

Idiosyncratic responses of grizzly bear habitat to climate change based on projected food resource changes

DAVID R. ROBERTS,^{1,3} SCOTT E. NIELSEN,¹ AND GORDON B. STENHOUSE²

¹Department of Renewable Resources, University of Alberta, Edmonton, Alberta T6G 2H1 Canada

²Foothills Research Institute, P.O. Box 6330, 1176 Switzer Drive, Hinton, Alberta T7V 1X6 Canada

Abstract. Climate change vulnerability assessments for species of conservation concern often use species distribution and ecological niche modeling to project changes in habitat. One of many assumptions of these approaches is that food web dependencies are consistent in time and environmental space. Species at higher trophic levels that rely on the availability of species at lower trophic levels as food may be sensitive to extinction cascades initiated by changes in the habitat of key food resources. Here we assess climate change vulnerability for *Ursus arctos* (grizzly bears) in the southern Canadian Rocky Mountains using projected changes to 17 of the most commonly consumed plant food items. We used presence–absence information from 7088 field plots to estimate ecological niches and to project changes in future distributions of each species. Model projections indicated idiosyncratic responses among food items. Many food items persisted or even increased, although several species were found to be vulnerable based on declines or geographic shifts in suitable habitat. These included *Hedysarum alpinum* (alpine sweet vetch), a critical spring and autumn root-digging resource when little else is available. Potential habitat loss was also identified for three fruiting species of lower importance to bears: *Empetrum nigrum* (crowberry), *Vaccinium scoparium* (grouseberry), and *Fragaria virginiana* (strawberry). A general trend towards uphill migration of bear foods may result in higher vulnerability to bear populations at low elevations, which are also those that are most likely to have human–bear conflict problems. Regardless, a wide diet breadth of grizzly bears, as well as wide environmental niches of most food items, make climate change a much lower threat to grizzly bears than other bear species such as polar bears and panda bears. We cannot exclude, however, future alterations in human behavior and land use resulting from climate change that may reduce survival rates.

Key words: climate change; ecological niche model; food; global warming; grizzly bear; North America; species distribution model; trophic levels; *Ursus arctos*.

INTRODUCTION

Climate change is altering habitats for a wide breadth of organisms, with plants being particularly sensitive given their limited ability to physically follow suitable environmental conditions (Parmesan 2006). While this vulnerability to plants is notable in itself, it also has implications for species that are dependent on plant resources for their habitat. This leaves open the possibility for extinction cascades to be initiated via bottom-up effects, thus increasing vulnerability for species at higher trophic levels that rely on the availability and health of primary producers. Climate change vulnerability assessments for species at higher trophic levels, such as large mammals, may therefore need to include assessments of plant communities and the food web interactions with mammals, under the assumption that food webs related to the target species are consistent in time and environmental space. While

such trophically based vulnerability assessments may be rare in the literature, it is apparent that interspecific interactions among species and trophic levels should be considered when assessing effects of climate change (but see Tuanmu et al. 2013).

For the North American grizzly bear (*Ursus arctos*; see Plate 1), the high energetic requirements of winter hibernation combined with the relatively short foraging season means that habitat tends to be selected based largely on resource availability (Schwartz et al. 2003). While faunal food sources such as ungulate predation are important energy sources, bears also dedicate much effort to foraging on vegetation, particularly in temperate forested habitats (Bojarska and Selva 2012), where isotopic diet assessments demonstrate that grizzly bears in the southern Canadian Rockies are among the most vegetarian of North American populations (Hilderbrand et al. 1999). In spring, and to a lesser extent throughout the active period, root digging for species such as *Hedysarum alpinum* (alpine sweet vetch) dominate the diet and thus the activity of bears (McLellan 1990, Hamer et al. 1991, Munro et al. 2006). As spring progresses with green-up, succulent herbaceous foods

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³ E-mail: drr3@ualberta.ca

high in protein, such as young *Equisetum arvense* (horsetail) and *Trifolium* spp. (clovers) become more important. And finally, during the late-summer and early-autumn hyperphagic period, bears in the southern Canadian Rocky Mountains rely predominantly on fruit from perennial shrubs for energy (Munro et al. 2006).

The threat of anthropogenic footprints and activities, such as roads, urban development, and resource extraction, which can all adversely affect grizzly bear survival rates, have been well described (Mattson 1990, McLellan 1990). However, little is known about how climate change may affect the foods and thus the habitats that bears depend on. A variety of empirical models of grizzly bear habitat have been developed, focusing primarily on parameterizing current bear habitat (but see Nielsen et al. 2008), mostly using complex environmental surrogates of food resources and human activity such as land cover type, forest crown closure, slope, aspect, elevation, and metrics of road density or urbanization (e.g., Nielsen et al. 2006, Ciarniello et al. 2007, Graves et al. 2011). Although some studies have focused directly on food resources on which bears depend (e.g., Nielsen et al. 2003, 2004, 2010), few have assessed how climate change would affect those resources and thus grizzly bear habitat. (See, however, the recent review by Butler [2012] on potential linkages between climate and bear foods.) First, woody encroachment of subalpine and alpine meadows threatens sweet vetch habitat and other important alpine sources of bear foods. Second, decreased winter snowpack may limit the number of new avalanche slopes, which also represent quality foraging habitat for bears. Rodriguez et al. (2007) presents the only study to our knowledge of changes in grizzly bear food source consumption in relation to changing climate conditions over a 30-year period in Spain. While the authors found relationships between changes in autumn bear diets and changes in climate regimes over the same period, changes in land use and grazing practices were also noted.

Species distribution models represent a different type of predictive model, often used to project future species ranges under climate change scenarios (Elith and Leathwick 2009). These models relate environmental predictors with the response of observed species presence or absence using any of a number of statistical procedures and then incorporate novel environmental data to project the ranges of suitable species habitat. Because of their empirical nature, species distribution models make a number of assumptions, including equilibrium of a species with its environment and the conservation of species niches over time. They also contain no mechanisms for incorporating biotic interactions such as competition, aside from indirectly through the observed presence and absences of species on the landscape, nor do they consider barriers to or limitations of species migration and colonization (see reviews by Pearson and Dawson 2003, Elith and



PLATE 1. A large adult male grizzly bear (*Ursus arctos*) in the foothills of Alberta, Canada. Forested habitats are common to the region. Photo credit: Gordon Court.

Leathwick 2009). Despite these limitations, species distribution models have been widely used to project future ranges under climate change for a variety of species.

In this study, we assess climate change vulnerability to grizzly bear food plant species using field data on bear food distribution and ecological niche models. Specifically, we project habitat changes for 17 species considered to be key grizzly bear food resources in the southern Canadian Rocky Mountains of Alberta and British Columbia (Fig. 1). To assess risk levels to habitat stability, we also examined seasonal changes in species prevalence across the southern Canadian Rocky Mountains and identified geographic trends of habitat changes. While the extensibility of food resource projections to habitat quality changes, for upper trophic level species like bears, ignores potentially complex adaptive behavioral responses of these habitat generalists, model predictions allow us to make inferences regarding general patterns among species and geographic space of future climate-related vulnerabilities to current key grizzly bear food resources.

METHODS

Ecological niche models

We incorporate eight individual modeling methods into a single, averaged ensemble output, which has been shown to improve accuracy (Araújo and New 2007,

Roberts and Hamann 2012): artificial neural networks, classification tree analysis, generalized additive models, generalized boosting models, generalized linear models, multivariate adaptive regression splines, a boosted regression tree known as Random Forest, and surface range envelopes (not included in the ensemble) (Thuiller 2003). All modeling methods, as an output variable, report a probability of presence (PoP) for each species.

Species niches were parameterized in the models using species presence-absence data from 7088 field vegetation plots located throughout the study area from three independent data sources. A total of 4090 vegetation plots were established in 1977–1979 within Banff National Park, Kootenay National Park, Jasper National Park, and Yoho National Park (Nielsen et al. 2003), 2849 plots were sampled between 2001–2008 in west-central Alberta by Nielsen et al. (2010), and 149 plots were sampled in the Willmore Wilderness Area in 2001–2003 (Gould 2007) and 2009–2010 (J. A. Gould, unpublished manuscript). Plots were distributed between 394 m and 2708 m elevation (mean 1603 m) and varied in location (alpine to valley bottoms) and aspect.

Environmental predictors for each plot included nine seasonal and annual climate variables, three topographic/radiative variables, and one remotely sensed variable of forest crown closure. Climate data were generated for the 1961–1990 historic period (prior to the influence of the recent anthropogenic warming signal and a likely period of recruitment for the generally long-lived shrubs that constitute most of the species we considered) using PRISM down-sampling (Daly et al. 1994) via a publically available software package that generates monthly, seasonal, and annual climate variables (Wang et al. 2012). Of the available climate variables, we selected nine that covaried least, including five temperature and precipitation metrics (mean annual temperature, average winter temperature, average summer temperature, winter precipitation, and summer precipitation); two dryness indices (annual heat moisture and summer heat moisture [Hogg 1997]); and two calculated temperature-based metrics (the number of frost-free days and the number of degree days above 5°C). Topographic/radiative predictor variables, which have previously been found important in describing species distributions for bear foods in the region (Nielsen et al. 2003, 2010), included a compound topographic index that incorporates moisture and drainage (Moore et al. 1991), a topographic heat load index that measures annual solar radiation with a lagged heat load effect for southwestern aspects using slope, aspect, latitude (McCune 2007), and finally a general slope/aspect topographic radiation based only on slope and aspect using the topographic radiation aspect (TRASP) index of Roberts and Cooper (1989) within the Geomorphometric and Gradient Metrics ArcGIS Toolbox (Evans 2011). Last, we included a remotely sensed metric of forest crown closure from McLane et al. (2009), as forest structure has been identified as an important local

predictor of occurrence for our species of interest (Nielsen et al. 2010).

Ecological niche models were validated using a random cross-validation of training data, where two-thirds of training points were used to build models, and the remaining one-third used to evaluate model projections. While cross-validations have been shown to be optimistic measures of model accuracy (Araújo et al. 2005), they have also been shown to be effective in selecting among modeling techniques (Roberts and Hamann 2012). Validations were performed using the area under the curve (AUC) of the receiver operating characteristic (Fawcett 2006). The AUC provides a threshold-independent evaluation of true presences vs. false presences for all probability of presence outputs simultaneously, where an AUC value of 1.0 is a perfect match, and where random PoP data would produce an AUC of 0.5.

Species habitat projections

Present day and future species' habitats were projected at 300 × 300 m resolution, with environmental predictor data generated as described previously. Future-climate grids were estimated for the area by calculating the arithmetic average of 14 general circulation model (GCM) outputs as temperature and precipitation anomalies from the present day, averaged across the 2071–2100 period (hereafter referred to as the "2080s"). The effectiveness of averaged multi-GCM climate projections has been questioned (Fordham et al. 2011), as using multi-model averages of climate has the effect of centralizing more extreme climate projections, which may be equally likely to occur. As a means of bookending the extent of potential future warming, two emissions scenarios, the aggressively warming A2 scenario and the moderately warming B1 scenario (IPCC 2007), were averaged separately, and results from both emissions scenario projections are presented.

Apart from the climate variables, future predictor data were left unchanged from present-day values, with the exception of estimates of crown closure. Projections of future crown closure were estimated using a separate niche modeling procedure, incorporating the same predictor variables as described above for the species models, but using only the Random Forest bootstrapped regression tree method (Breiman 2001). Crown closure models were evaluated by training the model with data from the northern half of the study area, and validating models with data from the southern half, to simulate a projection into warming climates. The correlation between modeled and observed crown closure in the southern half of the study area was $r = 0.49$.

Areas of agricultural use, surface water, and high alpine rock and ice were removed from the species habitat projections, as they were considered unsuitable future habitat. These areas were masked as absences and were not considered in any of the summary analyses.

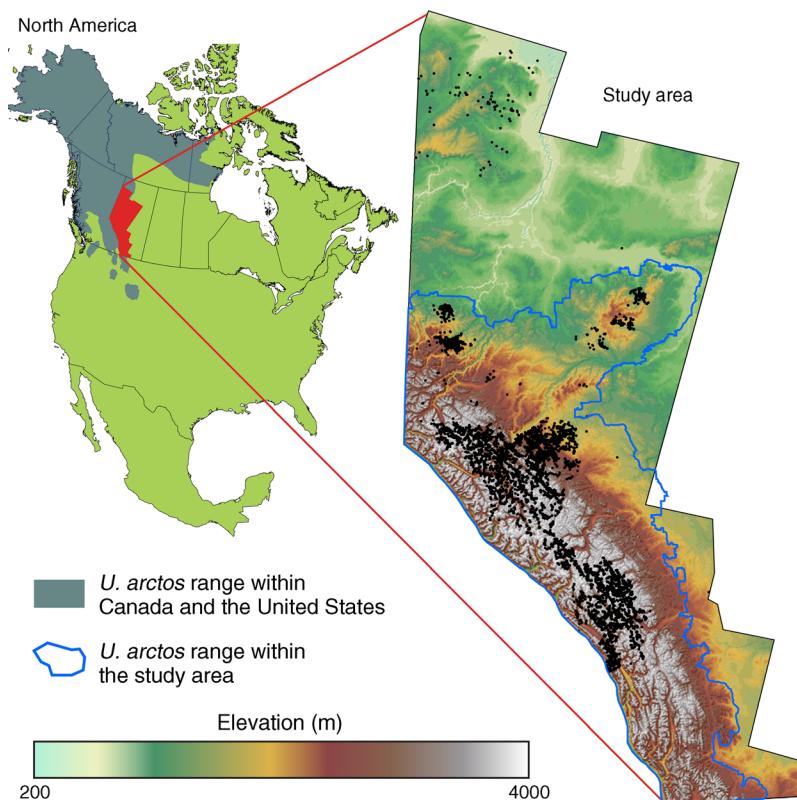


FIG. 1. Location of the study area in the western Canadian Rocky Mountains, showing topographic profile. Present-day grizzly bear range for the southern Canadian Rockies (Nielsen et al. 2009) is outlined in blue.

Masking these areas did not affect model validation statistics, as neither training nor validation data were located in these areas. To convert all other PoPs to binary presence–absence outputs, a threshold PoP was selected for each species. Threshold criteria that balance sensitivity and specificity have been shown to be more accurate than arbitrary thresholds or those based on maximizing Cohen’s kappa statistic (Jimenez-Valverde and Lobo 2007), but tend to favor errors of commission in the data (i.e., favoring sensitivity, or potential overestimates of species presence). To select a threshold for presence–absence delineation from the PoP data, the average of two methods was used: (1) the PoP that maximized the sum of sensitivity and specificity, and (2) the PoP that minimized the difference between the absolute values of sensitivity and specificity.

While maps show species projections for the entire study area, summary statistics of elevation profile and change in total distribution (area) were completed only for data within the boundary of present-day grizzly bear habitat (as defined by Nielsen et al. 2009) in order to quantify threats to bear foods for their currently inhabited range (shown in blue in Fig. 1).

Software

All modeling, analysis of results, and generation of output files were done within the R programming

environment (R Development Core Team 2013); all eight individual models were generated with the *BIO-MOD* package (Thuiller et al. 2009), AUC and associated statistics were calculated using the *ROCR* package (Sing et al. 2005), the PCA was performed using the base stats package, and rasters and graphics were generated using the *raster* package (Hijmans and van Etten 2012) and the *ggplot2* package (Wickham 2009).

RESULTS

Model validation

Area under cover (AUC) for all methods within each species is shown in Fig. 2. All AUC values for all species and all methods, including the number of observed presences and absences, are provided in Appendix A. With the exception of the surface range envelopes, which showed very poor model performance (median AUC = 0.61; maximum AUC = 0.68), model validations indicated good to excellent model fit for all methods, with median AUC values ranging from 0.74 for the classification tree method to 0.83 for Random Forest. The ensemble method of averaging outputs from all other methods performed better than any individual method (median AUC = 0.84). While it has previously been shown that including even poor-performing models in the ensemble calculations may increase the accuracy

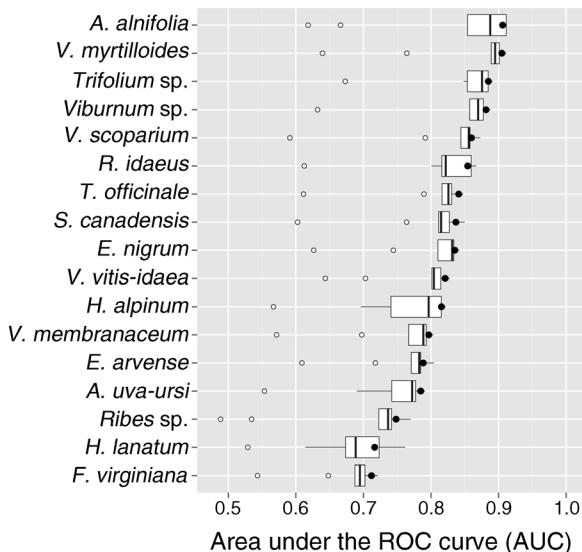


FIG. 2. Boxplot showing model accuracy as measured by the area under the curve (AUC) of the receiver operating characteristic (ROC) for each species and all modeling methods, including the ensemble mean method, the AUCs for which are shown as black circles. The boxes represent the interquartile range, with heavy lines as the median. Whiskers represent the range of the data, omitting Tukey outliers (greater than 1.5× the interquartile range), which are shown as open circles. A complete table of AUC values for each species within each method and number of observed presences and absences, including complete scientific names, is provided in Appendix A.

of the ensemble (Roberts and Hamann 2012), including the surface range envelope outputs in the ensemble decreased its accuracy and was thus omitted from the calculation. AUC values for individual species for the ensemble method ranged from 0.72 for *Fragaria virginiana* (wild strawberry) to 0.91 for *Amelanchier alnifolia* (saskatoon). As a simple metric of model agreement, we also examined the standard deviations of PoPs in the ensemble model. Within present-day grizzly habitat, PoP standard deviations tended to be low to moderate, with the greatest model agreement occurring in areas of higher elevation. The highest model disagreements in both B1 and A2 scenarios appear in the low-elevation prairies in the southern extent of the study area, along the bottoms of some southern river valleys, and in some of the warmer and drier low-elevation areas in the north.

Changes in species distributions

Complete summaries of habitat gained and lost for each species are shown in Table 1. Maps of PoP and plots of the distribution for each species along the observed elevation gradients for the modern and future periods are presented in Appendix B. Within present-day grizzly bear range, most species (with some notable exceptions) experienced increased PoPs in the 2080s projections for both the B1 and A2 warming scenarios relative to the 1961–1990 period. PoPs also typically increased from the B1 to the A2 scenario, suggesting a trend of increased habitats with increased warming. When PoPs were converted to presence or absence, most species demonstrated a corresponding increase in

TABLE 1. Summary of species’ projected elevation and area changes within occupied grizzly bear habitat (Nielsen et al. 2009) for the 2080s period for two emissions scenarios: B1 (moderate warming) and A2 (aggressive warming).

Species	Common name	Season	Elevation (m)		
			1961–1990		
			p10	p50	p90
<i>Amelanchier alnifolia</i>	saskatoon	aut	880	1378	1822
<i>Arctostaphylos uva-ursi</i>	bearberry	aut	1096	1497	1995
<i>Empetrum nigrum</i>	crowberry	aut	1587	1901	2176
<i>Equisetum arvense</i>	horsetail	spr	766	1036	1360
<i>Fragaria virginiana</i>	strawberry	aut	794	1219	1776
<i>Hedysarum alpinum</i>	sweet vetch	spr–aut	1219	1518	2111
<i>Heraclium lanatum</i>	cow parsnip	sum	809	1237	1846
<i>Ribes</i> spp.	gooseberry	aut	808	1218	1733
<i>Rubus idaeus</i>	raspberry	aut	778	1080	1493
<i>Shepherdia canadensis</i>	buffaloberry	aut	803	1459	1921
<i>Taraxacum officinale</i>	dandelion	spr–sum	791	1127	1582
<i>Trifolium</i> spp.	clover	spr–sum	781	1099	1552
<i>Vaccinium membranaceum</i>	huckleberry	aut	1139	1616	2035
<i>Vaccinium myrtilloides</i>	blueberry	aut	773	1046	1386
<i>Vaccinium scoparium</i>	grouseberry	aut	1634	1940	2239
<i>Vaccinium vitis-idaea</i>	lingonberry	aut	792	1134	1711
<i>Viburnum</i> spp.	cranberry	aut	786	1105	1501

Notes: Median elevations for the 1961–1990 period and the projected changes (Δ elev.) in 10th percentile (p10), median (p50), and 90th percentile (p90) elevation under each future-climate scenario are listed, as are total range area (Area) and percentage change in range area (Δ area) for the 1961–1990 observed climate and the two 2080s climate projections. The percentage of stable area (Stable area) represents the proportion of the species’ 1961–1990 range that is maintained in the projections for the 2080s. Trends of species’ seasonal use by bears (Season) are based on findings of Munro et al. (2006). Seasons are abbreviated as: aut, autumn; spr, spring; sum, summer.

projected range for the 2080s period for both scenarios (again, typically larger in the A2 than B1 scenario). *Amelanchier alnifolia* gained the most suitable habitat, increasing in projected area by 186% and 199% in the B1 and A2 scenarios, respectively. *Vaccinium membranaceum* (huckleberry) and *Vaccinium myrtilloides* (blueberry) also showed substantial increases in habitat, by 84–112% and 66–78%, respectively. Notable exceptions to increased trends include *Vaccinium scoparium* (grouseberry), which was projected to lose 92–95% of its habitat, *Empetrum nigrum* (crowberry), which was projected to lose 72–89% of its habitat, and wild strawberry, which was projected to lose 30–58% of its habitat. The remaining species gained or lost projected habitat in more moderate amounts, ranging from losses of 18% to gains of 70%.

In addition to the area of total habitat by species, the amount of stable habitat was also summarized within present-day grizzly bear range. The measure of stable area represents the proportion of a species' 1961–1990 habitat that remains suitable habitat in future projections (Table 1). While most species were projected to maintain between 94% and 100% of their 1961–1990 habitat, some species were projected to lose substantial amounts of habitat. *Empetrum nigrum*, *Vaccinium scoparium*, *Fragaria virginiana*, and *Arctostaphylos uva-ursi* (bearberry) in both scenarios, and *Hedysarum alpinum* in the A2 scenario, all lost considerable amounts of stable habitat (retaining between 3% and 67%). *Hedysarum alpinum* in the B1 scenario predicted an

increase in habitat area of 45% but a loss of stable area (only 56% stable), indicating that, while net habitat area may increase, just over half of the present-day range of the species remains suitable habitat in future projections.

In addition to changes in projected area of habitat, all species showed changes in their elevation profile, with a general future trend towards increasing median elevation, increasing 10th percentile elevation (the trailing downslope edge), and increasing 90th percentile elevation (the leading upslope edge) (Table 1; Appendix B). The largest increases in median elevation were projected in the A2 scenario for *Hedysarum alpinum* and *Fragaria virginiana*, with increases of 525 m and 423 m, respectively. With only one exception, the 90th percentile elevation of all species increased in both emissions scenarios. Median and 10th percentile elevation decreases were projected for some species including *Vaccinium membranaceum* (median decrease of 203 m in the A2 scenario), *Arctostaphylos uva-ursi* (median decrease of 101 m in the A2 scenario), and *Amelanchier alnifolia* (median decrease of 68 m in the A2 scenario). All three of these species are wide ranging in their present-day elevation profile. *Empetrum nigrum* was the only species exhibiting contradictory trends in elevation profiles for different emissions scenarios. Projected 10th percentile and median elevations for the species increased moderately in the B1 scenario (by 242 m and 193 m, respectively), but decreased substantially in the A2 scenario (by 993 m and 767 m, respectively).

TABLE 1. Extended.

Δ elevation (m)						Area 1961–1990 (×10 ⁵ km ²)	Δ area 2080s (%)		Stable area 2080s (%)	
2080s (B1)			2080s (A2)				B1	A2	B1	A2
p10	p50	p90	p10	p50	p90					
(-57)	-96	(+91)	(-51)	-68	(+153)	4.47	+186	+199	100	100
(-136)	-57	(+70)	(-109)	-101	(+49)	5.42	-11	-18	67	58
(+242)	+193	(+181)	(-993)	-767	(+201)	2.89	-72	-89	22	3
(+25)	+96	(+315)	(+34)	+152	(+513)	6.94	+30	+45	100	100
(+244)	+212	(+187)	(+440)	+423	(+329)	9.71	-30	-58	61	34
(+133)	+357	(+108)	(+449)	+525	(+207)	1.37	+45	-15	56	31
(+20)	+74	(+131)	(+20)	+74	(+131)	11.42	+17	+17	100	100
(+20)	+92	(+233)	(+21)	+94	(+245)	11.34	+17	+18	100	100
(+23)	+89	(+169)	(+44)	+192	(+404)	8.10	+28	+55	99	100
(+33)	-66	(+87)	(+19)	-124	(+61)	7.40	+42	+70	97	100
(+15)	+69	(+221)	(+31)	+153	(+374)	9.23	+16	+36	99	100
(+11)	+42	(+107)	(+20)	+80	(+244)	8.27	+13	+22	99	99
(-114)	-111	(+24)	(-335)	-203	(-4)	4.96	+84	+112	100	100
(+49)	+224	(+480)	(+56)	+265	(+591)	7.50	+66	+78	100	100
(+382)	+288	(+296)	(-414)	+171	(+319)	2.11	-92	-95	7	3
(+6)	+24	(+57)	(+17)	+85	(+107)	8.75	+13	+30	94	97
(+37)	+176	(+390)	(+43)	+205	(+474)	8.85	+44	+51	100	100

Changes in distribution of seasonal resources

When summarized by foraging season for grizzly bears (as per Munro et al. 2006), the diet richness (number of species present) during spring (hypophagia), summer (early hyperphagia), and autumn (hyperphagia) periods tended to be either stable or increasing (Fig. 3; Appendix C). It should be noted that these summaries reflect only the net balance of diet items (species counts), and do not reflect the loss of one species that is replaced by the arrival of another species (i.e., community turnover in diet composition). Springtime conditions showed no major change in diet richness for most of the present-day grizzly bear range, with the exception of some high mountainous areas that gain habitat for one species and for some regions along the eastern slopes and river valleys of the Rocky Mountains that lose a single species, reflecting the loss of *Hedysarum alpinum* habitat (Fig. 3). Grizzly bear habitat in the summertime is projected to maintain present-day diet richness or increase diet richness in the higher-elevation areas of the Rocky Mountains, with up to four additional species. Decrease in diet richness in summer occurs in the southernmost valley bottoms, losing up to two of the four summer species considered. The same trends as in the spring and summer were also present during the fall: a general stability of diet richness within present-day grizzly bear range. Decreases in habitat of up to three species occurred in the eastern slopes, while increases in high-elevation habitat of up to 11 of the 12 species considered.

DISCUSSION

Climate change vulnerability of grizzly bear food items

The lack of extensive projected range loss due to climate change for most plant-based grizzly bear food items suggests that widespread collapse of habitats due to losses in trophic web linkages on which bears depend is unlikely. In fact, the general trend within present-day grizzly bear range of the southern Canadian Rocky Mountains is towards more widespread availability and increased diet richness of bear foods. Changes in model projections that have high uncertainty could, however, alter responses. For instance, the general projection of increased diet richness ignores key species interactions such as competition, which may, despite environmental suitability for a new site, prevent future establishment (successful colonization).

Our models also assume an “equilibrium and perfect dispersal” scenario where species are expected to reach all suitable habitats by the 2080s. Owing to steep elevation clines in the area, this may be a reasonable assumption for many species, since emerging habitat would be geographically proximate to current habitat. However, some bear food items, particularly the ericaceous shrubs that are an important source of fruit (energy) to bears, are known to have low dispersal–establishment capacity, with their long-term persistence

in an area predominantly due to vegetative reproduction (Vander Kloet and Hill 1994, Regan et al. 2012). These species may therefore only persist in habitats that they currently occupy, and are projected to be within the environmental niche of the species in the 2080s (i.e., zero dispersal scenario). Less topographically diverse locations may be vulnerable to losing a large complement of their species richness, since the rate of migration would need to be higher, especially considering that these areas are more likely to be fragmented by anthropogenic barriers.

In addition to changes in specific locations of habitats, there were notable changes in the elevation profile of food items that have meaningful implications for bears. A general trend of uphill migration of species may increase habitat quality at higher elevations, thus offsetting losses elsewhere, and further providing a source population for rescue effects of sink populations. Given the propensity for human interactions to negatively affect bears and bear survival rates (Mattson 1990), the persistence of grizzly populations under such a scenario relies on the continued preservation of upslope habitats free from anthropogenic disturbance and human activity, as is a feature of the National Parks and other protected areas within current grizzly bear range. However, due to this trend of upslope movement, many downslope locations, such as lower foothills and valley bottoms, are projected to lose species richness by as much as 50% for summer species or 25% of the seasonally important hyperphagic season in late summer and autumn. In locations where increased upslope foraging is not possible or convenient, this may increase human–bear conflict, since food may be more limiting in these areas, as periods of food scarcity are known to increase human–bear conflict rates (Mattson et al. 1992, Pease and Mattson 1999, Gunther et al. 2004). However, given the mobility of the species and the general availability of higher-elevation habitats in the bear range examined here, bears may be able to adapt to these losses by using upslope resources or alternate food items. Indeed, prior studies have demonstrated seasonal adaptations in diet to interannual changes in resources, illustrating their dietary plasticity. For instance, in Yellowstone National Park, whitebark pine nuts are an important seasonal food source for grizzly bears when abundant, but when scarce, are replaced by false-truffles (*Rhizopogon* spp.) (Fortin et al. 2013). Overall, our models predict general increases in seasonal food resources, although changes in habitat for individual food items are predicted to occur, necessitating seasonal adaptation in resources consumed by bears or spatial adjustments in their habitat use relative to changes in food resource distribution.

While not entirely positive, our prognosis for the overall vulnerability of northern Rocky Mountain grizzly bears to climate change is markedly better than those for similar high-trophic-level mammals, including other species of bears. Recent assessments of food

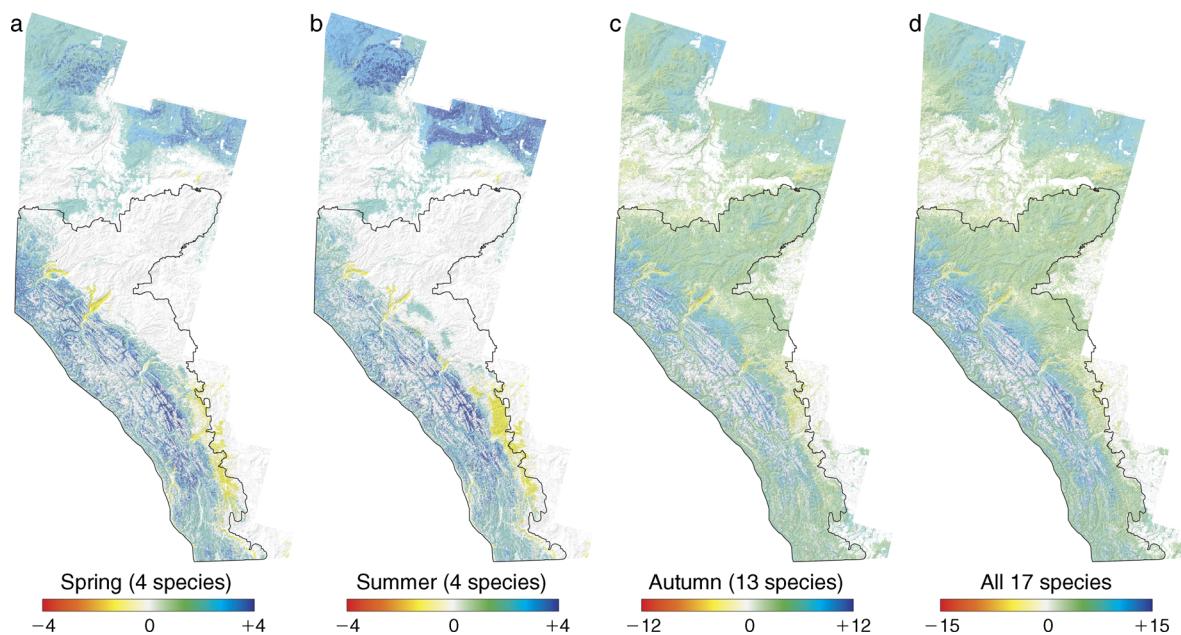


FIG. 3. Maps showing the change from the 1961–1990 period in number of species projected present for the A2 scenario of the 2080s period. Changes are shown by season for (a) spring, (b) summer, and (c) autumn, with the seasonally important bear food source species (see Table 1). (d) Changes in counts of all 17 species considered (all seasons together), are also shown. Areas of unsuitable range (agriculture, rock, ice, water, etc.) are masked in white. The range of present-day grizzly bear habitat in the southern Canadian Rockies is shown as a black outline. Maps of absolute counts of species are shown in Appendix C.

resources for a population of giant pandas (*Ailuropoda melanoleuca*) in China project substantial reductions in availability of many bamboo species (Tuanmu et al. 2013), representing an acute threat to this species. As a second example, the polar bear (*Ursus maritimus*) is a species of conservation concern that has received extensive public exposure in terms of its sensitivity to climate change (Courtland 2008). Primary threats to polar bears from climate warming relate to habitat loss, and in particular, losses of sea ice, which can adversely affect hunting and breeding. Less sea ice coverage and earlier spring sea ice breakup results in less ideal seal-hunting conditions, shorter on-ice feeding periods, and more energy expended in swimming activities, leading to a general decrease in reproduction rates and litter sizes (Derocher et al. 2004). While grizzly bears in the Canadian Rockies do not appear to face such challenges, the implications for all upper-trophic-level species is one of general uncertainty regarding the availability of food resources and habitat quality. A reiteration of the conclusions by Tuanmu et al. (2013) would serve well here: it is important to consider interspecific interactions when assessing effects of climate change.

Most vulnerable species

Species considered in our study that could be labeled “vulnerable” take two forms. First, we identify noncritical bear food species that show major reductions and/or changes in habitat. In this case, the species in question may itself be at high risk, but the effect of its loss on the

overall quality of bear habitat may be minimal due to the availability of other food resources and low use by grizzly bears. Second, we identify critical bear food species, such as those that form a substantial proportion of diets throughout the year, or those that are highly important to bears in a given season, which are projected to have reduced range sizes or to have limited stable habitat between the present and future.

An example in the first case, *Vaccinium scoparium*, shows the largest habitat loss of any species considered in the B1 and A2 scenarios for the 2080s (92% and 95% loss, respectively) and the smallest amount of stable habitat (only 7% and 3% for B1 and A2, respectively). While not a critical food source by itself, bears rely heavily on fruit from all forms of ericaceous shrubs during the autumn hyperphagic period. Other ericaceous species such as *Vaccinium myrtilloides*, *Vaccinium vitis-idaea* (lingonberry), and the more critical *Vaccinium membranaceum* all show increases in habitat and nearly complete maintenance of their present-day ranges, thus suggesting lower vulnerability and risk to climate change. Projections for *Empetrum nigrum* are similar to *Vaccinium scoparium*, with habitat losses of up to 89% and amount of stable habitat as low 3%. Not surprisingly, these two species have the highest-elevation ranges in the present day of all species considered. This, in combination with projected upward elevation shifts in suitable climate conditions, suggests that suitable habitat for these species may be pushed out of alpine areas and “off” mountain tops entirely by future

warming. Other high-elevation species considered, including *Vaccinium membranaceum*, do not exhibit the same increases in elevation and habitat losses under future-climate scenarios. *Vaccinium membranaceum* is less elevation restricted than either *Vaccinium scoparium* or *Empetrum nigrum*, as is evident by their much lower 10th percentile elevations. This wider climate niche may make them less sensitive to changes, particularly in temperature.

Hedysarum alpinum, the other notable high-elevation species considered in our study, is of particular concern, as root digging of this species represents an important spring and autumn food source for bears (Munro et al. 2006). While this species exhibits a less-restrictive elevation profile, much like *Vaccinium membranaceum*, habitat projections shows large increases in elevation in future scenarios, similar to *Vaccinium scoparium* and *Empetrum nigrum*. However, corresponding changes in area of habitat are not consistent between future scenarios, with *Hedysarum alpinum* gaining 45% area of habitat in B1, while losing 15% area in A2. This difference is explained by the increased amount of habitat lost along the east slopes of the Rocky Mountains in the A2 scenario, while new upslope habitat emerges in roughly equal amounts in both scenarios. Density plots of elevation for future-climate scenarios (Appendix B), show equal probabilities of high-elevation habitat in both scenarios but disappearing habitats of mid-elevation in the A2 scenario. The net result for *Hedysarum alpinum* is that, while available habitat may not be drastically restricted in the future, proportions of stable area suggest that half to two-thirds of populations will be required to physically migrate into new locations to be maintained within the landscape. While these migrations may only be short upslope distances, the simple necessity of physical migration for the survival of the majority of this species raises concern, especially given the species' critical importance as a bear food source. Future research exploring the ecological niche of this species is needed given its seasonal importance to bears and the contradictory results observed here for different magnitudes of climate warming.

Two less critical food sources for bears, *Fragaria virginiana* and *Arctostaphylos uva-ursi*, are predicted to decrease in range. In both cases, this result was unexpected, as these species are widespread within the present-day study area as well as throughout western North America, suggesting a tolerance for warmer conditions such as those projected for our future study area. In these cases, the projected habitat losses could be a result of the limits of the model training data, which may not adequately capture the full climate niche of these species, particularly the warmer end of the niche that would be represented to the south of our study area. This is especially visible in *Fragaria virginiana*, which loses extensive habitat through the warmest areas of its present-day range through the center of the study area.

By contrast, future projections for *Arctostaphylos uva-ursi* suggest substantial loss of habitat in the low-elevation river valleys throughout the Rocky Mountains, with no emergence of higher-elevation habitats, as is the case with other widespread species such as *Taraxacum officinale* (dandelion). This would be an expected trend if the range of *Arctostaphylos uva-ursi* is not temperature driven, but rather defined by other environmental predictors, which may be the case.

CONCLUSIONS

This first examination of grizzly bear plant food resources under anthropogenic climate warming provides reasons for optimism, but also reasons for concern. With only a few exceptions, most species considered in this study appear to be at low risk of widespread extirpation, and often do not have large migration requirements to reach locations of suitable future habitat given regional topographic heterogeneity. In fact, many species show the potential to increase in range under future climate warming. This would suggest that the majority of plant-related grizzly bear food items should continue to be available to bears within their current range through the coming century. We have, however, identified a few species of particular interest that show severe projected range losses under future climate warming: high-elevation, restricted species such as *Empetrum nigrum* and *Vaccinium scoparium*, both of which are projected to lose nearly all their range within present-day grizzly bear habitat. However, the effect of the loss of these individual species on bear habitat quality is difficult to assess, given the continued availability of most other autumn fruit resources (including the fact that these species are less commonly used by bears) and the uncertainty around the species' capacity to adapt to these losses through changes in foraging behavior. Of greater concern are the high rates of projected habitat loss or instability of *Hedysarum alpinum*, a spring and autumn food resource for grizzly bears when little else is available.

It should be noted that this study does not consider food quality (i.e., energetics), local abundance, or the potential introduction of new, invasive food resources, which may also be affected in unpredictable ways by anthropogenic alterations in the climate regime. We also did not consider how climate change may affect local sources of animal protein that bears rely on, including ungulates and ants (Munro et al. 2006), although generally warmer climates for cool mountain environments would be expected to benefit these species, particularly ants. Future investigations into how climate change will affect quality and abundance of these food resources, as well as research into potential behavioral responses of bears to changing resource availability, both seasonally and spatially, is needed to fully understand the impacts of climate change on grizzly bear habitats.

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SUPPLEMENTAL MATERIAL

Appendix A

Table of validation statistics for all modeling methods for all species, including the area under the curve of the receiver operating characteristic (AUC), sensitivity, specificity, and sample sizes ([Ecological Archives A024-065-A1](#)).

Appendix B

Maps and summary plots of model projections for each species for the present and future, including (A) maps of model projections of probability of presence (PoP) for the present and future scenarios; (B) maps of projected change in habitat based on changes of modeled species presence/absence; (C) probability density function plots for projected PoPs; and (D) probability density function plots for elevations of projected suitable habitat ([Ecological Archives A024-065-A2](#)).

Appendix C

Seasonal and annual maps showing counts of projected species for the present and future periods ([Ecological Archives A024-065-A3](#)).