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Climate-informed forecasts reveal dramatic local habitat shifts and population uncertainty for northern boreal caribou

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Open Research statement

Data (Stewart, et al. 2023) are available in Dryad at https://doi.org/10.5061/dryad.gmsbcc2p6. Burned area classes were derived from the Canadian National Fire Database (up to 1985; Natural Resources Canada: https://cwfis.cfs.nrcan.gc.ca/ha/nfdb) and the National Burn Area Composite (1986–2017; Natural Resources Canada: http://cwfis.cfs.nrcan.gc.ca/datamart/datarequest/nbac). Anthropogenic disturbance footprint within boreal caribou ranges were obtained from the Boreal Ecosystem Anthropogenic disturbance data provided by the Canadian Government in 2010 (Environment and Climate Change Canada, 2010) and 2015 (Environment and Climate Change Canada, 2015). All code necessary to reproduce all analyses, including acquisition of the above-mentioned data sets used within this paper, is archived in Zenodo in Micheletti and Chubaty (2023) and Micheletti, Chubaty, and McIntire (2023) at https://doi.org/10.5281/zenodo.7503130 and https://doi.org/10.5281/zenodo.7503113, respectively.

ABSTRACT

Most research on boreal populations of Woodland caribou (*Rangifer tarandus caribou*) has been conducted in areas of high anthropogenic disturbance. However, a large portion of the species' range overlaps relatively pristine areas primarily disturbed by natural disturbances, such as wildfire. Climate-driven habitat change is a key concern for the conservation of boreal-dependent species, where management decisions have yet to consider knowledge from multiple ecological domains integrated into a cohesive and spatially explicit forecast of species-specific habitat and demography. We used a novel ecological forecasting framework to provide climate-sensitive projections of habitat and demography for five boreal caribou monitoring areas within the Northwest Territories (NWT), Canada, over 90 years. Importantly, we quantify uncertainty around forecasted mean values. Our results suggest habitat suitability may increase in central and southwest regions of the NWT's Taiga Plains ecozone but decrease in southern and northwestern regions driven by conversion of coniferous to deciduous forests. We do not project boreal caribou population growth rates to change despite forecasted changes to habitat suitability. Our results emphasize the importance of efforts to protect and restore northern boreal caribou habitat despite climate uncertainty while highlighting expected spatial variations that are important considerations for local people who rely on them. An ability to reproduce previous work, and critical thought when incorporating sources of uncertainty, will be important to refine forecasts, derive management decisions, and improve conservation efficacy for northern species at risk.

Keywords: anthropogenic change, climate change, critical habitat, ecological forecasting, fire, *Rangifer*, SpaDES, species at risk, vegetation, Woodland boreal caribou

INTRODUCTION

The habitat selection and population growth of boreal populations of Woodland caribou (*Rangifer tarandus caribou*; hereafter boreal caribou) are driven by multiple factors including anthropogenic activities, natural disturbances, and associated habitat changes (Environment Canada, 2011). In the northern boreal forest – an area of highly variable anthropogenic disturbance – future natural ecosystem disturbances may have a large impact on caribou due to climate change. These include an increased probability of vegetative drought and wildfires (Boulanger et al., 2014, 2017; Gauthier et al., 2015; but see Marchal et al., 2019), associated changes to forest composition and structure (Boulanger et al., 2014, 2017; Baltzer et al. 2021), and permafrost thaw (Baltzer et al., 2014; Helbig et al., 2016; Schneider et al., 2016). The effects of such habitat changes are not well encompassed by current policy primarily originating from analyses conducted on southern populations largely impacted by human disturbance (Stewart et al. 2020; Neufeld et al. 2021). Nonetheless, these environmental changes have important implications for inferring species northward range shifts, demographic change, and downstream consequences for reliant northern societies.

Johnson et al. (2020) compared boreal caribou demographic rates across Canada and found a strong relationship between anthropogenic disturbances, calf recruitment and adult survival. A weaker relationship was found with fire. However, in regions where anthropogenic disturbance is variable (e.g., northern Canada), drivers such as wildfires or primary productivity may better predict caribou population status (Fortin et al., 2017; Neufeld et al., 2021; Palm et al. 2022); uncertainty regarding recruitment is high where anthropogenic disturbance is low (Johnson et al., 2020; Neufeld et al., 2021; Rudolph et al., 2017). Calf recruitment declines with climate-induced phenological and predatory changes in other caribou ecotypes (Post and

Forchhammer 2008; Vors and Boyce 2009; Mallory and Boyce 2018), with similar fecundity declines shown in other northern ungulates (e.g. Post et al. 1997). With climate change, the relative demographic influence of anthropogenic and wildfire drivers may change through important range-wide indirect (e.g., habitat-mediated) effects on boreal caribou (Neilson et al. 2022; Leblond et al. 2022).

The contemporary rate of northern environmental change requires a predictive (Mouquet et al., 2015; Travers et al., 2019) rather than reactive approach to resource conservation. Given uncertainty with forecasting species dynamics, we must be able to reliably and repeatedly update forecasts with the best available information about system drivers and anticipate the spatial and temporal requirements of effective and efficient conservation across broad extents. Within the circumpolar boreal forest – the world's largest land biome – this 'conservation forecasting' (Travers et al., 2019) requires process-driven forecasts of landscape change that include updateable models (Dietze et al., 2018; McIntire et al., 2022), and from which changes in species habitat and populations may be inferred (*sensu* Cadieux et al., 2020; Micheletti et al., 2021). Climate change indirectly affects boreal caribou through its relation to habitat (Neilson et al., 2022) making climate-informed forecasts of landscape change important.

However, integration of models from diverse areas of ecology – such as wildlife ecology, climate change, wildfire, and forest ecology – is challenging. The field of ecological forecasting is in its infancy (Clark, 2001; Dietze, 2017; Dietze & Lynch, 2019; Travers et al., 2019), and uncertainty is rarely reported. Existing model integrations (e.g., Rempel et al., 2021) are often written in specialized languages (e.g., ALCES, LANDIS-II) and use simulation platforms whose parameters are often estimated from other studies; scientists' direct involvement in iteratively performing projections is hampered as updating models with the latest data sources, or changing study areas, is unattainable. Frequently, existing work is neither repeatable nor reproducible, both hallmarks of the scientific process (Hayward et al., 2015) and an essential requirement for predictive modeling (Bodner et al., 2020). Moving conservation forecasting towards an opensource platform capable of adaptable and updateable model integrations would be an asset for ecology generally, and species conservation planning specifically (McIntire et al., 2022; Micheletti et al., 2021).

To understand the potential effects of climate-driven landscape change on threatened boreal caribou we forecast the future trajectories of five caribou population monitoring areas (hereafter 'monitoring areas') across the Taiga Plains of the Northwest Territories, Canada, throughout the 21st century. We forecast habitat suitability and population trends using the most recently available resource selection (DeMars et al., 2020) and demographic (Johnson et al., 2020) models by incorporating future landscape conditions based on integrated climate-sensitive vegetation and wildfire models. We conduct this work in a northern area of the boreal caribou range to specifically investigate the effects of climate-driven habitat change on this species at risk.

METHODS

Study area

At 50 million ha, the Taiga Plains of Canada's Northwest Territories (NWT) overlaps with several Indigenous lands including the Gwich'in, Inuvialuit, and Sahtú Settlement Areas, Wek'èezhìı Management Area, and the Southern NWT region which is comprised of several ongoing land claim agreements that overlap the Dehcho Region and Akaitcho Territory. Anthropogenic disturbance covers 8% of the NWT Taiga Plains (Environment Canada, 2012), is highly variable (comprising 6.7 to 28.0 % of monitoring areas; Appendix S1: Table S2) and is not anticipated to increase drastically due to ongoing land claim negotiations, limited road access, high operating costs, and low commodity prices. This study area has an average annual precipitation of 230-500 mm and is largely composed of forested land (Ecosystem Classification Group, 2007); roughly 78% of forests are coniferous, 11% are mixed wood, and 10% are deciduous (NFI, 2013). The upland forests of the Taiga Plains are dominated by black spruce (*Picea mariana*), white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and tamarack (*Larix laricina*; Ecosystem Classification Group, 2007).

Federal and territorial governments in Canada estimate there are up to 7,000 boreal caribou across the NWT Taiga Plains (Environment Canada, 2011). Five monitoring areas were used in the initial scientific assessment (Environment Canada, 2011) and subsequent analyses (Johnson et al. 2020) informing species recovery (Figure 1). The NWT Taiga Plains region approximates the NT1 local population unit of boreal caribou used in the national Recovery Strategy (Figure 1; Environment Canada, 2012). This local population unit is considered threatened but self-sustaining (Environment and Climate Change Canada, 2019; Government of Northwest Territories, 2019) and may become endangered if causes of population decline (e.g., changes to forest composition and wildfire regimes) are not considered in recovery planning (Environment and Climate Change Canada 2019).

An integrated forecasting framework

We sought to integrate models of important boreal forest ecological processes to inform projections of boreal caribou habitat and demography. Our integration incorporates openly available landscape models of climate-sensitive forest vegetation dynamics, climate-sensitive wildfire dynamics, northern boreal caribou habitat selection, and boreal caribou demographics (Figure 2). We implemented these models within an integrative forecasting framework coded in R (R Core Team, 2021) using the *SpaDES* toolkit (Chubaty & McIntire, 2021). We followed the PERFICT approach to predictive ecology (McIntire et al. 2022) supporting high levels of accessibility, interoperability, and reusability. Future changes to data and model components presented here can be readily updated with more relevant, more precise, or more advanced models for the study area should they become available.

Our integration is implemented as a suite of two collections, each composed of two modules. The first collection – the dynamic modules – fits statistical models and parameters, and then simulates the dynamics of (1) climate-sensitive forest vegetation change (*LandR Biomass CS*) and (2) climate-sensitive wildfire (*FireSense*). The second collection – the non-dynamic modules – implements published statistical parameters and models and predicts (3) boreal caribou habitat suitability (*caribouRSF*) and (4) boreal caribou population growth (*caribouPopGrowth*). Integrating these models, and iteratively projecting them through time allows us to understand how landscape-driven impacts of climate change may affect both caribou habitat suitability and population growth within one ecological forecast that is linked to original data sources where possible.

Forecasting northern climate-sensitive landscape change

Our methods to project climate-sensitive landscape change through forest vegetation dynamics and wildfire follow those of Micheletti et al. (2021). Briefly, *LandR Biomass CS* is a climate-sensitive, spatially explicit model of vegetation dynamics composed of four SpaDES modules and two R packages. Two data treatment and parameterization modules estimate the parameters governing species-specific biomass change (*Biomass_borealDataPrep* and

Biomass_speciesParameters), a core dynamic vegetation model (*Biomass_core*) and a module that simulates vegetation responses to disturbances (i.e., fire; *Biomass_regeneration*). The core dynamic vegetation module simulates forest biomass succession dynamics similarly to the LANDIS-II Biomass Succession Extension v3.2 model (Barros et al., 2022a; Scheller & Miranda, 2015; Scheller & Mladenoff, 2004). These modules together with the LandR R package (Barros et al. 2022b) generate "baseline" (i.e., non-climate sensitive) growth and mortality; climate sensitivity is simulated by adding a separate R package, LandR.CS, to the simulation.

FireSense is a spatially dynamic wildfire model that simulates the processes of ignition, escape, and spread as spatially varying probabilities predicted by climate and vegetation. Fire spread is simulated as a percolation process (sensu Hargrove et al., 2000). The parameters linking climate and vegetation to these three processes are described in Marchal et al. (2017a, 2017b, 2020). Here, we classified the landscape into one of four vegetative land cover classes: deciduous leading, conifer leading, young vegetation (i.e., < 15 years since disturbance), and other. Fires stop burning when no further spreading occurs.

The outputs of these dynamic models required some adaptations to reflect the inputs required for boreal caribou habitat selection and demographic models. We converted the species-specific aboveground tree biomass values obtained from the vegetation simulations into one of four vegetative land cover classes: deciduous leading, conifer leading, young vegetation (i.e., < 15 years since disturbance), and other. Leading within a pixel is defined for the species type (deciduous or conifer) that represents more than 50% biomass. Following Micheletti et al (2021), we used the Monthly Drought Code (MDC) to estimate the climate effect on wildfire ignition, escape, and spread. We took these values from three, spatially explicit, General Circulation Model (GCM) projections (CCSM4, CanESM2, and INM-CM4; *sensu* Bergeron et al., 2010) within the fifth IPCC Assessment Report (IPCC 2014), under the Relative Concentration Pathway (RCP) 8.5, to represent our climate change scenarios. We used annual temperature anomaly (ATA) and climate moisture index (CMI) to evaluate and forecast the spatially explicit effect of climate on vegetation change. Yearly data from CCSM4, CanESM2, and INM-CM4 represent average, higher, and lower levels of projected temperature (°C) and precipitation (mm), respectively (Fajardo et al., 2020). Although RCP 8.5 may be considered as a worst-case climate change scenario for 2100 (Hausfather & Peters, 2020), the average increase in temperature in the present century will likely exceed RCP 4.5 (Sherwood et al., 2020), supporting the use of this RCP for 21st century forecasts (Schwalm et al., 2020).

Incorporating existing anthropogenic disturbance

We developed two sets of anthropogenic layers that matched the available statistical models for resource selection (DeMars et al., 2020; implemented in *caribouRSF*) and population growth (Johnson et al., 2020; implemented in *caribouPopGrowth*), respectively. Both sets of layers incorporate current anthropogenic disturbances across the study area and were kept constant through time, based on the fact that 1) anthropogenic disturbance is not anticipated to increase significantly in NWT (GNWT 2021 Economic Review), and 2) no realistic model of future anthropogenic change exists currently for this area.

For *caribouRSF*, anthropogenic disturbance layers were based on both linear and polygonal disturbance derived from 30 m resolution Landsat imagery by the Canadian Government in 2010 (Environment and Climate Change Canada, 2010) and 2015 (Environment and Climate Change Canada, 2015). The 2015 layer did not have data for every pixel; we backfilled these pixels with 2010 data. An exception includes the roads component of these layers: for the distance to major public roads layer (described below), we used the *road_segment1* shapefile from the National Road Network data for both Northwest Territories and Yukon (Natural Resources Canada, 2018) at 50 km resolution to differentiate private and public roads. We created four distinct disturbance layers from these products for use in our forecasts: (i) a line density layer of linear disturbances; (ii) a layer incorporating a decay function to increase the emphasis of areas in close proximity to roads (Leblond et al., 2011; St. Laurent et al. 2022); (iii) a layer with the distance to polygonal disturbances to reflect caribou behaviour near polygonal disturbances (Johnson et al., 2015; Vors et al., 2007); and (iv) a distance to settlements to reflect caribou behaviour near settlements (Polfus et al., 2011). As in DeMars et al., (2020), line density (i.e., linear disturbances) included roads, railways, seismic exploration lines, pipelines, powerlines, air strips, and unknown linear features. Polygonal disturbances included forestry cutblocks, settlements, well sites, mines, oil and gas facilities, agriculture, and unknown polygonal features.

We followed the same methods as Johnson et al., (2020) when generating disturbance layers for the *caribouPopGrowth* model, and again used the 2010 and 2015 Landsat imagery to quantify disturbance products (Environment and Climate Change Canada, 2010, 2015). 'Anthropogenic disturbance' was defined as the percent of non-overlapping anthropogenic disturbance (buffered by 500m, with reservoirs removed; *anthro*) within the range of a caribou local population. 'Fire excluding anthropogenic disturbance' is defined as the percentage of non-overlapping, unbuffered, fires less than or equal to 40 years old within a range; any overlap with anthropogenic disturbance is removed in this metric (*fireExclAnthro*). We obtained historical wildfire data when available (pre-2017; see below) and forecasted wildfire data through *FireSense* model outputs (post-2017).

Forecasting boreal caribou habitat suitability

We forecast habitat suitability using the most recently available boreal caribou resource selection function (RSF; DeMars et al., 2020) for the region. Within a predictive context, this model translates species-habitat associations of resource selection into spatial and temporal predictions of habitat suitability proportional to the probability of use (sensu DeCesare et al., 2012). We assumed two processes remain constant through time and across habitat types: i) caribou resource selection behavior, and ii) the probability of false caribou occurrences. We binned forecasted RSF values to represent discrete habitat suitability categories across space and time (*sensu* DeMars et al., 2020). These forecasts describe areas that caribou are more likely to select or avoid in future, based on changes in the underlying landscape.

RSFs contrast the ratio of used Global Positioning System (GPS) locations to available locations animals could have used as predicted by landscape variables; selection of a landscape feature occurs when the proportion of used GPS locations is significantly higher than the proportion of total random locations available for the same landscape variable. This ratio of used vs. available habitat predicts relative (as opposed to absolute) resource selection probability (Manly et al., 2007). For the Taiga Plains ecozone, we used the previously estimated RSF that used data from GPS collars collected from 194 female caribou across the NT1 local population unit within the NWT (average monitoring duration per collar = 690 days; see DeMars et al., 2020 for additional details on the capture and humane handling of animals).

The RSF included (i) four anthropogenic disturbance layers as described above, (ii) land cover types kept static through the simulation (non-vegetated, bryoids, shrubs, herbs, wetlands, and water), (iii) time since fire per the following specific land cover types: upland-non-treed, lowland, upland-conifer and upland-deciduous, and (iv) landscape features representing landscape context within a 1-km radius surrounding each location (Table 1). Static land cover was determined by the Earth Observation of Sustainable Development (EOSD) of Forests layer at 30 m resolution and reclassified to 250 m pixel resolution by nearest neighbor resampling to match the spatial resolution of all model inputs and outputs. The EOSD classification was developed by Wulder et al., (2008) using imagery from the year 2000. Part of the NT1 had EOSD based on imagery circa 2007 and the other part based on imagery circa 2010.

Previous boreal caribou RSF models generated for this region distinguished recent and old burns by their time since fire; ≤ 40 years indicates a recent burn and > 41 years indicates an old burn (Environment Canada, 2011). However, there is evidence that both forest burn age and type may affect caribou use at finer temporal scales (Fisher & Wilkinson, 2005; Kansas et al., 2016), and may be different for northern landscapes and under climate change (Palm et al. 2022). As in DeMars et al., (2020), we categorized burned areas across decadal increments (10 - 60 years) generating 6 categories for each burned forest type (Table 1). We used the Canadian National Fire Database (up to 1985; Natural Resources Canada: https://cwfis.cfs.nrcan.gc.ca/ha/nfdb) and the National Burn Area Composite (1986 - 2017; Natural Resources Canada: http://cwfis.cfs.nrcan.gc.ca/datamart/datarequest/nbac) to derive these burned forest classes. To reconcile the differences between *LandR Biomass CS* outputs (i.e., biomass per tree cohort per pixel) and the inputs needed for the *caribouRSF* model (i.e., land cover classes) we translated tree biomass into land cover classes following the EOSD land cover interpretation. This allowed us to generate both the forest type required for different burn classifications and landscape context layers.

We applied the DeMars et al. (2020) resource selection model within a SpaDES module (caribouRSF_NT; Micheletti and Chubaty 2022). This module was integrated with landscape simulations provided by the forest (*LandR Biomass CS*) and wildfire (*FireSense*) model collection described above (Figure 2). To ensure comparability between existing caribou habitat suitability maps (DeMars et al. 2020) and changing boreal caribou habitat suitability through time, we binned the predicted values following the table used by DeMars et al. (2020). Briefly, random points were sampled from the predicted RSF values and partitioned into decile bins. The cut points between bins were used to create a map with values equally binned between 1 and 10. To evaluate the differences between initial maps of the RSF predictions using biomass-to-land-cover and the predictions using land cover directly (sensu DeMars et al., 2020), we calculated the mean absolute deviation of bins between the predicted maps using both methods for the year 2017 – the original year for which the RSF was produced (DeMars et al., 2020). We compared two RSF maps for the year 2017 – one from DeMars et al. (2020) and one involving our dynamic biomass-to-land-cover map to ensure both methods of landscape classification were comparable. The biomass-to-land-cover map had a mean and median decrease of 0.8 and 0 bins, respectively, across the study area (min = -9 bins, max = +9 bins; Appendix S2: Figure S3). If the two methods produced the exact same maps we would expect to see a mean difference of 0 bins; this suggests equivalency to the original RSF conducted by DeMars et al., (2020) at the study area-scale.

We present the predicted mean change in binned RSF values from 2011 to 2100 (mean pixel RSF value at 2100 - mean pixel RSF value at 2011); we started the simulations in 2011 to match the year of the input biomass dataset. We evaluated mean change in predicted RSF values within the five monitoring areas. We present RSF prediction uncertainty as the standard deviation of the predicted values generated across all replications and simulations; this approach encompasses fire and vegetation stochasticity, and differences among climate GCMs, as uncertainty.

Forecasting boreal caribou demography

To determine changes in the rate of boreal caribou population growth (lambda; λ) through time, we used a simple two-stage population model of adult female survival and juvenile recruitment:

$$\lambda = S*(1+R/2) \qquad \text{Eq. 1}$$

where S is the annual survival of adult females and R is the rate of juvenile recruitment (calf:cow ratio, including both male and female calves). R and S are predicted by landscape features using the regression models in Johnson et al. (2020):

$$R \sim \text{Beta}(\mu^R, \phi^R); \log(\mu^R) = \beta^R{}_0 + \beta^R{}_a anthro + \beta^R{}_f fireExclAnthro \qquad \text{Eq. 2}$$

$$S \sim \text{Beta}(\mu^S, \phi^S); \log(\mu^S) = \beta^S{}_0 + \beta^S{}_a anthro + \beta^S{}_f fireExclAnthro \qquad \text{Eq. 3}$$

where $\phi^R \sim$ Norm(19.862, 2.229) and $\phi^S \sim$ Norm(63.733, 8.311) are precision parameters of the Beta distributed recruitment and adult female survival errors (as defined in Ferrari & Cribari-Neto, 2004; C.A. Johnson & J. Hughes pers. com.). All regression coefficients ($\beta^R{}_0$, $\beta^R{}_a$, $\beta^R{}_f$, $\beta^S{}_0$, $\beta^S{}_a$, $\beta^S{}_f$) are assumed to be Gaussian distributed, with expected values and 95% confidence intervals given in Johnson et al. (2020); note that regression coefficients for anthropogenic disturbance (*anthro*) are generally larger than regression coefficients for fire (*fireExclAnthro*) (Table 2). We opted to use an adult female survival model that includes fire as well as anthropogenic disturbance rather than the top adult female survival model, according the Akaike Information Criterion corrected for small sample sizes (AIC_c, Johnson et al., 2020), because the primary focus of this study is on climate-mediated boreal caribou habitat change. The support for these two models was similar, with 1.86 deltaAICc.

The regression models were not designed for the purpose of projecting population growth trajectories within ranges, and some additional assumptions about the distribution of variability within and among populations are necessary to use the models for this purpose. Here, we assume uncertainty in the model represents variation in demographic rates among, rather than within, populations. For each sample population, regression model parameter values are selected at the beginning of the simulation and each sample population is assigned to quantiles of the error distributions for survival and recruitment. Sample populations remain in their quantiles as the landscape changes over time. Thus, the model assumes a great deal of variability in growth rate among sample populations, and less variability in the effects of changing disturbance on the growth rate of a sample population over time.

We implemented this caribou demographic model as a SpaDES module (*caribouPopGrowth*; Micheletti et al. 2022). For each climate scenario, we ran five replicates of the dynamic landscape simulations (*LandR Biomass CS* and *FireSense*) to account for climate-sensitive stochasticity arising from vegetation and fire dynamics in our forecasts. For each of these simulations, we ran 500 replicate sample caribou population growth trajectories, with each sample population randomly assigned to quantiles of the error distributions between 2.5% and 97.5%. We present the mean λ values and range of variation in λ among replicate sample populations for each caribou monitoring area from 2011 to 2100.

We ran all models at a spatial resolution of 250 m, and results are reported at 20-year time intervals. We used R (v 4.0.4 R Core Team, 2021) for all simulations, forecasts, and analyses and present results as means ± either standard deviation (SD) or standard error (SE), as specified.

RESULTS

Anticipated boreal caribou habitat suitability under climate change

Across all simulations, GCMs, and replicates, boreal caribou habitat suitability showed a non-significant average decline during the simulated period (Figure 3; Appendix S2: Figure S1). The average change in the mean binned RSF value across the five boreal caribou monitoring areas was -0.06 ± 0.43 SD. However, significant spatial variations exist. Mean binned RSF values significantly increased in Dehcho North, Gwich'in Settlement Area (GSA) North, and GSA South (Table 3). Dehcho North was predicted to contain the largest average increase in caribou habitat suitability (mean binned RSF value = 0.75), while Hay River Lowlands was predicted to contain the largest average decrease (mean binned RSF value = -1.64). The two most southern caribou monitoring areas (Dehcho South and Hay River Lowlands) showed significant decreases in habitat suitability (Table 3).

Anticipated boreal caribou population growth under climate change

Mean λ across all five caribou monitoring areas, simulations, GCMs, and replicates shows little change during the simulated period (Figure 4). All five areas contain the contemporary observed field-based 2011 λ estimate lending support for initialization conditions (Table 4). Average values for GSA North and GSA South showed larger discrepancies from observed values but observed confidence intervals were not available (Table 4). Calculated initial (2011) estimates for landscape-informed adult female survival (S) and recruitment (R) within each simulation varied from 0.84 ± 0.05 SE (Dehcho South) to 0.86 ± 0.08 SE (Hay River

Lowlands) for *S*, and from 0.21 ± 0.02 SE (Dehcho North) to 0.28 ± 0.01 SE (GSA North) for *R* (Appendix S1: Table S2). Variance around the mean of each λ simulation demonstrates no difference between GCMs (Figure 4). Importantly, our results predict current λ values will not improve through time; mean annual λ changes little (maximum mean difference = 0.02; Dehcho North) between initial (2011) and end (2100) simulation values within each caribou monitoring area (Figure 4).

Underlying landscape changes affecting caribou

Our projections of boreal caribou habitat suitability and population growth were independently informed by our integrated landscape simulations of climate-sensitive forest vegetation and climate-sensitive wildfire. We projected a net increase in forest biomass across the Taiga Plains ecozone in NWT. Climate-sensitive tree growth and mortality result in an average increase of 76 t/ha of forest biomass across the 21st century (Appendix S3: Figure S2). We also observe a general shift from conifer (mainly black spruce) towards deciduous/mixed forests (trembling aspen), with exception of the southwestern region overlapping Dehcho South. In this region we observe a conversion from deciduous (trembling aspen) and mixed forests (with white spruce leading) to pure conifer forests (white spruce; Appendix S2: Figure S4 and Appendix S3: Figure S1). These results were consistent across replicates and climate scenarios. *FireSense* simulations projected a significant increase (19%) in the mean annual area burned compared to historical fire data obtained from the Canadian National Fire Database (Canadian Forest Service, 2019) for the NWT's Taiga Plains region, as well as a significant increase (27%) in the number of fires (Appendix S3: Figure S3). However, there was a non-significant decrease (17%) in the mean fire size (Appendix S3: Figure S3).

Across the five caribou monitoring areas (Figure 1) forecasted fire disturbance – excluding anthropogenic features – in the year 2100 varied between 14.3 and 31.53%, with the Gwich'in Settlement Area North (GSA North) containing the least fire disturbance and Hay River Lowlands containing the most. Combining both disturbance types (wildfire and anthropogenic disturbance) GSA North represents the least, and Dehcho South represents the most disturbed area by 2100.

DISCUSSION

Our integrated ecological forecast quantifies important climate-induced changes to critical northern boreal caribou habitat over the next century. It demonstrates the potential for all but one monitoring area to exceed the federal 35% disturbance threshold due to changing wildfire regimes alone. We show a reduction in habitat suitability in the southeast and northwest parts of the Northwest Territories (NWT) within the century, suggesting the potential for boreal caribou to shift their range. Despite this spatial variation in habitat suitability, the potential for caribou populations to change is reflected in the uncertainty estimation of our forecasts; on average monitoring areas are expected to remain similar to current conditions, with southern areas continuing to decline over the next century. If these dramatic changes in forecasted habitat were to directly affect demography, the magnitude of boreal caribou demographic change could be devastating for the people who rely on them. This climate-sensitive forecast of landscape and anticipated associated caribou population change is an important step in identifying areas for critical habitat protection for this species at risk.

Spatial and temporal considerations affecting boreal caribou conservation

Despite minimal changes in the intrinsic rate of population growth (λ) we did see important spatial variation in projected changes to landscape composition and associated boreal caribou habitat suitability. We projected a net increase in forest tree biomass across the NWT's Taiga Plains within the 21st century. The most change may occur in the southern region of the study area, the area with the highest amount of disturbance. Our results show a gradient of trembling aspen being replaced by white spruce in the west, and trembling aspen replacing black spruce in the east (Appendix S2: Figure S4 and Appendix S3: Figure S1). Given the parameters of our fire model dictate deciduous burns less than conifers, the conversion to more deciduous tree cover (Appendix S2: Figure S4 and Appendix S3: Figure S1) may have reduced fire size due to vegetation feedbacks, as observed in eastern Canada (Marchal et al., 2017a, 2020) and is similar to previous reports elsewhere in the Canadian boreal forest (Boulanger et al., 2014; Gauthier et al., 2015; Masson-Delmotte et al., 2019). Because both fire and vegetation models interact and are sensitive to climate this predicted change is the result of east-west gradients in initial forest vegetation and in projected climate changes, which generate differential response of forest composition by the year 2100 (Appendix S4: Figure S4). Gradients of differential climate, fire distribution and associated mechanisms are documented in data sheet 1 and figure S2 from Micheletti et al. (2021), which used the same forecasting framework for landscape change in a largely overlapping study area. These results reinforce the importance of integrating different models in the same analysis and could be further investigated for other regions.

For boreal caribou, habitat suitability is related to lichen biomass which is expected to increase with time since fire (Environment and Climate Change Canada, 2019; Environment Canada, 2011; Greuel et al., 2021). The DeMars et al. (2020) RSF model used here predicts high selection for early post-burn areas (1-10 years) followed by selection of late successional forests

(41-60 years, and >60 years unburned; Table 1). This selection for a recent post-fire landscape reflects current investigations of resource use by GPS collared female caribou in fire-dominated landscapes (Kansas et al., 2016; Konkolics et al., 2021; Silva et al., 2019), but the cyclical nature of this process should not contribute to the uncertainty quantified within our 90-year forecast as each year of the forecast was updated with an annual projection of climate-sensitive vegetation change and fire. This annual independence in forecast start-time is a unique feature of the SpaDES framework not possible in other landscape simulation software and offers an adaptable approach to simulating cyclical or stochastic ecological processes.

Addressing model limitations and management uncertainties

Some model uncertainty within our integrated framework is accounted for by incorporating different climate change scenarios. Still, much uncertainty remains. We attribute this to model and reproducibility limitations, all of which can be addressed in future iterations of this work. For example, boreal caribou rely on unfragmented lowlands throughout the year (Walker et al. 2021; DeMars et al. 2020); we can currently only simulate changes in forested areas, not unforested areas composed of shrub, bryoid, or wetland vegetative cover (i.e., successional change, see Micheletti et al., 2021; Appendix II for details). Predicting changes to anthropogenic disturbance is difficult, relies on socioeconomic drivers, and outside the scope of this work; hence landscape fragmentation by linear features is held static within our integrated framework. Moreover, reproducing models from published tables (as done here) rather than from fitted model objects forces the assumption that uncertainty within each model parameter is independent, heightening the risk of overestimating uncertainty (e.g., Figure 4, Table 4); an assumption that could be addressed by ensuring model objects and their variance-covariance matrices are made available upon publication (McIntire et al. 2022). As additional information, new models, and their code become available, these limitations can be addressed through the adaptive, and repeatable, management approach enabled by SpaDES.

Identification of critical habitat and conservation in the form of protected areas represent one form of spatially explicit resource management strategy that may reduce the uncertainty of species persistence in the face of climate change. Promoted globally under the post-2020 Global Biodiversity Framework (CBD, 2020), the NWT contains several recently established protected areas co-managed under various jurisdictions (GNWT, 2019). Some of these overlap the southernmost caribou monitoring areas investigated here, which are anticipating a decline in predicted RSF values (Table 3), have the largest amount of anthropogenic disturbance, and are all predicted to exceed the 35% federal disturbance threshold before the end of this century despite any assumed anthropogenic change (Appendix S1: Table S2). Our simulations suggest the Edéhzhíe Indigenous protected area (IPA), which overlaps the Dehcho North monitoring area (Appendix S1: Figure S1), is well placed for both landscape and caribou conservation within the next century. In contrast, the Ka'a'gee Tu candidate area, which overlaps with the Hay River Lowlands monitoring area (Appendix S1: Figure S1), may experience larger amounts of landscape change resulting in declining caribou habitat suitability and population growth across this same time horizon. Iteratively conducting integrated spatially explicit 'wildlife forecasts', and ensuring short-term forecasts receive higher weighting than long-term forecasts, will help identify important spatial and temporal locations where management efforts may be most effective.

Next steps for integrated wildlife forecasting

Integrating components of habitat and population change remains an important research avenue within wildlife ecology (Avgar et al., 2013; DeCesare et al., 2014; Manly et al., 2007), with real ramifications for local people who rely on the assumed positive association between critical habitat protection and species persistence. Here, our resource selection and demographic forecasts are not empirically linked; they represent separate modeled results that generally align. Caveats associated with both types of models should be considered when interpreting these results simultaneously. The resource selection model represents averaged annual resource selection, a time scale consistent with our other integrated models (i.e., *LandR Biomass CS* and *FireSense*) and does not account for important seasonal variations in caribou life history stages (e.g., calving season); the open-source philosophy of SpaDES ensures this could be changed in future iterations of this work. Caribou behavior is also assumed to remain unchanged throughout our simulations despite changes to the availability of suitable habitat; a simplification, considering ample empirical evidence suggesting functional responses in resource selection for the species (e.g., Moreau et al., 2012; Mumma et al., 2019). Furthermore, models of survival and juvenile recruitment were generated from nationally derived demographic boreal caribou data, which are unlikely to capture some of the regional variation in environmental conditions driving boreal caribou dynamics and may underestimate the importance of wildfire in the NWT. Finally, developing an integrated population model (Schaub & Kerry 2021), able to incorporate projected habitat selection values as a predictor of spatially explicit demographic change would help test the assumed link between critical habitat and demography, refining our reported uncertainty in population growth forecasts and associated implications for northern people who rely on caribou as a critical food source.

Conclusion

Our integrated simulations represent a state-of-the-art tool for applied ecology. We define, quantify uncertainty around, and accomplish spatially explicit forecasts of integrated ecological models to better understand future conditions of a species at risk. Within a northern context, we demonstrate that the management and recovery of boreal caribou critical habitat deserves heightened attention as climate-induced vegetation shifts and wildfire, alone, will greatly alter its spatial extent and availability. These types of conservation forecasts can, and should, be refined under an adaptive management approach.

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CONFLICT OF INTEREST

None.

AUTHOR CONTRIBUTIONS

FS, TM, EM, and SC conceived the idea. FS, TM, and EM designed the study. TM led the analyses. TM, CB, EM, IE, and AC implemented all components of the models, with additional contributions from JH. FS led the writing. All authors provided guidance on results interpretation and contributed to editing the manuscript into its final version.

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TABLES

Table 1. Category, name, coefficient and standard error of landscape variables modeled as fixed effects within the *caribouRSF* SpaDES module for the Taiga Plains of the Northwest Territories (adapted from the annual model presented in DeMars et al. 2020).

Variable category	Variable name*	Coefficient	StdErr	Variable nature	Post-fire classification
Intercept	Dense conifer forest	-8.22	0.28	Dynamic	uplands conifer
Local land cover	Bryoids	1.23	0.04	Static	uplands non-treed
	Tall shrub	0.67	0.04	Static	uplands non-treed
	Short shrub	0.55	0.02	Static	uplands non-treed
	Treed wetland	0.96	0.01	Dynamic	lowlands
	Shrub wetland	0.81	0.01	Static	lowlands
	Herbed wetland	1.02	0.02	Static	lowlands
	Herb	0.54	0.05	Static	lowlands
	Open conifer forest	0.49	0.01	Dynamic	uplands conifer
	Sparse conifer forest	0.55	0.01	Dynamic	lowlands
	Dense deciduous forest	-1.13	0.09	Dynamic	deciduous
	Open deciduous forest	-0.43	0.07	Dynamic	deciduous
	Open mixedwood forest	0.66	0.04	Dynamic	deciduous
	Dense mixedwood forest	0.29	0.02	Dynamic	deciduous

	Water	-1.33	0.02	Static	NA
	Non vegetated	-0.71	0.05	Static	NA
	Burned lowlands (1-10 years old)	0.69	0.02	Dynamic	NA
	Burned lowlands (11-20 years old)	-0.98	0.02	Dynamic	NA
	Burned lowlands (21-30 years old)	-0.62	0.02	Dynamic	NA
	Burned lowlands (31-40 years old)	0.75	0.02	Dynamic	NA
	Burned lowlands (41-60 years old)	0.46	0.03	Dynamic	NA
	Burned uplands non-treed (1-10 years old)	0.66	0.02	Dynamic	NA
	Burned uplands non-treed (11-20 years old)	-0.94	0.03	Dynamic	NA
	Burned uplands non-treed (21-30 years old)	-0.3	0.02	Dynamic	NA
	Burned uplands non-treed (11-40 years old)	-0.14	0.03	Dynamic	NA
	Burned uplands non-treed (41-60 years old)	0.5	0.04	Dynamic	NA
	Burned uplands conifer (1-10 years old)	-0.34	0.02	Dynamic	NA
	Burned uplands conifer (11-20 years old)	-0.64	0.05	Dynamic	NA
	Burned uplands conifer (21-30 years old)	-0.31	0.05	Dynamic	NA
	Burned uplands conifer (31-40 years old)	0.11	0.03	Dynamic	NA
	Burned uplands conifer (41-60 years old)	0.33	0.03	Dynamic	NA

	Burned uplands deciduous (1-10 years old)	0.11	0.07	Dynamic	NA
	Burned uplands deciduous (11-20 years old)	-1.54	0.15	Dynamic	NA
	Burned uplands deciduous (11-30 years old)	-0.65	0.12	Dynamic	NA
	Burned uplands deciduous (31-40 years old)	0.21	0.05	Dynamic	NA
	Burned uplands deciduous (41-60 years old)	-0.7	0.14	Dynamic	NA
Landscape context	Proportion of deciduous (1-km radius)	-7.67	0.05	Dynamic	NA
	Proportion of sparse conifer (1-km radius)	-0.56	0.02	Dynamic	NA
Anthropogenic disturbance	Linear feature density (1-km radius)	-0.16	0.01	Static	NA
	Distance to nearest major road	4.42	0.14	Static	NA
	Distance to nearest polygonal road	4.13	0.14	Static	NA
	Distance to nearest settlement	-1.79	0.08	Static	NA

* Variables names without a fire decade represent unburned landcover types > 60 years old.

Table 2. Response, variable name, coefficient and standard error of landscape variables modeled as fixed effects within the *caribouPopGrowth* SpaDES module for the Taiga Plains of the Northwest Territories (adapted from Table 3 of Johnson et al. 2020).

Model	Variable name	Coefficient	95% CI	Variable nature
Calf-cow ratio, model	Intercept	-1.023	-1.143 to -0.903	Static
	Anthro	-0.017	-0.020 to -0.014	Static
	Fire excluding anthro	-0.008	-0.012 to -0.004	Dynamic
Adult female survival, model	Intercept	-0.148	-0.170 to -1.126	Static
	Anthro	-0.0008	-0.001 to -0.0004	Static
	Fire excluding anthro	0.0002	-0.0004 to 0.0008*	Dynamic

*Table 3 in Johnson et al. 2020 reports this value as -0.0008 to which we confirmed, and used, the corrected value of 0.0008.

Table 3. Predicted change in regional mean binned RSF values for five woodland boreal caribou monitoring areas within the Taiga Plains of Canada's Northwest Territories, generated from an integrated ecological forecast incorporating three climate models. Predicted means were calculated as the difference between two points in time (2100 - 2011) and represent the change in regional mean RSF across our simulations. Bin values vary between 0 and 10.

Caribou monitoring area	**Predicted change in regional mean RSF bin values (CI 95%)**
GSA North	0.525 (0.522 to 0.528)
GSA South	0.281 (0.279 to 0.284)
Dehcho North	0.753 (0.751 to 0.755)
Dehcho South	-0.258 (-0.259 to -0.258)
Hay River Lowlands	-1.646 (-1.649 to -1.643)

Table 4. Predicted and observed mean intrinsic rate of population growth (λ) values for five woodland boreal caribou monitoring areas within the Taiga Plains of Canada's Northwest Territories generated from an integrated ecological forecast incorporating three climate models. Observed values were obtained from recent population trend estimates reported by the Government of the Northwest Territories (Government of Northwest Territories 2019).

	Predicted		Observed
Caribou monitoring area	**Mean λ 2011 (min - max)**	**Mean λ 2100 (min - max)**	**Mean λ^a (min - max)**
GSA North	1.00 (0.77 - 1.30)	1.00 (0.80 - 1.33)	1.08
GSA South	0.98 (0.76 - 1.24)	0.99 (0.78 - 1.27)	1.20
Dehcho North	0.96 (0.77 - 1.21)	0.98 (0.77 - 1.29)	0.94 (0.72-1.60)
Dehcho South	0.95 (0.75 - 1.19)	0.94 (0.74 - 1.18)	0.97 (0.72-1.28)
Hay River Lowlands	0.98 (0.76 - 1.26)	0.97 (0.77 - 1.22)	0.97 (0.72-1.14)

[a]Observed lambda values are based on long-term geometric means (pre-2016 through 2018). GSA North lambda based on data from 2005 – 2007, GSA South lambda based on data from 2003 – 2007. Dehcho North, Dehcho South were based on data from 2006 – 2018 and Hay River Lowlands was based on data from 2004 – 2018.

FIGURE CAPTIONS

Figure 1. Location of five boreal caribou monitoring areas within the Taiga plains ecozone of Canada's Northwest Territories where a portion of Hay River Lowlands and Dehcho South areas overlap (Johnson et al. 2020).

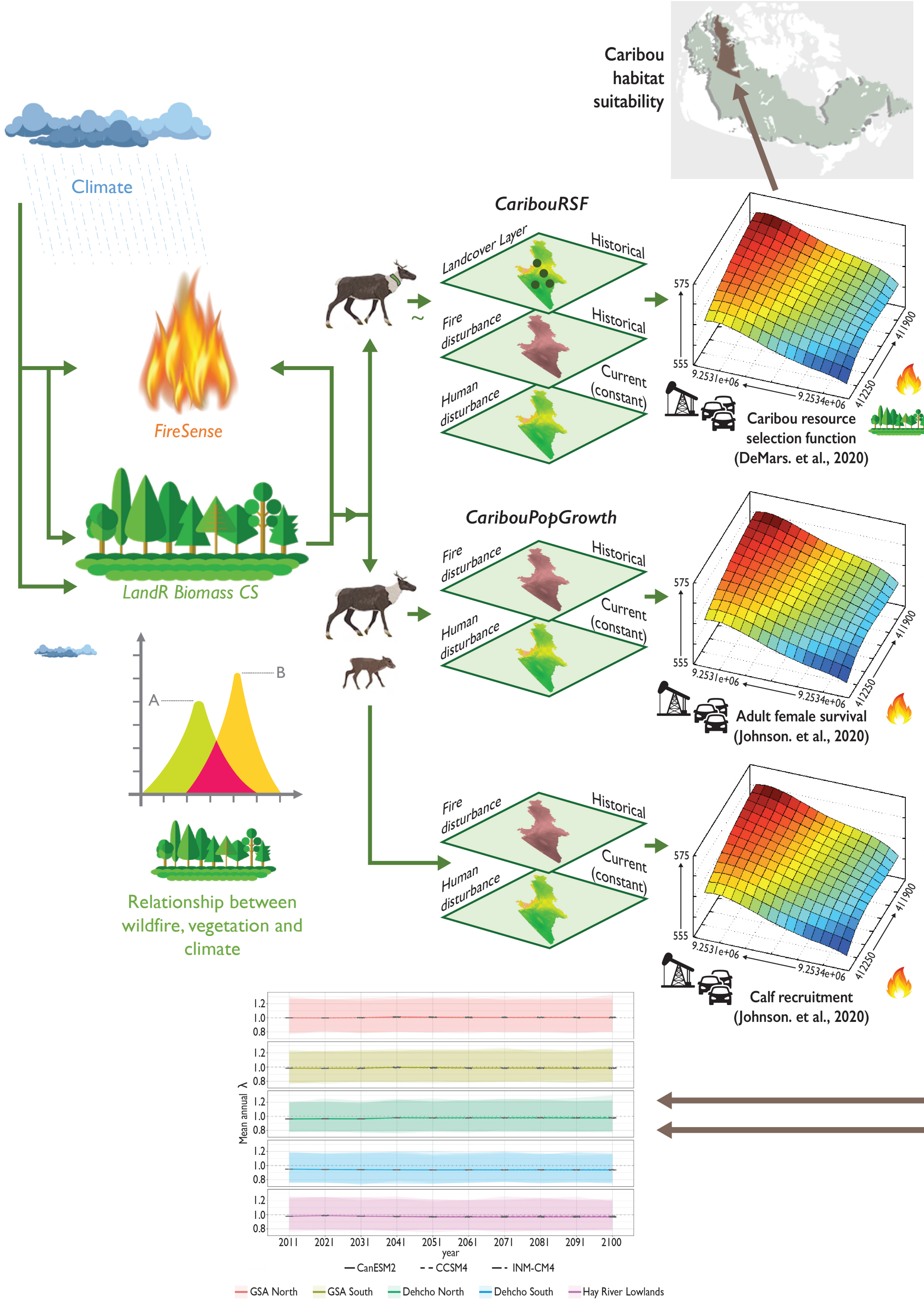
Figure 2. Conceptual framework connecting forest growth (*LandR Biomass CS*) and wildfire (*FireSense*) simulation to caribou resource selection (*CaribouRSF*) and population growth (*CaribouPopGrowth*). Caribou resource selection and population growth models were adapted from DeMars et al., 2020 and Johnson et al. 2020, respectively.

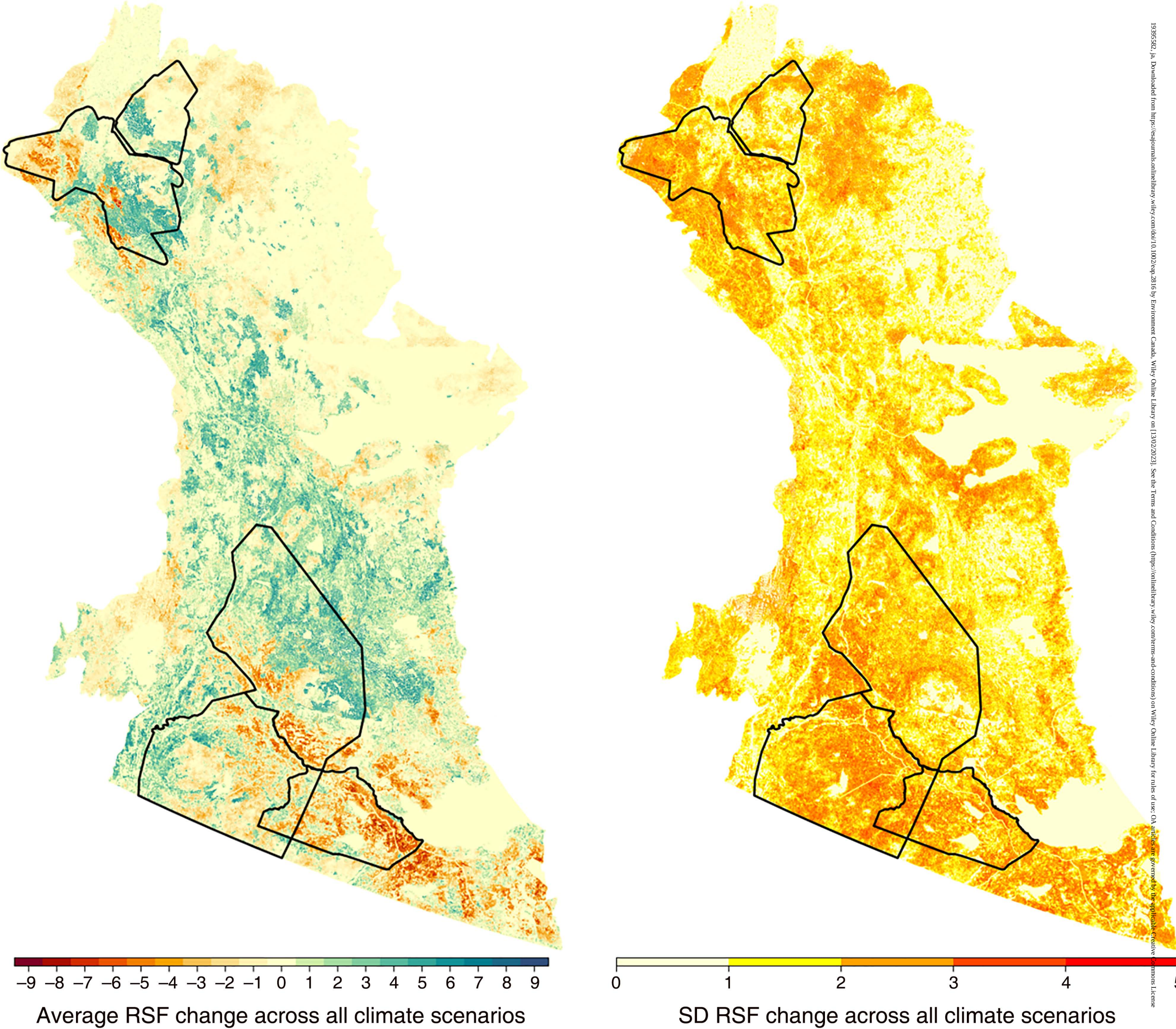
Figure 3. Projected average difference, and standard deviation, in boreal woodland caribou resource selection across climate-sensitive predictions of three Global Circulation Models for the Northwest Territories Taiga Plains. We compared projected resource selection (RSF) values from the end and start dates (RSF value for year 2100 – RSF value for year 2011) within an integrated ecological forecast. Blue areas represent a net increase in the average RSF value, whereas orange-red areas represent a net decrease in average RSF values (left). For the standard deviation map (right), red areas represent a net increase in the standard deviation of RSF values, and yellow areas represent a net decrease. Polygons represent locations of the five boreal caribou monitoring areas.

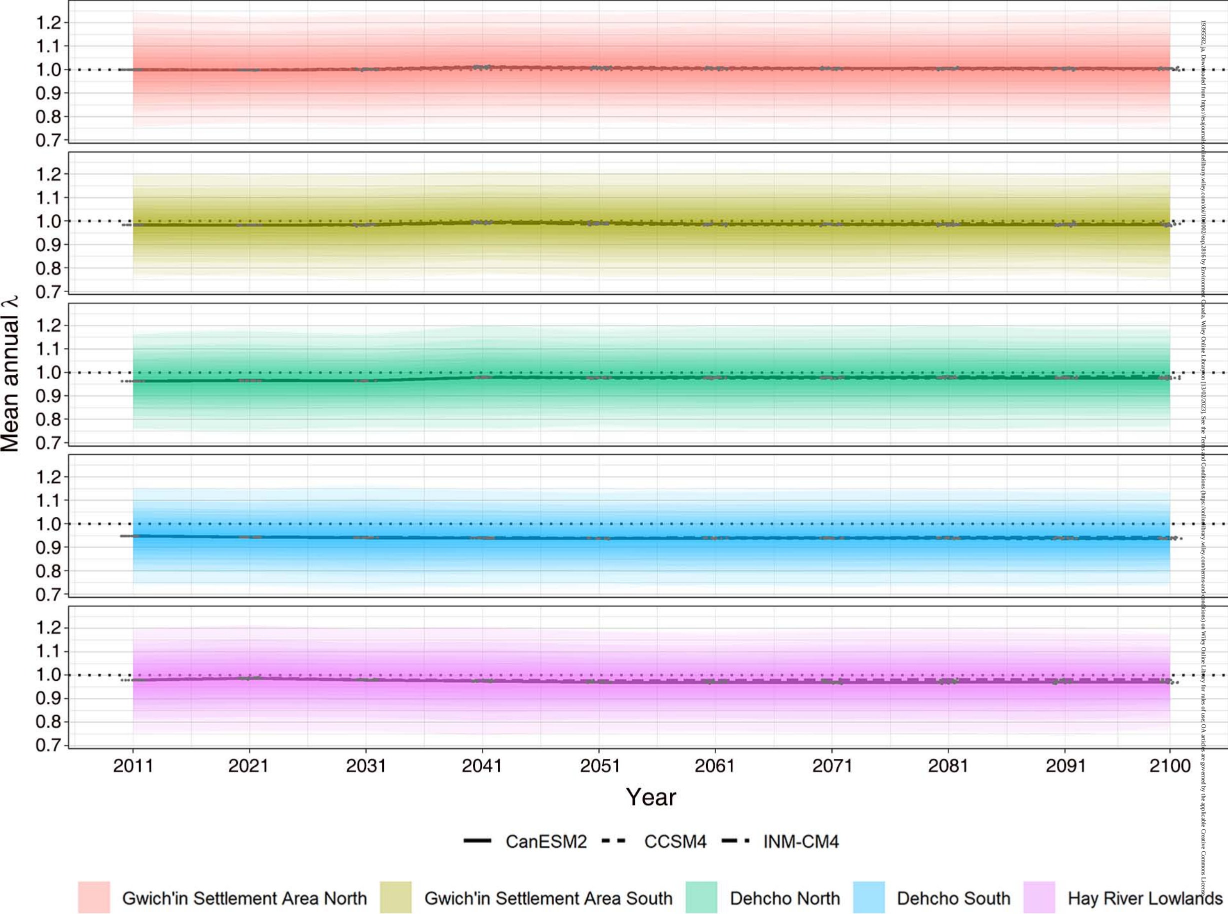
Figure 4. Projected mean annual rate of intrinsic population change (λ) for five woodland caribou monitoring areas under three climate change scenarios within our ecological forecast. Each projection was informed by one of three climate models, CanESM2, CCSM4, or INM-

CM4, each receiving five iterations; values at 20-year increments are plotted as grey dots and confidence bands are composed of confidence intervals at 5% increasing increments around the mean (5, 10, 15….95%). Vital rates were determined from adult female survival and recruitment models in Johnson et al. (2020).


N
GSA North
GSA South
Dehcho North
Dehcho South
Hay River
Yellowknife
NT1 Local Population Unit
Caribou monitoring areas
Taiga plains
0
75
150
300
Km


Caribou habitat suitability
Climate
FireSense
LandR Biomass CS
A
B
Relationship between wildfire, vegetation and climate
CaribouRSF
Landcover Layer
Historical
Fire disturbance
Historical
Human disturbance
Current (constant)
575
555
9.2531e+06
9.2534e+06
411900
412250
Caribou resource selection function (DeMars. et al., 2020)
CaribouPopGrowth
Fire disturbance
Historical
Human disturbance
Current (constant)
Adult female survival (Johnson. et al., 2020)
Calf recruitment (Johnson. et al., 2020)
Mean annual λ
year
2011
2021
2031
2041
2051
2061
2071
2081
2091
2100
CanESM2
CCSM4
INM-CM4
GSA North
GSA South
Dehcho North
Dehcho South
Hay River Lowlands


−9 −8 −7 −6 −5 −4 −3 −2 −1 0 1 2 3 4 5 6 7 8 9
Average RSF change across all climate scenarios
0 1 2 3 4 5
SD RSF change across all climate scenarios


Mean annual λ
1.2
1.1
1.0
0.9
0.8
0.7
2011
2021
2031
2041
2051
2061
2071
2081
2091
2100
Year
CanESM2
CCSM4
INM-CM4
Gwich'in Settlement Area North
Gwich'in Settlement Area South
Dehcho North
Dehcho South
Hay River Lowlands