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Climate change alone cannot explain boreal caribou range recession in Quebec since 1850

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Abstract

The contraction of species range is one of the most significant symptoms of biodiversity loss worldwide. While anthropogenic activities and habitat alteration are major threats for several species, climate change should also be considered. For species at risk, differentiating the effects of human disturbances and climate change on past and current range transformations is an important step towards improved conservation strategies. We paired historical range maps with global atmospheric reanalyses from different sources to assess the potential effects of recent climate change on the observed northward contraction of the range of boreal populations of woodland caribou (*Rangifer tarandus caribou*) in Quebec (Canada) since 1850. We quantified these effects by highlighting the discrepancies between different southern limits of the caribou's range (used as references) observed in the past and reconstitutions obtained through the hindcasting of the climate conditions within which caribou are currently found. Hindcasted southern limits moved ~105 km north over time under all reanalysis datasets, a trend drastically different from the ~620 km reported for observed southern limits since 1850. The differences in latitudinal shift through time between the observed and hindcasted southern limits of distribution suggest that caribou range recession should have been only 17% of what has been observed since 1850 if recent climate change had been the only disturbance driver. This relatively limited impact of climate reinforces the scientific consensus stating that caribou range recession in Quebec is mainly caused by anthropogenic drivers (i.e. logging, development of the road network, agriculture, urbanization) that have modified the structure and composition of the forest over the past 160 years, paving the way for habitat-mediated apparent competition and overharvesting. Our results also call for a reconsideration of past ranges in models aiming at projecting future distributions, especially for endangered species.

KEYWORDS
anthropogenic disturbances, climate niche, eastern Canada, modelling, *Rangifer tarandus caribou*, species distribution model

1 | INTRODUCTION

The negative impacts of human activities on ecosystems are not recent news (Chapin III et al., 2000; Plass, 1956; Sanderson et al., 2002). The ongoing loss of biodiversity worldwide weakens functioning ecosystems and compromises the benefits human societies gain from them (Chapin III et al., 2000; Díaz et al., 2018, 2019). Species range contraction happens to be an important symptom of this phenomenon, as it is often linked to population sustainability (Ceballos et al., 2017; He, 2012; Laliberté & Ripple, 2004). Different mechanisms can lead to range contraction (Yackulic et al., 2011), but anthropogenic habitat alteration stands out as one of the most critical, yielding high extinction risks (Ceballos & Ehrlich, 2002; Di Marco et al., 2018; Pacifici et al., 2020). In fact, agriculture, hunting, land-use change and increased human density are some of the factors that caused a significant shrinkage of ranges described in the past decades for many mammals, especially megafaunal species (Karanth et al., 2010; Ripple et al., 2015; Torres-Romero et al., 2020).

In addition, the impacts of climate change on species distribution have been growing increasingly visible (Colwell et al., 2008; Hughes, 2000; Parmesan, 2006). Since the end of the Little Ice Age (~1850), a clear accelerating and anthropogenic-driven warming trend is observed at the surface of the globe (Free & Robock, 1999; IPCC, 2013, 2021), resulting in a displacement of isotherms towards higher latitudes and altitudes that induces a shift in phenology and biome distribution at a global scale (Gonzalez et al., 2010; Lenoir et al., 2020; Parmesan & Yohe, 2003). While some species benefit from these changes (e.g. white-tailed deer *Odocoileus virginianus*; Dawe & Boutin, 2016), many high-altitude and high-latitude adapted mammals are at risk (Freeman et al., 2018; Gilg et al., 2012; Pauchard et al., 2016). Severe range contraction is observed and predicted for many of them, as global warming is happening at a greater speed at higher latitudes because of Arctic amplification (Cai et al., 2021; Miller et al., 2010; Parry et al., 2007). For instance, temperatures have warmed by 1.7°C on average between 1948 and 2012 in Canada, while average arctic temperatures have been increasing two to four times as fast as the rate of the rest of the world (Bush & Lemmen, 2019; IPCC, 2021; Rantanen et al., 2022). For this reason, the survival of vulnerable populations may be critical because of the cumulative impacts of anthropogenic and climatic threats (Sultaire et al., 2016; Wan et al., 2019). Although important range contractions caused by future global warming are projected for many mammal species (La Sorte & Jetz, 2010; Zanin et al., 2021), much is yet to be understood and quantified regarding the recent effects of climate change on past and current species distribution (but see McCain et al., 2021; Moritz et al., 2008). As climate change and human disturbances have occurred simultaneously for the past decades, it is important to be able to disentangle their effects on the contraction, expansion or shift of mammal distributions.

Across the northern hemisphere, caribou (*Rangifer tarandus*) is one of the high-profile species that have been suffering from a northward range contraction over the last century (D'Orangeville et al., 2023; Festa-Bianchet et al., 2011; Schaefer, 2003). The boreal population (hereafter boreal caribou), an ecotype of the woodland caribou subspecies (*R. t. caribou*) (COSEWIC, 2014; Environment Canada, 2012), thus represents a great subject to study range contraction as a result of environmental pressures. Although the boreal caribou is listed as Threatened under the federal Species at Risk Act since 2002 (Species at Risk Act, 2002), the southern limit of its distribution has been shrinking northwards for several decades (Drever et al., 2019; Vors et al., 2007). Boreal caribou rely heavily on mature coniferous forests for foraging and spacing away from predators (Courtois et al., 2004; DeCesare et al., 2012; Hornseth & Rempel, 2016). Human-induced resource extraction activities have converted most of these old-growth stands into a matrix of recent cutblocks, mixed/hardwood regenerating stands and small remnants of residual older stands, all intersected by a dense network of forest roads (Courtois et al., 2007; Dickie et al., 2017; Fryxell et al., 2020).

In Canada, the spatial progression of anthropogenic disturbances over time presents a rather similar northward trend as the one shown by climate-induced shifts in isotherms (Gagné et al., 2016; Parmesan & Yohe, 2003). Anthropogenic disturbances are the most important, well-recognized driver of habitat alteration for boreal caribou populations (Courtois et al., 2007; Lafontaine et al., 2019; Serrouya et al., 2019; Vors & Boyce, 2009); for example, Schaefer (2003) identified forestry as the main driver of northward range recession for caribou in Ontario. Nevertheless, the role of recent global warming in the northward displacement of the southern trailing edge of boreal caribou distribution is still poorly understood and so are its future consequences on boreal caribou distribution. Although anthropogenic disturbances are systematically designated as the number one driver of caribou decline until 2050 (Barber et al., 2018; Leblond et al., 2022; Neilson et al., 2022; St-Laurent et al., 2022), numerous potential effects of climate change have been identified (Masood et al., 2017; Racey, 2005), and we are not certain of their magnitudes nor of their interactions. Considering that many factors may have contributed to shape the current distribution of the subspecies, it is crucial to isolate the specific influence of climate change, as it could orient and constrain our recovery strategies and contribute to middle- and long-term sustainable development goals.

Consequently, our study aimed at assessing the potential effects of climate change on the northward contraction of the boreal caribou's distribution in the province of Quebec (eastern Canada) since 1850. More precisely, we modelled and delineated the climate conditions under which boreal caribou occur today and defined them as their realized climate niche. Then we hindcasted where these climate conditions prevailed in the past, from 1970 back to 1850, to contrast the past locations of these climate conditions with the observed past ranges of boreal caribou. To do so, we paired historical range maps with global atmospheric reanalyses from different sources. Much is still to be done regarding past distribution hindcasting in large mammals, but the combined

use of such data types in this context is a first to our knowledge. We hypothesized that the current distribution of boreal caribou results partially from the influence of climate change, but that climate change is not the most important factor in the contemporary northward contraction of caribou range. According to previous findings on small mammals and plants (Davis et al., 2014; Williams et al., 2013), we predicted that the distribution hindcasted through climate niche modelling would not accurately match the past observed distribution of boreal caribou because its current realized climate niche is not representative of the actual diversity of regional climate conditions suitable for its presence.

2 | METHODS

2.1 | Study area

Our study area covers the whole province of Quebec, and also includes the Maritimes, a part of Labrador and Ontario (Canada), as well as the northeastern region of New England (the United States) (63°N to 42°N and 80°W to 56°W; Figure 1). This area was chosen to incorporate the past southern limits of boreal caribou range in eastern Canada and also its current range in Quebec. Two important ecological gradients exist between ecoregions within the study area, from tundra in the north to eastern temperate forests in the south, and from Hudson plains in the west to Atlantic highlands in the east (Berteaux, 2014; Wiken et al., 2011). The climate in the tundra is much colder and drier than that of eastern temperate forests (annual averages of −13°C to −11°C with 100–300 mm of total precipitation vs. about 5–9°C with 720–1200 mm of total precipitation respectively), while the climate of Atlantic highlands is milder and more humid than the Hudson plains' climate (annual averages of 1–8°C with 850–2000 mm of precipitation vs. −3.5°C to −2°C with 500–800 mm of precipitation, respectively) (Wiken et al., 2011). European colonisation and its impacts on natural environments have historically been mostly concentrated in the St. Lawrence River valley between the early 1600s and 1800s (Bélanger & Grenier, 2002; Moreau et al., 2007; Terrail et al., 2020). Additional colonization and more intensive forestry activities occurred further north and away from the valley during the 19th century (Boucher et al., 2021). Industrialized forestry became more important in the 20th century, especially after the 1950s (Boucher et al., 2009).

2.2 | Data acquisition

2.2.1 | Boreal caribou data—Current and historical distributions

While raw contours of the current distribution exist for the province, fine-scale occurrence maps are not common. We thus delineated the current distribution using telemetry relocations of 253 boreal caribou monitored from 2004 to 2019 and belonging to populations in the continuous range in Quebec, but also to isolated populations in the province (Val-d'Or, Charlevoix and Atlantic-Gaspésie, hereafter Gaspésie caribou), thus covering all the known populations in the province. These three isolated populations are small, southern populations that are remnants of the past continuous range of the boreal caribou in Quebec (Banfield, 1961; COSEWIC, 2014).

Adult females were captured and fitted with GPS collars by field technicians, biologists of the ministère de l'Environnement, de la Lutte contre les changements climatiques, de la Faune et des Parcs du Québec (hereafter referred to as MELCCFP) and their collaborators. Capture and manipulation of study animals were approved by the Animal Welfare Committee (according to the guidelines of the Canadian Council on Animal Care) of the Université du Québec à Rimouski (certificates #36-08-67 and #27-07-53), Université de Laval (certificate #2008026–3) and the MELCCFP (certificates #07-00-02, #04-005, #06-00-27, #07-00-04, #11-03, #12-03, #12-07, #13-09, and #14-05). We created a binary map of the current distribution of boreal caribou in Quebec fitted to the spatial resolution of each climate data source (see the Section 2.2.2) by defining every cell with at least one location recorded as 1 and other cells as 0.

We examined archives and other sources to find reliable information on past boreal caribou distributions. We gathered southern boundary clues for three past time steps: ~1850 (Courtois et al., 2003), ~1900 (Banfield, 1961) and ~1970 (Courtois et al., 2003) (Figure 1). As our sources for past distributions and southern boundaries were digital images from online books and articles, we extracted the boundaries by tracing them as precisely as possible and georeferencing them using ArcMap 10.6.1 (ESRI, 2018). We considered the isolated Gaspésie caribou population as part of the boreal caribou range, despite its current assignation to the montane ecotype, as they used to be included in the broader boreal caribou range back in 1850 and 1900 (Banfield, 1961).

2.2.2 | Climate data

We extracted the climate data used in this study from three datasets, that is, ERA5 (Hersbach et al., 2020), CERA-20C (Laloyaux et al., 2018) and 20CRv3 (Slivinski et al., 2019), to limit the bias generated by the use of only one data source (Zanin et al., 2021). Data from ERA5 (ECMWF, 2022a), CERA-20C (ECMWF, 2022b) and 20CRv3 (NOAA, 2022) covered 1950–2019, 1901–2010 and 1850–2015 respectively. Spatial resolution varied between climate datasets with ERA5 having a 0.25°×0.25° spatial resolution, while CERA-20C and 20CRv3 had a resolution of 1°×1°. From these datasets, we built specific climate variables (listed in Table 1) that were further used in our models. We built these variables using the following data: 2 m air temperature (i.e. above ground level), total (liquid and solid) precipitation and ground surface snow depth, in order to fit what was considered most important according to literature when studying a large herbivore such as caribou (Mallory & Boyce, 2018; Masood et al., 2017; Weladji et al., 2002) (see Table S1.1 for detailed description of variable extraction).
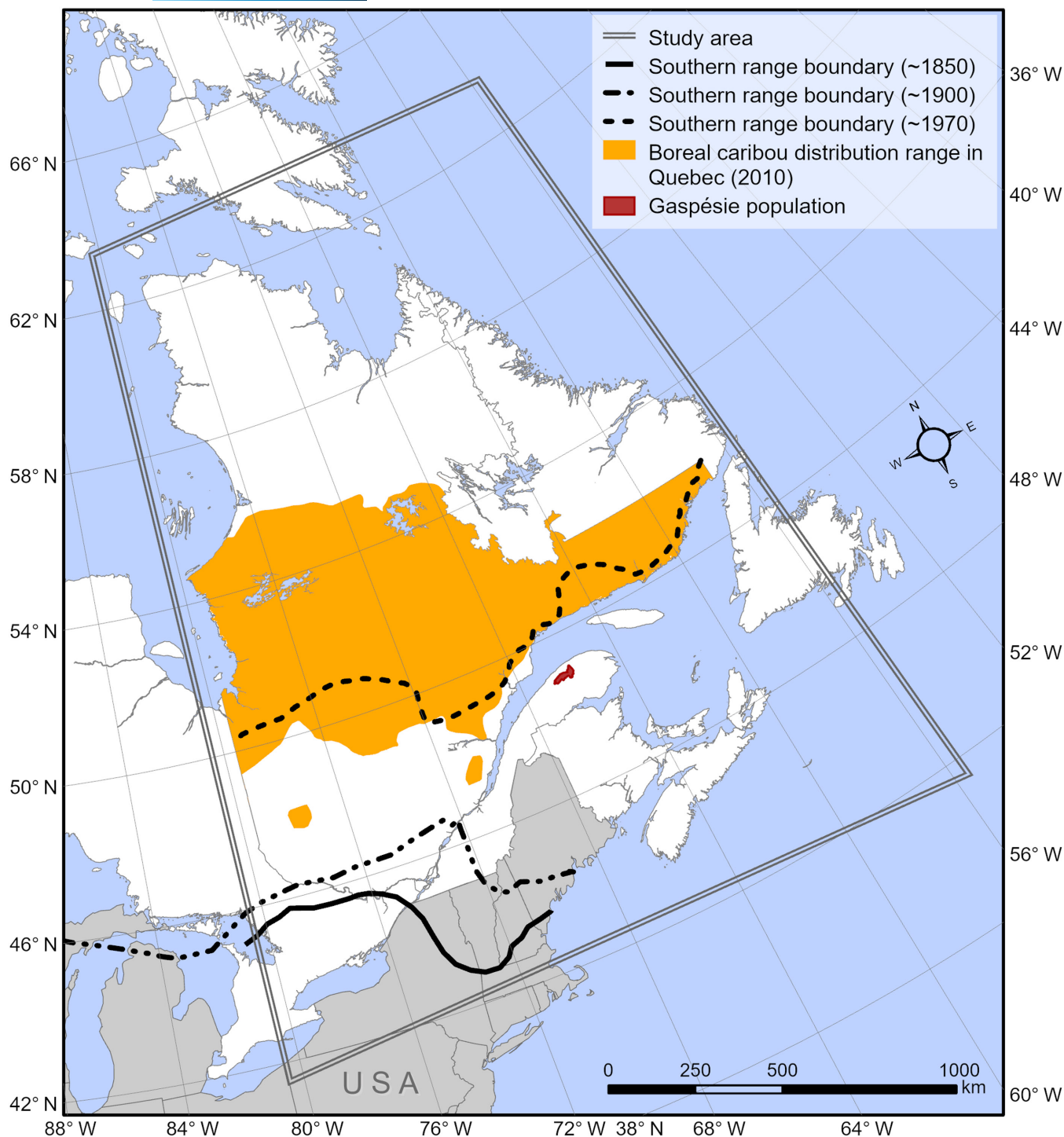
FIGURE 1 Historical southern boundaries of boreal caribou distribution across time: ~1850 (solid line); ~1900 (dot-dashed); ~1970 (dashed). The current continuous ranges of boreal caribou, as well as the ranges of the three isolated populations (from west to east: Val-d'Or, Charlevoix and Gaspésie) are also shown. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

2.3 | Data analysis

2.3.1 | Model building and hindcast

We modelled the realized climate niche of boreal caribou by linking current climate conditions and occurrences of caribou. We then hindcasted past boreal caribou distributions using the identified climatic niche. Different algorithms were used: Generalized linear models (GLMs), generalized additive models (GAMs), random forests (RFs) and boosted regression trees (BRTs) (Araújo & New, 2006; Guisan & Zimmermann, 2000; Shabani et al., 2016). This variety of approaches served to minimize the bias produced by the use of only one algorithm to build models (Shabani et al., 2016). We tested for correlation and multicollinearity among climate variables using the

TABLE 1 List of the climate variables selected to build hindcast models.

Name	Unit	Description
Maximum winter temperature	Kelvin (K)	Monthly maximum between December and March
Mean winter temperature	Kelvin (K)	Monthly average between December and March
Minimum winter temperature	Kelvin (K)	Monthly minimum between December and March
Maximum summer temperature	Kelvin (K)	Monthly maximum between June and August
Mean summer temperature	Kelvin (K)	Monthly average between June and August
Minimum summer temperature	Kelvin (K)	Monthly minimum between June and August
Total summer rainfall	Metre (m)	Monthly sum of rainfall between June and August
Total winter rainfall	Metre (m)	Monthly sum of rainfall between December and March
Total winter snowfall	Metre (m)	Monthly sum of snowfall between December and March
Mean snow depth	Metre of water equivalent (mwe)	Monthly average of ground surface snow depth
Total number of rain-on-snow events	Event (number)	Monthly sum of rain-on-snow events
Start of the growing season	Julian Day (JD)	Date of the first day of a series of over 5 consecutive days with an average daily temperature above 5°C
End of the growing season	Julian Day (JD)	Date of the first day of a series of over 5 consecutive days with an average daily temperature under 5°C
Duration of the growing season	Days (number)	Number of days between the date of start and the date of end of the growing season

Pearson correlation coefficient (*r*, threshold absolute value of 0.7; Dormann et al., 2013) and the variance inflation factor (VIF, threshold value of 10; Senaviratna & Cooray, 2019). Variables presenting indices above threshold values were used in separate models. Out of the entire set of climate variables tested, only a few were eventually used to comply with the thresholds selected for VIF and *r* values. Hence, different sets of variables were selected to build models for each reanalysis dataset. The variables selected were mean summer temperature, total summer rainfall, total winter rainfall and total winter snowfall for models built using the 20CRv3 dataset; mean summer temperature, total summer rainfall, total winter snowfall and total number of rain-on-snow events for models built using the CERA-20C dataset; and finally, mean summer temperature, total summer rainfall, total winter rainfall, total winter snowfall, mean snow depth and total number of rain-on-snow events for models built using the ERA5 dataset.

A k-fold cross-validation was conducted with a 70/30 data ratio for calibration and validation of the models respectively, and 20 iterations were produced to minimize sampling bias (as suggested by Berteaux, 2014), generating 80 models in total. Considering that the current distribution was defined using several years of telemetry monitoring on an extensive number of individuals in all caribou populations over the province, and given the coarse spatial scale used here (Lobo et al., 2010), we assumed that cells with no presence recorded could be considered as true absences. The models produced were evaluated using the true skill statistic (TSS) performance index, a measurement of sensitivity and specificity independent of prevalence (see Allouche et al., 2006), and then combined in an ensemble model, improving the robustness of projections by considering several models and algorithms instead of a single one (see Araújo & New, 2006). We used the weighted mean as an ensemble modelling method, according to the TSS values obtained (Berteaux, 2014). An ensemble model was produced, from all 80 models generated, for each reanalysis dataset using the 1981–2010 period, hereafter named the 'baseline' period. The past distributions of boreal caribou in Quebec were then hindcasted, or reconstructed, at specific past time steps under each reanalysis dataset by using the ensemble model pertaining to the appropriate reanalysis dataset (Figure 2). Model building and hindcasts were conducted on R 4.1.3 with the BIOMOD2 v.3.5.1 package (Thuiller et al., 2016).
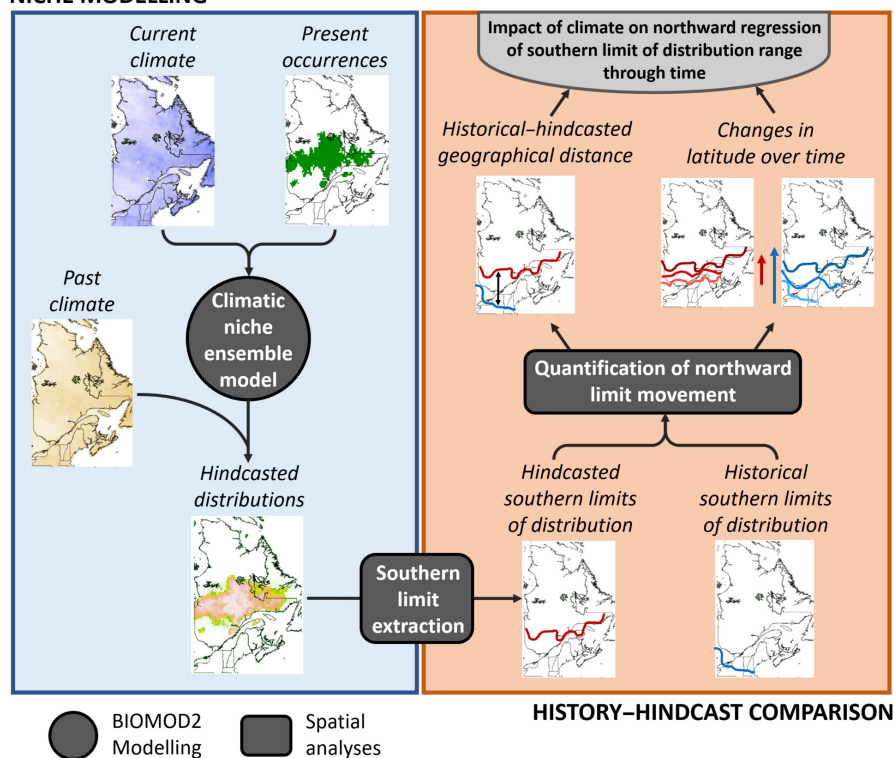
NICHE MODELLING

FIGURE 2 Schematic workflow depicting the different analytical steps used. Hindcasted boreal caribou distributions (maps of probability of occurrence) were produced by climatic niche ensemble modelling for each source of data and time step of interest. Southern boundaries extracted from those distributions are compared to the historical southern boundaries for each time step, by quantifying their respective movements northward, to underline the discrepancies between history and hindcast. These spatial analyses bring forward the impact of climate on the regression of the southern boundary of distribution through time. The circle represents the ensemble modelling done through BIOMOD2, and the rectangles represent spatial analyses.

2.3.2 | Quantification of spatial discrepancies

We compared the results of hindcasted distributions with the historical (observed) distributions of boreal caribou for the four time steps investigated (~1850, ~1900, ~1970, ~2010) to evaluate if there were spatial discrepancies produced by our models (and if so, quantify to what extent; Figure 2). Since the contraction of the historical caribou range followed a clear south-to-north pattern, we measured geographical distances between observed (historical) and hindcasted southern limits for points of the same longitude, and for each time step of interest. We also compared the latitudes of observed southern limits versus hindcasted southern limits to identify their respective trends of northward movement through time.

A threshold of 0.3 probability of occurrence was used to extract southern boundaries from model outputs (i.e. mapped contours of the distribution). We selected this value as it best fitted the position of hindcasted southern limits when compared with the position of the observed southern limit of the caribou distribution for the most recent time step (2010). Doing so, we aimed at ensuring that there was minimal error generated in the inference of southern range boundaries from hindcasted distributions. We conducted a sensitivity analysis, presented in Figures S2.1–S2.3, with other thresholds (0.1 and 0.5). Our focus was on the fit of the southern limit of the distribution, and as such we did not use a threshold that would have maximized the value of the TSS (Liu et al., 2005). When compared to the 0.1 and 0.5 thresholds, the 0.3 threshold presented the shortest median distance between observed and hindcasted southern limits of distribution for 2010, all reanalyses combined (Figure S2.1). We still tested the sensitivity of our analyses to the choice of such a threshold by running them for all considered values (0.1, 0.3 and 0.5), yielding different results but an identical overall trend (Figures S2.2 and S2.3). As expected, the chosen value of the threshold has an impact on the results, and each option represents a different focus in terms of modelling. A threshold of 0.5 illustrates mainly the stability of the core range throughout time, whereas a threshold of 0.1 is more representative of its shifting margins.

The three small, isolated populations found south of the continuous range (i.e. from west to east: Val-d'Or, Charlevoix and Gaspésie) could potentially bias our modelling exercise when tracing the southern range boundaries, despite their low weight compared to the other populations belonging to the continuous distribution of boreal caribou. We thus also evaluated the effect of including these three small populations by hindcasting past distributions while including and excluding them from our dataset (see Figure S3.1 for results).

The data that support this study are archived and openly available on DRYAD (see Morineau et al., 2023), except for the GPS locations, as caribou is a species at risk in Canada.

3 | RESULTS

3.1 | Past caribou distributions inferred from climate reanalysis show little effects of climate variation

Ensemble models show very high goodness-of-fit when modelling the current realized climate niche of boreal caribou. Indeed, average TSS values of ensemble models (with [lower: upper] 95% CI bounds)

were 0.926 [0.918: 0.926], 0.945 [0.945: 0.945] and 0.901 [0.896: 0.901] using 20CRv3, CERA-20C and ERA5 datasets respectively (for Kappa-type statistics, according to Landis & Koch, 1977: 0.81 < TSS < 1.00 = almost perfect; as used in Eskildsen et al., 2013: TSS > 0.75 = excellent). The fact that the TSS value of the weighted-mean ensemble model is equal to the TSS value of either one of the upper- or lower-bound ensemble models may seem surprising, but it results from the way the BIOMOD2 v.3.5.1 package calculates the confidence intervals (see Thuiller et al., 2016). The hindcasted locations of the climate conditions fit for caribou occurrence, obtained through ensemble modelling, showed rather similar trends in probability of occurrence through time and space under all reanalyses, except for CERA20C between 1900 and 1970 (Figure 3). These analyses also presented very similar patterns of probabilities of occurrence for a given time step. Probabilities of occurrence over the entire study area and for all data sources were overall higher for recent time steps than for older ones. Furthermore, areas of probable occurrence (>0.3) showed a slight northward trend with time. In other words, hindcasted ranges described here resided at rather consistent longitudes but slightly increasing latitudes, with no visible expansion nor shrinkage over time and across all reanalysis datasets.

Observed southern boundaries of boreal caribou range presented a clear northward displacement with time (Figure S4.1). Indeed, limits for all time steps were easily visually distinguishable from each other, and latitudinal positions of limits started around 44–45°N in 1850–1900 to end up around 49–50°N in 1970–2010.

However, southern boundaries of the hindcasted locations of climate conditions fit for boreal caribou occurrence showed limited spatial displacement through time, with minimal northward migration between 1850 and 2010 (Figure S4.1). Boundaries of consecutive time steps from hindcasted climate niche analyses tended to strongly overlap or to lay just one cell away from each other.

3.2 | Discrepancies between observed and hindcasted southern limits increase as we go back in time

Distances between southern limits of observed caribou ranges and southern limits of hindcasted locations of climate conditions fit for caribou occurrence largely increased when looking back from today to 1850, regardless of the reanalysis dataset used (Figure 4). Indeed, 20CRv3 presented hindcasted locations of climate conditions suitable for boreal caribou that nearly overlapped the southern boundaries of past caribou ranges in 2010, and the distance between these limits increased over time to reach ~280 km in 1850. Although distributions could be relatively wide for certain time steps, especially 1970, similar trends were observed under CERA-20C and ERA5, for which median distances went from ~100 km in 2010 to ~425 km in 1900, and ~25 km in 2010 to ~90 km in 1970 respectively. These results displayed similar trends whether southern boundaries were defined using a probability of occurrence threshold of 0.1, 0.3 or 0.5 (Figures S2.2 and S2.3).
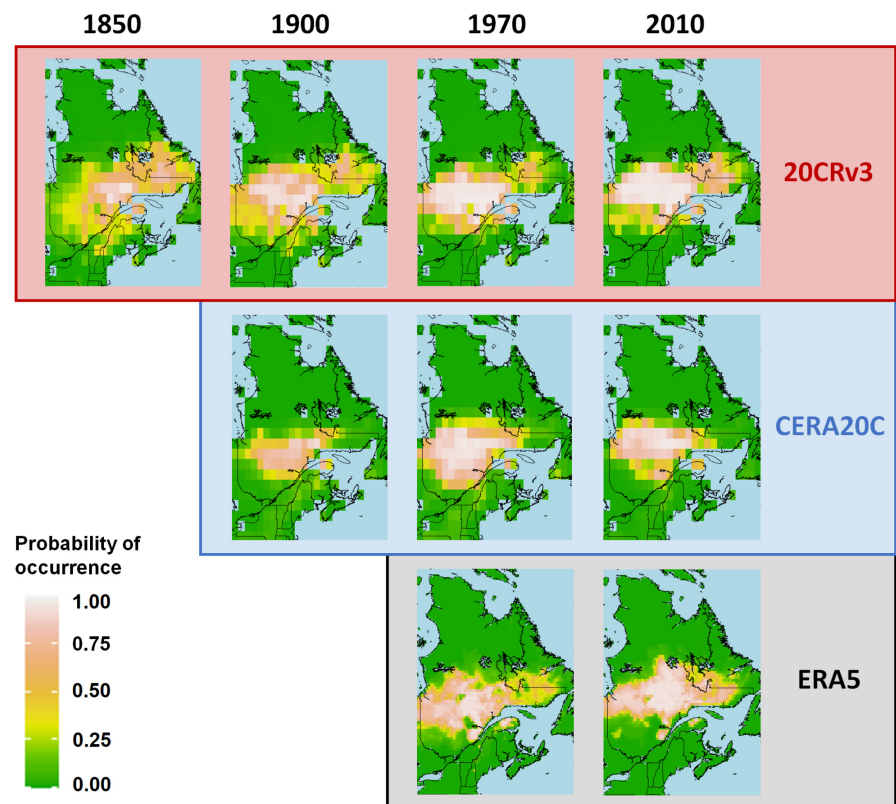

FIGURE 3 Hindcasted probabilities of boreal caribou occurrence over the study area obtained by ensemble modelling for each data source (20CRv3, CERA-20C and ERA5) and each available time step (1850–1900–1970–2010, 1900–1970–2010 and 1970–2010 respectively).
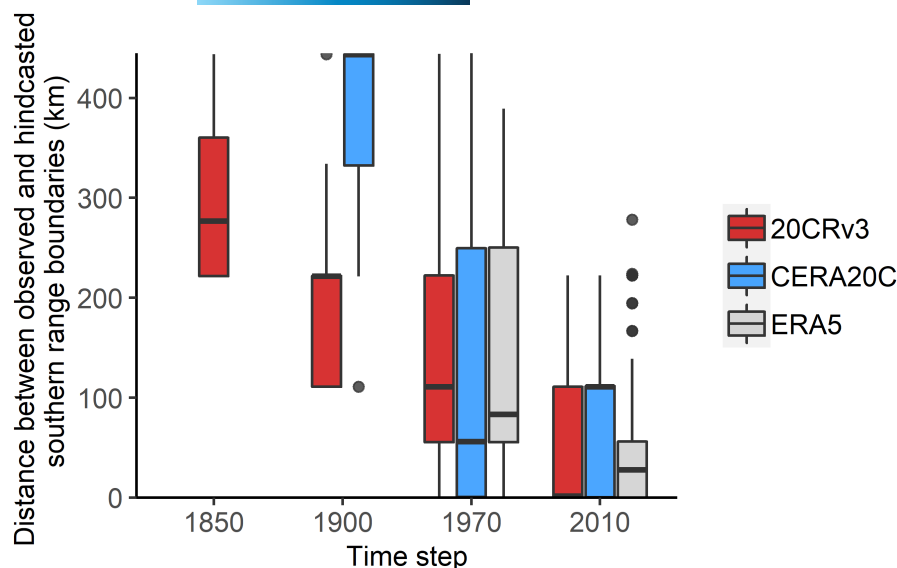
FIGURE 4 Boxplot (black line: median value, box: upper and lower quartiles, whiskers: distribution outside of the upper and lower quartiles) of distances between observed southern range boundaries and hindcasted southern range boundaries for each time step of interest and the three reanalysis datasets available. Distances were measured in kilometres between points of same longitude on observed and hindcasted southern limits.
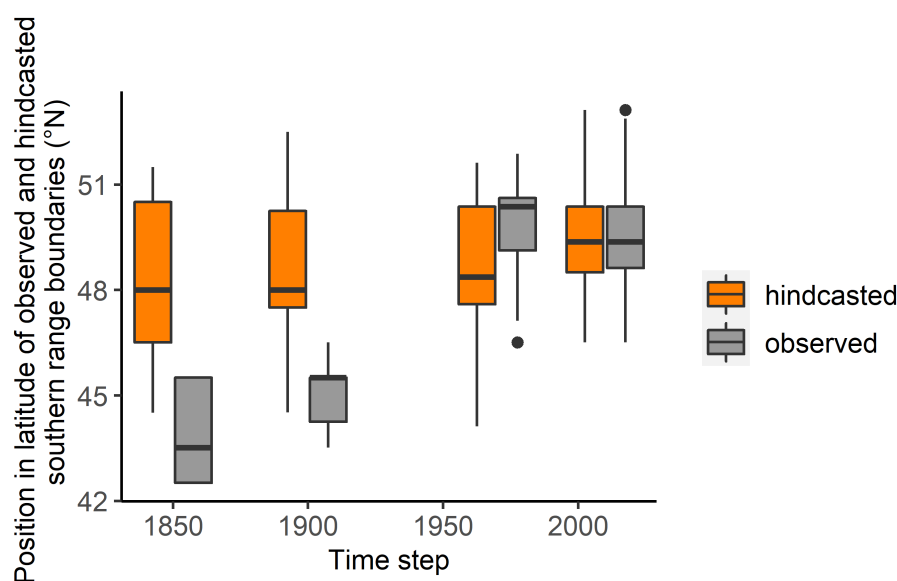

FIGURE 5 Latitudinal position in degrees north of observed and hindcasted southern boundaries through time. Boxes for hindcasted southern boundaries were obtained by combining data from all reanalysis datasets.

3.3 | Observed and hindcasted southern limits show distinctly different trends of latitudinal displacement through time

Trends of latitudinal movement through time were markedly different between southern boundaries of observed caribou range and southern boundaries of hindcasted locations of climate conditions suitable for boreal caribou (Figure 5). Hindcasted southern boundaries presented a slight northward displacement across time steps, with median latitudes showing a northward range recession of the southern limit from ~48° to 49°N. In contrast, the observed past southern boundaries of caribou range showed an important displacement (Figure 5), with a more pronounced northward range recession from ~43° to 49°N over time according to median latitude values. The median latitude of the observed southern boundary in 1970 also happens to be located at more northern latitudes than in 2010. From these results (see Figure 5), we calculated that the

distance between the median positions in latitude of southern limits of hindcasted locations of climate conditions fit for caribou occurrence in 1850 and the one estimated in 2010 reached 105 km. In comparison, the distance between the median latitude of the observed southern limit of caribou range in 1850 and the one observed in 2010 is of ~620 km, which equals to a rate of range contraction of approximately 39 km/decade. This trend was similar whether southern boundaries were defined using a threshold of probability of occurrence of 0.1, 0.3 or 0.5, though distances in km varied between threshold values (see Figure S2.3).

4 | DISCUSSION

We successfully hindcasted climatic conditions in the boreal caribou's current range (e.g. its current realized climate niche) in the province of Quebec (eastern Canada). More interestingly,

by comparing the southern limits of occurrence of these climate conditions with the southern boundaries of observed past boreal caribou range, we highlighted discrepancies between available historical information, used as reference, and reconstitutions through climate niche modelling. Doing so, we showed that if climate change was the only factor driving the northward recession of the southern limit of boreal caribou range, this recession would have been only a fraction (~17%) of what has been observed since 1850. We also tested for different thresholds of probability of occurrence when hindcasting southern boundaries and highlighted the robustness of this main trend.

4.1 | Hindcasted-observed southern limit discrepancies: Consequences of a truncated niche

Hindcasted maps of boreal caribou occurrence based on climate conditions where the species is currently ranging presented a trailing edge of probable distribution moving very slightly northward under all reanalysis datasets, that is, ~105 km on average for the trailing edge of distribution between 1850 and 2010 (which is equivalent on average to 6.5 km/decade). As a result, the southern limits of the hindcasted locations of climate conditions fit for boreal caribou occurrence under all reanalysis datasets showed minor northward displacement. In contrast, observed southern limits of caribou range presented drastic northward movement through time (i.e. 39 km/decade). Distances between both types of southern limits were also largest in 1850 and decreased over time up to the calibration period (i.e. 2010; see Figures 4 and 5).

Overall, the reliable ensemble models we built and that accounted for parameters such as temperature, precipitation, snow cover and phenology could not reconstitute locations and southern limits of caribou range similar to those observed in the past despite a high statistical robustness and a high quality of both caribou and climate data. Such inconsistency, resulting in the inability of these models to recreate past southern distribution limits of caribou range, suggests that the current distribution of boreal caribou in Quebec might not be representative of the actual diversity of regional climate conditions suitable for its presence, which we define here as its fundamental climate niche. More specifically, the current distribution of boreal caribou should extend further south if the range contraction was driven by climate only. This observation stems from a key condition of niche model building, which is that the species must be at equilibrium with its environment (Dormann et al., 2012; Wiens et al., 2009). In fact, niche modelling relies on the direct ecological link between environmental clues and a species' presence, and this link must be intact for niche models to perform. If the species' distribution is '*an environmentally biased subset of abiotically suitable areas*' (sensu Anderson, 2013), the predictive power of the niche model can be strongly hindered and projected distributions biased and inaccurate (Anderson, 2013; Davis et al., 2014; Williams et al., 2013).

The few studies that hindcasted past ranges of mammal species based on models delineating climate conditions within which the species reside showed similar results (Davis et al., 2014; Guralnick & Pearman, 2010; McGuire & Davis, 2013). As these studies showed partial reconstitutions of observed fossil presence, several of the potential explanations they raised for such mismatches most likely do not apply to our case. In fact, considering the relatively short duration of our study (160 years), changes in the climate niche of boreal caribou through time, such as niche shifts through evolution or phenotypic plasticity (Guralnick & Pearman, 2010; McGuire & Davis, 2013), are probably irrelevant. Similarly, climate conditions seem very unlikely to have changed enough since 1850 to produce complete non-analogue climates (Davis et al., 2014) that would generate a niche bias as significant as the one presented here. Aside from that, the statistical quality of the models used can partly explain the situation. Yet, the ensemble models, suitable algorithms and model calibrations (see the Section 2.3.1), as well as the high scores obtained from a reliable performance index, are all elements that indicate that our models have very high goodness-of-fit and are likely robust. For all these reasons, it seems very unlikely that the inability of our reconstitutions to match past boundaries could be due to the poor quality of our data or models.

Differences between the actual distribution of a species and the area designated by their climate niche are nevertheless expected, as factors such as predation, competition or dispersal limitations also weigh into the geographical distribution of species (Colwell & Rangel, 2009; McGuire & Davis, 2013). That being said, the continuous northward movement for over one and a half centuries and its magnitude exhibited in the case of the range recession of boreal caribou seem unlikely to originate mainly from natural biotic factors. Schaefer (2003) reached the same conclusion in the case of woodland caribou in Ontario, with a similar rate of observed northward range recession during approximately the same period (about 34 km/decade).

Thus, we suggest that the distribution of boreal caribou has probably been shaped by anthropogenic drivers (e.g. Laliberté & Ripple, 2004; Vors et al., 2007) that have disrupted the state of equilibrium of the species with its climate environment since 1850. This would result in its current distribution being a subset of what it used to be and what it could be in terms of climate conditions. Indeed, there is now growing evidence that anthropogenic activities and space use have affected species range enough to create a significant disconnection between the fundamental climate niche of species and their realized niche (Nogués-Bravo, 2009; Pineda-Munoz et al., 2021; Veloz et al., 2012). In mammals, this phenomenon is especially true for large-sized and specialist species whose current distributions are only a portion of what they used to be about 100 years ago (Pineda-Munoz et al., 2021). A major consequence of this mismatch is the great difficulty to rely on current presence data only to calibrate niche models, even though they are usually the most precise available (Faurby & Araújo, 2018). Including past distributions and anthropogenic impacts on range alteration in the calibration of climate niche models is, for that reason, often highly recommended (Faurby & Araújo, 2018; Nogués-Bravo, 2009). Unfortunately, we did not find detailed, spatially explicit data of the

growing anthropogenic footprint for the entire Province of Quebec since 1850, and thus could not reach a spatiotemporal resolution for anthropogenic disturbance factors that is similar to the resolution of climate reanalysis data.

4.2 | Limited effect of climate change on range shift suggests important impact of anthropogenic land use since 1850

Southern limits of observed past caribou ranges and southern limits of hindcasted areas where climate conditions are suitable for boreal caribou presented two very distinct trajectories of displacement in latitude, with observed limits showing a much more dramatic northward trend. According to our findings, the northward movement of observed southern limits of boreal caribou distribution between 1850 and 2010 was of ~620 km, whereas it was of only ~105 km for southern limits of the hindcasted locations of climate conditions fit for caribou occurrence. This implies that if climate was solely responsible for the current and past changes in caribou distribution, the latter should have shifted only ~105 km north in the past 160 years, which represents only ~17% of the observed recession (calculated from median latitudes for a 0.3 threshold of probability of occurrence; see Figures S2.2 and S2.3 for results using less performing 0.1 and 0.5 thresholds). As discussed above, anthropogenic drivers referring to land use (i.e. loss, fragmentation and alteration of caribou habitat induced by natural resource extraction, urbanization or agriculture) or caribou harvest (i.e. subsistence Indigenous hunting, but also poaching or past sport hunting, the latter being prohibited since 2001) are most likely the main cause for the remaining 83% (at least). In the absence of detailed mapping of all human activities from 1850 to now, we cannot precisely identify which anthropogenic driver can explain the part of the boreal caribou range recession that was not associated with climate change, but such an important effect of habitat loss on the distribution is consistent with a large body of knowledge on the decline of this species, as reviewed by Festa-Bianchet et al. (2011).

As in many other places in the world, the human footprint has grown rapidly in the province of Quebec since 1850 (Boucher et al., 2014). Lumber as well as pulp and paper were some of the province's biggest industries in the 19th century (Minville, 1946; Natural Resources Canada, 2014), and forest harvesting became an important economic activity in most of southern Quebec (Girard, 1989). The economic development of the province came with a dense network of roads and railways, first covering the southern part of the province before progressing north to the region of Lac-St-Jean by the beginning of the 20th century (Editions Forest, 1935; Letarte, 1971; Rinfret & Taché, 1907), and with a rapid conversion of forests (i.e. caribou habitat) into agricultural lands around the valley of the St-Lawrence River (Behiels, 2020; Dick & Taylor, 2015). Industrial forestry from 1950 and onward progressed northward to reach north of the 50° N, encouraging

post-disturbance stand renewal by pioneer deciduous species in a sequential pattern from the southern to the northern regions (Marchais et al., 2022). In addition to this increasing anthropogenic land-use change, boreal caribou was commonly hunted by non-Indigenous populations (Government of Quebec, 2022; Minville, 1946), until endangered species laws started protecting it under federal and provincial jurisdictions in the 2000s (Environment Canada, 2012; MFFP, 2021a). For all these reasons, we suggest that anthropogenic land use and activities have been an important driver of the historical extirpation of boreal caribou from the southern part of the province, exceeding climate change in terms of impact and leading to the northward range recession recorded since 1850. Indeed, in Quebec there is a close correspondence between the southern range limits of boreal caribou and the northern limits of forest fragmentation (Schindler & Lee, 2010).

The literature is rich regarding studies focusing on the negative impacts of various types of anthropogenic disturbances on boreal caribou in Quebec and other Canadian provinces, such as forest harvesting (Fryxell et al., 2020; Lafontaine et al., 2019; Lochhead et al., 2022; Vors et al., 2007), railways, paved and forest roads (Leblond et al., 2013; Lochhead et al., 2022; Newton et al., 2017; Whittington et al., 2011) and other types of industrial resource exploitation (Dyer et al., 2001; MacNearney et al., 2021; Stewart et al., 2020). Many of these disturbances lead to an apparent competition phenomenon (DeCesare et al., 2012; Frenette et al., 2020; Wittmer et al., 2005) by inducing an increase in early regeneration stands that provokes a rise in moose (*Alces alces americana*) and white-tailed deer populations, which in turn generates growing wolf (*Canis lupus*) or coyote (*C. latrans*) populations, increasing predation pressure on caribou populations. All these elements further support the scientific consensus that the land-use changes driven by industrial activities in caribou range have been exerting their detrimental effects on boreal caribou populations in Quebec for over a century and a half. Although several factors, such as diseases (Environment and Climate Change Canada, 2019; MFFP, 2021b), nutrition and access to key resources (Bergerud & Mercer, 1989; MFFP, 2021b) and dispersion (Bergerud & Mercer, 1989), have been put forward over the last few decades to explain caribou decline, the major direct or indirect implications of anthropogenic land use are now clearly identified (COSEWIC, 2014; Schaefer, 2003). Moreover, predation and fires, both historical drivers that have shaped the boreal ecosystem, now represent threats to caribou population sustainability because of their link with human land-use activities (Environment and Climate Change Canada, 2019). In a landscape historically modelled by forest fires, the deep modifications caused by human presence reduce even further the area of available suitable habitat (Environment and Climate Change Canada, 2019; Racey & Armstrong, 2000). In addition, high predation rates are inherent to the apparent competition phenomenon identified as a considerable factor of caribou decline across Canada and a result of anthropogenic habitat alteration (DeCesare et al., 2012; Frenette et al., 2020). Hence, the relatively limited impacts of climate change in the past boreal caribou range recession tend to align with these assertions.

4.3 | Limits

As climate niche modelling relies on climate data, any inaccuracies in the reconstitution of past climates by the reanalysis data used here definitely affects the quality of hindcasted distributions. Despite scarce literature on the local performances of ERA5, CERA-20C and 20CRv3 over the province specifically, some studies indicate that these data are sufficient for analyses on a broader geographical scale and for various uses (Alves et al., 2020; Crossett et al., 2020; Slivinski et al., 2021; Tarek et al., 2020; Wazneh et al., 2021).

An important assumption made in this study is that the historical southern boundaries are representative of the situation for the time steps they describe and can therefore be used to test the predictive capacity of our models. Considering the different methods and sources most likely used to trace these boundaries through time (archive descriptions, aerial surveys, etc.), their quality can obviously be questioned, as for any historical source of information. Because they describe the past, sometimes in a biased or imprecise manner, they still bring a new perspective into the topic of boreal caribou conservation and hold unique information that could not be accessed otherwise. For that reason, we chose to use these sources in analyses designed to understand the mechanisms that lead to the current situation regarding boreal caribou distribution. That being said, the fact that our results show the median latitude of the 1970 observed southern range boundary north of the one observed for 2010 is most likely due to the difference in precision between the methods used to define those limits. The southern boundary observed in 1970 was based on data from aerial surveys carried out during winter, whereas the 2010 observed southern boundary was obtained using telemetry data, which is more spatiotemporally precise and more geographically extensive. Such a problem can be faced by other research teams for other species in future work, making our case study an interesting example of how to deal with inaccuracy in historical range limits. The sensitivity analyses we conducted (see Figures S2.1–S2.3) as well as the integration (or not) of the three isolated herds (see Figure S3.1) offered us an opportunity to evaluate the influence of niche modelling responses to imprecise input data. Moreover, the boundary observed in 1850 could also be imprecise, but it was described by at least two different sources (Courtois et al., 2003; Environment Canada, 2011), suggesting that the reliability might be high enough for our analyses, considering the relatively coarse spatial resolution of climate data (i.e. 0.25°–1.0° in latitude and longitude). Furthermore, the observed recession described in our results presents a distance that is much greater than the potential imprecision held by each archival boundary used in our analyses, despite the potential variations in the relative contribution of climate to the observed recession (Figure S2.3).

Our study also tends to consider the effects of anthropogenic pressures and climate change as separate, additive factors. We know that this representation of the system studied here is simplistic and that the synergistic effects of human land use and climate change on biodiversity worldwide have been brought to light before (Brodie, 2016; Brook et al., 2008; Carroll, 2007; García-Valdés et al., 2015; Penjor et al., 2021). In our case, the difficulty to precisely quantify these synergistic effects made us consider the effects of climate and land use separately, though such an approach leads to optimistic conclusions regarding the impact of anthropogenic land use on boreal caribou habitat in Quebec since 1850.

Apparent competition is mostly described via impacts of anthropogenic disturbances on caribou habitat (DeCesare et al., 2012; Frenette et al., 2020; Wittmer et al., 2005), but this phenomenon can also imply—at least partially—the influence of climate change. As proposed by Bergerud (2007), the milder climate conditions and the increasing proportion of deciduous stands resulting from climate change can contribute to the increase in local abundance of alternative prey (i.e. cervids) and predators as well as to the change in their space use patterns, thus being part of the northward displacement of the boreal caribou distribution and contributing to the caribou's extinction debt. Recent studies have shown that climate change has already induced subtle modifications in forest composition over the last decades in the province of Quebec in boreal forests (Boisvert-Marsh et al., 2014; Brice et al., 2019), and will remain a marginal agent of change in the future (Leblond et al., 2022; St-Laurent et al., 2022). Nevertheless, it is recognized that climate-induced changes in forest landscapes strongly lag behind shifts in climate variables (Taylor et al., 2017). Consequently, climate change impacts on caribou habitat—and ultimately on climate-mediated apparent competition—have potentially occurred at a quite slow pace in areas free of anthropogenic disturbances although we acknowledge that they could have had impacts at a faster rate in sectors where human-induced disturbances (mostly timber harvesting) have converted the old-growth forests into early-seral forests. Such a lag effect in the northward shift of caribou's southern range limit may explain partially the discrepancies between the hindcasted and current southern limits of the caribou distribution in our study.

5 | CONCLUSION

By highlighting the limited role of climate change in the northward recession of the southern boundaries of boreal caribou range since 1850, our study suggests that anthropogenic land use (i.e. timber harvesting, agriculture and the development of cities, villages and road networks) and caribou harvest (hunting and poaching) were the most important drivers at play during the last 160 years. This implies that management measures aiming at limiting the detrimental impacts of human activities on boreal caribou habitat are far from irrelevant. As such, our results do not align with the idea that the caribou's northward range recession in Quebec is mainly driven by climate change and that land-use practices (mainly timber harvesting and oil and gas extraction) have nothing to do with this major, pan-Canadian decline, an argument commonly raised by opponents to caribou conservation (e.g. Alliance Forêt Boréale, 2019; St-Gelais & Gilbert, 2021). As suggested by Boan et al. (2018), such denial

campaigns can have detrimental effects on decision-maker commitment and on stakeholder involvement towards caribou recovery actions, especially when caribou conservation threatens socioeconomic development (Hebblewhite, 2017). Whereas the evidence for climate-driven range contraction is scant, the evidence for habitat loss is immense (Courtois et al., 2007; D'Orangeville et al., 2023; Festa-Bianchet et al., 2011; Schaefer, 2003; Serrouya et al., 2019; Vors & Boyce, 2009) and constitutes a major cause for concern for the sustainability of endangered species such as the boreal caribou in Quebec.

Although the changes in climate observed during the last 160 years have had a relatively minor impact on the northward recession of the boreal caribou distribution, we recognize that our conclusion might not stand for the future. The combined negative effect of anthropogenic pressures and global warming has been identified as an important threat to many endangered species, with climate change growing in magnitude and aggravating the decline of species made vulnerable by human activities (Carroll, 2007; García-Valdés et al., 2015; Penjor et al., 2021). Climate changes are expected to be more severe for the upcoming decades than those observed during the last century (IPCC, 2021) as a result of increased anthropogenic climate forcing that could accelerate the ongoing processes and further cumulate with anthropogenic disturbances (Boulanger & Puigdevall, 2021). For eastern Canada, these impacts include changes in forest composition and stand age as a result of the gradual northward migration of temperate deciduous species, the decrease in boreal conifer competitiveness and increased mortality in temperate and mixedwood forest biomes and the increased area burned (Boulanger et al., 2016, 2021; Boulanger & Puigdevall, 2021). Although harvesting impacts would remain high especially in the short to medium term, future climate-induced changes would contribute to increasing fire regimes in the boreal forest (Barber et al., 2018; Boulanger et al., 2014), and to a lesser extent subtle changes in species composition, thus decreasing habitat suitability for boreal caribou, especially under severe anthropogenic climate forcing (Leblond et al., 2022; St-Laurent et al., 2022). Moreover, other factors of uncertainty could become particularly detrimental to caribou if cumulated over an already deteriorated habitat. For example, a northward displacement of isotherms could negatively affect caribou thermoregulation capacities within its current range (Masood et al., 2017; Racey, 2005; see also Williamsen et al., 2019 for Svalbard reindeer) as well as the distribution of parasites, pathogens, predators and competitors (Barber et al., 2018; Latham et al., 2011; Pickles et al., 2013), further intensifying the northward recession of its southern limit. Nevertheless, many compound effects from the ongoing amplification of climate change will need to be further identified and assessed, as they can have serious consequences on the survival of caribou. The recent extent, magnitude and location of concomitant wildfires in Quebec over the summer of 2023 pose significant challenges for several species, as wildfires are projected to increase in a warmer world (Barnes et al., 2023).

From a theoretical perspective, our results suggest that future distribution predictions should be made with caution when using species distribution models based on climate (only), notably for species currently recognized as threatened or endangered, as they are not necessarily at equilibrium with their environment. Taking into account such non-equilibrium states, notably by considering information from past distributions, is required to obtain accurate predictions even when using recent, high-quality presence data.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that supports the analysis and findings of this study are archived on DRYAD, except for the GPS locations of the collared caribou as these data are under embargo to protect this threatened species. Data can be accessed at Morineau et al. (2023).

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