

## Article

# Effects of Natural Land Cover, Anthropogenic Disturbance, Space, and Climate on Oribatid Mite Communities in Canada's Oil Sands Region

Lisa M. Lumley<sup>1,2,\*</sup> , Ermias T. Azeria<sup>1</sup> , Victoria A. Giacobbo<sup>1</sup> and Tyler P. Cobb<sup>1,2</sup>

<sup>1</sup> Alberta Biodiversity Monitoring Institute, CW 405 Biological Sciences Building, University of Alberta, Edmonton, AB T6G 2E9, Canada

<sup>2</sup> Department of Biological Sciences, CW 405 Biological Sciences Building, University of Alberta, Edmonton, AB T6G 2E9, Canada

\* Correspondence: lisa.lumley@ualberta.ca

**Abstract:** Soil contains a diverse fauna and microflora that are vital for maintaining healthy soils and their various ecosystem services. Oribatid mites are typically highly abundant arthropods in the soil and are used as indicators for environmental monitoring. The aim of this study was to determine oribatid mite community response to natural land cover, anthropogenic disturbance, space, and climate in the oil sands region of Alberta, Canada. Our results found that oribatid mite total abundance was significantly reduced by mining, cultivation, and well sites. Species richness was significantly reduced by mining and cultivation. Shannon's diversity index was significantly higher for all natural land cover types, seismic lines, and forest harvest. Additionally, species diversity was lower under the relative influence of energy-related soft linear disturbances than for naturally vegetated sites and forest harvesting, and was lowered further by anthropogenic disturbances with more impact on soil integrity (cultivation, mines, urban/industrial, road/trail verges, well sites). Abundance, richness, and diversity also increased with increased frost free period and with eastward longitude. Mite community composition included a notable composition difference between lowland habitats and upland forest types, and between natural land cover and intense anthropogenic disturbance types (e.g., mines, cultivation). Our study highlighted oribatid mite communities' response to natural land cover, anthropogenic disturbance and spatial-climatic factors assessed over broad spatial scales and the potential utility of oribatid mites as ecosystem health indicators under multiple ecological drivers.

**Keywords:** Acari; biodiversity; environmental monitoring; indicator species; mesofauna; microarthropod; oil sands; Oribatida; soil health; soil quality



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## 1. Introduction

Soil biodiversity drives ecological processes associated with soil formation and functioning that are intimately linked to various ecosystem services by soils, including food security, ecological resilience, carbon sequestration, air and water purification, and climate regulation [1–5]. The provisions of these ecosystem services are linked to the wide range of activities undertaken by the enormous diversity of soil organisms adapted to different habitats and environmental conditions [1]. For example, soil organisms form complex food webs that promote nutrient cycling through the breakdown and decomposition of organic materials [6,7]. As a result, the abundance and diversity of belowground soil biota play vital roles in both above- and belowground nutrient availability, which are linked to many essential ecological processes such as primary productivity [6–9]. Thus, intact soil food webs are critically linked to both above- and belowground ecosystem productivity and function [5,8]. The recognition of soil biodiversity as vital for healthy ecosystem functioning

has placed it at the heart of international policy frameworks, including the United Nation's Sustainable Development Goals [5].

Many human activities result in soil degradation, which has negative consequences for soil biodiversity [2,10]. Energy-related disturbances such as well sites and seismic lines have significant impact on soil structure, including compaction, reduced porosity, and increased bulk density, which in turn impact above- and belowground vegetation structure and function [11–13]. In addition, salvaging and long-term stockpiling of soil for post-mining reclamation purposes can modify nutrient availability and create anaerobic conditions that reduce the survival of soil organisms [14,15]. These changes decrease the available space and food for soil organisms and can also affect other soil properties that soil organisms are sensitive to, such as hydrology [11]. Similarly, replacing or sealing the upper soil horizons with sand, gravel, or pavement (e.g., transportation, urban–industrial), mixing the mineral and organic soil layers (e.g., cultivation), and other landscape conversions can negatively impact the abundance and diversity of soil-associated biota [16–20]. Anthropogenic contaminants carried by water or dust can eventually make their way to the soil and therefore to the food chains of the organisms that live within it [10,21–24]. In addition, introduction of non-native species as a result of human activity has resulted in substantially altered soil communities [10,25,26]. Overall, monitoring for changes in soil biodiversity associated with human activities is an integral component of understanding, managing, and conserving the ecological services these organisms provide [1–5].

Oribatid mites are among the most abundant soil organisms and possess important biological/ecological attributes that make them strong indicators for environmental monitoring [17,27–36]. Oribatid mites play a major role in soil nutrient cycling, as they feed on and break down organic materials, and concentrate these materials into faecal pellets for colonization and further breakdown by fungi and bacteria [17]. Through their activities, they disperse other organisms and move soil sediments and nutrients through the soil profile [17,37]. Unlike most smaller-bodied invertebrates, oribatids have a relatively long lifespan (lasting multiple years), low fecundity, and slow growth rates [17,38], which make them amenable to disturbances and degradation in soil over long term [39]. Oribatid mites are diverse, abundant, found in almost every terrestrial habitat, and their relatively low motility means that they are likely to produce a strong signal of local environmental change [17,40,41]. Oribatids have shown sensitivity to fine-scale environmental gradients [42–45]. Their taxonomy is also relatively well established compared to many other soil-dwelling organisms, including the availability of regional checklists [46–49], which supports the ability to provide species-level identifications. As a result, oribatid mites have been studied as bioindicators of soil quality in many parts of the world [28,35,50–60], including for the aim of this study, which is to examine the effect of multiple ecological drivers on mite community structure in the oil sands region of Alberta, Canada.

The oil sands region (OSR) of Canada is situated within the provinces of Alberta and Saskatchewan, and hosts a rich diversity of boreal flora and fauna. The region has been subjected to various types of natural and anthropogenic disturbance. As of 2019, anthropogenic disturbance (i.e., human development or “human footprint”) occupied 16.1% of the OSR in Alberta, including agriculture (7.8%; 10,895 km<sup>2</sup>), forestry (4.2%; 5819 km<sup>2</sup>), energy (2.3%; 3155 km<sup>2</sup>), transportation (0.9%; 1220 km<sup>2</sup>) and urban/industrial (0.8%; 1192 km<sup>2</sup>) [61]. The OSR encompasses the Athabasca, Cold Lake, and Peace River oil sands deposits, a combined area of 142,200 km<sup>2</sup> containing 95% of Canada's proven oil reserves and the fourth largest oil reserves in the world [62]. About 4800 km<sup>2</sup> of reserves are shallow enough to access using surface mines, while the remaining reserves are deeper and require access through in situ drilling and production methods [62]. Thus, intensive oil and gas exploration and production in the region have created several human footprint types including surface mining, in situ well sites, seismic lines for energy exploration, transmission lines, and pipelines. In addition, industrial facilities, urban centres, and roads have expanded to access these economic resources.

Alberta's monitoring data for oribatid mites show that individual species are responding to the human footprint in the OSR [63]. Community metrics using a subset of these data have previously revealed that oribatid mites respond to forest harvest and linear disturbance in the OSR [36]. However, the full dataset has not yet been assessed to determine how oribatid mite communities are responding to all broad classes of human footprint types through changes in total abundance, diversity, and community composition. Therefore, our objectives in this study were to: (1) assess the relationship between OSR human footprint and oribatid mite abundance, diversity, and community composition, (2) assess oribatid mite community responses to natural land cover types, space, and climate, and (3) use this information to discuss how oribatid mites may be useful as environmental indicators in the OSR.

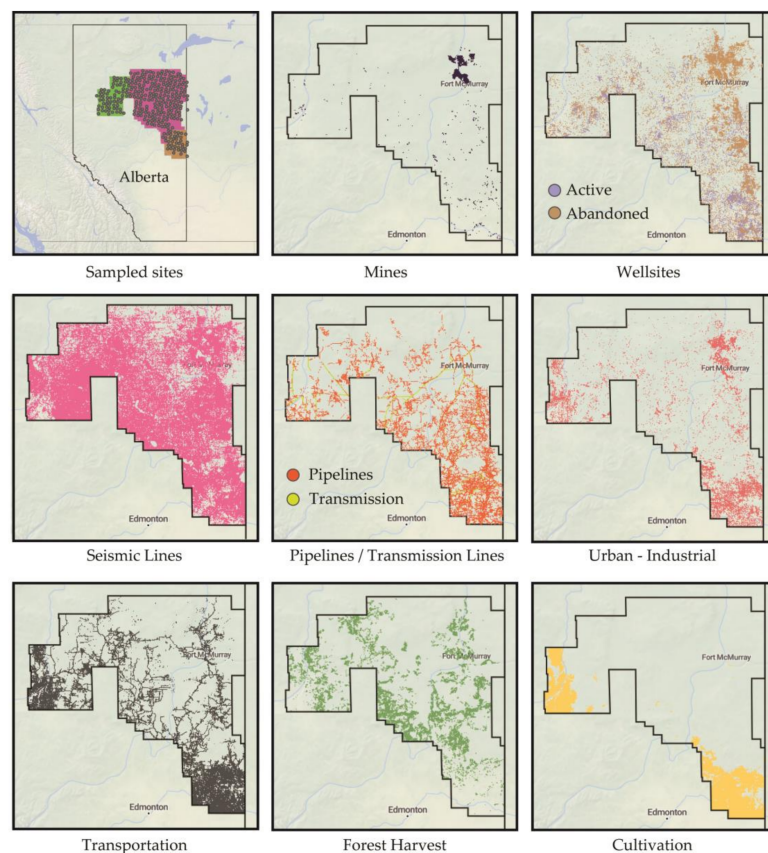
## 2. Materials and Methods

**Study Area.** Our study focused on long term environmental monitoring sites located within the OSR of Alberta, which encompasses the Athabasca, Cold Lake, and Peace River oil sands deposits, a combined area of 140,213 km<sup>2</sup> (Figure 1). Natural land cover in the OSR includes large areas covered by upland and lowland forests and low-lying wetlands, bogs, and fens. Upland forests are treed by trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* (L.) P. Mill.), balsam poplar (*Populus balsamifera* L.), jack pine (*Pinus banksiana* Lamb.), lodgepole pine (*Pinus contorta* Dougl. ex Loud), paper birch (*Betula papyrifera* Marshall), and white spruce (*Picea glauca* (Moench) Voss); the lowlands by black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenburg) and tamarack (*Larix laricina* (Du Roi) K. Koch). There is a wide diversity of understory plants, including flora associated with peatlands. These regions also contain human footprint, including surface mines, in situ well sites, roads, urban and industrial developments, seismic exploration, pipeline and transmission lines, cultivation, and forest harvest. In our study, we analysed data from 420 sites sampled between 2007 and 2019. Some sites received more than one sampling visit, which provided a dataset from a total of 583 site-level collection events during this 13 year time period.

**Field soil sampling.** Sites were selected throughout the OSR following a 20 km systematic grid [64]. Soil samples were taken at each site to monitor oribatid mites following established terrestrial field protocols [65]. In brief, at each 1 ha study site, four 1 m radius soil plots were placed 80 m diagonally from the site centre, i.e., 10 m outside of the northeast, northwest, southeast, and southwest corners of the site. The soil plots were established outside of the main 1 ha site to minimize soil disturbance within the site for other measurements. At each soil plot, at least four 40 cm depth soil cores were taken and laid out on a sheet. The organic layer from these cores was composited, and then 500 mL was measured and placed into a labelled cloth soil bag. If the four cores did not result in enough soil volume, then more soil cores were taken to reach the 500 mL requirement for each plot. Thus, 2 L of organic soil was collected from each site. The soil was placed in coolers with ice and shipped to the ABMI Processing Centre, Edmonton, Alberta, Canada for further processing.

**Oribatid mite extraction and identification.** We used established standard operating procedures to process the soil and oribatid mites [66]. In brief, each organic soil collection was placed on a modified Tullgren funnel for one week with the collection cups containing 100% ethanol for invertebrate preservation. To increase ease of sorting and identification, each invertebrate collection was sieved using stacked 300 µm and 53 µm metal sieves. The 53 µm fractions were labelled and stored in glass scintillation vials in 100% ethanol. The 300 µm fractions were each sorted using a stereoscope to retain all adult oribatid mites > 300 µm in ventral length, and the remaining invertebrates were returned to separate, labelled scintillation vials. All retained oribatid mites were identified to species or morphospecies via stereoscope or compound microscopy using available taxonomic keys and species descriptions [46], then databased and curated as outlined in the standard operating procedures. All resulting slide-mounted and ethanol collections of mites were deposited

in the PMAE Invertebrate Zoology collection at the Royal Alberta Museum, Edmonton, Alberta, Canada.



**Figure 1.** (Top left) is a map of Alberta, Canada showing oribatid mite collection localities within the oil sands region (Athabasca Oil Sand Area in pink, Cold Lake Oil Sand Area in orange, Peace River Oil Sand Area in green), and the remaining maps are of the main human footprint types in the oil sands region in 2018 (available on the ABMI mapping portal at <https://maps.abmi.ca> (accessed on 8 March 2023)).

*Land cover, space, and climate variables.* We examined how natural land cover types, human footprint types, and spatial and climate characteristics impact oribatid mite community structure. We used detailed vegetation and human footprint GIS layers [67] to characterize each of the soil plots using a 10 m buffer radius from the plot centre. The 10 m scale was chosen because oribatid mite communities are thought to show strong microhabitat preference [43–45]. This scale also improves capture of the full characteristics of the soil plot and accounts for potential deviation in plot centre location that may occur due to error in signal propagation while using a handheld GPS receiver. We described the fine-scale habitat characteristics of the 10 m area as proportional area of broad natural land cover types and human footprint types. For our analyses, broad natural land cover types included bog, fen, swamp, pine, deciduous, mixedwood, white spruce, and shrub/grass cover types. We characterized human footprint types as mines, well sites, urban–industrial developments, energy-related seismic lines, and other soft linear features (pipelines, transmission lines), transportation-related soft linear features (vegetation along roads and railways, trails), forest harvesting, and cultivation (e.g., crop, tame pasture). Proportional areas of the natural land cover and human footprint types were calculated for each site by pooling data for the four soil plots, i.e., NE, NW, SE, and SW quadrants. This site-level summary was generated for each site and survey year (Table S1). In addition to spatial variables (latitude, longitude), we considered a broad suite of climate variables including annual heat–moisture index (AHM), frost free period (FFP), mean annual precipitation (MAP), mean annual temperature (MAT), mean coldest month (January) temperature (MCMT), mean warmest month

(July) temperature (MWMT), and potential evapotranspiration (PET). Climate variables were derived from historical weather station data (500 m<sup>2</sup> spatial resolution) using the parameter-elevation regressions on independent slopes model (PRISM) method [68]. We assessed collinearity between climate variables and location using variance inflation factor (VIF) analysis [69]. We performed a stepwise removal process using the *vifstep* function (*usdm* package) [70] in the R statistical package [71] to remove variables with VIF > 5 which led to the retention of FFP, MAP, PET, latitude and longitude.

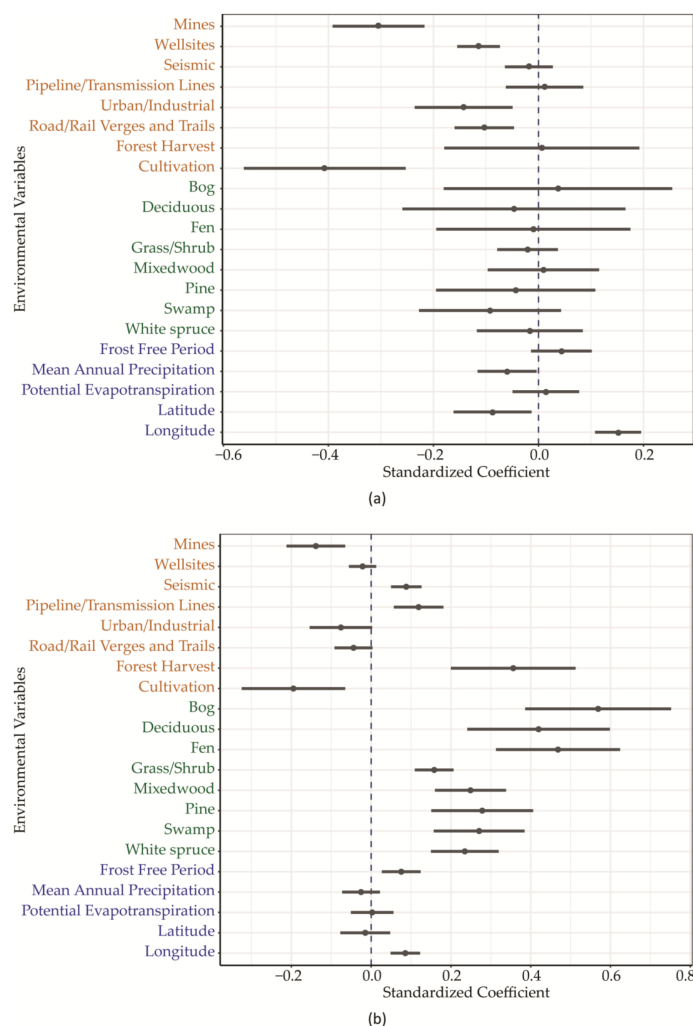
*Statistical analyses.* To reduce within-site variability across soil collections we aggregated the plot (quadrant)-level species abundance of a given site and sampling year to create a site-by-species matrix (Table S2). We used these data as a basis to examine oribatid mite community structure in response to the landscape and spatial-climatic variables in the R statistical package [71]. We calculated total abundance, species richness, Shannon's diversity indices, and the effective number of species (exponential of Shannon's diversity) [72], then assessed their response to the environmental variables using linear regression models. For the models, we transformed the species data by  $\log(x + 1)$  for abundance and richness. We scaled the species and environmental data for all tests to obtain standardized coefficient values across different environmental data types. This allowed us to obtain standardized effect size statistics of different predictors that are measured on different scales and make it possible to compare the relative effects or importance of each of the predictors. Permutational multivariate analysis of variance (PERMANOVA) was used to assess the influence of the environmental variables on mite community composition using the *adonis2* function (*vegan* package) [73] with Bray–Curtis dissimilarity. We used 999 permutations to test the statistical significance of the overall model and of each variable. Because there were sites with no mites recorded that can make their Bray–Curtis dissimilarities meaningless, we added a single dummy species with a negligible abundance (0.00001) so that all sites could be included in the analysis. In addition, we performed redundancy analysis (RDA) to assess overall patterns of association of oribatid mite species with the 21 environmental variables. RDA is a constrained ordination method that summarises the variance explained by the dependent variables by a linear combination of explanatory variables. We assessed the full model and each constrained axis for significance using *anova.cca*. We conducted variance partitioning using the function *varpart* with three categories of the variable: natural land cover types, human footprint types, and climate-space variables.

### 3. Results

*Species data summary.* Within the oil sands region in Alberta, we identified a total of 29,301 oribatid mites between 2007 and 2019, from 583 collection events at 420 sites (Figure 1). These mites were identified to 123 described species and 78 morphospecies, representing 93 genera, 47 families, 25 superfamilies and five infraorder/hyporders (Table A1). Total abundance ranged between 0–239 individuals per site (mean  $\pm$  SD = 50.3  $\pm$  36.8), species richness ranged between 0–33 species per site (mean  $\pm$  SD = 13.2  $\pm$  6.02), Shannon's diversity ranged between 0–3.1 indices per site (mean  $\pm$  SD = 2.0  $\pm$  0.62), and the effective number of species ranged between 1–23.3 species per site (mean  $\pm$  SD = 8.9  $\pm$  4.14) (Table S3).

*Effect of land cover, space, and climate on species abundance, richness and diversity.* The multiple linear regression model for total abundance indicated that the natural land cover, human footprint, space, and climate variables explained 24.3% (adjusted R<sup>2</sup>) of the variation (Table A2). Mines, well sites, cultivation, and longitude significantly explained ( $p < 0.05$ ) variation, while road/rail verges and trails showed a marginally significant ( $p < 0.07$ ) impact on total abundance. Abundance responded negatively to these footprint types and responded positively eastward in longitude (Table A2, Figure 2). The model for species richness explained 43.2% (adjusted R<sup>2</sup>) of the variance. Richness was significantly reduced by mines and cultivation, and significantly increased eastward with longitude. The model showed overall higher species richness with natural land cover and forest harvesting. In addition, less intense human footprint types had greater species richness than intense human footprint types (Table A3). The model for Shannon's diversity revealed that the in-

dependent variables explained 46.4% (adjusted  $R^2$ ) of the variance (Table A4). The diversity increased with natural land cover types (bog, deciduous, fen, grass/shrub, mixedwood, pine, swamp, white spruce), less intense human footprint types (forest harvesting, seismic, pipelines and transmission lines), and longitude. In contrast, intense human footprint types (mines, urban–industrial, cultivation) and vegetated road/trail/verges (transportation soft linear) had a negative effect (Table A4, Figure 2). The model for effective number of species explained 31.7% (adjusted  $R^2$ ) of the variance and the pattern of its relationship with environmental variables was similar to that obtained for Shannon’s diversity.

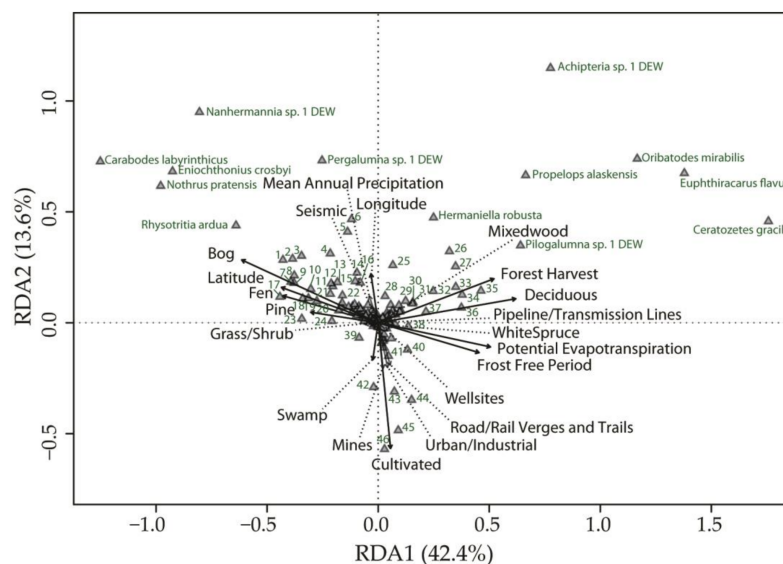


**Figure 2.** Linear regression plots for oribatid mite (a) total abundance and (b) Shannon’s diversity, against 21 land cover and climate–space variables in the oil sands region of Alberta, Canada. Standardized coefficients (i.e., beta weights) allow a better comparison of the relative influence of environmental variables on response variables. For example, total abundance is expected to respond strongly (negatively) to cultivation and mines compared to seismic lines. Word colour: yellow = human footprint; green = natural land cover; blue = climate–space.

*Species composition.* PERMANOVA analysis indicated that mite composition was impacted by land cover composition and spatial climatic variables that together explained 24.5% of the total variance (Table A5). All included variables except seismic, well sites, and mixedwood were significant ( $p < 0.05$ ). Similarly, redundancy analysis indicated that the environmental variables explained 20.8% of the total variance of mite community composition (Figure 3). The overall RDA model was significant ( $p = 0.001$ ), as were the first six axes ( $p < 0.05$ ). The first three RDA axes included 42.4%, 13.6%, and 8.0% of the explained variation, respectively. The ordination plot (Figure 3) showed that the first axis represented

a change in mite composition along a gradient from upland habitat types (positive loading: e.g., deciduous, mixedwood, white spruce, forest harvesting) to lowland habitat types (negative loading: e.g., bog, fen). In addition, it was linked to a gradient in climate (positive loading: FFP, PET) and spatial variables (negative loading: latitude). The second RDA axis represented a change in mite composition from natural land cover types and less intense human footprint types (positive loading: bog, deciduous, fen, forest harvesting) to more intense human footprint types (negative loading: mines, urban–industrial, transportation soft linear, cultivation). The second axis was also linked to a gradient in climate and spatial variables (positive loading: MAP, latitude, longitude; negative loading: FFP, PET). The third axis had a very high positive loading for pine and latitude, and a negative loading for PET and FFP.

Variance partitioning indicated that natural land cover types (adjusted  $R^2$ : 11.8%) contributed the most to differences in oribatid mite community structure, and human footprint types (adjusted  $R^2$ : 5.5%) and climate–space (adjusted  $R^2$ : 5.6%) contributed equally (Table A6). The adjusted  $R^2$  value gives the full contribution of each partition, including unique contribution (natural land cover = 7%, human footprint = 3%, climate–space = 3%) and overlap (natural land cover/human footprint = 2%, natural land cover/climate–space = 2%, and natural land cover/human footprint/climate–space = 1%).



**Figure 3.** Redundancy analysis (RDA) plot of oribatid mite composition against 21 land cover and climate–space variables in the oil sands region of Alberta, Canada. The proportion of variance explained in each axis is shown. The triangles represent 201 oribatid mite species. The most visible triangles are labelled with the species name or numbered as follows: 1. *Cepheus* sp. 1 DEW, 2. *Allosuctobelba* sp. 2 DEW, 3. *Hoplophthiracarus illinoisensis*, 4. *Trhypochthonius tectorum*, 5. *Schelorbates pallidulus*, 6. *Ceratoppia quadridentata arctica*, 7. *Scutozetes lanceolatus*, 8. *Hydrozetes* sp. E RAN, 9. *Roynortonella* sp. 1 DEW, 10. *Mainothrus badius*, 11. *Dentizetes ledensis*, 12. *Protoribates haughlandae*, 13. *Carabodes granulatus*, 14. *Tectocephus velatus*, 15. *Nothrus* sp. B DEW, 16. *Hypochthonius rufulus*, 17. *Unduloribates diana*, 18. *Eremaeus translamellatus*, 19. *Heminothrus longisetosus*, 20. *Neonothrus humicola*, 21. *Platynothrus peltifer*, 22. *Trimalaconothrus maior*, 23. *Mycobates incurvatus*, 24. *Eueremaeus quadrilamellatus*, 25. *Diapterobates humeralis*, 26. *Phthiracarus boresetosus*, 27. *Chamobates cuspidatus*, 28. *Peloribates* sp. 3 DEW, 29. *Zetomimus francisi*, 30. *Ceratozetes cuspidatus*, 31. *Carabodes polyporetetes*, 32. *Phthiracarus borealis*, 33. *Epidamaeus* sp. 2 DEW, 34. *Epidamaeus coxalis*, 35. *Gymnodamaeus ornatus*, 36. *Platynothrus yamasakii*, 37. *Quatrobelba montana*, 38. *Dorycranosus acutidens*, 39. *Epidamaeus arcticolus*, 40. *Fuscozetes fuscipes*, 41. *Trichoribates striatus*, 42. *Peloribates pilosus*, 43. *Tectocephus sarekensis*, 44. *Anachipteria howardi*, 45. *Peloptulus* sp. 1 DEW, 46. *Oribatula* sp. 1 DEW. See Table S4 for species scores, Table S5 for site scores, and Table S6 for biplot scores for constraining variables.

#### 4. Discussion

We found that natural land cover, human footprint, climate, and space significantly contributed to mite community structure in Canada's oil sands region. Our results showed a differential impact of human footprint types on abundance, species richness, and diversity indices in mite communities. Among energy-related footprint types, oribatid mites were more affected in mines, with lower abundance and richness than at well sites, seismic lines, pipelines, or transmission lines. However, the relative impact of mines appeared to be lower than for cultivation, and it is likely that sites with mine footprint were located within the mine buffer zone which may have undergone some degree of reclamation, in contrast to active mining sites. This may also have been the case for well sites. In addition, the sample size with energy-related footprint was small (for mines and well sites) and the sampled sites included a mosaic of other habitat types besides energy-related footprints which may obscure the full impact of these human footprint types on oribatid mites detected in our analyses. These results suggest that targeted sampling of oribatid mites in these footprint types, and relating their abundance and diversity metrics to soil and habitat quality parameters (including post-reclamation) will be of particular importance for future study. Using oribatid mites as an indicator of soil organism response to reclamation practices has been successful both within [34] and outside [28,74–76] the boundaries of the OSR, supporting their use as bioindicators for this purpose.

We found that total oribatid mite abundance was similar across natural land cover types as well as most human footprint types (e.g., forestry, seismic lines) except for being significantly negatively impacted by mines, well sites, and cultivation. This suggests the latter human footprint types could have a more significant effect on soil health due to the practice of removing or recurrently disturbing the topsoil and the supported fauna and flora. Several studies have revealed that the abundance of oribatid mites, and consequently their richness, typically increases in the topsoil because of the rich supply of food sources, including dead organic material in the litter (LFH), fungi, and bacteria [77–79]. However, when land use practices severely alter or remove the topsoil, such as through surface mining and cultivation, the soil fauna are also impacted. For example, studies have found that soil mite abundance and diversity were lower in agricultural sites than in forest sites [51,79], a finding that our study also supports. However, the same negative effect on abundance was not evident for other energy related activities (e.g., seismic lines) or for forest harvesting, which showed similar abundance to that found in natural land cover types. This suggests that such successional human footprint types that retain most of the topsoil biological legacy, including the organic matter, can sustain abundant oribatid mite fauna. Finally, forest type differences, which can include differences in understory plant composition, litter composition, and abiotic soil conditions, appear to have limited effect on the total abundance of oribatid mites at broad spatial scale.

Despite their similar influence on total mite abundance, the relative responses of mite diversity indices appear to differ among natural land cover, forest harvesting, and energy-related soft linear human footprints (seismic lines, pipelines, and transmission lines). In particular, the relative influence of energy-related linear human footprints on species diversity, albeit positive, was lower than that of natural land cover and forest harvesting. Differences in linear human footprints such as area, shape, and associated physico-chemical changes could have contributed to such differences [11]. Our analyses also emphasize that the other human footprint types (cultivation, mines, road/trail verges) with more impact on soil integrity (e.g., through prolonged removal, mixing of soil horizons, change in soil structure, or soil compaction) lowered diversity further. More focused efforts to study linear disturbances would be helpful as we have little to no understanding of how edge effects from these disturbance types impact soil mite biodiversity in the OSR, including transportation-related pollutants, seismic-related compaction and shock waves, and changes to microclimate (e.g., light, temperature, moisture). Distance-to-edge transects that include soil sampling and analyses of oribatid mites would improve understanding of soil condition and soil biodiversity within these linear features.



Our study also showed differentiation of mite community composition along gradients of land cover composition. In particular, there was a notable difference in mite composition between lowland bog and fen habitats and the upland forest types, including deciduous and mixedwood forests and harvested sites, indicating a strong link between above- and belowground biodiversity. Soils influence the occurrence and distribution of different biomes globally, including both overstory composition and belowground biodiversity [80]. In turn, overstory composition influences soil characteristics, including the amount and diversity of litter, peat, and other biotic (e.g., fungal diversity) and abiotic (e.g., pH) properties that potentially drive community structure of oribatid mites [81–85]. In our study, species such as *Epidamaeus coxalis* and *Euphthiracarus flavus* were more abundant in upland forests, while species such as *Carabodes labyrinthicus* and *Hoplophthiracarus illinoisensis* were differentially abundant in lowland habitats. Our results also support that changes to overstory composition (e.g., through human disturbance) can lead to changes in belowground mite composition. We detected a compositional difference between intense human footprint types (e.g., mines, cultivation) from the natural land cover and forest harvest sites. This is not surprising given the low abundance and richness of mites in those human footprint types compared to in natural habitats. In addition, we found dominance by a small number of species in those human footprint types; for example, the morphospecies *Oribatula* sp. 1 DEW and *Tectocephus sarekensis* were associated with cultivated sites. Further work is needed to study and clarify the relationships of individual oribatid mite species to natural land cover and human footprint types within the OSR, along with their functions within these systems.

Our analyses also showed that space and climate variables influence mite communities. Total abundance, richness, and diversity of oribatid mites significantly increased with eastward longitude. Variance partitioning also showed that, although natural land cover types contributed the most to differences in oribatid mite community structure, both human footprint types and large scale space and climate variables related to temperature (FFP, PET, Latitude) and precipitation (MAP) also contributed to differences in mite community composition. The species composition relationship to these broad scale environmental variables might reflect individual species' tolerances (preferences) to climate variables, biogeographical or land-use history, or other spatially structured unmeasured environmental variables such as soil properties [84,86] that are known to influence mite communities. For example, *Epidamaeus coxalis* correlated with both westward longitude and the increased mean annual precipitation that follows along the foothills to the southwest, indicating that these large-scale climate patterns are influencing species distributions. Other species were influenced by frost-free period, which was highly positively correlated with annual heat-moisture index (AHM), mean warmest month (July) temperature, and mean annual temperature (MAT). Some species were positively correlated with increased FFP (e.g., *Atropacarus striculus*) whereas others were negatively correlated (e.g., *Malaconothrus mollisetosus*, *Neonothrus humicola*). These differences may reflect species' preferences or tolerance to temperature gradients in this large expanse of boreal forest, including those associated with elevation gradients such as the Birch Mountains and the eastward extension of the foothills into the region. We note that disturbance has been advocated as the primary factor driving plant and animal abundance and distribution [79] and there are spatial differences in human footprint types across the OSR, such as higher mining activity in the northeast, higher concentration of well sites and pipelines towards the east, higher density of cultivated sites along the western and southern borders, and different patterns of density across the landscape in forest harvest and seismic lines (see Figure 1 or ABMI mapping portal at <https://maps.abmi.ca> (accessed on 8 March 2023)). We also note that large-scale quantification of abiotic variables will not have captured fine scale (microclimate) differences that arise due to factors such as habitat structure and topography differences, which can also be important for mite community structure. For example, forest harvesting can modify local soil temperature and moisture regimes [87], moisture differences in peatland hummocks and hollows have been associated with differences in oribatid community struc-

ture [45], and air temperature has been found to influence the dispersion of oribatid mites among forest microhabitats [44].

The current study has some important limitations that need to be addressed to answer more targeted environmental effects monitoring or ecological questions specific to the OSR. First, due to the limitations of the existing dataset being used, the number of sites sampled with energy-related human footprints is relatively small, in particular those related to surface mines and well sites. Second, the sampled sites included a mosaic of habitat and land use types, which may obscure the full impact of each human footprint type. Third, further work to assess functional groups may help to provide greater insight into stability, resistance, and resilience of lands significantly altered by intense human footprint types (cultivation, mines, well sites). There is a limit to the number of individuals that can fill a community, or a standardized volume of soil as was our sampling method, and changes to soil conditions may decrease available food and space. However, the much debated diversity–stability theory [88] proposes that multiple species present in the community can stabilize ecosystem processes if these species vary in response to environmental conditions, such that an increase in abundance of one species can compensate for the decreased abundance of another. In addition, the insurance hypothesis [89] suggests that biologically diverse communities provide resilience to an ecosystem because the accumulation of species increases the probability that any one of them will have the necessary traits to adapt to a changing environment and to act as a buffer against loss of other species. As such, the comparison of patterns in total abundance and species richness and diversity may provide information on ecosystem resilience. We found less intense human footprint types to have similar total abundance to natural land cover types but reduced species richness and diversity, indicating that there were species negatively impacted by the human footprint but also other species present that could adapt and act as a buffer with increased abundance. For intense human footprint types, the combined reduction in total abundance, richness and diversity may indicate that these ecosystems are destabilized, lacking the diverse community needed to compensate for species-level changes in abundance and thereby facing a loss in resilience. Similar results have been found by other studies on intense disturbance practices, for example with soil microbial communities [90]. Assessing oribatid mite functional groups may help to further connect changes in abundance and diversity to stability, resistance, and resilience of ecosystems in the OSR.

A focal research question in the energy industry has been the challenge of reclaiming lands impacted by the various energy-related human footprints [91]. For example, in Alberta there are more than 239,000 drilled well sites, of which ~24% have been certified as reclaimed or exempted [92]. The long-term goal of reclamation of Alberta's well sites is to return the disturbed land to support biodiversity and various land uses similar to what existed prior to exploitation/development activities (i.e., equivalent land capability) [93,94]. Various ecological indicators are used to assess the long-term recovery of reclaimed lands including soil biodiversity and physico-chemical attributes [12,34,86,93] and aboveground plant communities [13,95,96]. The assessment of soil health recovery might be considered a key component in the evaluation of post-reclamation ecological recovery of mines, and oribatid mites have been studied and suggested as biological indicators of soil recovery for this human footprint type [34]. Future investigation of soil conditions could benefit from targeted sampling of oribatid mite communities in energy footprints, including following post-mining reclamation and recovery.

In conclusion, oribatid mite communities show a clear response at the landscape-level to natural land cover, anthropogenic disturbance, space, and climate in the Canadian oil sands region. As a result, this taxonomic group could be a strong bioindicator for future efforts to assess soil condition in the OSR. Their response to land use in the region could be further delineated with an experimental design specific to studying footprint and cumulative effects such as the Hierarchical Before-After Dose–response (BADR) monitoring design currently under investigation using other taxa [97]. In addition, experimental design specific to assessment of management strategies within land use types (e.g., reclamation

practices in energy, management practices in forestry or agricultural production) are necessary to make further conclusions on best management practices to maintain soil biodiversity in the OSR.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15040469/s1>, Table S1: Environmental data including spatial-climatic, human footprint, and broad natural land cover data for each site collection event in the oil sands region of Alberta, Canada; Table S2: Site by species matrix with species abundance data summed for each site collection event in the oil sands region of Alberta, Canada; Table S3: Site summary with oribatid mite total abundance, species richness, Shannon’s diversity index, and effective number of species.; Table S4: Species scores from redundancy analysis (RDA) of oribatid mite composition against 21 land cover and climate–space variables in the oil sands region of Alberta, Canada; Table S5: Site scores from redundancy analysis (RDA) of oribatid mite composition against 21 land cover and climate–space variables in the oil sands region of Alberta, Canada; Table S6: Biplot scores from redundancy analysis (RDA) of oribatid mite composition against 21 land cover and climate–space variables in the oil sands region of Alberta, Canada.

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## Appendix A

**Table A1.** Summary of oribatid mite species detected in the oil sands region of Alberta, Canada.

Superfamily	Family	Species	Author
Parhypochthonioidea	Gehypochthoniidae	<i>Gehypochthonius</i> sp. 1 LML	
Brachychthonioidea	Brachychthoniidae	<i>Eobrachychthonius latior</i>	(Berlese, 1910)
Hypochthonioidea	Eniochthoniidae	<i>Eniochthonius crosbyi</i>	(Ewing, 1909)
		<i>Eniochthonius mahunkai</i>	Norton and Behan-Pelletier, 2007
		<i>Eniochthonius minutissimus</i>	(Berlese, 1903)
	Hypochthoniidae	<i>Eniochthonius</i> sp. 1 LML	
		<i>Hypochthonius luteus</i>	Oudemans, 1917
		<i>Hypochthonius rufulus</i>	C.L. Koch, 1836

Table A1. Cont.

Superfamily	Family	Species	Author	
Euphthiracaroida	Euphthiracaridae	<i>Euphthiracarus</i> cf. <i>flavus</i>	(Ewing, 1908)	
		<i>Euphthiracarus</i> cf. <i>fulvus</i>	(Ewing, 1909)	
		<i>Rhysotritia ardua</i>	(C.L. Koch, 1841)	
	Oribotritiidae	<i>Mesotritia nuda</i>	(Berlese, 1887)	
		<i>Protoribotritia</i> sp. 1 DEW		
Phthiracaroida	Phthiracaridae	<i>Atropacarus striculus</i>	(C. L. Koch, 1835)	
		<i>Hoplophthiracarus illinoisensis</i>	(Ewing, 1909)	
		<i>Phthiracaridae</i> sp.		
		<i>Phthiracarus boresetosus</i>	Jacot, 1930	
Crotonioidea	Crotoniidae	<i>Phthiracarus</i> cf. <i>borealis</i>	(Trägårdh, 1910)	
		<i>Camisia biurus</i>	(C.L. Koch, 1839)	
		<i>Camisia biverrucata</i>	(CL Koch, 1839)	
		<i>Camisia horrida</i>	(Hermann, 1804)	
		<i>Camisia</i> sp. 1 DEW		
		<i>Camisia spinifer</i>	(C.L. Koch, 1835)	
		<i>Heminothrus longisetosus</i>	Willmann, 1925	
		<i>Heminothrus thori</i>	(Berlese, 1904)	
		<i>Neonothrus humicola</i>	Forslund, 1955	
		<i>Platynothrus peltifer</i>	(C.L. Koch, 1839)	
	<i>Platynothrus sibiricus</i>	Sitnikova, 1975		
			<i>Platynothrus</i> sp. 1 DEW	
			<i>Platynothrus yamasakii</i>	Aoki, 1958
		Malaconothridae	<i>Malaconothrus</i> cf. <i>mollisetosus</i>	Hammer, 1952
			<i>Trimalaconothrus foveolatus</i>	(Willmann, 1931)
			<i>Trimalaconothrus maior</i>	(Berlese, 1910)
			<i>Trimalaconothrus</i> sp. 3 DEW	
	Nanhermanniidae	<i>Nanhermannia</i> sp. 1 DEW		
	Nothridae	<i>Nothrus anauniensis</i>	Canestrini and Fanzago, 1876	
		<i>Nothrus borussicus</i>	Sellnick, 1928	
		<i>Nothrus</i> cf. <i>pratensis</i>	Sellnick, 1928	
		<i>Nothrus</i> sp. B DEW		
	Trhypochthoniidae	<i>Mainothrus badius</i>	(Berlese, 1905)	
		<i>Mucronothrus nasalis</i>	(Willmann, 1929)	
		<i>Trhypochthoniellus setosus</i>	Hammer, 1952	
		<i>canadensis</i>		
		<i>Trhypochthonius</i> cf. <i>cladonicola</i>	(Willmann, 1919)	
		<i>Trhypochthonius</i> cf. <i>nigricans</i>	Willmann, 1928	
		<i>Trhypochthonius tectorum</i>	(Berlese, 1896)	
Achipterioidea	Achipteriidae	<i>Achipteria coleoprata</i>	(Linnaeus, 1758)	
		<i>Achipteria</i> sp. 1 DEW		
		<i>Anachipteria</i> cf. <i>howardi</i>	(Berlese, 1908)	
		<i>Anachipteria</i> sp. 1 DEW		
		<i>Parachipteria bella</i>	(Sellnick, 1928)	
		<i>Parachipteria</i> sp.		
		<i>Parachipteria</i> sp. 1 DEW		
	Tegoribatidae	<i>Tegoribates americanus</i>	Hammer, 1958	
		<i>Tegoribates subniger</i>	Ewing, 1917	
Carabodoidea	Carabodidae	<i>Carabodes granulatus</i>	Banks, 1895	
		<i>Carabodes labyrinthicus</i>	(Michael, 1879)	
		<i>Carabodes polyporetetes</i>	Reeves, 1991	
		<i>Carabodes wonalancetanus</i>	Reeves, 1990	

Table A1. Cont.

Superfamily	Family	Species	Author
Cepheoidea	Cepheidae	<i>Cepheus</i> sp. 1 DEW <i>Cepheus</i> sp. 2 DEW <i>Cepheus</i> sp. 2B DEW <i>Oribatodes mirabilis</i>	Banks, 1895
Ceratozetoidea	Ceratozetidae	<i>Ceratozetes cuspidatus</i> <i>Ceratozetes gracilis</i> <i>Ceratozetes mediocris</i> <i>Ceratozetes parvulus</i> <i>Ceratozetes</i> sp. 1 LML <i>Ceratozetes</i> sp. 2 LML <i>Ceratozetes thienemanni</i> <i>Dentizetes ledensis</i> <i>Diapterobates humeralis</i> <i>Diapterobates</i> sp. <i>Diapterobates variabilis</i> <i>Fuscozetes fuscipes</i> <i>Lepidozetes singularis</i> <i>Lepidozetes</i> sp. 1 DEW <i>Neogymnobates luteus</i> <i>Neogymnobates</i> sp. 1 DEW <i>Scutozetes lanceolatus</i> <i>Sphaerozetes arcticus</i> <i>Sphaerozetes</i> sp. 1 DEW <i>Trichoribates copperminensis</i> <i>Trichoribates</i> sp. <i>Trichoribates</i> sp. 2 DEW <i>Trichoribates</i> sp. 3 DEW <i>Trichoribates</i> sp. 5 LML <i>Trichoribates striatus</i>	Jacot, 1939 (Michael, 1884) Berlese, 1908 Sellnick, 1922  Willmann, 1943 Behan-Pelletier, 2000 (Hermann, 1804)  Hammer, 1955 (C.L. Koch, 1844) Berlese, 1910  (Hammer, 1955)  Hammer, 1952 Hammer, 1952  Hammer, 1952
	Chamobatidae	<i>Chamobates</i> cf. <i>cuspidatus</i> <i>Chamobates</i> sp. 2 DEW	(Michael, 1884)
	Punctoribatidae	<i>Mycobates hylaeus</i> <i>Mycobates incurvatus</i> <i>Mycobates perates</i> <i>Pelopsis bifurcatus</i> <i>Punctoribates palustris</i>	Behan-Pelletier, 1994 Hammer, 1952 Behan-Pelletier, 1994 (Ewing, 1909) (Banks, 1895)
	Zetomimidae	<i>Heterozetes aquaticus</i> <i>Zetomimus francisi</i>	(Banks, 1895) (Habeeb, 1974)
Cymbaeremaeoidea	Cymbaeremaeidae	<i>Scapheremaeus palustris</i>	(Sellnick, 1924)
Damaeioidea	Damaeidae	<i>Dyobelba</i> sp. 1 DEW <i>Epidamaeus arcticolus</i> <i>Epidamaeus canadensis</i> <i>Epidamaeus</i> cf. <i>fortispinosus</i> <i>Epidamaeus coxalis</i> <i>Epidamaeus floccosus</i> <i>Epidamaeus koyukon</i> <i>Epidamaeus</i> sp. 1 DEW <i>Epidamaeus</i> sp. 2 DEW <i>Epidamaeus</i> sp. 3 DEW <i>Epidamaeus</i> sp. 4 DEW <i>Epidamaeus</i> sp. 5 DEW <i>Epidamaeus</i> sp. 8 DEW <i>Epidamaeus tritylos</i> <i>Quatrobrelba montana</i>	(Hammer, 1952) (Banks, 1909) Hammer, 1967 (Hammer, 1952) Behan-Pelletier and Norton, 1985 Behan-Pelletier and Norton, 1985             Behan-Pelletier and Norton, 1983 Norton, 1980
Galumnoidea	Galumnidae	<i>Galumna</i> sp. 1 DEW <i>Pergalumna</i> sp. 1 DEW <i>Pilogalumna</i> sp. <i>Pilogalumna</i> sp. 1 DEW <i>Pilogalumna</i> sp. 2 DEW	

Table A1. Cont.

Superfamily	Family	Species	Author		
Gustavioidea	Astegistidae	<i>Astegistes</i> sp. 1 DEW			
	Gustaviidae	<i>Gustavia</i> sp. 1 DEW			
	Liacaridae	<i>Dorycranosus</i> cf. <i>acutidens</i>	(Aoki, 1965)		
		<i>Dorycranosus parallelus</i>	(Hammer, 1967)		
		<i>Dorycranosus</i> sp. 4 DEW			
	Peloppiidae	<i>Ceratoppia bipilis</i>	(Hermann, 1804)		
<i>Ceratoppia quadridentata arctica</i>		Hammer, 1955			
Hermannelloidea	Tenuialidae	<i>Hafenferrefia</i> sp. 1 DEW			
	Hermannelliidae	<i>Hermannella robusta</i>	Ewing, 1918		
Licneremaeoidea	Passalozetidae	<i>Bipassalozetes</i> cf. <i>intermedius</i>	(Mihelčič, 1954)		
Limnozetoidea	Hydrozetidae	<i>Hydrozetes octosetosus</i>	Willmann, 1932		
		<i>Hydrozetes</i> sp.			
		<i>Hydrozetes</i> sp. 1 DEW			
		<i>Hydrozetes</i> sp. 2 DEW			
		<i>Hydrozetes</i> sp. 3 DEW			
	Limnozetidae	<i>Hydrozetes</i> sp. E RAN			
		<i>Limnozetes canadensis</i>	Hammer, 1952		
		Oppioidea	Autognetidae	<i>Autogneta</i> sp. 2 DEW	
			Oppiidae	<i>Moritzoppia</i> sp. 1 DEW	
				<i>Multioppia</i> sp. 1 DEW	
<i>Oppiella</i> cf. <i>washburni</i>	(Hammer, 1952)				
<i>Oppiella</i> sp. 2 DEW					
Oribatelloidea	Thyrisomidae	<i>Oppiella</i> sp. 3 DEW			
		<i>Oppiella</i> sp. 4 LML			
		<i>Ramusella</i> sp. 2 DEW			
		<i>Banksinoma lanceolata canadensis</i>	Fujikawa, 1979		
		<i>Banksinoma spinifera</i>	(Hammer, 1952)		
	Oribatellidae	<i>Oribatella banksi</i>	Behan-Pelletier and Walter, 2012		
		<i>Oribatella ewingi</i>	Behan-Pelletier and Walter, 2012		
		<i>Oribatella jacoti</i>	Behan-Pelletier, 2011		
		<i>Oribatella reticulatoides</i>	Hammer, 1955		
		<i>Oribatella yukonensis</i>	Behan-Pelletier and Walter, 2012		
Oripodoidea	Haplozetidae	<i>Peloribates canadensis</i>	Hammer, 1952		
		<i>Peloribates pilosus</i>	Hammer, 1952		
		<i>Peloribates</i> sp.			
		<i>Peloribates</i> sp. 3 DEW			
		<i>Peloribates</i> sp. 4 DEW			
		<i>Protoribates haughlandae</i>	Walter and Latonas, 2013		
		<i>Protoribates robustior</i>	(Jacot, 1937)		
		<i>Protoribates</i> sp.			
		<i>Protoribates</i> sp. 3 LML			
		<i>Podoribates longipes</i>	(Berlese, 1887)		
	Mochlozetidae	Oribatulidae	<i>Eporibatula</i> sp. 1 DEW		
			<i>Lucoppia burrowsii</i>	(Michael, 1890)	
			<i>Oribatula</i> sp. 1 DEW		
			<i>Oribatula</i> sp. 2 LML		
			<i>Phauloppia boletorum</i>	(Ewing, 1913)	
Parakalummidae	Schelorbitidae	<i>Zygoribatula bulanovae</i>	Kulijew, 1961		
		<i>Zygoribatula</i> sp. 1 DEW			
		<i>Zygoribatula</i> sp. 2 DEW			
		<i>Neoribates</i> sp. 1 DEW			
		<i>Neoribates</i> sp. 2 DEW			
	Schelorbitidae	<i>Domatorina plantivaga</i>	(Berlese, 1895)		
		<i>Hemileius haydeni</i>	(Higgins and Woolley, 1975)		
		<i>Paraleius leontonycha</i>	(Berlese, 1910)		
		<i>Scheloribates laevigatus</i>	(C.L. Koch, 1835)		
		<i>Scheloribates pallidulus</i>	(C.L. Koch, 1841)		
		<i>Scheloribates</i> sp.			
		<i>Scheloribates</i> sp. 3 DEW			

Table A1. Cont.

Superfamily	Family	Species	Author
Phenopeloidea	Phenopelopidae	<i>Eupelops</i> cf. <i>septentrionalis</i>	(Trägårdh, 1910)
		<i>Eupelops</i> sp. 2 DEW	
		<i>Eupelops</i> sp. 3 DEW	
		<i>Peloptulus</i> sp. 1 DEW	
		<i>Propelops alaskensis</i>	(Hammer, 1955)
		<i>Propelops canadensis</i>	(Hammer, 1952)
Plateremaeoidea	Unduloribatidae	<i>Unduloribates diana</i>	Behan-Pelletier and Walter, 2009
	Gymnodamaeidae	<i>Gymnodamaeus</i> cf. <i>ornatus</i>	Hammer, 1952
		<i>Pleodamaeus</i> sp. 1 DEW	
		<i>Roynortonella gildersleeveae</i>	(Hammer, 1952)
Tectocephoidea	Tectocephidae	<i>Tectocephus sarekensis</i>	Trägårdh, 1910
		<i>Tectocephus velatus</i>	(Michael, 1880)
Trizetoidea	Suctobelbidae	<i>Allosuctobelba gigantea</i>	(Hammer, 1955)
		<i>Allosuctobelba</i> sp. 2 DEW	
		<i>Suctobelbella punctata</i>	(Hammer, 1955)
		<i>Suctobelbella</i> sp. 2 DEW	
Zetorchestoidea	Eremaeidae	<i>Suctobelbella</i> sp. 3 DEW	
		<i>Eremaeus</i> sp.	
		<i>Eremaeus translamellatus</i>	Hammer, 1952
		<i>Eueremaes</i> cf. <i>quadrilamellatus</i>	(Hammer, 1952)
		<i>Eueremaes foveolatus</i>	(Hammer, 1952)
		<i>Eueremaes marshalli</i>	Behan-Pelletier, 1993
		<i>Eueremaes masinasin</i>	Behan-Pelletier, 1993
		<i>Eueremaes trionus</i>	(Higgins, 1979)

Table A2. Summaries of multiple regression model of total abundance of oribatid mites in the oil sands region of Alberta, Canada.

	Coefficient	Standard Error	Standardized Coefficient	Standard Error	
Energy Footprint					
Mines	−2.314	0.664	−0.305	0.087	***
Well sites	−3.733	1.329	−0.114	0.041	**
Seismic	−0.426	1.062	−0.018	0.045	
Pipeline/Transmission Lines	0.108	0.696	0.011	0.074	
Other Human Footprint					
Urban/Industrial	−0.982	0.641	−0.143	0.093	
Road/Rail Verges and Trails	−2.181	1.197	−0.103	0.057	
Forest Harvest	0.021	0.619	0.006	0.186	
Cultivation	−1.653	0.626	−0.407	0.154	**
Natural Land Cover					
Bog	0.104	0.610	0.037	0.218	
Deciduous	−0.134	0.611	−0.047	0.212	
Fen	−0.033	0.618	−0.010	0.185	
Grass/Shrub	−0.279	0.773	−0.021	0.058	
Mixedwood	0.056	0.640	0.009	0.106	
Pine	−0.178	0.621	−0.043	0.152	
Swamp	−0.430	0.630	−0.092	0.135	
White spruce	−0.107	0.654	−0.017	0.101	
Climate					
Frost Free Period	0.006	0.008	0.044	0.058	
Mean Annual Precipitation	−0.002	0.002	−0.060	0.056	
Potential Evapotranspiration	0.000	0.002	0.014	0.063	

**Table A2.** *Cont.*

	Coefficient	Standard Error	Standardized Coefficient	Standard Error	
Space					
Latitude	−0.077	0.066	−0.087	0.074	
Longitude	<b>0.068</b>	0.020	<b>0.152</b>	0.044	***

Significant relationships shown in bold: \* <0.05, \*\* <0.01, \*\*\* <0.001.

**Table A3.** Summaries of multiple regression model of species richness for oribatid mites in the oil sands region of Alberta, Canada.

	Coefficient	Standard Error	Standardized Coefficient	Standard Error	
Energy Footprint					
Mines	− <b>1.291</b>	0.381	− <b>0.257</b>	0.076	***
Well sites	−1.058	0.761	−0.049	0.035	
Seismic	0.757	0.609	0.049	0.039	
Pipeline/Transmission Lines	0.409	0.399	0.066	0.064	
Other Human Footprint					
Urban/Industrial	−0.653	0.367	−0.144	0.081	
Road/Rail Verges and Trails	−0.961	0.686	−0.069	0.049	
Forest Harvest	0.418	0.355	0.190	0.161	
Cultivation	− <b>0.937</b>	0.359	− <b>0.349</b>	0.134	**
Natural Land Cover					
Bog	0.612	0.349	0.330	0.188	
Deciduous	0.365	0.350	0.192	0.184	
Fen	0.585	0.354	0.265	0.160	
Grass/Shrub	0.681	0.443	0.077	0.050	
Mixedwood	0.572	0.367	0.143	0.092	
Pine	0.268	0.356	0.099	0.131	
Swamp	0.301	0.361	0.098	0.117	
White spruce	0.469	0.375	0.109	0.087	
Climate					
Frost Free Period	0.005	0.004	0.055	0.050	
Mean Annual Precipitation	−0.001	0.001	−0.038	0.049	
Potential Evapotranspiration	0.001	0.001	0.030	0.055	
Space					
Latitude	−0.017	0.038	−0.030	0.064	
Longitude	<b>0.036</b>	0.011	<b>0.121</b>	0.038	**

Significant relationships shown in bold: \* <0.05, \*\* <0.01, \*\*\* <0.001.

**Table A4.** Summaries of multiple regression model of Shannon's diversity for oribatid mites in the oil sands region of Alberta, Canada.

	Coefficient	Standard Error	Standardized Coefficient	Standard Error	
Energy Footprint					
Mines	−0.716	0.380	−0.139	0.074	
Well sites	−0.477	0.760	−0.021	0.034	
Seismic	<b>1.398</b>	0.608	<b>0.088</b>	0.038	*
Pipeline/Transmission Lines	0.764	0.398	0.119	0.062	
Other Human Footprint					
Urban/Industrial	−0.355	0.367	−0.076	0.078	
Road/Rail Verges and Trails	−0.634	0.685	−0.044	0.048	
Forest Harvest	<b>0.807</b>	0.354	<b>0.356</b>	0.156	*
Cultivation	−0.538	0.358	−0.195	0.130	



**Table A4.** *Cont.*

	Coefficient	Standard Error	Standardized Coefficient	Standard Error	
Natural Land Cover					
Bog	<b>1.085</b>	0.349	<b>0.569</b>	0.183	**
Deciduous	<b>0.821</b>	0.350	<b>0.420</b>	0.179	*
Fen	<b>1.065</b>	0.354	<b>0.469</b>	0.156	**
Grass/Shrub	<b>1.439</b>	0.442	<b>0.158</b>	0.049	**
Mixedwood	<b>1.022</b>	0.366	<b>0.249</b>	0.089	**
Pine	<b>0.775</b>	0.355	<b>0.278</b>	0.128	*
Swamp	<b>0.857</b>	0.360	<b>0.271</b>	0.114	*
White spruce	<b>1.035</b>	0.374	<b>0.235</b>	0.085	**
Climate					
Frost Free Period	0.007	0.004	0.075	0.049	
Mean Annual Precipitation	−0.001	0.001	−0.025	0.047	
Potential Evapotranspiration	0.000	0.001	0.003	0.053	
Space					
Latitude	−0.009	0.038	−0.015	0.062	
Longitude	<b>0.026</b>	0.011	<b>0.086</b>	0.037	*

Significant relationships shown in bold: \* <0.05, \*\* <0.01, \*\*\* <0.001.

**Table A5.** Permutational Multivariate Analysis of Variance (PERMANOVA) results showing the significance for each natural land cover, human footprint, space, and climate variable on differences in community structure of oribatid mites for 583 site-level collection events within the oil sands region of Alberta, Canada. The total variance explained by the model was 24.5% (Pr (>F) = 0.001).

	Df	Sum of Sqs	R <sup>2</sup>	F	Pr (>F)	
Energy Footprint						
Mines	1	1.604	0.008	5.717	<b>0.001</b>	***
Well sites	1	0.410	0.002	1.462	0.080	
Seismic	1	0.380	0.002	1.354	0.116	
Pipeline/Transmission Lines	1	1.049	0.005	3.737	<b>0.001</b>	***
Other Human Footprint						
Urban/Industrial	1	1.292	0.006	4.603	<b>0.001</b>	***
Road/Rail Verges and Trails	1	1.083	0.005	3.859	<b>0.001</b>	***
Forest Harvest	1	6.713	0.032	23.920	<b>0.001</b>	***
Cultivation	1	7.534	0.036	26.847	<b>0.001</b>	***
Natural Land Cover						
Bog	1	6.531	0.031	23.271	<b>0.001</b>	***
Deciduous	1	9.256	0.044	32.982	<b>0.001</b>	***
Fen	1	2.335	0.011	8.319	<b>0.001</b>	***
Grass/Shrub	1	0.473	0.002	1.685	<b>0.025</b>	*
Mixedwood	1	0.400	0.002	1.426	0.094	
Pine	1	2.651	0.013	9.445	<b>0.001</b>	***
Swamp	1	0.857	0.004	3.055	<b>0.001</b>	***
White spruce	1	0.645	0.003	2.297	<b>0.003</b>	**
Climate						
Frost Free Period	1	3.147	0.015	11.213	<b>0.001</b>	***
Mean Annual Precipitation	1	1.066	0.005	3.797	<b>0.001</b>	***
Potential Evapotranspiration	1	1.362	0.007	4.852	<b>0.001</b>	***
Space						
Latitude	1	0.778	0.004	2.774	<b>0.003</b>	**
Longitude	1	1.519	0.007	5.414	<b>0.001</b>	***

Significant relationships shown in bold: \* <0.05, \*\* <0.01, \*\*\* <0.001.

**Table A6.** Variance partitioning of the mite assemblage RDA by three explanatory variables: natural land cover (NLC), human footprint (HF), and climate–space (CS).

	Df	R <sup>2</sup>	Adj.R <sup>2</sup>
NLC	8	0.131	0.118
HF	9	0.070	0.055
CS	5	0.064	0.056
NLC + HF	17	0.173	0.148
NLC + CS	13	0.165	0.146
HF + CS	14	0.126	0.105
NLC + HF + CS	22	0.209	0.178

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