An uncertain future for woodland caribou (*Rangifer tarandus caribou*): The impact of climate change on winter distribution in Ontario

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Abstract: Habitat alteration and climate change are two important environmental stressors posing increasing threats to woodland caribou, *Rangifer tarandus caribou*, in Ontario. Our first objective was to identify the importance of linear features, habitat, and climate on the occurrence of woodland caribou during the winter season using over 30 years of records (1980-2012). Our second objective was to forecast the impacts of climate change on the future occurrence and range of woodland caribou. Woodland caribou occurrence and environmental data collected during 1980 to 2012 were obtained from the Ontario Ministry of Natural Resources (OMNR). Logistic regression models were used to identify the importance of linear features, habitat, and climate on woodland caribou. We then forecast future caribou occurrences using 126 future climate projections. Woodland caribou preferred coniferous forests and mixed forests that tended to be associated with increased lichen coverage, and regions with colder winters. Woodland caribou also avoided anthropogenically disturbed regions, such as areas associated with high road density or developed areas. Caribou range extent was projected to contract by 57.2-100% by 2050 and 58.9-100% by 2070. Furthermore, all 126 climate change scenarios forecast a range loss of at least 55% for woodland caribou in Ontario by 2050. We project complete loss of woodland caribou in Ontario if winter temperatures increase by more than 5.6°C by 2070. We found that woodland caribou in Ontario are sensitive to changes in climate and forecasted that an average of 95% of Ontario's native woodland caribou could become extirpated by 2070. The greatest extirpations were projected to occur in the northernmost regions of Ontario as well as northeastern Ontario, while regions in western Ontario were projected to have the lowest rates of extirpation. This underscores the importance of mitigating greenhouse gases as a means to protect this iconic species.

Key words: climate change; woodland caribou; habitat selection; linear features; threatened species; winter habitat.

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Introduction

The decline of the iconic non-migratory woodland caribou (*Rangifer tarandus caribou*) (Figure 1) in North America can be attributed to habitat alteration and climate change, among other environmental stressors (e.g., Vors *et al*., 2007; Vors & Boyce, 2009; Yannic *et al*., 2014).

Figure 1. A photograph of our study organism, the woodland caribou (*Rangifer tarandus*) taken by Tim Timmermann, retired from the Ontario Ministry of Natural Resources and Forestry.

Woodland caribou were historically found across much of North America's boreal forests, but their populations and ranges have declined drastically since European settlement (de Vos & Peterson, 1951; Bergerud, 1974). For example, forest-dwelling woodland caribou population ranges have contracted by 40-50% of their historical range in Ontario since 1880 receding at a rate of approximately 34 km per decade (Schaefer, 2003). Forest-dwelling woodland caribou have subsequently been listed as a "threatened" species by both the Committee on the Status of Endangered Wildlife in Canada and the Committee on the Status of Species at Risk in Ontario (COSEWIC, 2000; COSSARO, 2005). Future changes to precipitation and temperature regimes will also likely have a net negative impact on woodland caribou by altering resource availability and increasing predation pressure (Thompson *et al*., 1998; Vors & Boyce, 2009), suggesting that woodland caribou populations will continue to be put under increasing stress in the future.

Woodland caribou occurrence is related to landcover, climatic, and other biotic factors. Woodland caribou prefer coniferous regions characterized by old growth forests (Racey, 2005; Wittmer *et al*., 2005), that are found in large contiguous zones (O'Brien *et al*., 2006; Brown *et al*., 2007) with lichen rich understories (Hebert & Weladji, 2013). This association reflects life-history strategies adopted by woodland caribou to obtain preferred forage and to avoid interactions with predators and insects (O'Brien *et al*., 2006; Wittmer *et al*., 2007). Similarly, woodland caribou tend to show strong preference for areas with water bodies, wetlands, and peatlands alongside hilly areas to cope with heat stress (Racey, 2005), avoid predators, and ease of movement in winter (O'Brien *et al*., 2006; Fortin *et al*., 2008; Courbin *et al*., 2014). Linear features (e.g., roads, railways, trails, utility lines), forest developments (e.g., timber harvest), and natural disturbances (e.g., forest fires, blow downs) fragment the boreal forest and negatively impact woodland caribou (Rettie & Messier, 1998; James & Stuart-Smith, 2000; Joly *et al*., 2003; Vors *et al*., 2007; Fortin *et al*., 2008; Courbin *et al*., 2014). These disturbances alter the composition and structure of forests by changing mature forests to early successional stages (Joly *et al*., 2003). Such habitat modification results in the loss of primary habitat, reduced forage, and increased risk of predation (through apparent competition with other ungulates; Courtois *et al*., 2007; Wittmer *et al*., 2007).

The decline of caribou has recently been studied in relation to climate change (e.g., Sharma *et al*., 2009; Yannic *et al*., 2014; Murray *et al.,* 2015; Le Corre *et al.,* 2016). Projected changes in air temperatures and precipitation can influence caribou population dynamics both directly and indirectly. For example, climate change may lead to shifts in the habitat suitability and distribution of caribou populations (Sharma *et al*., 2009; Yannic *et al*., 2014; Murray *et al.,* 2015; Le Corre *et al.,* 2016). Habitat suitability for woodland caribou across the boreal forest in North America is projected to decline by up to 51.5% under an A2 climate change scenario and 28.7% under the best-case climate change scenario, B2 (Murray *et al.,* 2015). Migratory caribou distributions are forecast to change significantly in all seasons under a scenario of climate change in eastern North America (Sharma *et al*., 2009). Extreme winter weather is forecast to degrade caribou body condition, by reducing their mobility and foraging opportunities (Brotton & Wall, 1997; Couturier *et al*., 2009; Vors & Boyce, 2009). For example, unhealthy Svalbard reindeer experienced increased incidences of starvation and death in years with heavy snowfall and icing (Aanes *et al*., 2000; Solberg *et al*., 2001).

In our study, we directly incorporated all currently available general circulation models (GCMs) of future climate and their corresponding greenhouse gas emission scenarios for the mid- and late-century (IPCC, 2013). We fill a key knowledge gap in understanding how a range of scenarios of climate change influence the likelihood of woodland caribou extirpation by directly incorporating uncertainty in the projected degree of warming. Our overall objective was to forecast the impacts of climate change on the likelihood of extirpation of woodland caribou over the winter season in Ontario. More specifically our objectives were threefold: i) identify the climate variables that can forecast future occurrence of woodland caribou in the winter exclusive of linear features and habitat; ii) forecast the future winter occurrence of woodland caribou across Ontario using all 126 General Circulation Models (GCMs) and their corresponding representative concentration pathways (RCP) for 2050 and 2070; and iii) forecast changes in woodland caribou winter range extent in Ontario over the coming century. To our knowledge, this is the first study examining the impacts of climate change on future woodland caribou occurrence in Ontario that incorporates the uncertainty from all 126 GCMs.

Material and Methods

Caribou data

Woodland caribou presence across the province have been recorded by the Ontario Ministry of Natural Resources (OMNR), with records dating back to the late 1800s (OMNR, 2012). Woodland caribou occurrence records from the OMNR consisted of a compilation of surveys including: observations from research based activities (e.g., aerial, telemetry, ground surveys) and casual observations (e.g., Off-hour OMNRF staff sightings, forest workers, hunters). Although occurrences from any type of observation were recorded in this survey, the vast majority (above 95% for all decades between 1980-2012) of recorded observations occurred as a result of survey activities. All woodland caribou occurrences from 1980-2012 for the winter months (January, February, and March) were used in this study (Figure 2; O'Brien *et al.,* 2006; Basille *et al.,* 2013).

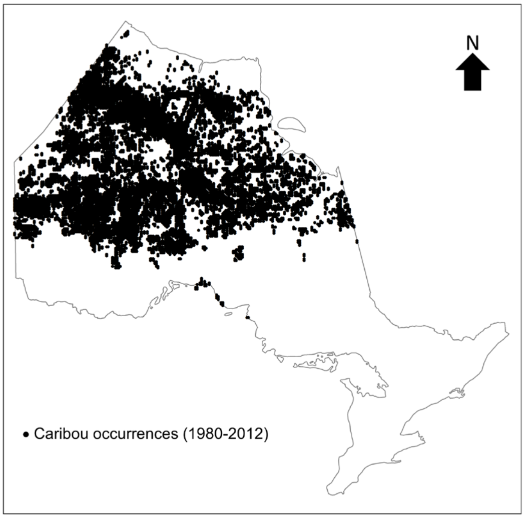

Figure 2. The presence (black) and absence (white) of woodland caribou throughout the province of Ontario during winter (Jan – Mar) between 1980 and 2012.

We selected records after 1980, as this period encompasses the most spatially extensive woodland caribou surveys within the province. We only used records from the winter months because >70% of woodland caribou occurrence data over the period of 1980-2012 came from those months. The winter period also represents a critical time period to assess woodland caribou persistence because of the potential for harsher weather, reduced mobility, and limited resources. We assumed that caribou were absent in locations where they were not observed. True absences were only available for data collected using aerial surveys. A single presence in any year from any type of observation was sufficient for the grid cell to be recorded as a "presence". Incorporating presence-absence data by site reduces the possibility of introducing sampling error and bias in the analysis (Sharma *et al.,* 2009), as population size estimates can introduce large errors (i.e., 30-50% of estimates; Couturier *et al.,* 2009). However, woodland caribou observations may exhibit positive spatial autocorrelation (Segurado *et al.,* 2006). Presence-absence of woodland caribou and all corresponding environmental data were summarized on a 25 km² grid (5 km x 5 km spatial resolution).

Linear features, climate and habitat data

Data on 20 environmental variables were used as predictor variables in our models, including linear features, habitat, and climate data (Table S1). Data on elevation and four different types of linear features in Ontario were compiled from Ontario Base Maps (OMNR, 2003) to assess the impacts of elevation and linear anthropogenic disturbances on woodland caribou distribution (Vors *et al.,* 2007). The occurrence of linear features including roads, trails, utility lines, and railways within each 25 km² grid cell were summarized in ArcGIS 10.1.

Land cover information was compiled from the Ontario Land Cover Classification (OLC). These data were acquired from multispectral Landsat thematic mapper imagery (OMNR, 2000). Land cover was classified into 1 of 26 classes of vegetation and non-vegetation surfaces at a spatial resolution of 25 m x 25 m (Table S1 and Figure S1). Of these 26 classes, 2 were unknown (could have been clouds or shadows blocking the region from the satellite) and therefore omitted. Eighteen classifications contained data that overlapped with other classifications and were therefore combined to make 7 composite classes listed as follows: coniferous cover, deciduous cover, open forests, wetlands, water, agriculture, and industry (see Table S2 for descriptions of what is contained in each). The remaining 6 classes were left in their original form as follows: tundra, bedrock, mudflats, mixed forest, burned forest (that occurred within 10 years), and cutovers (that occurred within 10 years). The occurrence (presence/absence) of each habitat within each 25 km² grid cell was summarized in ArcGIS 10.1 to investigate habitat associations with caribou occurrence.

Vegetation and snow cover data were obtained from NASA Earth Observations (NEO) (https://earthobservatory.nasa.gov/GlobalMaps/) collected using Moderate Resolution Imaging Spectroradiometer on NASA's Terra satellite. Monthly vegetation values were based on the Normalized Difference Vegetative Index (NDVI) and were averaged to derive winter vegetation for the period of 2001-2012. In addition, we acquired the average percentage of snow cover during January to March for 2001-2012 (i.e., snow covering a given parcel of land measured as the percentage of cover).

Historical climate data were obtained from the Intergovernmental Panel on Climate Change (IPCC) as 1950–2000 averages. These values were interpolations of observed data from weather stations and summarized at a spatial resolution of approximately 1 km² (*see* Hijmans *et al.*, 2005). The variables included were elevation (derived from the shuttle radar topography mission at NASA), monthly mean precipitation, monthly mean maximum temperature, monthly mean minimum temperature, and monthly mean temperature (calculated as the average between maximum and minimum monthly temperatures; see http://www.worldclim.org/format for more details). We used climate data averaged over a 50-year period as recommended by the IPCC to reduce inter-annual and inter-decadal variation in the climate data (IPCC, 2013). We calculated winter climate as the average of values for January, February, and March.

Future climate projections were obtained from the IPCC fifth assessment (IPCC, 2013). Projected total annual precipitation, average minimum temperature, average mean temperature, and average maximum temperature for the winter period (average values for January to March) were summarized at a 30 arc-second spatial resolution (equivalent to approximately 1 kilometer). All 19 General Circulation Models (GCMs) and greenhouse gas emission scenarios represented by all 4 representative concentration pathways (RCPs) used by IPCC fifth assessment for 2050 (2041-2060) and 2070 (2061-2080) were acquired for this study. A total of 126 climate projections were available: fifteen RCP 2.6, nineteen RCP 4.5, twelve RCP 6.0, and seventeen RCP 8.5 scenarios were available in both 2050 and 2070. The GCMs and RCPs have different assumptions about atmospheric greenhouse gas emissions (IPCC, 2013). For example, RCP 2.6 represents a reduction in greenhouse gas emissions where there is a predicted peak in greenhouse gas concentration by the mid-century before declining in late-century (van Vuuren et al., 2007). RCP 4.5 and 6.0 represent stabilization scenarios where greenhouse gas concentrations stabilize by the year 2100 (Fujino et al., 2006; Smith & Wigley, 2006; Clark et al., 2007; Hijioka et al., 2008; Wise et al., 2009). Finally, RCP 8.5 is the worst-case scenario, where greenhouse emissions continue to rise past the year 2100 (Riahi et al., 2007).

Data analysis

i) Woodland caribou occurrence

Prior to analysis, collinearity among variables was assessed using Pearson correlations. Monthly winter climate variables were found to be highly correlated with one another (monthly precipitation, minimum temperature, maximum temperature, and mean temperature). The collinearity among climate variables would have an impact on parameter estimation and the order of importance of these variables in our final models (Graham, 2003), so we only included two independent seasonal and annual climate variables following forward selection in the models: minimum winter temperature and mean annual precipitation.

Logistic regression was used to identify the relationship among linear features, habitat features, and climate on woodland caribou occurrence in Ontario. We implemented variable and model selection approaches to choose our model: i) Only significant predictor variables based on a dual-criterion (α = 0.05 and significant contribution to R^2_{adj}) forward selection procedure were retained using the *packfor* library in R software (Blanchet *et al.,* 2008; R Team, 2015) and ii) model selection criterion such that the model with the lowest Akaike Information Criterion (AIC) was selected. Logistic regression models were implemented using *glm* in the *base* library in R.

Training and validation datasets were used to assess how well the multiple logistic regression model performed. Eighty percent of the data were randomly allocated to the training dataset (n = 23,279) and 20% of the data were allocated for validation of the model (n = 5,820). A Receiver Operator Characteristic (ROC) curve was used to identify a threshold of caribou occurrence (rather than the traditional designation of 0.5 as species presence; Fielding & Bell, 1997; Olden & Jackson, 2002; Sharma & Jackson, 2008). Using the ROC curve, we determined a threshold by altering the sensitivity (percentage of presences correctly predicted) and specificity (percentage of absences correctly predicted) of the model such that the predicted occurrence rate resembled current occurrence rates throughout our study area. Following the selection of the optimal threshold based on ROC, confusion matrices (consisting of true presences, true absences, false absences, and false presences) using the validation data were created to calculate the classification rate (percentage of presences and absences correctly predicted), sensitivity and specificity of the model (Fielding & Bell, 1997). This procedure was implemented using the *pROC* and *caret* packages in R software (Kuhn, 2008; Robin *et al.*, 2011). We also evaluated the performance of our model by calculating a Cohen's Kappa statistic (Fielding & Bell, 1997).

ii) Uncertainty in climate change on woodland caribou occurrence

The probability of caribou occurrence was summarized for each 25 km^2 grid cell across our study area based on changes in temperature and

Table 1. Significant (p<0.05) coefficient values for the logistic regression model. Those with no value indicate that the predictor does not significantly contribute to caribou occurrence in Ontario.

Type of Feature	Variables	Value
	Intercept	48.67
Linear	Roads	-0.767
	Trails	
	Utility Lines	
	Railway	
Habitat Class	Tundra	
	Bedrock	
	Mudflats	
	Mixed Forest	0.519
	coniferous Cover	0.917
	Deciduous Cover	-0.493
	Burns (within 10 years)	-0.294
	Cutovers (within 10 years)	-0.947
	Open Forests	
	Lake Waters	
	Wetland	0.406
	Agriculture	
	Settlement/Industry	
Elevation	Altitude	0.007
Climate	Minimum Winter Temperature	-0.293
	Average Annual Precipitation	0.027
	Snow	0.37

precipitation in each of the 126 climate change scenarios. Only changes in temperature and precipitation were modelled, as habitat and linear features were held constant. Caribou were expected to be extirpated if the log likelihood of caribou occurrence was 0 (Sharma *et al.*, 2011). We then used the model predictions (or the probability density function of likelihood) to determine caribou occurrence rates across the study region.

iii) Climate change and woodland caribou range

To summarize uncertainty in caribou predictions across all GCM scenarios we used an interpolation method, Ordinary Kriging with 12 of the nearest neighbours, to visualize the proportion of models that forecast a caribou presence across both periods (2050 and 2070) and all climate scenarios (Cressie, 1993). The current range extent of caribou was used as a baseline comparison for projected future range extents under each GCM scenario.

Results

i) Woodland caribou occurrence

Landscape characteristics related to habitat, linear features, and climate significantly influence the occurrence of woodland caribou in Ontario in the winter season (Table 1). In terms of habitat, woodland caribou are found at higher elevations (uplands), in regions with greater areas of wetland, mixed forests, and coniferous forests (Table 1). They tend to avoid areas near cutovers, roads, deciduous forest and burned regions (Table 1). With respect to climate, woodland caribou show a preference for colder minimum winter temperatures, higher snow cover, and higher annual precipitation across the study region (Table 1). Upon testing the model with the validation data set, the logistic regression model had an overall correct classification rate of 72.0%. More specifically, the model had an overall sensitivity (true presences) of 61.9% and a specificity (true absences) of 73.1%.

ii) Uncertainty in climate change effects on woodland caribou occurrence

Presently, woodland caribou occur on 30.3% of our grid cells. By 2050, woodland caribou are forecast to occur in 2.2% of the grid cells on average (ranging from 0% to 13%) and 1.5% in 2070 (ranging from 0% to 12.5%; Table 2). The majority of climate change scenarios indicated that woodland caribou are more likely to be found within the western region of northern Ontario in the coming century (Figure 3). In contrast, the likelihood of woodland caribou occurrence decreased with increasing distance from the core region. Very few scenarios forecast the occurrence of woodland caribou in central Ontario, northeastern Ontario, as well as the northernmost limit of current woodland caribou occurrence in Ontario (Figure 3).

iii) Climate change and woodland caribou range

The current range extent of woodland caribou in Ontario is forecast to decrease by 92.2% on average by 2050 and 95.3% on average by 2070 (Table 2). For mid-century (2050), the lowest greenhouse gas emission scenario (RCP 2.6) forecast the loss of caribou range to be 85.6% (with a range of uncertainty of 57.2-99.8%). The highest greenhouse emission scenario (RCP 8.5) forecast a 98% (with a range of uncertainty of 87.5-100%) loss of woodland caribou range by 2050 (Table 2). Woodland caribou range was projected to contract even further by the late-century (2070). For example by 2070, caribou range was forecast to decrease by 99.7% on average across all business as usual (RCP 8.5) climate change scenarios, with numerous scenarios forecasting 100% losses of caribou across Ontario (Table 2).

Further, there was a strong relationship between increasing minimum winter temperatures in both 2050 and 2070 and declines in

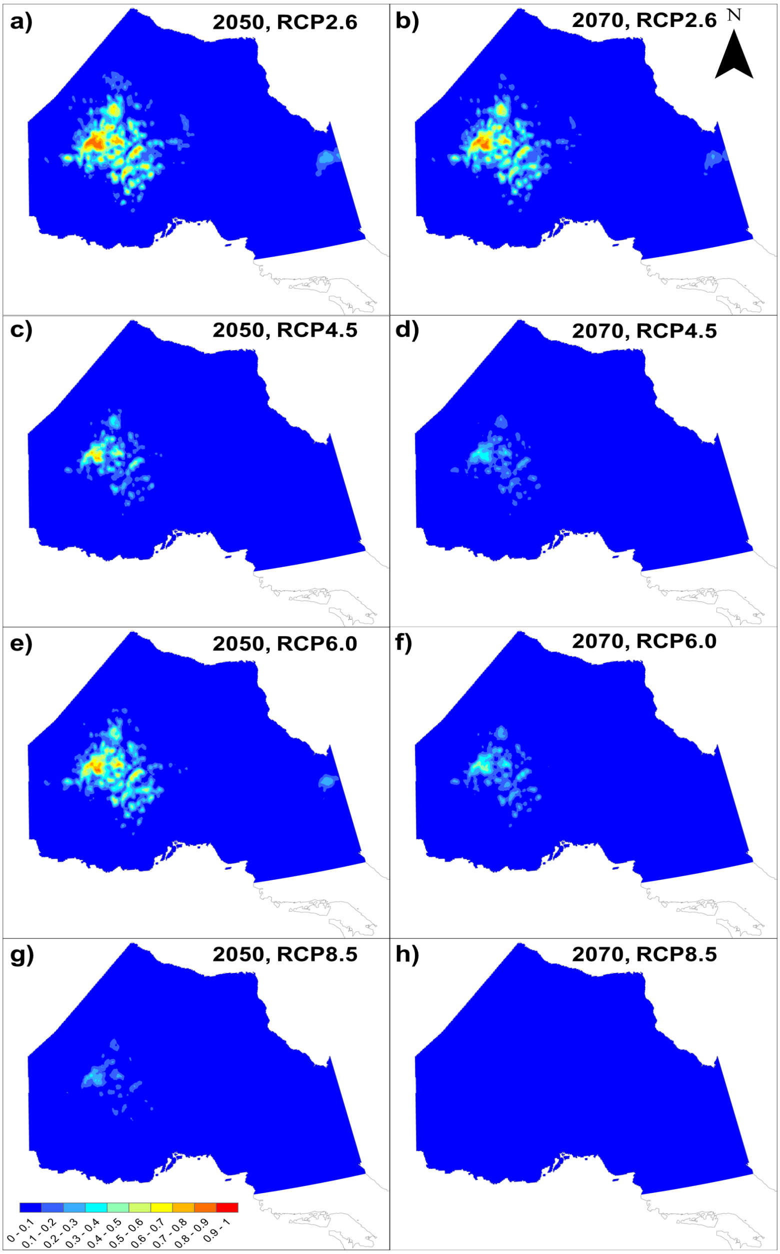

Figure 3. Future projections of caribou occurrence using 126 General Circulation Models (GCM) and greenhouse gas emission representative concentration pathway (RCP) scenarios. All fifteen RCP 2.6 (a,b), nineteen RCP 4.5 (c,d) , twelve RCP 6.0 (e,f), and 17 RCP 8.5 (g,h) projections were utilized in the projections of future caribou occurrence. Woodland caribou occurrence was forecasted using scenarios from 2050 (a, c, e and g) and 2070 (b, d, f and h). Blue regions represent low likelihoods of woodland caribou occurrence while orange, yellow, and red regions represent areas of higher likelihoods of caribou occurrence. Values are interpolated using Ordinary Kriging and shown at a 25 km^2 resolution.

caribou range extents in Ontario (Figure 4a). For mid-century, four scenarios forecast that an average increase above 5.3°C in winter minimum temperatures can elicit complete caribou extirpation across Ontario (Figure 4a). By late-century, twenty-four scenarios forecast an increase in minimum winter temperature of more than 5.8°C could lead to complete caribou extirpation across Ontario (Figure 4a). Although annual precipitation was revealed to be a significant, positive predictor of caribou occurrence in northern Ontario in our model, its impact on caribou occurrence under scenarios of future climate change was not as consistent as temperature variables (Figure 4b).

Discussion

We found that linear features, habitat types, and climatic conditions all influenced the occurrence of woodland caribou in Ontario in the winter. Overall, our assessment of the sensitivity of winter woodland caribou occurrence to all available climate change scenarios revealed a strong range recession and a high degree of variability in the forecasted woodland caribou range. Increases in the minimum winter temperature by the year 2070 demonstrated that on average, 95% of all caribou populations in Ontario may become extirpated as a result of climate change (Table 2; Figure 3). There is a high likelihood that woodland caribou will be extirpated from a large proportion of their range in the northernmost regions of Ontario, in addition to northeastern Ontario. In contrast, the lowest likelihood of woodland caribou extirpation is in the western region of northern Ontario.

Woodland caribou habitat preferences

Our models revealed habitat preferences for woodland caribou that largely agree with previous studies (e.g., O'Brien *et al.,* 2006; Vors *et al.,* 2007). We found that woodland caribou were positively associated with regions with dense coniferous forests, in addition to open forest, during winter (Table 1). The positive association of woodland caribou with coniferous forests is expected as contiguous coniferous zones, often composed of black spruce (*Picea mariana)* and jack pine (*Pinus banksiana*), serve

Table 2. The forecasted average and range of woodland caribou occurrence, and forecasted average range reduction (%) and range of values for the change in range extent of woodland caribou in northern Ontario for mid-century (2050) and late-century (2070) based on 63 climate change scenarios each. Shown are values for four greenhouse gas emission scenarios, representative greenhouse gas concentration (RCP) pathways and the number of models that are available for each scenario and time period (n).

Year	RCP (Greenhouse gas emission scenario)	n	Average Occurrence (%)	Range of Occurrence (%)	Average Range Reduction (%)	Range of Range Reduction (%)
2050	2.6	15	4.4	0.06-13.0	85.6	57.2-99.8
	4.5	19	1.5	0.05-6.1	95	79.8-99.8
	6	12	3	0.3-8.0	90.2	73.7-99.0
	8.5	17	0.6	0-3.9	98	87.5-100
2070	2.6	15	3.6	0.3-12.5	88.3	58.9-99.1
	4.5	19	1	0-5.1	96.8	83.4-100
	6	12	1.2	0-4.7	96.1	84.44-100
	8.5	17	0.1	0-1.2	99.7	96.0-100

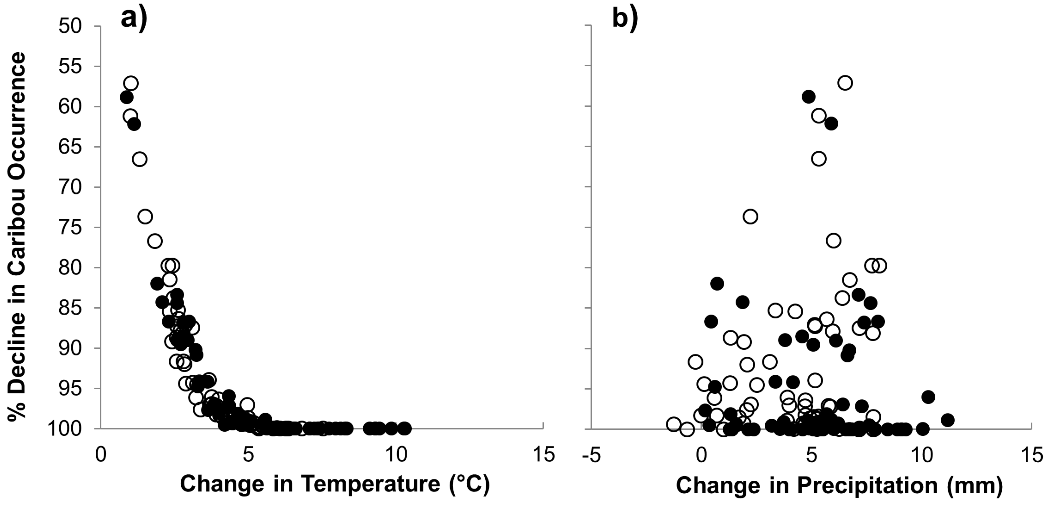

Figure 4. The percent reduction in the range extent of caribou with forecasted changes in minimum winter temperatures (a) and annual precipitation (b) for all 2050 (open circles) and 2070 (closed circles) climate change scenarios. Each point represents an average percent of caribou reduction across all grid cells in Ontario for one General Circulation Model (GCM).

as the primary habitat of woodland caribou in winter (O'Brien *et al.,* 2006). The preference of woodland caribou for open forest is explained by their increased ability to move around to successfully avoid predation (Brown *et al.,* 2003). Furthermore, open forests are associated with arboreal and terrestrial lichen rich understories, which are the primary food source of woodland caribou (O'Brien *et al.,* 2006; Courtois *et al.,* 2007, Thompson *et al.,* 2014). Caribou tend to also be associated with water and wetlands in the winter months as frozen water presents an easy means to navigate through the landscape and may facilitate "slushing" (Bergerud *et al.,* 1983; Leroux *et al.,* 2007; Fortin *et al.,* 2008). Finally, the association with wetland and elevation reflects the preference of caribou to be associated with muskegs or bogs alongside hilly areas to avoid predation (O'Brien *et al.,* 2006; Environment Canada, 2012).

The presence of fires (burns) and deforestation within a site was found to be negatively associated with woodland caribou occurrence (Table 1). Woodland caribou have been reported to avoid disturbed forests, both those that have been harvested and have undergone fire activities (Darby & Duquette, 1986; Rettie & Messier, 1998; Joly *et al.*, 2003). The disturbance of forest through timber harvesting and fire activities is known to alter predator-prey interactions as it can facilitate apparent competition (Wittmer *et al.*, 2007). However, Courtois *et al.* (2007) found that caribou can increase their home range sizes and reduce their fidelity to home ranges to combat the effects of forest disturbances.

Finally, woodland caribou tended to avoid roads (Table 1). The presence of road networks tends to increase the abilities of hunters, vehicles, and predators to access woodland caribou, thereby increasing mortality (Darby & Duquette, 1986; James & Stuart-Smith, 2000). Anthropogenic disturbances in caribou habitat can also result in behavioural changes in woodland caribou in an effort to avoid regions with high sensory disturbance (Dyer *et al.*, 2001; Fortin *et al.*, 2008). Extensive road networks that have high levels of traffic may increase energetic costs associated with travelling, thereby disrupting caribou movements that are essential for their survival (Darby & Duquette, 1986). As a result of these adverse effects, a strong relationship between woodland caribou extirpation and distance to roads has been previously documented for Ontario (Vors *et al*., 2007).

Climate change and woodland caribou

Climate change is expected to influence woodland caribou occurrence in the winter season both directly (e.g., extreme weather events) and indirectly (e.g., fire regimes). We found that woodland caribou preferred regions with colder minimum winter air temperatures and more snow cover (Table 1). This direct association resulted in our forecast that there may be a high risk of extirpation for woodland caribou in Ontario under all available scenarios of climate change and do not account for increased disturbance (e.g., roads) or habitat (landcover) changes that may also be associated with climate change. For example, by 2050, under the most conservative greenhouse gas emissions scenarios, with a range of increase in minimum winter temperature between 0.9-5.3ºC, we projected a loss of 57.2-99.8% of woodland caribou range in Ontario (Table 2; Figure 3). The high degree of variability in the likelihood of woodland caribou extirpation depends upon the degree of climate change and illustrates the sensitivity of woodland caribou to changing climates. Further, we showed that all 126 climate change scenarios forecast woodland caribou loss of at least 55% across Ontario by 2050 (Table 2; Figure 3). Similarly, Murray *et al.* (2015) forecasted the decline of woodland caribou suitable habitat in the boreal forest in North America to decline by up to 51.5% under an A2 climate change scenario by 2080, with a potential total loss projected for woodland caribou in Ontario (Murray *et al.,* 2015). Sharma *et al*. (2009) found that the occurrence and distribution of two migratory caribou herds in eastern North America during the winter season were also expected to change significantly by 2040-2069 as a result of climate change. For example, the distribution of the Rivière-George herd in the winter season decreased significantly (overall range contraction of 36.1%) under one scenario of climate change, whereas the distribution of Rivière-aux-Feuilles expanded and shifted north (overall range expansion of 47.4%; Sharma *et al*., 2009). Poleward range expansions are a common response to climatic change by numerous species (Parmesan and Yohe 2003). As such, one might expect some northward range expansion by migratory (Le Corre *et al.,* 2017) and woodland caribou given that the northern limit of sedentary caribou coincides with open water in mid-June (Bergerud *et al.,* 2008), an isoline that will also shift northward in a warming world. Molecular data confirm that caribou distributions have been tracking suitable climatic conditions across the entire range of caribou in response to changing climates over the past 21,000 years (Yannic *et al*., 2014). Yannic *et al.* (2014) also forecasted changes in caribou distributions under scenarios of future climate change by 2070, with potential extirpations of caribou inhabiting southern regions of their global extent.

Woodland caribou also showed a positive association with areas that have higher amounts of snow cover and precipitation (Table 1). The absence of sufficient snow cover can reduce ice thickness on freshwater lakes and rivers (Brown & Duguay, 2010), which may subsequently hinder woodland caribou movements as well as their migration across the landscape. Warmer winter temperatures, as forecast by climate change scenarios, can also result in the absence of proper ice formation and can increase ice-free periods (Magnuson *et al*., 2000; Sharma *et al*., 2013). The absence of thick ice could increase the risk of drowning and energetic costs of navigating the winter landscape for woodland caribou when moving on or around water bodies (Nault & LeHénaff, 1988). In contrast, extreme weather events, such as heavy snowfall or lightning-caused fires, are also projected to become more prevalent as climate changes (Thompson *et al.*, 1998; IPCC, 2013). For example, some Peary caribou populations in the Canadian High Arctic failed to survive during extreme winter weather conditions (Tews *et al.*, 2007).

Improvements to our models, if data permitted, could be made by incorporating other direct and indirect impacts of climate change, which might include: alterations in land cover and snowfall, biotic interactions, changes to forest composition, alterations to disturbance regimes (e.g., fire), and the interactions between land cover and climate. However, the lack of forecasted land cover and snowfall for the region and high range of uncertainty with how each of these processes may manifest in the boreal forest in the future may render this endeavour less useful. Our model forecasted a high likelihood of woodland caribou persistence within the southwest region of northern Ontario based on expected changes in minimum temperatures and precipitation (Figure 3). For the most part, woodland caribou also showed an extirpation along the most southerly margins of their range in northern Ontario (with the exception of a few models; Figure 3). Some previous assessments of future woodland caribou range under climate scenarios in Ontario demonstrated a straightforward northward range recession from their southern range limit (Thompson *et al.*, 1998; Yannic *et al.*, 2014). There are a few reasons why our model did not show this same pattern. First, the highest degree of change in winter temperatures from the current IPCC scenarios occurs along the northernmost portions of Ontario following the coast of Hudson Bay. As a result, woodland caribou, which prefer colder winters, may not prefer areas in the far north and east of northern Ontario in the future where we may find warmer winter temperatures. Second, the preferred habitat type of woodland caribou identified within our models (e.g., dense coniferous forest) was currently found in greater quantity in the southwestern portion of northern Ontario. If distributions of preferred habitat shift in response to climate change (as has been suggested by other studies; e.g., Lui, 1990; Parker *et al.*, 2000; Price *et al.*, 2013) our predictions of woodland caribou occurrence would follow changes in landscape patterns of this habitat. Thus, future woodland caribou ranges will not be a straightforward northerly shift, but a function of several sources of uncertainty including habitat, climate and linear disturbances across northern Ontario.

We have identified climate change as a large threat to woodland caribou persistence. Depending upon the extent of climate change, there is some degree of uncertainty with woodland caribou range alterations, where their current distributions may contract by 58.9-100% by 2070 (Table 2; Figure 3). Mitigating greenhouse gas emissions could reduce the risk of extirpation for woodland caribou (Schaefer, 2003; Sharma *et al.*, 2009). The decline of woodland caribou could foreshadow the likelihood of extirpation of other boreal forest species due to climate change. Thus, the reduction of greenhouse gas emissions would contribute much to the persistence of woodland caribou and the sustainability of boreal forest ecosystem.

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Supplementary Material

Table S1. Summary of predictor variables used to create caribou occurrence models. The 12 habitat variables were grouped based on their similarities from 26 total habitat variables.

Feature Type	Variables	Units	Mean	Range
Linear	Roads	binary	-	0 or 1
	Trails	binary	-	0 or 1
	Utility Lines	binary	-	0 or 1
	Railway	binary	-	0 or 1
Habitat	Tundra	binary	-	0 or 1
	Bedrock	binary	-	0 or 1
	Mudflats	binary	-	0 or 1
	Mixed Forest	binary	-	0 or 1
	Coniferous Cover	binary	-	0 or 1
	Deciduous Cover	binary	-	0 or 1
	Burns (within 10 years)	binary	-	0 or 1
	Cutovers (within 10 years)	binary	-	0 or 1
	Open Forest	binary	-	0 or 1
	Lake Waters	binary	-	0 or 1
	Wetland	binary	-	0 or 1
	Agriculture	binary	-	0 or 1
	Settlement/Industry	binary	-	0 or 1
Elevation	Altitude	m	250.95	0.04 - 549.56
Climate	Min. Winter Temperature	°C	-23.37	-28.16 - -14.23
	Avg. Annual Precipitation	mm	56.87	19.38 - 83.49
	Snow	% cover	98.82	53.03 - 100

Table S2. Summary of the 7 composite variables that were created by combining 18 land cover classification variables with overlapping values.

Composite variable name	Variables included within each composite
Coniferous Cover	Dense coniferous forests
	Coniferous cover over swamps
Deciduous Cover	Dense deciduous forests
	Deciduous cover over swamps
Open Forest	Sparse forests
	Forests regenerating from depletion
Wetland	Marsh intertidal
	Marsh supertidal
	Fen open
	Fen treed
	Bog open
	Bog treed
Lake Waters	Shallow/sedimented water
	Deep/clear water
Agriculture	Pasture/abandoned fields
	Croplands
Settlement/Industry	Settlement/Infrastructure
	Mine tailings/sand/gravel

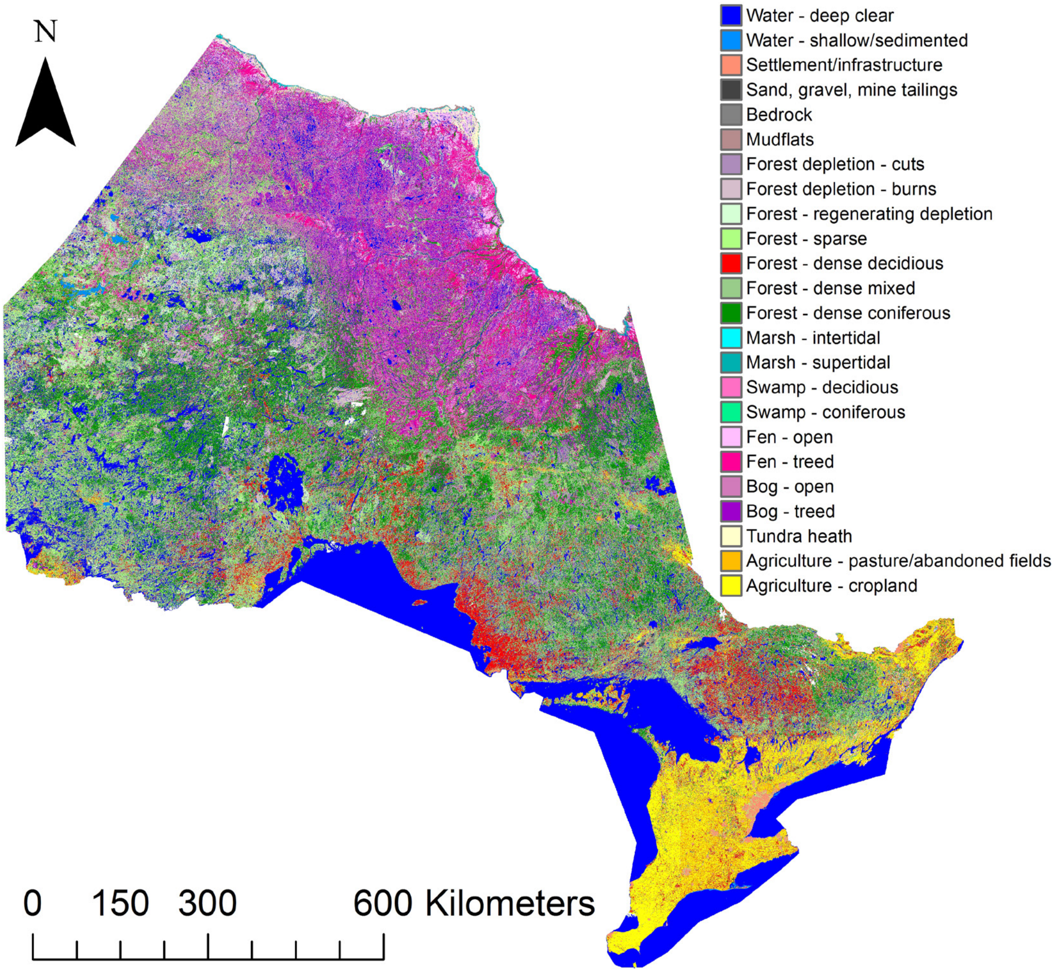

Figure S1. Classification of 24 land types in Ontario in between 1999-2002 by the Ontario Ministry of Natural Resources Landsat-7 Thematic Mapper satellite. Two of the original 26 variables were left out of this figure because their classification was labelled as "unknown".