Received: 29 January 2024 | Revised: 9 December 2024 | Accepted: 3 February 2025

DOI: 10.1002/eap.70038

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

ARTICLE

Shifting and expanding ranges of a sub-Arctic caribou herd and associated changes in vegetation

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Funding information
U.S. National Science Foundation (NSF), Grant/Award Number: 2127272; National Science Foundation Graduate Research Fellowship Program, Grant/Award Number: 1938054; U.S. National Aeronautics and Space Administration (NASA), Grant/Award Number: NNX15AW71A

Handling Editor: Juan C. Corley

Abstract

Rapid climate warming has contributed to significant changes in Arctic and boreal vegetation over the past half century. Changes in vegetation can impact wildlife by altering habitat and forage availability, which can affect behavior and range use. However, animals can also influence vegetation through foraging and trampling and therefore play an important role in determining ecosystem responses to climate change. As wildlife populations grow, density-dependent processes can prompt range expansion or shifts. One mechanism for this is density-dependent forage reduction, which can contribute to nutritional stress and population declines, and can also alter vegetation change trajectories. We assessed the range characteristics of a migratory caribou (*Rangifer tarandus*) herd in east-central Alaska and west-central Yukon Territory as it grew (1992–2017) then declined (2017–2020). Furthermore, we analyzed the correlation between caribou relative spatial density and vegetation change over this period using remotely sensed models of plant functional type cover. Over this period, caribou population density increased in all seasonal ranges. This was most acute in the calving range where density increased 8-fold, from 1.5 to 12.0 animals km^{-2}. Concurrent with increasing density, we documented range shifts and expansion across summer, post-calving and winter ranges. In particular, summer range size doubled (12,000 km^2 increase) and overlap with core range (areas with repeated year-round use) was halved. Meanwhile, lichen cover, a key forage item,

Authorship statement: Authorship, besides lead and last author, is alphabetical.

declined more in areas with high caribou density (2.4% absolute, 22% relative decline in cover) compared to areas where caribou were mostly absent (0.3% absolute, 1.9% relative decline). Conversely, deciduous shrub cover increased more in high caribou density areas. However, increases were dominated by less palatable shrubs whereas more palatable shrubs (i.e., willow [*Salix* spp.]) were stable or declined slightly. These changes in vegetation cover were small relative to uncertainty in the map products used to calculate change. Nonetheless, correlations between vegetation change and caribou range characteristics, along with concerning demographic trends reported over this same period, suggest changing forage conditions may have played a role in the herd's subsequent population decline. Our research highlights the potential of remotely sensed metrics of vegetation change for assessing the impacts of herbivory and trampling and stresses the importance of in situ data such as exclosures for validating such findings.

KEYWORDS
caribou, climate change, density dependence, forage, Fortymile Caribou Herd, herbivory, range expansion, *Rangifer tarandus*, remote sensing, shrub expansion, vegetation change

INTRODUCTION

Caribou and reindeer (*Rangifer tarandus*) are some of the most ecologically, economically, and culturally important species across Arctic and sub-Arctic ecosystems (Gagnon et al., 2020; Hummel & Ray, 2008; Parlee et al., 2018). These ecosystems are warming over three times faster than the rest of the planet (Rantanen et al., 2022) and are particularly at risk from climate change and its downstream ecological effects such as shifting phenology, intensified wildfire regimes, permafrost degradation, altered nutrient cycling, and changing vegetation communities (Post et al., 2009). *Rangifer* are vulnerable to climate-induced changes in the structure and function of tundra vegetation, and research suggests warming temperatures will have a predominantly negative effect on these animals (Mallory & Boyce, 2018).

Rangifer also have the potential to affect vegetation, creating complex plant–herbivore interactions (Olofsson & Post, 2018). Animals play a critical role in shaping ecosystem structure and function (Schmitz et al., 2014) and are therefore crucial to understanding interactions between ecosystems and climate change (Hempson et al., 2015; Schmitz et al., 2018). Animals can impact vegetation directly by consuming or trampling plant biomass, or indirectly by contributing to soil nutrients via urine and feces, altering wildfire regimes, and influencing soil temperatures and microbial activity (Cahoon et al., 2012; Schmitz et al., 2014, 2018; Väisänen et al., 2014). In Arctic and sub-Arctic regions, experimental studies have shown that large herbivores can trigger significant declines in lichens (Bernes et al., 2015; Joly et al., 2007; Suominen & Olofsson, 2000), promote transitions to graminoid-dominated communities (van der Wal, 2006), impact tree recruitment (Biuw et al., 2014), constrain shrub expansion (Christie et al., 2015; Olofsson et al., 2009; Zamin & Grogan, 2013), limit shrub height via "browse traps" (Bråthen et al., 2017), and alter vegetation community composition through selective foraging (Bryant et al., 2014). *Rangifer*-induced changes in vegetation can also alter forage quantity and quality, causing density-dependent negative feedback on caribou populations themselves (Manseau et al., 1996).

Impacts of *Rangifer* herbivory and trampling can intensify as population density increases, leading to high grazing pressure on vegetation and accelerated forage depletion (Rickbeil et al., 2015). Density-dependent habitat selection predicts that when animal density increases, overlap with primary range decreases as individuals expand into secondary ranges (Morris, 2003). Range expansion can curtail forage depletion by opening new areas for foraging, but can also be associated with the use of lower quality habitat (van Beest et al., 2014) and/or increased movement rates (Fancy & White, 1985).

Empirical studies of *Rangifer* impact across a range of animal densities are rare, and a significant knowledge gap exists in understanding how *Rangifer* herbivory and trampling might impact Arctic vegetation change. Existing studies examining *Rangifer* impacts on vegetation have mostly been small-scale experiments (Bernes et al., 2015; Suominen & Olofsson, 2000) or large-scale remote sensing studies at coarse spatial resolution (1 km) that focus on metrics of vegetation greenness or productivity (Campeau et al., 2019; Rickbeil et al., 2015), although recent work leverages higher resolution imagery to assess reindeer impacts at local scales in Fennoscandia and Siberia (Spiegel et al., 2023;

Villoslada et al., 2023). Experimental studies, such as exclosures, are crucial to understanding *Rangifer* impacts on vegetation but are context-dependent and limited in spatial scale, often covering only a small fraction of the area of interest. Conversely, remote sensing studies cover larger spatial extents but are subject to additional sources of error. Past remotely sensed studies have focused on metrics of vegetation greenness, which research shows are weakly correlated with *Rangifer* forage quality (Johnson et al., 2018). Therefore, greenness-based metrics are not likely to accurately capture caribou forage availability or *Rangifer* impacts on vegetation. Quantifying the differential impacts of *Rangifer* on individual vegetation taxa is thus important for understanding how herbivory and trampling impact vegetation communities.

In this study, we tracked changes in caribou population and distribution, and concurrently examined vegetation changes across different levels of caribou spatial density. Our approach was unique in that we assessed vegetation changes concurrent with caribou movement data across large spatial and temporal scales using annual maps of plant functional type (PFT) cover derived from Landsat satellite imagery (Macander et al., 2022; Macander & Nelson, 2022). These maps are the first for the area to move beyond vegetation "greenness" and categorical land cover and provide quantitative measures of PFT fractional cover.

We focused on the Fortymile Caribou Herd (FMCH) in interior Alaska, USA, and Yukon Territory, Canada. The FMCH is a large migratory herd that concentrates in higher elevation upland tundra during the calving and summer periods and disperses into adjacent spruce (*Picea* spp.)–moss taiga during the winter (Valkenburg et al., 1994). However, FMCH seasonal ranges often overlap; therefore, critical upland areas receive year-round use and are potentially vulnerable to density-dependent forage reduction. Over recent decades, the FMCH population grew from fewer than 8,000 individuals to a peak of over 80,000 by 2017 (Gross, 2023), and density increased across the critical upland range. Concurrently, signs of nutritional stress and range expansion were reported within the herd, and the population ultimately declined from 2017 to 2022 (Boertje et al., 2017; Gross, 2023). The FMCH's 40-year history of increasing numbers and overlapping seasonal ranges provides a unique opportunity to assess whether differences in caribou density are correlated with changes in PFT cover and if forage reduction across critical range may have contributed to range expansion and/or population declines. Specifically, our objectives were to: (1) assess whether range expansion occurred by tracking changes in annual, seasonal range size and overlap with primary range (i.e., areas with repeated year-round use); (2) evaluate whether grazing pressure likely increased on these ranges by tracking annual changes in caribou density; (3) investigate whether areas of high sustained use by caribou were associated with changes in vegetation by comparing temporal changes in remotely sensed PFT cover to spatial distributions of caribou density.

DATA AND METHODS

Study area

Our study area encompassed the extended range of the FMCH, approximately 125,000 km^2 across Alaska, USA and Yukon Territory, Canada (Figure 1a). This includes the current range of the FMCH and historically used areas to the northwest and the southeast (Boertje et al., 2012). The climate is subarctic and continental, with long, cold winters (1958–2020 average minimum = −28°C) and short, warm summers (1958–2020 average maximum = 20°C; Abatzoglou et al., 2018; Appendix S1: Figure S1). The landscape spans lowland and upland areas (85–2,300 m elevation) and includes boreal forest, shrublands, tussock tundra, and sparsely vegetated alpine communities. Wildfires are prevalent at lower elevations. The calving and summer ranges of the FMCH are concentrated in sparsely treed, moderately rugged upland areas referred to as the Core Uplands (Figure 1a; Boertje et al., 2017; Valkenburg et al., 1994). The Core Uplands represent the most used and presumably highest quality habitat for FMCH from 1992 to 2008. These areas see use in all seasons and were subject to increasing caribou density as the herd's population grew from 1992 to 2017 (Figure 1b).

Caribou location data

To estimate trends in caribou seasonal range use, we used location data from Very High Frequency (VHF) and Global Positioning System (GPS) collars placed on caribou captured by the Alaska Department of Fish and Game (ADFG) and Environment Yukon biologists following approved state capture and handling protocols (Appendix S1: Table S1). VHF collars were placed on 388 female caribou in the FMCH from 1991 to 2008. Animals with VHF collars were located monthly from fixed-wing aircraft, resulting in 21,412 total locations with an estimated location accuracy of ~3 km (T.W. Bentzen, personal observation, July 18, 2022; Appendix S1: Section S1). VHF locations were mapped to check for outliers due to relocation or plotting errors. ADFG and Environment Yukon placed GPS collars on 223 female caribou in the FMCH from 2011 to 2021. GPS data were

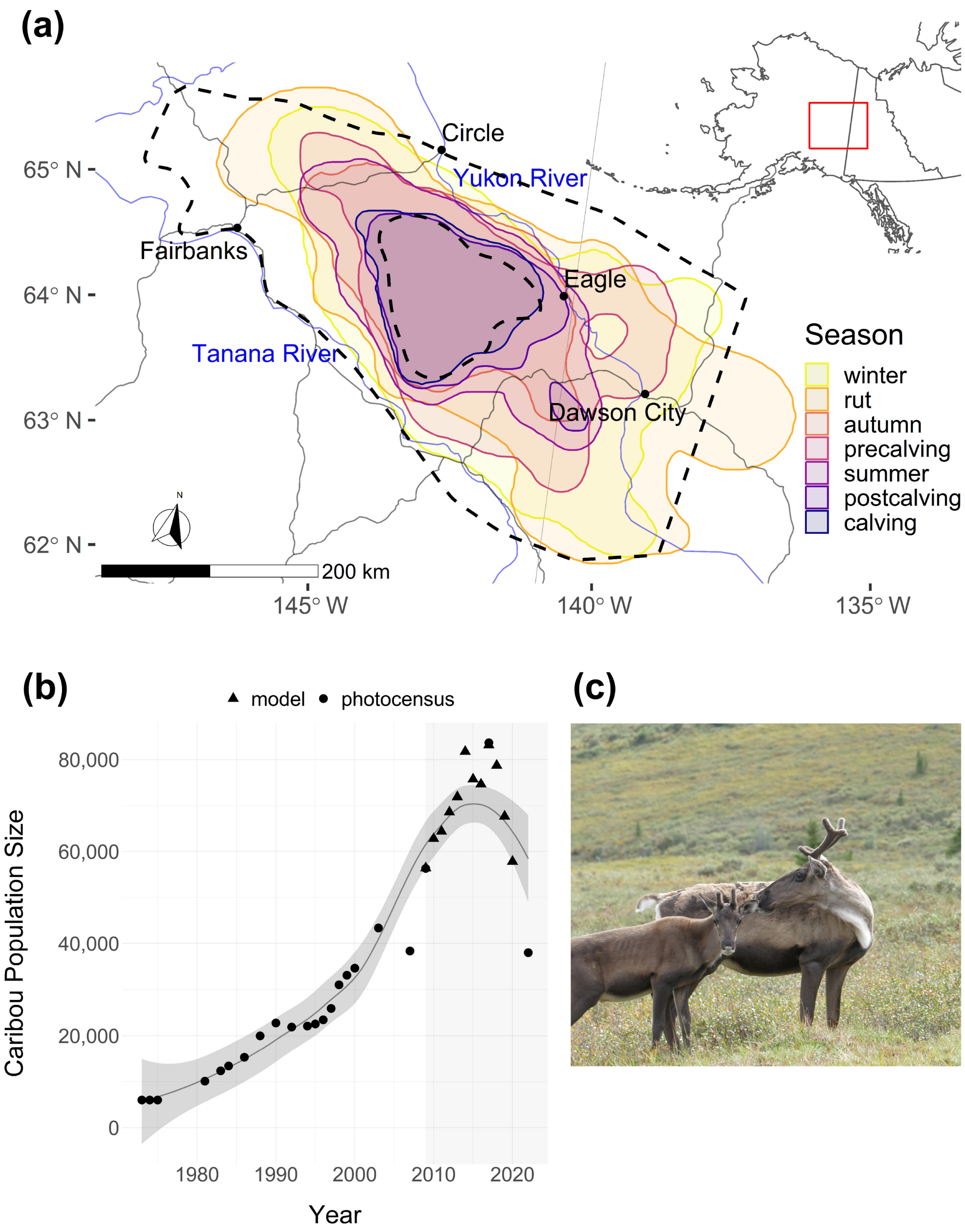


FIGURE 1 (a) Map of study area with seasonal ranges for radio-collared adult female caribou (*Rangifer tarandus*) in the Fortymile Caribou Herd (FMCH), 1992–2021. Black dashed lines show the extended range of the FMCH (outer) and the Core Uplands (inner). (b) Annual FMCH population size estimates derived from photo census (circles) or population models (triangles). Population estimates within the shaded gray rectangle were derived using the Rivest method, which corrects for caribou aggregations missed during photo census (Rivest et al., 1998). Estimates derived using the Rivest method are generally higher than those derived without it. (c) A female Fortymile caribou and her calf travel and forage across core summer range. Photo credit: Jim Herriges and Libby Ehlers.

filtered to one location every 5 h for each caribou ID/season/year combination. We included animals whose collars were active for over 67% of the season/year and had at least twice as many locations as the number of days active. This resulted in 595,567 locations with estimated location accuracy ≤10 m (Jung et al., 2018).

Vegetation data

To assess vegetation change within the FMCH range, we used annual 30 m resolution maps of plant percent top cover (i.e., the proportion of area where a vegetation class comprises the top layer, ≤100%; Wilson, 2011). Maps were partitioned by five common PFTs: deciduous shrubs, evergreen shrubs, forbs, graminoids, and light-colored macrolichens (e.g., white/yellow lichens, predominantly genus *Cladonia*, henceforth "lichens") (Macander et al., 2022; Macander & Nelson, 2022), as well as three deciduous shrub genera: alder (*Alnus* spp.), birch (*Betula glandulosa, Betula nana* ssp. *exilis*) and willow (*Salix* spp.) (M.J. Macander, unpublished data, 2022). PFT cover maps were produced using a dataset of over 14,000 in situ observations across Alaska and the Yukon Territory and rigorously validated using a spatially blocked cross-validation approach. Model root mean squared error (RMSE) ranged from 5.7% (birch shrubs) to 19.0% (deciduous shrubs), R^2 ranged from 0.2 (forbs) to 0.5 (lichens, alder) and bias ranged from 1.4 (lichens) to 3.6 (deciduous shrubs) (Appendix S1: Table S2). For further information on PFT cover modeling and accuracy assessment, see Macander et al. (2022).

To isolate the effects of caribou on vegetation, we masked out water, persistent snow, historic fire perimeters, and areas of forest loss or flooding (Appendix S1: Table S3). For each season, we also restricted our analysis to the 30% of the study area with the highest relative probability of caribou use using seasonal maps of resource use probability derived from step-selection functions (SSFs, Boyce & McDonald, 1999) that were developed for the FMCH (Palm, 2021; Palm, unpublished manuscript, 2023, further details in Appendix S1: Section S2). This helped ensure that habitat characteristics were similar across caribou density classes, as it restricted analysis to only areas deemed suitable caribou habitat. For example, calving SSFs indicated a high probability of use for higher elevation areas, so further analysis across the calving range was restricted to mostly higher elevation areas across all caribou density classes. As a result, our results were less likely to be confounded by different distributions of habitat types or landscape features across caribou density classes. To check the effectiveness of this method, we compared distributions of habitat and landscape variables across caribou density classes. Distributions were compared visually and using Kolmogorov–Smirnov (K-S) tests (Massey, 1951). To facilitate computation, we sampled 10% of pixels across each caribou density class, which resulted in a large number of observations per class (>80,000). At such large sample sizes, the K-S test is very sensitive, and even small deviations between distributions will result in small *p*-values (Lin et al., 2013). Therefore, we reported the K-S distances (*D*), a metric of dissimilarity, rather than the *p*-values. Because caribou themselves can impact some environmental characteristics, we focused on variables that are not easily impacted by herbivore presence: elevation, northness, eastness, topographic position index (TPI), topographic ruggedness index (TRI), and day-of-year of the start of the snow-free season. Topographic variables were derived from the National Elevation Dataset (>60° N, >120° W; Gesch et al., 2002) and the Canadian Digital Elevation Model (>60° N, ≤120° W; Natural Resources Canada, 2015). TPI and TRI were calculated using 3 × 3 pixel windows, and the TRI formula from Wilson et al. (2007). Snow-free date data were derived from Landsat seasonal imagery and created by Macander et al. (2022).

Range trend analysis

We estimated seasonal and annual population ranges for the FMCH from 1991 to 2021 using the "amt" package in R (R Core Team, 2020; Signer et al., 2019). Seasons were defined based on annual patterns of range expansion and contraction (Boertje et al., 2012) and annual data availability varied by season (Appendix S1: Table S5). First, we grouped the VHF and GPS data by season and year, then estimated probabilistic relative frequency distributions of caribou location using a kernel density estimator. To account for greater location error in VHF data, we used a spatial resolution of 3 km. We calculated the smoothing parameter for the kernel density estimator using the reference method (Worton, 1989). Smaller smoothing parameters were chosen for larger sample sizes (Fieberg, 2007; Appendix S1: Figure S2), which resulted in mostly contiguous home ranges (Appendix S1: Section S3).

We derived 95% (range extent) and 50% (high use area) isopleths for each season/year combination using the kernel density estimate, then calculated the total area (in square kilometers) covered by each isopleth. To estimate caribou population density (animals per square kilometer) across each range, we weighted the FMCH population estimate for each year (Figure 1b) by the isopleth percentage, then divided these annual population estimates by the seasonal range areas for that specific year. We also calculated centroids for the 50% isopleths using the sf package in R (Pebesma, 2018) and compared annual centroids to test for range shifts.

We produced rasterized relative utilization probability (0–1) distributions (UDs) for each season/year from 1991 to 2021. To delineate the area of greatest use during the FMCH's period of population growth, we created an overall UD for the period 1992–2008 using population-weighted averages of the season/year UDs, normalized this raster to 0–1, and calculated the 50% isopleth. We henceforth refer to this area as the "Core Uplands" as it broadly aligned with the Core Uplands defined by Boertje et al. (2012). Finally, we calculated the area of overlap between each season/year range and the Core Uplands and converted this to a percentage by dividing it by the season/year range area.

To assess temporal trends in range size, population density, and range overlap with the Core Uplands, we created a time series of these metrics, applied linear regressions, and assessed whether slopes were significantly different from zero. In most cases, the assumptions of linear regression were met (Appendix S1: Table S6).

Vegetation change analysis

To test how caribou density was related to vegetation change, we examined changes in PFT-weighted area (total mapped area weighted by top cover, Figure 2a) from 1992 to 2020 within caribou spatial density classes. For each season, we calculated population-weighted averages of the annual season/year UDs (described in *Range trend analysis*) for the period 1992–2020 and normalized these to 0–1. We also averaged all seasons to create an "overall" season. Areas that had a normalized relative utilization probability <0.01 were assigned to the lowest caribou spatial density class, representing areas with very few or no caribou. Where the normalized relative utilization probability was ≥0.01 we binned the data into three equal interval classes of caribou spatial density (low, medium, and high, Figure 2b). These density classes are unitless and do not represent animals per unit area, but rather relative spatial density. We refer to them as "caribou spatial density" to differentiate them from "caribou population density" which denotes annual estimates of animals per square kilometer (described in *Range trend analysis*). Caribou spatial density classes do not vary annually and therefore do not incorporate shifting habitat use within the study period.

We partitioned our analysis of the effects of caribou spatial density on PFT by land cover type using the 1992 land cover map from Wang et al. (2019) (Figure 2c). This accounted for differences in the distribution of land cover types across the caribou spatial density classes. For each unique combination of land cover type and caribou spatial density class, we summed the cover weighted area for each PFT across the study area for both the start (1992) and end year (2020) of the time series using the PFT cover maps from Macander et al. (2022) (after applying the masking steps outlined in *Vegetation data*; Figure 2d,e). We then converted from cover weighted area to percent cover and calculated absolute and relative changes in percent cover from 1992 to 2020 for each PFT (Appendix S1: Section S4).

To account for annual variation in PFT cover, we also produced a time series of PFT cover change across the study period and calculated average Sen's slopes across the land cover and caribou spatial density classes described above (Appendix S1: Section S5). PFT cover maps were subject to uncertainty during the modeling process (Macander et al., 2022). We incorporated this uncertainty into our PFT change results by tabulating, for each caribou spatial density class, the proportion of pixels that experienced no change, less certain change, or more certain change (for more details on this analysis, see Appendix S1: Section S6). This categorical analysis allowed us to assess trend certainty for PFT changes over the study period.

RESULTS

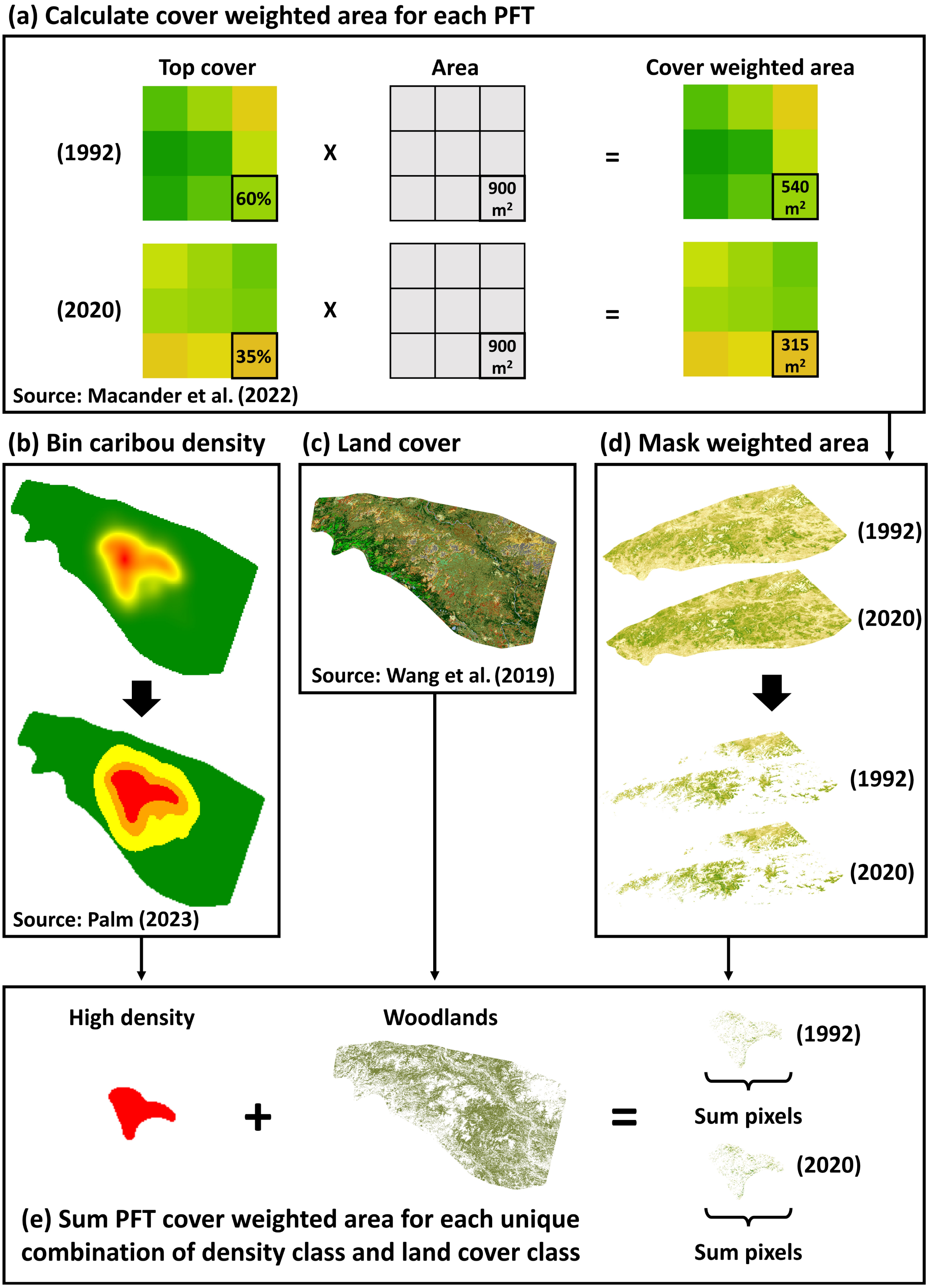
Annual changes in FMCH seasonal ranges

Range size and caribou population density

From 1991 to 2021, and concurrent with population growth in the FMCH (Figure 1b), summer 95% isopleth range size increased significantly, by approximately 500 $\text{km}^2\ \text{year}^{-1}$ ($R^2 = 0.59$, $p < 0.001$; Figure 3). In contrast, sizes for calving, post-calving, and winter 95% isopleth ranges showed no clear trend ($R^2 < 0.05$, $p > 0.1$; Figure 3). Winter range sizes were larger and more variable than other seasonal ranges, whereas calving and post-calving ranges were the smallest. Caribou population density increased significantly across all seasonal 95% isopleth ranges ($p \leq 0.01$; Figure 3) and increases in population density were most pronounced within calving and post-calving ranges where range size did not increase. Calving range caribou population density increased by 0.3 animals $\text{km}^{-2}\ \text{year}^{-1}$ ($R^2 = 0.28$; Figure 3) and post-calving density increased by 0.23 animals $\text{km}^{-2}\ \text{year}^{-1}$ ($R^2 = 0.42$; Figure 3). Across the calving range, this resulted in an 8-fold increase from 1.5 animals km^{-2} in 1992 to 12.0 animals km^{-2} during the 2017 population peak. Caribou population density across the winter range was lower overall but still increased 9-fold from 0.5 animals km^{-2} in 1992 to 4.6 animals km^{-2} in 2017. Summer caribou population density also increased modestly, roughly doubling from 1.4 animals km^{-2} in 1994 to 3.2 animals km^{-2} in 2017 (Figure 3) despite increases in summer range size. Similar trends were observed for 50% isopleths (Appendix S1: Figure S4).

Range overlap with Core Uplands

As predicted by the theory of density-dependent habitat selection, seasonal range overlap with the Core Uplands primary range decreased as caribou abundance and density increased. From 1991 to 2021, range overlap decreased for post-calving, summer, and winter 95%



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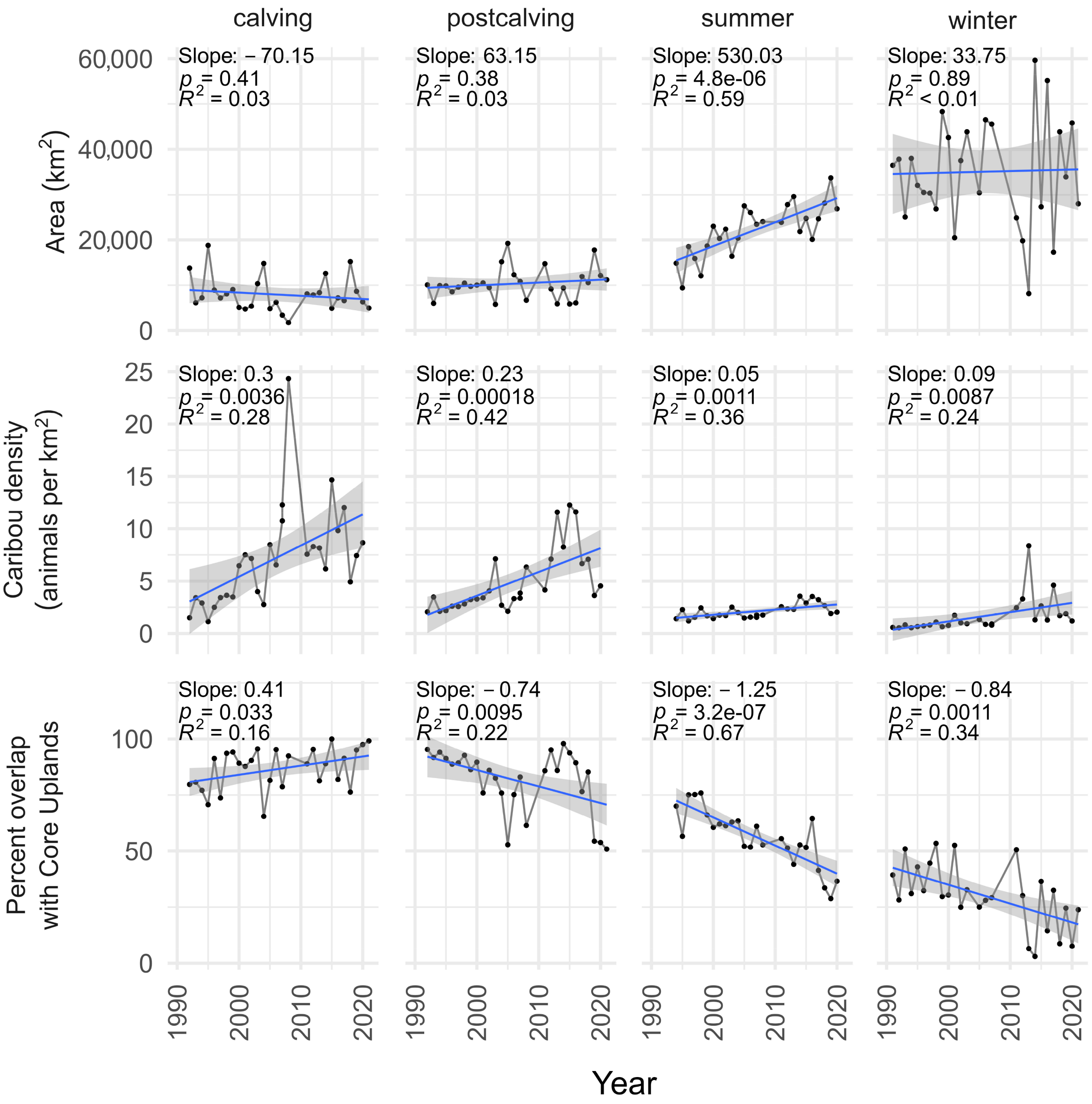

FIGURE 3 Change in Fortymile Caribou Herd 95% isopleth range area (top), population density across range (middle), and percent overlap with the Core Uplands (bottom) from 1991 to 2021.

FIGURE 2 Workflow for vegetation change analysis. (a) Cover weighted area was calculated by multiplying plant functional type (PFT) cover (as a proportion) by pixel area. This was done on a pixel-wise basis. Weighted area was calculated separately for each PFT and for the start and end year, producing ten 30-m resolution maps of weighted area in total. (b) Continuous utilization distributions are binned into four caribou spatial density classes. Here, density refers to relative spatial density, not absolute density. These density values are unitless and do not represent animals per unit area. (c) Land cover for the year 1992 (the start of the time series) was retrieved from Wang et al. (2019). (d) Before they were used in the analysis, the weighted area maps were masked following the steps in *Vegetation data*. (e) For each unique combination of caribou spatial density class and land cover class, all weighted area pixels within those areas were retrieved and summed to provide the overall area covered for that density class and land cover class. Here, we show an example using the high caribou spatial density class and the Woodlands land cover class. The summed weighted area values were then used to calculate absolute and relative changes in PFT top cover.

isopleth ranges ($p \leq 0.001$) but not for calving 95% isopleth ranges (Figure 3). Summer range overlap decreased most at a rate of -1.2% year^{-1} ($R^2 = 0.68$; Figure 3). From 1994 to 2020, summer range overlap with the Core Uplands was roughly halved from 68.2% to 35.2%. Winter range overlap also decreased from 37.5% in 1991 to 22.8% in 2021 (slope $= -0.82\%$ year^{-1}, $R^2 = 0.35$; Figure 3). Post-calving range overlap showed a decreasing trend (slope $= -0.79\%$ year^{-1}, $R^2 = 0.24$; Figure 3), but annual overlap was more variable. Calving range overlap increased slightly (slope $= 0.40\%$ year^{-1}), although the trend was less definitive ($R^2 = 0.14$, $p = 0.05$; Figure 3). Similar trends were observed for 50% isopleths (Appendix S1: Figure S4).

Congruent with range overlap trends, calving 50% isopleth range centroids remained within the Core Uplands for the duration of the study period, although they shifted within this area (Appendix S1: Figure S5). Shifting and expanding ranges were observed from the summer 50% isopleth range centroids (Figure 4), and to a lesser degree for post-calving and winter centroids (Appendix S1: Figures S6 and S7). From 1994 to 2014, the herd's summer 50% isopleth range remained within the Core Uplands, although range size increased. Starting in 2015, summer range centroids shifted outside the Core Uplands as the herd expanded into new upland habitats to the northwest and the southeast.

Density-dependent trends in PFT cover

Distributions of elevation, northness, eastness, start of the snow-free season, TPI, and TRI were broadly similar across caribou density classes. The K-S D statistic is a metric of dissimilarity that ranges from [0–1] with 0 representing identical distributions and 1 representing completely distinct distributions. We found that 85% of pairwise comparisons had a D statistic ≤ 0.2, indicating general similarity between distributions (Appendix S1: Table S7, Figures S8–S13). Small differences were present, mostly for the winter range. Across winter range, areas with no caribou were somewhat lower elevation and less rugged than areas with higher caribou density ($D > 0.4$, Appendix S1: Table S7, Figures S9 and S13). Frequency

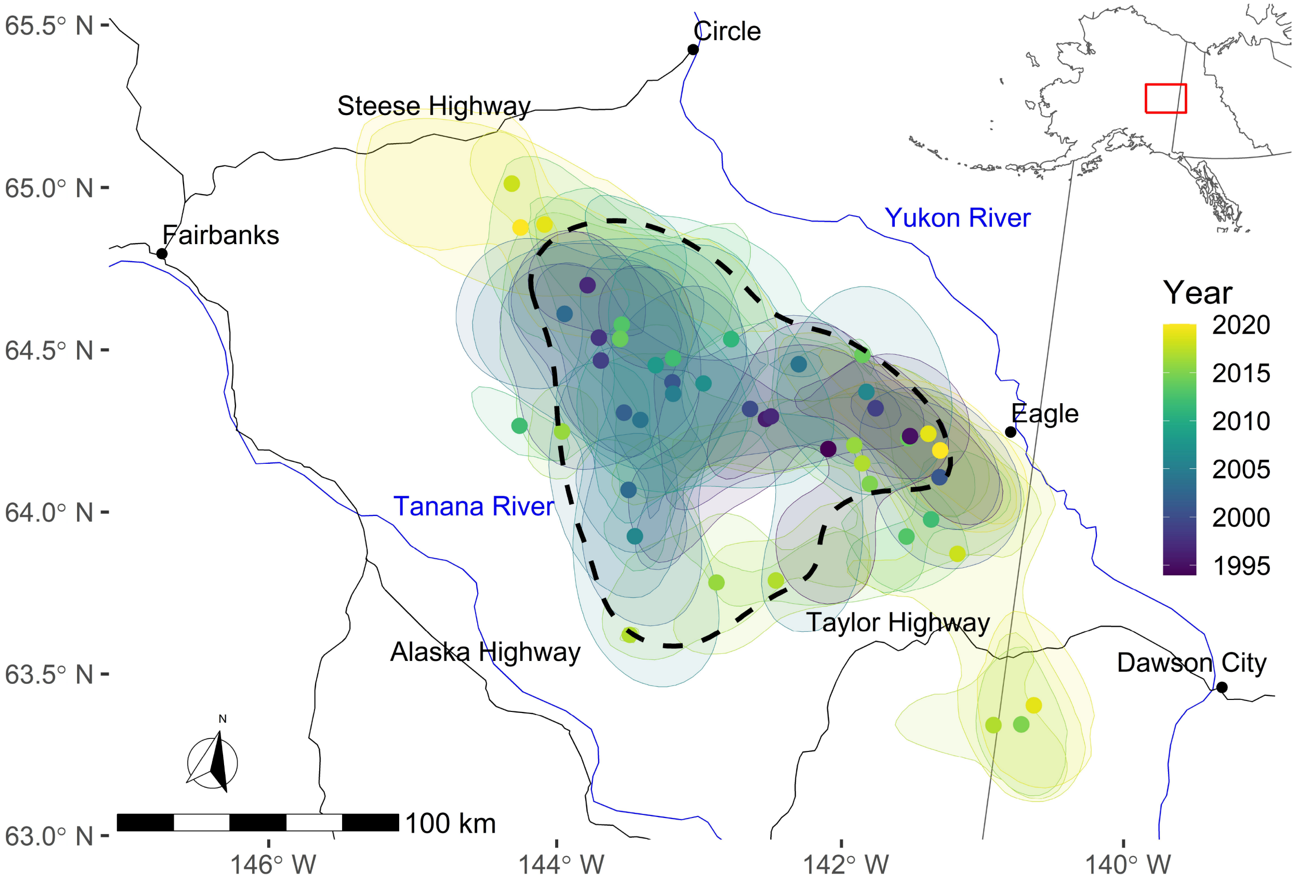

FIGURE 4 Annual summer 50% isopleth ranges for radio-collared adult female caribou (*Rangifer tarandus*) in the Fortymile Caribou Herd, 1992–2021. Polygons denote range boundaries, points denote range centroids. The dashed black area denotes the Core Uplands, which is the area of greatest caribou use across all seasons.

distributions varied somewhat for snow-free date, but distribution peaks occurred around broadly similar dates, with the possible exception of post-calving and summer ranges ($D > 0.3$, Appendix S1: Table S7, Figure S11). The overall similarity of habitat and environmental conditions across caribou density classes provides confidence that these areas are comparable and that observed PFT cover trends across density classes are not driven by major discrepancies in environmental conditions.

From 1992 to 2020, areas with high FMCH spatial density were associated with greater declines in cover of some preferred forage classes (e.g., lichens and graminoids) than areas with low caribou spatial density. Conversely, high FMCH spatial density areas were associated with greater increases in deciduous shrubs than low-density areas. PFT cover trends were mostly monotonic across the study period, but small relative to the uncertainty in the mapped products used to calculate change (Appendix S1: Figures S14–S16). Trends in less palatable evergreen shrub cover did not change across caribou spatial density classes. Forb cover change did not show a clear trend across caribou density classes (Appendix S1: Table S8). Forbs also represented a very small area proportion of the study area (~200 km^2) and had the highest model uncertainty amongst PFTs ($R^2 = 0.2$, Macander et al., 2022). Evergreen shrubs and forbs were thus excluded from further analyses. Lichen cover declined somewhat more in areas with high caribou spatial density compared to areas where caribou were largely absent. This trend was consistent across seasons and land cover types (Figure 5, Appendix S1: Figures S17–S19). Overall, lichen cover declined from 16.1% to 15.8% (−0.3% absolute change, −1.9% relative change) where caribou were largely absent and from 10.9% to 8.5% (−2.4% absolute change, −22.0% relative change) where caribou spatial density was high (Appendix S1: Table S8, see Appendix S1: Section S4 for change metric formulas). To assess total lichen lost across high caribou spatial density areas, we converted pixel-wise lichen cover loss to weighted area lost (e.g., $\frac{10\%\text{ absolute cover decline}}{100} \times 900\,\text{m}^2$ pixel area $= 90\,\text{m}^2$ area lost) and summed across all pixels. This resulted in 139 km^2 of total lichen area lost in high caribou spatial density areas.

Similarly, slightly more graminoid cover was lost where caribou spatial density was high, compared to areas where caribou were absent. This trend was most pronounced across the calving and post-calving range (Figure 5, Appendix S1: Figure S17). Across the calving range, graminoids declined from 8.5% to 7.9% (−0.6% absolute change, −7.1% relative change) where caribou were largely absent and from 8.0% to 6.1% (−1.9% absolute change, −23.8% relative change) where caribou spatial density was high. Across the post-calving range, graminoids declined from 8.6% to 8.0% (−0.6% absolute change, −7.0% relative change) where caribou were

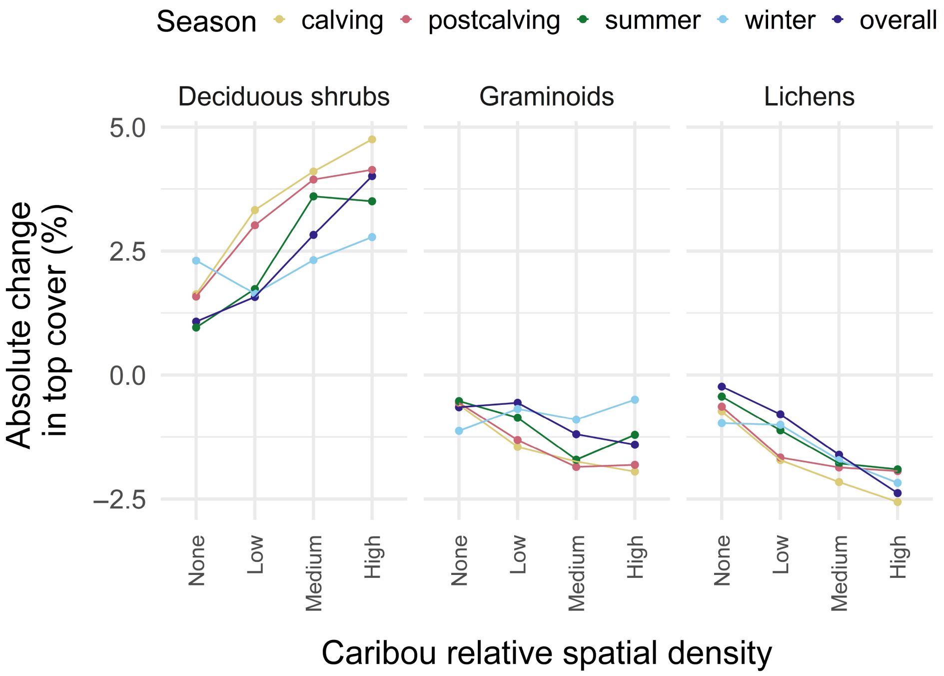

FIGURE 5 Relationship between caribou spatial density and absolute percent change in plant functional type (PFT) top cover from 1992 to 2020. The *x*-axis shows levels of relative caribou spatial density, from "None" (or very low density) to "High" density. Each facet represents a different PFT, and each color represents a different season. The seasons dictated the spatial extent of each caribou density bin and the probability of selection mask used. The "overall" season represents an aggregate of caribou use across all seasons.

largely absent and from 8.4% to 6.5% (−1.9% absolute change, −22.6% relative change) where caribou spatial density was high (Appendix S1: Table S8). Graminoid cover decreased more at higher caribou spatial density for most land cover types (Appendix S1: Figures S18 and S19).

Deciduous shrub cover increased more at high versus very low caribou spatial density (Figure 5). At high caribou spatial densities, deciduous shrub top cover increased from 26.4% to 30.4% (4.0% absolute change, 15.2% relative change; Appendix S1: Table S8). Where caribou were largely absent, deciduous shrub top cover increased from 19.6% to 20.6% (1.0% absolute change, 5.1% relative change). Within shrub genera, alder cover increased more (1.3% vs. 0.2% absolute increase) and shrub birch cover increased more (2.4% vs. 0.5% absolute increase) in areas with high versus very low caribou spatial density (Figure 6, Appendix S1: Table S9). Conversely, willow cover was relatively stable (−0.2% absolute change, −2.9% relative change) across caribou spatial density classes (Figure 6, Appendix S1: Table S9). Relative cover increases were greatest for alder (Appendix S1: Figure S20), but alder had lower cover across the study area (0.5%–2.7%) than shrub birch (10.2%–16.4%) or willow (5.2%–6.8%; Appendix S1: Table S9). Shrub genera trends were mostly consistent across land cover types, with the largest changes taking place in the tall shrub type (Appendix S1: Figures S21 and S22).

For all PFTs and shrub genera, trends in Sen's slopes were similar to trends in top cover change: Lichen and graminoid slopes were more negative in areas with higher caribou spatial density, whereas alder and birch slopes were more positive (Appendix S1: Figures S23 and S24). Likewise, within high caribou spatial density areas a larger proportion of pixels experienced more certain decreases in lichen and graminoid cover (Appendix S1: Figure S15). In these same high caribou density areas, a larger proportion of pixels experienced more certain increases in alder and birch cover (Appendix S1: Figure S16).

DISCUSSION

From 1992 to 2020, we documented a 4-fold increase in caribou abundance and increases in caribou population density across all seasonal ranges. Increased density can lead to greater impacts on vegetation within highly used areas via herbivory and trampling, with potential negative consequences for individual nutrition. During our study period, we also observed an increase in summer

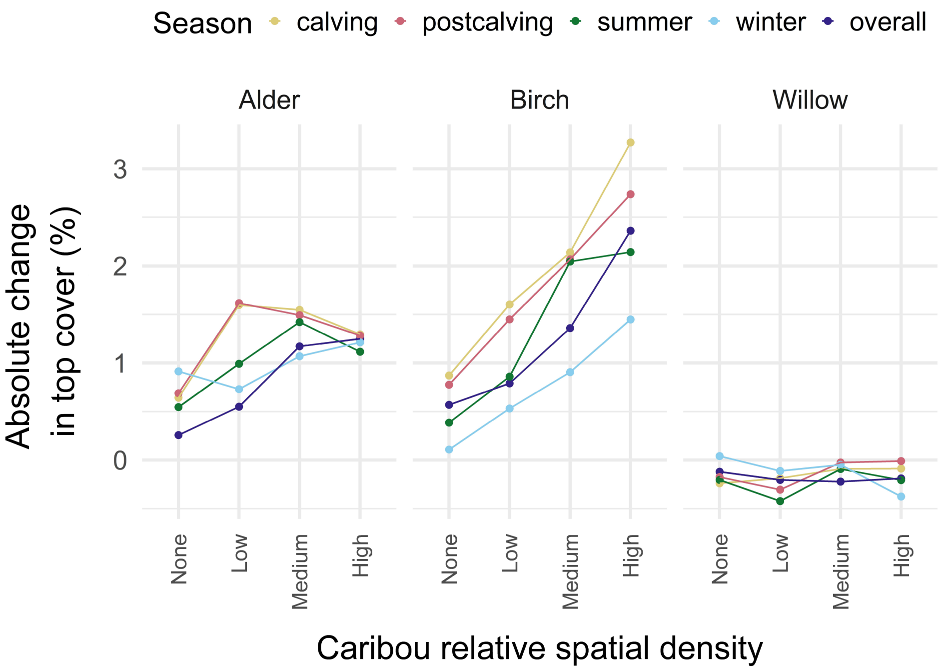

FIGURE 6 Relationship between caribou spatial density and absolute percent change in shrub genus top cover from 1992 to 2020. The *x*-axis shows levels of relative caribou spatial density, from "None" (or very low density) to "High" density. Each facet represents a different shrub genus, and each color represents a different season. The seasons dictated the spatial extent of each caribou density bin and the probability of selection mask used. The "overall" season represents an aggregate of caribou use across all seasons.

range size and a decrease in post-calving, summer, and winter range overlap with the primary FMCH range (the Core Uplands). These trends are indicative of range expansion occurring within the FMCH and consistent with forage reduction and/or increased intra-specific competition within the Core Uplands and the theory of density-dependent habitat selection. Demographic data from the herd further suggest declines in herd nutritional status over this time (Boertje et al., 2012, 2017; Gross, 2023). Using remotely sensed maps of PFT and shrub genus cover, we observed greater decreases in cover of some preferred forage (lichens and graminoids) where caribou spatial density was highest. Contrary to expectations, deciduous shrubs increased more where caribou spatial density was highest. However, these increases were driven by less palatable shrubs such as alder and dwarf birch, whereas willow, a critical forage shrub, remained relatively stable. Although modest, declines in key forage plants in combination with observed trends in range distribution, nutritional condition, and demography suggest forage reduction might have played a role in the recent population declines reported for this herd. Our study provides some of the first large-scale, remote-sensing informed evidence of correlation between sub-Arctic herbivore abundance and vegetation change. Our results suggest vegetation trajectories in Arctic/boreal regions could be influenced by caribou abundance, but vegetation changes were small compared to the uncertainty in the underlying map products used to calculate them. Thus, these findings would ideally be validated by in situ data.

Caribou density-dependence and range expansion

Density-dependent processes can be a crucial driver of population dynamics in large herbivore populations (Bonenfant et al., 2009). According to the theory of density dependence, the population growth rate slows as density increases (Getz, 1996). For ungulates, Fowler (1987) proposed that competition for food is the main density-dependent process influencing demographic rates. For wild reindeer and caribou, Skogland (1985) further suggested winter forage availability (e.g., lichen) is most critical, whereas other studies have shown summer range conditions can regulate caribou populations (Manseau et al., 1996; Messier et al., 1988). Recent studies on migratory caribou in an adjacent population demonstrated the importance of digestible protein obtained from the summer use of willow species in maintaining parturition, while overall survival has been tied to digestible energy obtained from lichen (Johnson et al., 2022).

FMCH population density increased across all seasonal ranges from 1992 to 2020, prompting management concerns that density-dependent impacts on forage might lead to population declines (Boertje et al., 2012). Increases in population density were pronounced in calving and post-calving range, peaking at 24.3 and 12.3 caribou km^{-2}, respectively. Winter range population densities also increased, averaging 0.9 caribou km^{-2} during the first half of the study period (1991–2005) and 2.4 caribou km^{-2} during the second half of the study period (2006–2020). This latter winter density greatly exceeded the 1.08 caribou km^{-2} that Messier et al. (1988) deemed excessive for the George River Herd in Quebec and the 1.35 caribou km^{-2} reported for the Western Arctic Herd (WAH) in northwest Alaska (Joly et al., 2007). In both cases, reported high winter range densities preceded large population declines. Because FMCH caribou seasonal ranges often overlap, increased population density across multiple seasons could result in intense, year-round grazing pressure within the herd's primary range, the Core Uplands (Skoog, 1968). This is relatively unique among migratory caribou herds and could lead to more pronounced density-dependent forage reduction in sympatric ranges than in caribou populations with completely allopatric seasonal ranges (Festa-Bianchet et al., 2011; Theoret et al., 2022).

Density-dependent processes can be alleviated or delayed via range expansion, which can open new areas for forage. Range size often increases with population size (Schaefer & Mahoney, 2003), possibly driven by social facilitation or density-dependent forage limitation (Duquette & Klein, 1987; Manseau et al., 1996). Skoog (1968) further postulated that as populations increase, caribou move farther away from their "center of habitation." However, range expansion may come with consequences such as increased energetic costs or use of lower quality habitat (Fancy & White, 1985; Morris, 1987; van Beest et al., 2014).

We documented the expansion of FMCH summer range size and decreases in summer, post-calving, and winter range overlap with the herd's center of habitation. These trends corroborate and expand on those reported by Boertje et al. (2012) who hypothesized the FMCH summer range expansion from 1994 to 2008 was caused by localized overgrazing in the Core Uplands. Boertje et al. (2017) also reported declines in 3-year-old parturition rates and October calf weights from 1995 to 2010, and these declines have continued through 2022 (Gross, 2023). These trends are consistent with ungulate life-history theory (Eberhardt, 1977, 2002; Fowler, 1987) which suggests reproductive rates and juvenile survival are most responsive to density dependence, but were also likely influenced by harsh winter conditions towards the end of this period (2020–2022). Starting in 2015, we observed FMCH range expansion into a high-quality summer range not used since the 1930s (for details on FMCH historic range, see Appendix S1: Section S7), which could alleviate nutritional stress within the herd. However, after reaching a maximum of 84,000 individuals in 2017, population models based on survival and reproduction indicated the herd had begun to decline (Alaska Department of Fish and Game, unpublished data, 2023). While other factors such as changes in predator management, harvest regime, and poor winter conditions likely influenced the change in herd trajectory (Gross, 2023), our analyses indicate cumulative forage reduction across seasons may have also played a role (for details on FMCH population and management history, see Appendix S1: Section S7).

Vegetation change and forage availability

Rangifer can disturb vegetation through grazing and trampling, especially as animal density increases. Impacts on vegetation can have consequences for ecosystem structure and function and can impact caribou themselves if forage is reduced. Our analysis revealed population trends within the FMCH that could be precursors to forage reduction such as increased population density across core ranges or symptoms of forage reduction such as range expansion. Over this same time period, other researchers reported troubling demographic trends such as reduced parturition and reduced calf weights, which could be indicative of nutritional stress and forage reduction (Boertje et al., 2017; Gross, 2023). These observations of apparent density dependence in demographic trends, independent of observations in this manuscript, led managers to intentionally reduce the population through harvest (Gross, 2023). To assess whether *Rangifer* has measurable impacts on vegetation, we analyzed changes in modeled PFT and shrub genera cover across levels of caribou relative spatial density. Recognizing that caribou spatial density can vary significantly over small time scales, we assessed cumulative impacts over nearly 3 decades. Across the FMCH range from 1992 to 2020, lichen and graminoid declines were most pronounced where caribou spatial density was highest. Furthermore, at the highest levels of caribou spatial density, less palatable shrubs expanded (alder, birch) whereas more palatable shrubs (willow) did not. These results indicate caribou spatial density might influence rates of vegetation change. However, absolute vegetation changes were modest relative to changes in herd size and density; therefore, our remotely sensed results would ideally be validated by on-the-ground data.

Lichens

We found the strongest potential impacts of caribou on lichen, consistent with a meta-analysis of field studies (Bernes et al., 2015). Because portions of FMCH seasonal ranges overlap, grazing and trampling during high-density calving, post-calving, and summer aggregations may influence winter lichen availability (for details on FMCH range overlap, see Appendix S1: Section S8). This contrasts with most migratory Arctic herds where winter and summer ranges are geographically separate (Festa-Bianchet et al., 2011; Theoret et al., 2022). Lichens also constitute a large proportion (25%–50%) of the FMCH diet during the growing season (Ehlers et al., 2021), which is unusual among migratory herds. We observed greater losses of lichen cover where caribou spatial density was higher across all seasons and land cover types. Over 28 years we observed a 2.4% absolute reduction (22% relative reduction) in lichen cover across areas with high caribou spatial density, with up to a 4.0% absolute reduction (29.2% relative reduction) in lichen-rich land cover types. Over the same time period, absolute lichen top cover declined only 0.7% across all of Alaska and the Yukon, 0.6% across the range of the Porcupine Caribou Herd, 0.3% across the range of the WAH, and 1.4% across the entire FMCH extended range (Macander & Nelson, 2022; Appendix S1: Table S10).

Past research has documented declines in lichen cover coincident with increasing caribou populations. An extreme example comes from St. Matthew Island, Alaska, where lichens were almost completely eliminated after caribou were introduced to the island and grew to high densities (18 animals km^{-2}), leading to extirpation of caribou on the island (Klein, 1968, 1987), but see Miller et al. (2005). In Finnmark, Norway, an analysis of remotely sensed lichen cover across a semi-domesticated reindeer winter range showed lichen cover decreased 0.6%–1.1% year^{-1} (relative declines 3.0%–2.5% year^{-1}), depending on the range district, as the reindeer population doubled (Johansen & Karlsen, 2005). Within the winter range of the WAH, field-measured lichen cover decreased ~0.9% year^{-1} (relative decrease −2.7% year^{-1}) as population numbers rose (Joly et al., 2007). In both Finnmark and Alaska, concerning reindeer/caribou demographic trends (decreased body weights, high mortality, low calving rates) were observed coincident with decreases in lichen across the winter range, possibly influenced by overgrazing.

Our remotely sensed measures of lichen cover suggest a slower decline of lichens in high-use areas with absolute declines of 0.09% year^{-1} overall (0.8% year^{-1} relative decline) and up to 0.14% year^{-1} (1.0% year^{-1} relative decline) in lichen-rich land cover types. Both Johansen and Karlsen (2005) and Joly et al. (2007) report higher initial lichen cover, and reindeer densities in Finnmark were 9–22 times higher than average winter FMCH density. These factors could have contributed to the faster rates of lichen decline reported by those studies. Regardless, our analysis suggests the rate of lichen decline across the FMCH range is modest compared to other *Rangifer* ranges.

It is important to note we cannot directly link lichen declines to caribou grazing and trampling since our analysis relies on modeled estimates of PFT cover subject to uncertainty and is not experimental, that is, cannot identify causation. For example, the deciduous shrub expansion we observed could also reduce lichen cover via competitive exclusion (Cornelissen et al., 2001; Mekonnen et al., 2018; Walker et al., 2006) or overtopping (Macander et al., 2022). Regardless of the main driver, observed lichen reductions could have energetic consequences for the FMCH. Because lichens are an important component of the migratory caribou diet, the reduction of winter lichen cover can have negative impacts on caribou overwinter survival, neonatal survival, postpartum mass, and ultimately population size (Joly et al., 2010). These effects can be ameliorated if caribou expand their winter range (Ferguson et al., 1998, 2001), although viable alternative ranges are not always available (Joly et al., 2010).

Graminoids

Graminoids are resilient to grazing and capable of compensatory growth responses (Post & Klein, 1996). Therefore, caribou can facilitate graminoid growth, especially when other PFTs decline (Joly et al., 2007; Klein, 1987; Post & Pedersen, 2008). Some research suggests caribou are capable of initiating or maintaining productive grasslands (Thing, 1984; van der Wal, 2006), akin to the "grazing lawns" facilitated by large herbivores in the Serengeti (McNaughton, 1984) or the Mammoth Steppe of the Late Pleistocene (Olofsson & Post, 2018). In other cases, caribou cause graminoid declines or have no effect (Bråthen et al., 2007; Bernes et al., 2015). The intermediate disturbance hypothesis predicts the highest graminoid productivity at intermediate levels of grazing pressure (McNaughton, 1979), although this is not always observed (Olofsson et al., 2001).

Because graminoids are a small part of the FMCH diet (Ehlers et al., 2021), we expected little influence of caribou spatial density on graminoid cover change. Instead, we observed somewhat greater declines in graminoid cover as caribou spatial density increased. This trend was strongest across calving and post-calving ranges, possibly because graminoids are most prevalent in the FMCH diet during May and June (Ehlers et al., 2021) and caribou density is high during these months. However, few of these changes exceeded the level of uncertainty in mapped predictions of graminoid cover (Appendix S1: Figure S15).

Shrubs

Caribou herbivory has the potential to reduce deciduous shrub cover, potentially constraining shrub expansion, which has been widely documented across tundra ecosystems (Christie et al., 2015; Macander et al., 2022; Mekonnen et al., 2021; Orndahl et al., 2022). However, shrub responses to herbivory are highly context-dependent (Bernes et al., 2015; Morrissette-Boileau et al., 2018). Historic caribou density and local shrub palatability likely play a role. For example, most evidence for *Rangifer*-induced reductions in shrubs comes from Greenland and Europe, where semi-domesticated reindeer herds are managed at high densities (Bernes et al., 2015), and a palatable dwarf birch subspecies (*B. nana* ssp. *nana*) is prevalent (Bryant et al., 2014; Cahoon et al., 2012; Olofsson & Post, 2018; Post, 2013). Conversely, minimal impacts of caribou herbivory on shrubs have been reported in North America, where caribou herds occur at relatively low densities and a less palatable dwarf birch subspecies (*B. nana* ssp. *exilis*) is prevalent (Bryant et al., 2014; Joly et al., 2007; Morrissette-Boileau et al., 2018).

Our findings were not consistent with the idea that caribou suppress shrub expansion. In fact, we observed greater increases in deciduous shrub cover where caribou spatial density was higher. We cannot definitively identify the causes of observed shrub changes; however, several explanations are possible for the correlation between shrub increase and high caribou density.

First, areas selected by caribou might also have attributes favorable for shrub expansion. For example, higher elevation regions can exhibit rapid rates of shrub cover increase as shrubline expands upwards (Berner et al., 2020; Hallinger & Martin, 2010; Myers-Smith & Hik, 2018). In this scenario, greater shrub increase might be expected at higher caribou densities if caribou density is positively correlated with elevation. We did not find a positive correlation between caribou spatial density classes and elevation (Appendix S1: Table S7, Figure S10). However, we did find higher relative shrub increases in areas that were classified as "barren" or "sparsely vegetated" at the start of the study period (Appendix S1: Figure S19). Regardless, shrubline advance could be problematic for migratory caribou that utilize alpine calving and summer habitat, as these areas will shrink as shrubs expand. Furthermore, shrub expansion might inhibit travel by cutting off linkage habitat, making it more difficult for caribou to perform seasonal migrations and seek out new ranges with intact forage (Rickbeil et al., 2018).

Selective herbivory may also alter shrub community composition by suppressing palatable shrub species, thereby allowing less palatable species to expand. This is especially important as ongoing climate warming promotes shrub expansion across the Arctic (Bryant et al., 2014; Christie et al., 2014; Mekonnen et al., 2021). Less palatable shrub species like alder and dwarf birch (*B. nana* ssp. *exilis*) were most prevalent across our study area, which could dampen impacts of herbivory on shrub cover and further favor the expansion of less palatable shrubs. Consistent with selective herbivory, we found well-defended alder and dwarf birch increased more across high versus low caribou spatial density areas, whereas highly palatable willow remained relatively stable or decreased slightly. This suggests caribou may reduce diet quality across their range over time by enabling the expansion of less palatable shrubs, possibly resulting in important trade-offs between forage quantity and quality (Christie et al., 2015; Johnson et al., 2021). Such impacts on diet could create additional downward pressure on an already declining herd.

However, changes in willow cover were consistent across caribou spatial density classes (−0.2%), and similar changes were observed across all of Alaska and the Yukon Territories (−0.1%). This suggests trends of stable or slightly declining willow are widespread and not solely driven by caribou herbivory. Herbivory from other species such as moose (*Alces alces*) might also keep willows in check or contribute to widespread, albeit modest, declines. Moose and other herbivore populations are influenced by a variety of factors including predators, wildfires, and climate. Quantifying the factors affecting other herbivore populations is beyond the scope of this paper, but herbivory from these species could have impacted the shrub and other vegetation changes we observed. For example, predator control (i.e., culling wolves [*Canis lupus*]) occurred across our study area from 1998 to 2018, which could have influenced the impacts of moose herbivory (Boertje et al., 2017; Wells, 2023). Because willows are known to respond positively to ongoing climate warming, herbivory might inhibit willow expansion rather than causing measurable declines (Bråthen et al., 2017; Mekonnen et al., 2021; Olofsson et al., 2009). Herbivory might also impact willow structure (e.g., height and/or biomass), and these changes may not be captured by estimates of plant cover (Bråthen et al., 2017; Christie et al., 2015). Willows are generally resilient to browsing, but summer browse can reduce their utility as forage by reducing leaf nitrogen concentrations (Christie et al., 2014; Danell et al., 1994). Willows are a crucial source of protein for female caribou as they enter critical life periods such as peak lactation, early calf survival, and the rut (Crête & Huot, 1993; Ehlers et al., 2021; Klein, 1990). Although we did not find strong evidence of willow decline, modest declines in willow abundance coupled with browsing-induced changes in willow forage quality and accelerated expansion of less palatable shrubs could reduce caribou summer range quality in general.

Edaphic factors such as soil moisture and nutrient supply might also influence shrub expansion. Preliminary analyses using remotely sensed maps of soil properties suggested total soil nitrogen levels at 0–30 cm depth were higher at higher levels of caribou spatial density (Poggio et al., 2021; Appendix S1: Figures S25–S27). Fertilization from caribou urine or feces can lead to higher soil nitrogen, particularly in upper soil levels (Hobbs, 1996; McKendrick et al., 1980; Olofsson et al., 2004). This can in turn facilitate deciduous shrub growth, particularly that of shrub birch (Barthelemy et al., 2015; Gough et al., 2012; Shaver et al., 2001). Higher soil nitrogen can also be a consequence of shrub expansion (Myers-Smith et al., 2011; Mekonnen et al., 2021). These results provide a cursory look at how caribou density is correlated with edaphic properties, but these patterns warrant further research.

Finally, uncertainty in the mapped products used to assess vegetation change must be considered. Although our analysis reveals dominant trend directionalities that are consistent with density-dependent caribou impacts, change magnitude was small compared to uncertainty in the PFT cover maps used to calculate change. Thus, it is possible that some of the change quantified in this study does not represent on-the-ground vegetation change, but rather noise in the remotely sensed products. Conversely, we may have underestimated change if the uncertainty metric (RMSE) used here overestimates pixel-level uncertainty. Advances in computing are facilitating better constrained uncertainty estimation which can provide a clearer picture of spatially variable uncertainty—this is discussed further in *Limitations*.

Quantifying herbivory with remote sensing

Remote sensing has been used to identify negative relationships between caribou abundance and vegetation productivity across the ranges of the George River, Pen Islands, Cape Bathurst, Bluenose East, and Bluenose West caribou herds (Campeau et al., 2019; Newton et al., 2014; Rickbeil et al., 2015). We similarly identified a negative relationship between caribou spatial density and graminoid and lichen cover. However, we observed a positive relationship between caribou spatial density and deciduous shrub cover. This highlights the utility of partitioning by vegetation type. Because the expansion of deciduous shrubs across our study area would manifest as a greening trend, declines in graminoid and lichen cover might have gone unnoticed using metrics of vegetation greenness alone. Further partitioning shrubs by genera allowed us to examine trade-offs in expanding shrub forage quantity versus diet quality. Our remote sensing approach could be applied to other caribou herds or herbivore assemblages in other ecosystems and, in conjunction with field research, might provide a more comprehensive understanding of how animals impact vegetation change trajectories. For example, remotely sensed analyses of herbivory could complement large-scale herbivore exclusion experiments underway across African savannas (Goheen et al., 2018). Furthermore, regional analyses such as these could inform future research by identifying ideal locations for on-the-ground experiments such as herbivore exclosures.

Limitations

It is crucial to note that remotely sensed map products also have limitations and are subject to uncertainty introduced during the modeling process. For the vegetation cover maps we utilized, pixel-level changes in percent cover from 1985 to 2020 were mostly not significant at $p < 0.05$ (Macander et al., 2022). For example, we observed a greater number of pixels with more certain lichen decline (|% cover change| > root-mean-squared-error) in areas with high caribou density than in areas with low caribou density, but pixels with more certain declines represented a small proportion (2.8%) of total pixels across the study area (Appendix S1: Figure S1). Overall, absolute changes in vegetation cover were more modest than expected given the 4-fold increase in caribou population and increases in density over most seasonal ranges. Remotely sensed data is also limited in that it can only assess vegetation top cover. This means that reported changes in vegetation could be influenced by overtopping as vegetation in the canopy grows over understory plants. In these instances, real declines in understory plants, particularly shade-intolerant lichens and bryophytes, can, but do not always, occur due to light competition. Given uncertainties in the remotely sensed data, the vegetation change trends we report here would ideally be validated with in situ data. Change trends from this analysis could be used to identify optimal locations for such long-term monitoring plots.

The PFT cover maps do capture ecologically sensible changes in vegetation following disturbances such as fire, which suggests they are able to identify acute vegetation change trends across larger areas (Macander et al., 2022). Our lichen and graminoid change results are consistent with density-dependent forage reduction, but we cannot directly tie changes in vegetation cover to caribou herbivory since our study was not designed to establish causation. Most likely, observed changes in PFTs were influenced by a variety of factors. Caribou herbivory and trampling may have played a role alongside other potential drivers such as biogeochemical conditions, climate, phenology, snow properties, and/or topography.

The maps we used are at the edge of what is possible with currently available remote sensing data and modeling techniques. As remote sensing technology advances and the archive of available data grows, map precision and accuracy should improve. For example, time series of structural data (e.g., lidar) or hyperspectral data would likely improve vegetation cover predictions and allow for mapping of vegetation structural metrics, such as height and biomass. In addition, the RMSE-based uncertainty estimates we used are useful but have a few key limitations. First, RMSE values are restricted to 101 unique values (0%–100%) and second, they are applied based only on the starting amount of cover for each PFT. Assigning statistical significance to aggregate trends observed in remote sensing data is challenging due to the presence of temporal and spatial autocorrelation, as well as the large volume of pixels, which renders many statistical tests impractical. However, emerging techniques might allow for more robust quantification of trend certainty in the future (Ives et al., 2021). Although imperfect, the maps we used provide information that would not otherwise be available (i.e., data across large spatiotemporal scales).

CONCLUSION

Large herbivore population dynamics are driven in part by bottom-up controls such as forage availability and diet quality, which may be influenced by the density of animals on the landscape. As populations approach carrying capacity, density-dependent reduction of preferred forage species can affect range distribution, demography, and population trends. We analyzed changes in vegetation within the range of a sub-Arctic caribou herd whose abundance, range size, and density rose over the past 30 years. Using a novel remote-sensing approach, we found evidence of vegetation changes consistent with herbivory and/or trampling on preferred forage species. Across areas of high-density caribou use, lichen and graminoid cover declined. These declines were modest compared to uncertainty in the underlying remotely sensed data, but in aggregate suggest a trend of declining forage in high-use regions. Long-term reduction of these critical forage items, especially slow-growing lichen, and regardless of the cause, could have negative impacts on the FMCH. Some of these impacts may have already been observed, and others might be revealed in years to come. Conversely, we did not find evidence that caribou were able to constrain shrub expansion. This contrasts with research from other regions but confirms synthesis research suggesting patterns of Arctic shrub expansion might be influenced by regional shrub palatability, along with herbivore density and diversity. Our results suggest increases in deciduous shrub can be biased towards low-palatability species. This can lead to decreases in diet quality that are not beneficial to caribou. Using remotely sensed data, we were able to assess caribou impacts across a broad spatiotemporal extent. These methods could be applied to other large herbivores across the globe to understand how impacts on vegetation change differ based on demography and ecology. Combining large-scale analyses such as ours with detailed manipulative experiments such as exclosures would help validate remotely sensed results and might provide more insight than either can produce alone.

AUTHOR CONTRIBUTIONS

Kathleen M. Orndahl, Scott J. Goetz, Mark Hebblewhite, Jim D. Herriges, and Michael J. Suitor conceived the ideas. Kathleen M. Orndahl, Mark Hebblewhite, Jim D. Herriges, Matthew J. Macander, and Eric C. Palm designed the methodology. Kathleen M. Orndahl, Torsten W. Bentzen, Jim D. Herriges, Matthew J. Macander, Eric C. Palm, and Michael J. Suitor processed and curated the data. Kathleen M. Orndahl analyzed the data with input from Torsten W. Bentzen, Logan T. Berner, Libby P. W. Ehlers, Scott J. Goetz, Mark Hebblewhite, Jim D. Herriges, Kyle Joly, Matthew J. Macander, Eric C. Palm, and Michael J. Suitor. Kathleen M. Orndahl led the writing of the manuscript. All authors contributed to writing and editing.

ACKNOWLEDGMENTS

This research was supported by the National Science Foundation Graduate Research Fellowship under Grant No. 1938054 (to Kathleen M. Orndahl) and U.S. National Aeronautics and Space Administration (NASA) grant NNX15AW71A (to Scott J. Goetz). This material is based upon work supported by the U.S. National Science Foundation (NSF) under Grant No. 2127272 (to Logan T. Berner). Data analysis was supported through the use of Northern Arizona University's high-performance computing cluster (Monsoon), funded by Arizona's Technology and Research Initiative Fund. The authors thank the Yukon Government, the U.S. Bureau of Land Management, and Parks Canada for providing logistical and financial support to facilitate field research supporting this work. We extend thanks also to Yukon–Charley Rivers National Park (YUCH-2018SCI-0004), Yukon Government (19-64S&E), Ivvavik National Park (IVV-2019-32638), the Wildlife Management Advisory Council—North Slope, the Tetlin Renewable Resource Council, the Gwich'in Renewable Resources Board, and the Aklavik Hunters and Trappers Committee for their support of this research. The authors are grateful to the U.S. Bureau of Land Management, Alaska Department of Fish & Game, Yukon Government, and all individuals who collected the caribou radio-collar data without which this research would not be possible. We also thank one anonymous reviewer whose thoughtful feedback greatly improved the quality of the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and novel statistical code (Orndahl, 2025) are available on Zenodo at https://doi.org/10.5281/zenodo.14927215. Additional data (Orndahl et al., 2025) are available on the Arctic Data Center at https://doi.org/10.18739/A2C824G8W. Caribou locality data, season-year isopleths, and season-year occurrence distributions are sensitive data and not available publicly; these data are owned by the Alaska Department of Fish and Game and are available to qualified researchers by contacting the Division of Wildlife Conservation, Alaska Department of Fish and Game with the following details. For caribou locality data, request VHF and GPS collar locations for the Fortymile caribou herd for the years 1991–2021, all seasons, and all cohorts. For season-year isopleth data, request Fortymile caribou season-year isopleths for the years 1991–2021, all seasons, and isopleth levels 0.95 and 0.5. For season-year occurrence distribution data, request Fortymile caribou season-year occurrence distributions for the years 1991–2021 and all seasons.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Orndahl, Kathleen M., Torsten W. Bentzen, Logan T. Berner, Libby P. W. Ehlers, Mark Hebblewhite, Jim D. Herriges, Kyle Joly, et al. 2025. "Shifting and Expanding Ranges of a Sub-Arctic Caribou Herd and Associated Changes in Vegetation." *Ecological Applications* 35(4): e70038. https://doi.org/10.1002/eap.70038