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Nested Population Structure of Threatened Boreal Caribou Revealed by Network Analysis

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ABSTRACT

Delineating relevant local populations of widely distributed species is a common challenge in conservation ecology. Caribou and reindeer (*Rangifer tarandus*) are in general decline throughout their global range, despite ongoing conservation efforts. In Canada, recovery actions for the threatened boreal population of woodland caribou (*Rangifer tarandus caribou*) are stratified by 'local population units' (LPUs) on ranges distributed across $2.4 \times 10\ km^2$ of the species' geographic range. To estimate local population dynamics, LPUs are assumed to be geographically closed, though supporting evidence varies widely. We assembled an exceptionally large database of GPS telemetry locations (891,306 telemetry days, 1998–2020) from 1,586 adult female caribou across the 19 northwesternmost LPUs. We generated a many-to-many Gaussian Bayesian Network to identify candidate local populations at range-level extents, as well as subpopulations, termed 'communities' in network analysis. We detected local population boundaries that in some cases were consistent with accepted LPUs and consistent with the assumption of geographic closure. In other cases, local population boundaries did not map well to currently delineated LPUs. Several communities at smaller spatial extents were consistent with expert and local knowledge of caribou movements and support recovery planning and actions "stepped down" from entire ranges. Evidence consistent with population fragmentation was confirmed along the southern and southwestern boundaries of the species' geographic range within the study area, as were more continuous distributions confirmed to the north. We suggest that network analysis can help to inform conservation planning for boreal caribou and other wide-ranging species that would benefit from data-driven characterizations of multiscale population spatial structure.

Keywords

Boreal woodland caribou, *Rangifer tarandus caribou*, spatial analysis, Gaussian Bayesian Networks, community detection, species recovery planning

1 INTRODUCTION

Information about population structure at different spatial and temporal scales is required to inform policies intended to conserve demographic and genetic processes important to species persistence (*e.g.,* Mager et al., 2014; Zannèse et al., 2006). Wide-ranging species are potentially exposed, across the entirety of their geographic ranges, to multiple factors that operate at different spatial and temporal scales, emphasizing a need to account for multi-scale population structure when delineating meaningful spatial units for policy and management interventions.

Despite a long tradition of telemetry studies that yielded, in some cases, exceptionally fine-grained data over large spatial and temporal dimensions, the challenge of identifying spatial structure in apparently continuous populations has received relatively little empirical attention. Taylor et al. (2001) clustered median telemetry locations collected from polar bears (*Ursus maritimus*) in the Canadian Arctic to inform the delineation of population units. A similar approach was used by Shuter and Rodgers (2013) to characterize boreal woodland caribou (*Rangifer tarandus caribou*; hereafter boreal caribou) ranges in Ontario, Canada, and by Schaefer et al. (2000) to examine within-range spatial structure of boreal caribou in Labrador, Canada. These studies generated relatively low-resolution groups because spatial information was limited to median coordinates by radio-collared animal and season.

Caribou and reindeer (*Rangifer tarandus*) are declining throughout their global range, despite ongoing conservation efforts (Vors and Boyce, 2009), and in Canada, the boreal population of woodland caribou is designated as *Threatened* under Canada's *Species at Risk Act* (Environment and Climate Change Canada, 2020). Recovery actions are stratified nationally across 51 local population units (LPUs), within discrete ranges and across a gradient of industrializing landscapes that are also undergoing climate change. LPUs are assumed to be geographically closed for purposes of population assessment, *i.e.*, "experience a limited exchange of individuals with other populations, such that the demography is affected mainly by local factors and not by immigration or emigration among groups" (Environment Canada, 2011:6). However, data and methods used to define range boundaries varied widely; in some cases, ranges were geopolitically bounded (Environment and Climate Change Canada, 2020). Calls ensued to further investigate spatial population structure as new data emerged (Environment and Climate Change Canada, 2017, 2020).

Here we model, to our knowledge, the largest telemetry dataset yet collated for boreal caribou: $>4.0 \times 10^6$ Global Positioning System telemetry locations, collected between 1998 and 2020, from 1,586 adult female caribou across northeast British Columbia, southern Northwest Territories and northern Alberta and Saskatchewan. We generated a novel Gaussian Bayesian Network (Geiger and Heckerman, 2021) coupled with a community detection analysis (Fortunato and Hric, 2016) to characterize multiscale spatial structure among boreal caribou with 4 times the telemetry locations over a study area 3 times the size analysed by Wilson et al. (2020). We demonstrate a data-driven method to characterize multiscale population spatial structure within the geographic range of this wide-ranging species, amenable to informing policy and management interventions intended to conserve multiple population processes.

2 MATERIAL AND METHODS

2.1 Study area

The study area spanned 19 LPUs across the southern Northwest Territories (NT), northwest British Columbia (BC), northern Alberta (AB) and northern Saskatchewan (SK) in western Canada (Figure 1), across the Taiga Plains, Boreal Plains, and Boreal Shield Ecozones (Statistics Canada, 2017).

The area is dominated by conifer and mixedwood boreal forests, bogs, wetlands, and lakes. The climate is continental, with long, cold winters and short, warm summers. The human population is small throughout the region, but many communities are linked by major highways and there is an extensive industrial footprint in much of the area, consisting of forestry and oil and gas exploration and development. Landscape change associated with these activities, as well as climate, are considered to be the most significant cause of caribou declines via habitat-mediated apparent competition with moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*; *e.g.*, Johnson et al., 2020; Dawe and Boutin 2016, Latham et al., 2011).

The study area was located within territories of a diversity of Indigenous peoples, including the Woodland Cree, Dene, Gwich'in, Dane-zaa, and Chipewyan. Woodland caribou are essential to the culture, identity, and survival of First Nations and Métis people, and hunting rights are protected under treaties and by Canada's constitution.

2.2 Data and pre-processing

GPS telemetry data collected from boreal caribou in the study area were acquired from provincial jurisdictions, academic researchers, and industry partners. Sampling varied among LPUs, within and among datasets, as did makes and models of collars and relocation frequencies. Adult females were primarily targeted for collaring but there were a small number of adult males in the dataset. We excluded males from the analysis because adult males are known to have different movement characteristics and larger home ranges than females (*e.g.*, Edmonds, 1988).

To reduce potential bias introduced by long range, return movements, we generated an index, ξ (Keating 1994), of such movements to identify and remove 'outlier' telemetry locations. Specifically, in the case of 3 sequential telemetry points $A \rightarrow B \rightarrow C$, the longer the vector $A \rightarrow B$, the smaller the angle formed by the vectors, and the more similar the length of $B \rightarrow C$ to $A \rightarrow B$, the more likely point B is to be a telemetry error. We assumed values of ξ >10 km were errors and excluded them from further analysis.

The calculation of ξ was scripted in Python 3.9 (Python Software Foundation, Beaverton, OR) using packages *pandas* (McKinney, 2010) and *NumPy* (Harris et al., 2020). Reproducible code is available in the Supplementary Materials.

The outlier detection routine did not capture all errors; occasionally, clusters of points that were obvious errors remained. Long step lengths between sequential telemetry locations were also examined visually. Locations detected near airports and offices were removed, as well as a small number of points, despite they may have been clustered, but located >100 km from an animal's centre of activity. Data cleaning procedures removed approximately 0.005% of locations from the dataset.

2.3 Spatial analysis

We laid 10 km x 10 km grid squares over the extent of telemetry data and assigned unique grid IDs to each telemetry location. Data were summarized for further analysis as a table of location frequencies, where each case (row) was a grid cell ID and each node (column) a caribou ID. Where >1 location fix was acquired for a caribou during a given day, all but the first fix were censored from the dataset. Spatial analyses were completed in QGIS 3.20 (QGIS Development Team, 2021).

2.4 Network structural learning

We learned the structure of an undirected, Gaussian Bayesian Network (Nagarajan et al., 2013; Geiger and Heckerman, 2021) from the table of location frequencies using the semi-interleaved variant of the *Hiton Parents and Children* (si.hiton.pc) algorithm (Aliferis et al., 2010). The resulting network structure consisted of nodes representing each caribou and connections where the patterns of grid cell occupancy by caribou were similar. Using a Gaussian learning routine meant that no *a priori* discretization of location frequencies was required, and nodes were parameterized as probability density functions rather than as tables of discrete probabilities. The si.hiton.pc algorithm was chosen for its relative speed among constraint-based local discovery algorithms and its accuracy in comparison to similarly efficient algorithms based on pairwise mutual information (*e.g.,* Chow and Liu, 1968).

Arcs between network nodes were added based on Pearson's correlation conditional independence test with an α threshold of 0.05. As a result, connections were not forced among all caribou nodes to create a single graph, but spatially related caribou could be grouped into subgraphs disconnected from each other where there was little evidence (*i.e.*, $P > 0.05$) of spatial coincidence. Caribou networked together into the same subgraphs were considered members of the same coarse-scale groups. Telemetry points were assigned membership to the corresponding groups and group boundaries were estimated as 100% minimum convex polygons. Caribou that were not sufficiently spatially coincident with other caribou to generate an arc in the network, as well as small subgraphs consisting of <5 caribou, were not included in coarse-scale groups.

We used package *bnlearn* 4.6.1 (Scutari and Ness, 2021) in *R* 4.0.5 (R Core Team, 2021) for structural learning. Reproducible code is available in the Supplementary Materials. Plausible local ranges were generated using the QGIS implementation of the *R* package *adehabitat* Minimum Convex Polygon script (Calenge, 2006).

2.5 Community detection

Finer-scale groups, termed "communities" in the field of network analysis, were identified by applying a community detection algorithm within network subgraphs (Fortunato and Hric, 2016; Javed et al., 2018). Whereas the network structure analysis identified spatially coincident caribou, community detection focused on within-group structure based on the density of arcs. Community detection algorithms use various schemes to optimize scores of *modularity*, an index of graph clustering quality, where more intra-group arcs and few inter-group arcs signals a better clustering solution (Brandes et al., 2008). We detected communities within coarse-scale groups composed of >50 caribou using *fast greedy*, a bottom-up hierarchical clustering algorithm that merges nodes together to locally optimize modularity (Clauset et al., 2004).

We used package *igraph* 1.2.6 (Csardi and Nepusz, 2006) in *R* 4.0.5 (R Core Team, 2021) for community detection. Reproducible code is available in the Supplementary Materials.

3 RESULTS

3.1 Processed dataset

The processed dataset consisted of 4,053,049 telemetry locations and 891,306 telemetry-days collected on 1,586 boreal caribou from 1998 to 2020 (Table 1).

Table 1. GPS telemetry sources and sample sizes used in the network and community detection analysis of boreal caribou in western Canada. Only the first location acquired from each GPS-collared caribou during a given day (i.e., a "telemetry day") was analysed.

Data source	Collared animals	Telemetry Locations	Telemetry days	Start date	End date
University of Saskatchewan	94	360,417	82,847	2014-04-01	2017-12-31
Government of Northwest	463	1,202,428	322,796	2005-01-01	2020-06-30

Territories					
Government of British Columbia	287	429,796	156,956	1999-11-30	2020-09-30
Government of Alberta	735	2,045,440	327,257	1998-02-22	2020-08-15
Cenovus Energy Ltd	7	14,968	1,450	2012-12-24	2015-11-05
Total	**1,586**	**4,053,049**	**891,306**		

3.2 Network analysis

Structural learning resulted in a network composed of 2,883 arcs among the 1,586 caribou nodes. The network was not fully connected, but was composed of 70 subgraphs, 39 of which were single nodes (i.e., caribou not significantly coincident with any others) and 17 more of which were subgraphs of <5 nodes. The unconnected caribou and those in groups of <5 (n = 45 caribou) were omitted from coarse scale groups and the community analysis. Unconnected caribou and small groups occurred most often near the edges of the geographic distribution (e.g., near Fort Nelson, BC, and Cold Lake, AB) or were separated from larger concentration of caribou by a presumed barrier (e.g., Highway 3 between Fort Providence and Behchokǫ̀, NT). Some caribou remained unconnected because too few telemetry locations were available to characterize their spatial patterns of use with respect to other caribou.

The remaining 24 subgraphs varied in size from 5 to 781 nodes; 5 of these were groups comprised ≥50 caribou. A plot of coarse-scale group membership among the telemetry points revealed broad relationships among boreal caribou in western Canada (Figure 2). A large network of caribou comprising most of the collared adult females in NT, BC and northwest AB dominated the distribution. Smaller coarse-scale groups were evident, particularly along the southern extent of caribou range in Alberta. Groups did not necessarily occupy distinct areas but overlapped in several instances.

3.3 Community detection

Community detection revealed finer-level groups within the 5 largest groups composed of ≥50 caribou. The largest of these, comprising 781 caribou in NT, BC, and AB, was resolved into 16 separate communities (Figure 3A). Communities spanned jurisdictional boundaries but tended to break along major rivers in the region (*e.g.*, Hay, Mackenzie, Liard, Petitot and Fontas). Highways also tended to separate communities, but less consistently; for example, movements by 5 caribou across Highway 3 in NT was sufficient to group caribou on either side into the same community, although some unconnected caribou were separated by the highway to the west of the main group.

The second largest group, composed of 224 caribou in eastern AB, resolved into 12 communities (Figure 3B). These communities were distributed among several existing, recognized ranges (*i.e.*, Red Earth, West Side Athabasca, East Side Athabasca). The third-largest group of 120 caribou was located entirely within the existing Chinchaga range spanning the BC and AB boundary and resolved into 6 communities (Figure 3C). The fourth group spanned the AB-SK boundary and resolved into 8 communities among 67 collared caribou (Figure 3D). The final large group was composed of 56 caribou and resolved into 5 communities in the southernmost portion of the boreal caribou distribution in AB (Figure 2B).

Community sizes tended to be larger in larger coarse-scale groups. Communities within the largest coarse-scale group ranged between 10 and 100 caribou, with a median community size of 50. The other groups had median community sizes of 16, 21, 8 and 12).

4 DISCUSSION

4.1 Comparison with results of spatial cluster graph analysis

Wilson et al. (2020) proposed a Bayesian "spatial cluster graph" that treated the presence or absence of woodland caribou in landscape grid cells as observations and individual caribou as random variables. They used >1.2M locations from >1200 GPS and VHF-collared caribou from across northeast British Columbia, northwest Alberta, and southwestern Northwest Territories.

Their “spatial cluster graph” also comprised coarse-scale groups, some of which also differed from recognized ranges of local population units. Similar to our results, one large group spanned >136,000 km^2 across all three jurisdictions and subsumed seven currently recognized local populations.

The “spatial cluster graph”, however, was limited to a binary representation of use of landscape cells and clusters based on pairwise mutual information which might have led to either of two types of error (Wilson et al. 2020). Animals might have clustered together despite little real spatial interaction (*i.e.*, type II error). In that case, a continuous distribution might suggest greater potential for population resilience via a “rescue effect” (Tallmon, 2017) among subgroups than would actually exist. On the other hand, due to gaps in sampling, separate clusters of animals might actually be part of the same group (*i.e.*, type I error) and local populations might be more resilient than assumed. Whereas the addition of community detection addressed type II errors, as elaborated in section 4.2, undersampling in northern SK might have led to over-stratification (type 1 errors).

Where portions of study areas used by Wilson et al. (2020) and this study were coincident, results were largely consistent, even with significantly greater sample sizes and more aggressive removal of suspected GPS telemetry errors in the latter. Specifically, we confirmed evidence that in the northwestern extent of the species’ range, caribou are distributed more continuously than suggested by current LPU boundaries. Nearly half of all collared caribou were captured in a single large group that spanned parts of three jurisdictions and eight currently defined local population ranges.

Many of the small groups and unconnected caribou were concentrated along the southern edge of the species' range, consistent with an ongoing process of fragmentation and range contraction (Johnson et al., 2020, p10-11, Murray et al., 2017). There was also evidence of this along the southwestern extent of boreal caribou range in BC, where the small Parker and Fort Nelson Core ranges were resolved (as they were by Wilson et al. 2020). The shape of the Parker group was influenced to the southwest by the movement of an adult female that migrated into the ranges of the Rocky Mountains, a behaviour characteristic of mountain caribou (Watters and DeMars, 2016).

4.2 Insights from community detection

The community detection analysis additionally identified discrete groups smaller than currently delineated populations, at spatial extents that often aligned with land-use planning focused on caribou recovery. Its use to identify finer-scale structuring within groups is a novel application to a conservation problem of a technique that is becoming more common in human social theory research (*e.g.*, Papadopoulos et al., 2012). In our application, the network structural analysis generated groups that often spanned landscape features such as major river corridors and highways, which boreal caribou rarely cross, according to both telemetry information and Indigenous knowledge (Wilson et al., 2020). However, the addition of community detection analysis resolved groups that were often, but not always, bounded by these features. Based on our analysis, major rivers appeared to generate stronger spatial structuring than major roads.

In some cases, communities generally aligned with currently defined local population ranges (*e.g.*, Maxhamish, Snake-Sahtaneh, Yates, Caribou Mountains; Figure 2A), while in other cases, network analysis identified finer-scale structuring that had not been previously delineated (*e.g.*, within the NWT, Chinchaga, and Richardson ranges; Figure 2).

This finer level of spatial structuring revealed by the community analysis effectively resolved initial challenges encountered by Wilson et al. (2020) and resulted in an improved fit of clustering results to traditional and local knowledge of researchers, managers, and land users. The analysis also provided some supporting evidence for some of the current local population range delineations, although not at a consistent scale; some current ranges aligned with groups while others aligned with communities within groups. We believe this is largely a legacy of how LPUs were initially drafted. For example, the community analysis identified finer-scale structuring within the NWT LPU; however, this boundary was drafted before most of the telemetry data were collected and a largely continuous distribution of caribou was assumed. Radio-collaring efforts in northeast AB have a longer history and LPU boundaries more closely approximated the results of our analysis. The presumed role of major rivers and highways in structuring subpopulations was supported by our analysis.

Notwithstanding the very large sample of animals and telemetry locations, the analysis remains subject to spatial biases and sampling intensity. For example, the situation in SK may represent type 1 error insofar as data spanned <4 years, which is a comparatively short period compared to other areas. The six identified groups within that jurisdiction might amalgamate into fewer, larger groups if more data were collected, especially because fire, as opposed to anthropogenic features, is the dominant source of landscape disturbance there and might be expected to drive caribou movements and local distribution over long time scales. This is less likely along the southern and southwestern edges of our study area because telemetry data in these areas generally represent the southern limits of boreal caribou range in Canada (with the exception of the isolated Little Smoky range in west-central AB; Environment and Climate Change Canada 2020). Along this edge of the range, habitat fragmentation may constrain caribou movements to smaller, more discrete ranges and less fluid spatial dynamics than in landscapes with smaller human-related infrastructure footprints.

4.3 Comparison with social network analysis

Caribou and reindeer groups have been recently analysed as social or familial networks (Robitaille et al., 2018; Bonoan, 2020; McFarlane et al., 2021) that estimate behavioural interactions among caribou. The structural network analysis with community detection presented here differs from social network analyses by searching for persistent spatial structure over greater time and spatial scales with which to rationalize ecological boundaries. In fact, the structural network grouped animals that might not have been collared at the same time but nevertheless shared the same space. As a result, we capture multigenerational spatial structure that is important to consider for species like boreal caribou that can exhibit strong fidelity to seasonal ranges and calving grounds (*e.g.*, Schaefer et al., 2000; Popp et al., 2011).

4.4 Policy and research implications

We addressed repeated calls for approaches and standards to identify range boundaries that should be transparent and repeatable across variable landscapes, and appropriate for reporting at a national scale (*e.g.*, Environment and Climate Change Canada, 2017, 2020). We suggest that the network structural analysis generated coarse-scale groups which, for purposes of estimating population dynamics, are more plausibly geographically closed than currently defined ranges of several local populations. At the same time, the method identified smaller groups that reconciled with local knowledge of caribou behaviour. Groups at this scale are amenable to “stepped down” recovery planning and management.

Our analysis of spatial structure indicated insufficient support for several of the currently defined LPUs of boreal caribou in the northwest portion of the species' range in Canada. This suggests that some realignment of range boundaries with existing ecological evidence might assist planning to recover boreal caribou. It is widely acknowledged, however, that such realignment complicates implementation of recovery plans, especially where it would result in ranges that span provincial and territorial boundaries. In Canada, though boreal caribou are listed federally as at-risk, constitutional authority for management of the species rests with provinces and territories.

We suggest that network analysis provides a powerful tool to resolve the spatial structuring of populations, even where such populations appear largely continuous, We further contend that such analyses could be expanded to accommodate additional sources of location information. For example, advances in molecular ecology and landscape genetics have been used to detect population structure and animal movement over comparatively large spatial and temporal dimensions (*e.g.*, Frantz et al., 2009; Hobbs et al. 2014), to delineate local population management units (*e.g.*, Zannèse et al. 2006) and to apportion spatiotemporal variation in population structure to different drivers (*e.g.*, Priadka et al., 2018; Galpern et al., 2014). Genetic approaches are proving particularly useful where non-invasive methods for estimating distribution and abundance are preferred to traditional means, such as telemetry (*e.g.*, MacFarlane et al., 2021). To date there are few examples of studies that integrate genetic and telemetric data among groups of boreal caribou (*e.g.*, Boulèt et al., 2007). Structural network analysis with community detection affords an opportunity to do so at unprecedented spatial scales.

CRediT authorship contribution statement

S.F. Wilson: Conceptualization, data curation, methodology, formal analysis, writing, editing. **W. Crosina:** Funding acquisition. **E. Dzus:** Editing, funding acquisition. **D. Hervieux:** Data curation, editing. **P.D. McLoughlin:** Data curation, editing. **L.M. Trout:** Funding acquisition. **T.D. Nudds:** Conceptualization, methodology, writing, editing, funding acquisition, supervision.

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Figure 1. Local Population Units (LPUs) for boreal woodland caribou in western Canada.

Figure 2. Results of network structure analysis of boreal woodland caribou in western Canada. The GPS telemetry points of groups identified by the analysis are illustrated by different colours and bounded by 100% minimum convex polygons. Telemetry points from unconnected caribou and small groups are illustrated in grey.

Figure 3. Results of the community detection analysis for the 5 largest coarse-scale groups composed of ≥50 collared caribou. Network subgraphs are illustrated for each, as well as the existing range boundaries defined by Environment and Climate Change Canada (2020). Currently accepted local populations and range boundaries are colour contrasted and labelled

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Highlights

- Delineating relevant local populations of continuously distributed species is a common challenge in conservation ecology.
- Local populations of threatened boreal caribou are distributed across a gradient of industrializing landscapes on ranges assumed to be discrete and geographically closed for purposes of population assessment.
- Network analysis identified multiscale spatial structure of caribou populations based on 891,306 telemetry days spanning 22 years from 1,586 caribou in western Canada.
- To the north, small groups or “communities” of caribou tended to be nested within larger groups that were less discrete than currently recognized ranges of local populations.
- To the south, small, discrete groups were detected along the edge of the species' range, consistent with ongoing fragmentation and extirpation.

- Network analysis can inform conservation planning and management for wide-ranging species, from operational levels on working landscapes to large spatial scales.

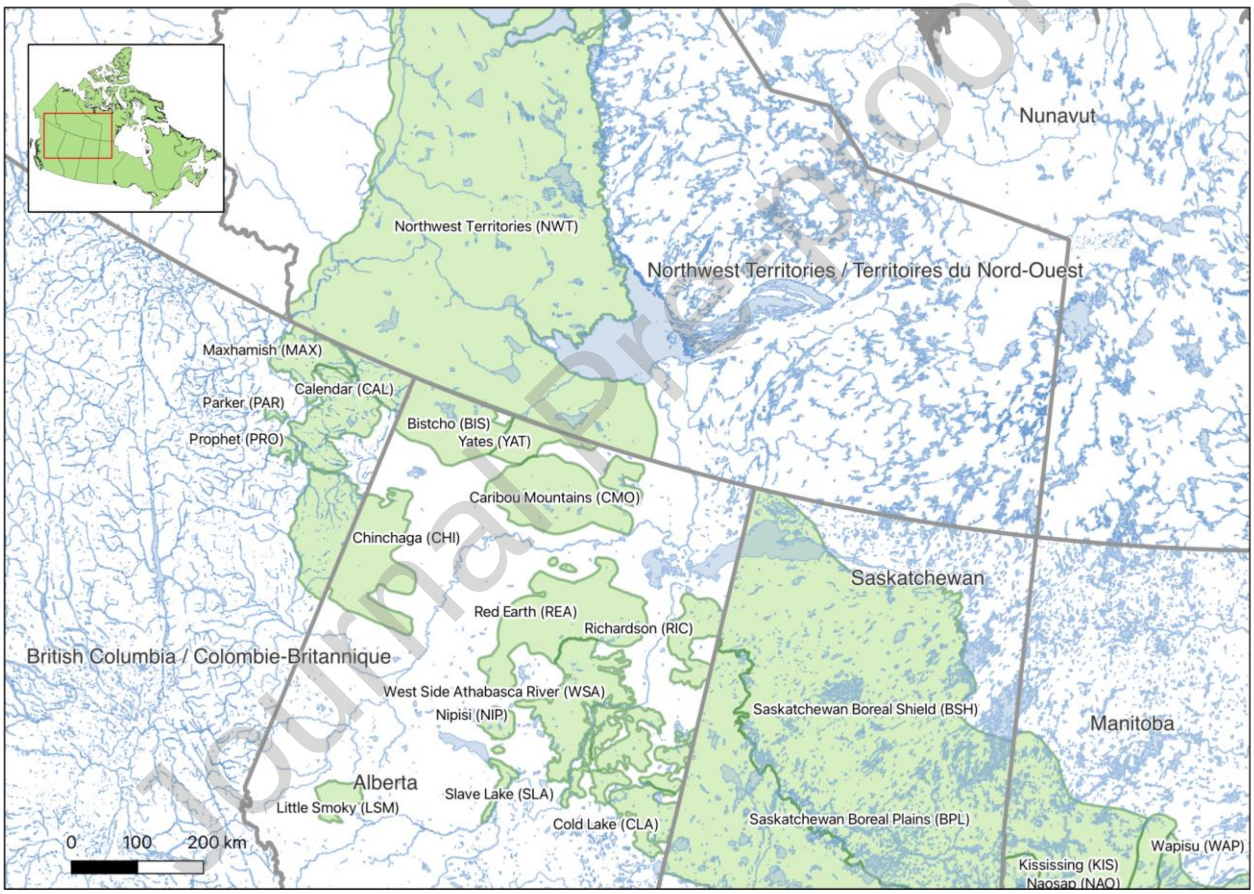

Fig 1

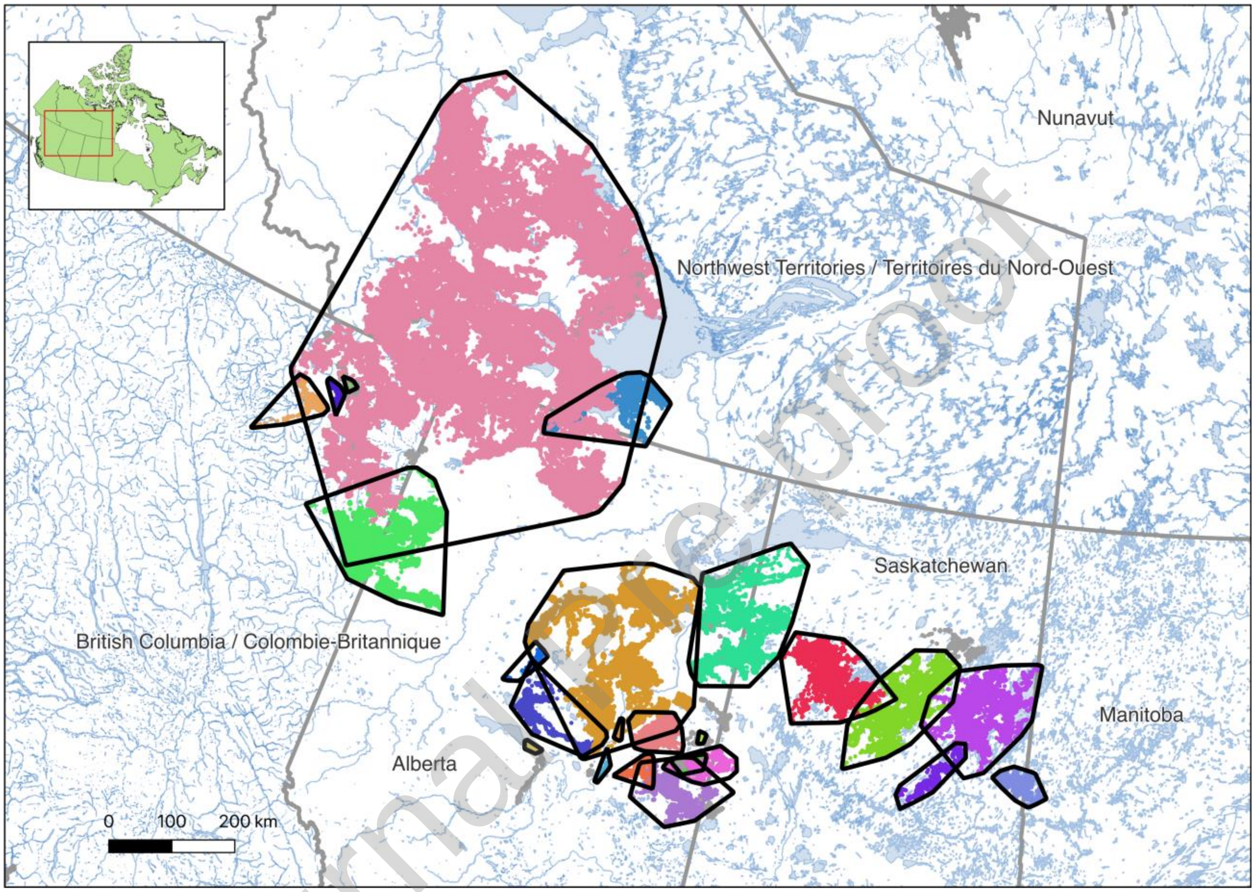
Nunavut
Northwest Territories / Territoires du Nord-Ouest
Saskatchewan
British Columbia / Colombie-Britannique
Manitoba
Alberta
0
100
200 km

Fig 2

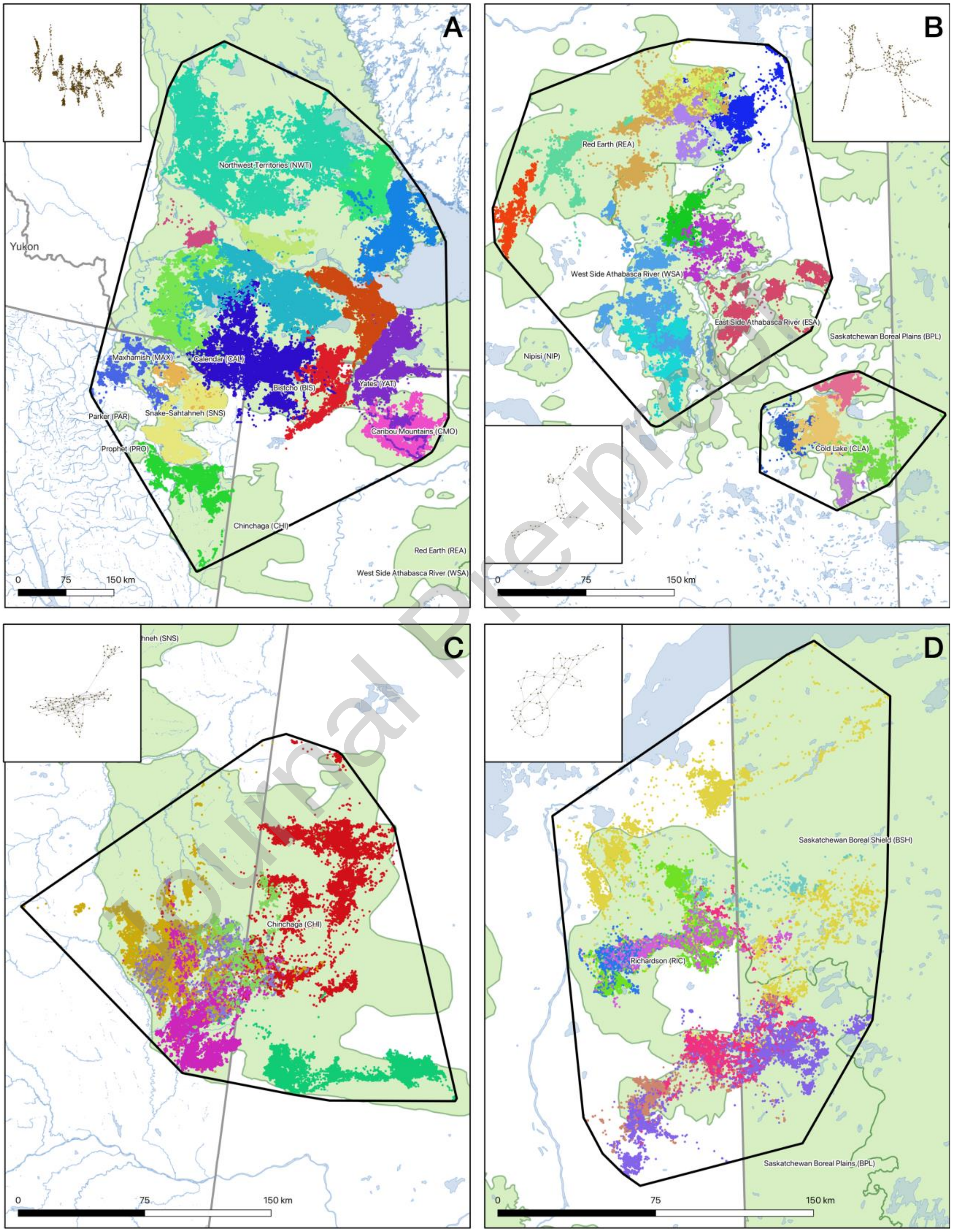
A
Northwest Territories (NWT)
Yukon
Maxhamish (MAX)
Calendar (CAL)
Bistcho (BIS)
Yates (YAT)
Parker (PAR)
Snake-Sahtahneh (SNS)
Caribou Mountains (CMO)
Prophet (PRO)
Chinchaga (CHI)
Red Earth (REA)
West Side Athabasca River (WSA)
0
75
150 km
B
Red Earth (REA)
West Side Athabasca River (WSA)
East Side Athabasca River (ESA)
Saskatchewan Boreal Plains (BPL)
Nipisi (NIP)
Cold Lake (CLA)
0
75
150 km
C
Chinchaga (CHI)
0
75
150 km
D
Saskatchewan Boreal Shield (BSH)
Richardson (RIC)
Saskatchewan Boreal Plains (BPL)
0
75
150 km

Fig 3