present, our identifications to the ordinal level may have been too coarse to detect changes in diversity. Within the order Hymenoptera and at the family or subfamily scale, we did not find a relationship between diversity and road proximity either. We had assumed that beta diversity would be low close to the road because all near-road habitats would be similar. However, our results suggest that near-road habitats are not as homogenous as we had presumed.

CONCLUSIONS

Roads are one of humanity's oldest inventions, having existed since at least 2000 BCE (depending how "road" is defined; Lay and Vance, 1992). They provide a necessary service, allowing the flow of people and resources between communities. In the case of the Dempster Highway, the road connects remote northern communities to southern Yukon, as well as allowing access to recreation and traditional food harvesting in the area surrounding the road. While the utility of roads cannot be denied, this study and others demonstrate that roads are not without consequences for the surrounding ecosystem. The Dempster Highway alters the nearby habitat, fostering an ecological community that differs from what would normally be present, with implied consequences for ecosystem services and functions. More Diptera close to the road, for example, could mean more biting insects, or more Hymenoptera could mean more pollination of harvested plants. Furthermore, changes in the arthropod community affect all members of the broader ecosystem, from insectivorous vertebrates to flowering plants. Further research is needed to understand the extent to which ecosystem services and functions are altered in these disturbed arthropod communities. As infrastructural and industrial development continues in the North, and as the climate continues to warm, it is vital that we develop the capacity to anticipate the impact of these projects.

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APPENDIX 1

The following tables are available in a supplementary file to the online version of this article at:
http://arctic.journalhosting.ucalgary.ca/arctic/index.php/arctic/rt/suppFiles/4702/0

TABLE S1. The functional group designation of each Hymenoptera family or subfamily present in our pan trap samples.

TABLE S2. The coordinates of pan traps set out at 1 m, 10 m, and 100 m from the road along a 56 km segment of the Dempster Highway (Yukon, Canada) in July 2016. Each row represents a single pan trap and shows the abundance of individuals in each arthropod order.

TABLE S3. The coordinates of pan traps set out at 1 m, 10 m, and 100 m from the road along a 56 km segment of the Dempster Highway (Yukon, Canada) in July 2016. Each row represents a single pan trap and shows the abundance of individuals in each Hymenoptera family or subfamily.

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