

# Earth's Future

## RESEARCH ARTICLE

10.1029/2020EF001537

### Key Points:

- Early spring snowpack declines sharply in the lower half of wolverine den elevations studied but persists through midcentury higher up
- Springtime snowpack is less affected by climate change on north and east facing slopes leading to potential for climate refugia
- High-resolution modeling that resolves topographical aspect may provide useful information to support conservation decisions

### Supporting Information:

- Supporting Information S1

### Correspondence to:

J. J. Barsugli,  
joseph.barsugli@colorado.edu

### Citation:

Barsugli, J. J., Ray, A. J., Livneh, B., Dewes, C. F., Heldmyer, A., Rangwala, I., et al. (2020). Projections of mountain snowpack loss for wolverine denning elevations in the Rocky Mountains. *Earth's Future*, 8, e2020EF001537. <https://doi.org/10.1029/2020EF001537>

Received 3 MAR 2020

Accepted 2 SEP 2020

©2020. The Authors.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

## Projections of Mountain Snowpack Loss for Wolverine Denning Elevations in the Rocky Mountains

Joseph J. Barsugli<sup>1,2</sup> , Andrea J. Ray<sup>2</sup> , Ben Livneh<sup>1,3</sup> , Candida F. Dewes<sup>1,2</sup> , Aaron Heldmyer<sup>3</sup>, Imtiaz Rangwala<sup>1,4</sup> , John M. Guinotte<sup>5</sup>, and Stephen Torbit<sup>5</sup>

<sup>1</sup>Cooperative Institute for Research in Environmental Sciences, University of Colorado Boulder, Boulder, CO, USA,

<sup>2</sup>NOAA Physical Sciences Laboratory, Boulder, CO, USA, <sup>3</sup>Department of Civil, Environmental and Architectural

Engineering, University of Colorado Boulder, Boulder, CO, USA, <sup>4</sup>North Central Climate Adaptation Science Center,

University of Colorado Boulder, Boulder, CO, USA, <sup>5</sup>United States Fish and Wildlife Service (USFWS), Lakewood, CO, USA

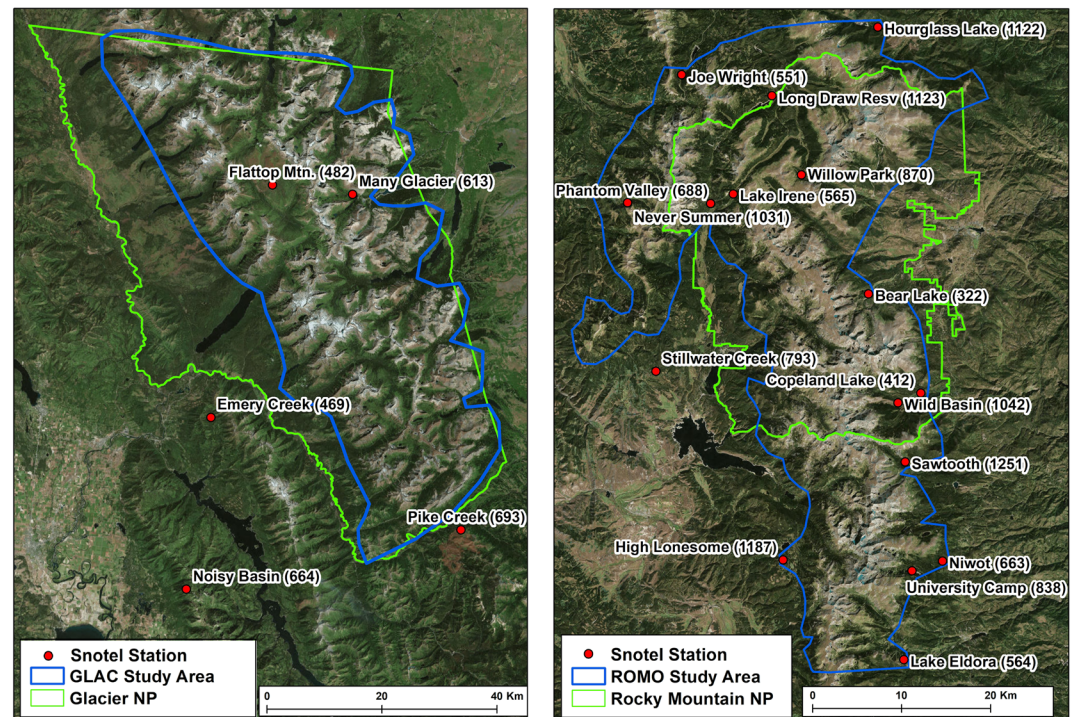
**Abstract** Future reduction in mountain snowpack due to anthropogenic climate change poses a threat to many snow-adapted species worldwide. Mountain topography exerts a strong control on snowpack not only due to elevation but also through the effect of slope and aspect on the surface energy balance. We develop high-resolution projections of snowpack in order to provide improved, physically based estimates of the spatial distribution of future snowpack to inform species conservation efforts for the wolverine (*Gulo gulo*) in two study areas in the Rocky Mountains: one in Montana with known den sites and one in Colorado with recent wolverine activity and potential for reintroduction. Here we assess springtime snowpack loss in actual and potential denning areas under five future climate scenarios for the mid-21st century. Snowpack in April and May is likely to persist into the mid-21st century in the upper half of current denning elevations in all but the warmest future climate scenario, while large declines are projected for the lower half of the denning elevations. We gain new insight into the influence of topographical aspect on future snowpack and quantify the potential for enhanced snow persistence on north and east facing slopes under future scenarios that is only revealed in simulations where terrain slopes are resolved.

**Plain Language Summary** Climate change and its effect on snow are a threat to high mountain ecosystems and species worldwide. The future of mountain snowpack is complex, with multiple drivers, and with a strong elevation dependence. What has received much less attention is the dependence on topographical aspect—how will the snowpack on north facing versus south facing slopes respond differently under climate change. In this paper we develop snow projections motivated by a conservation issue for the wolverine: the future of the springtime snowpack at elevations of observed and potential wolverine denning for two study areas in the Rocky Mountains by the mid-21st century. While there is significant snowpack loss in the lower half of denning elevations, the upper denning elevations retain springtime snowpack, supporting conservation actions through midcentury in these regions.

## 1. Introduction

Climate change is a threat to high mountain ecosystems and species worldwide (Hock et al., 2019; Huss et al., 2017). In particular, the future of mountain snowpack is an important factor in assessing the vulnerability of many snow-adapted species (e.g., Boelman et al., 2019; Carroll, 2007; Jackson et al., 2015; Johnston et al., 2012; Mahoney et al., 2018; McKelvey et al., 2011; Sivy et al., 2018). The future of mountain snow is complex (Brown & Mote, 2009; Kapnick & Delworth, 2013), with a strong elevation dependence. What has received less attention is the dependence on topographical aspect (López-Moreno et al., 2014; Lundquist & Flint, 2006), which requires much finer-scale modeling to resolve yet may be important information to support conservation efforts. In this paper we develop high-resolution snow projections motivated by a conservation issue for the wolverine: the future of the springtime snowpack at elevations of observed and potential denning for two study areas in the Rocky Mountains, one in Montana and one in Colorado (Figure 1).

Wolverines (*Gulo gulo*) are the largest member of the mustelid family. They are Holarctic in their distribution (Copeland & Whitman, 2003; Hash, 1987) with generally low population density and correspondingly low reproductive rates, compared to most carnivores (Persson et al., 2006; Royle et al., 2011). In North



**Figure 1.** The high-resolution modeling study area domain (blue outline) consists of high-elevation areas within and in the vicinity of Glacier (GLAC, left) and Rocky Mountain (ROMO, right) national parks. SNOTEL stations used for model validation are indicated by red dots. Study areas were chosen to encompass drainages with elevations from the ridgetops down to approximately 250 m below tree line and do not follow National Park boundaries.

America, wolverines (*G. g. luscus*) declined at the turn of the 19th century and were extirpated from much of their formerly occupied habitat (Aubry et al., 2007; Schwartz et al., 2007). The recent population in the conterminous United States has been estimated through statistical modeling to be 318 (range 249–626) individuals, with the largest numbers in the states of Washington, Montana, Idaho, and Wyoming (Inman et al., 2013). This population is currently being re-evaluated for listing as a threatened species under the Endangered Species Act (ESA) due to recent litigation (Defenders of Wildlife et al. vs. Sally Jewell et al., 2016). Past regulatory action (United States Fish and Wildlife Service [USFWS], 2014) identified climate change as a potential threat yet expressed significant uncertainty regarding how fine-scale spatial changes in the springtime snowpack might affect denning site availability, providing the specific motivation for this work.

Persistent spring snowpack has been cited as an important factor in determining suitable habitat for the wolverine (e.g., Aubry et al., 2007; Peacock, 2011) and in particular for den site location. This empirical relationship was the motivation for the climate envelope analysis by Copeland et al. (2010) and McKelvey et al. (2011), henceforth McKelvey. In McKelvey, climate change projections of snowpack using coarse-scale hydrologic modeling ( $>30 \text{ km}^2$  per gridcell) were then used to characterize future wolverine habitat. Reduction in the area of this climate envelope of 33% by 2045 and 67% by 2085 (for the mean of an ensemble of climate model projections) and a fragmentation of this envelope were cited as a potential threat to the viability of this wolverine population by the end of the 21st century. Availability of snow at current wolverine denning elevations was only considered indirectly in these studies. Recent work (Aronsson & Persson, 2017; Jokinen et al., 2019) has documented wolverine denning in areas with minimal or no persistent spring snow cover, questioning the absolute necessity of persistent springtime snow for wolverine denning success. Nonetheless, the strength of the above empirical relationships, and the use of Copeland et al. (2010) and McKelvey studies in prior regulatory litigation, justifies the investigation into the future of snowpack amount and extent.

Numerous studies document declines in western U.S. snowpack (Mote et al., 2005, 2018; Pederson et al., 2011; Pierce et al., 2008). Reduction in western U.S. snow water equivalent (SWE) has been formally attributed to anthropogenic climate change (Pierce et al., 2008) through the impacts of warmer temperatures on accumulation and melt. A common feature of these studies is that the greatest losses are documented for elevations and latitudes where winter temperatures are near freezing, particularly in coastal mountain ranges and the lower elevations of interior ranges (Regonda et al., 2005). At higher elevations in the Rockies the observed trends have been dominated by precipitation forcing rather than by temperature (Mote et al., 2018).

Western U.S. snowpack is projected to decline further as the climate warms. The resolution of global climate models is typically insufficient to directly simulate snowpack in mountainous regions. Dynamical downscaling (~50 km, McCrary & Mearns, 2019; Rhoades et al., 2017), variable-resolution climate models (~28 km, Rhoades et al., 2017) and statistical downscaling followed by fine scale hydrologic modeling (6–12 km, Christensen & Lettenmaier, 2007; Littell et al., 2011; Mote et al., 2018) have all been used to model snowpack change over the Western United States and project overall decline in snowpack, while considering multiple future climate scenarios. As with historical snowpack changes, the vulnerability of snowpack has a strong elevation dependence in mountainous terrain (Christensen & Lettenmaier, 2007; Rhoades et al., 2017). Additionally, for much of the northern tier of the United States, most of the climate models in the Coupled Model Intercomparison Project, Phase 5 (CMIP5, Taylor et al., 2012) project an increase in winter-time precipitation (Collins et al., 2013). Increasing precipitation may offset temperature-driven snow loss at higher elevations within a mountain range, provided winter temperatures remain cold enough such that sufficient snowpack may accumulate before the critical denning period of March through May in this region. While snowfall (vs. rain) is directly affected by air temperature (and humidity), snowmelt depends on the net energy flux into the snowpack, and hence on solar and longwave radiation, sensible and latent turbulent fluxes, and heat flux from the ground and from precipitation (e.g., Jennings et al., 2018). Solar radiation depends strongly on topographic aspect. The differing energy balance on north vs. south facing slopes has been shown, for a small number of individual locations (López-Moreno et al., 2014) and for small areas (Keller et al., 2005), to lead to greater snow persistence on north facing slopes under climate warming scenarios. Snow albedo (modulated by dust deposition, for example) also strongly affects the surface energy balance during the melt season and interacts nonlinearly with other climate change drivers (Deems et al., 2013). However, we do not consider changes in dust deposition in this study.

The current study assesses the persistence of spring snow at the landscape scale with 250 m spatial resolution for midcentury climate scenarios (nominally the climate of 2041–2070, centered on the year 2055) for the purpose of ecological application. It builds on and refines the methods in McKelvey (see supporting information for a methodological comparison). McKelvey and the other papers on which that study was based used bulk measures of snowpack (extent and depth) as proxies for wolverine denning and habitat, motivating our use of an energy-balance snow model rather than a more detailed model of snowpack structure. Further motivation for this modeling choice comes from the observation that wolverine are relatively plastic in their denning, with dens in rugged and steep mountains often associated with boulders, wood debris, and fallen trees under the snow (Jokinen et al., 2019; Magoun & Copeland, 1998), so that snowpack internal structure may be of less concern.

A key advance of this study, enabled by the high resolution, is to quantify the role of topographical aspect in snow persistence under climate change scenarios and to include this effect in assessing the extent of snow cover in climate projections. Furthermore, we explicitly consider a range of temperature and precipitation change consistent with CMIP5 model projections and consider the role of variability—how snowpack in wet and dry years may be impacted differently by climate change, whereas McKelvey chose future scenarios based only on the range of temperature change. While climate studies at this resolution and scale are not common, two are worth noting here. Cooper et al. (2016) simulated two large river basins in Oregon at 250 m resolution using an energy balance snow model and concluded that recent low-snow years were not a close analog for future warming. Bavay et al. (2013) use a detailed snow process model, Alpine3D (Lehning et al., 2006), for three future climate scenarios at 250 m resolution for a 7,000 km<sup>2</sup> domain in Switzerland, finding an upward shift in snow climate of 200–400 m by midcentury and 400–800 m by the end of this century.



## 2. Methods and Data

### 2.1. Study Areas

Two study areas were selected in consultation with USFWS personnel. They comprise a northern, relatively wet, and low-elevation mountainous area in Glacier National Park, Montana (Figure 1a, abbreviated GLAC) that is currently occupied by wolverines, and a comparatively dry and high elevation area located about 1,000 km south in and near Rocky Mountain National Park, Colorado (Figure 1b, abbreviated ROMO) that has had recent documented wolverine occurrence (Packila et al., 2017) and could be a potential reintroduction site for wolverines. Both model domains encompass contiguous hydrologic drainages that span elevations from approximately 250 m below tree line to the maximum elevation in each domain (962–3,166 m in GLAC, and 2,563–4,253 m in ROMO). This elevation range includes a denning elevation band determined from observed den sites (1,500–2,300 m) in GLAC and inferred denning elevations (2,700–3,600 m) in ROMO (see below).

### 2.2. DHSVM Model and Inputs

The Distributed Hydrology Soil Vegetation Model (DHSVM version 3.1.2) provides a physically based simulation of land surface hydrology, including snowpack. The physical processes include a full surface water and energy balance model, a two-layer canopy model, a multilayer soil model, a two-layer snowpack model (Wigmosta et al., 1994). It has been used in many studies that have provided realistic hydrologic simulations in topographically complex areas (e.g., Livneh et al., 2015). The model has explicit treatment of topographic slope and aspect. The model was selected for developing snowpack projections because it can be run at a fine spatial scale yet is able to be run over extensive domains.

The model was set up for both study domains on a 250 m grid in Universal Transverse Mercator coordinates within the modeling domain defined within the polygons shown in Figure 1. Soil properties (STATSGO, Miller & White, 1998) and geologic information (Green, 1992) based on soil survey data, land cover at 30 m resolution (Wickham et al., 2014) as well as a digital elevation model (DEM) at 1/3 arc-second ( $\sim 10 \text{ m} \times 7 \text{ m}$  at 45 N, Gesch et al., 2002) were adapted to the model grid, in order to generate the necessary model input layers. A soil hydraulic routing network was also determined from the DEM, though in this project we do not investigate the runoff. The effect of slope and aspect on incoming solar radiation is implemented through a computation of the degree of shading for each 250 m pixel that was variable throughout the day and differed from month to month based on the solar angle and the DEM. The model requires inputs of time-varying meteorological fields on subdaily time scales. Snow water equivalent was output on the 1st and 15th of the month from 1 March to 1 June for every year of the simulation and projections (1998–2013 and their future analogs using the delta method). The twice-monthly output is consistent with the time-scales investigated in previous literature (Copeland et al., 2010; McKelvey et al., 2011), and with the paucity of landscape-scale biological data on CONUS wolverine at submonthly scales. Future work on the impacts of daily weather variations (of the type proposed in Boelman et al., 2019, for example) could incorporate daily model output.

The DHSVM model inputs were derived in a multistep process. First, values of daily minimum temperature, daily maximum temperature, and precipitation were extracted from the Livneh gridded dataset (Livneh et al., 2015), which has a grid resolution of 1/16th degree in latitude and longitude ( $\sim 7 \times 5 \text{ km}$  at 45 N). These daily values were disaggregated in time using the VIC modeling system's utilities (Bohn et al., 2013). Solar radiation, downwelling longwave radiation, and specific humidity were derived from empirical relationships using the MTCLIM algorithms in VIC modeling system. In addition to the global evaluation in Bohn et al. (2013) the MTCLIM algorithms have been evaluated at two alpine sites in Colorado (Livneh et al., 2014) finding small overall positive biases ( $< 3\% \text{ RH}$ ,  $< 17 \text{ W m}^{-2}$  shortwave, and  $< 8 \text{ W m}^{-2}$  longwave). The radiative biases are small compared to the seasonal cycle in radiation, so the effect on snowmelt timing is likely to be small and to affect the historical and future simulations similarly. The Livneh data were then interpolated to the 250 m DHSVM grid using an inverse-distance weighting algorithm along with assumed elevational dependence in temperature and precipitation. The baseline historical simulation was run for January 1997–December 2013, with the first year removed from analysis as a model spin-up period. (Note that a longer spin-up would be required to study soil moisture and runoff).



Primary validation of the DHSVM historical simulation was done in comparison against snow data from nine Snow Telemetry (SNOTEL, Natural Resources Conservation Service, n. d.) sites in the ROMO study area that were in operation during 1998–2013, and three SNOTEL sites in and adjacent to the GLAC study area that are noted in Figure 1. The spatial distribution of snow cover was assessed by comparison with MODIS remotely sensed snow cover data (MODIS/Terra daily snow cover version 6, MOD10A1.006, K. Hall & Riggs, 2015). Details of the model validation and parameter adjustment procedure are provided in the supporting information, along with a discussion of caveats for our modeling approach.

### 2.3. Snow Depth Computation

DHSVM does not compute snow depth (SD) as a separate quantity but instead returns snow water equivalent (SWE). To approximate the snow depth from SWE we adopt a uniform value of 2.5:1 for the SD:SWE ratio, corresponding to a bulk snow density of 0.4 for 1 May and 15 May. For 15 April conditions, we adopt a bulk density of 0.33 which yields a conversion factor of 3.0:1. Median 2000–2013 density among SNOTEL stations in Figure 1 of 0.33 for April average and 0.38 for May average conditions. These values are typical for mature springtime snowpack in this region as determined from observations (Mizukami & Perica, 2008). Two spatially extensive products that model variable snow density were also investigated for comparison. The Snow Data Assimilation System product (SNODAS, National Operational Hydrologic Remote Sensing Center, 2004) from the NOAA National Operational Hydrologic Remote Sensing Center points to a very narrow density range of about 0.37–0.39 for 1 May conditions (not shown). Snow depth and SWE products from the Littell et al. (2011) hydrologic model runs (data downloaded from <https://cig.uw.edu/datasets/wus/> on 30 September 2016) used in McKelvey also indicate bulk snow densities in this range (not shown). In the interest of simplicity, the above values were adopted for this study. Because snow depth is considered here mainly as a proxy for the snow environment at denning elevations, the conclusions of this study are not sensitive to the choice of conversion factor within the ranges indicated by the above analysis. In addition, we show analyses for the elevation dependence of SWE changes (see Figure S6), which is not dependent on assumptions about snow density.

### 2.4. Inferred Denning Elevation Band in ROMO

As there are no documented wolverine dens in the ROMO study area, the potential denning elevation band was inferred from a least squares linear regression of den site elevations versus latitude for 47 documented wolverine dens in the contiguous United States (Idaho, Montana, Wyoming, Washington, and California). Taking into account the scatter in elevations about the regression line, the model indicates that potential den sites in the ROMO study area would lie approximately between 2,700 and 3,600 m elevation. The procedure is documented in more detail in the USFWS species status assessment for the wolverine (J. Guinotte, pers. comm.). The total change in snow covered area and the analysis of SWE change versus aspect are not strongly dependent on whether only the denning band is considered, or the entire domain.

### 2.5. Snow Depth Threshold

We analyze snow-covered area with depth of at least 1.0 m (denoted by  $SCA_{1.0}$ ) on 15 April and at least 0.5 m ( $SCA_{0.5}$ ) on 15 May. The snow depth thresholds were arrived at by an analysis of the DHSVM modeled snow depth at known wolverine denning sites in Glacier National Park (Table 1). With the exception of one site that had melted out by 15 May, the other sites all have snowpack between 0.5 and 2.4 m on that date, with a median of 0.6 m. For 15 April the median modeled snow depth is 1.3 m with a range from 0.7 to 3.0 m, with only one site below 1.0 m depth. Subgrid variations would result in locations of deeper and shallower snow within the 250 m pixel that are not explicitly modeled, so we interpret modeled snow depth as an indicator of snow availability at typical denning locations and times of year rather than an exact site-specific value.

### 2.6. Climate Change Scenarios

Climate change scenarios are implemented using a change-factor, or “delta” method. Some benefits and drawbacks of the delta method for conservation applications are discussed in (Sofaer et al., 2017). Five future climate scenarios are considered which encompass the range of CMIP5 cold-season temperature and precipitation changes between the periods 1986–2015 and 2041–2070 (Table 2). We first compiled output for temperature and precipitation projections for 34 CMIP5 GCMs (Table S3) from the Reclamation Downscaled CMIP3 and CMIP5 Archive of 1-degree re-gridded raw GCM output for Representative Concentration Pathways (RCP) 4.5 and 8.5, for a total of 68 GCM projections (Reclamation, 2013). Figure S11 shows

**Table 1**  
*Modeled Snow Depth at Den Sites in the Glacier Study Area as Compiled by USFWS*

Den site	Date observed (month-year)	Melt-out date (MODIS)	15 April snow depth dhsvm (m)	1 May snow depth dhsvm (m)	15 May snow depth dhsvm (m)	Den type
1	3 April	25/5/2003	1.32	1.07	1.04	Natal
2	3 May	25/5/2003	1.32	1.07	1.05	Maternal
3	4 April	4/6/2004	1.96	1.46	1.13	Natal
4	4 April	29/6/2004	1.0	0.75	0.54	Maternal
5	4 May	29/6/2004	1.07	0.83	0.65	Maternal
6	5 March	11/6/2005	1.6	1.11	0.58	Maternal
7	5 April	11/6/2005	1.6	1.11	0.58	Natal
8	5 May	11/6/2005	1	0.76	0.47	Maternal
9	6 March	25/5/2006	3.05	2.56	2.44	Unknown
10	6 April	14/5/2006	0.68	0.26	0	Unknown
11	6 April	7/6/2006	2.83	2.4	2.38	Unknown
12	6 May	31/5/2006	1.14	0.79	0.61	Maternal
13	6 May	31/5/2006	1.14	0.79	0.61	Natal
14	7 May	4/6/2007	1.82	1.28	0.68	Natal

*Note.* Melt-out date determined at each pixel from MODIS remotely sensed snow cover as the first day after March 1 when NDSI  $\leq 0.1$ .

these changes averaged over a latitude-longitude box encompassing the GLAC and ROMO study areas for each of the 68 projections (red circles). We found a large range in daily average temperature increases (1–4°C) and changes in precipitation (–5% to +20%) for these regions, reflecting uncertainty in model sensitivity and to a lesser extent internal variability. Five GCM projections were chosen for each study area (black circles) to largely span this uncertainty range. The filled blue circles show the three scenarios considered in the McKelvey study for the 2030–2059 period, as inferred from the Littell et al. (2011) hydrologic data, indicating that their choice of scenarios does not adequately represent the range of possible precipitation futures for the ROMO study area. For each of these GCMs, we calculated changes in average daily maximum temperature, minimum temperature, and precipitation for each month of the year. These monthly change factors were applied to the maximum temperature, minimum temperature, and precipitation inputs to DHSVM resulting in changes to humidity and radiation inputs through the use of the MTCLIM algorithm. The chosen scenarios are listed in Table 2.

### 3. Results

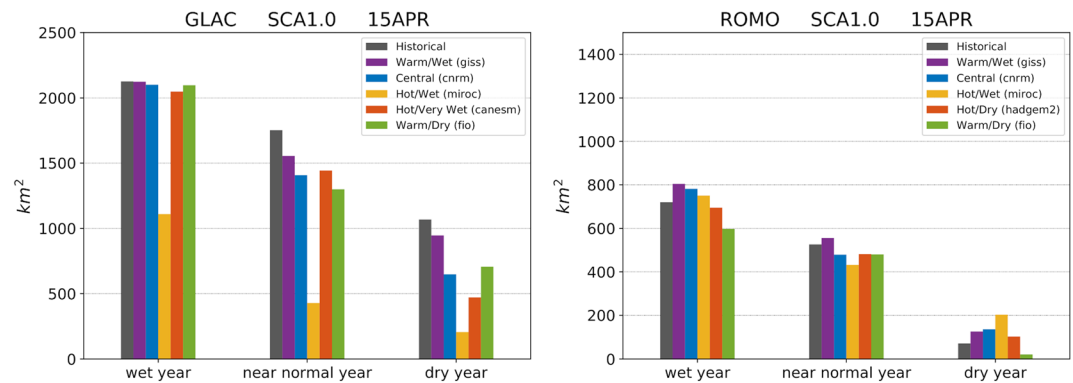
#### 3.1. Overview

To orient the reader, a brief overview of the methods is presented here. Results are shown for the two study areas defined above: GLAC in Montana and ROMO in Colorado (Figure 1). The DHSVM model at 250 m horizontal resolution is used to simulate the evolution of the snowpack over the historical period 1998–2013. Five future climate scenarios are considered that largely encompass the range of CMIP5 cold-season temperature and precipitation changes between the periods 1986–2015 and 2041–2070 (Table 2). These

**Table 2**  
*Change in Cold Season (October–April Average) Temperature and Precipitation, and Change in Snow Covered Area of 1 m Depth on 15 April and 0.5 m on 15 May, for Five Climate Change Scenarios*

Scenario (GCM)	GLAC study area (Montana)				ROMO study area (Colorado)			
	$\Delta T$ (K)	$\Delta P$ (%)	$\Delta SCA_{1.0\ 15}$ April (%)	$\Delta SCA_{0.5\ 15}$ May (%)	$\Delta T$ (K)	$\Delta P$ (%)	$\Delta SCA_{1.0\ 15}$ April (%)	$\Delta SCA_{0.5\ 15}$ May (%)
Central (cnrm)	2.2	5	–23	–31	2.5	8	+1	–24
Hot Very Wet (canesm)	3.2	20	–32	–39	—	—	—	—
Hot Dry (hadgem)	—	—	—	—	3.5	–5	–7	–43
Hot Wet (miroc)	4.2	10	–71	–60	3.7	18	+1	–32
Warm Wet (giss)	1	10	–11	–13	2.3	7	+8	–8
Warm Dry (fio)	1.6	–5	–26	–22	0.8	–5	–26	–20

*Note.* The CMIP5 GCM from which the scenario was developed is noted below the scenario name.



**Figure 2.** Snow covered area (km<sup>2</sup>) for dry, near normal, and wet years in the historical simulation and five future scenarios. (a) GLAC 15 April 1.0 m depth (SCA<sub>1.0</sub>), (b) ROMO 15 April 1.0 m depth. Only the denning elevation bands were included in the calculation of snow covered area. See supporting information for choice of representative years.

simulations form the basis for our analysis of the change in snow covered area, and how this change depends on elevation and aspect.

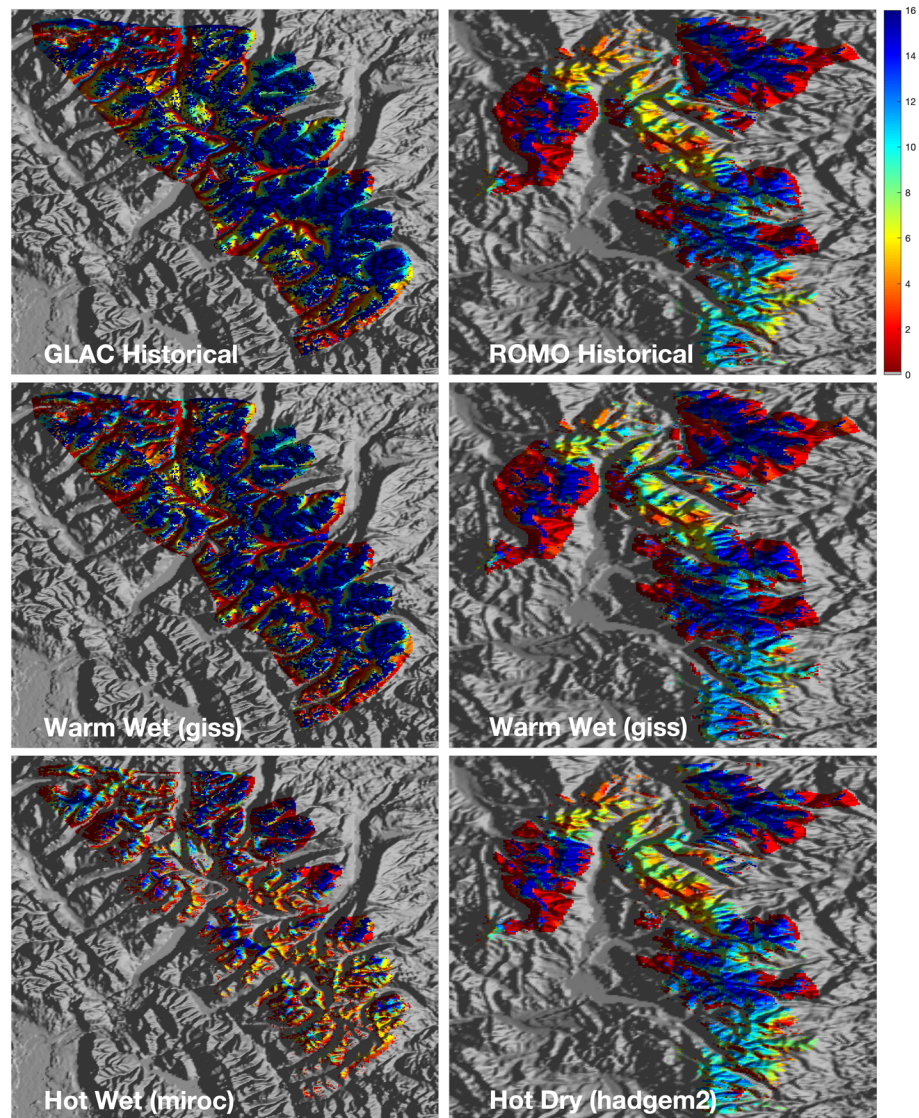
### 3.2. Change in Snow Covered Area

As noted above, we consider the area with modeled snow depths of at least 1.0 m (SCA<sub>1.0</sub>) on 15 April and at least 0.5 m (SCA<sub>0.5</sub>) on 15 May as indicators of snow availability at typical denning locations and times of year. On average SCA<sub>1.0</sub> on 15 April decreases in all scenarios for GLAC, with changes ranging from −11% to −71%. SCA<sub>0.5</sub> on 15 May shows similar declines. For the ROMO study area the changes on 15 April range from +8% to −26% and on 15 May from −8% to −43%. Overall, this suggests that the ROMO study area may be more resilient to snow loss than GLAC, particularly for April snowpack.

Variability in the snowpack from year to year is large in these regions; therefore we evaluate snow covered area for representative wet, near normal, and dry years (Figure 2). The wet and near normal years retain large areas of snow cover at denning elevations under all scenarios, with the exception of the Hot/Wet scenario for GLAC. Conversely, the dry year in GLAC has a large loss of SCA in all but the Warm/Wet scenario. The pattern in ROMO is quite different, with several scenarios showing an increase in 15 April SCA<sub>1.0</sub>, while the Warm/Dry scenario loses almost all its deep snow cover in dry years, indicating the influence of changes in wintertime precipitation on the early springtime snowpack. The two driest years in the historical simulation for ROMO (2002 and 2012) had excessive snow cover in the eastern part of the ROMO domain compared to MODIS snow cover observations, even with the best set of model parameters (see supporting information), so that the future percent reduction in snow covered area is likely to be underestimated for dry years. All scenarios show a decrease for SCA<sub>0.5</sub> on 15 May with the exception of the representative wet year in GLAC (Figure S1).

Given the year-to-year variability in snowpack, it is useful to see where on the landscape reliable (at least 14 out of 16 years) snowpack will persist in the future scenarios. This summary statistic is analogous to that used by the Copeland et al. (2010) study, who found denning preference where there was persistent snow in 6–7 out of the 7 years they analyzed. We consider more than twice as many years, and these maps use a higher threshold of modeled snow appropriate for denning elevations. Figure 3 shows the number of years with at least 1.0 m of snow on 15 April (out of 16 years that were simulated for the current and future climates) for the historical simulations, and the scenarios that show the least change, and greatest snowpack loss for each study area. Results for the three other scenarios and for 15 May are shown in Figures S2 and S3. As expected in a generally warming climate, by 15 May (and by 15 April in GLAC) the most reliable snowpack retreats to smaller, higher elevation areas. However, the effects vary widely among future climate scenarios. For 15 April in ROMO, only the Warm/Dry scenario shows this retreat, again indicating the potential resilience of early springtime snowpack in ROMO.

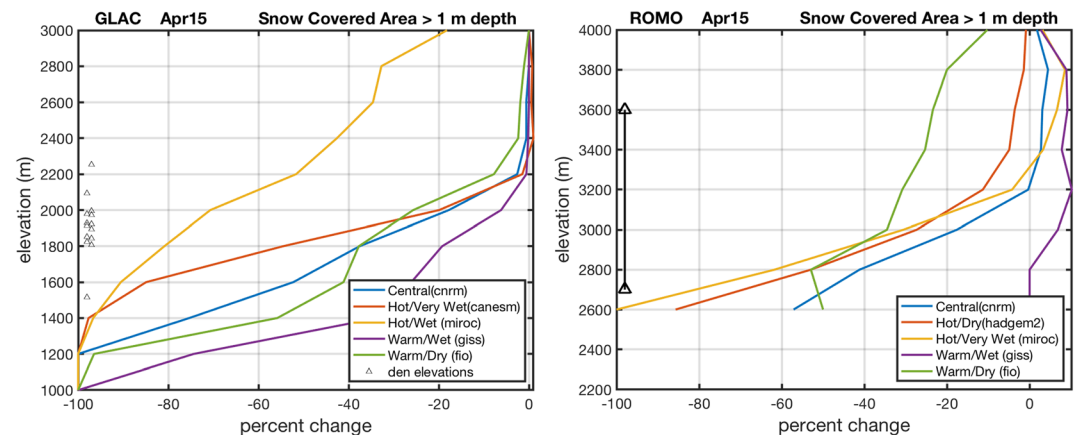




**Figure 3.** Number of years (out of 16 simulated) with snow depth  $>1.0$  m on 15 April for GLAC (left column) and ROMO (right column). Historical simulation (top row); Warm/Wet scenario (second row), and Hot/Wet (GLAC)/Hot/Dry (ROMO) scenario. Scenarios are described in Table 1. Shaded topography is that used in the modeling study. North is up, and for distance scale see Figure 1.

### 3.3. Elevation Dependence of Snow Loss

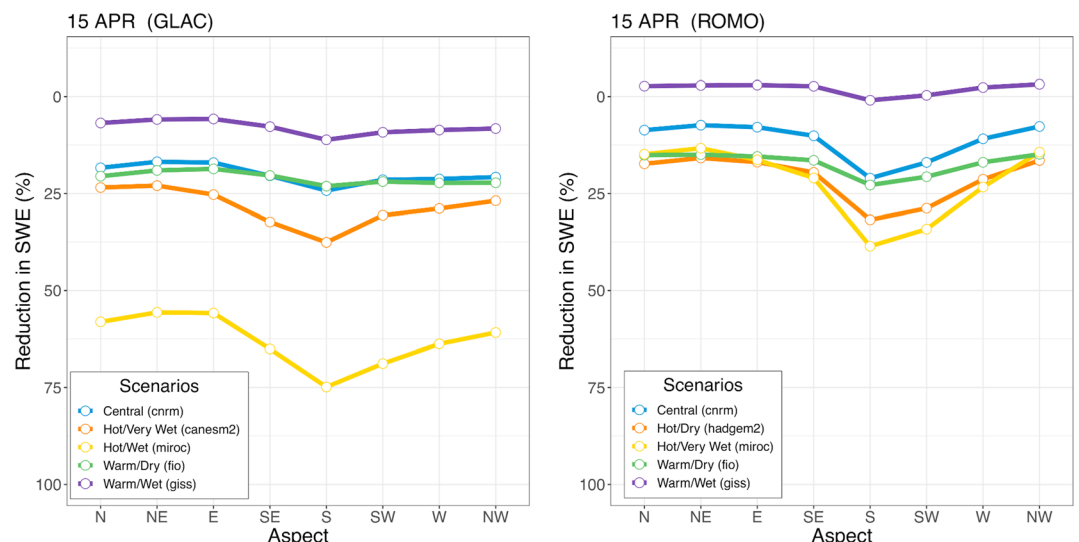
We find a strong dependence of snowpack loss with elevation. In the Warm/Dry and Hot/Dry scenarios, reduction in precipitation and warming conspire to reduce Spring snowpack. For the other scenarios, the effects of warming can be offset by an increase in precipitation, provided that the midwinter temperature remains cold enough to accumulate snow. Figure 4a shows the percent change in 15 April  $SCA_{1.0}$  for GLAC, computed for 200 m elevation bands. The elevations of observed den sites are noted by triangles, ranging from approximately 1,500 to 2,300 m. In the denning elevation band, snowpack change is very sensitive to elevation and to the particular future climate scenario. There is a stark difference between the upper and lower portions of the denning elevations. There is only moderate change ( $<30\%$ ) at 2,000 m for four of the five scenarios and almost no change above 2,200 m, yet there is greater than 50% loss of  $SCA_{1.0}$  below 1,400 m for all but one scenario. Changes in 15 May  $SCA_{0.5}$  (Figure S4) show a similar elevational gradient, with even more severe losses at low elevations.



**Figure 4.** Elevation dependence of snow covered area (SCA): (a) GLAC projected change in  $SCA_{1.0}$  on 15 April (b) ROMO projected change in  $SCA_{1.0}$  on 15 April. Elevations of observed den sites in GLAC and the modeled elevation range of potential denning in ROMO are indicated by triangles.

Comparison between changes in SCA and changes in SWE (Figure S6) indicates that modest declines in SWE may have little appreciable effect on SCA at high elevations for the depth thresholds we have chosen. The implication is that the relatively wet, cold climate of GLAC, in addition to the generally increasing winter precipitation in this study area can act as a buffer to change, but only above 2,000 m elevation. A vertical displacement of approximately 200 m in the denning band would offset much of the risk of depleted snow from four of the five scenarios, provided suitable terrain is available at these higher elevations. This vertical shift in snow climate is at the low end of the 200–400 m range projected by Bavay et al. (2013) for midcentury in the Alps.

Figure 4b shows the 15 April  $SCA_{1.0}$  for ROMO. As there are no currently observed den sites in ROMO, the denning elevation band is inferred from a linear regression model (see Methods). For elevations above 3,200 m only modest losses are seen (under 30%, with four of the five scenarios), and the Warm/Wet scenario shows an increase. Below 3,200 m the losses in SWE are much larger. By 15 May losses have increased at 3,200 m, but the snowpack at 3,400 m largely persists. The overall picture is similar to GLAC, with the upper range of (potential) denning relatively insensitive to warming for four of the five scenarios, and the lower



**Figure 5.** Topographical aspect dependence of 15 April snowpack loss for five future midcentury climate scenarios for (a) GLAC and (b) ROMO. Only areas within the denning elevation band in each study area were included in the analysis.

range of potential denning subject to large losses in snowpack. However, comparison with SWE changes (Figure S6) shows that the relationship between SWE loss and SCA loss in ROMO is not always straightforward as in GLAC, with a more complicated elevation dependence for SCA than for SWE.

The existence of a critical elevation below which temperature dominates snowpack variability is well supported in the literature (e.g., Sospedra-Alfonso et al., 2015, for a site near the GLAC study area). Scalzitti et al. (2016) find that this critical elevation is projected to rise by about 200–250 m by late-century for the central and northern Rockies (for a single RCP 6.0 climate scenario). While it is difficult to compare these results directly to the present study due to differences in methodology, the qualitative picture remains—projected warming has a much larger effect at lower elevations whereas projected precipitation changes dominate the future springtime snowpack in the high country for most midcentury scenarios. This study shows that the transition between temperature and precipitation dominance for early-to-mid spring lies in the middle of the denning elevation bands.

### 3.4. Aspect Dependence of Snow Loss

We also find a strong dependence of snowpack loss on aspect—the compass direction that the slope faces. South and southwest facing slopes are projected to have considerably greater loss of snow water equivalent (SWE) than other aspects (Figure 5). The magnitude of this effect varies widely depending on the future climate scenario. Most scenarios have upwards of 50% greater loss on southerly exposures, but, for example, the Hot/Very Wet scenario for ROMO on 15 April has almost a threefold difference. The analysis for 15 May (Figure S5) shows a similar dependence on aspect, but with greater differentiation among the climate change scenarios. How the future energy balance on north versus south facing slopes may change in a warmer climate depends on many factors, including latitude, slope angle, and time of year (Lundquist & Flint, 2006). A qualitative consideration of these effects led Lundquist and Flint (2006) to suggest that north-facing slopes may react more slowly to anthropogenic warming and thus provide the potential for ecological refugia. Our results quantitatively support this hypothesis.

## 4. Discussion

We investigated projections of snowpack loss in two study areas: a northern, relatively wet and low-elevation area in Montana (GLAC), and a southern, relatively dry and high elevation area in Colorado (ROMO). In both areas we find general declines in snow-covered area for 15 May (both areas) and for 15 April in GLAC. For ROMO 15 April 1.0 m snow covered area in the denning elevation band is controlled by precipitation change, for which there is a considerable range among projections. However, we report that the springtime snowpack is projected to persist in roughly the upper half of the current denning zone for many future scenarios to the mid-21st century. We also find a strong dependence of snow loss on topographical aspect supporting the hypothesis of Lundquist and Flint (2006) that northerly slopes could provide refugia for snow adapted species.

The present study paints a more complex picture of the evolution of the snowpack by midcentury than does McKelvey. Much of their modeled snow loss was located at the lower margins of the springtime snowpack as would be expected in a warming climate, albeit the results were not resolved at the scale of individual mountain slopes. In contrast, this study focuses explicitly on snow cover at current observed and inferred denning elevations. Deliberate sampling of the range of precipitation projections in this study improves the characterization of risk, given that increased winter precipitation in some of the CMIP5 scenarios may buffer the loss of snowpack at high elevations. It should be noted that even in the most extreme scenario in McKelvey, “miroc 2080”, the highest elevation model pixels in the Rocky Mountains retain snow cover even to the end of the century.

Assuming that persistent spring snowpack plays a significant, if not determinative, role in den site availability, these findings support the viability of continued conservation efforts through at least midcentury, including the potential for reintroduction of wolverines in certain areas. This study does not address the questions of wolverine biology related to snowpack, such as whether den site availability is a limiting factor for this wolverine population, or whether other effects of climate change such as the loss of lower elevation snow and subsequent ecological disturbance will be significant stressors.



The much higher resolution of this analysis compared to previous studies allows the simulation to better represent many influences of the mountainous terrain on snowpack within the study areas, including the influence of slope and aspect on the surface energy balance (with some caveats, see supporting information). The strong dependence of snow loss on both elevation and aspect motivate the production of high-resolution snow projections in order to identify terrain characteristics of where snow may persist in the future. Finally, the improved ability to relate the snowpack projections to fine scale terrain features allows specific biological and ecological hypotheses related to topography to be investigated in order to support conservation of wolverine and other snow-adapted species. Since mountain snow loss and its potential threat to species is a global phenomenon, we see high-resolution snow studies as potentially useful for a wide variety of conservation applications, though we agree with Boelman et al. (2019) that the choice of snow processes represented in the model must be motivated by the particular conservation concern.

## Data Availability Statement

A complete set of snow projection data is available from the NOAA Physical Sciences Laboratory at [ftp://ftp2.psl.noaa.gov/Projects/FAIR\\_paper\\_data/20200914\\_01/](ftp://ftp2.psl.noaa.gov/Projects/FAIR_paper_data/20200914_01/). We gratefully acknowledge the United States Forest Service Rocky Mountain Research Station (<https://www.fs.usda.gov/rmrs/contact>) for providing J. Guinotte with the wolverine den site locations for Glacier National Park that were used to delineate the denning elevation band in the GLAC study area and to derive the results shown in Table 1.

## Acknowledgments

Funding was provided by the U.S. Fish and Wildlife Service, Region 6, the NOAA Physical Sciences Laboratory and CIRES, University of Colorado Boulder. The snow modeling described herein was used to inform the USFWS Species Status Assessment process. The final decision on the threatened or endangered status of the wolverine under ESA is allocated to a separate decision-making body within USFWS, not involving any of the authors, and ultimately to the Department of the Interior. We are grateful to the many USFWS Region 6 biologists and managers who provided feedback and in particular to Kevin Swensen. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service or the National Oceanic and Atmospheric Administration. We also acknowledge the World Climate Research Programme's Working Group on Coupled Modeling, and the modeling groups that supplied data to CMIP5. We gratefully acknowledge the United States Forest Service Rocky Mountain Research Station (<https://www.fs.usda.gov/rmrs/contact>) for providing J. Guinotte with the wolverine den site locations for Glacier National Park that were used to delineate the denning elevation band in the GLAC study area and to derive the results shown in Table 1.

## References

- Aronsson, M., & Persson, J. (2017). Mismatch between goals and the scale of actions constrains adaptive carnivore management: The case of the wolverine in Sweden. *Animal Conservation*, 20(3), 261–269. <https://doi.org/10.1111/acv.12310>
- Aubry, K. B., McKelvey, K. S., & Copeland, J. P. (2007). Distribution and broadscale habitat relations of the wolverine in the contiguous United States. *Journal of Wildlife Management*, 71(7), 2147–2158. <https://doi.org/10.2193/2006-548>
- Bavay, M., Grünwald, T., & Lehning, M. (2013). Response of snow cover and runoff to climate change in high Alpine catchments of Eastern Switzerland. *Advances in Water Resources*, 55, 4–16. <https://doi.org/10.1016/j.advwatres.2012.12.009>
- Boelman, N. T., Liston, G. E., Gurarie, E., Meddens, A. J. H., Mahoney, P. J., Kirchner, P. B., et al. (2019). Integrating snow science and wildlife ecology in Arctic-boreal North America. *Environmental Research Letters*, 14(1), 010401. <https://doi.org/10.1088/1748-9326/aaec1>
- Bohn, T. J., Livneh, B., Oyler, J. W., Running, S. W., Nijssen, B., & Lettenmaier, D. P. (2013). Global evaluation of MTCLIM and related algorithms for forcing of ecological and hydrological models. *Agricultural and Forest Meteorology*, 176, 38–49. <https://doi.org/10.1016/j.agrformet.2013.03.003>
- Brown, R. D., & Mote, P. W. (2009). The response of Northern Hemisphere snow cover to a changing climate. *Journal of Climate*, 22(8), 2124–2145. <https://doi.org/10.1175/2008JCLI2665.1>
- Carroll, C. (2007). Interacting effects of climate change, landscape conversion, and harvest on carnivore populations at the range margin: Marten and Lynx in the Northern Appalachians. *Conservation Biology*, 21(4), 1092–1104. <https://doi.org/10.1111/j.1523-1739.2007.00719.x>
- Christensen, N. S., & Lettenmaier, D. P. (2007). A multimodel ensemble approach to assessment of climate change impacts on the hydrology and water resources of the Colorado River Basin. *Hydrology and Earth System Sciences*, 11(4), 1417–1434. <https://doi.org/10.5194/hess-11-1417-2007>
- Collins, M., Knutti, R., Arblaster, J., Dufresne, J.-L., Fichet, T., Gao, X., et al. (2013). Long-term climate change: Projections, commitments and irreversibility. In T. F. Stocker, et al. (Eds.), *Climate Change 2013: The Physical Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 1029–1136). Cambridge, UK and New York, NY: Cambridge University Press.
- Cooper, M. G., Nolin, A. W., & Safeeq, M. (2016). Testing the recent snow drought as an analog for climate warming sensitivity of Cascades snowpacks. *Environmental Research Letters*, 11(8), 084009. <https://doi.org/10.1088/1748-9326/11/8/084009>
- Copeland, J. P., McKelvey, K. S., Aubry, K. B., Landa, A., Persson, J., Inman, R. M., et al. (2010). The bioclimatic envelope of the wolverine (*Gulo gulo*): Do climatic constraints limit its geographic distribution? *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 88(3), 233–246. <https://doi.org/10.1139/Z09-136>
- Copeland, J. P., & Whitman, J. S. (2003). Wolverine (*Gulo gulo*). In G. A. Feldhamer, B. C. Thompson, J. A. Chapman (Eds.), *Wild mammals of North America: Biology, management, and economics* (pp. 672–682). Baltimore, Maryland USA: The Johns Hopkins University Press.
- Deems, J. S., Painter, T. H., Barsugli, J. J., Belpnap, J., & Udall, B. (2013). Combined impacts of current and future dust deposition and regional warming on Colorado River Basin snow dynamics and hydrology. *Hydrology and Earth System Sciences*, 17(11), 4401–4413. <https://doi.org/10.5194/hess-17-4401-2013>
- Defenders of Wildlife et al. vs. Sally Jewell et al., (2016). No. CV 14–246-M-DLC (United States District Court for the State of Montana April 4, 2016). Retrieved from [http://blogs2.law.columbia.edu/climate-change-litigation/wp-content/uploads/sites/16/case-documents/2016/20160404\\_docket-14-246-M-DLC\\_order.pdf](http://blogs2.law.columbia.edu/climate-change-litigation/wp-content/uploads/sites/16/case-documents/2016/20160404_docket-14-246-M-DLC_order.pdf)
- Gesch, D. B., Oimoen, M. J., Greenlee, S. K., Nelson, C. A., Steuck, M. J., & Tyler, D. J. (2002). The national elevation data set. *Photogrammetric Engineering and Remote Sensing*, 68, 5–11.
- Green, G. N. (1992). *The digital geologic map of Colorado in ARC/INFO format (U.S. geological survey open file report No. 92–0507)* (p. 9). Denver, CO: U.S. Geological Survey. Retrieved from <https://pubs.usgs.gov/of/1992/ofr-92-0507/>
- Hall, D. K., & Riggs, G. A. (2015). *MODIS/Terra snowcover daily L3 global 500 m grid, version 6 [data set]*. Boulder, CO: National Snow and Ice Data Center. <https://doi.org/10.5067/MODIS/MOD10A1.006>

- Hash, H. S. (1987). Wolverine. In M. Novak, J. A. Baker, M. E. Obbard, B. Malloch (Eds.), *Wild furbearer management and conservation in North America* (pp. 575–585). Ontario, CA: Ontario Ministry of Natural Resources.
- Hock, R., Rasul, G., Adler, C., Cáceres, B., Gruber, S., Hirabayashi, Y., et al. (2019). Chapter 2: High mountain areas. In H.-O. Pörtner, et al. (Eds.), *IPCC special report on the ocean and cryosphere in a changing climate* (pp. 131–202).
- Huss, M., Bookhagen, B., Huggel, C., Jacobsen, D., Bradley, R. S., Clague, J. J., et al. (2017). Toward mountains without permanent snow and ice. *Earth's Future*, 5, 418–435. <https://doi.org/10.1002/2016EF000514>
- Inman, R. M., Brock, B. L., Inman, K. H., Sartorius, S. S., Aber, B. C., Giddings, B., et al. (2013). Developing priorities for metapopulation conservation at the landscape scale: Wolverines in the Western United States. *Biological Conservation*, 166, 276–286. <https://doi.org/10.1016/j.biocon.2013.07.010>
- Jackson, M. M., Gergel, S. E., & Martin, K. (2015). Effects of climate change on habitat availability and configuration for an endemic coastal alpine bird. *PLoS ONE*, 10(11), e0142110. <https://doi.org/10.1371/journal.pone.0142110>
- Jennings, K. S., Kittel, T. G., & Molotch, N. P. (2018). Observations and simulations of the seasonal evolution of snowpack cold content and its relation to snowmelt and the snowpack energy budget. *The Cryosphere*, 12(5). <https://doi.org/10.5194/tc-12-1595-2018>
- Johnston, K. M., Freund, K. A., & Schmitz, O. J. (2012). Projected range shifting by montane mammals under climate change: Implications for Cascadia's National Parks. *Ecosphere*, 3(11), art97. <https://doi.org/10.1890/ES12-00077.1>
- Jokinen, M. E., Webb, S. M., Manzer, D. L., & Anderson, R. B. (2019). Characteristics of Wolverine (*Gulo gulo*) dens in the lowland boreal forest of north-central Alberta. *The Canadian Field-Naturalist*, 133(1), 1. <https://doi.org/10.22621/cfn.v133i1.2083>
- Kapnick, S. B., & Delworth, T. L. (2013). Controls of global snow under a changed climate. *Journal of Climate*, 26(15), 5537–5562. <https://doi.org/10.1175/JCLI-D-12-00528.1>
- Keller, F., Goyette, S., & Beniston, M. (2005). Sensitivity analysis of snow cover to climate change scenarios and their impact on plant habitats in alpine terrain. *Climatic Change*, 72(3), 299–319. <https://doi.org/10.1007/s10584-005-5360-2>
- Lehning, M., Völksch, I., Gustafsson, D., Nguyen, T. A., Stähli, M., & Zappa, M. (2006). ALPINE3D: a detailed model of mountain surface processes and its application to snow hydrology. *Hydrological Processes*, 20(10), 2111–2128. <https://doi.org/10.1002/hyp.6204>
- Littell, J. S., Elsner, M. M., Lutz, E., Hamlet, A. F., Mauger, G., & Salathé, E. (2011). Regional climate and hydrologic change in the Northern US Rockies and Pacific Northwest: Internally consistent projections of future climate for resource management. In *Climate Impacts Group* (pp. 1–109). Seattle, WA: University of Washington. Retrieved from [http://cse.washington.edu/picea/USFS/pub/Littell\\_etal\\_2010/](http://cse.washington.edu/picea/USFS/pub/Littell_etal_2010/)
- Livneh, B., Bohn, T. J., Pierce, D. W., Munoz-Arriola, F., Nijssen, B., Vose, R., et al. (2015). A spatially comprehensive, hydrometeorological data set for Mexico, the U.S., and Southern Canada 1950–2013. *Scientific Data*, 2(1), 150042. <https://doi.org/10.1038/sdata.2015.42>
- Livneh, B., Deems, J. S., Buma, B., Barsugli, J. J., Schneider, D., Molotch, N. P., et al. (2015). Catchment response to bark beetle outbreak and dust-on-snow in the Colorado Rocky Mountains. *Journal of Hydrology*, 523, 196–210. <https://doi.org/10.1016/j.jhydrol.2015.01.039>
- Livneh, B., Deems, J. S., Schneider, D., Barsugli, J. J., & Molotch, N. P. (2014). Filling in the gaps: Inferring spatially distributed precipitation from gauge observations over complex terrain. *Water Resources Research*, 50, 8589–8610. <https://doi.org/10.1002/2014wr015442>
- López-Moreno, J. I., Revuelto, J., Gilaberte, M., Morán-Tejeda, E., Pons, M., Jover, E., et al. (2014). The effect of slope aspect on the response of snowpack to climate warming in the Pyrenees. *Theoretical and Applied Climatology*, 117(1–2), 207–219. <https://doi.org/10.1007/s00704-013-0991-0>
- Lundquist, J. D., & Flint, A. L. (2006). Onset of snowmelt and streamflow in 2004 in the western United States: How shading may affect spring streamflow timing in a warmer world. *Journal of Hydrometeorology*, 7(6), 1199–1217. <https://doi.org/10.1175/Jhm539.1>
- Magoun, A. J., & Copeland, J. P. (1998). Characteristics of wolverine reproductive den sites. *Journal of Wildlife Management*, 62(4), 1313–1320. <https://doi.org/10.2307/3801996>
- Mahoney, P. J., Liston, G. E., LaPoint, S., Gurarie, E., Mangipane, B., Wells, A. G., et al. (2018). Navigating snowscapes: Scale-dependent responses of mountain sheep to snowpack properties. *Ecological Applications*, 28(7), 1715–1729. <https://doi.org/10.1002/eap.1773>
- McCrary, R. R., & Mearns, L. O. (2019). Quantifying and diagnosing sources of uncertainty in midcentury changes in North American snowpack from NARCCAP. *Journal of Hydrometeorology*, 20(11), 2229–2252. <https://doi.org/10.1175/JHM-D-18-0248.1>
- McKelvey, K. S., Copeland, J. P., Schwartz, M. K., Littell, J. S., Aubry, K. B., Squires, J. R., et al. (2011). Climate change predicted to shift wolverine distributions, connectivity, and dispersal corridors. *Ecological Applications*, 21(8), 2882–2897. <https://doi.org/10.1890/10-2206.1>
- Miller, D. A., & White, R. A. (1998). A conterminous United States multilayer soil characteristics dataset for regional climate and hydrology modeling. *Earth Interactions*, 2(2), 1–26. [https://doi.org/10.1175/1087-3562\(1998\)002<0001:ACUSMS>2.3.CO;2](https://doi.org/10.1175/1087-3562(1998)002<0001:ACUSMS>2.3.CO;2)
- Mizukami, N., & Perica, S. (2008). Spatiotemporal characteristics of snowpack density in the mountainous regions of the western United States. *Journal of Hydrometeorology*, 9(6), 1416–1426. <https://doi.org/10.1175/2008JHM981.1>
- Mote, P. W., Hamlet, A. F., Clark, M. P., & Lettenmaier, D. P. (2005). Declining mountain snowpack in western North America. *Bulletin of the American Meteorological Society*, 86(1), 39–50. <https://doi.org/10.1175/BAMS-86-1-39>
- Mote, P. W., Li, S., Lettenmaier, D. P., Xiao, M., & Engel, R. (2018). Dramatic declines in snowpack in the western US. *Npj Climate and Atmospheric Science*, 1(1). <https://doi.org/10.1038/s41612-018-0012-1>
- National Operational Hydrologic Remote Sensing Center (2004). *Snow data assimilation system (SNODAS) data products at NSIDC, version 1 [Data set]*. Boulder, CO: National Snow and Ice Data Center. <https://doi.org/10.7265/n5tb14tc>
- Natural Resources Conservation Service (n. d.). *SNOW TELEmetry (SNOTEL) data [Data set]*. Retrieved from <https://www.wcc.nrcs.usda.gov/snow/>
- Packila, M. L., Riley, M. D., Spence, R. S., & Inman, R. M. (2017). Long-distance wolverine dispersal from Wyoming to historic range in Colorado. *Northwest Science*, 91(4), 399–407. <https://doi.org/10.3955/046.091.0409>
- Peacock, S. (2011). Projected 21st century climate change for wolverine habitats within the contiguous United States. *Environmental Research Letters*, 6(1), 014007. <https://doi.org/10.1088/1748-9326/6/1/014007>
- Pederson, G. T., Gray, S. T., Woodhouse, C. A., Betancourt, J. L., Fagre, D. B., Littell, J. S., et al. (2011). The unusual nature of recent snowpack declines in the North American cordillera. *Science*, 333(6040), 332–335. <https://doi.org/10.1126/science.1201570>
- Persson, J., Landa, A., Andersen, R., & Segerström, P. (2006). Reproductive characteristics of female wolverines (*Gulo gulo*) in Scandinavia. *Journal of Mammalogy*, 87(1), 75–79. <https://doi.org/10.1644/04-1>
- Pierce, D. W., Barnett, T. P., Hidalgo, H. G., Das, T., Bonfils, C., Santer, B. D., et al. (2008). Attribution of declining western U.S. snowpack to human effects. *Journal of Climate*, 21(23), 6425–6444. <https://doi.org/10.1175/2008JCLI2405.1>
- Reclamation (2013). *Downscaled CMIP3 and CMIP5 Climate and Hydrology Projections: Release of Downscaled CMIP5 Climate Projections, Comparison with preceding Information, and Summary of User Needs* (p. 47). Denver, Colorado: U.S. Department of the Interior, Bureau

- of Reclamation, Technical Services Center. Retrieved from [https://gdo-dcp.ucllnl.org/downscaled\\_cmip\\_projections/techmemo/downscaled\\_climate.pdf](https://gdo-dcp.ucllnl.org/downscaled_cmip_projections/techmemo/downscaled_climate.pdf)
- Regonda, S. K., Rajagopalan, B., Clark, M., & Pitlick, J. (2005). Seasonal cycle shifts in hydroclimatology over the western United States. *Journal of Climate*, 18(2), 372–384. <https://doi.org/10.1175/JCLI-3272.1>
- Rhoades, A. M., Ullrich, P. A., & Zarzycki, C. M. (2017). Projecting 21st century snowpack trends in western USA mountains using variable-resolution CESM. *Climate Dynamics*, 50(1–2), 261–288. <https://doi.org/10.1007/s00382-017-3606-0>
- Royle, J. A., Magoun, A. J., Gardner, B., Valkenburg, P., & Lowell, R. E. (2011). Density estimation in a wolverine population using spatial capture-recapture models. *Journal of Wildlife Management*, 75(3), 604–611. <https://doi.org/10.1002/jwmg.79>
- Scalzitti, J., Strong, C., & Kochanski, A. (2016). Climate change impact on the roles of temperature and precipitation in western US snowpack variability. *Geophysical Research Letters*, 43, 5361–5369. <https://doi.org/10.1002/2016gl068798>
- Schwartz, M. K., Aubry, K. B., McKelvey, K. S., Pilgrim, K. L., Copeland, J. P., Squires, J. R., et al. (2007). Inferring geographic isolation of wolverines in California using historical DNA. *Journal of Wildlife Management*, 71(7), 2170–2179. <https://doi.org/10.2193/2007-026>
- Sivy, K. J., Nolin, A. W., Cosgrove, C. L., & Prugh, L. R. (2018). Critical snow density threshold for Dall's sheep (*Ovis dalli dalli*). *Canadian Journal of Zoology*, 96(10), 1170–1177. <https://doi.org/10.1139/cjz-2017-0259>
- Sofaer, H. R., Barsugli, J. J., Jarnevich, C. S., Abatzoglou, J. T., Talbert, M. K., Miller, B. W., & Morissette, J. T. (2017). Designing ecological climate change impact assessments to reflect key climatic drivers. *Global Change Biology*, 23(7), 2537–2553. <https://doi.org/10.1111/gcb.13653>
- Sospedra-Alfonso, R., Melton Joe, R., & Merryfield William, J. (2015). Effects of temperature and precipitation on snowpack variability in the Central Rocky Mountains as a function of elevation. *Geophysical Research Letters*, 42, 4429–4438. <https://doi.org/10.1002/2015GL063898>
- Taylor, K. E., Stouffer, R. J., & Meehl, G. A. (2012). An overview of CMIP5 and the experiment design. *Bulletin of the American Meteorological Society*, 93(4), 485–498. <https://doi.org/10.1175/Bams-D-11-00094.1>
- United States Fish and Wildlife Service (2014). *Threatened status for the distinct population segment of the North American wolverine occurring in the contiguous United States* (Vol. 79, pp. 47,522–47,545). 79 Fed. Reg. <https://www.federalregister.gov/d/2014-18743/page-47522>
- Wickham, J. D., Homer, C. G., Vogelmann, J. E., McKerrow, A., Mueller, R., Herold, N., & Coluston, J. (2014). The multi-resolution land characteristics (MRLC) consortium: 20 years of development and integration of USA national land cover data. *Remote Sensing*, 6(8), 18. <https://doi.org/10.3390/rs6087424>
- Wigmosta, M. S., Vail, L. W., & Lettenmaier, D. P. (1994). A distributed hydrology-vegetation model for complex terrain. *Water Resources Research*, 30(6), 1665–1679. <https://doi.org/10.1029/94wr00436>

## References From the Supporting Information

- Abatzoglou, J. T. (2013). Development of gridded surface meteorological data for ecological applications and modeling. *International Journal of Climatology*, 33, 121–131. <https://doi.org/10.1002/joc.3413>
- Alder, J. R., & Hostetler, S. W. (2019). The dependence of hydroclimate projections in snow-dominated regions of the western United States on the choice of statistically downscaled climate data. *Water Resources Research*, 55, 2279–2300. <https://doi.org/10.1029/2018WR023458>
- Brekke, L. D., Dettinger, M. D., Maurer, E. P., & Anderson, M. (2008). Significance of model credibility in estimating climate projection distributions for regional hydroclimatological risk assessments. *Climatic Change*, 89(3–4), 371–394. <https://doi.org/10.1007/s10584-007-9388-3>
- Curtis, J. A., Flint, L. E., Flint, A. L., Lundquist, J. D., Hudgens, B., Boydston, E. E., & Young, J. K. (2014). Incorporating cold-air pooling into downscaled climate models increases potential refugia for snow-dependent species within the Sierra Nevada Ecoregion, CA. *PLoS ONE*, 9(9), e106984. <https://doi.org/10.1371/journal.pone.0106984>
- Hall, A., Cox, P., Huntingford, C., & Klein, S. (2019). Progressing emergent constraints on future climate change. *Nature Climate Change*, 9(4), 269–278. <https://doi.org/10.1038/s41558-019-0436-6>
- Marshall, A. M., Link, T. E., Robinson, A. P., & Abatzoglou, J. T. (2020). Higher snowfall intensity is associated with reduced impacts of warming upon winter snow ablation. *Geophysical Research Letters*, 47, e2019GL086409. <https://doi.org/10.1029/2019GL086409>
- Symstad, A. J., Fisichelli, N. A., Miller, B. W., Rowland, E., & Schuurman, G. W. (2017). Multiple methods for multiple futures: Integrating qualitative scenario planning and quantitative simulation modeling for natural resource decision making. *Climate Risk Management*, 17, 78–91. <https://doi.org/10.1016/j.crm.2017.07.002>
- Zappa, M. (2008). Objective quantitative spatial verification of distributed snow cover simulations—An experiment for the whole of Switzerland/Vérification quantitative spatiale objective de simulations distribuées de la couche de neige—une étude pour l'ensemble de la Suisse. *Hydrological Sciences Journal*, 53(1), 179–191. <https://doi.org/10.1623/hysj.53.1.179>