

## Article

# Boreal Sand Hills are Areas of High Diversity for Boreal Ants (Hymenoptera: Formicidae)

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Received: 11 December 2018; Accepted: 31 January 2019; Published: 8 February 2019



**Abstract:** The boreal forest in Canada comprises a wide variety of ecosystems, including stabilized (overgrown) sand dunes, often referred to as sand hills. Globally, sandy soils are known for supporting a high diversity of invertebrates, including ants, but little is known for boreal systems. We used pitfall trap sampling in sand hill, aspen parkland and peatland ecosystems to compare their ant diversity and test the prediction that areas with sandy soils have higher invertebrate diversity compared to more mesic/organic soils. Overall, sand hills had ~45% more ant species compared to other sampled ecosystems from Alberta. Similar to other studies, local canopy cover within sand hills was found to be inversely related to ant species richness and diversity. Although sand hills are rare across the region, they are high biodiversity areas for ants, with the sand hills of north-central Alberta having higher species richness of ants compared to other studied areas in Canada.

**Keywords:** Formicidae; ants; sand hills; biodiversity; boreal

## 1. Introduction

Ants (Hymenoptera: Formicidae) are an important component of northern temperate ecosystems in the Nearctic [1]. They act as predators and prey, and influence soil turnover, nutrient cycling, the breakdown of wood, and dispersal of herbaceous seeds [2–4]. They are often the most numerous ground dwelling invertebrates, and are therefore useful for measuring levels of biodiversity [4]. However, despite their ecological importance, little research has been done on the diversity of ants in the northern temperate areas of North America, especially the prairie provinces of Canada.

Sand hills are often defined as sand dunes that have been stabilized by vegetation [5]. In Alberta, Canada, sand dunes first formed at the end of the Wisconsin glaciation, about 11,000 years ago [6]. Since their formation, periods of active blowing sand have been correlated with extreme drought conditions, with the southern parts of Alberta having their last major active dune period during the 1930s [7]. In contrast, the majority (excluding the Lake Athabasca sand dunes [5,7]) of northern and central dune fields in Alberta have been stabilized by vegetation for several centuries [7]. The sand hills of central Alberta are typically covered by jack pine (*Pinus banksiana*) barrens, a heterogeneous environment with variable canopy cover, grassland openings, and jack pine or mixed jack pine/aspen (*Populus tremuloides*) forests [8]. These distinctive environments are situated within a transition zone between the aspen parkland ecoregion and the boreal forest [9] with sand hills representing distinct ecological “islands” when viewed at regional scales. Compared with sand hills, aspen parkland is underlain by a substrate of glacial till and clay, and vegetated by grassland and dense aspen or mixed aspen/black spruce (*Picea mariana*) forests [8], while boreal/peatland forests have more organic soils, including peat, and are dominated by mixed woodlands of black spruce, white spruce, aspen, balsam

poplar (*Populus balsamifera*) and in wetter areas, larch (*Larix laricina*) [9]. Unlike the sand hills, much of the surrounding parkland and boreal vegetation has been converted to cropland and rangelands.

Sand hills are important areas for invertebrate diversity because sand is a substrate that allows for easy burrowing, offers thermal benefits, and is often topographically heterogeneous with high dune crests and low inter-dune valleys [5,10]. Being dominated by jack pine, these areas also have a higher fire frequency, which further increases the structural diversity of vegetation [11]. This is important, as habitat structure heterogeneity is positively correlated with ant species diversity [12,13]. Like other invertebrates, ant diversity has also been found to be higher in sandier soils compared to soils with higher clay content [14] and in forest areas having more open canopy [15].

Here, our objectives were three-fold: (1) test the prediction that ant diversity is higher on sand hills compared to more common aspen parkland and peatland forest types; (2) test the prediction that ant diversity is inversely related to canopy cover within the sand hill ecosystem; and (3) compare ant faunas in the central Alberta sand hills with other similar faunas in the northern Holarctic.

## 2. Materials and Methods

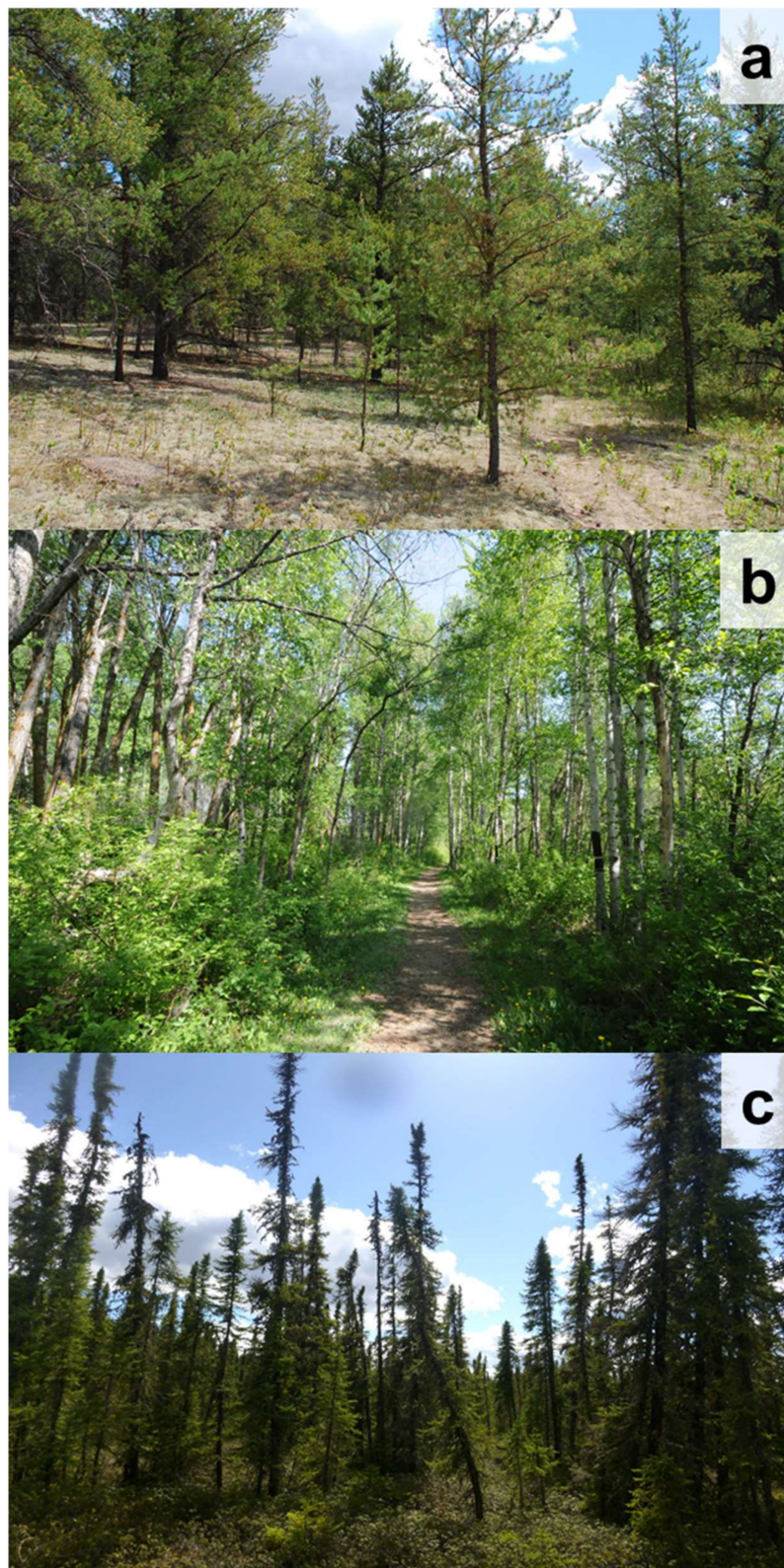
### 2.1. Study Sites

Research was conducted at seven sites in Alberta, Canada. Four of the sites are located in the Redwater sand hills complex, one within the Stony Plain sand hills, one within aspen parkland near Elk Island National Park (Cooking Lake—Blackfoot Grazing, Wildlife and Provincial Recreation Area) and one within peatland forest south of Fort McMurray, Alberta (Table A1). The majority of the Redwater sand hills sites are covered by heterogeneous jack pine woodlands, with intermixed aspen-jack pine forest (Table A1). The Stony Plain sand hills site (Woodbend Forest) is forested with a mix of aspen, jack pine, and black spruce (Table A1). All sand hill sites were on overgrown sand dunes, with little topsoil and just a thin top soil over underlying sand [5,6] (Figure 1a). At Cooking Lake—Blackfoot Grazing, Wildlife and Provincial Recreation Area, sampling was done within the Waskahegan day use area. Vegetation at Waskahegan is comprised of a mix of open grazed grassland and aspen forest with some black spruce (Figure 1b). Waskahegan is typified by glacial moraines and hummocks, a similar rolling topography to the sand hills, but with high clay mesic soils (Table A1) [8]. The Fort McMurray area is forested peatland, dominated by black spruce, larch with some aspen and represents a wetter organic peat-based soil typical of most of Alberta's boreal forest [9] (Figure 1c).

### 2.2. Research Plots and Vegetation Physiognomies

A total of 72 plots were sampled. Each sand hill area had 10 plots sampled, except for Woodbend Forest which had seven, for a total of 47 sand hill plots. At the Waskahegan aspen parkland site, 10 plots were sampled, while 14 plots were sampled in forested peatland near Fort McMurray. Aspen forests and peatland forests are dominant forest types in northern Alberta, while sand hills are relatively rare [5]. Plots in the sand hill sites were 0.1 ha rectangular (20 m by 50 m) areas, with 10 pitfall traps (sub-samples) per plot, placed in pairs 10 m perpendicular to and away from a center line (50 m tape) at intervals of 5, 15, 25, 35 and 45 m. The center lines were orientated to maintain the most homogeneous conditions (canopy cover) possible. Plots in the peatland were 0.25 ha (50 m by 50 m), with 15 pitfall traps (sub-samples) per plot, placed in 3 parallel transects of 5 traps each.

To simplify comparisons of ant diversity among sites within only sand hills, we identified four vegetation physiognomy types: grassland, savannah, woodland, and forest. On sand hills, we had 11 grassland plots, 13 savannah plots, 10 woodland plots, and 13 forest plots. This division of vegetation type was not done for the aspen parkland and peatland forest sites. These types were based in part on site canopy cover, using average densiometer [16] values over each pitfall trap. Sites were then classified with respect to vegetation physiognomy using the United States National Vegetation Classification System (Table A2).



**Figure 1.** (a) Vegetation representative of sand hill ecosystems dominated by jack pine; (b) Typical vegetation of aspen parkland ecosystems, dominated by trembling aspen; and (c) Typical vegetation of peatland forest ecosystems, dominated by black spruce. Photos taken by JRNG, JA and JP respectively.

### 2.3. Specimen Sampling and Identification

For the sand hills and parkland sites, ants were sampled twice in 2010 using pitfall traps, with the exception of Woodbend forest, which was sampled twice during the summer of 2009. Sampling at the sand hill and parkland sites was completed as part of J.R.N.G.'s Master of Science thesis research [17]. For the Fort McMurray peatland forest sites, ants were sampled twice over 2017, and then ant richness was combined. Sampling dates were dependent on weather and available time. The first sampling session occurred between 20 May and 30 June, while the second sampling session occurred between 20 July and the 31 August. Pitfall traps were polypropylene sample containers, 64 mm in diameter, 76 mm deep, and filled with 30 mL of propylene glycol, a solution that is non-toxic to vertebrates [18,19]. Traps were placed flush with the ground, retrieved after 24 h (Fort McMurray traps were collected after 3 weeks), with specimens transferred into 75% ethanol for storage [19].

Ants were identified using a number of published keys [20–25]. Voucher specimens were deposited in E. H. Strickland Entomological Museum, Department of Biological Sciences, University of Alberta, Edmonton, Alberta, the Northern Forestry Centre Arthropod Museum, Edmonton, Alberta and the J.R.N. Glasier Collection.

### 2.4. Statistical Analysis

Sample-based rarefaction curves were used to assess whether samples were large enough to give a reliable measure of ant species richness, and to compare species richness between ecosystems (sand hills vs. parkland vs. peatland) and within sand hill vegetation physiognomies (forests vs. woodland vs. savannah vs. grassland). Sample-based rarefaction (Mao Tau) curves were generated for 50 samples using EstimateS Version 8.0 [26]. EstimateS was also used to calculate common diversity indexes: Michaelis-Menton estimator (MMMeans), Fischer's Alpha (Alpha), Shannon Index and Simpson Index. Sampling efficiency was calculated by comparing number of sampled species with estimated species predicted by MMMeans. Species Rank-Abundance curves were also produced to qualitatively compare evenness of ant faunas among sampled areas.

## 3. Results

### 3.1. Sampling Comparison

A total of 37,439 ants were identified and counted. Overall, 35 species in ten genera were sampled in the sand hills, 20 species in six genera were sampled in aspen parkland, and 20 species from five genera were sampled in the peatland (Table 1; Table S1). One species, *Myrmica incompleta*, was found exclusively within in the aspen parkland, three exclusively within peatland forests (*Myrmica lobifrons*, *Myrmica quebecensis* and *Myrmica lampra*), and 17 exclusively in the sand hills (Table 1).

**Table 1.** Ant species presence/absence among vegetation physiognomies.

Species	Aspen Parkland	Peatland Forest	Sand Hill Grassland	Sand Hill Savannah	Sand Hill Woodland	Sand Hill Forest
<i>Camponotus herculeanus</i>	x	x	x	x	x	x
<i>Camponotus nearcticus</i>	x			x		
<i>Camponotus novaeboracensis</i>	x	x	x	x	x	x
<i>Dolichoderus taschenbergi</i>			x	x	x	x
<i>Formica accreta</i>	x	x	x	x	x	x
<i>Formica adamsi</i>		x	x	x	x	
<i>Formica aserva</i>	x	x	x	x	x	x
<i>Formica dakotensis</i>	x	x	x	x	x	
<i>Formica densiventris</i>		x	x	x	x	x
<i>Formica hewitti</i>	x	x	x	x		x
<i>Formica impexa</i>			x		x	
<i>Formica lasioides</i>	x		x	x	x	x
<i>Formica neorufibarbis</i>	x	x	x	x	x	x
<i>Formica obscuriventris</i>		x	x	x	x	x

Table 1. Cont.

Species	Aspen Parkland	Peatland Forest	Sand Hill Grassland	Sand Hill Savannah	Sand Hill Woodland	Sand Hill Forest
<i>Formica oreas</i>			x	x	x	x
<i>Formica podzolica</i>	x	x	x	x	x	x
<i>Formica subintegra</i>			x			
<i>Formica ulkei</i>	x	x	x	x	x	
<i>Formicoxenus hirticornis</i>						x
<i>Formicoxenus quebecensis</i>	x	x			x	
<i>Harpagoxenus canadensis</i>						x
<i>Lasius americanus</i>						x
<i>Lasius aphidicolus</i>			x	x		
<i>Lasius crypticus</i>			x	x		
<i>Lasius neoniger</i>			x	x	x	x
<i>Lasius pallitarsis</i>	x		x	x	x	x
<i>Leptothorax canadensis</i>	x	x	x	x	x	x
<i>Myrmica ab001</i>	x		x	x	x	x
<i>Myrmica alaskensis</i>	x	x	x	x	x	x
<i>Myrmica brevispinosa</i>			x	x	x	x
<i>Myrmica detritinodis</i>	x	x	x	x	x	x
<i>Myrmica fracticornis</i>	x	x	x	x	x	x
<i>Myrmica incompleta</i>	x					
<i>Myrmica lampra</i>		x				
<i>Myrmica lobifrons</i>		x				
<i>Myrmica nearctica</i>			x	x	x	x
<i>Myrmica quebecensis</i>		x				
<i>Polyergus mexicanus</i>	x		x	x		
<i>Tapinoma sessile</i>			x	x	x	x
Total Genera	7	5	8	8	7	8
Total Species	20	20	30	29	26	25

Sampled species richness on the sand hills was equal to the predicted species richness (based on MMMeans) at a 100.0% sampling efficiency (Table 2). For vegetation physiognomies within sand hills, sampling efficiency was 88.3% for grassland, 90.9% for savannah, 86.3% for woodlands and 86.3% for forests. For non-sand hill areas, sampling efficiency was 83.8% for aspen parkland and 100% for peatland forest (Table 2).

**Table 2.** Diversity indexes of ant species on sand hills compared to on aspen parkland and peatland forest in Alberta (Standard deviations reported in parentheses).

Ecosystem	Species (Generic) Richness	MMMeans	Fisher's Alpha	Shannon Index	Simpson Diversity Index
Sand Hills					
Overall	35 (10)	34.91	3.99 (0.21)	2.58 (0)	9.98
Grassland	30 (8)	33.94	4.07 (0.26)	2.52 (0)	9.31
Savannah	29 (8)	31.90	3.67 (0.23)	2.30 (0.12)	6.88
Woodland	26 (8)	30.12	3.48 (0.23)	2.27 (0)	6.70
Forest	25 (8)	28.97	3.64 (0.27)	2.15 (0)	5.94
Aspen Parkland	20 (7)	23.87	3.07 (0.26)	1.69 (0.05)	5.45
Peatland Forest	20 (5)	20.71	2.42 (0.18)	1.85 (0)	4.64

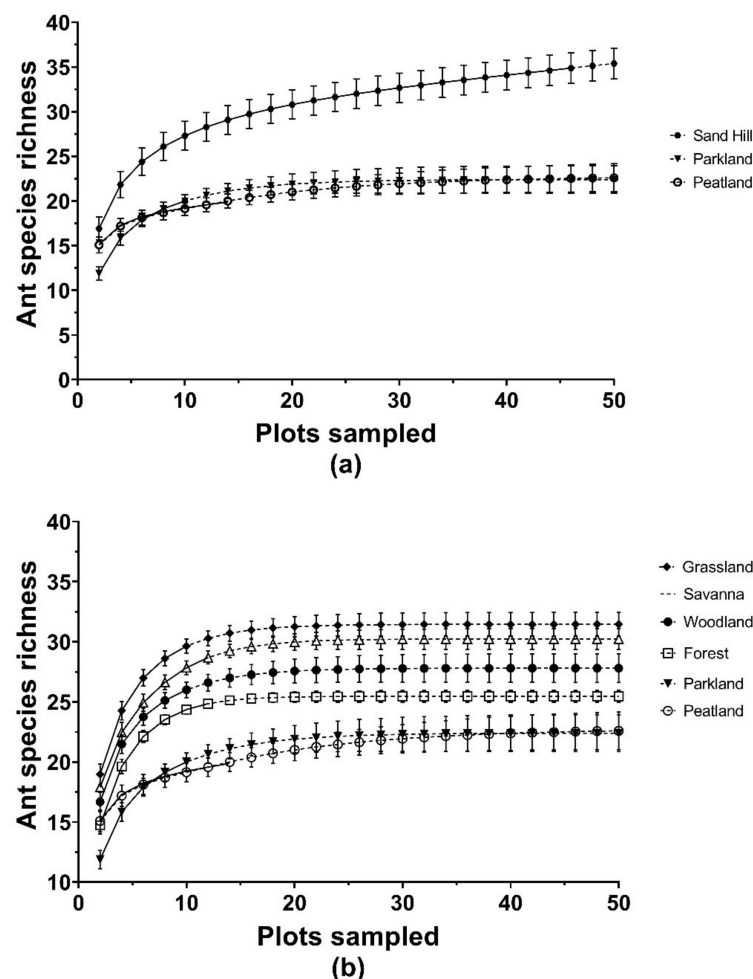
### 3.2. Diversity Comparisons

The various diversity indexes show similar patterns: sand hills had higher levels of diversity than aspen parklands and peatland forests, regardless of the index used (Table 2). All four sand hill vegetation physiognomies also had higher diversity when compared to the aspen parkland sites. Values from the Shannon index (H) (Table 2) showed that grassland plots were the most diverse ( $H = 2.52$ , effective number of species = 12.48) within the sand hill ecosystem, while forests were the least diverse ( $H = 2.15$ , effective number of species = 8.55). Woodland (2.28, effective number of species = 9.75) and savannah (2.30, effective number of species = 9.98) areas exhibited intermediate

diversity, although woodlands were slightly less diverse. Aspen parkland diversity was much lower (1.69, effective number of species = 5.45) than sand hills, as was diversity in peatland forests (1.85, effect number of species = 6.39). Fisher's alpha was highest for grasslands (4.07), and lowest in woodlands (3.48) (Table 2). Values from the Simpson index (Table 2) show a pattern similar as those obtained from Shannon's, with grasslands being the highest, forests the lowest, and woodlands and savannahs intermediate.

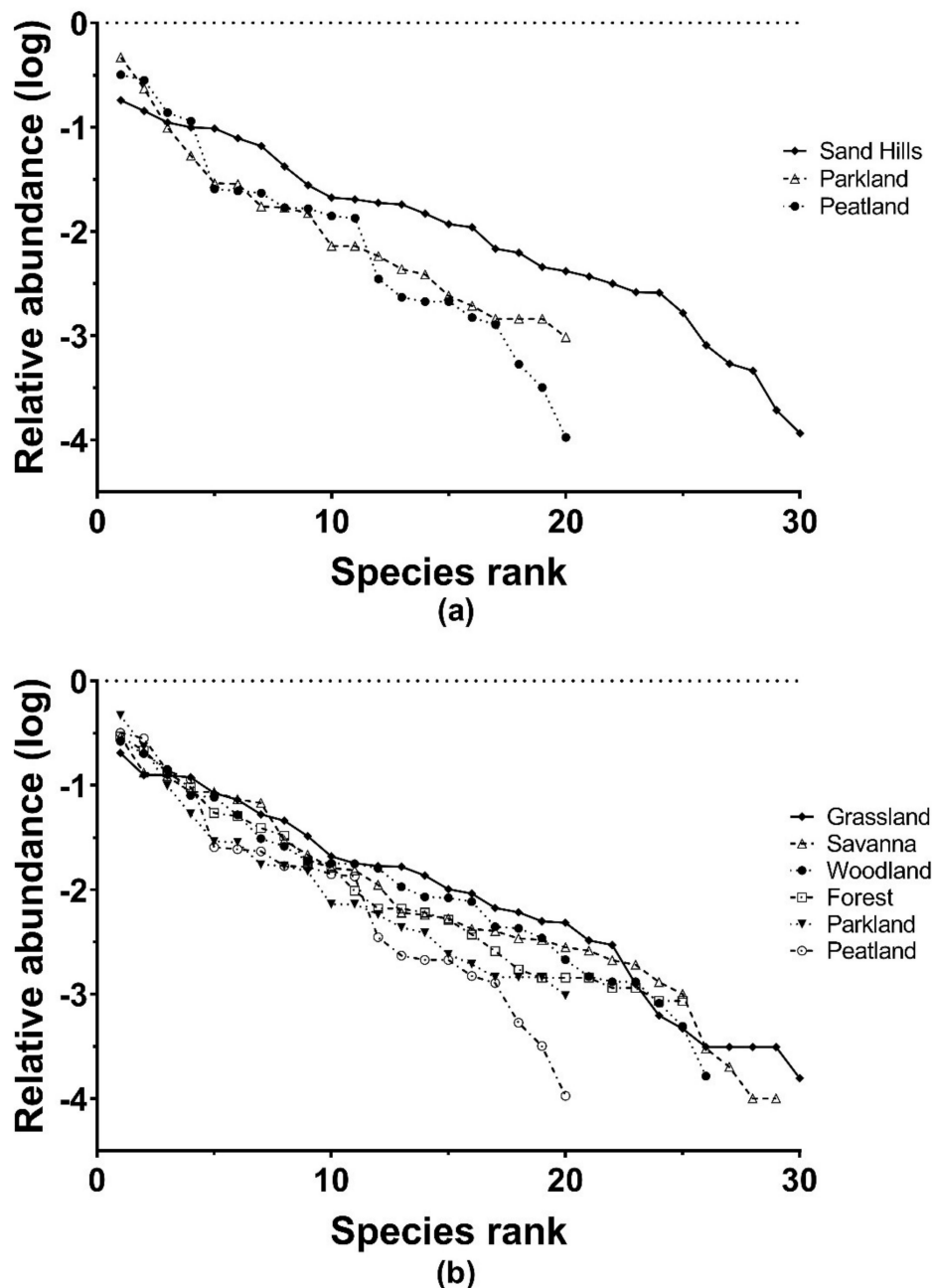
### 3.3. Species Accumulation and Species Rank Curves

Species accumulation curves for sand hills, aspen parkland and peatland forests appear to level out after approximately 20 sampled plots (Figure 2a). Species richness is clearly lower in aspen parklands ( $S = 20$ ) and peatland forests ( $S = 20$ ) than in sand hills ( $S = 35$ ) or any of the four sand hill vegetation physiognomy types (Figure 2b). Moreover, there is a clear inverse relationship between ant diversity and canopy cover (grasslands > savannah > woodland > forest) (Figure 2b). Total predicted species richness of ants for each sand hill vegetation physiognomy type, at sample sizes of 50 plots, is ~31 for grasslands, ~30 for savannah, ~28 for woodland, and ~25 for forests (Figure 1b). For aspen parkland and peatland forest, predicted species richness at 50 samples is ~22 for both (Figure 2a,b).



**Figure 2.** (a) Results of ant species rarefaction curves, comparing overall sand hill ant species richness with aspen parkland and peatland forest ecosystems. (b) Species rarefaction curves of ant species richness from different vegetation physiognomies within the sand hill ecosystem compared to topographically similar aspen parkland ecosystem and to the northern peatland forest. Rarefaction was based on a series of 1000 randomizations of species data [26]. Error bars represent standard errors. Solid lines indicate number of plots sampled, while dotted lines indicates extrapolated numbers.

Species rank-abundance curves for all sand hill sites have a gradual slope, indicating a high level of evenness in ant diversity (Figure 3a). In contrast, the rank-abundance curves for aspen parklands and peatland forests have higher slopes and lower total species richness (Figure 3a). Within sand hills, the forest physiognomy has the least even community, with woodland, savannah, and grasslands showing similar degrees of evenness (Figure 3b).



**Figure 3.** (a) Species rank-abundance (log scale) curve for all sand hill ant species in central Alberta and from sampled aspen parkland and peatland forest. (b) Species rank-abundance (log scale) curves for the different vegetation physiognomies within sand hills and for sampled aspen parkland and peatland forest.

Based on published information about ants in Canada, the central Alberta sand hills had higher diversity compared to the majority of other similar boreal areas or areas reported elsewhere in the country, with 35 reported species (Tables 1 and 3). The closest area of diversity was the Southern

Okanagan with 31 species (Table 3). Most other boreal or pine barren areas were nearer to 20–24 species (Table 3).

**Table 3.** Diversity of ant species on several northern Holarctic localities. The highest species richness is found in the sand hills of central Alberta.

Locality	Ecosystem	Ant Species (Genera) Richness	Author(s)
Central Alberta Sand Hills, Alberta, Canada	Pine Barrens	35 (10)	This Paper
Waskahegan, Alberta, Canada	Aspen Parkland	20 (8)	This Paper
Fort McMurray, Alberta, Canada	Peatland Forest	20 (6)	This Paper
Southern Okanagan Grassland, British Columbia, Canada	Brush Shrub Steppe	31 (13)	Heron 2001 [27]
Prince George, British Columbia, Canada	Boreal Forest	23 (10)	Higgins and Lindgren 2005 [28]
Great Sand Hills, Saskatchewan, Canada	Open Dunes Grassland	20 (6)	Glasier and Acorn 2014 [29] Personal Collection
Molson Reserve, Quebec, Canada	Maple-Beech Forest	24 (12)	Lessard and Buddle 2005 [30]
Hanko Peninsula, Finland	Pine Barrens	24 (7)	Galle 1991 [12]
Kampinos National Park, Poland	Pine Barrens	22(7)	Galle et al. 1998 [13]

## 4. Discussion

### 4.1. Diversity on Sand Hills

The most abundant ant species in the sand hills were common to all vegetation physiognomy types, while some species were unique to, or most abundant in, a single physiognomy type (Table 1). Species richness by sand hill vegetation physiognomy was difficult to quantify, since some single plots sampled multiple physiognomy types. Other site variables, such as ground cover, shrub density, and soil moisture, could have improved our understanding of local influences of habitat on ant species [14], but were not reported here. However, both the Shannon and Simpson indices indicated higher ant diversity in grasslands, with a general trend toward reduced diversity with increased canopy cover, as reported in other studies [15,31]. By all measures, except perhaps Fisher’s alpha, grassland openings clearly showed the highest ant diversity (Table 2).

Despite being uncommon ecosystems, the Alberta sand hills are a habitat for approximately one third of the ant species of Alberta (35 of 92 species) [5,25]. Furthermore, sand hills in central Alberta have the highest species richness of any reported Canadian localities (Table 3). The more southerly Okanagan Grasslands of British Columbia were expected to have higher ant species richness because of latitude and climate [26], but they did not. Similarly, open sand dunes within the Great Sand Hills of southern Saskatchewan also had lower species richness, most likely because they represent a harsher and less heterogeneous environment compared to the overgrown sand hills further north [30]. All other reported Canadian localities are forested with lower ant diversity, likely due to higher canopy cover, fewer edges, vegetation homogeneity, and more mesic soils. Ants are associated with forest edges where they take advantage of the sun for warmth, and the ability to use multiple vegetation

types for foraging [15]. However, in stabilized sand dunes in Europe, ant species diversity was lower than what was observed in Alberta (Table 3) [12,13].

We wish to bring to attention some important caveats of our study. First, the collecting methods differed between the peatland forest, aspen parkland and sand hill plots. The sampling area differed for the peatland forest (50 m × 50 m; 0.25 ha) and that of the aspen parkland/sand hills sites (50 m × 20 m; 0.10 ha), as did the time lengths for pitfall trapping (3 weeks for peatland; 24 h for aspen parkland and sand hills). Other studies have shown that sampling a larger area, or increasing pitfall trap time, increases the sampling of ant species richness [19,32]. Assuming that this bias exists, peatland plots were therefore more efficiently sampled compared to aspen parkland and sand hills, but still had a lower ant species richness (Table 3), suggesting that the pattern we are presenting is real.

We were also constrained to comparing samples from different years with respect to ant species richness (Table 3). However, other published accounts of ant richness give similar estimates for the diversity of ants species in northern temperate region of Canada (Table 3), and thus, we believe that our results still provide an excellent representative comparison of sand hills to other ecosystems with broad inferences of greater diversity in the sand hills supported regardless of sampling methods, given that diversity was higher even though plots sizes and sample lengths were shorter than in peatland forests.

#### 4.2. Notable Species Records

Several ant species records for the province of Alberta are limited to the sand hills, some of which were previously reported in Glasier et al. [25]. *Dolichoderus taschenbergi* was found to be tightly associated with Jack pine in all five sampled sand hill areas, and its discovery represents a range extension of over 1200 km [33]. *Myrmica nearctica* appears to be another sand hill specialist, known in Alberta only in sand hills, but previously recorded in B.C. and Montana. *Formicoxenus hirticornis* has been found in Alberta only on sand hills, in *Formica oreas* nests, although it is expected anywhere its host species in the *Formica rufa*-group are found in the province [34]. An undescribed species *Myrmica* ab001, may be a new species closely related to *M. crassirugis*; however more research is needed before this can be confirmed [25]. Lastly, the first and only record of *Harpagoxenus canadensis* in Alberta, a species listed as Vulnerable in the IUCN redlist [35], was found in only one plot (in only one pitfall trap site) in the Redwater Natural Area, approximately 2000 km from other known localities. As *H. canadensis* is a slave-making species utilizing *Leptothorax canadensis* (and allies), it may be present across Canada with its hosts, although it is vulnerable to disturbances and fluctuations of its host species [36].

There were two additional records of species on the IUCN redlist [35] from the Fort McMurray peatland forest. *Myrmica quebecensis* and *Myrmica lampra* (both social parasites of *Myrmica alaskensis*) were found in relatively high numbers (over 10 specimens of *M. lampra* were collected). Both species are ranked as vulnerable and are in need of further study. *Myrmica quebecensis* had been previously reported from Elk Island National Park, Alberta, by the Barcode of Life Data System [37]. *Myrmica lampra*, however, has only been recorded in Canada from two localities in Quebec [38], and a range extension of over 2500 km indicates that this species likely exists across Canada and the boreal forest.

#### 5. Conclusions

The central Albertan sand hills are speciose areas for ants. They represent higher ant diversities compared to the surrounding aspen parkland, boreal/peatland forest, and other Canadian localities. Sand hills, being islands of higher biodiversity, represent important ecosystems within central Alberta [5]. As such, further research is needed to determine whether sand hills should be more prominently protected and conserved for their diversity.

**Supplementary Materials:** The following are available online at <http://www.mdpi.com/1424-2818/11/2/22/s1>, Table S1: Species abundance and richness data of plots sampled.

**Author Contributions:** Conceptualization, Methodology, Validation, & Formal Analysis, J.R.N.G.; S.E.N. & J.A.; Investigation, Data Collection & Resources, J.R.N.G. & J.P. Writing-Original Draft Preparation, J.R.N.G.; Writing-Review & Editing, J.R.N.G., S.E.N., J.A. & J.P.; Supervision, S.E.N. & J.A.; Funding Acquisition, J.R.N.G.; S.E.N. & J.A.

**Funding:** This research was funded by Alberta Conservation Association Biodiversity Grant 2012.

**Acknowledgments:** For help in the field, we would like to thank Caroline LeCourtois, and Sonya Odsen. At the E.H. Strickland Entomological Museum, we thank Danny Shpeley and Felix Sperling.

**Conflicts of Interest:** The authors declare no conflict of interest.

## Appendix A

**Table A1.** Descriptions of study areas sampled for ants in northern Alberta. Areas include five sand hill areas dominated by Jack Pine forests, as well as and aspen parkland and peatland forest area for comparison.

Study Area	Latitude/Longitude	Area Type	Vegetation	Date of Recent Fires	Disturbance
Waskahagan Natural Area	53°30'21.96" N 112°56'8.81" W	Aspen Parkland	Aspen Parkland (mixed Aspen and Black Spruce)	Has not burned recently	Grazed by cattle
Fort McMurray Peatland Forest Area	56°25'43.59" N 111° 4'49.89" W	Peatland Forest	Black Spruce and Larch	May 2016	Cut lines
North Bruderheim Natural Area	53°52'8.54" N 112°56'40.10" W	Sand Hills	Jack Pine Forest and mixed aspen/jack pine forest	May 2009	All terrain vehicle and petroleum industry
Northwest Bruderheim Natural Area	53°52'8.54" N 112°56'40.10" W	Sand Hills	Jack Pine Forest and mixed aspen/jack pine/forest	May 2009	All terrain vehicle and petroleum industry
Opal Natural Area	53°59'13.59" N 113°18'34.96" W	Sand Hills	Jack Pine Forest and mixed aspen/jack pine/black spruce forest	May 2010	All terrain vehicle
Redwater Natural Area	53°56'27.66" N 112°57'17.19" W	Sand Hills	Jack Pine Forest and mixed aspen/jack pine forest	Has not burned recently	All terrain vehicle and petroleum industry
Woodbend Forest	53°23'31.66" N 113°45'15.38" W	Sand Hills	Jack Pine Forest and mixed aspen/jack pine/black spruce forest	Has not burned recently	Petroleum industry

**Table A2.** Classification scheme and description for the vegetation physiognomies used in sampling ants in central Alberta sand hills.

Vegetation Type in Sand Hills	Description	Canopy Cover
Grassland	Areas of open canopy often located on the tops of dunes. Open sand patches are common. Lichen, sedges, and small shrubs such as roses or pin cherry make up common ground cover.	0–5%

Table A2. Cont.

Vegetation Type in Sand Hills	Description	Canopy Cover
Savannah	Openings with a few jack pine and aspen. Often dominated by lichen, with bryophytes in shaded areas. Sedges and grasses are common, with scattered shrubs such as saskatoons, pin cherry and roses.	>5–25%
Woodland	Jack pine and aspen with mix of lichen and bryophyte ground cover. Roses and saskatoons are common. Grasses and sedges are uncommon	>25–60%
Forest	Jack pine forest interspersed with rare aspen. Ground cover dominated by bryophytes. Sometimes thick shrubs, sometimes none.	>60–100%

## References

- Holldöbler, B.; Wilson, E.O. *The Ants*; The Belknap Press of Harvard University Press: Cambridge, MA, USA, 1990; pp. 1–746.
- Handel, S.H.; Finch, S.B.; Schatz, G.E. Ants disperse a majority of herbs in a mesic forest community in New York State. *Bull. Torrey Bot. Club* **1981**, *108*, 430–437. [\[CrossRef\]](#)
- Briese, D. The effects of ants on the soil of a semi-arid saltbush habitat. *Insectes Sociaux* **1982**, *29*, 375–386. [\[CrossRef\]](#)
- Folgarait, P. Ant biodiversity and its relationship to ecosystem functioning: A review. *Biodivers. Conserv.* **1998**, *7*, 1221–1244. [\[CrossRef\]](#)
- Acorn, J.H. Sand Hill Arthropods in Canadian Grasslands. In *Arthropods of Canadian Grasslands: Inhabitants of a Changing Landscape*; Floate, K.D., Ed.; Biological Survey of Canada: Ottawa, ON, Canada, 2011; Volume 2, pp. 25–43.
- Wolfe, S.; Huntley, D.; Ollerhead, J. Relict Late Wisconsinan Dune Fields of the Northern Great Plains, Canada. *Géogr. Phys. Quat.* **2014**, *58*, 323–336. [\[CrossRef\]](#)
- Wolfe, S.A.; Huntley, D.J.; David, P.P.; Ollerhead, J.; Sauchyn, D.J.; McDonald, G.M. Late eighteenth century drought induced sand dune activity, Great Sand Hills, Saskatchewan. *Can. J. Earth Sci.* **2001**, *38*, 105–117. [\[CrossRef\]](#)
- Lewis, F.; Dowding, E.S. The vegetation of Alberta: II. the swamp, moor and bog forest vegetation of central Alberta. *J. Ecol.* **1928**, *16*, 19–70. [\[CrossRef\]](#)
- Downing, D.J.; Pettapiece, W.W. Natural Regions and Subregions of Alberta. Natural Regions Committee Government of Alberta. 2006. Available online: [https://www.albertaparks.ca/media/2942026/nrsrcomplete\\_may\\_06.pdf](https://www.albertaparks.ca/media/2942026/nrsrcomplete_may_06.pdf) (accessed on 13 November 2018).
- Howe, M.A.; Knight, G.T.; Clee, C. The importance of coastal dunes for terrestrial invertebrates in Wales and the UK, with particular reference to aculeate Hymenoptera (bees, wasps & ants). *J. Coast. Conserv.* **2010**, *14*, 91–102.
- Larsen, P. Spatial and temporal variations in boreal forest fire frequency in Northern Alberta. *J. Biogeogr.* **1997**, *24*, 663–673. [\[CrossRef\]](#)
- Galle, L. Structure and succession of ant assemblages in a north European sand dune area. *Holarct. Ecol.* **1991**, *14*, 31–37. [\[CrossRef\]](#)
- Galle, L.; Körmöcz, L.; Hornung, E.; Kerekes, J. Structure of ant assemblages in a Middle-European successional sand-dune area. *Tiscia* **1998**, *31*, 19–28.
- Boulton, A.M.; Davies, F.D.; Ward, P.S. Species richness, abundance and composition of ground-dwelling ants in northern California grassland: Role of plants, soil, and grazing. *Environ. Entomol.* **2005**, *34*, 96–104. [\[CrossRef\]](#)
- Palladini, J.D.; Jones, M.G.; Sanders, N.J.; Jules, E.S. The recovery of ant communities in regenerating temperate conifer forests. *For. Ecol. Manag.* **2007**, *242*, 619–624. [\[CrossRef\]](#)
- Lemon, P. A spherical densitometer for estimating forest overstory density. *For. Sci.* **1956**, *2*, 314–320.
- Glasier, J.R.N.G. Community Ecology of Ants (Hymenoptera: Formicidae) on the Central Sand Hills of Alberta, and a Key to the Ants of Alberta. Master's Thesis, University of Alberta, Edmonton, AB, Canada, 2012.

18. Weeks, R.D., Jr.; McIntyre, N.E. A comparison of live versus kill pitfall trapping techniques using various killing agents. *Entomol. Exp. Appl.* **1997**, *82*, 267–273. [[CrossRef](#)]
19. Bestelmeyer, B.T.; Agosti, D.; Alonso, L.E.; Brandão, C.R.F.; Brown, W.L., Jr.; Delabie, J.H.C.; Silvestre, R. Field techniques for the study of ground-dwelling ants: An overview, description, and evaluation. In *Ants Standard Methods for Measuring and Monitoring Biodiversity*; Agosti, D., Majer, J.D., Alonso, L.E., Schultz, T., Eds.; Smithsonian Institution Press: Washington, DC, USA, 2000; pp. 122–144.
20. Creighton, W.S. The ants of North America. *Bull. Mus. Comp. Zool.* **1950**, *104*, 1–585.
21. Wheeler, G.C.; Wheeler, J. *The Ants of North Dakota*; University of North Dakota Press: Grand Forks, ND, USA, 1963; pp. 1–325.
22. Francoeur, A. Revision taxonomique des espèces nearctiques du groupe Fusca, genre *Formica* (Formicidae, Hymenoptera). *Mem. De La Soc. Entomologique Du Que.* **1973**, *3*, 1–316.
23. Mackay, W.; Mackay, E. *The Ants of New Mexico (Hymenoptera: Formicidae)*; The Edwin Mellen Press: Lewiston, NY, USA, 2002; pp. 1–398.
24. Hasen, L.D.; Klotz, J.H. *The Carpenter Ants of the United States and Canada*; Cornell University Press: Ithaca, NY, USA, 2005; pp. 1–204.
25. Glasier, J.R.N.; Acorn, J.H.; Nielsen, S.; Proctor, H. Ants (Hymenoptera: Formicidae) of Alberta: A key to species based primarily on the worker caste. *Can. J. Arthropod Identif.* **2013**, *22*, 1–104.
26. Colwell, R.K.; Estimate, S. Statistical Estimation of Species Richness and Shared Species from Samples, Version 8.2, User's Guide and Application. 2009. Available online: <http://purl.oclc.org/estimate> (accessed on 12 August 2018).
27. Heron, J. Ants of the south Okanagan grasslands, British Columbia. *Arthropods Can. Grassl.* **2005**, *11*, 17–22.
28. Higgins, R.; Lindgren, S. Species List of Ants Collected in Central and North-Central British Columbia. 2005. Available online: [http://web.unbc.ca/~jllindgren/ants\\_species\\_list.html](http://web.unbc.ca/~jllindgren/ants_species_list.html) (accessed on 8 October 2018).
29. Glasier, J.R.N.; Acorn, J.H. An Annotated List of Ants (Hymenoptera: Formicidae) from the Grasslands of Alberta and Saskatchewan. In *Arthropods of Canadian Grasslands (Volume 4): Biodiversity and Systematics Part 2*; Giberson, D.J., Cárcamo, H.A., Eds.; Biological Survey of Canada: Ottawa, ON, Canada, 2014; pp. 299–314.
30. Lessard, J.; Buddle, C.M. The effects of urbanization on ant assemblages (Hymenoptera: Formicidae) associated with the Molson nature reserve, Quebec. *Can. Entomol.* **2005**, *137*, 215–225. [[CrossRef](#)]
31. Lassau, S.A.; Hochuli, D.F. Effects of habitat complexity on ant assemblages. *Ecography* **2004**, *27*, 157–164. [[CrossRef](#)]
32. Delabie, J.H.C.; Fisher, B.L.; Majer, J.D.; Wright, I.W. Sampling effort and choice of methods. In *Ants Standard Methods for Measuring and Monitoring Biodiversity*; Agosti, D., Majer, J.D., Alonso, L.E., Schultz, T., Eds.; Smithsonian Institution Press: Washington, DC, USA, 2000; pp. 122–144.
33. Mackay, W. A review of the New World ants of the genus *Dolichoderus* (Hymenoptera: Formicidae). *Sociobiology* **1993**, *22*, 1–148.
34. Francoeur, A.; Buschinger, A. Biosystematique de la tribu Leptothoacini (Formicidae, Hymenoptera) 1. Le genre *Formicoxenus* dans la région Holarctique. *Nat. Can.* **1985**, *112*, 343–403.
35. Social Insects Specialist Group. *Harpagoxenus canadensis*. In IUCN 2011. IUCN Red List of Threatened Species, Version 2011.1. 1996. Available online: [www.iucnredlist.org](http://www.iucnredlist.org) (accessed on 7 December 2018).
36. Stuart, R.J.; Alloway, T.M. The slave-making ant, *Harpagoxenus canadensis*, M. R. Smith, and its host-species, *Leptothorax muscorum* (Nylander): Slave raiding and territoriality. *Behaviour* **1983**, *85*, 58–90. [[CrossRef](#)]
37. Ratnasingham, S.; Hebert, P.D.N. Barcoding, BOLD: The barcode of life data system ([www.barcodinglife.org](http://www.barcodinglife.org)). *NPR Mol. Ecol. Notes* **2007**, *7*, 355–364. [[CrossRef](#)] [[PubMed](#)]
38. Francoeur, A. Les fourmis de la forêt boréale du Québec. *Nat. Can.* **2001**, *125*, 108–114.

