



The direct and habitat-mediated influence of climate on the biogeography of boreal caribou in Canada

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ABSTRACT

Effective species conservation efforts require insight into whether a species' extent of occurrence may shift due to changing climate, habitat loss, or both. The extent of occurrence of the threatened boreal population of woodland caribou (*Rangifer tarandus caribou*; caribou) has contracted due to environmental and anthropogenic disruption, with further contractions predicted as boreal habitat shifts with the changing climate. However, the direct and indirect climate drivers of caribou extent of occurrence have not been explicitly investigated. We estimated and compared the influence of climate and habitat drivers on the occurrence of caribou ranges across the Canadian boreal forest. We fit path models that estimated the direct effects of climate on caribou range occurrence and its indirect effect through climate's influence on caribou habitat (i.e., forest cover, presence of peatland, human disturbance and wildfire). Our analysis suggests that the distribution of caribou ranges is less sensitive to the direct effects of climate than to those of habitat and human disturbance. However, through its relationship to caribou habitat, climate exerts indirect influence over the distribution of caribou. As the climate changes, future distributions of caribou may be more heavily relegated to refuge habitats, particularly peatlands in the western boreal forest. Our biogeographical approach enables more informed decisions for large-scale caribou conservation efforts (e.g. establishment of protected areas, habitat restoration) that account for potential shifts in the distribution of caribou under changing environmental and climatic conditions.

Introduction

Revealing the determinants of a species' spatial extent of occurrence or geographic range is a fundamental goal of ecology and is critical for species at risk conservation planning [3,47,61]. Species are limited by abiotic and biotic constraints that are currently undergoing global shifts due to a changing climate and habitat alteration, loss, and fragmentation [82,22]. Consequently, human disturbance and climate change are reducing the extent and shifting the locations over which species occur, leading to an increased extinction risk [108,66,62,102,18,14,9]. Effective habitat and population management requires models that compare the geographic ranges of species to environmental gradients to provide insight into whether that range has or will shift due to changing climate, habitat loss, or both [78,52,111,12].

Biogeographical models identify and parse the relative importance of the environmental controls on where, and in what abundance, a species occurs across its geographic range [4,8]. Environmental gradients con-

trol species occurrence directly by limiting survival, reproduction, and other vital rates [103], or indirectly through their influence over factors that exert direct control on occurrence. Models that do not account for direct and indirect effects may disregard important interactions and provide biased conclusions about how a species will react to landscape and climate dynamics [79,31]. For instance, climate may limit species occurrence directly because population vital rates are sensitive to thermal conditions [103], and indirectly by limiting the extent of suitable forage [24,77,108,62,75]. In such cases, estimating the direct correlation between climate and species occurrence without understanding the dependence of forage availability on climate could underestimate the importance of climate as an environmental control [69].

In North America, the boreal populations of woodland caribou (*Rangifer tarandus caribou*; hereafter, caribou) are closely associated with Canada's boreal forest [38], which has experienced an accumulation of human disturbance in recent decades and is predicted to experience accelerated changes in climate and the distribution of habitat over the coming century [87,21,105,96]. Caribou are listed as threat-

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ened in Canada under the Species at Risk Act [50], and many local populations are decreasing in abundance [106,19,34], due largely to human disturbance-mediated predation. Caribou occupy mature coniferous forests and peat complexes, which are avoided by other ungulates (moose *Alces americanus* and deer *Odocoileus* spp.) and their predators (primarily wolves *Canis lupus* and bears *Ursus* spp.) [11,98,20,80,46]. Human disturbance such as timber harvesting and natural disturbance from wildfire and insect infestations generate early seral habitats and foraging opportunities for ungulate herbivores [16,45]. The resulting larger ungulate populations drive predator population growth [88,13,46], increasing predation risk for caribou [90]. Linear disturbances that intersect multiple forest types increase predation of caribou because they are used by predators [60,67]. Predator movement speed [30] and access to caribou occupied areas [67,27] increases when using linear features, thereby increasing their encounter rates with caribou [112,72,71].

Human disturbance has also caused a contraction of the caribou's distribution [42,38]. This contraction is predicted to accelerate due to indirect climate effects such as more recurrent wildfires, changing plant phenology, and shifts in the distribution of caribou pathogens, competitors and predators [106,73,5,6]. Environment Canada [36] compared past contractions of caribou occurrence to climate effects, but because their models included either habitat, such as forest patch metrics and the presence of peatland, or climate drivers (not both), the variation in caribou occurrence explained by either is not clear, leaving the direct and indirect effects of climate and habitat on caribou occurrence untested.

The goal of our study was to estimate and compare the magnitudes of the multiple pathways by which climate and habitat (defined as biotic environmental gradients, and human and natural disturbance) influence the distribution of caribou ranges across the boreal forest of Canada, explicitly accounting for the relationship between climate and habitat [79,4]. To this end, we modeled caribou range occurrence using path analysis, a type of structural equation model that fits complex pathways between multiple predictors and responses using regression analysis [91,51]. As opposed to simple regression analyses, path analysis provides additional insight into causal relationships by parsing the direct and indirect effects among a series of ecological variables [115]. In path analysis, a variable can be both a predictor and a response. This allowed us to estimate the magnitudes of the direct effects of climate and topography on caribou habitat and caribou occurrence, while also accounting for the effect of habitat on caribou occurrence.

Material and methods

Study area

We defined our study area as the ecozones occupied by caribou [39,37], which encompass Canada's boreal forest (hereafter, the boreal forest, Fig. 1). The climate varies broadly across the boreal forest, with greater amounts of annual precipitation in the east, and generally much lower annual precipitation in the continental interior, such as the western Taiga Shield ecozone. To account for, and examine the effects of, the broad gradient in precipitation and the resulting variation in wildfire history, we divided the boreal forest into eastern and western study areas (hereafter, ESA and WSA, respectively) following Amiro et al. [2]. We used the Hudson/James Bay to split the Taiga Shield and Hudson Plain ecozones, and split the Boreal Shield ecoregions into the ESA and WSA along the Boreal Shield's narrowest portion between Lake Superior and James Bay. In both resulting study areas, there is a north-south temperature gradient exhibiting short warm summers and long cold winters in the southern regions, and cool summers and very cold winters in the northern regions [39].

Both study areas exhibit broad gradients in forest cover and human land use. The main deciduous species found across the boreal forest are trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*), whereas the main coniferous species are white spruce (*Picea*

glauca), black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), lodgepole pine (*Pinus contorta*), and balsam fir (*Abies balsamea*). Deciduous and coniferous species co-occur, but there is a general increase in the proportion of conifers with increasing latitude. The intensity of human land use, including forestry, agriculture, mining and oil and gas, occurs mainly in the southern half of both study areas. Wildfires are the dominant natural disturbance type occurring in both study areas; these fires often result in extensive tree mortality and stand replacement ([17], Fig. 2).

Distribution of boreal caribou

Geographic ranges occupied by a group of caribou (hereafter, 'caribou ranges') are the appropriate unit for assessing conservation status because each encloses similar environmental conditions that drive caribou demography and life history [37]. We therefore defined caribou occurrence across their geographic range as the distribution of ranges ($n = 51$) delineated by Environment and Climate Change Canada (ECCC) in the Federal Recovery Strategy [38]. ECCC used the best and most up-to-date descriptions of caribou locations collected by provinces and territories, beginning in the 1970s but frequently updated with data from new methods up to 2012, to estimate the boundaries of each caribou range [36,37]. Data used to delineate range boundaries varied from low certainty, including maps of forest cover and habitat, and short-term ground and aerial surveys for specific study areas and adjacent areas; to high certainty, including long-term data such as Indigenous Knowledge and caribou telemetry from the specific area of interest [37]. We assumed that incremental changes to the human footprint and environmental layers have trivial effects on the occurrence and boundaries of caribou ranges during the timespan over which the environmental spatial data were collected (see 'Spatial Data' below).

The methods and data used to estimate caribou range boundaries varied among jurisdictions, resulting in variable accuracy and precision of estimates of range size and shape [37]. To reduce bias from variable estimation methods, we redefined the distribution of caribou ranges with a grid of hexagonal cells (hereafter referred to as "hexels"; Fig. 1). Each hexel that overlapped the caribou distribution described in the Federal Recovery Strategy by at least 50% was labeled as occupied, and assigned to the ESA or WSA by majority overlap. To determine the most suitable hexel size, we bootstrap sampled the median caribou range area. For 10,000 iterations, we sampled with replacement the distribution of caribou range areas and extracted the median value, then extracted the 50% quantile of the resulting distribution. This resulted in a hexel grid area of 13,159 km² and 523 hexels (path model χ^2 tests p -values did not vary among hexel sizes in either study area; Fig. B1 Appendix B1), leading to 60 and 114 occupied and 116 and 233 unoccupied hexels in the ESA and WSA respectively (Fig. 1) (see Fig. A2, Appendix A2 for a map of the caribou range overlaid with hexels; see Table B1, Appendix B2 for an analysis of inclusion of the areas occupied by caribou in Newfoundland).

Spatial data

We used climate data developed by the AdaptWest Project from 30-year normal (1981–2010) data from WorldClim and PRISM [1] to describe the climate of our two study areas. AdaptWest estimates climate variables at a 1 km² resolution (Table A1, Appendix A1). We summarized the climate metrics using principal component analysis (hereafter, PCA) (e.g. [55,109]). We only used the first two climate principal components (hereafter, PC1 and PC2), as they explained 78.5% of the variation among the climate variables (Fig. A1, Appendix A1). Initially, the majority (81%) of the variation in mean annual precipitation (MAP) across the study area was contained in just 0.22% (12,789 km²) of the pixels, i.e. in the coastal mountains of the western Boreal Cordillera where MAP was > 2000 mm. To enhance the variation within the second principal component across the continental interior, we removed

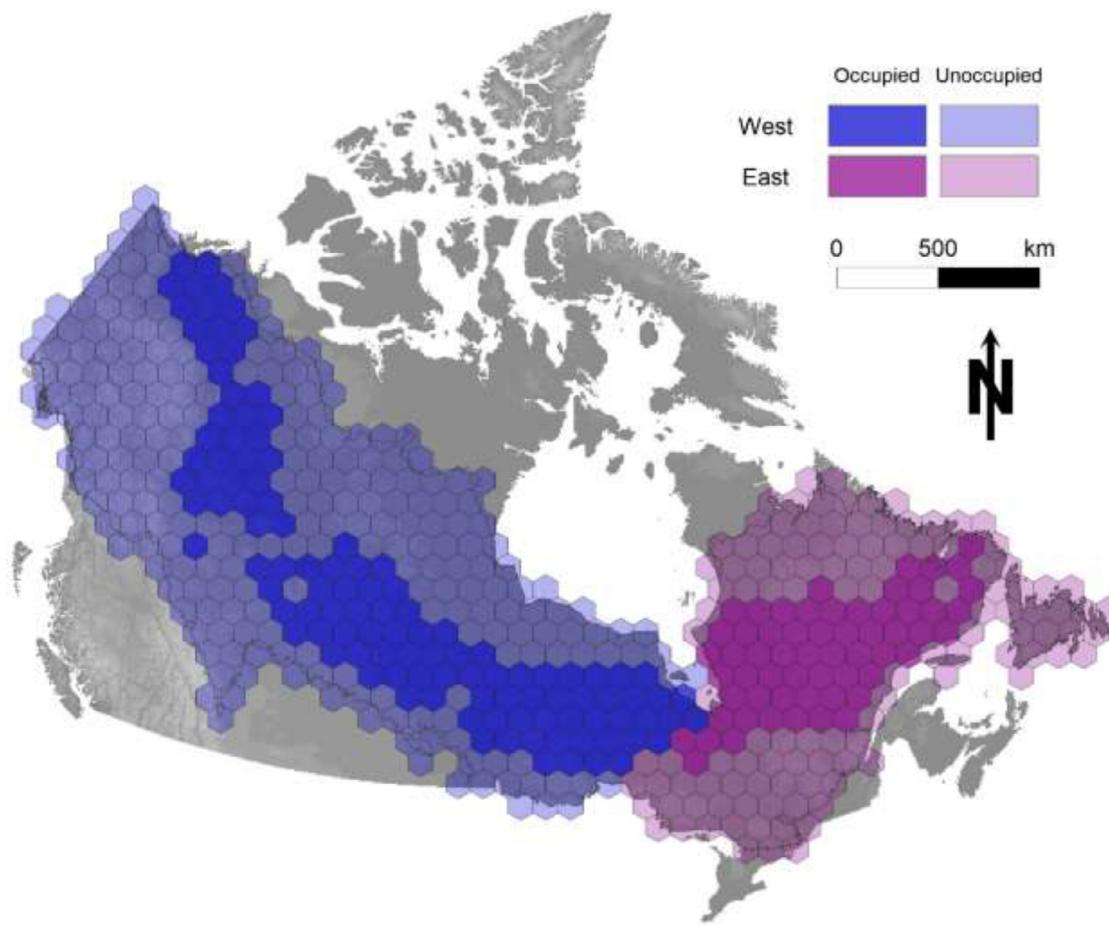


Fig. 1. Study area defined as the union of the seven ecozones occupied by the woodland boreal caribou. We split the boreal forest into two regions to account for variations between eastern and western Canada. East and west study areas with associated occupied and unoccupied hexels. Occupied hexels defined as occupied by caribou, where 50% of the hexel intersects the current estimated distribution of caribou.

pixels with MAP > 2000 mm from the study area then refit the PCA. We described topography across the two study areas using slope, calculated from a digital elevation model [74] using the ‘terrain’ function from the ‘raster’ package in R [58].

We included variables known to contribute to biophysical caribou habitat (Fig. 2): peatlands, forest composed of a high proportion of needle-leaf tree species, wildfire events, and human disturbance [11,98,83,20,59,65]. We summarized conifer cover across the two study areas using the estimated proportion of above-ground biomass for each 250-m pixel classified as needle-leaf species in 2011 (hereafter, “conifer”) [7]. Peatland cover (hereafter, peat) was extracted from the product of Thompson et al. [104], who modeled the probability that each 250 m is a treed peatland in the boreal forest for 2001. For both study areas, we calculated the minimum distance (km) to any wildfire in the National Burned Area Composite, the most recent wall-to-wall wildfire dataset for boreal Canada, which includes wildfires from 2004 to 2016 (hereafter, fire) [53]. We used wildfire proximity rather than density per unit area because it is less sensitive to a clumped distribution of wildfires. We excluded wildfires < 200 ha because small fires are often reported inconsistently among fire agencies and through time [95]. We described human disturbance using the Wildlife Conservation Society and Center for International Earth Science Information [113] index of human footprint summarized between 1995 and 2004. The index, which ranges from 0 to 100, estimates a snapshot of anthropogenic disturbance for a 1 km grid by combining global data layers including human population density, urban areas, roads, navigable rivers, and various agricultural land use.

The hexels used to describe the distribution of caribou were the analytical unit of our path model (see below). We resampled all landscape and climatic variables to a raster with a 1 km resolution using the Canada Albers equal-area conic projection (Fig. 2), then calculated the mean value for each variable for each hexel (see Table A2, Appendix A3 for the Spearman rank correlation among predictor variables). We standardized each predictor around its mean using a z transformation in order to compare the coefficient estimates among predictors. For ease of interpretation, the distance to wildfire variable was reversed by subtracting each value from the max distance such that the values increased with increasing proximity to wildfire.

Statistical analysis

We fit a path model including two regressions: caribou range occurrence as a function of habitat (peatlands, conifer, fire, human disturbance) and abiotic variables (climate, slope), and habitat variables as a function of abiotic variables (Figs. 3A, 3B) (see Table B2 and Fig. B2, Appendix B3 for a description of methods and resulting path model performance with quadratic climate predictors). We used a subset approach to fit path models and estimate path model parameters, for which we iteratively sampled a proportion of the hexels to reduce spatial autocorrelation and to ensure equal sample sizes between occupied and unoccupied hexels in each study area. To determine the maximum proportion of hexels that effectively reduced spatial autocorrelation, we iteratively (1000 times) randomly sampled without replacement a subset of hexels, from 0.1 to 1 by 0.1 increments, keeping occupied and unoccupied hexels

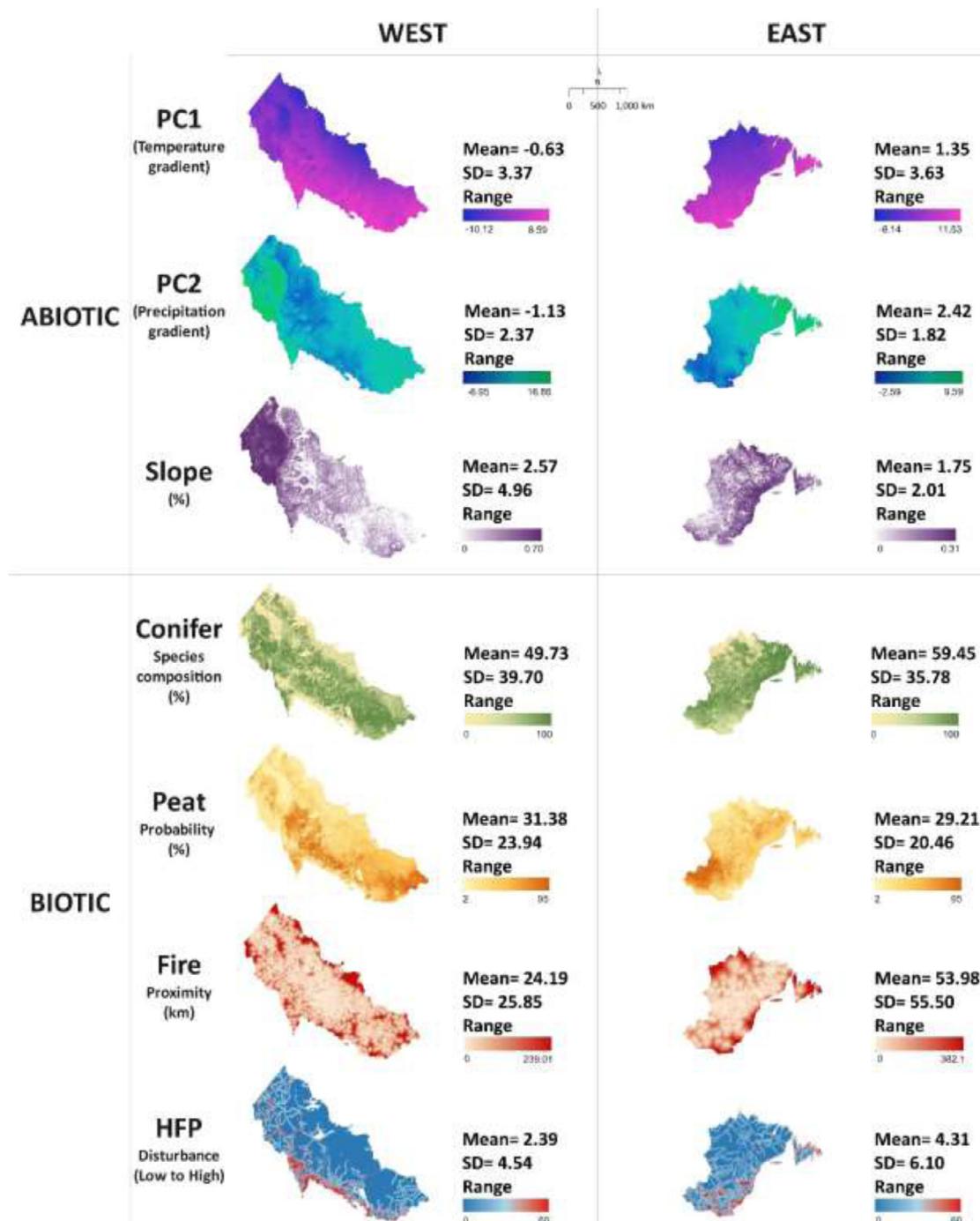
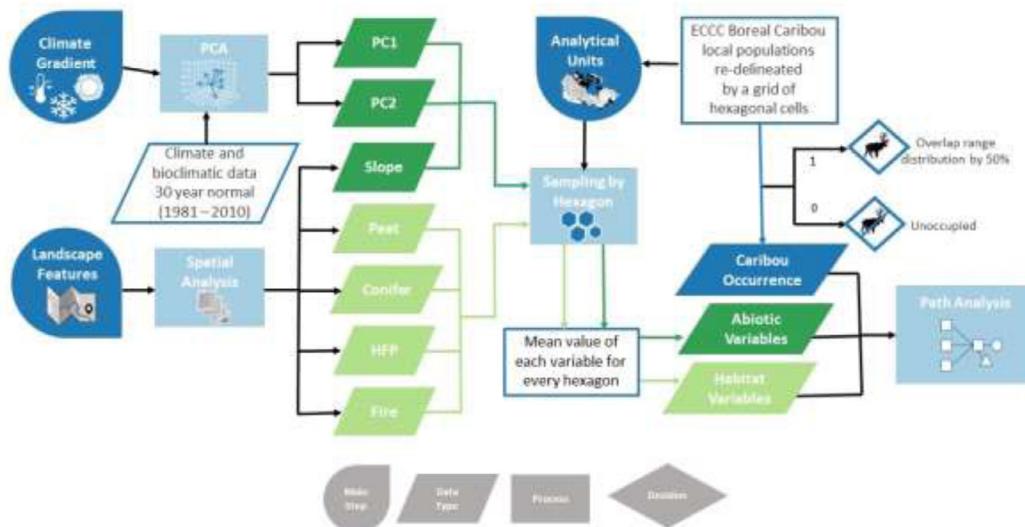


Fig. 2. Abiotic and biotic variables used to evaluate effects on caribou occurrence for the east and west study areas using a path analysis approach. We calculated the mean value of each variable for all hexagons for each study area. Abiotic variables are depicted by the percent of landscape Slope [74], as well as the first (PC1) and the second (PC2) principal components derived from a set of 27 climate variables developed by the AdaptWest Project (2015) from 30-year normals (1981–2010) using data from WorldClim and PRISM (Supplementary material Appendix A, A1–Boreal Climate, Table A1). Biotic variables comprise Conifer or the proportion of above-ground biomass consisting of needle-leaf species [7], Fire as the distance in km to fires >200 ha that burnt between 2004 and 2016 [53] HFP the Human Footprint 1995–2004 (Wildlife Conservation Society and Center for International Earth Science Information, 2005), and Peat as the probability of a pixel being a wetland [104].

equal. To each sample, we fit a logistic regression model predicting caribou occurrence with all path model variables (Fig. 3B). We then selected the largest proportion for which the mean Moran's I p-value, calculated for the spatial distribution of the model residuals, was > 0.05 (i.e. insignificant; Fig. B3, Appendix B4). As a result of this process, we sampled without replacement a random 60% of occupied hexels (with equivalent unoccupied hexels) per study area without replacement for each of 1000

iterations, and fit our path model to that sample. We then calculated the mean and bootstrapped 95% confidence intervals of the resulting distribution of all model regression coefficients. We identified significant predictors as those for which the 95% confidence interval did not cross zero. To compare the direct effects of climate and habitat on the relative probability of caribou range occurrence, we calculated the ratio between significant climate predictors (either PC1 or PC2) and signifi-

A



B

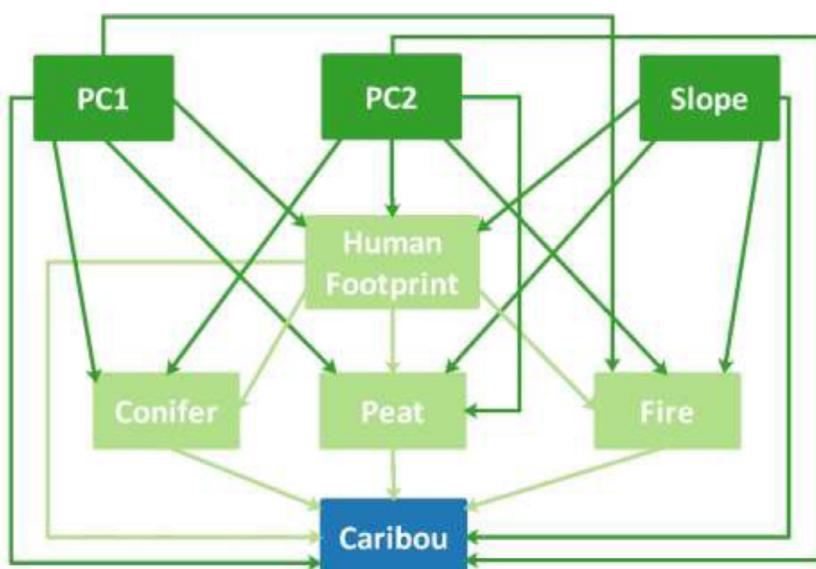


Fig. 3. A Schematic diagram depicting the steps used to prepare species, climate and habitat data to model caribou occurrence by means of a path analysis. Hexagons were used as analytical units to redefine caribou distribution and to calculate mean values of landscape and climate data. Data types are represented by parallelograms while rectangles represent main processes, and diamonds represent the decisions made on caribou distribution. B Path model used to estimate the relative importance of abiotic (in dark green) and biotic (in light green) variables on the occurrence of caribou (in blue). Arrows point from predictor variables to response variables. The path model included a regression for each response variable. In both diagrams PC1 is a gradient of temperature, and PC2 a gradient of precipitation.

cant habitat predictors. We fit our path model to data from both study areas using the ‘sem’ function and the diagonally weighted least squares (DWLS) estimator in the lavaan (version 0.6.3 [84]) package in R (version 3.4.3 (<https://cran.r-project.org/bin/windows/base.old/3.4.3/>)). We tested model fit using a χ^2 test [51].

Results

The proposed path model successfully distinguished direct and indirect associations with caribou occurrence, with similarities and contrasts between the ESA and WSA. The PCA factor loadings (Fig. A1, Appendix A1) indicated that PC1 described an expected latitudinal gradient of decreasing temperature (hereafter ‘temperature’) and PC2 a continental gradient of decreasing precipitation with increasing distance to oceanic coastlines (hereafter ‘precipitation’) (Fig. 2). In the WSA path model, the relative probability of caribou range occurrence increased with the

proportion of peat, and decreased with increasing topographic mean slope, and with increasing density of the human footprint (Fig. 4). The relative probability of caribou range occurrence also decreased consistently as precipitation increased (Fig. 4). The precipitation coefficient was 1.35 and 2.03 times that of peat and the human footprint respectively (Fig. 4). In the ESA path model, the relative probability of caribou range occurrence increased with conifer biomass and proximity to fire and decreased with the density of human footprint (Fig. 4), whereas neither climate PCA component had a significant direct effect. Path models showed good model fit across model fitting iterations (ESA, χ^2 test p -values = 0.62, 95% CI = 0.18, 0.98; WSA, χ^2 test p -values = 0.71, 95% CI = 0.29, 0.98).

Abiotic variables and human footprint exhibited strong and consistent effects on habitat variables in both study areas (Fig. 4). The mean probability of peat increased with temperature (PC1) in both study areas and with precipitation (PC2) in the WSA. The mean proportion of conifer

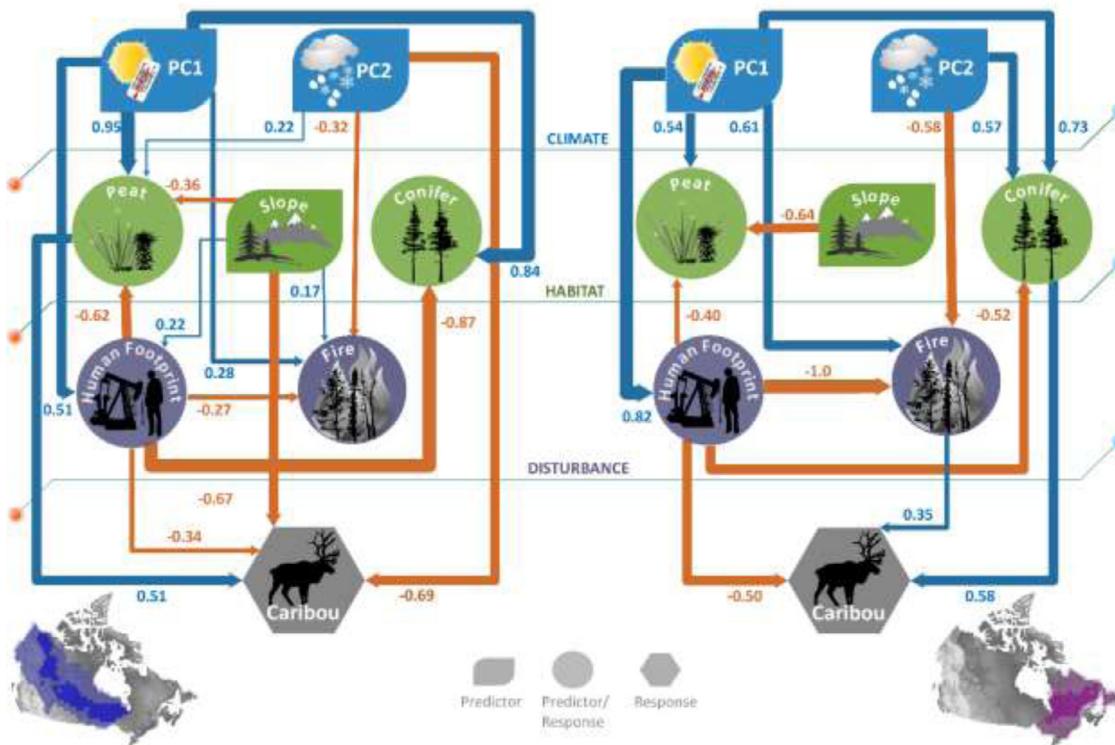


Fig. 4. Path model main results (for which the bootstrapped 95% confidence interval did not cross zero) of the relative importance of climate, habitat and disturbance variables on the occurrence of caribou in the west (blue map insert) and the east (magenta map insert) study area. PC1 represents a gradient of temperature, and PC2 is a gradient of precipitation. For ease of interpretation, the distance to wildfire variable was reversed by subtracting each value from the max distance such that the values increased with increasing proximity to wildfire. Each arrow shows path coefficient values, and widths of the arrows are proportional to the absolute magnitude of the corresponding path coefficient. Blue and orange lines represent positive and negative values respectively.

increased with both PC1 and PC2 in both study areas. Both the mean probability of peat and the proportion of conifer decreased consistently as the density of human footprint increased in both study areas. Distance to fires decreased with increasing temperature (PC1) and increased with increasing precipitation (PC2) human footprint in both study areas. Increasing slope corresponded to a decreasing distance to fire in the WSA (Fig. 4, see Table B3 Appendix B5). The probability of peat decreased, and the density of human footprint increased with slope in both study areas. See Appendix B6 for a description of indirect coefficient effects.

Discussion

Our results indicate that climate indirectly distributes caribou ranges across Canada's boreal forest. We found that climate drives the extent over which caribou occur through its influence on the distribution of peatlands, wildfire, human disturbance and conifer forest across the boreal forest. However, despite the important indirect effects of climate, habitat was a more important direct driver of caribou range occurrence than climate in our analysis. In particular, human disturbance was a consistent constraint of caribou range occurrence, with caribou occurrence decreasing with increasing disturbance. Our results indicated that climate may not be directly responsible for the contraction of the extent of caribou occurrence of recent decades. However, because climate exerts a direct influence on caribou habitat, it is likely that accelerating climatic and ecological changes will greatly affect caribou biogeography in the future.

Through its direct effect on the distribution of caribou habitat, climate exerted indirect influence on caribou range occurrence in both study areas. Both peatlands and conifer forests, which provide caribou with refuge from predation because other ungulates generally avoid them [11,98,20,80], were sensitive to climate. Our path model showed

that caribou selection for open and treed peat complexes in western Canada [83], and mature forests and open lichen woodlands in eastern Canada [59] are evident at the biogeographical scale and is driven in part by climate. In western Canada, where precipitation is relatively low, we corroborate previous work showing that large peatland complexes tend to form in areas with increased precipitation [54], resulting in wide spatial separation between core peatland areas and upland mixed-wood forest. Further, lower amounts of precipitation in the western boreal forest contribute to increased wildfire in forest uplands [76], supplying early seral habitat for other ungulates and thereby increasing the importance of the large, conifer-dominated peatlands as predator refugia for caribou [11,98]. Where stand-renewing wildfires are less prevalent in the eastern boreal forest [2], mature conifer forests provide caribou with refuge because moose and deer, which attract caribou predators, are more commonly found in younger mixed or deciduous forest uplands [32,33,44].

Interestingly, there was a direct positive effect of wildfire on caribou range occurrence in eastern Canada, but not in the west. Previous studies of caribou habitat use have shown avoidance [93,64] or use of recently burned areas (non-calving season, [92]) or a mixed response depending on age of recent burns [65]. Our fire layer, which included fires dating back to 2004, did not include sufficiently old fires, which may be avoided by caribou [29]. However, these studies examined caribou responses using individual animal GPS collar data, at the home-range scale. We revealed that the occurrence of entire caribou ranges, within which home-range habitat use is averaged among individual caribou sharing a range, does not respond to recent wildfires in western Canada, similar to the relationship between wildfire and caribou population size and growth [94]. Our results align with observations that whereas caribou in western Canada preferred older forest stands, they maintain their home range size and location following recent fires [23].

In eastern Canada, we suggest that the importance of conifer-dominated areas for caribou has led to increased overlap between caribou and wildfire. Fortin et al [44] suggests that increased foraging opportunities and a quick return to close canopy forest may allow caribou to tolerate higher levels of disturbances in highly productive areas in eastern Canada. Caribou may cope with increased wildfire by shifting home range location after recent natural disturbances and avoiding recent fires within their home range [40,65]. In contrast, caribou in western Canada prefer low productive areas, such as peatland that are more resilient to fire, because the high densities of caribou competitors in these habitats increase predation risk [89]. Differences in fire histories, forest productivity and landscape alteration (amount, type and configuration) have likely all contributed to differences in the dynamics and space use of caribou, their competitors and their predators in eastern versus western Canada.

Adult female caribou survival is not negatively affected by increasing snow depth, and caribou recruitment responds positively to longer snow periods and deeper snow [28]. Our results show that when examining the effect of snow depth on the occurrence of caribou ranges, rather than among range demographic rates, caribou occurred less frequently where snowfall was highest (snowfall was the most important variable in our precipitation PCA axis, Fig. 1, Appendix A), indicating that caribou strategies for living in deep snow are limited at the upper range of snow depth. Their large feet, and trail breaking and digging behaviors make caribou relatively more adapted to life in severely snowy environments compared to other ungulates [100,15] but previous work has observed reduced caribou movement with increasing snow depth [97]. Across the boreal forest, the deepest snow occurs in the mountainous boreal cordillera [1], where boreal caribou occurrence is minimal [37]. Northern mountain woodland caribou contend with deep snow by migrating seasonally into lower elevations during the winter [43,57].

Caribou occurrence was insensitive to temperature in both the eastern and western study areas at the spatio-temporal scale of this study. Our results are in contrast to previous work which indicated that caribou selected areas for their home range with cooler temperatures during the fall and mid-winter [70]. In the eastern study area, caribou ranges are located in mid-range temperatures, suggesting that range occurrence may have a non-linear response to temperature. However, because the addition of the quadratic term (see Table B2, Appendix B3) caused high model convergence failures, we make the conservative conclusion that the direct effect of temperature on the occurrence of caribou ranges in eastern Canada is minimal.

Implications for boreal caribou conservation

The distribution of caribou has contracted over the past 100 years, particularly in the western boreal forest, chiefly due to human activities [85] but also partly due to climate change [36]. We showed that direct impacts of human disturbance on caribou range occurrence outweighed that of temperature and precipitation in eastern and temperature in western Canada. Given the consistent, direct effect of the human footprint, our results provide further support to previous work showing the historical and continuing contraction of the distribution of woodland caribou, including mountain caribou [68,114], was driven largely by human development [85,107,36,42]. However, additional work modeling the distribution of caribou with an estimate of their historical extent of occurrence is needed to assess how climate change and human disturbance have caused caribou range contractions or shifts [41].

Ongoing and future conservation and restoration efforts (e.g. protected areas, habitat restoration) that do not account for shifts in the distribution of caribou due to climate change may be ineffective at maintaining population viability over long time periods [99,48]. Our work suggests that as the climate changes, the distribution of caribou ranges will be more sensitive to the effects of habitat-mediated climate changes than to the direct effects of changing climate conditions. As such, the current and projected distributions of caribou habitat, in par-

ticular habitat disturbance [63], are likely the most effective targets for conservation efforts. Future distributions of caribou may be even more heavily relegated to refuge habitat, either peatlands in the western boreal or patches of mature conifer forest in eastern boreal forest. In western Canada, peatlands are projected to transition at a slower rate than other boreal ecotypes under climate change [86], but the surrounding conifer-dominated forest is projected to shift to generally younger forest with increasing proportions of deciduous species, due primarily to an increase in droughts and fires [10,96,56]. Increasing numbers of caribou competitor and predator populations in the areas around peatlands would increase the importance but degrade the effectiveness of refugia in peat complexes. Based on the fire data used in this study, the association between caribou range occurrence and wildfire-prone areas in eastern Canada suggests additional resilience to increased natural disturbance. However, caribou adaptations for avoiding predators in wildfire-prone areas of eastern Canada, including small-scale avoidance of fires [65] and searching out mature stands [20], may become ineffective as wildfires become larger and more frequent in eastern Canada.

Whereas climate exerted direct control over the distribution of caribou habitat, the indirect effect of climate on caribou ranges varied with its relationship to habitat and the region of the boreal forest, making the full effect of a changing climate on caribou ranges difficult to predict. Further, climate may also indirectly affect caribou through a projected increase in exposure to parasites, as the distribution of parasites' alternative hosts moves northward into the boreal forest of North America [81]. Similarly, the distribution of white-tailed deer is moving northward as winter severity decreases with climate change, invading areas occupied by caribou, particularly in western Canada, which could increase predator numbers [25,26].

Study limitations

Despite the advances of our multi-factor assessment of environmental controls on woodland caribou distribution, it remains a conceptual and simplistic model that would require further refinement to address additional questions. Testing a range of direct or indirect, and non-linear mechanistic links between caribou demography and climate [28], such as heat stress or thermoregulation [117], forest succession [101,49], and the expansion of parasites and diseases are important next steps in evaluating caribou responses to a changing climate. Additional habitat descriptions of present and future caribou habitat connectivity would provide an opportunity to assess the viability of the populations across the caribou's distribution [110,5,116]. We defined anthropogenic footprint as a single measure of intensity of human use, including urban and rural communities, agriculture, navigable rivers, and permanent roads. We considered the average density of permanent roads within each hexel to approximate the effect of other anthropogenic feature such as seismic exploration lines and forestry harvest blocks, which contribute to caribou habitat loss and range contraction [85,107,36,42]. Additional path models that include each of these features could parse their individual effects on caribou range size and occurrence in the context of climate drivers.

The distribution of caribou ranges used as the response variable in our path model somewhat overestimates the current range of caribou for two reasons. First, 18 of the 51 ranges included in our description of the extent of occurrence of caribou ranges were delineated from 'low certainty' data, meaning that caribou are likely to occur there, rather than having been actually observed there [37]. Second, boreal caribou live at low densities and in small groups such that the full extent of the range is never fully occupied and likely includes areas that are not used over long periods [37]. As such, our path model likely represents an inclusive description of the current drivers of caribou range occurrence, whereas in reality caribou may not occupy all climates and habitats represented here.

Conclusions

Our results indicated that climate exhibits habitat-mediated effects on the occurrence of caribou ranges, suggesting that as climate changes, the distribution of caribou will likely change accordingly. The associations between climate (temperature and precipitation gradients), caribou range occurrence, and caribou habitat vary between eastern and western Canada. The presence of peat is crucial to caribou occurrence in the west, and conifer forests drive caribou range occurrence in the east. Proximity to recent wildfires has no direct influence on caribou range occurrence in the west and a positive influence in the east. In the west, caribou occurrence decreases in areas with steep slopes and deep snow. Across the west and east, human-caused disturbance is a direct and negative driver of caribou occurrence. By assessing the factors that control the geographic distribution of woodland caribou, our results may help refine the projections of future caribou distribution and, as such, provide guidance to current conservation initiatives. Given that the laws protecting species at risk are federally mandated in Canada, our analysis may facilitate informed decision-making for caribou recovery planning across regional jurisdictions. Moreover, our results could contribute to a large-scale, biogeographical definition of caribou critical habitat that complements the wealth of smaller-scaled regional studies [35].

Author contributions

EWN, CCA, JB, NM, DP, AK, MHS, CAJ and MAP Conceptualization; CCA and EWN Data curation; EWN, CCA and JB Data curation; EWN, CCA, MHS and MAP Visualization; EWN Writing - original draft; EWN, CCA, JB, NM, DP, AK, MHS, CAJ and MAP Writing - review & editing.

Declaration of Competing Interest

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Data Availability

Climate data supporting the findings of this study was derived from climate data for North America that are available in AdaptWest at <https://adaptwest.databasin.org/pages/adaptwest-climatena>. Other spatial data that support the findings of this study are openly available in the following public repositories: Boreal Caribou Populations- Canada in Open Government at <https://open.canada.ca/data/en/dataset/4eb3e825-5b0f-45a3-8b8b-355188d24b71>, or in Environment and Climate Change Canada Data at <http://data.ec.gc.ca/data/species/protectrestore/boreal-caribou-populations-canada/>. Needle-leaf species composition [7], data available in Open Government at <https://doi.org/10.1139/cjfr-2017-0184>; <https://open.canada.ca/data/en/dataset/ec9e2659-1c29-4ddb-87a2-6aced147a990>. Slope data were derived from the Digital Elevation Model of Canada available in Open Government at <https://open.canada.ca/data/en/dataset/042f4628-94b2-40ac-9bc1-ca3ac2a27d82>. Distance in km to fires was calculated using the National Burned Area Composite (NBAC) database available through the Canadian Wildland Fire Information System at <https://cwfis.cfs.nrcan.gc.ca/datamart/download/nbac?token=619bc065246fe7e55e91957a92106f56>. Human Influence Index (HII) is available in Socioeconomic Data and Applications Center (SEDAC) at <https://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-influence-index-ighp/data-download>. Wetland probability data is

available upon reasonable request. Please contact Daniel Thompson (daniel.thompson@canada.ca) at Natural Resources Canada, Canadian Forest Service, Northern Forestry center, Edmonton, Canada. All derived and summarized data will be archived in <http://datadryad.org>.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:[10.1016/j.ecochg.2022.100052](https://doi.org/10.1016/j.ecochg.2022.100052).

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