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Biotic interactions govern the distribution of coexisting ungulates in the Arctic Archipelago – A case for conservation planning

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ABSTRACT

Climate change and biodiversity loss underscore the need for conservation planning, even in remote areas. Species distribution models (SDMs) can help identify critical habitat for reserve design and selection, and have quickly advanced to the fore of ecological inquiry. Such models are typically dominated by abiotic factors, following the Eltonian Noise Hypothesis (ENH) that physical features set the limits of species distributions. Nevertheless, recent studies challenge this notion and highlight the importance of biotic interactions. Resolving this discrepancy could have significant implications for conservation and ecological understanding. To test these ideas, we built distribution models for two large herbivores, muskoxen (*Ovibos muschatus*) and Peary caribou (*Rangifer tarandus pearyi*), systematically observed across a vast spatial extent – 65 islands spanning 800,000 km^2 in the Canadian High Arctic. To test the ENH we fit SDMs with two sets of predictors: (1) abiotic only (i.e. topographic, climatic) and (2) abiotic + biotic (i.e. vegetation communities, distance-to-heterospecifics). We evaluated these models and spatially estimated habitat suitability for each species. We found both sets of models had good predictive ability, although biotic variables (i.e. proportion of grass-lichen-moss) improved model performance and substantially narrowed areas of high habitat suitability. Niche overlap between caribou and muskoxen was moderate and highly suitable areas were spatially disjunct between species and largely outside protected areas. These results fail to support the ENH. Our study implies that biotic features, although often overlooked, may be important to the performance of SDMs and vital in identifying priority areas for conservation. For these large herbivores, reflecting trophic interactions in SDMs was essential when estimating areas of conservation value. Our approach helps prepare the way for improved projections regarding the prospects for wildlife while laying the foundation for biologically relevant protected areas.

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1. Introduction

Understanding the geographic and ecological distributions of species is a longstanding quest (Grinnell, 1914; Hutchinson and MacArthur, 1959). With global disruptions in climate, declines in wildlife, and growing anthropogenic disturbance, the need has become urgent (Young et al., 2016). In response, broad-scale species distribution models (SDMs) have emerged as a fundamental tool in conservation assessment, planning, and decision-making (Kremen et al., 2008; Schmolke et al., 2010) with emphasis on protecting biodiversity, habitat, biocultural landscapes, and climate refugia (Keppel et al., 2012; Guisan et al., 2013; Li et al., 2016). SDMs, often based on abiotic features alone, have proliferated due to the availability of abiotic variables on a global scale (Araújo et al., 2019). SDMs typically assume species are distributed independent of other species (Guisan and Thuiller, 2005). This focus on abiotic features conforms to the Eltonian Noise Hypothesis – i.e., that species distributions are unaffected by biotic interactions (e.g. competition, herbivory) at large spatial extents and coarse resolutions (Soberon and Nakamura, 2009). Yet, recent broad-scale studies illustrate biotic predictors can constrain a species range, and that including these features can consequently improve species distribution models (Heikkinen et al., 2007; Broennimann et al., 2012; Araújo et al., 2014; Atauchi et al., 2018). By reflecting biotic interactions, such models can provide more robust predictions and a strong foundation for planning (Thuiller et al., 2018; Palacio and Girini, 2018).

Despite their utility, accounting for biotic interactions can be difficult owing to their complexity (Aragon et al., 2018) and the challenge of representing dynamic and potentially fine-grained interactions at a macro scale (Soberon and Nakamura, 2009; Wisz et al., 2013). On the other hand, the distributions of species can be valuable proxies for biotic interactions (e.g., commensalism, Atauchi et al., 2018; herbivory, Thuiller et al., 2018) when supported by knowledge of interspecific interactions (Wisz et al., 2013). Accounting for competition is less straightforward, however, owing to the dynamic nature of predictors (Anderson, 2017) and the scarcity of methods to represent competition in grid cells (Mpakairi et al., 2017).

Multi-herbivore ecosystems provide valuable test cases. Among ungulates, for example, interactions with heterospecifics may include direct and indirect competition for resources and space, but also apparent competition mediated by shared predators or parasites (Rettie and Messier, 2000; Rostro-Garcia et al., 2015). Species responses to competition have led to the enduring concepts of competitive exclusion (Hardin, 1960) and niche (Hutchinson and MacArthur, 1959). Notably, these processes are difficult to uncover using correlative distribution models (Wisz et al., 2013; Anderson, 2017), but adding biotic variables in SDMs could improve our understanding of biogeographical patterns and interspecific relationships.

Relatively uncomplicated in structure, the Arctic lends itself to testing ecological relationships (Schaefer et al., 1996). In Canada, endangered Peary caribou *Rangifer tarandus pearyi* and muskoxen *Ovibos moschatus* (Fig. 1) occur on remote islands – the only ungulates adapted to this environment (Festa-Bianchet et al., 2011; Dobson et al., 2015). Interactions between these species is a longstanding and widespread issue that remains unresolved (Smits, 1989; Larter and Nagy, 1997; Rozenfeld et al., 2012), and a concern voiced by many Arctic Indigenous communities (Taylor, 2005; Jenkins et al., 2010a,b; COSEWIC, 2015). On some islands, numbers have risen and fallen in tandem; others show caribou population growth coincident with muskox extirpation or, conversely, the near-extirpation of caribou with rising muskox numbers (Klein, 1999; Gunn et al., 2006; Jenkins et al., 2011). Indeed, morphological, physiological and behavioral differences may limit interspecific competition and promote exploitation of different habitats (Klein, 1992, 1999; Larter and Nagy, 2004). Further, the patchiness of food resources, particularly during periods of snow cover, may be limiting for these large herbivores (Schaefer et al., 1996), and result in patchiness in species distributions. By uncovering environmental relationships and patterns (Araújo et al., 2014), the addition of biotic interactions in SDMs may enhance knowledge of both species and highlight areas of conservation value (Guisan et al., 2013).

Here, we use SDMs to quantify the distribution and niche characteristics of Peary caribou and muskoxen across the Canadian Arctic Archipelago – an immense swath of these species' ranges. We focus on late winter, a season of heightened environmental stress and depleted body condition, coincident with the fitness and physiological demands of calving (Miller and Gunn, 2003a,b). We tested the Eltonian Noise Hypothesis by using abiotic predictors alone, and then incorporating vegetation types and proximity to heterospecifics, as proxies for biotic interactions. Following Araújo et al. (2014), we predicted that (P1) models using *abiotic-only* variables would perform at least as well as models that included biotic predictors; and (P2) abiotic variables would remain the most important features of both *abiotic-only* and *abiotic + biotic* models. Finally, using our best models, we compared spatial estimates of high habitat suitability, and identified areas of conservation value in relation to protected areas in this vast and largely intact wilderness.

2. Materials and methods

2.1. Study area and study species

Our study extends across the eastern Canadian range of Peary caribou and muskoxen: 65 islands and roughly 800,000 km^2 (Fig. 2A; Jenkins et al., 2011; Cuyler et al., 2019). Both species are ecologically and culturally significant (Taylor, 2005; Yannic et al., 2014, Yannic et al., 2017). At a broad scale, their primary predator, the Arctic grey wolf (*Canis lupus arctos*), occurs at low numbers and can be scarce or absent from many islands (Miller and Reintjes, 1995). Wolves are generally associated with areas of high muskox density, although non-ungulate prey are also important (Mech, 2007; Larter, 2013; Dalerum et al., 2018). Muskoxen predator-prey relationships, including associated impacts on Peary caribou, have been identified as a knowledge gap (COSEWIC, 2015; Cuyler et al., 2019). Observations of wolves during our study were infrequent.

Fig. 1. Peary caribou (A, B) and muskoxen (C, D) in the rugged treeless habitat of the Canadian High Arctic Islands. Photos by Kevin Rawlings $_{(A,\ C)}$, and D.A.J. $_{(B,\ D)}$.

This landscape varies (west-east) from low, rolling tundra in the Northern Arctic ecozone to mountains, exposed bedrock, and ice fields in the Arctic Cordillera ecozone (Ecological Stratification Working Group, 1995). The climate is cold and dry, with extensive periods of snow cover (~10 months a year; Canadian Climate Normals 1981–2010) and darkness (6–18 weeks without daylight; https://www.timeanddate.com/sun/canada; Coops et al., 2008). The short growing season and shallow soils support sparse, patchy vegetation dominated by dwarf herbs, lichens, and moss (Walker et al., 2005). Six protected areas include national parks, national wildlife areas, and migratory bird sanctuaries (Fig. 2). According to national and international targets, the Northern Arctic Ecozone is underrepresented by protected areas (7.1% protected; Environmental and Climate Change Canada, 2019).

2.2. *Species distribution models*

To predict late-winter distributions and to assess the contribution of biotic interactions, we built SDMs from abiotic predictors and a combination of abiotic and biotic variables. We used maximum entropy modelling (MaxEnt Version 3.4.1; Phillips and Dudık, 2008), given its predictive performance, extensive use, suitability for presence-only data, and continuous prediction of habitat suitability (Elith et al. 2006, 2011; Broennimann et al., 2012). MaxEnt contrasts background environmental conditions with conditions at known species locations. As an index of habitat suitability, this approach estimates species distributions across the landscape (Phillips et al., 2006; Phillips and Dudık, 2008). We used the presence-only approach, recognizing true absences are difficult to record, particularly for mobile species (Lobo et al., 2010). Instead, we generated random points (n = 20,000) to sample the terrestrial environment (Phillips and Dudık, 2008; Elith et al., 2011; Barbet-Massin et al., 2012; Merow et al., 2013); the marine environment was excluded, despite possible sea-ice crossings (Jenkins et al., 2016; Schmidt et al., 2016). To improve model performance and predictions of habitat suitability, we followed recommendations for species-specific tuning of model settings and minimizing spatial autocorrelation (described below; Anderson and Gonzalez, 2011; Muscarella et al., 2014; Radosavljevic and Anderson, 2014).

2.3. *Occurrence records and environmental variables*

2.3.1. *Occurrence data*

Caribou and muskoxen are gregarious, so we used georeferenced observations to represent individuals in separate social groups. These observations were of animals, trails, and feeding sites in snow cover (Fig. 2) derived from systematic late-winter (April–May) aerial surveys (2001–2008) and unsystematic ground surveys (2000–2006; ~10% of the data; Jenkins et al., 2011; Environment, 2013). The number of locations varied by year, species and survey type (see Jenkins et al., 2011).

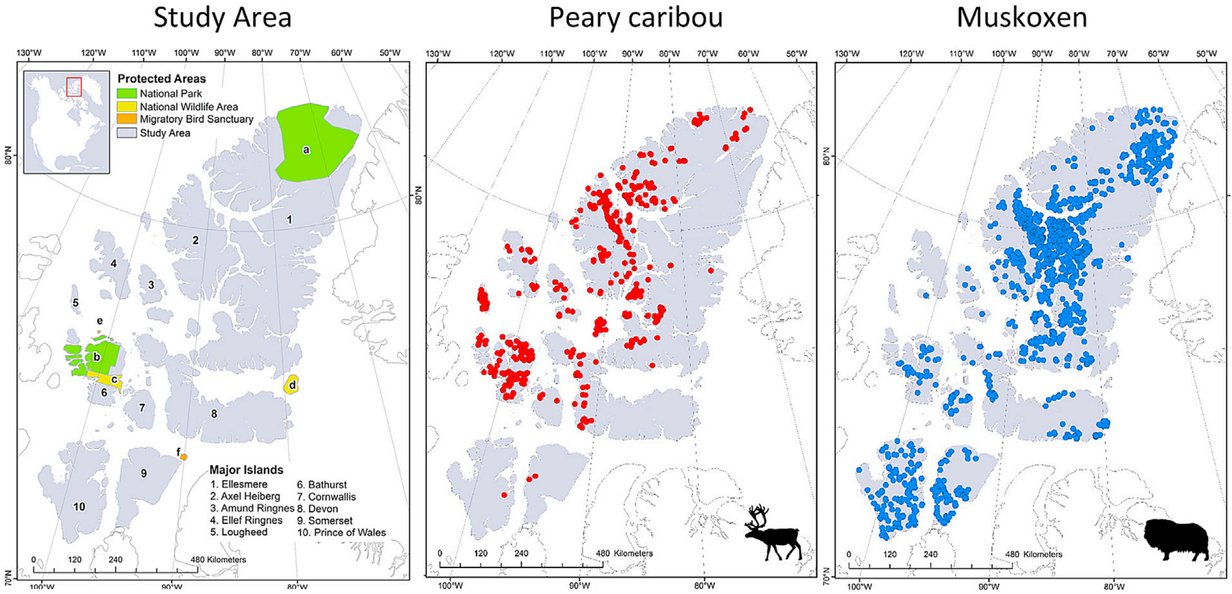

Fig. 2. Study area in the Arctic Archipelago (71° - 83°N, 61° - 106°W), Canada, including six protected areas: (a) Quttinirpaaq National Park (37,775 km^2), (b) Qausuittup National Park (11,000 km^2), (c) Polar Bear Pass National Wildlife Area (2636 km^2), (d) Nirjutiqavvik National Wildlife Area (1783 km^2), (e) Seymour Island Migratory Bird Sanctuary (53 km^2) and (f) Prince Leopold Island Migratory Bird Sanctuary (304 km^2). Occurrence records for Peary caribou (red) and muskoxen (blue), 2000–2008, derived from aerial and ground surveys. We geoprocessed the data to one geographic datum (i.e. WGS84) and projection (North Pole Lambert Azimuthal Equal Area, centered on 84°W, 78°N. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

We considered systematic aerial observations representative of geographic and environmental space (Wisz et al., 2008). In contrast, ground surveys were non-systematic and occasionally overlapped with aerial surveys (Jenkins et al., 2011). We buffered ground observations by 2 km (average daily winter movement of muskoxen; Jingfors, 1982). Overlapping observations were thinned to one location, unless separated by at least one day; aerial locations were preserved over ground locations (Radosavljevic and Anderson, 2014). We further reduced observations to one per grid cell (Phillips and Dudık, 2008) – in all, retaining 535 caribou and 1519 muskox locations. All geoprocessing occurred in ArcMap 10.6.1 (ESRI, 2018a) unless stated otherwise.

2.3.2. Environmental variables

To characterize habitat variation, we considered a suite of 18 abiotic and biotic predictors (see Appendix A, Table A.1) of putative ecological relevance to our species (Elith et al., 2011). We used geophysical variables that were derived from a digital elevation model (DEM) at 1-km resolution – a resolution to match the grain of our other environmental data – downloaded from the National Centers for Environmental Information (Globe Version 1.0; Hastings et al., 1999), from which aspect and slope were calculated using Spatial Analyst Tools (Surface) in ArcMap 10.6.1 (ESRI, 2018a). Average monthly climate data (1970–2000; April and May) were downloaded at a 30-s (~1 km at equator) spatial resolution (including minimum temperature [°C], maximum temperature [°C], average temperature [°C], precipitation [mm], solar radiation [kJ m^{-2} day^{-1}], and wind speed [m s^{-1}]; WorldClim2, Fick and Hijmans, 2017) which we then averaged across the winter study period. Snow depth was derived from the Canadian Meteorological Centre (CMC) Daily Snow Depth Analysis Data using monthly means of snow depth (24-km resolution, April and May, 2000–2008), which we then averaged across months and years.

Land cover types (Table A.1) were derived from the 2010 North American Land Cover categorical dataset from the Canada Centre for Remote Sensing/Canada Centre for Mapping and Earth Observation, Natural Resources Canada (30-m resolution; Latifovic et al., 2017). To develop continuous layers for each land cover type, from entirely unproductive land cover (i.e. snow and ice) to a series of vegetation types, we resampled the data and determined the proportion of each land cover type in each grid cell (577 m) using ArcGIS Pro (ESRI, 2018b). To incorporate heterospecifics as a biotic predictor, we generated separate continuous Euclidean distance rasters, distance-to-muskoxen and distance-to-caribou, based on our field observations of animals.

In ArcMap 10.6.1, we standardized all layers in extent and projection (North Pole Lambert Azimuthal Equal Area; Elith et al., 2006). For our base layers, i.e., elevation and climate, this resulted in a cell size of approximately 577 m × 577 m, which we standardized across layers. To address collinearity between predictor layers, we ran pair-wise Pearson correlations (r) using SDMtoolbox v2.2c (Brown, 2014; Brown et al., 2017), and excluded one variable from any pair where $|r| \geq 0.6$ (Dormann et al., 2007; Phipps et al., 2017). Our results revealed strong positive correlations among late-winter average, maximum, and minimum temperatures ($r > 0.90$). Additionally, snow and ice was positively correlated with elevation

($r = 0.74$) and negatively correlated with barren land ($r = -0.65$). We removed maximum and minimum temperature, as well as snow and ice, maintaining elevation and barren land (areas of low primary productivity) within the final set of 15 abiotic and biotic factors (Table 1).

2.4. Model tuning and performance

To derive input parameters, we ran models for each species. We used *abiotic-only* and *abiotic + biotic* predictors and tested 7 combinations (L, Q, H, LQ, LQH, LQHP, LQHPT; where L = linear, Q = quadratic, H = hinge, P = product, and T = threshold) and 8 regularization multiplier values (RM: 0.5, 1, 1.5, 2, 2.5, 3, 3.5, 4) – a total of 224 models. Due to the large study area, and the potential for environmental gradients, heterogeneity, and spatial autocorrelation, we employed spatially independent cross-validation (Radosavljevic and Anderson, 2014). Specifically, we used checkerboard2 partitioning in ENMeval R package, an approach that masks geographical structure (Radosavljevic and Anderson, 2014). The data were subdivided into 4 bins based on a hierarchical checkerboard distribution (i.e. 4 x 4) to equally partition geographic space and represent environmental heterogeneity in each bin (Radosavljevic and Anderson, 2014; Muscarella et al., 2014). Cross-validation for final models followed Beumer et al. (2019).

For each model, we assessed predictive performance, overfitting, goodness-of-fit, and model complexity (Radosavljevic and Anderson, 2014). These analyses were completed using the ENMEval package in R (Muscarella et al., 2104), unless stated otherwise.

A common measure of predictive performance is the area under the curve (AUC) of the receiver operating characteristic plot (ROC), where $AUC = 1$ represents perfect discriminatory ability, $AUC > 0.75$ useful models, and $AUC = 0.5$ no better than random (Elith et al., 2006; Phillips and Dudık, 2008). We generated AUC for training and testing (AUC_{TRAIN}, AUC_{TEST}; Muscarella et al., 2104) and evaluated performance using AUC_{TEST}.

We also calculated the partial receiver operating characteristic (PROC) area under the curve (AUC_{PROC}; ENMGadgets package in R; Barve and Barve, 2013) which gives priority to omission over commission errors, as recommended for presence-only data (Peterson et al., 2008; Lobo et al., 2010). We estimated ratios (AUC_{RATIO}) by comparing AUC_{PROC} to null expectations with bootstrapping (1000 replicates, 50% of evaluation data; 2% error among occurrence data). When AUC_{RATIOS} are significant and greater than one, model performance is better than random (Peterson et al., 2008).

To detect overfitting, we calculated the difference between AUC_{TRAIN} and AUC_{TEST} (AUC_{DIFF}), the minimum training presence omission rate (OR_{MIN}), and the 10% training omission rate (OR_{10}). Overfitting is typically indicated by higher AUC_{DIFF} and by $OR_{MIN} > 0$ and $OR_{10} > 10\%$ (Warren and Seifert, 2011). To balance goodness-of-fit and model complexity (Palacio and Girini, 2018), we calculated Akaike's Information Criterion for small sample size (AIC_c: Burnham and Anderson, 2002). We favored models with low ΔAIC_c (i.e. $AICc_{OPT}$).

Finally, we evaluated candidate models and selected optimal settings to balance low omission rates (i.e. OR_{MIN}), high predictive performance (i.e. AUC_{TEST}, AUC_{PROC}), and low model complexity (i.e. ΔAIC_c; Atauchi et al., 2018). To allow replication, our final model set was run in MaxEnt Version 3.4.1, using optimization settings, 20 replicates, 20,000 background points, and cross-validation on a subsample of presence data (75% training, 25% testing) with a random seed.

2.5. Variable importance and response curves

As measures of variable importance, we generated percent contribution and permutation importance in MaxEnt Version 3.4.1. The first identifies the contribution of each environmental variable to model fitting; the second identifies the change in training AUC when the variable is randomized across presence and background data (Phillips, 2017). The influence of a variable on the model is demonstrated by the change in AUC, where a large decrease in AUC corresponds to strong dependence (Searcy and Shaffer, 2016). Response curves show the relationship between each predictor variable and the prediction of habitat suitability while holding other variables constant (Merow et al., 2013; Phillips, 2017).

2.6. Spatial predictions of habitat suitability, niche characteristics, and protected areas

Using the logistic output, we mapped potential habitat suitability for caribou and muskoxen based on the best *abiotic-only* and *abiotic + biotic* models. We estimated spatial niche overlap, contrasting *abiotic-only* models vs *abiotic + biotic* models, using Schoener's D (Schoener, 1968; ENMTools Version 1.4.4; Warren et al., 2010; Warren and Seifert, 2011). Using two thresholds of habitat suitability ($HS \geq 0.5$; $HS \geq 0.75$), we measured extent and overlap of habitat (sum of pixels) and calculated the proportion of habitat in protected areas.

3. Results

3.1. Model performance

Species-specific tuning resulted in 224 *abiotic-only* and *abiotic + biotic* models, with moderate to good explanatory power ($0.73 \leq AUC_{TEST} \leq 0.88$; $0.74 \leq AUC_{PROC} \leq 0.90$) and predictive accuracy ($0.00 \leq OR_{MIN} \leq 0.01$) for both species in all but one model. According to AUC_{DIFF} and OR_{MIN}, overfitting was low for *abiotic-only* and *abiotic + biotic* models, further supported by

OR_{10} (0.074–0.136) across models and species. Best models based on $AICc_{OPT}$ and AUC_{PROC} revealed $AICc_{OPT}$ with only slightly lower predictive power (e.g. AUC_{TEST}) but reduced complexity (i.e. fewer parameters; Table A.2). For both species, there was high spatial overlap between all model predictions ($0.64 \leq$ Schoener's D ≤ 0.99).

For caribou and muskoxen, biotic variables improved model performance (AUC_{PROC} and AUC_{TEST}); AIC_c declined when biotic variables were included. Notably, caribou models had slightly higher performance (AUC_{PROC} and AUC_{TEST}) than muskox models (Table A.2). Below, we report $AICc_{OPT}$ models, given their reduced complexity but strong similarity to AUC_{PROC}.

3.2. Environmental predictors of habitat suitability

In *abiotic-only* models, elevation and precipitation were the main influences on habitat suitability for caribou; elevation and wind were most important for muskoxen (Table 1). For both species, the relative contribution of these variables was >50%. Aspect and slope were consistently minor influences. High habitat suitability (HS > 0.75) differed slightly between species – i.e., for caribou, low-moderate elevation (<626 m asl) and low precipitation (2.2–9.1 mm), whereas for muskoxen, low elevation (<219 m asl) and light winds (<2.87 m s^{-1}; Fig. 3).

When we added biotic variables, the proportion of grass-lichen-moss and barren-lichen-moss had the greatest influence on habitat suitability, with a combined contribution >60% for both species (Table 1). For muskoxen, wind was third in importance, while precipitation and wind were the next most influential features for caribou. For both species, distance to heterospecifics contributed little (<2%) to habitat suitability. Even small proportions of grass-lichen-moss (>0.0 for muskoxen; >0.28 for caribou) and barren-lichen-moss (>0.0 for muskoxen; >0.09 for caribou) had high habitat suitability (HS > 0.75). For muskoxen, such areas had near-zero to low winds (0.22–5.12 m s^{-1}) whereas for caribou, areas of high habitat suitability exhibited moderate winds (2.1–5.67 m s^{-1}) and low precipitation (2.6–9.35 mm; Fig. 3).

3.3. Spatial predictions of habitat suitability, niche characteristics, and protected areas

Regardless of species, we found modest differences between *abiotic-only* and *abiotic + biotic* model predictions of habitat suitability (Schoener's $D_{PC\ A\text{-}AB} = 0.73$; Schoener's $D_{MX\ A\text{-}AB} = 0.74$). Suitable habitat for caribou occurred in the northwest, particularly Axel Heiberg, Amund Ringnes, Lougheed, and Bathurst Island Complex (Fig. 4). In contrast, the most suitable habitat for muskoxen occurred primarily in the northeast, particularly the low-lying areas of eastern Axel Heiberg Island, west-central Ellesmere Island, and the far-eastern peninsula on Devon Island (Fig. 4). Spatial niche overlap between caribou and muskoxen was moderate (Schoener's $D_{PC\text{-}MX\ A} = 0.64$; Schoener's $D_{PC\text{-}MX\ AB} = 0.66$). For both species, areas of high habitat suitability were limited (Table 2, Fig. 5); they declined by as much as 42% when we included biotic variables.

From our best *abiotic + biotic* models, the estimated area of habitat suitability (HS > 0.5) for caribou and muskoxen overlapped by 42%, but by 17% at the higher threshold (HS > 0.75). These areas represent a small portion of the study area (i.e. 6.9% and 1.3%, respectively; Table 2). The majority of important habitat (>85%) occurred outside protected areas (Table 2, Fig. 5) – i.e., only 13% of prime late-winter caribou habitat and 9% of prime late-winter muskoxen habitat (HS > 0.75) is

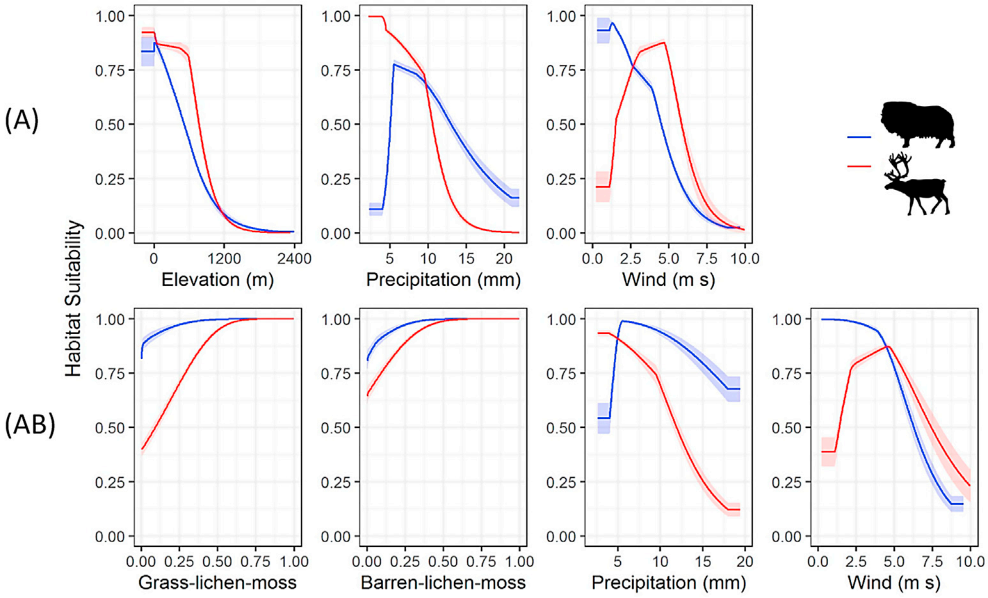

Fig. 3. Response curves (+/-std) showing the relationship between habitat suitability and the most important predictor variables in *abiotic* models (A) and *abiotic + biotic* models (AB).

Table 1
The estimated relative contribution of each environmental variable, percent contribution and permutation importance (in parentheses), to habitat suitability models for Peary caribou (PC) and muskoxen (MX) for best *abiotic-only* and *abiotic + biotic* models based on $AICc_{OPT}$ (see Table A.2 and Results). An em dash (–) marks variables not included in the models.

Variables	*Abiotic-only*		*Abiotic + biotic*	
	PC	MX	PC	MX
Aspect	1.7 (1.2)	2.4 (2.4)	0.3 (0.1)	0.8 (1.0)
Elevation	30.7 (26.8)	33.1 (32.4)	3.7 (6.2)	3.0 (5.3)
Precipitation	26.7 (22.6)	7.2 (7.1)	6.1 (7.6)	2.3 (3.3)
Solar Radiation	0.9 (0.4)	16.4 (12.1)	1.7 (0.2)	2.9 (1.9)
Avg. Snow Depth	8.5 (13.3)	10.2 (6.9)	4.3 (8.3)	2.0 (2.7)
Slope	1.2 (1.3)	1.7 (2.8)	0.1 (0.1)	0.4 (0.7)
Avg. Temperature	20.8 (25)	2.7 (5.3)	5.4 (5.7)	1.6 (3.1)
Wind Speed	9.5 (9.2)	26.3 (31.1)	5.7 (3.4)	10.2 (13.1)
Shrubland-Lichen-Moss	–	–	0 (0)	4.0 (3.5)
Grassland-Lichen-Moss	–	–	46.5 (40.9)	23.2 (19.6)
Barren-Lichen-Moss	–	–	21.7 (16.3)	45.5 (34.2)
Wetlands	–	–	0 (0)	0.0 (0.4)
Barren Land	–	–	2.9 (8.8)	2.2 (8.9)
Distance-to-caribou	–	–	–	2.1 (2.3)
Distance-to-muskoxen	–	–	1.6 (2.4)	–

protected. Of this, the majority was in two parks: Qausuittuq National Park for caribou (~70%) and Quttinitpaaq National Park for muskoxen (~90%).

4. Discussion

Increasingly, researchers are emphasizing biotic interactions in species distributions, even at broad spatial scales (Atauchi et al., 2018; Palacio and Girini, 2018). Such findings challenge the Eltonian Noise Hypothesis that abiotic factors govern species distributions over large extents (Soberon and Nakamura, 2009). Contrary to our predictions, we found (P1) SDMs of late-winter distribution of Peary caribou and muskoxen improved by including vegetation communities (Table A.2), and (P2) abiotic variables failed to remain the most important predictors in *abiotic + biotic* models (Table 1). In our study, biotic features, representing vegetation and heterospecifics, were not correlated with abiotic variables ($|r| < 0.6$), implying that they captured new aspects of habitat (Soberon and Nakamura, 2009; Araújo et al., 2014). As well, the strong positive relationship between habitat suitability and grass-lichen-moss and barren-lichen-moss suggest forage resources are critical for both species (Schaefer and Messier, 1995a; Rettie and Messier, 2000), and signal herbivory as the likely driver of species distributions. During winter, muskoxen consistently select for higher forage abundance across spatial scales (Schaefer and Messier, 1995a) while regional studies, like ours, identified vegetated areas as important muskox habitat across seasons and years (Table 1, Fig. 3; Beumer et al., 2019). That caribou favored grass-lichen-moss while muskoxen were most strongly associated with barren-lichen-moss communities (Table 1) emphasizes the metabolic requirements and high-quality diet of caribou (Parker and Ross, 1976; Klein, 1992, 1999) – a largely mobile species in contrast to predominantly sedentary muskox (Klein, 1999; Beumer et al., 2019). Nevertheless, whether these differences in niche reflect biotic interactions, such as competitive exclusion and apparent competition (Holt and Bonsall, 2017), is not reconcilable with our data.

Demonstrating competition is difficult (Araújo and Guisan, 2006); including competitive interactions in SDMs is rare (Mpakairi et al., 2017). This rarity is likely due to the complexity of rasterizing this mechanism and difficulties in establishing competitive interactions from simple, static observations (Connell, 1980; Yackulic, 2017). We expected caribou habitat suitability might improve with increasing distances-to-muskoxen, potentially indicative of apparent competition and the avoidance of shared enemies. However, proximity to heterospecifics contributed little to our models (Table 1). Indeed, including potential competitors may not improve model performance while vegetation can be an important predictor of animal-plant interactions (Bateman et al., 2012; cf. Mpakairi et al., 2017).

Our study focused on late winter, a period of energetic and demographic stress for arctic caribou and muskoxen (Thomas and Edmonds, 1983; Miller and Gunn, 2003a,b; Joly, 2011). While our analysis was restricted to this season, arctic snow cover can impose appreciable fitness costs (Miller and Barry, 2009; Callaghan et al., 2011). For caribou and muskoxen, severe snow and icing can result in reproductive failure and mass die-offs (Miller and Gunn, 2003b; Miller and Barry, 2009; Schmidt et al., 2019). Our finding that muskox habitat suitability was related to low winds, rather than precipitation or snow cover (Spencer and Lensink, 1970), was unexpected. While snow depth is not static, and the resolution of our analysis was rather coarse, arctic snow cover is renowned for its strong spatial variation and relative consistency across years (Pruitt, 1978; Schaefer and Messier 1995b). Our study likely captured this coarse-scale variation, but muskoxen may react to snow at a finer grain (Schaefer and Messier, 1995a), using micro-habitats to overcome unfavorable conditions (Klein et al., 1993). Additionally, the absence of wind may provide energetic benefits, particularly to parturient cows and neonates. Our study overlapped with the calving season of muskoxen (April–June; Lent, 1991) and we observed ~1500 newborns throughout the study area (Jenkins et al., 2011). In contrast, low precipitation was important to caribou, underscoring winter precipitation as energetically and

Table 2
Total area, protected area, and overlapping area with habitat suitability (HS) scores above 0.5 and 0.75 for Peary caribou (PC) and muskoxen (MX), based on *abiotic* + *biotic* models ($AICc_{OPT}$). *Abiotic-only* values provided for contrast.

	Area with HS > 0.5		Area with HS > 0.75		Protected Area of HS > 0.5		Protected Area of HS > 0.75	
Model	km^2	%[a]	km^2	%[a]	km^2	%[b]	km^2	%[b]
Abiotic + *biotic* models								
Peary caribou	67,068	16.2	33,021	8.0	10,311	15.4	4,294	13.0
Muskoxen	68,333	16.5	31,938	7.7	7,773	11.4	2,888	9.0
Overlap	28,582	6.9	5,384	1.3	2,611	9.1	378	7.0
Abiotic-only models								
Peary caribou	114,977	27.7	41,425	10.0				
Muskoxen	102,688	24.8	34,706	8.4				

[a] in relation to the terrestrial study area (414,639 km^2).
[b] in relation to the Area of HS (>0.5 or >0.75).

demographically taxing to ungulates (Thomas and Edmonds, 1983; Joly, 2011). Snow and rain-on-snow can limit access to forage, already sparse and low in nutrients (Albon et al., 2017; Schmidt et al., 2018), and snow can amplify movement costs (Parker et al., 1984). Thus, areas of low precipitation likely favor access to forage (i.e. potentially higher-quality foods), a determinant of caribou survival during the energetically stressful pre-calving period (Thomas and Edmonds, 1983; Biddlecomb, 1992; Larter and Nagy, 2004; Joly, 2011).

Mapping species-environment relationships provides a geographic depiction of potential habitat (Araújo and Guisan, 2006). In our study, biotic interactions drove the distributions and appeared to constrain muskox and caribou habitat (Fig. 4). Our *abiotic-only* models performed well, but they underperformed in comparison to *abiotic* + *biotic* models (Table A.2) and estimated broader areas of habitat suitability (Atauchi et al., 2018), potentially devoid of critical forage resources. In contrast, Johnson et al. (2016) modeled range-wide Peary caribou distribution by season with the selected abiotic top model for late-winter distribution including precipitation, snow depth and wind speed as predictors. These models combined spatially and temporally disjointed observations (i.e. from surveys, radio-telemetry, Inuit Knowledge) and used predictors from coarse climate data (25 km) to fine categorical land cover (30 m). Our models differed in output and approach. By accounting for data resolution and independence, sample period, and spatial autocorrelation, and by incorporating continuous, fine-resolution predictors, our models had stronger predictive performance (average test AUC = 0.87 vs 0.78) and revealed a strong association with vegetation cover. Indeed, robust models of current and future distributions are often strongly influenced by plant species (Atauchi et al., 2018; Palacio and Girini, 2018; Thuiller et al., 2018).

Mapping habitat suitability can serve conservation, especially in determining areas of high conservation value as candidate protected areas for rare and endangered species (Guisan and Thuiller, 2005; Guisan et al., 2013). Our results reveal that protection of late-winter habitat is limited for caribou and muskoxen (Fig. 5, Table 2). These areas of conservation value lie largely outside protected habitat (≥85%), a circumstance not uncommon for mobile caribou (Taillon et al., 2012). The National Parks system in Canada has focused on geographic and bioregional representation; less on protecting biodiversity, viable populations, and ecosystem integrity (Manseau et al., 2001; Deguise and Kerr, 2004). We were not, therefore, surprised by our findings. Bias in siting new parks is a national and global issue; the potential for agriculture and resource extraction has typically been favored over ecological considerations (Joppa and Pfaff, 2009; Lopoukhine et al., 2012). Indeed, critical winter habitat, calving grounds, and climate refugia have long been emphasized in the ecology of muskoxen and Peary caribou (Thomas et al., 1981; Ferguson, 1995; Jenkins et al., 2011; Poole et al., 2015), species that are central to the culture and security of Arctic Indigenous communities. As our study underscores, such areas are strikingly absent from protected areas.

5. Conclusions

Species distribution modeling can be a powerful conservation tool. When based on robust location data and meaningful predictors, SDMs can inform conservation, with potentially better prospects for wildlife. To date, however, biotic features have largely been ignored. Contrary to Eltonian Noise Hypothesis, biotic predictors were essential to identifying late-winter habitat of these large herbivores. Habitat that is likely important to their physiological and metabolic requirements and a reflection of trophic interactions.

Suitable conditions for wildlife often occur outside protected areas (Deguise and Kerr, 2004), as our study shows. We focused on a biologically crucial period in a remote, but increasingly threatened area. Still largely intact, the Arctic represents important but vanishing opportunities to protect large areas of wildlife habitat. Such areas help meet national and international conservation obligations while supporting the persistence of key Arctic species, crucial for tundra ecosystems and for Inuit communities, in a changing environment. More generally, our approach helps prepare the way for improved large-scale projections regarding the prospects for wildlife, while laying the foundation for biologically relevant protected areas.

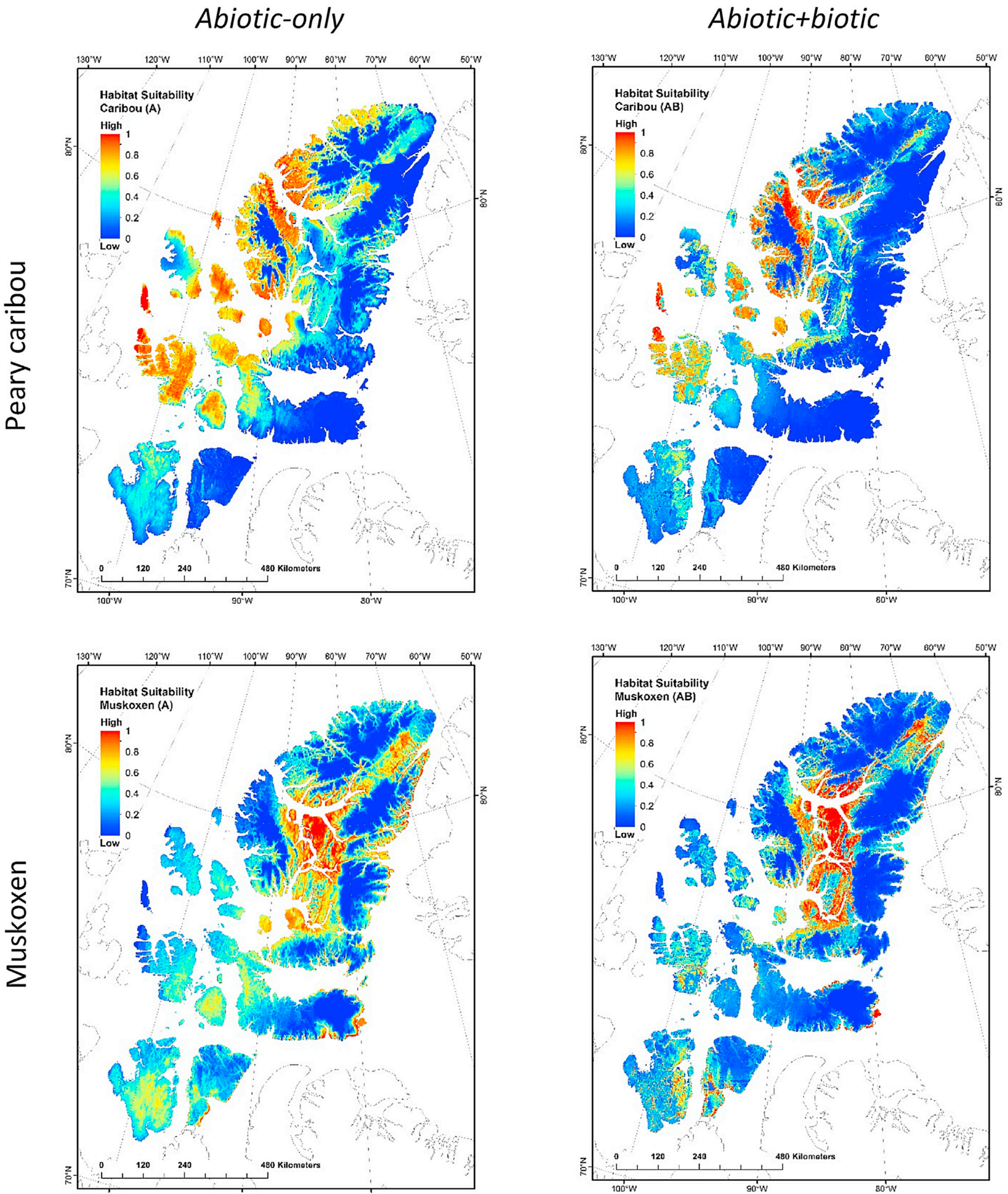

Fig. 4. Predictions of habitat suitability for Peary caribou and muskoxen across the north-eastern Arctic Archipelago, representing species-specific *abiotic-only* and *abiotic + biotic* models.

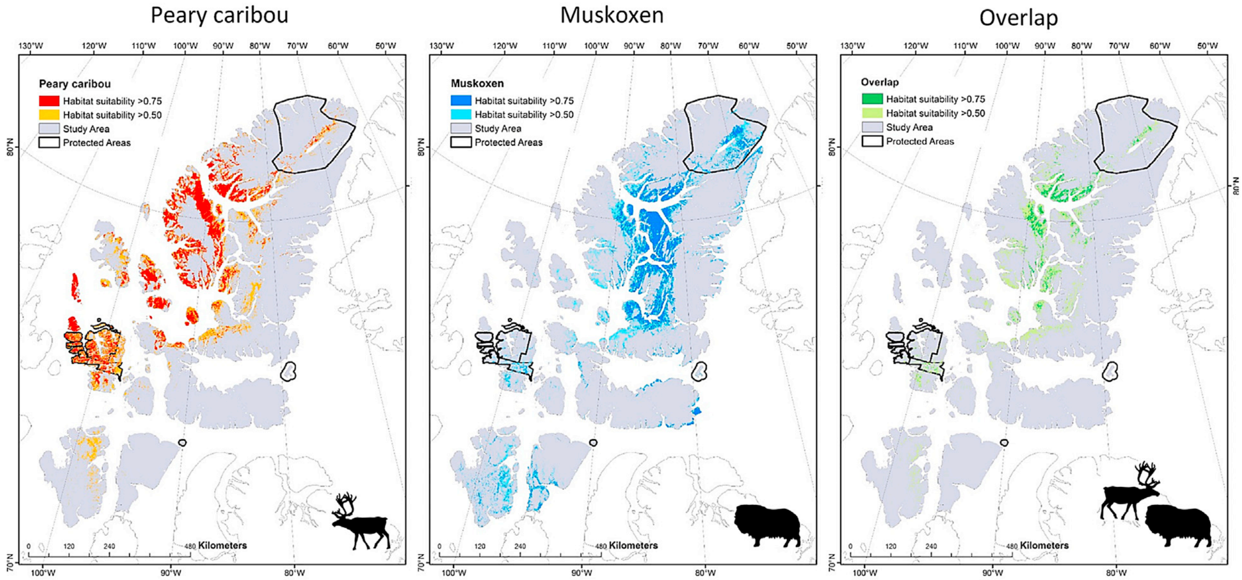

Fig. 5. Areas with high habitat suitability from two habitat suitability thresholds (HS > 0.5, HS > 0.75) for Peary caribou and muskoxen, in relation to protected areas. Overlap between species is highlighted separately.

Data availability statement

Observation data are sensitive and archived with the Nunavut Department of Environment. Environment, 2013. Peary caribou and muskoxen observations, High Arctic Islands, 2000–2008. Unpublished Data. Government of Nunavut, Iqaluit, Nunavut. Raster file sources are identified in Table A.1 and freely available.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

Table A.1
Original (grey) and derived environmental layers for *abiotic-only* and *abiotic + biotic* distribution models of Peary caribou and muskoxen, Canadian Arctic Archipelago.

Environmental Predictor	Spatial Resolution	Description	Source
Elevation	~ 1 km	DEM; Elevation above mean sea level; continuous 1 - 2394 m	National Centers for Environmental Information
Elevation	577 m	Elevation above mean sea level	Hastings, D.A., Dunbar, P. K., Elphingston, G.M., Bootz, M., Murakami, H., Maruyama, H., … MacDonald, J.S. 1999.
Aspect	577 m	9 categories; Flat, North, Northeast, East, Southeast, South, Southwest, West, Northwest	
Slope	577 m	Continuous; 0-50 degrees	
Bioclimatic Variables	~ 1 km	Monthly Long-term Average 1970-2000	WorldClim Version 2
Min Temp (°C)	577 m	Avg April -May	Fick, S.E. and Hijmans, R.J. 2017.
Max Temp (°C)	577 m	Avg April -May	
Avg Temp (°C)	577 m	Avg April -May	
Prec (mm)	577 m	Avg April -May	
Solar Rad. (kJ m^{-2} day^{-1})	577 m	Avg April -May	
Wind Speed (m s^{-1})	577 m	Avg April -May	
Snow depth	~24 km	Monthly average snow depth by year (2000 to 2008); averaged across months (April-May), and years.	National Snow and Ice Data Center, Canadian Meteorological Centre, Daily Snow Depth Analysis Data
Avg. Snow Depth (cm)	577 m		
Land cover	30 m	2010 Land Cover Map of North America; categorical	Natural Resources Canada
Shrubland-Lichen-Moss	577 m	proportion of subpolar or polar shrubland-lichen-moss (Code 11)	Latifovic, R., Pouliot, D., and Olthof, I. 2017.
Grassland-Lichen-Moss	577 m	proportion of subpolar or polar grassland-lichen-moss (Code 12)	
Barren-Lichen-Moss	577 m	proportion of subpolar or polar barren-lichen-moss (Code 13)	
Wetland	577 m	proportion of wetland (Code 14)	
Barren Land	577 m	proportion of barrenland; <10% vegetation cover (Code 16)	
Snow and Ice	577 m	proportion of snow and ice (Code 19)	
Euclidean distance		Derived in ArcMap using animal observations for each species	Animal observations collected during aerial and ground surveys.
Distance-to-muskox (m)	577 m		
Distance-to-caribou (m)	577 m		

Table A.2
Evaluation of selected models based on $AICc_{OPT}$ and AUC_{PROC} for Peary caribou (PC) and muskoxen (MX) using *abiotic-only* (A) and *abiotic + biotic* (AB) predictors.

Model	Feature Class	RM	AUC_{TRAIN}	AUC_{TEST}	AUC_{DIFF}	AUC_{PROC}	AUC_{RATIO}	OR_{MIN}	OR_{10}	AICc	# of Para.
$AICc_{OPT}$											
PC − A	LQHP	1.5	0.83	0.81	0.02	0.83	1.66	0.002	0.128	14540	91
PC − AB	LQHP	3	0.88	0.87	0.01	0.88	1.75	0.002	0.109	14076	62
MX − A	LQHP	1	0.81	0.80	0.01	0.81	1.62	0.001	0.102	41223	153
MX − AB	LQHP	2	0.87	0.86	0.01	0.87	1.73	0.003	0.113	40007	96
AUC_{PROC}											
PC − A	LQHP	0.5	0.85	0.83	0.03	0.85	1.70	0.005	0.124	14578	145
PC − AB	LQHP	0.5	0.91	0.88	0.03	0.90	1.80	0.009	0.134	14342	206
MX − A	H	0.5	0.81	0.80	0.01	0.81	1.63	0.001	0.106	41307	185
MX − AB	LQHP	1.5	0.87	0.85	0.01	0.87	1.74	0.002	0.109	40055	134

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