



# An integrated modeling approach for considering wildlife reintroduction in the face of climate uncertainty: A case for the North Cascades grizzly bear

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## ABSTRACT

As Earth faces a crisis of biodiversity loss, reintroduction of imperiled species has become an important tool toward mitigating extirpation. Current habitat quality for a reintroduced species may change dramatically under future climate scenarios, undermining or supporting species conservation efforts. Models designed to understand such change must consider the niche plasticity of a species to assess the costs and benefits of reintroduction. We integrated spatially-explicit individual-based population models with a dynamic vegetation model, using combinations of global climate models and greenhouse gas scenarios to better understand potential future carrying capacity for grizzly bears in the North Cascades Ecosystem (NCE). We estimated the ecosystem could support a grizzly bear population under several climate change scenarios through the 2080s, with the amount of high quality habitat increasing across all models, scenarios, and time periods, as compared to current conditions. Projected future habitat quality remained consistent or increased slightly along the eastern portion of the ecosystem, and increased along its central and western portions, for a net increase in high quality habitat through time. At the most plausible female home range size of 280 km<sup>2</sup>, we estimated carrying capacity would increase from a baseline of 139 female bears to 241–289 female bears. Estimated changes in habitat over time could increase grizzly bear density to 20–22 bears/1000 km<sup>2</sup> (males and females) from the previous estimate of 17 bears/1000 km<sup>2</sup>. Species with broad ecological niches (i.e., generalists), such as grizzly bears, may be especially good candidates for reintroduction efforts in some ecosystems. Our integrated model structure provides an innovative tool for advancing reintroduction initiatives while considering some long-term risks for species.

## 1. Introduction

Reintroduction of many imperiled wildlife species is often our last great hope for their conservation (Seddon et al., 2014). Across animal taxa, 95 % of 349 assessed reintroductions have been deemed at least partially successful (Soorae, 2018). Many such successes point to habitat quality as a critical factor in determining reintroduction outcome (Griffith et al., 1989; Wolf et al., 1998; Cochran-Biederman et al., 2015); yet, habitat for many species is changing rapidly in response to climate (Bellard et al., 2012; Groffman et al., 2014). A central question to conservation must thus be: how can managers better assess the potential viability of wildlife reintroductions in the face of unknown future habitat?

Most wildlife species in natural ecosystems are subject to changes in the plant communities on which they rely, and plant communities are directly affected by climate (Stephenson, 1990; Churkina and Running, 1998; Nemani et al., 2003). Species with specialized ecological niches may dramatically shift their range or abundance, or be impacted by changing phenology and complex trophic interactions (Gilman et al., 2010; Thackeray et al., 2016; Pacifici et al., 2017). As such, reintroduction efforts today could be undermined or bolstered by future climate change. Species with broad ecological niches (i.e., generalists) may be better candidates for reintroduction simply because their plasticity in resource demands allows them to occupy changing habitats more efficiently. Grizzly bears (*Ursus arctos*), for example, are expected to be relatively insensitive to climate change in the Canadian Rocky

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Mountains, where more of their broad array of food resources are expected to increase in abundance than those projected to become more scarce (Roberts et al., 2014).

Regardless of their plasticity in ecological space, wildlife reintroductions are expensive, inherently place individuals of rare species at risk, and can be controversial (Moehrenschrager et al., 2013). Public values around conservation of iconic carnivores are diverse (Treves and Bruskotter, 2014; Carter and Linnell, 2016), and real or perceived threats to human safety and property can inflate the socio-political landscape and further obfuscate conservation actions (Williams et al., 2002). Public support of the Endangered Species Act, the central law guiding many reintroductions in the U.S., remains strong despite these challenges (Bruskotter et al., 2018). As a recent case example, approximately 21,200 public comments were received from people living within the U.S. state of Washington on a proposal to restore grizzly bears to the North Cascade Ecosystem (NCE), and 88 % voiced support of restoration (USNPS/USFWS, 2021).

Grizzly bears were once present across much of western North America, but direct killing and extensive habitat loss over the last century extirpated them from 98 % of their historic range (USFWS 1993, 1997; Servheen et al., 1999). The NCE is home to the most imperiled grizzly bear population in the U.S.: the last confirmed sighting of a grizzly bear in the U.S. portion of the ecosystem was in 1996, and there have been only two confirmed sightings of this species in the Canadian portion of the ecosystem in the last decade (USNPS/USFWS, 2017; Rine et al., 2020). Even though grizzly bears have largely disappeared from this landscape, large intact areas of habitat remain. This habitat includes vast areas of designated wilderness with minimal anthropogenic infrastructure, extensive montane denning habitat, and at least 2668 plant and fungi species and 448 animal and insect species that have either been documented as grizzly bear diet components in other ecosystems or are possible natural food resources based on biological similarities to those confirmed foods (Ransom et al., 2018).

The potential carrying capacity for grizzly bears in the NCE has been estimated as approximately 274 bears (Mowat et al., 2013) and 250–300 bears (Lyons et al., 2018) using different methods. The Lyons et al. (2018) estimate was developed using individual-based models, and incorporated demographics and complex life histories, spatial habitat data, and anthropogenic influences. The grizzly bear parameters for that model were based on empirical grizzly bear life history metrics from similar ecosystems, as well as input from the Interagency Grizzly Bear Committee (IGBC) and the USNPS/USFWS (2017) Science Team (Lyons et al., 2018). The Lyons et al. (2018) framework also used a Resource Selection Function (RSF) based grizzly bears in the British Columbia, Washington, Idaho, and Montana trans-boundary region (Proctor et al., 2015), which are expected to be similar to those found in the NCE.

The Lyons et al. (2018) modeling framework and estimates provide robust information about carrying capacity of grizzly bears in the NCE given current habitat metrics, but the NCE is expected to experience significant future changes in climate that will likely alter habitat, and specifically natural bear foods (Raymond et al., 2014; Ransom et al., 2018). Climate change projections for the NCE over the next century suggest warming temperatures, drier summer months and wetter winter and spring months, decreased snowpack, and an increased number of disturbance events (Raymond et al., 2014). Such changes may influence the ecosystem's ability to sustain grizzly bear populations into the future. Should resources be dedicated to grizzly bear restoration in the NCE, models of future habitat quality and carrying capacity will be critical for supporting regional wildlife managers in assessing and responding to potential climate risks to grizzly bear populations.

To address this need, we integrated projections of future climate in the NCE, dynamic vegetation models, and adapted the Lyons et al. (2018) grizzly bear population models to better understand how climate change projections of vegetation abundance and distribution may influence grizzly bear distribution, abundance, and carrying capacity. While climate envelope models have frequently been used to provide

coarse correlative estimates of future habitat suitability, this is the first attempt (to our knowledge) to provide a more biologically relevant, process-based estimate of future habitat suitability to directly inform species reintroduction under a climate change paradigm. This information will be vital to guiding decisions about grizzly bear population restoration in the NCE, and offers a model for consideration of future habitat quality in other wildlife reintroduction scenarios.

## 2. Methods

### 2.1. Study area

The NCE is a 34,965 km<sup>2</sup> transboundary ecosystem located in north-central Washington State and southern British Columbia, Canada (Fig. 1). The U.S. portion of the NCE is 25,322 km<sup>2</sup> of designated wilderness, multiple use resource lands, and small rural communities, with 97 % of the area managed as public lands. Administratively, the NCE is one of six designated recovery zones for grizzly bears in the conterminous U.S. (USFWS, 1997) and is subdivided into 42 Bear Management Units (BMUs) for monitoring and evaluation of cumulative effects (IGBC, 1998; Gaines et al., 2003).

Humans have been a part of the NCE for at least 9000 years (Hoffman et al., 2015; Rine et al., 2020). Most human activity in the core of the ecosystem today consists of recreational use by visitors (>4 million visits/year), hydroelectric power generation, subsistence use by Native American tribes and First Nations, management and research use by administering agencies, and travel across four major highways that cross the otherwise largely roadless landscape. Several gateway communities persist around the edges of the ecosystem with low population densities (see USNPS/USFWS, 2017:71).

The NCE is divided orographically into the temperate marine west slope of the Cascades and semi-arid continental east slope of the Cascades. A transitional zone is created in the lower elevations of the Skagit watershed by the Cascade-Pacific, Skagit (west of the Cascade crest), and North Cascade orographic divides, which splits flow north to the Fraser River and south to the Skagit River. Marine temperate lowland forests dominate the western valleys, with lush subalpine forests and meadows along the central spine of the Cascades, descending to dry forests and lowland valleys in the east. Elevation ranges 25–3200 m. The NCE receives average precipitation of 400 cm/yr west of the Cascade crest and 130 cm/yr east of the Cascade crest, but orographic effects reduce precipitation to an average of only 25 cm/yr on the easternmost edge of the ecosystem. The NCE currently supports many of the primary natural food sources used by grizzly bears in other populations, including graminoids, starchy tubers like *Hedysarum* spp., montane forbs like glacier lilies (*Erythronium* spp.), forest plants like horsetails (*Equisetum* spp.) and cow parsnip (*Heracleum lanatum*), clovers (*Trifolium* spp.), and a wide variety of berry-producing plants (*Vaccinium* spp. and others), as well as ants, ungulates, and carrion (Ransom et al., 2018).

Climate change models for the NCE project a 3.1–3.3 °C increase in mean annual temperature by the 2080s (2070–2099) under a moderate greenhouse gas scenario (RCP 4.5), and as much as 5.2–5.6 °C increase in mean annual temperature under a high greenhouse gas scenario (RCP 8.5), relative to 1970–1999 (Raymond et al., 2014). Estimated decreases in snowpack by the end of the century occur under both moderate and high greenhouse gas scenarios, particularly at lower elevations and on the western slopes of the NCE. Projected increases in growing season length, winter and spring water surplus, summer water deficit, wildfire, and decreases in snowpack may lead to substantial vegetation changes through the end of the century (Littell et al., 2014). Disappearing glaciers may also reduce freshwater influx into watersheds, ultimately influencing associated riparian plant communities (Hoffman et al., 2015). Any of these changes could impact availability of specific natural food sources for grizzly bears either directly or through trophic interactions, and thus could influence their population dynamics through time.



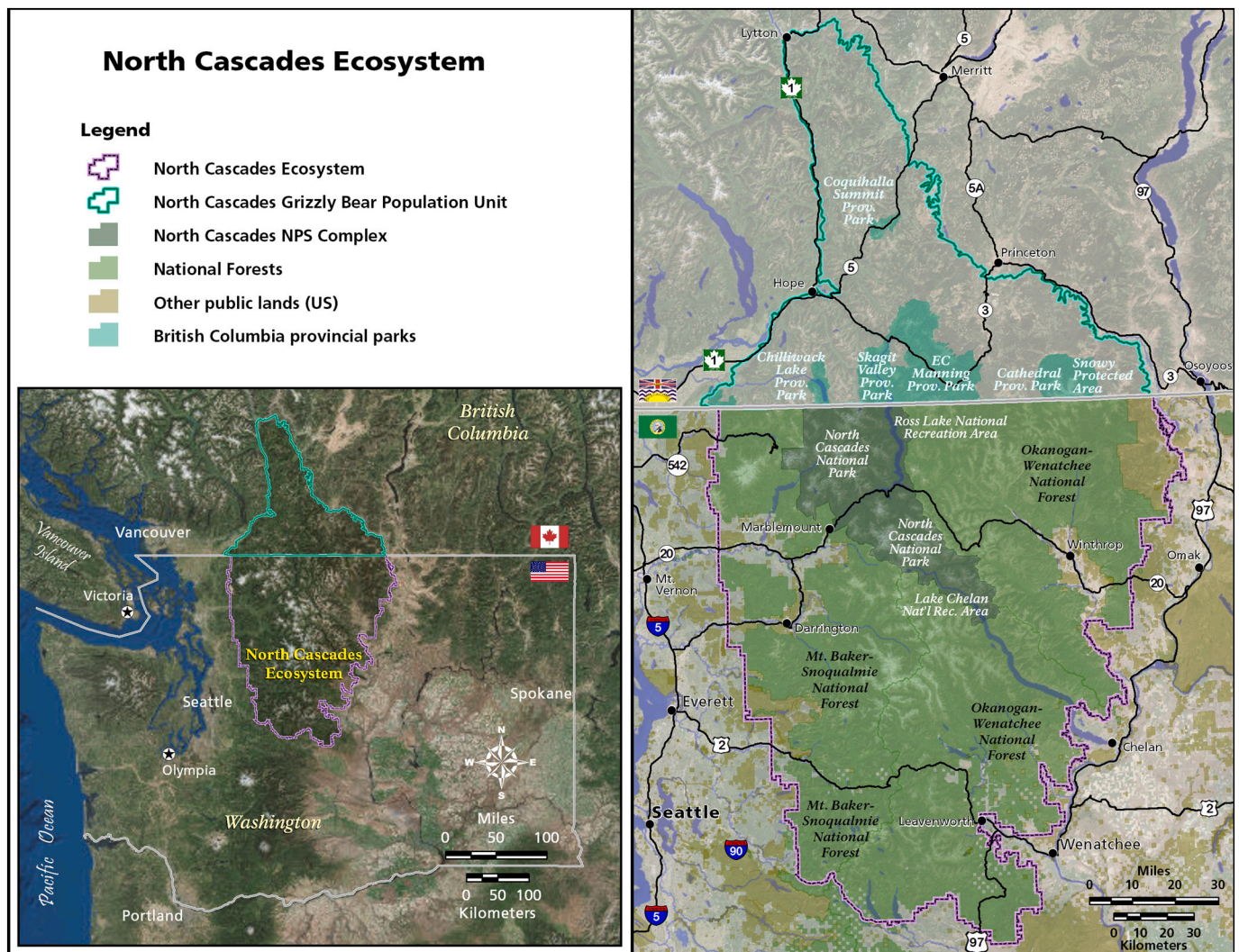


Fig. 1. The North Cascades Ecosystem is administered as a Grizzly Bear Recovery Zone in the U.S. and as a Grizzly Bear Population Unit in British Columbia, Canada.

## 2.2. Carrying capacity modeling framework

We estimated future carrying capacities for grizzly bears in the NCE by pairing individual-based population models of carrying capacity with the dynamic vegetation model MC2 (Bachelet and Turner, 2015; Bachelet et al., 2015) under a range of future climate scenarios. We used the HexSim platform (version 4.0.17, Schumaker and Brookes, 2018) to generate a suite of spatially-explicit, individual-based population models that integrate empirical information on habitat selection, human activities, demography, and population dynamics (Heinrichs et al., 2010; Spencer et al., 2011; Huber et al., 2014) in the same framework as Lyons et al. (2018). The resulting integrated modeling structure produced 36 different model combinations, arising through the progression of four major elements: 1) the population model (four age classes [each with different survival and reproductive rates], three home range sizes, two movement classes), 2) a crosswalk from RSF parameters to MC2 vegetation parameters, 3) climate modeling (22 climate models, and two circulation scenarios), and 4) the complete model output for each of three time periods (Fig. 2).

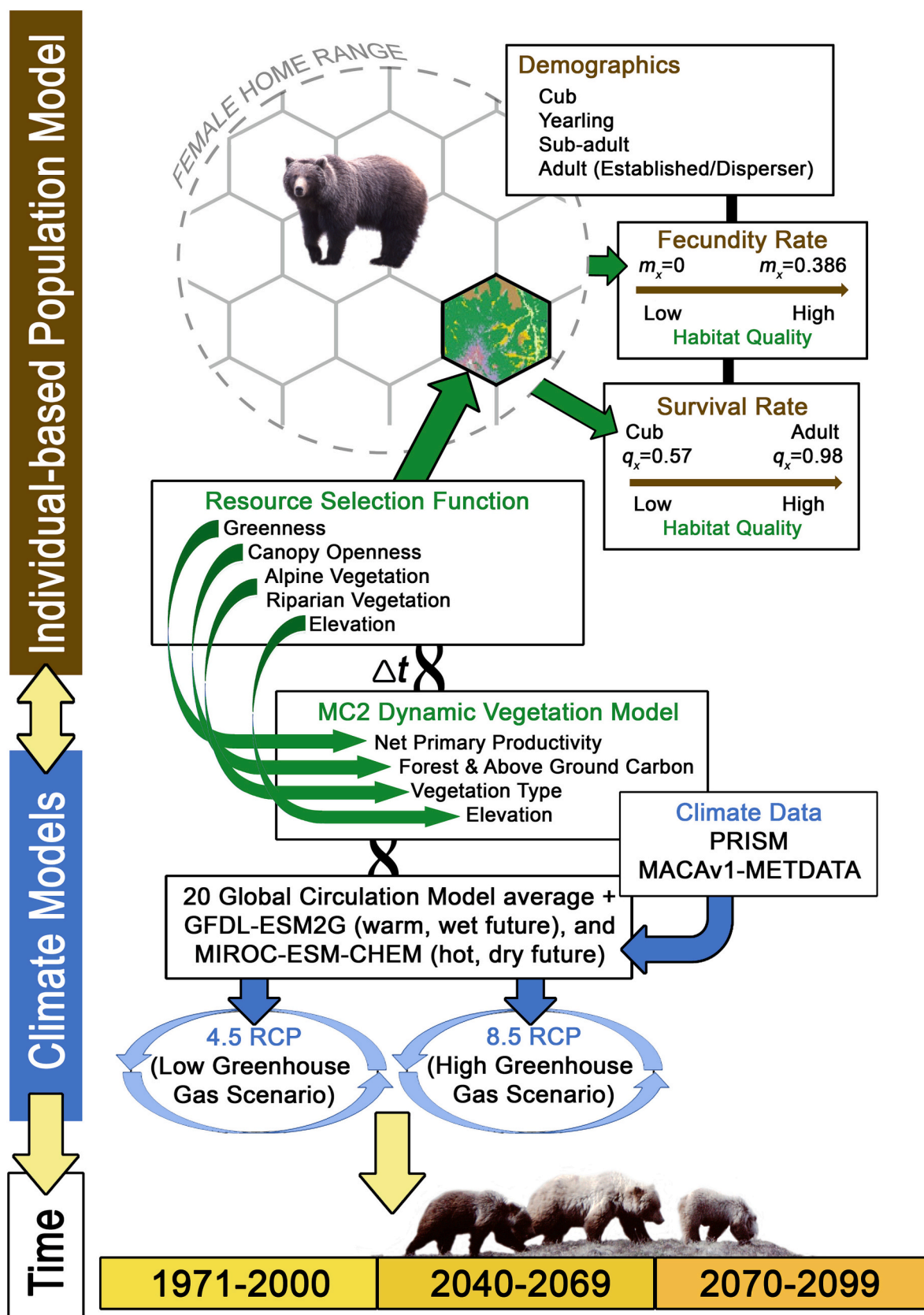
### 2.2.1. Resource selection function

We used resource values and habitat quality classifications for grizzly bears in the NCE developed by Lyons et al. (2018), based on a RSF originally developed by Proctor et al. (2015). Similar to methods in Proctor et al. (2015), we used logistic regression to estimate the

parameters of the exponential RSF (Manly et al., 2002). We then transformed RSF predictions using a logistic function to normalize right skewing, and mapped predictions at a 30 m scale. We estimated the parameters of greenness (2005 Landsat 5 Imagery (USGS)), canopy openness (Gradient Nearest Neighbor method: Ohmann and Gregory, 2002), alpine vegetation (Ohmann et al., 2011; Richardson, 2013), riparian vegetation (Krosby et al., 2014), and elevation (Digital Elevation Model). We also made adjustments to habitat quality based on proximity to open roads: resource values were decreased by 60 % within 250 m of an open road, and by 40 % when 250–500 m from an open road (Lyons et al., 2018). Lyons et al. (2018) defined these adjustment values based on data from other ecosystems (IGBC, 1998) and input from the USNPS/USWFS (2017) Science Team, with consideration of black bear resource selection in the NCE (Gaines et al., 2005) and differences in how bear species are influenced by human activities (Kasworm and Manley, 1990). To examine potential climate impacts on grizzly bear habitat quality, we incorporated MC2 vegetation model output under different climate scenarios directly into the RSF (Fig. 2).

### 2.2.2. MC2 dynamic vegetation model

MC2 is a global dynamic vegetation model designed to simulate vegetation type, plant growth, biogeochemical cycles, and their responses to wildfire (Bachelet and Turner, 2015; Bachelet et al., 2015). This model projects how four tree and shrub lifeforms (evergreen needleleaf, evergreen broadleaf, deciduous needleleaf, and deciduous



**Fig. 2.** Integration of a HexSim individual-based population model and MC2 dynamic vegetation model across climate scenarios, two individual global circulation models that bracket the range of climatic conditions (GFDL-ESM2G and MIROC-ESM-CHEM), and two representative concentration pathways (RCPs), to estimate future carrying capacity of grizzly bears (*Ursus arctos*) in the North Cascades Ecosystem. Models were run for three grizzly bear home range sizes (100 km<sup>2</sup>, 280 km<sup>2</sup>, 440 km<sup>2</sup>) for 100 years (preceded by a 50 year “burn-in” period).



broadleaf) and two graminoid lifeforms (C3 and C4 grasses and sedges) respond to changes in climate and atmospheric carbon dioxide concentration, including how vegetation competes for light, nitrogen, and available soil water. These simulations also estimate net primary production (greenness), decomposition, soil respiration, and nutrient release through time. Nitrogen inputs considered include release from organic matter turnover, wet and dry deposition, and nitrogen fixation.

MC2 is available for a historical time period (1895–2010), utilizing monthly climate data from the PRISM dataset (Daly et al., 2002) and for a future time period (2011–2100), utilizing monthly climate data from MACAv1-METDATA (Abatzoglou and Brown, 2012). MC2 was down-scaled for 20 global circulation models and two representative concentration pathways (RCPs) from the Coupled Model Intercomparison Project Phase 5 (CMIP5): RCP 4.5 (a low greenhouse gas scenario) and RCP 8.5 (a high greenhouse gas scenario) (Taylor et al., 2012).

We adjusted habitat quality derived from the RSF model using variables available in the MC2 vegetation models that were similar to those used in the RSF: net primary productivity (approximates greenness), forest and above ground carbon (to estimate canopy openness), vegetation type, and elevation (Fig. 2). The scale of the MC2 models (4 km) is coarse relative to the RSF (30 m); thus, we ultimately could not include some fine scale detail such as small canopy openings and riparian areas, which were originally included in the Lyons et al. (2018) RSF model. While inferences around these fine scale habitat features were precluded by the inherent coarse scale of MC2 data, it should be noted that riparian vegetation can represent a seasonally important forage source for grizzly bears in some ecosystems (Boyce and Waller, 2003). Our calculations of carrying capacity at fixed points in time rely on the underlying assumption that the relationship between RSF parameters and grizzly bear foods are mostly maintained in future growing conditions. This assumption is supported based on the range of plant communities represented in the RSF parameters and the incredibly diverse and flexible diet exhibited by interior grizzly bears during the 6–8 months/yr that they actively forage (see Ransom et al., 2018).

### 2.2.3. HexSim population model

HexSim relies on a set of hexagons on the landscape that are assigned a habitat resource value based on the quality of habitat within the hexagon. To develop the initial resource value map and classify habitat for the HexSim population model, we needed to crosswalk the MC2-reconciled RSF cell values with the HexSim cells. We classified the RSF scores into four categories ranging from 1 (low quality habitat) to 4 (high quality habitat), with non-habitat (i.e., ice, rock, large water bodies) removed (Fig. 2). Habitat class categories scaled linearly, such that 'high' quality habitat represented four times the resource value of 'low' quality habitat. Hexagons were then attributed with the sum of RSF score values within 250 m of the 21.7 ha hexagon center. We used 250 m for this calculation because that was the defined threshold at which proximity to a road changed habitat quality value. We calculated the percent difference in habitat quality values between time steps (historical, 2050s, and 2080s) and then used those differences to adjust the original RSF map to estimate relative change in habitat quality over time (Fig. 2).

To run our HexSim model, we simulated female grizzly bear population dynamics in the NCE based on grizzly bear metrics from populations in similar ecosystems, as described by Lyons et al. (2018). We used the same rates for age- and habitat quality-specific individual female annual fecundity ( $m_x$ ), annual survival ( $q_x$ ), and average dispersal distance detailed in Lyons et al. (2018). As in that study, we specified that only adult females with home ranges classified in HexSim as moderate (Class 2 or 3) or high (Class 4) quality habitat were allowed to reproduce. While female grizzly bears in low quality habitat have been documented reproducing, we chose a conservative classification to avoid over estimation of performance. Females in high quality habitat were assigned  $m_x = 0.386$ , in moderate quality habitat were assigned  $m_x = 0.302$ , and in low quality habitat were assigned  $m_x = 0.000$ . From low

to high habitat quality,  $q_x$  for cubs ranged 0.57–0.88, yearlings ranged 0.63–0.94, sub-adults ranged 0.65–0.86, and adults ranged 0.71–0.98.

Grizzly bears are not spatially territorial and females do not typically disperse long distances (mean distances range 9.8 km–14.3 km: McLellan and Hovey, 2001; Proctor et al., 2004). We used a female dispersal distance of 12.1 km, as did Lyons et al. (2018), and as in that study, we considered low quality habitat to be less permeable to movement than high quality habitat. We also considered large water bodies and expansive ice or rock as impermeable to movement. HexSim population estimates have been shown to have low sensitivity to movement (Marcot et al., 2015), and in our simulations only individuals that failed to establish a home range due to inadequate resources could disperse.

### 2.3. Modeling scenarios

We estimated future carrying capacity for female grizzly bears in the NCE using MC2 output summarized over three time periods: historical (1971–2000), 2050s (2040–2069), and 2080s (2070–2099). We used MC2 output from a 20 global circulation model average computed using a 20-model median (mode for vegetation type) of MC2 metrics, as well as two individual global circulation models that bracket the range of climatic conditions for the study area projected across all individual global circulation models: a relatively warm and wet future (GFDL-ESM2G: Dunne et al., 2012) and a relatively hot and dry future (MIROC-ESM-CHEM: Watanabe et al., 2011).

We estimated future carrying capacities for three home range sizes based on reported metrics for females in other grizzly bear populations (as described in Lyons et al., 2018): 100 km<sup>2</sup>, 280 km<sup>2</sup> and 440 km<sup>2</sup>. In these models, we classified individual bears as group members (female grizzly bears with established home ranges), or floaters (dispersing female grizzly bears without home ranges). We started model simulations with 1000 individuals randomly placed across the landscape, assuming that restoration had already occurred and the population exceeded carrying capacity. This allowed us to address the question of how carrying capacity could be affected by future climate, as opposed to climate effects on a small population that persisted under carrying capacity. We ran each model scenario for a total of 150 years, including a 50-year "burn-in" period followed by a 100-year simulation period. The "burn-in" period allowed populations to then approach equilibrium in the landscape and develop a representative distribution of age classes prior to the simulation period that included projected vegetation and climate influences on habitat amount, quality, and configuration.

We ran five population simulation replicates per scenario, because Lyons et al. (2018) found that five replicates adequately captured the variability in annual population size and distribution estimates. We used the 100-year simulation-duration mean number of individuals to represent the NCE carrying capacity metric. We summarized patterns of spatial distribution of the modeled populations across the NCE by calculating the annual mean number of female grizzly bears by BMU. All model output compilation, statistical analysis and mapping were conducted using R software (version 3.5.1, R Development Core Team, Vienna, Austria) and ArcGIS (version 10.6, ESRI, Inc.).

## 3. Results

### 3.1. Habitat quality

The habitat quality data layers developed as the foundation for this modeling exercise were consistent with the general climate trends anticipated for the NCE. Percent change of habitat quality ranged from a 77 % decrease in the lowest habitat (Class 1) to 197 % increase in the highest quality habitat (Class 4) across climate scenarios, as compared to historical conditions (Table S1). Estimated carrying capacity changed proportionately with habitat class distribution: current habitat quality conditions decreased moderately across low and moderate habitat classes, but increased substantially in high quality habitat (Table 1).

**Table 1**

Proportional change in habitat class distribution across the North Cascades Ecosystem relative to estimated carrying capacity under current habitat quality conditions, given two representative concentration pathways (RCP) (low greenhouse gas scenario [RCP 4.5] and a high greenhouse gas scenario [RCP 8.5]), for climate change and dynamic vegetation models over two time periods: 2050s (2040–2069), and 2080s (2070–2099).

Climate change model	RCP	Time period	Habitat class 1	Habitat class 2	Habitat class 3	Habitat class 4
GFDL-ESM2G (warm-wet)	4.5	2050s	−0.03	−0.32	−0.10	0.39
GFDL-ESM2G (warm-wet)	4.5	2080s	−0.02	−0.47	−0.16	0.59
GFDL-ESM2G (warm-wet)	8.5	2050s	−0.04	−0.27	−0.16	0.39
GFDL-ESM2G (warm-wet)	8.5	2080s	−0.25	−0.27	−0.28	0.72
MIROC-ESM-CHEM (hot-dry)	4.5	2050s	0.01	−0.27	−0.19	0.37
MIROC-ESM-CHEM (hot-dry)	4.5	2080s	−0.09	−0.21	−0.18	0.40
MIROC-ESM-CHEM (hot-dry)	8.5	2050s	−0.06	−0.26	−0.19	0.43
MIROC-ESM-CHEM (hot-dry)	8.5	2080s	−0.24	−0.25	−0.40	0.81
GCM 20-model mode	4.5	2050s	0.04	−0.21	−0.09	0.18
GCM 20-model mode	4.5	2080s	−0.08	−0.29	−0.11	0.41
GCM 20-model mode	8.5	2050s	−0.03	−0.35	−0.14	0.44
GCM 20-model mode	8.5	2080s	−0.25	−0.29	−0.39	0.84

High quality habitat increased across all models, scenarios, and time periods (Fig. 3). The largest increase was observed between the 2050s and 2080s under the high greenhouse gas scenario (RCP 8.5), an increase that was seen across global circulation models. Projected habitat quality remained fairly consistent or increased slightly along the eastern portion of the ecosystem, but increased along its central and western portions, for a net increase in high quality habitat (Fig. 3).

### 3.2. Carrying capacity estimates

The range of model outputs across future climate scenarios estimated that grizzly bear carrying capacity in the NCE would likely increase from 83 to 402 female bears under current conditions to 148–820 female bears (Tables S2–S4). At the most plausible home range size of 280 km<sup>2</sup>, the estimated carrying capacity increased from a baseline of 139 female bears to 241–289 female bears (Table S3). Changes in habitat resulting from climate change impacts would increase grizzly bear density in the NCE to 20–22 bears/1000 km<sup>2</sup> (males and females) from the previous

estimate of 17 bears/1000 km<sup>2</sup> (Lyons et al., 2018), given a home range size of 280 km<sup>2</sup> and assuming a 50:50 sex ratio (Fig. 4).

Spatial patterns of grizzly bear occupancy within the NCE were generally consistent across the range of future scenarios (Fig. 4). Predicted grizzly bear abundance was spatially similar to historical distributions along the drier eastern side of the ecosystem, with slight density increases (i.e., more bears in areas of higher quality habitat). A noticeable shift to higher quality habitat was projected for the interior of the ecosystem with a corresponding increase in grizzly bear density. The lowest concentration of bears was observed in the Toats, Lower Chewuch, Salmon and Middle Methow BMUs (Fig. 4). An increase in the concentration of bears was observed in the central portion of the ecosystem in the Upper Wenatchee, Chiwawa, and Suitttle BMUs (Fig. 4). The density of bears varied with global circulation model, greenhouse gas emission scenario, and time step, but the pattern was similar across future scenarios.

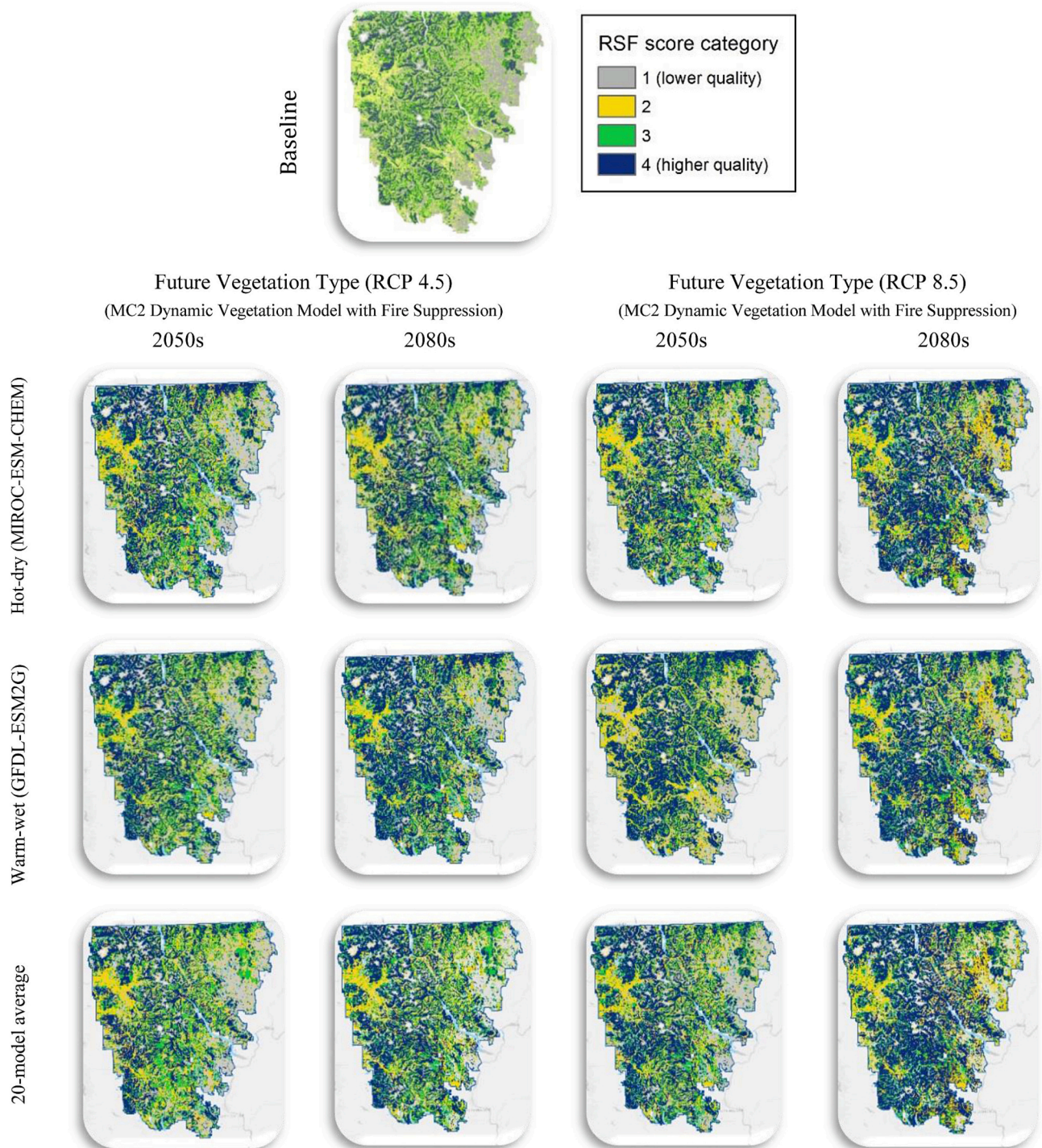
## 4. Discussion

Reintroduction or augmentation of wildlife is often a last resort after all other conservation measures have failed, but these tools are increasingly used worldwide (Seddon et al., 2014; Moehrenschlager et al., 2013). While many nuances such as species interactions and trophic cascades may arise after wildlife reintroductions (e.g., Ripple and Beschta, 2012), changing climate poses a potentially large systemic source of uncertainty. The NCE, for example, is expected to experience warming temperatures, more extreme seasonal patterns of precipitation (i.e., drier summers, wetter winters), reductions in snowpack and increasing disturbance events (Raymond et al., 2014). The increases in growing season length, winter and spring water surplus, summer water deficit, and wildfire, and decreases in snowpack projected under current climate models could result in substantial vegetation changes through the end of the century (Littell et al., 2014). Climate change impacts on wildlife species may include changes to food availability as well as altered interspecific relationships, predator-prey dynamics and competition, disease and parasite prevalence and distribution, and invasive species colonization (Kareiva et al., 1993; Schneider et al., 2002; Lawler et al., 2014). Reintroducing a species like the grizzly bear could thus result in future bears facing new ecological paradigms, and their success will depend greatly on their dietary plasticity and ability to travel across landscapes (Hamilton and Bunnell, 1987; Stirling and Derocher, 1990).

Our results suggest that the projected future shifts in vegetation in the NCE may result in high quality grizzly bear habitat increasing across all climate scenarios, while low quality grizzly bear habitat may decrease in some areas. These results are consistent with expectations from projected climate impacts on the NCE (Littell et al., 2014). For example, the projected declines in snowpack would result in a decrease in alpine and subalpine vegetation and an increase in montane vegetation. This may lead to an increase in important grizzly bear foraging habitat (e.g., grasses and sedges, *Vaccinium* species) found in high-elevation meadows (Munro et al., 2006). *Vaccinium* species are the most abundant fruit-bearing food resources in the NCE and a seasonally important grizzly bear food (Ransom et al., 2018); those species are projected to increase their range across the west by 66–112 %, depending on greenhouse gas scenario (Solomon et al., 2007; Roberts et al., 2014). At lower elevations along the eastern slopes of the NCE, dry meadows may provide early season foraging habitat, but become less available as soil moisture decreases (Littell et al., 2014). Forests can also provide important grizzly bear habitat, hosting a variety of plant- and animal-based foods, including ungulates, ants, and termites. Forested vegetation will be impacted by fire, but is projected to generally increase across the ecosystem, though tree species diversity will likely change (Ransom et al., 2018).

All of our model outcomes suggest that grizzly bears should persist in the ecosystem through time, but it should be noted that the coarse resolution required to effectively crosswalk the complex framework of

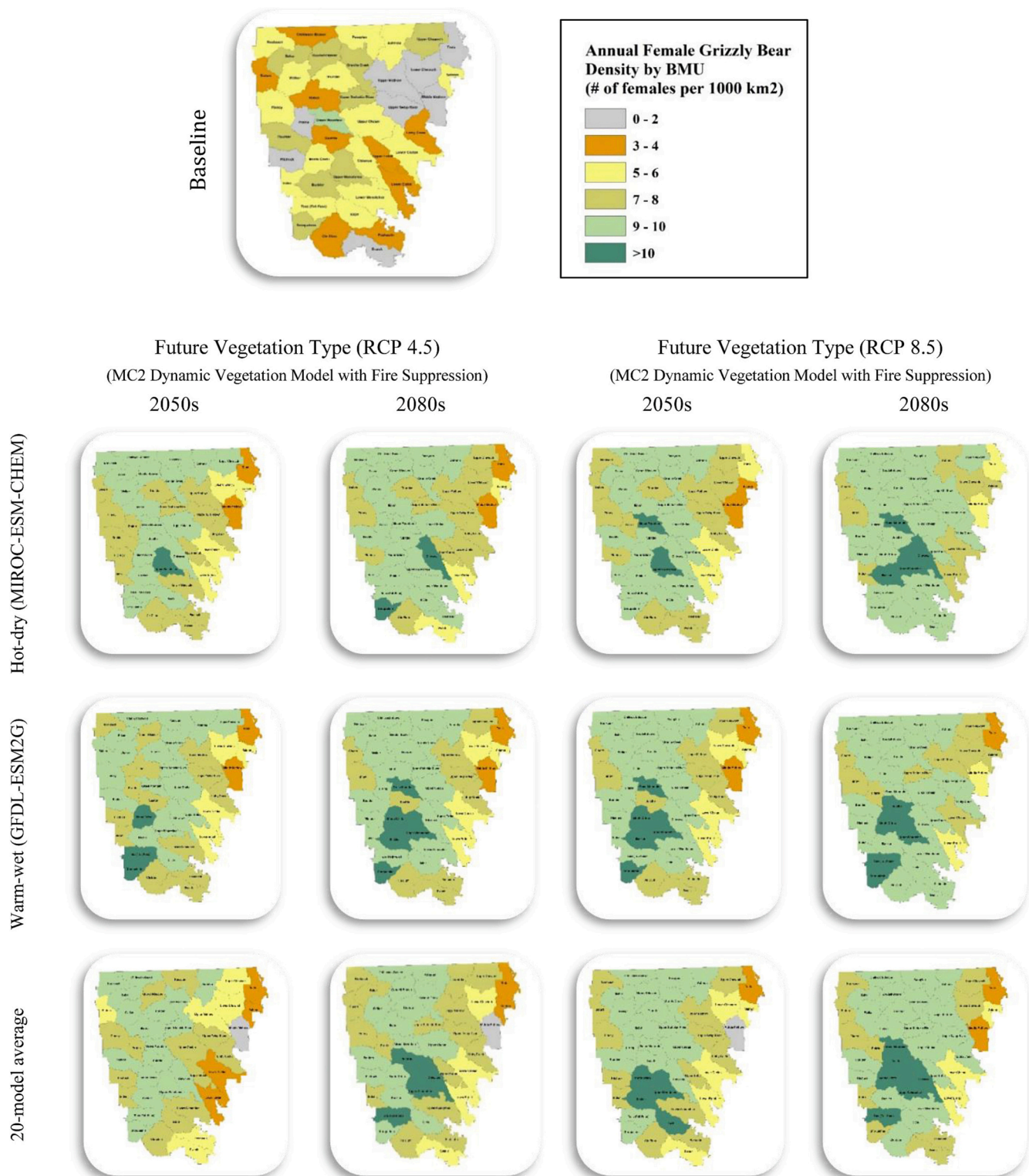




**Fig. 3.** Grizzly bear habitat in the North Cascades Ecosystem (NCE) derived from an exponential Resource Selection Function logistic regression and MC2 Climate Projections. Habitat classifications were divided into four classes to display relative habitat quality across the NCE (1/gray = lower quality habitat to 4/blue = best quality habitat). Projected changes in habitat quality were estimated by applying projected changes in net primary productivity, from the MC2 dynamic global vegetation model with fire suppression for the North Cascades Grizzly Bear Recovery Zone. Changes are relative to historical conditions for two global circulation models (MIROC-ESM-CHEM [hot-dry] and GFDL-ESM2G [warm-wet]) under a low (RCP 4.5) and high (RCP 8.5) greenhouse gas scenario. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

population, vegetation, and climate models we used may not fully capture the fine-scale nuances of grizzly bear diet, and phenology of specific food availability. Grizzly bears are known to rely heavily on some specific foods seasonally, and the phenology and availability of those foods could change through time (Ransom et al., 2018). Whitebark pine (*Pinus albicaulis*) seeds, for example, are an important source of fat,

protein, and minerals for wildlife (Lanner and Gilbert, 1994). On Montana's eastern slope of the Rocky Mountains, whitebark pine seeds and were detected in 15 % of grizzly bear scat samples from one location; however, in the other three areas of the same study, whitebark pine seeds were only detected in 0.3–4 % of scat samples (Mace and Jonkel, 1986). Whitebark pine, though relatively common, did not occur in the



**Fig. 4.** Change in spatial distribution of mean annual female grizzly bear (*Ursus arctos*) density (number/1000 km<sup>2</sup>) by Bear Management Unit in the North Cascades Ecosystem as a result of applying different climate change scenarios. Results are shown only for the most plausible, mid-range home range size of 280 km<sup>2</sup>.

1100 scat samples analyzed by McLellan and Hovey (1995) for grizzly bears in southeastern British Columbia. It is unknown how important this food source would be for grizzly bears in the NCE, and our vegetation models and projections through time could not differentiate between whitebark pine and other tree species, nor do they capture the phenology of specific mast foods within any given year.

The broad time scale of our modeling (1971–2000, 2040–2069,

2070–2099) also does not robustly capture short-term effects of stochastic events like fire on grizzly bear foods, but such impacts also are not expected to produce a net loss of natural grizzly bear foods (Ransom et al., 2018). Fire ignitions are strongly related to low spring snowpack in parts of the NCE (Cansler, 2011), and by the 2080s, fire in the NCE is expected to burn an average of nearly four times the area that was burned between 1980 and 2006 (Littell et al., 2014). While fire is a



natural ecosystem process in the NCE, high fuel loads combined with increasing summer temperatures in the NCE are projected to result in a 29–41 % increase in burn severity, as compared to 1971–2000 (Rogers et al., 2011). Such burns will locally change forest structure such as creating significant openings of the canopy and consequent irruption of graminoids and forbs that are grizzly bear foods. Such openings can also be beneficial to small mammal and ungulate populations across successional stages, which may further improve food resources for grizzly bears. Because of this regeneration and recolonization of nutritious foods, grizzly bears have been shown to strongly select for recently burned forest habitats, at least under low and moderate burn severity conditions (Hamer and Herrero, 1987). This type of specific food transition is generally captured in our RSF through the parameters of greenness and canopy openness, as well as through incorporation of fire in the MC2 vegetation model structure, but the timing of such changes within a single growing season is not fully captured at the multi-decadal time scale of the model estimates.

While climate change may affect grizzly bears in disparate ways, their primary threat remains interactions with humans in an increasingly human-dominated world (Wilson et al., 2005). The most significant anthropogenic impact to grizzly bears is direct killing by humans, with 77–85 % of 99 mortalities across British Columbia, Alberta, Washington, Idaho, and Montana, coming from intentional human action (McLellan et al., 1999). Given 97 % of the NCE is public land, the vast expanse of designated wilderness and absence of urban development greatly reduces the potential for bear-human conflict. Eighty-nine percent of the NCE has also been managed under a “no-net-loss-of-core area” agreement between NPS and USFWS since 1997 (USNPS/USFWS, 2017), which in practice prevents creation of new roads and trails in grizzly bear core habitat, and this practice is expected to endure through time. Nonetheless, decreased snowpack and increased temperatures could exacerbate human-bear interactions and potential disturbance through habitat loss, conflicts and access to anthropogenic food sources that may arise from increased recreational use and duration of access, and bear mortality from collisions with vehicles and poaching. Climate projections for the NCE do suggest a generally uphill migration of species, which may provide more bear foods as well as adequate denning habitat, while lower elevation habitats are projected to decrease in species richness (Roberts et al., 2014). Although some bears will likely use lower elevation habitats, particularly as population densities increase and some bears are displaced to lower quality habitats, this general uphill migration could lead to selection of higher quality habitat located in the more remote portions of the NCE that are farther from roads and human development, thus reducing human-bear interactions and bear mortality.

Our estimates of carrying capacity in the future NCE project an increase of at least 70 % across scenarios of future climate as compared to current conditions. Our results vary greatly depending on home range size, with larger home ranges resulting in smaller carrying capacity estimates. Estimates of future population size are similar across climate change scenarios, with a marked increase for mid-century (2050s) and a modest additional increase by end-of-century (2080s). These results do not imply that we would expect a recovering grizzly bear population to increase at this rate (we did not model population growth rate), but rather provides insight into how many bears the ecosystem could be capable of supporting under different climate change scenarios. It should also be noted that our results arise from home range sizes that represent static categorical sizes in the models, but in reality as populations grow and resources change through time, home ranges may expand or reduce in size; thus influencing carrying capacity at the ecosystem scale (Clutton-Brock and Harvey, 1978; Edwards et al., 2013). We used a span of home range sizes that contain the expected range of area a female grizzly bear would use in the NCE across resource conditions and reproductive status differences, and while grizzly bear habitat selection has been shown to be scale dependent, the parameter of greenness (as was captured in our RSF) has been shown to be a strong

predictor of female presence across habitat types (Ciarniello et al., 2007).

Our findings of increasing and spatially shifting carrying capacity in the NCE are consistent with grizzly bears' plasticity as habitat generalists: predicted increases in high quality habitat would generally allow for greater availability of preferred food resources that in turn could support a larger population of grizzly bears. At the most plausible home range of 280 km<sup>2</sup> and across climate scenarios, we estimated a carrying capacity of 241–289 female grizzly bears by the 2080s. Assuming a 50:50 sex ratio, the estimated grizzly bear density in the NCE would thus be 20–22 bears/1000 km<sup>2</sup> (male and females) by the 2080s. Lyons et al. (2018) estimated density under the same demographic scenarios as 17 bears/1000 km<sup>2</sup> given current habitat conditions. Other ecosystems have reported population density estimates ranging from a low of 8 bears/1000 km<sup>2</sup> in the Yahk Population Unit, British Columbia (Proctor et al., 2007) to a high of 30 bears/1000 km<sup>2</sup> in the Glacier National Park in Montana, US (Kendall et al., 2008). Our models fall within this range and further support the plausibility that the NCE may be capable of supporting a grizzly bear population as habitat quality changes under several climate change scenarios through the 2080s.

## 5. Conclusions

Reintroducing wildlife, and especially large carnivores, is not a trivial endeavor and understanding future habitat quality is critical toward successful long-term conservation of species. Uncertainty still pervades the world's wildest places as the anthropogenic footprint grows and interacts with species on multiple scales (Dirzo et al., 2014). Despite this daunting conservation miasma, hope lies in science-based tools that inform actions with a diligent regard to adaptive management as more data are gathered through time (Allen et al., 2011). In the case of the North Cascades grizzly bear, integrating population models with dynamic vegetation models under a range of climate scenarios provides a quantitative framework to inform thoughtful reintroduction initiatives. This novel integrated model structure may be used for other species and help managers to make informed decisions around wildlife reintroduction in the face of unknown future resources, based on the best available data. The complex relationship between presence of grizzly bears, changes in climate, natural processes, and anthropogenic features will ultimately determine the future quality of grizzly bear habitat across the NCE.

## CRedit authorship contribution statement

**Jason I. Ransom:** Conceptualization, Funding acquisition, Methodology, Visualization, Writing – original draft. **Andrea L. Lyons:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Visualization, Writing – review & editing. **Katherine C. Hegewisch:** Resources, Validation, Writing – review & editing. **Meade Krosby:** Conceptualization, Methodology, Resources, Validation, Writing – review & editing.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Andrea Lyons reports financial support was provided by Skagit Environmental Endowment Commission.

## Data availability

No empirical bear data were used for this work. All vegetation and climate data are public-sourced as cited in the manuscript.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2023.109947>.

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