RESEARCH ARTICLE

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A genus at risk: Predicted current and future distribution of all three *Lagopus* species reveal sensitivity to climate change and efficacy of protected areas

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Abstract

Aim: Cold-adapted species are considered vulnerable to climate change. However, our understanding of how climate-induced changes in habitat and weather patterns will influence habitat suitability remains poorly understood, particularly for species at high latitudes or elevations. Here, we assessed potential future distributions for a climate-sensitive genus, *Lagopus*, and the effectiveness of protected areas in tracking shifting distributions.

Location: British Columbia, Canada.

Methods: Using community science observations from 1970 to 2020, we built species distribution models for white-tailed (*L. leucura*), rock (*L. muta*) and willow ptarmigan (*L. lagopus*) across British Columbia, a globally unique region harbouring all three ptarmigan species. We assessed the impact of climate (direct) and climate-induced habitat change (indirect) on potential future distributions of ptarmigan.

Results: White-tailed and rock ptarmigan were associated with colder temperatures and tundra-like open habitats and willow ptarmigan with open, shrub habitats. Future projections based on climate and vegetation scenarios indicated marked losses in suitable habitat by the 2080s (RCP +8.5 W/m^2), with range declines of 85.6% and 79.5% for white-tailed and rock ptarmigan, respectively, and a lower 61.3% for willow ptarmigan. Predicted current and future suitable habitat occurred primarily outside of current protected areas (67%–82%), yet range size declined at a less pronounced rate within protected areas suggesting a capacity to buffer habitat loss.

Main conclusions: Ptarmigan are predicted to persist at higher elevations and latitudes than currently occupied, with the magnitude of elevation shifts consistent with trends observed elsewhere in the Holarctic. Our spatially explicit assessment of potential current and future distributions of ptarmigan species provides the first comprehensive evaluation of climate change effects on the distribution of three congeneric, cold-adapted species with different habitat preferences and life-history

traits. We also highlight the potential role of protected areas in preserving suitable future sites for ptarmigan and other climate-sensitive or high-elevation species.

KEYWORDS
Alpine, Arctic, high elevation, high latitude, mountain fauna, ptarmigan, species distribution models

1 | INTRODUCTION

Species occurring at high latitudes and elevations are considered to be particularly vulnerable to rising temperatures, variable precipitation patterns and frequent extreme weather events emblematic of climate change (Fei et al., 2017; Pacifici et al., 2017; Wernberg et al., 2013). Warming climate trends are more pronounced in these areas than in other terrestrial environments due to changes in albedo and surface-based feedbacks, water vapour, radiative fluxes and aerosol concentrations (Pepin et al., 2015; Serreze & Barry, 2011). Some high-latitude species have shifted their distribution poleward to match the latitudinal displacement of suitable climate, while high-elevation species are tracking cooler climates upslope (Flousek et al., 2015; Lehikoinen & Virkkala, 2016; Scridel et al., 2018; Zuckerberg et al., 2009). For high-mountain species, reduced land area at the highest elevations poses further concerns for the extinction of isolated populations (Caizergues et al., 2003; Freeman et al., 2018). Indeed, simulations of future climatic scenarios predict drastic changes for Arctic and alpine wildlife species, ranging from species redistribution to the extinction of rare and endemic plants and animals (Brambilla et al., 2017; La Sorte & Jetz, 2010; Zhang et al., 2015).

Despite the vulnerability of high-latitude and high-elevation biota to climate change, studies of species inhabiting these regions remain limited globally (Lehikoinen, Brotons, et al., 2019; Scridel et al., 2018). Yet, exploring the potential distribution of Arctic and alpine species has value in terms of targeting searches for unknown populations and informing conservation policy decisions (McCune, 2016). Assessing the future effectiveness of protected areas (PAs) in tracking shifting distributions under climate change is particularly relevant for planning biodiversity management and conservation areas.

For charismatic, habitat-specialized species such as grouse, assessing changing distributions can provide advanced warning of shifting habitat suitability and positively influence conservation of the wider community (Hanser & Knick, 2011; Henden et al., 2017; Storch, 2007). Within the grouse family, the three species comprising the avian genus *Lagopus*, commonly known as ptarmigan, are among the most iconic of the boreal hemisphere. White-tailed ptarmigan (*L. leucura*), rock ptarmigan (*Lagopus muta*) and willow ptarmigan (*L. lagopus*) are cold-adapted species with Holarctic distributions, inhabiting northern tundra and/or high elevations, often as isolated glacial relict populations (Martin & Wilson, 2011; Moss et al., 2010; Storch, 2007). While genetically similar, each species exhibits notable differences in their biology, ecology and life-history strategies

(Sandercock et al., 2005a, 2005b). White-tailed ptarmigan are alpine specialists, restricted to western North America and inhabiting the highest elevations of the three species, preferring greater rock cover and low-profile vegetation such as lichens and dwarf shrubs (Martin et al., 2020; Wilson & Martin, 2008). Rock ptarmigan have the widest latitudinal distribution (35°–83°N), inhabiting the high Arctic to the alpine tundra of southern Europe and Japan (Fuglei et al., 2020; Hotta et al., 2019; Montgomerie & Holder, 2020). They breed in lower alpine meadows at intermediate elevations, with graminoid ground cover interspersed with rock, woody shrubs and heather (Wilson & Martin, 2008). Willow ptarmigan, the most abundant tetraonid in the world, ranges from NW Alaska to Newfoundland and from Europe to northern Mongolia, occurring as far south as 47°N (Hannon et al., 2020; Storch, 2007). It selects wetter, lower elevation sites in thickets of dwarf vegetation (i.e. scrub birch *Betula* spp., heather *Calluna* spp.) in the low tundra or tree line ecotones of sub-Arctic and alpine habitats (Wilson & Martin, 2008).

Ptarmigan are considered sentinels of climate change, being sensitive to increasing temperatures, snow loss and severe weather events and to climate-amplified food limitations, predation risk and parasite occurrence (Henden et al., 2017). White-tailed ptarmigan are year-round alpine residents, with widely demonstrated susceptibility to changing spring and winter temperatures. Population growth declined following higher minimum winter temperatures in Colorado, USA (Wang et al., 2002), while breeding success was greatly reduced with multi-week delays in spring snow-melt (Martin & Wiebe, 2004). Changing climate regimes are predicted to result in extensive habitat loss and fragmentation of the coastal alpine that white-tailed ptarmigan inhabit on Vancouver Island, British Columbia (Jackson et al., 2015a). Similarly, rock ptarmigan in the European Alps (*L.m. helvetica*) are moving to higher elevations to track cooler climate (Pernollet et al., 2015; Revermann et al., 2012), contracting range sizes (Scridel et al., 2017) and displaying negative population trends across the world (Fuglei et al., 2020). Willow ptarmigan are also sensitive to changes in climate which influence recruitment rates (Hannon & Martin, 2006; Martin & Wiebe, 2004; Slagsvold, 1975; Steen et al., 1988). In Europe, Melin et al. (2020) demonstrated that population declines in Finland were more pronounced in years when the preceding April was snow-free, while Selås et al. (2011) showed that chick production in Norway was related negatively to summer temperatures in the two previous years.

Despite being closely related, variation in habitat preferences and life-history traits suggest ptarmigan species may differ in their response to changes in climate and consequently habitat availability. Currently, all three species of ptarmigan inhabit relatively

large ranges within British Columbia (B.C.), Canada. This provided a unique opportunity to conduct a comparative evaluation of potential climate-induced redistributions of a cold-adapted genus while controlling for regional geographic influences. While single-species ptarmigan studies exist (Table S1), they tend to predict future distributions independent of climate-induced changes in habitat. Critically evaluating the potential distribution of all ptarmigan, while accounting for changes in both climate and vegetation, will improve our understanding of future habitat suitability for these climate-sensitive species. It will also highlight the potential for species interactions or exclusions through patterns of co-occurrence (c.f. Brambilla et al., 2020), key parameters underlying future distributions.

We assessed current and future habitat suitability for all three congeneric ptarmigan species in B.C., one of the few areas in the world hosting the entire genus. We also examined how predicted redistribution of these species would match current coverage by protected areas (PAs). The static boundaries of PAs may undermine their effectiveness at protecting species under future climate change scenarios (Hannah et al., 2007). For current distributions based on species' ecological traits, we predicted that white-tailed and rock ptarmigan would occupy similar habitats at the highest elevations, while willow ptarmigan would favour lower elevations. Being cold-adapted birds, we hypothesized that all three species would shift towards higher elevations and higher latitudes in the future, with reductions in suitable habitats from direct climatic impacts (i.e. abiotic factors) and indirectly via climatic-induced changes in vegetation (i.e. biotic conditions). We expected white-tailed and rock ptarmigan to lose more habitat than willow ptarmigan as the latter prefers comparatively warmer, shrubby habitats which are encroaching on alpine grassland under a warming climate (Jackson et al., 2016; Wang et al., 2012).

2 | METHODS

2.1 | Study system

We modelled the potential current and future distributions of ptarmigan across the entire province of British Columbia (B.C.), Canada (approximate land area 945,000 km^2). B.C. is one of the most mountainous regions of North America, with 75% of land located above 1,000 m a.s.l. (Cannings & Cannings, 1996) and 18% considered rock, ice or tundra (Cannings & Cannings, 2015). Major mountain ranges of B.C. generally fall into four distinct regions: eastern (Canadian Rockies), interior (Cassiar Mountains, Omineca Mountains), western (Cascade Mountains, Coast Mountains) and insular systems (Vancouver Island, Haida Gwaii). Climate varies dramatically across B.C. given the complex topography, influence of the Pacific Ocean and large latitudinal (48°–60° North) and longitudinal (120°–140° West) ranges. Average annual temperature across the province has warmed by 1.4°C over the past century (1900–2013), a greater increase than the global average (0.85°; IPCC, 2013), with northern areas experiencing greater warming (1.6–2°C) than the south (0.8°C).

Annual precipitation has also increased by 12% in the past century (B.C. Ministry of Environment 2015).

2.2 | Bird data

Alpine birds are not systematically monitored in B.C., and therefore, to model potential current and future distributions of the three ptarmigan species, we used presence-only data compiled from georeferenced observations in B.C. between 1970 and 2020 during the breeding and brood-rearing period (May 1–October 31). We considered observations with a spatial accuracy of ≤1 km, reflecting a resolution that provided a good compromise among the need for high accuracy, sample size limitations, a large spatial extent and the climatic and habitat data resolution (see Section 2.3). Occurrence locations were obtained from published sources (Boyle & Martin, 2015; Campbell et al., 1990a, 1990b; Campbell & Preston, 1970–2019; Davidson et al., 2015; Jackson et al., 2015a, 2015b), open-access community science platforms (eBird: Sullivan et al., 2009, iNaturalist: available from https://www.inaturalist.org, Xeno-canto: http://www.xeno-canto.org) and personal communications supported by photograph identification or provided by experienced naturalists. All community science data records were checked carefully for correct species identification via photographs provided. Records were excluded if we were in any doubt about the correct species identification. To control for sample selection bias, duplicate records were removed manually from the dataset when multiple observations occurred within the same spatial unit even if they occurred at different times (1km^2 grid resolution). The final dataset included 87 unique locations for rock, 133 for willow and 476 for white-tailed ptarmigan (see Tables S2–S4).

2.3 | Climate and environmental data

To assess current habitat suitability, we obtained 19 bioclimatic variables from the CHELSA data base (Karger et al., 2017, Table S5), representing mean temperature and precipitation patterns from 1979 to 2013. To reduce potential multicollinearity, we selected a priori seven temperature and three precipitation variables considered ecologically and biologically meaningful for ptarmigan. Mean annual temperature (BIO1), temperature seasonality (BIO4; standard deviation of the monthly mean temperatures), temperature annual range (BIO7), annual precipitation (BIO12) and precipitation seasonality (BIO15; standard deviation of the monthly precipitation estimates expressed as a percentage of the mean of those estimates) were considered representative of general climate patterns and likely to influence vegetation distributions (Brambilla et al., 2017; Kozma et al., 2018). Maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), mean temperature of the warmest quarter (BIO10) and mean temperature of the coldest quarter (BIO11) were considered important for defining physiological tolerance limits (Jackson et al., 2015a; Smith

et al., 2013). Lastly, precipitation of the warmest quarter (BIO8) and precipitation of the coldest quarter (BIO19) were considered critical for defining foraging conditions with potential effects on reproductive success (Barrio et al., 2017). For habitat predictors, data were available between 2001 and 2009 for the Biogeoclimatic Ecosystem Classification, which classifies B.C. into 13 zones (hereinafter "BEC zones," Table S5) including three alpine-specific subzones (Boreal Altai Fescue Alpine—BAFA, Coastal Mountain-Heather Alpine—CMA, Interior Mountain-Heather Alpine—IMA), representing natural vegetation in the province based on local climate and geology (Pojar et al., 1987; accessed: www.climatebc.ca). Projections of future BEC zones are also available (see below). Given the importance of topographic variables for mountain biota, we used a 50-m digital elevation model (U.S. Geological Survey; https://earthexplorer.usgs.gov/) to derive slope, topographic position index and average summer solar radiation via GRASS 7.04 (Neteler et al., 2012, Tables S5 and S7). Although the overlapping temporal frame of the climatic (1979–2013) and habitat datasets (2001–2009) does not perfectly match the time period of the occurrence dataset (1970–2020), we do not expect temporal bias in the predictions as a result because only 6% ($n = 51$) of the occurrence records were prior to 1979. Indeed, for the ptarmigan occurrence dataset, 36% ($n = 289$) of the total observations occurred between 1978 and 1999 and 58% ($n = 458$) after 2000.

To predict future habitat suitability, we used climate scenario datasets available from the CHELSA data base (Karger et al., 2017) and selected three uncorrelated models (CESM1 (BGC), ACCESS1.0 and MIROC5) following Sanderson et al., (2015) based on the representative concentration pathway (RCP) +8.5 W/m^2 scenario averaged across the years 2061–2081 (2070s). We selected the most pessimistic scenario because: (a) it best matches the future projections of our target BEC zones (2080s: 2071–2100), which average projections across 20 different emission scenarios producing an overall emission scenario between RCP +6.0 and +8.5 W/m^2 (Wang et al., 2012; dataset available at www.climatebc.ca), (b) observed emission from 2005 to 2020 matches the RCP +8.5 W/m^2 (Peters et al., 2013) and the probability of realizing this scenario during the remainder of the century is large enough to merit its continued use (Schwalm et al., 2020), and (c) for conservation purposes, using intermediate scenarios would lead to intermediate changes; considering a worst scenario within a set of realistic predictions enables us to test for the potential effectiveness of protected areas under the more extreme conditions. Therefore, we reasonably accounted for both direct (i.e. climate) and indirect (i.e. climate-induced habitat alterations) impacts of climate change on the potential future distribution of ptarmigan (hereinafter defined as the 2080s).

2.4 | Modelling potential current and future distributions

We produced correlative species distribution models using a maximum entropy approach (MAXENT version 3.4.4; Phillips & Dudik, 2008)

through R package "SDMtune" (version: 1.1.3; Vignali et al., 2019) and dependent packages (i.e. "dismo" version 1.3-3, Hijmans et al., 2020; "ENMeval" version: 0.3.1, Muscarella et al., 2014). Maxent is widely used for broad-scale species distribution modelling (Elith et al., 2006, 2011) and is relatively insensitive to small sample sizes (Phillips et al., 2006). We estimated environmental suitability for each species as a function of climate and habitat variables in a gridded domain at ~1 km resolution (0.0083°). For Maxent models, the method of background point selection is critical to reducing potential effects of sampling effort bias. Here, background locations were chosen in a way that: (a) matched available landscapes for each species, considering both potential dispersal and sampling efforts, and (b) had sample sizes of at least 10,000 points (Phillips et al., 2006). We balanced the number of points required for this process with the placement of background points within reasonable proximity to the observations. This increases the certainty that background points were likely accessible to observers and within the area of occurrence for each species. To accommodate enough background points, we created species-specific buffers with radii inversely proportional to sample size (3, 6 and 5 km radii for white-tailed, rock and willow ptarmigan, respectively). This resulted in 14,460 background points for white-tailed, 13,387 for rock and 13,450 for willow ptarmigan.

For each species, occurrence data were partitioned into two groups (testing and training) using the "checkerboard1" function in the package "ENMeval" (version: 0.3.1; Muscarella et al., 2014) with each of the checkerboard units aggregating four original 1 km^2 cells. Considering the high heterogeneity and the broad environmental gradients of B.C., such a checkerboard subdivision at a rather fine scale is a compromise between each data partition being representative and spatial independence between the testing and training data. To limit the risk of overfitting, we considered linear and quadratic features only. We reduced model complexity and collinearity by applying two functions ("varSel" and "reduceVar") within "SDMtune" (Vignali et al., 2019) which removed highly correlated variables ($r_p > .7$) and variables with low importance (contribution <1%). After this, we tested different values of the regularization multiplier, training each model with 50 different values between 0.1 and 5 at 0.1 incremental steps. We selected the regularization multiplier resulting in the model with the highest test True Skill Statistic (TSS; Allouche et al., 2006) among those with a TSS difference (training – testing) lower than ±0.05.

To assess the relative importance of predictors in the final model, a leave-one-out jackknife procedure was applied, omitting each variable in turn and calculating the difference in TSS. Model accuracy was assessed comparing the area under the curve (AUC) of a receiver operating characteristic (ROC) and via TSS values estimated from the evaluation datasets. Models with AUC <0.60 or TSS <0.10 were considered no better than random. The final logistic (*cloglog*; complementary log-log) output of the model was then reclassified into a binary occurrence map using either the "maximum training sensitivity plus specificity" (MTSS) or the 10th percentile training presence threshold (Liu et al., 2013) according to the biological reliability of the reclassified output. The 10th percentile training

TABLE 1 Climate, habitat and topographic variables selected in the final models for each species (see Table S2 for full list of variables), with relative variable importance (%) and standard deviation (in brackets)

Variable type	Variable	White-tailed ptarmigan	Rock ptarmigan	Willow ptarmigan
Climate	Annual mean temperature (BIO1)			16.8 (0.02)+/−
Climate	Temperature seasonality (BIO4)			2.2 (0.01) +
Climate	Mean temperature of warmest quarter (BIO10)	43.8 (0.02)+/−	34.9 (0.03)+/−	
Climate	Mean temperature of coldest quarter (BIO11)		19.3 (0.01) +	
Climate	Annual precipitation (BIO12)		1.4 (0.005) -	
Climate	Precipitation of warmest quarter (BIO 18)		6.5 (0.01) +	19.5 (0.01)−/+
Climate	Precipitation of coldest quarter (BIO19)	34.5 (0.01)+/−		
Habitat	Boreal Altai Fescue Alpine (BAFA)		6.8 (0.01) +	23.1 (0.01) +
Habitat	Boreal White and Black Spruce (BWBS)			1.5 (0.005)0
Habitat	Coastal Mountain-Heather Alpine (CMA)			
Habitat	Coastal Western Hemlock (CWH)	4.2 (0.01)−		
Habitat	Engelmann Spruce-Subalpine fir (ESSF)	3.2 (0.004) +		7.5 (0.02)+
Habitat	Interior Cedar Hemlock (ICH)			1.6 (0.004)+
Habitat	Sub Boreal Spruce (SBS)			1.1 (0.004)+
Habitat	Spruce-Willow-Birch (SWB)			11.5 (0.01)+
Topography	Slope	9.9 (0.01)−	8.2 (0.01)−	15 (0.02)−
Topography	Solar radiation		4.2 (0.01)−	
Topography	Topographic position index (tpi)	4.4 (0.005)+	18.4 (0.02)−/+	

Note: The shape of the relationship is reported as: + (positive), −(negative), +/− (downward quadratic), −/+ (upward quadratic), +/−− (downward quadratic/negative), ++/− (downward quadratic/positive) and 0 (weak positive effect). Plots of species climate and environment relationships are shown in Figures S1, S3 and S5.

presence *cloglog* threshold was selected for all species because it (a) led to realistic binary predictions based on current knowledge of species distributions in B.C. and (b) had test omission rates closer to expected values (Muscarella et al., 2014). Predicted occurrence for each species was overlaid to calculate range overlap using the function *r.mapcalc* in GRASS 7.04. We then calculated the proportion of overlapping habitat among species by dividing by the largest species range, after accounting for latitudinal changes in pixel size (i.e. larger pixels in the north).

Prior to calculations, current and future suitability for rock and willow ptarmigan on Haida Gwaii and Vancouver Island were set to zero as there are no ptarmigan records for these two species in the past century. Future predictions of habitat suitability for each species were made by re-projecting the current bioclimatic environments into the future (i.e. future climate and BEC habitat data, while keeping topographic variables constant) and by reclassifying the output according to the same 10th percentile training presence thresholds established for the current scenario. To assess the efficacy of protected areas (PAs) for conserving *Lagopus* species under a changing climate, we compared the absolute and proportional range sizes of suitable ptarmigan habitat inside and outside PAs for both current and future scenarios. We used a standardized layer provided by the *World Database on Protected Areas* (www.protectedp lanet.net) and considered all terrestrial PAs in B.C. (*n* = 1,035) holding an international (*n* = 6) or national designation (IUCN category

I to VI; *n* = 1,029; Table S6). These terrestrial PAs cover a total of 146,069.3 km² (ca15% of terrestrial B.C.), of which 85,740.15 km² (ca59% of PAs) occur above 1,000 m a.s.l.

The ODMAP protocol of the modelling process following Zurell et al. (2020) is provided in Table S7.

3 | RESULTS

3.1 | Predicted current distributions and species overlap

From 1970 to 2020, breeding season observations occurred within 1 km² pixels representing 476 km² for white-tailed, 87 km² for rock and 133 km² for willow ptarmigan. Values of model performance over the test dataset ranged from 0.7 to 0.79 AUC and 0.33 to 0.45 TSS. Variation across partitions was limited (AUC_{diff} = 0.01–0.10, TSS_{diff} = 0.02–0.11) suggesting limited issues with overfitting, while omission rates over the test dataset were close to expected values indicating good prediction accuracy (10th percentile threshold omission rates = 0.07–0.24; Table S8; Brambilla, Gustin, et al., 2020; Brambilla, Scridel, et al., 2020; Muscarella et al., 2014). For rock ptarmigan, the lower sample size produced some potential signals of overfitting, such as slightly larger differences in AUC and TSS between testing and training datasets and larger omission rates.

However, prediction reliability was confirmed by the species–habitat relationships (Table 1; Figure S3), which were in agreement with the known ecology of rock ptarmigan in B.C. (Wilson & Martin, 2008), while the predicted current distribution matched well with the known species distribution (c.f. Davidson et al., 2015).

Variable importance suggested that temperature, precipitation, habitat and topographic variables were all important in defining the potential distribution of white-tailed, rock and willow ptarmigan (Table 1). All species displayed a quadratic or positive relationship with temperature variables (white-tailed ptarmigan: mean temperature of warmest quarter; rock ptarmigan: mean temperature of warmest and coldest quarter; willow ptarmigan: annual mean temperature), with the highest suitability being a few degrees above or below 0°C (Figures S1, S3 and S5). White-tailed and rock ptarmigan had a positive relationship with precipitation during the warmest and coldest quarter, respectively, while willow ptarmigan had a U-shaped relationship with the precipitation of warmest quarter. Rock and willow ptarmigan were positively associated with open habitats such as BAFA, but willow ptarmigan was also associated with tree line habitats such as Engelmann Spruce-Subalpine Fir (ESSF), Spruce-Willow-Birch (SWB), and less so with Interior Cedar Hemlock (ICH) and Sub Boreal Spruce (SBS). White-tailed ptarmigan had a limited preference for ESSF and was negatively associated with Coastal Western Hemlock (CWH). Habitat suitability for all species declined with steeper topography, while the topographic position index and slope were important in defining the potential distribution of white-tailed and rock ptarmigan.

According to our model predictions, white-tailed ptarmigan is the most widely distributed (19.9% of B.C.), compared to rock (16.3%) and willow ptarmigan (16.3%). On average, range suitability for white-tailed ptarmigan is predicted to be at higher elevations than rock or willow ptarmigan (Table 2). In B.C., willow ptarmigan was associated with the highest mean latitude, followed by rock and white-tailed ptarmigan (Table 2). Only 6.7% of B.C. (63,658.7 km²) was predicted to be occupied by all three species. Out of all combinations, white-tailed and rock ptarmigan were predicted to share the most suitable habitat: 68.6% of current rock ptarmigan range overlapped with white-tailed ptarmigan, followed by 50.1% for willow and white-tailed ptarmigan, and 44.8% for willow and rock ptarmigan (i.e. calculated as overlapping area/range of the more widely distributed species).

3.2 | Future distribution

While accordance among suitable areas (i.e. overlapping suitable pixels) for the three future uncorrelated models considered was limited (53% for white-tailed, 61% for rock and 52% for willow ptarmigan), agreement among model predictions highlighted similar suitability in general mountain regions (e.g. western Coast Mountains, interior Cassiar Mountains, eastern Canadian Rockies), confirming the robustness of our results with respect to different future climate assumptions. Models incorporating climate and vegetation for the

TABLE 2 Summary statistics of potential range size (km²), elevation (m) and latitude (°) under current and future modelled scenarios for each of the three ptarmigan species ("single species") and their combination ("co-occurrence")

Species	Mean elevation (m)—Current	Mean elevation (m)—2080s	Mean change in elevation (m)	Mean latitude (°)—Current	Mean latitude (°)—2080s	Mean change in latitude (°)	Suitable range (km²)—Current	Mean range (km²)—2080s (CESM1-BGC, ACCESS 1.0, MIROC5)	Mean range change %
Single species									
White-tailed ptarmigan	1,652 (0.59)	1,906 (31.77)	254 (31.77)	55.27 (0.005)	56.38 (0.41)	1.11 (0.41)	188,049.30	27,119.37 (3,952.93)	**−85.58% (2.57)**
Rock ptarmigan	1,598 (0.74)	1,841 (26.74)	242 (26.74)	55.62 (0.005)	56.83 (0.43)	1.2 (0.43)	154,046.30	31,602.99 (3,263.28)	**−79.48% (2.12)**
Willow ptarmigan	1,438 (0.51)	1,692 (30.4)	254 (30.4)	56.46 (0.005)	57.63 (0.04)	1.17 (0.04)	153,527.50	59,359.54 (10,025.26)	**−61.34% (6.51)**
Co-occurrence									
White-tailed +rock ptarmigan	1,662 (0.69)	1,892 (35.68)	230 (35.68)	55.55 (0.005)	56.7 (0.47)	1.15 (0.47)	128,935.10	21,046.52 (2,588.43)	**−83.68% (2.01)**
Rock +willow ptarmigan	1,621 (0.77)	1,914 (39.93)	293 (39.94)	56.28 (0.007)	58.09 (0.2)	1.81 (0.2)	68,996.85	13,028.07 (1,124.36)	**−81.12% (0.87)**
White-tailed +willow ptarmigan	1,626 (0.66)	1,945 (46.26)	319 (46.26)	55.95 (0.006)	57.73 (0.35)	1.78 (0.35)	94,186.65	10,472.36 (2,052.47)	**−88.88% (1.59)**
White-tailed +rock + willow ptarmigan	1,641 (0.79)	1,925 (54.96)	284 (54.96)	56.15 (0.007)	57.96 (0.30)	1.81 (0.3)	63,658.67	8,587.08 (1,302.47)	**−86.51% (1.01)**

Note: Future ranges (2080s) consider one habitat and three different climatic projections (CESM1-BGC, ACCESS 1.0, MIROC5; Table S8). Average change in elevation, latitude and range size between present and future predictions are included in bold with standard error in brackets.

2080s RCP 8.5 predicted that all species will experience a drastic reduction of their current potential range sizes (Tables 2, S8, and S9; Figures 1–4, S7–S9). White-tailed (Figure 1) and rock ptarmigan (Figure 2) are predicted to lose 85.6% (SE = 2.57) and 79.5% (SE = 2.12), of their current suitable habitat, respectively, while the range of willow ptarmigan (Figure 3) is predicted to contract by 61.3% (SE = 6.51; Table 2). About 50% (30,297.4 km^2) of willow ptarmigan future range occurs in areas currently considered unsuitable (i.e. gain in distribution), while for rock and white-tailed ptarmigan newly colonized areas represented a much lower proportion of potential future suitable habitats (12%, 3,781.8 km^2 and 13.8%, 3,738.64 km^2, respectively). For all species, predicted suitable climatic and habitat conditions persisted at or shifted to higher elevations and latitudes, with a predicted shift of 242–254 m upslope and 1.1–1.2° northwards (Table 3). For areas of sympatric co-occurrence, the most drastic declines in range overlap were predicted for willow and white-tailed ptarmigan (Table 2; Figure S8), followed by suitable areas where all three species could co-occur (Figure S10),

and then overlap of rock and white-tailed ptarmigan (Figure S7) and overlap of rock and willow ptarmigan (Figure S8). Similarly, by 2080s, co-occurrences are projected to occur at higher elevations (+230–319 m depending on the species combination) and higher latitudes (+1.1–1.8° northwards; Table 2). Range overlaps will decrease for all species combinations, with the exception of that between white-tailed and rock ptarmigan, which is predicted to increase from 69% to 78% of the area suitable for the former species (Table S11).

3.3 | Current and future suitable habitat in protected areas (PAs)

The current and future range for each ptarmigan species and their co-occurrences occurred mostly outside of PAs (i.e. 76%–82% of present suitable habitat is unprotected), with predicted strong declines in range sizes both inside and outside PAs (Tables 3 and S10). Range size declines were predicted to be less dramatic inside PAs
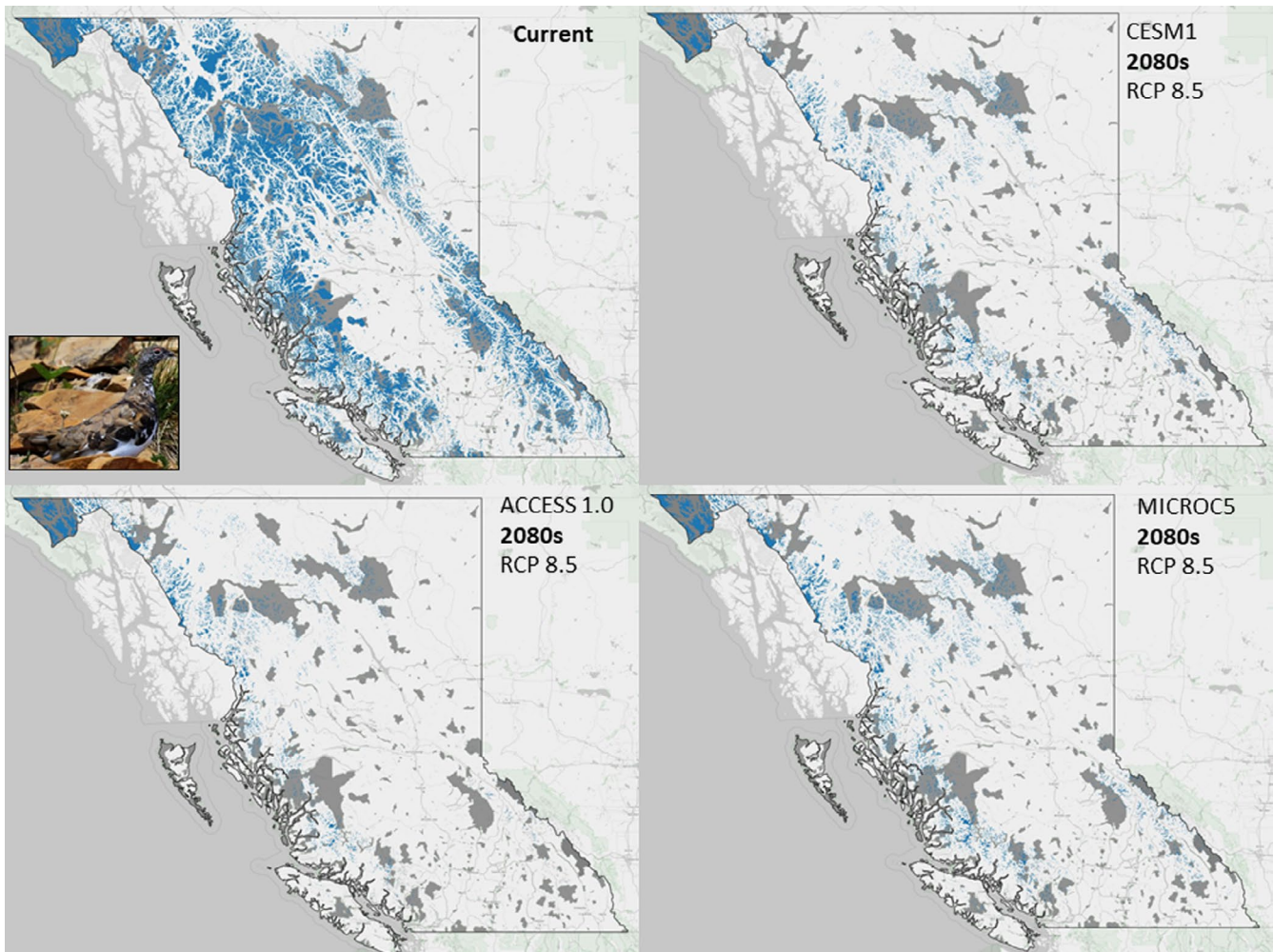

FIGURE 1 Modelled potential distributions of white-tailed ptarmigan in B.C. for current (top-left) and future scenarios (2080s) according to habitat and various climatic projections (top right: CESM1-BGC; bottom left ACCESS 1.0; bottom right: MIROC5) for RCP 8.5. Suitability according to the 10th percentile training presence cloglog threshold is depicted in blue, while dark grey polygons outline PA boundaries. Future models highlighted similar suitable areas with most resilient locations being in the western Coast Mountains, interior Cassiar Mountains and eastern Canadian Rockies. © OpenStreetMap contributors
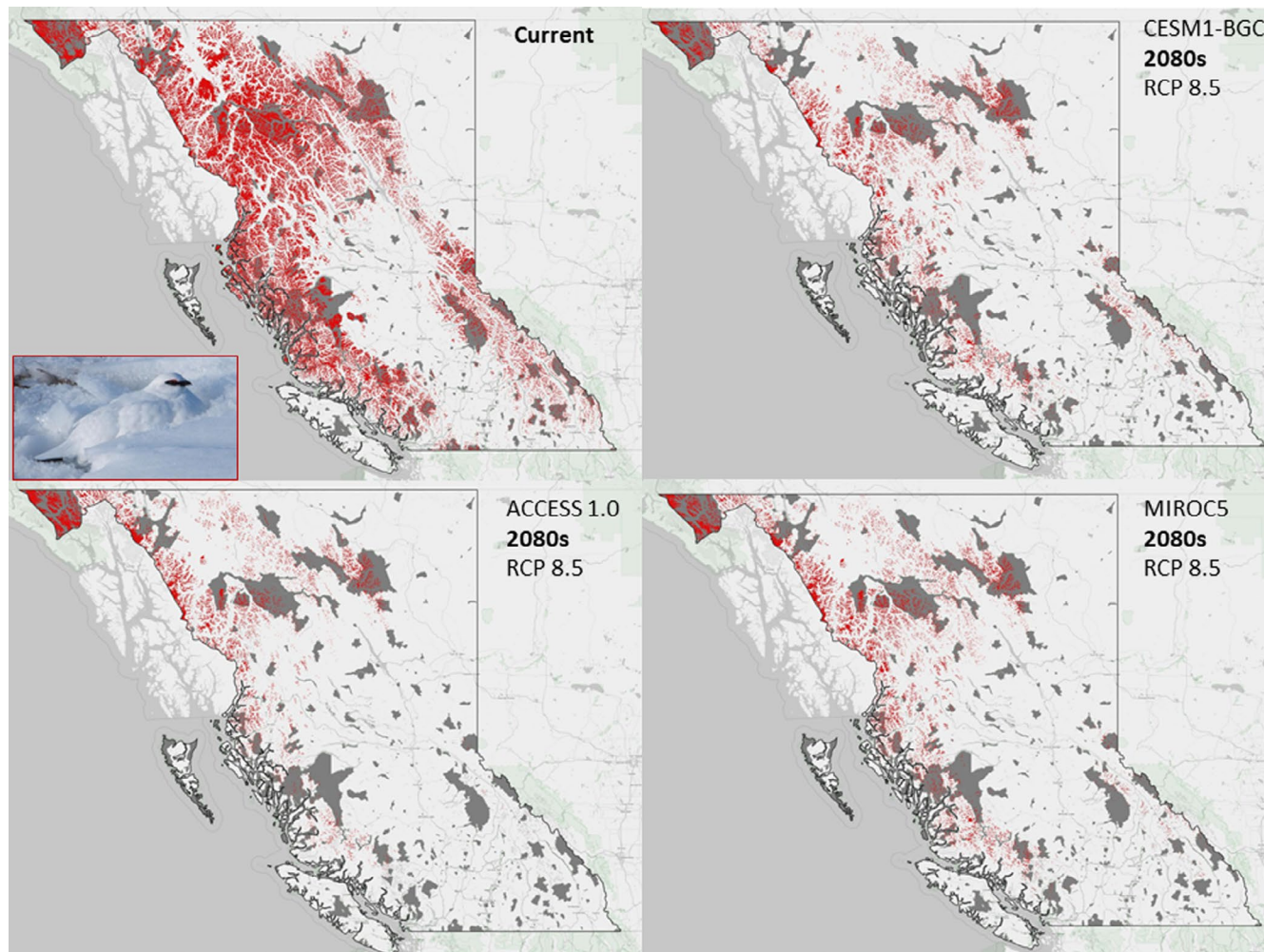
FIGURE 2 Modelled potential distribution of rock ptarmigan in B.C. for current (top-left) and future scenarios (2080s) under habitat and various climatic projections (top right: CESM1-BGC; bottom left ACCESS 1.0; bottom right: MIROC5) for RCP 8.5. Suitability according to the 10th percentile training presence cloglog threshold is depicted in red, while dark grey polygons outline PAs. Future models highlighted similar suitable areas with most resilient locations being in the western Coast Mountains, interior Cassiar Mountains and eastern Canadian Rockies. © OpenStreetMap contributors

such that the relative proportion of suitable habitats in PAs is expected to increase for all species. For all species, the suitable range was predicted to decline more severely outside PAs than inside and suitable range overlap between co-occurring ptarmigan species followed a similar pattern (Table 3).

4 | DISCUSSION

We provide the first comparison of potential climate change impacts on the current and future range distributions of the entire *Lagopus* genus, three flagship species representatives of high-elevation and high-latitude habitats that differ in their life-history traits and ecological requisites. The species–habitat associations and the predicted current distributions matched well with known habitat preferences and distributions of ptarmigan in B.C., one of the few regions globally that supports all *Lagopus* species. Habitat suitability of all *Lagopus* species was predicted to decline precipitously (61.3%–86.6%) by the

2080s due to changing climate and vegetation. Altered distributions under climatic change suggest a shift towards higher elevation and more northern latitudes, with white-tailed and rock ptarmigan that currently inhabit higher elevations predicted to experience greater habitat loss than willow ptarmigan. In contrast, willow ptarmigan will potentially gain some habitat through the effects of "shrubification" (i.e. advancing tree line) which may partially mitigate some of the predicted habitat loss for this species. Finally, while current suitable ptarmigan habitat predominantly exists outside protected area (PA) boundaries, we highlight the potential importance of PAs in buffering future range size declines. Due to their climate sensitivity and strong association with high-elevation and high-latitude habitats, our results highlight a role for ptarmigan as potential "sentinel" species, providing advanced warning of climate change effects where mitigation actions could benefit conservation of mountain biodiversity. While our predictions of future ptarmigan distribution may overestimate range declines if current greenhouse gas emissions are significantly reduced below the RCP 8.5 scenario, given current
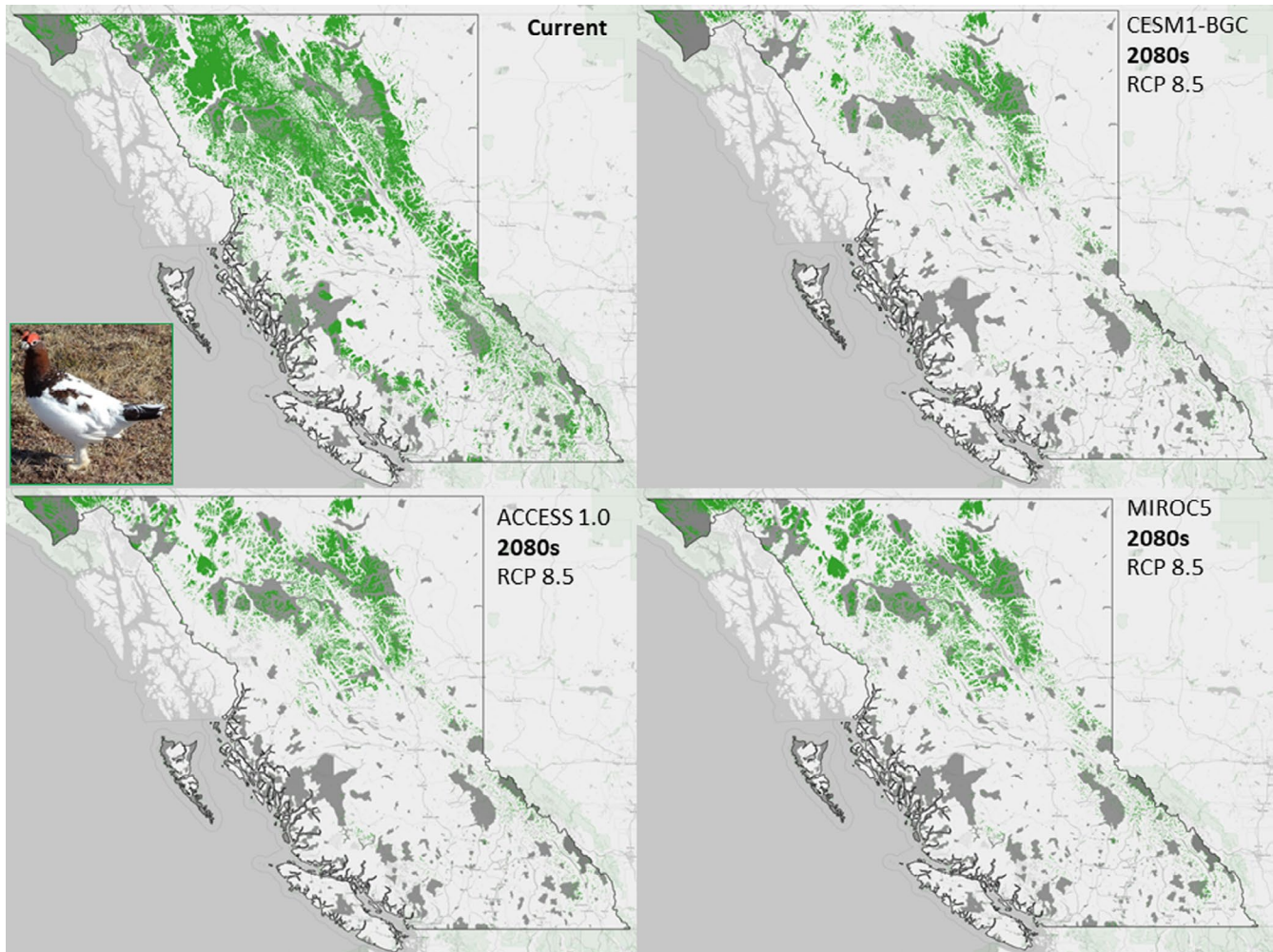
FIGURE 3 Modelled potential distribution of willow ptarmigan in B.C. for current (top-left) and future scenarios (2080s) under habitat and various climatic projections (top right: CESM1-BGC; bottom left ACCESS 1.0; bottom right: MIROC5). Suitability according to the 10th percentile training presence cloglog threshold is depicted in green, while dark grey polygons outline PAs. Future models highlighted similar suitable areas with most resilient locations being in the higher latitude Cassiar Mountains and to the east (Canadian Rockies). © OpenStreetMap contributors

trends our results highlight severe range declines for the *Lagopus* genus in the coming decades.

4.1 | Environmental correlates of species occurrence and overlap

The climatic, topographic and habitat associations we identified for breeding ptarmigan were generally consistent with findings from other geographic regions. As expected, all ptarmigan species were associated with high-elevation habitats (>1,400 m), complex topography (e.g. slopes, ridges, plateaus; see TPI and slope values), cooler breeding season temperatures (mean = −5 to 15°C) and variable temperature regimes (i.e. high temperature seasonality). Consistent with these results, ptarmigan are cold-adapted species with broods that can cope with subfreezing temperature (−5°C; Wiebe & Martin, 1998) but exhibit an upper thermal physiological limit above 21°C (Glutz von Blotzheim et al., 1973; Johnson, 1968).

White-tailed and rock ptarmigan selected similar environments, characterized by cold temperatures and high elevations (>1,500 m). Rock ptarmigan were positively associated with tundra meadow habitats (i.e. BAFA), but at slightly lower predicted elevations than white-tailed ptarmigan. This agrees with research at a finer spatial scale on sympatric populations in the Yukon Territory where white-tailed ptarmigan selected steeper breeding sites located at higher elevations with dominant rock and lichens ground cover, while rock ptarmigan occupied habitats with greater graminoid cover interspersed with woody shrubs and heather (Wilson & Martin, 2008). For example, these species display interspecific territoriality and may segregate based on shared habitats and diet (Wilson & Martin, 2008).

Our habitat suitability models indicated that willow ptarmigan was associated positively with BAFA, ESSF and SWB habitats and occupied lower elevation habitats than rock and white-tailed ptarmigan. This is consistent with studies suggesting preference for woody shrubs mixed with open patches of graminoids, heather and small
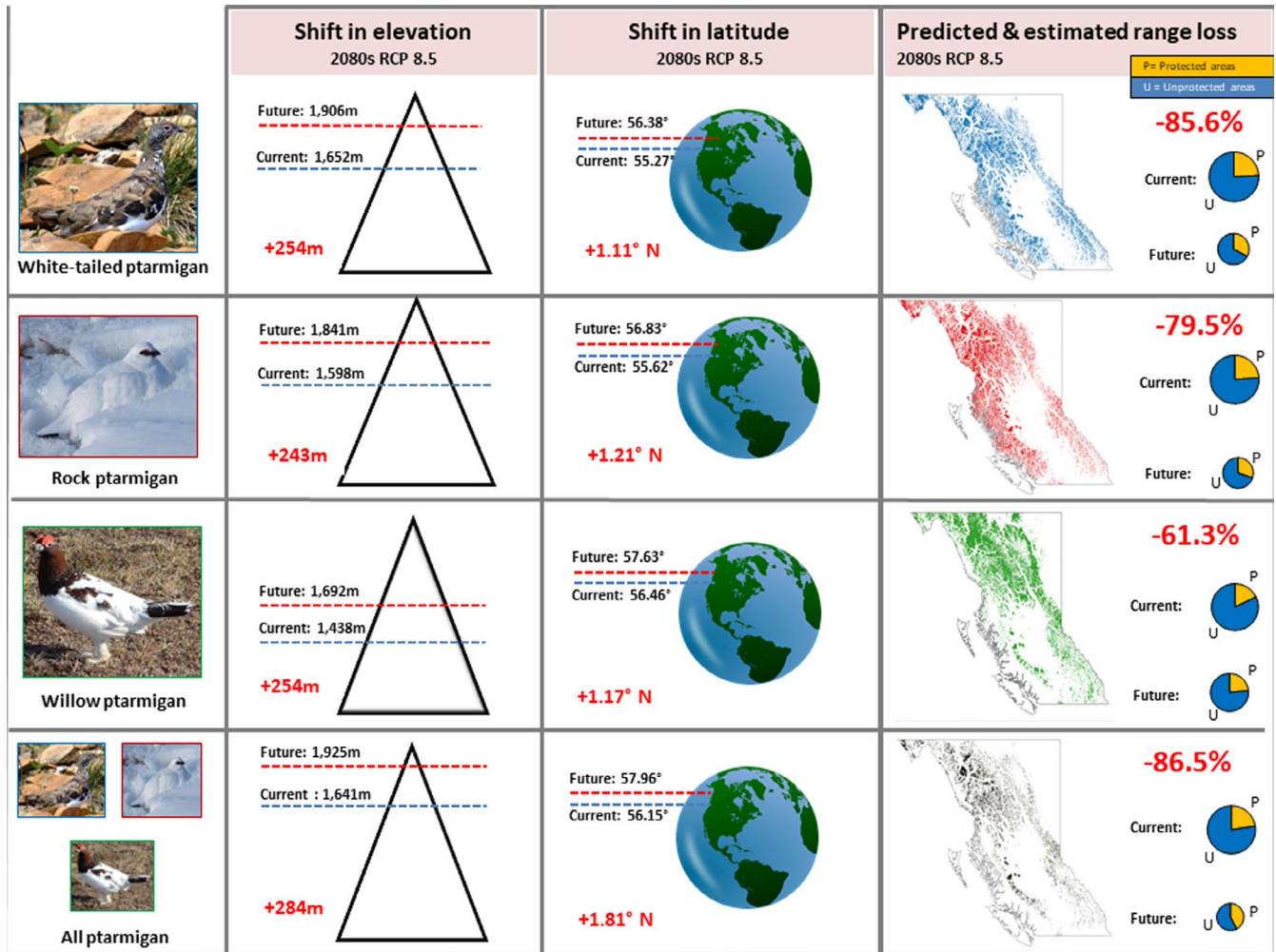
FIGURE 4 Summary of average current and future predictions for shifts in elevation, latitude and range size for the genus *Lagopus* in BC. Current and future potential range losses are shown with respect to protected (P) and unprotected areas (U) with size of pie charts being proportional to the relative value of current and future species' range

wetlands (Ehrich et al., 2012; Wilson & Martin, 2008). On average, willow ptarmigan also had greater suitability at high latitudes where many occurrence records for this species came from subalpine habitat dominated by willow (*Salix* spp.) and birch (*Betula* spp.) present at relatively low elevation (e.g. ~800 m, Hannon et al., 2020). Such patterns contrast with the potential distribution of rock and white-tailed ptarmigan, at least at the range of latitudes represented in B.C. where the latter are largely confined to the highest elevations.

4.2 | Predicted impacts of climate change: is the future already here?

By the 2080s, according to the future emission scenario considered, annual mean temperature is predicted to increase in B.C. by 3.96°C (*SE* = 0.21), while mean annual precipitation will increase by 60.63 mm (*SE* = 20.05). A warmer, wetter climate and associated vegetation change will lead to a strong decline in suitable habitat for all ptarmigan species. Warmer temperatures have been linked to upshifts in elevational range; however, species occurring on

mountaintops are likely to be more at risk of extinction than species at low elevations due to acute range restriction (Maggini et al., 2014; Rangwala & Miller, 2012; Tingley et al., 2012). As expected, model predictions suggest white-tailed ptarmigan, the species located at the highest elevations on average, will lose the greatest proportion of currently suitable habitat (−85.8%), followed by rock (−79.5%) and willow ptarmigan (−61.3%). Strikingly, observed records (1970–2020) for rock and willow ptarmigan (Figures S4 and S6) were better represented by potential future than current distributions based on visual comparison between predictions and observed records (Figures 2 and 3). This pattern could suggest that range shifts for both species may have already occurred in response to climatic alterations. This phenomenon has been suggested for other taxa (Archis et al., 2018) and is emblematic of a "sentinel" species, indicating a distributional change prior to shifts in habitat availability. While we cannot rule out factors alternative to breeding climate, such as non-breeding conditions, dispersal limitations or interspecific competition dynamics, current range restrictions highlight that ptarmigan populations in B.C. are potentially more vulnerable to future change than expected.

TABLE 3 Proportion (%) and range size (km²) of potential suitable habitat for ptarmigan within protected (PAs) and in unprotected areas (UPAs) in B.C. under the current and future scenarios (2080s) according to three different climatic projections (CESM1-BGC, ACCESS 1.0 and MIROC5; Table S9)

Species	Current suitable range in PAs	Current suitable range in UPAs	Suitable range in PAs—2080s (CESM1-BGC, ACCESS 1.0, MIROC5)	Suitable range in UPAs—2080s (CESM1-BGC, ACCESS 1.0, MIROC5)	Change in range size in PAs	Change in range size outside PAs
Single species						
White-tailed ptarmigan	24.14% (45,397.08 km²)	75.86% (142,652.22 km²)	32.87% (8,914.756 km²)	67.13% (18,204.62 km²)	−80.36% (2.12)	−87.24% (2.10)
Rock ptarmigan	23.82% (36,691.89 km²)	76.18% (117,354.41 km²)	30.22% (9,549.71 km²)	69.78% (22,053.28 km²)	−73.97% (1.56)	−81.21% (2.29)
Willow ptarmigan	17.86% (27,415.22 km²)	82.14% (126,112.28 km²)	23.45% (13,918.31 km²)	76.55% (45,441.22 km²)	−49.23% (7.54)	−63.97% (6.34)
Co-occurrence						
White-tailed +Rock ptarmigan	23.99% (30,936.16 km²)	76.01% (97,998.94 km²)	32.5% (6,840.59 km²)	67.5% (14,205.92 km²)	−77.89% (1.55)	−85.5% (2.16)
Rock +willow ptarmigan	22.88% (15,787.13 km²)	77.12% (53,209.72 km²)	37.86% (4,931.83 km²)	62.14% (80,96.24 km²)	−68.76% (2.56)	−84.78% (1.57)
White-tailed and willow ptarmigan	21.62% (20,364.33 km²)	78.38% (73,822.32 km²)	39.98% (4,186.38 km²)	60.02% (6,285.98 km²)	−79.44% (2.95)	−91.48% (2.05)
White-tailed +rock + willow ptarmigan	22.58% (14,373.04 km²)	77.42% (49,285.63 km²)	42.26% (3,628.69 km²)	57.74% (4,958.39 km²)	−74.75% (2.84)	−89.94% (1.99)

Note: Average changes in range size are included with standard errors in brackets. Bold values represent proportional changes (%) of suitable habitat inside and outside PAs.

Heterogeneous responses to climatic variation may also be driven by differences in BEC zones associated with each species. White-tailed and rock ptarmigan are associated with open alpine and Arctic tundra, habitats subject to rapid shrub and tree encroachment in response to climatic warming (i.e. Mountain Hemlock *Tsuga mertensiana*, Coastal Western Hemlock BEC zones, Douglas Fir *Pseudotsuga menziesii* and spruce *Picea spp*; Flower et al., 2013, Jackson et al., 2016). In B.C., high-elevation (BAFA, IMA and Mountain Spruce—MS) and sub-boreal ecosystems (Sub-boreal Pine Spruce—SBPS, SBS and SWB) are the most vulnerable to climate change, with over 80% of the area covered by their climate envelopes projected to be lost by the end of the century (Wang et al., 2012). Additionally, 23% of the geographic area in B.C. has already shifted to climate characteristic of different ecosystem zones (Wang et al., 2012). In our study, willow ptarmigan was forecasted to lose less suitable range than the other two species. Indeed, about 50% of the projected future range for willow ptarmigan occurs in areas currently considered unsuitable. A warmer, wetter climatic may favour the persistence and formation of highly suitable small wetlands (i.e. bogs, mires). Furthermore, the establishment of newly suitable habitats in former open tundra may support the resilience of this species, particularly at higher elevations and latitudes. Despite predicted declines of 44% and 33% in SWB and ESSF across B.C., respectively, these BEC zones are also projected to colonize new areas (+14% and +41%; Wang et al., 2012).

Our estimates of range losses in B.C. align with predicted climate sensitivity of ptarmigan across the globe: rock and/or willow ptarmigan in the European Alps (Brambilla et al., 2017; Revermann et al., 2012), in Fennoscandia and Russia (Virkkala et al., 2008), and Japan (Hotta et al., 2019), as well as global distributions (La Sorte & Jetz, 2010; Lagerholm et al., 2017; Table S1). While future projections for white-tailed ptarmigan are limited (Table S1), our results match those of Jackson et al. (2015a), who forecasted that Vancouver Island white-tailed ptarmigan (*L. l. saxatilis*), a threatened subspecies in B.C. (Campbell et al., 1990b; McTaggart-Cowan, 1939), will lose 74% of its current suitable habitat by the 2080s. Displacements of ptarmigan towards higher elevation and latitudes to track suitable climate and habitat have been observed in Europe, with an annual upward shift of rock ptarmigan between 1.5 and 9.4 m in the Swiss Alps (Pernollet et al., 2015). These estimates align with our projections of +242 m by the 2080s (~4 m upward shift/year). Similarly, Virkkala and Lehikoinen (2017) calculated a poleward shift in willow ptarmigan distribution of 145 km between 1974 and 1989 and 2006 and 2010, consistent with our projection of a northward shift of 1.2° (ca130 km) by the 2080s.

We projected a greater than 80% reduction for all combinations of sympatric occurrences between ptarmigan species with future suitable areas located at higher elevations and latitudes. The percentage of range overlap among species also decreased for all species pairs except for white-tailed and rock ptarmigan with a projected increase of 9% (Table S11). Given limited ecological knowledge of species interactions for the genus *Lagopus*, consequences of changing co-occurrence patterns are unclear (Parr et al., 1993). However,

occasional records of interspecific behaviours among these species in the form of resource competition, territoriality and hybridization indicate interspecific competition could partly influence range dynamics (Martin et al., 2020; Montgomerie & Holder, 2020). Additionally, while we could not account for the distribution of food resources or predators (e.g. gyrfalcon *Falco rusticolus*, fox *Vulpes vulpes*, coyote *Canis latrans*), changes in food availability and predator ranges can also significantly impact ptarmigan recruitment and habitat suitability (Bowler et al., 2020; Fuglei et al., 2020).

4.3 | Protected area (PA) effectiveness for ptarmigan facing climate change

Greater than 70% of the predicted current range of ptarmigan in B.C. occurs outside PAs. Being unprotected, these sites are more likely to be exposed to additional stressors such as hunting, mining and leisure activities. While we projected future range sizes will decline steeply overall, the estimated decline was steeper in unprotected PAs (UPAs) than PAs for all species. Protected areas have been associated with buffered declines for other climate-sensitive species, with the underlying mechanisms usually complex and difficult to isolate (Gaüzère et al., 2016; Lehikoinen, Santangeli, et al., 2019). Potentially by preserving intact habitats, PAs may maintain a greater diversity of microhabitats that allow species to adjust to temperature variations (Gaüzère et al., 2016). The less drastic habitat loss inside PAs for ptarmigan may be explained by geography, as 59% of PAs in B.C. are located above 1,000 m elevation, covering mountainous habitats that may partially accommodate ptarmigan shifts to higher elevations. Despite PAs accounting for a relatively small proportion of suitable habitat, PAs at higher latitudes and elevations will remain a stronghold for ptarmigan in future and most likely for communities of cold-dwelling wildlife in general.

4.4 | Caveats and limitations

We developed robust models by working with avian species within accessible areas, balancing model performance and quality and minimizing potential for overfitting (cf. Peterson et al., 2018), by considering different types of environmental predictors of species occurrence (cf. Brambilla, Gustin, et al., 2020; Brambilla, Scridel, et al., 2020). Nevertheless, we acknowledge that forecasting future distributions has some unavoidable potential weaknesses that should be considered when interpreting outputs (Peterson et al., 2018), especially for planning purposes. Maxent assumes that sampling is either random or representative throughout a landscape (Yackulic et al., 2013). Some of our standardized data might meet these requirements (e.g. Breeding Birds Atlas), but others may not (e.g. observations occurring in areas where actual sampling is limited by accessibility). Our models did not account for detectability as repeated surveys to high-elevation sites were limited; however, we worked with three open habitat birds, likely subject to comparable

detection functions, and we restricted background to sites close to observations to ensure that they match well with the actual sampled conditions.

To best match the time period of the climatic and habitat datasets, we modelled future ptarmigan suitable habitat based on only one pessimistic climatic scenario that might not occur in the future. This could reduce our ability to estimate uncertainty in future projections, but using less extreme scenarios would result in an intermediate distribution pattern between the current and future distribution forecast according to the pessimistic scenario adopted.

Finally, we could not use a number of observations from community science platforms for modelling because of poor spatial accuracy (>1 km). This primarily occurred when lists (i.e. eBird lists) encompassed long hikes that often started below the alpine zone with records that were georeferenced at the start of the walk rather than at the location of the detection. Given the importance of high spatial accuracy for modelling mountain birds, we encourage community scientists to submit avian observations as accurate as possible (e.g. routes <500 m) to maximize the value of these limited detection data for scientific purposes.

5 | CONCLUSION

We highlight the sensitivity of the genus *Lagopus* to future climatic alterations. Climate sensitivity, coupled with close associations with tundra habitat, supports the genus *Lagopus* as a charismatic indicator of climate change effects and an umbrella species for the wider tundra specialist wildlife community. In addition to demonstrating the sensitivity of ptarmigan to climate change, we also emphasize the general paucity of observations for high-elevation species in western Canada which limits our understanding of their distributions, unfortunately consistent with the general lack of information for high-elevation birds from other parts of the Holarctic (Scridel et al., 2018). Despite extensive searches for records over a 50-year period (1970–2020), observations for willow and rock ptarmigan were severely limited, contrasting with the modelled current suitable habitat and the extensive observed distribution of the ecologically similar white-tailed ptarmigan (Figure S2). We identified a large area of suitable habitat for ptarmigan which has never been subject to formal bird surveys. We strongly recommend targeted mountain bird monitoring schemes and community science calls (e.g. eBird) to build basic distributional knowledge of mountain birds at both local and regional scales before extensive change occurs.

Projecting habitat suitability scenarios are valuable for identifying hotspot areas for future PAs and the importance of existing PAs under climate-induced habitat change. In Europe, there is considerable evidence that willow and rock ptarmigan can be impacted by hunting and leisure activities such as hiking and skiing (Arlettaz et al., 2007; Imperio et al., 2013; Sandercock et al., 2011; Watson & Moss, 2004). In B.C., the negative effects of these stressors are likely to be spatially limited given the low human population density coupled with vast remote areas of high-quality alpine habitats

(111,189 km^2; ca12% of B.C.). Additionally, in BC, there is a wide selection of larger and more accessible game species for hunters, while air-supported recreational activities remain local and low intensity. This suggests that climate change is likely to be the main potential threat for ptarmigan in B.C. and northwestern America in general. We highlighted that range declines are less steep within PAs, confirming the conservation value of PAs for high-elevation habitats despite their limited coverage. Expanded, well-connected PAs will limit the potential impacts of human-related activities described above while also potentially buffering the effects of climate change on ptarmigan and the larger community of cold-adapted wildlife species (Lehikoinen, Santangeli, et al., 2019).

CONFLICT OF INTEREST

The authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest (such as honoraria; educational grants; participation in speakers' bureaus; membership, employment, consultancies, stock ownership or other equity interest; and expert testimony or patent-licensing arrangements), or non-financial interest (such as personal or professional relationships, affiliations, knowledge or beliefs) in the subject matter or materials discussed in this manuscript.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13366.

DATA AVAILABILITY STATEMENT

Data on species occurrences were obtained from various sources. Cleaned and thinned species occurrence data used for modelling can be found at alongside information of where each datapoint was obtain

(WTPT: https://doi.org/10.6084/m9.figshare.14546196.v1; WIPT: https://doi.org/10.6084/m9.figshare.14546184.v1; ROPT: https://doi.org/10.6084/m9.figshare.14546178.v1). To maximize repeatability, background data (WTPT https://doi.org/10.6084/m9.figshare.14546169.v1; WIPT: https://doi.org/10.6084/m9.figshare.14546166.v1; ROPT: https://doi.org/10.6084/m9.figshare.14546157.v1) and raster stacks including all predictors are also available (https://figshare.com/articles/dataset/Current_and_future_climate_and_habitat_stacks/14546262; PAs: https://doi.org/10.6084/m9.figshare.14546205.v1), as well as the script used to develop SDMs (https://doi.org/10.6084/m9.figshare.14559480.v1).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.