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How will snow alter exposure of organisms to cold stress under climate warming?

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Title: How will snow alter exposure of organisms to cold stress under climate warming?

Running head: Snow, climate warming and cold stress

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Biosketch

Michael Kearney is an ecophysiologist who's research focuses on integrating physical and biological principles to understand constraints on the behaviour, distribution and abundance of organisms. He is developing the NicheMapR package, a suite of programs in the R environment for modelling microclimates and their consequences for the heat, water and dynamic energy budgets of organisms.

Data availability

All data used in this study are publicly available and all required code to generate the results are publicly available and open source.

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Article type : Research Papers

Title: How will snow alter exposure of organisms to cold stress under climate warming?

Running head: Snow, climate warming and cold stress

Abstract

Aim: To test the capacity of an ecologically-focussed microclimate model to capture the interaction between snow cover and soil temperature and use it to assess how historical and future climate warming affects exposure of organisms to stressfully cold conditions in shallow soil.

Location: continental USA

Time Period: 1980 to 2017

Method: A snow heat budget algorithm was developed and integrated with the general-purpose microclimate model of the NicheMapR package. The gridMET daily historical weather grids were used as environmental forcing. The model was tested against hourly observations of soil temperature and snow cover for 590 SCAN/SNOTEL sites across the USA. It was then used to simulate ectotherm cold stress exposure and endotherm hibernation costs.

Results: The model captured soil and snow observations to within ~10-15 % of the range (r ~ 0.85). Air temperature exhibited a mean warming rate of 0.37 °C per decade across sites but in snow affected regions the predicted shallow-soil warming rates were one third lower. Biophysical analyses predicted increased activity ectotherm time as a result of contemporary climate change but little change in cold stress at most sites. For endotherms, hibernation costs were predicted to decline in

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general. However, both reduced and increased cold stress was simulated to occur for ectotherm and endotherms under simulated air temperature warming of up to 3 °C.

Main conclusions: Many of the direct biological consequences of climate warming will be mediated through soil temperature. Microclimatic processes linked to snow cover mean that exposure to cold stress for both ectotherms and endotherms may stay constant, decrease or even increase under climate warming depending on the local circumstances and species-specific biology. The idiosyncratic and season-specific decoupling of above- and below-ground environments under climate warming will have important ecological consequences in snow-affected regions and can now be computed mechanistically.

Key Words: snow, soil temperature, cold stress, hibernation, microclimate, NicheMapR, SCAN, SNOTEL, climate warming

Introduction

Snow has long been known for its ecological importance. Snow protects plants from exposure to cold and from desiccating winds, as well as contracting the growing season (Warming, 1909). Many cold-adapted animal and plant species rely on the stable, moist subnivean conditions that occur near the ground-snow interface during winter (Pauli *et al.*, 2013). Snow-mediated soil temperatures can also affect microbial dynamics with consequences for carbon cycling (Monson *et al.*, 2006). Climate warming will increase growing season length in cold environments but any associated reductions in snow depth and duration may increase exposure to extremely cold microclimates and outweigh any positive effects (Wipf *et al.*, 2009). For example, climate warming may increase activity time for ectotherms (Kearney, 2013) but reduced snow cover may increase exposure to extreme cold (Bale & Hayward, 2010). During the snow season, many endotherms enter hibernation where body temperature and hence energy requirements are dramatically reduced (e.g. Körtner & Geiser, 1998). Climate warming may reduce the overall hibernation period by reducing snow cover, but shallower snow may mean that hibernating endotherms experience colder conditions, with complex consequences for their energy budgets. Thus whole communities dependent on the 'subnivium' will be strongly affected by snow-mediated microclimatic effects of climate change (ávila-Jiménez *et al.*, 2010; Pauli *et al.*, 2013; Sanders-DeMott *et al.*, 2018, 2019) and we therefore need good models of how snow affects soil temperatures if we are to predict the ecological consequences.

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The interaction between climate change, snow, soil temperature and other microclimatic conditions is highly multidimensional and non-linear (Zhang, 2005; Zhang *et al.*, 2005; Thompson *et al.*, 2018). The ultimate outcome of climate warming in snow-affected areas will depend on the balance between the buffering effect of snow and the overall addition of heat to the soil profile (Campbell *et al.*, 2010; Aalto *et al.*, 2018). In certain circumstances, snow melt as a result of a warming climate may result in paradoxical cooling of soil with the warming of air (Groffman *et al.*, 2001; Decker *et al.*, 2003; Isard *et al.*, 2007; Sinha & Cherkauer, 2010; Brown & DeGaetano, 2011).

How can we incorporate these complexities introduced by snow cover into our understanding of species responses to climate change? One approach is to empirically compare spatially broad time series of snow cover and soil temperature data to better understand their interaction. In the USA, the Soil Climate Network Analysis (SCAN, Schaefer *et al.*, 2007) and SNOw TELemetry (SNOTEL, Serreze *et al.*, 1999) projects comprise over 600 stations recording snow and soil conditions dating back to the 1960s. However, it is difficult to infer the general nature of climate-snow-microclimate interactions from these sources because of data incompleteness, especially for concurrent measurements of soil temperature, snow cover and air temperature. Thus, in this study I take a simulation approach by forcing a general microclimate model with historical gridded data, using the historical point-observations to test model performance. I then use the simulation results to assess the consequences of historical climate change and future potential warming for the snow/soil temperature interaction, and their ecological consequences for ectotherms and endotherms.

Several modelling approaches have been developed for predicting soil temperature as a function of snow cover (e.g. Jordan, 1991; Liston & Sturm, 1998; Zhang, 2003; Anderson, 2006; Bartlett *et al.*, 2006; Essery *et al.*, 2013; Avanzi *et al.*, 2016; Lute & Luce, 2017; Cuntz & Haverd, 2018; Hamman *et al.*, 2018). These approaches range from fully physical schemes that explicitly consider energy and mass balances, to more phenomenological approaches that use descriptive formulations. Most ecologically-focused studies of microclimatic snow effects have been in the middle of this spectrum, balancing data input requirements with model transferability. For example, Isard et al. (2007) and Brown et al. (2011) integrated soil heat flow models with snow and soil moisture models in such a way that only air temperature and rainfall data were needed as forcing data. However, radiation and humidity interact in complex ways to affect snow cover (Harpold & Brooks, 2018) and more mechanistic approaches are therefore desirable.

In this study I use a fully physical microclimate model that simultaneously solves a complete energy and mass budget for the soil and snow profile, and uses radiation, wind and humidity forcing data in

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addition to air temperature and precipitation (NicheMapR, Kearney & Porter, 2017). This modelling framework is more generalisable than phenomenological ones, and more targeted to ecological-scale outputs (hourly time-step, fine-scale topographic adjustments, detailed soil profiles) than are Land Surface Models. Moreover, the NicheMapR package also includes algorithms for computing the biophysical consequences of microclimates for different kinds of organisms (Kearney & Porter, 2019).

Microclimate models can now be applied on broad spatial scales at fine temporal resolution due to the increasing availability of historical gridded meteorological forcing data (New *et al.*, 2002; Jones *et al.*, 2009; Kemp *et al.*, 2012; Abatzoglou, 2013). I integrated the NicheMapR microclimate with the gridMET historical climatology of the USA (Abatzoglou, 2013) and the data from 590 SCAN/SNOTEL sites (Schaefer *et al.*, 2007) to test the model's performance and to quantify the buffering influence of snow on soil temperature across continental USA as well as the pattern of historical change in shallow (5cm) soil temperature in relation to air temperature and snow cover. I then used the model output to explore the potential effects of snow on shallow soil temperature and the physiological consequences of these effects for ectotherms and endotherms. Specifically, I address the following questions: 1) To what extent are soil temperatures independent of, or reduced by, climate warming through the buffering effect of snow? 2) How will climate warming affect exposure to cold stress in overwintering ectotherms? and 3) How will climate warming affect the energetic costs of hibernation in endotherms?

Materials and Methods

Snow model formulation

All simulations were done with the microclimate model of the NicheMapR package, now fully open source (https://github.com/mrke/NicheMapR). The model can be installed and run for the USA from base R in 5 lines of code, with all meteorological forcing data accessible online via opendap (SI Supplementary Text). The snow model of the NicheMapR microclimate model was partially described by Kearney and Porter (2017) and here I provide an overview and additional details. Snow layers form an extension of a maximum of eight nodes above the ten nodes used to compute heat flux through the soil profile. These additional snow nodes are at 2.5, 5, 10, 20, 50, 100, 200 and 300cm, with the original soil surface node (0cm) acting as the snow surface node and the connection between the 300cm snow node and the depth of the soil surface node being allowed to grow to an arbitrary large extent. As the snow pack grows and shrinks, the subroutine 'snowlayer' checks whether to increase or decrease the number of snow nodes in use. Snow is set to zero if the

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predicted depth is less than 2.5 cm to ensure numerical stability but small rainfall events that would otherwise produce a snow layer shallower than this threshold are cumulated each hour until the threshold is met, conserving mass balance. Snow growth is driven by inputted precipitation for each day (or hour, if hourly rainfall data are available) and by the user-specified thresholds for the air temperature at which rain falls as snow. Snow density ρ_{snow} can be constant, vary as a linear function of snow age (with a maximum of 0.9167 Mg/m^3), or can vary with the non-linear asymptotic formulation of Sturm *et al.* (2010, eq. 5) $\rho_{snow} = (\rho_{max} - \rho_0)[1 - \exp(-k_1 h - k_2 D)] + \rho_0$ where ρ_{max} is the maximum allowable density, ρ_0 is the initial density, k_1 and k_2 are fitting parameters, h is the snow height (cm) and D is the age of the snow (days; note that this differs from Sturm *et al.* (2010) in that they used *D* as day of year). The latter function was used in all analyses presented here, using the parameters ρ_{max}= 0.9167, ρ_0= 0.27, k_1 = 0.004 and k_2 = 0.009.

All snow for a given day is assumed to fall at midnight if the rainfall input is daily (as in the present case), and the user can specify a multiplier to account for undercatch (wind-driven precipitation inaccuracies) if necessary (Rasmussen et al. 2012). When snow is present, the fractional surface albedo α changes as a function of the age of the snow pack as $\alpha = -9.8740 \ln (d_{snow} + 78.3434)$ where d_{snow} is the days since the last snowfall based on regressions fitted to Fig A-4 of Anderson (2006), and reverts to the user-specified value for the substrate when snow is absent. Snow thermal conductivity is estimated from Djachkova's formula following Anderson (2006) $k_{snow} = 0.0442 e^{5.181 \rho_{snow}}$. Snow melt occurs according to the heat load as computed by the heat budget for the substrate (including the snow), as well as melting due to rain. If there is a temperature increase between time steps for a given internode of the snowpack, this temperature difference is multiplied by the snow heat capacity (including the heat of fusion), snow density and distance between the nodes to obtain the heat input, and then divided by the heat of fusion to compute the mass of snow melted, with temperatures of the respective nodes set to 0 °C. Rain-melt is simulated following Anderson (2006) by multiplying the product of the rainfall and mean air temperature for the day by a rain melt factor (default value 0.0125) whenever rain falls at air temperatures above the snow threshold (this is the only phenomenological aspect of the model).

Environmental Forcing data

Meteorological forcing data were obtained from the gridMET dataset of 0.042° (~4 km) resolution daily grids of minimum and maximum air temperature, minimum and maximum relative humidity, daily cumulative precipitation, daily cumulative solar radiation and mean daily wind speed. Observed solar radiation was converted into a fraction of the maximum possible for each day under clear sky

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conditions using the micro_global function of the NicheMapR package, and used as cloud cover as per Kearney et al. (2014). Air temperature was adjusted via lapse rate corrections of 0.0039 °C m^{-1} and 0.0077 °C m^{-1} for minimum and maximum temperature, respectively (Ruddell *et al.*, 1990), for the reported elevation at each site, with relative humidity then recomputed for the new temperature. Soil properties were extracted from the SoilGrids global dataset (Hengl *et al.*, 2014, 2017), a ~250m resolution product, using the jsonlite package. Soil bulk density, and percent sand, silt and clay were extracted for 0, 5, 15, 30, 60, 100 and 200 cm and converted to soil hydraulic parameters (air entry potential, saturated hydraulic conductivity and Campbell's b) using the 'pedotransfer' function of the NicheMapR package that is based on Cosby et al. (1984), as described in more detail in Kearney and Maino (2018). These connections to the gridMET and SoilGrids data are encoded in a new function in the NicheMapR package, 'micro_usa'.

Sites and observation data

The model was tested at 590 SCAN and SNOTEL sites with time-series of snow depth, snow water equivalent (SWE), soil temperature and soil moisture (5, 10, 20, 50 and 100 cm) observations for between 0.9 and 24.4 years (mean 13.8). Two test scenarios were run. In the first scenario, slope, aspect, shading and horizon angles were all assumed to be zero. In the second scenario, these parameters were adjusted based on assessments of site photos available at https://www.wcc.nrcs.usda.gov/scan/. Each photo was used to estimate canopy shade level (to nearest 5%), slope (to nearest 5%), horizon angles (to nearest 5%, assumed either uniform in all 24 directions, or alternative between a single estimated value and zero in sites deemed as woodland), whether the substrate was rock or soil (used to determine whether an organic cap was absent or present, respectively), and the proportion of ground cover (nearest 5%) (Table S1). The ground cover fraction was used as an estimate of shade, but this shade was only imposed if no snow was present, on the assumption that the groundcover was under the snow. In addition, a preliminary run of the model for the year 2017 (using 2016 as a spin-up year) for all sites was done across all 11 soil types in Table 9.1 of Campbell and Norman (Campbell & Norman, 1998), and the best fitting hydraulic parameter set was used for each respective soil layer for the final simulation. All other parameters for the microclimate model were set to the default values to be found in the 'micro_usa' function.

Simulations and Analyses

A schematic of the overall simulation approach is shown in Figure 1. The model was run at all sites for the years 1979 to 2017 (the year 1979 used as a 'spin-up' year), with the soil depth nodes chosen to match the observation data (5, 10, 20, 50 and 100 cm - the depths were measured in inches and

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approximate the cm depths here). A total of six different scenarios were considered. First (DefaultTest) the model was run with all default settings and using the SoilGrids database for soil hydraulic properties. Second (LocalTest), it was run as in DefaultTest but with parameters adjusted as described in the section above, to match the local conditions as indicated in site photos and to use the best-fitting soil type for hydraulic properties. Third, the model was run with the snow module switched off (NoSnow), so that instead of precipitation falling as snow it fell as rain and only affected soil temperature via its effect on soil moisture. Finally, simulations were run incrementing the air temperature by one degree to a maximum of three degrees higher than base level (Warm1, Warm2 and Warm3). The latter four simulations used the DefaultTest settings to obtain a picture of the effect of snow and warming with all else being equal.

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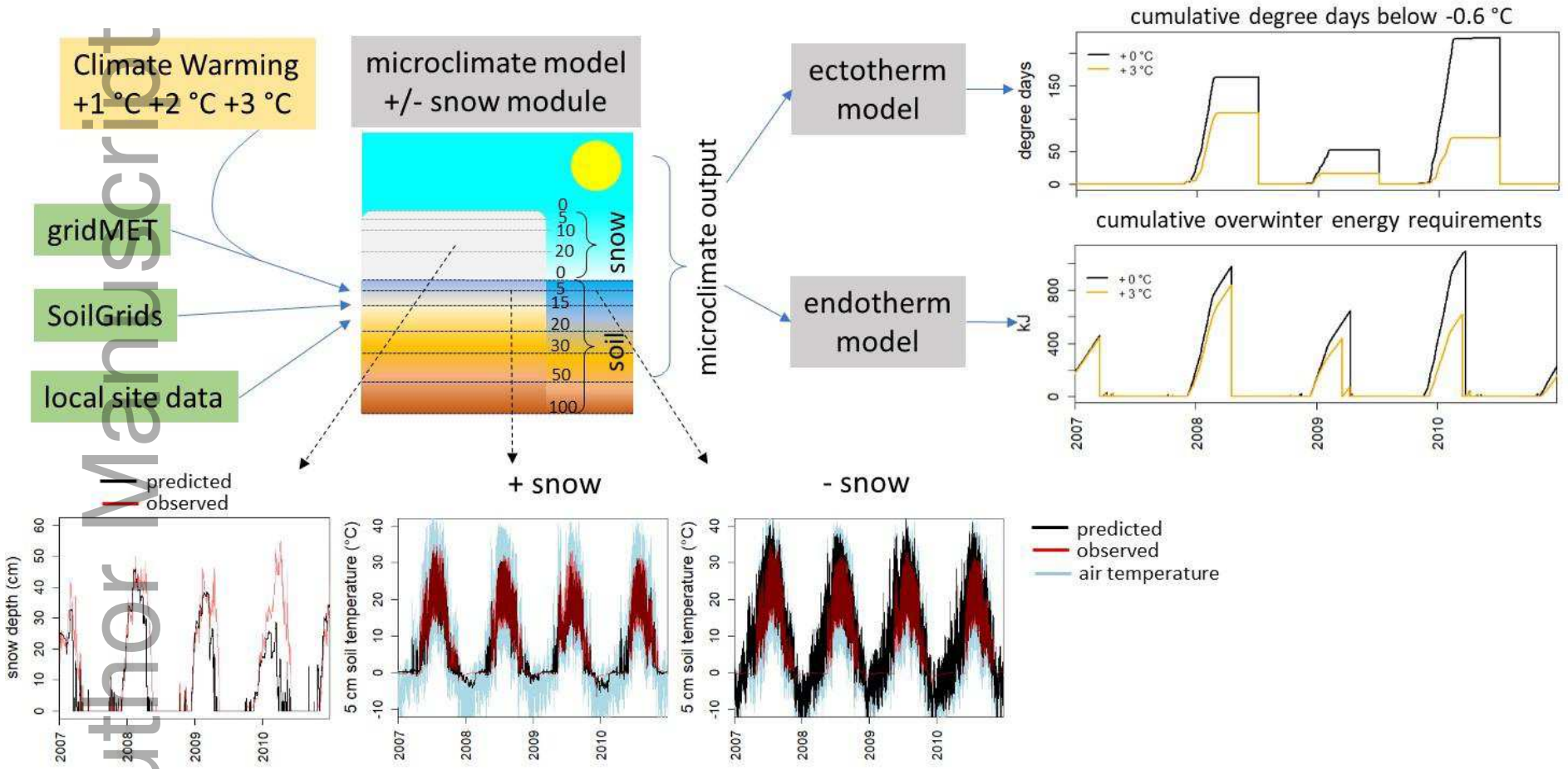

Figure 1. Overview of the scheme for modelling snow-mediated microclimatic effects on organisms using the NicheMapR package. The environmental data (green boxes) includes forcing weather data (gridMET for the USA), soil characteristics (sourced from the SoilGrids database) and local site information on topography, shading etc. The microclimate model predicts above- and below-ground environments, including the accumulation and melting of snow and its

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influence on ground temperature. The snow model can be turned on or off to study the direct effect of snow. The outputs of the microclimate model can then be used to simulate the biophysical consequences for ectotherms (e.g. cumulative exposure to below-zero body temperature for a given winter) and endotherms (e.g. hibernation energy costs of overwintering). Example simulations (back, blue) and observations (red) are given for Dorsey Basin, Nevada USA (SNOTEL site 453) and the consequences for ectotherms and endotherms are shown for current climate (black) and a uniform warming of 3 °C (orange). The code to generate these simulations is provided in the Supplementary Text.

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For each simulation, hourly output of reference (2 m) and local (1 cm above surface, i.e. of soil or of snow if present) air temperatures were saved as well as estimates of snow depth, snow density, and soil temperature and moisture at each depth. The hourly model predictions for DefaultTest and LocalTest were compared to hourly observations using the correlation coefficient *r* and the root mean square deviation *rmsd*, as in Kearney and Maino (2018), as well as the *rmsdp* (*rmsd*/range, expressed as %) and mean bias error. Observation data were filtered to remove negative values (for snow depth, snow water equivalent and soil moisture), and hourly spikes above or below a threshold level (> 20 cm for snow depth, > 20 inch for snow water equivalent, > 5% for soil moisture and > 20 °C for temperature) (see also Avanzi *et al.*, 2014). All observation data sets were checked for aberrant data and variables were excluded from analyses where necessary; these were sites with clearly impossible values (some likely due to incorrect units, e.g. °F rather than °C, and others apparently due to sensor mix-up, e.g. highly fluctuating temperatures in deep soil).

The hourly air temperature (1 cm and 2 m), snow depth and soil temperature data from DefaultTest, NoSnow and Warm1-3 were then aggregated to provide annual summary statistics of snow depth, snow days, air and soil temperature and degree days below 0 °C per height/depth, offsetting by half a year to ensure that statistics referred to a whole winter. Where annual means are presented, these are the means of the aggregated yearly values. Linear regression analysis of relationships between these variables with year and with each other were undertaken and the slopes, R^2 and *P*-values saved (all mapped results are for cases where $P < 0.05$).

Finally, two example biophysical simulations were run to assess the physiological consequences of snow-mediated soil temperatures under the DefaultTest and Warm1-3 scenarios. First, a simulation of a 20 g thermoregulating lizard was run using the 'ectotherm' model of the NicheMapR package (Kearney & Porter, 2019). The activity body temperature range was assumed to be 32-37 °C, between 0 and 90% shade could be selected when active and the retreat site was at 5 cm below the soil surface. Annual activity time and exposure to cold stress (degree days below super-cooled body temperature of -0.63 °C) was then collated. Second, the total energy requirements of a hibernating 20 g endotherm at 5 cm depth was simulated during periods of snow cover using the 'ellipsoid' function of NicheMapR (Porter & Kearney, 2009). The required metabolic rate to balance the heat budget at basal metabolic rate (BMR) for core temperatures ranging from 2 to 20 °C in 1 °C increments was computed for all hours that snow cover was > 5 cm depth (assuming this represented times when food was inaccessible). Basal metabolic rate was adjusted from the expected normothermic value at 37 °C to the simulated body temperature using a typical Q10 of 2.5

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(Geiser, 2004). For each hour, the core temperature that resulted in the lowest BMR was chosen and the overall trajectory then summed for a given winter to obtain the total energetic cost of hibernation (See Supplementary Text for all ectotherm and endotherm model parameters).

Results

Tests of the model predictions of snow depth and SWE were within 15% of the observed range and highly correlated with the observations (r ~ 0.85), with the model skill and bias (slightly positive) differing little between DefaultTest (default settings) and LocalTest (shade, soil and terrain tuned to local site conditions) (Table 1). Soil temperature predictions showed similar skill, being within between 10% and 15% of observed ranges across all depths to 50 cm and showing high correlation with the observations (r 0.83-0.96) and a small positive bias. Predictions of 100 cm soil temperature had lower skill, especially for LocalTest (Table 1). Again, little difference was found in model performance between DefaultTest and LocalTest. Soil moisture predictions were within ~27% of observed ranges for depths down to 50 cm under DefaultTest but this improved to ~ 20% under LocalTest (r ~ 0.6 in both tests) and bias was substantially reduced, again with 100 cm predictions being of lower skill (Table 1). Figure 1 shows a typical match between time series of observed and predicted snow depth and snow temperature. Simulated snow removal reduced minimum soil temperature by around 10 °C, and in some places by as much as 19 °C (Fig. 1 & Fig. S1). Histograms of the summary statistics per site for DefaultTest and LocalTest are provided in Appendix S1, and plots of observed and predicted values for all 590 sites for snow, soil temperature and soil moisture (DefaultTest) are in Appendices S2, S3 and S4, respectively.

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Table 1. Correlation coefficients (*r*), root mean square deviation (*rmsd*), percent root mean square deviation (*rmsdp*) and bias error (*bias*) for hourly snow depth (cm), snow water equivalent (SWE), soil temperature (T_{soil}) and soil moisture (M_{soil}) at different depths under DefaultTest (default settings) and LocalTest (shade, soil and terrain matched to local conditions).

	DefaultTest				LocalTest			
	r	*rmsd*	*rmsdp*	*bias*	*r*	*rmsd*	*rmsdp*	*bias*
snow depth (cm)	0.86	9.15	14.32	1.34	0.86	9.43	14.7	1.13
T_{soil} 5 cm (°C)	0.87	4.81	12.66	0.21	0.88	4.45	11.81	0.24
T_{soil} 10 cm (°C)	0.94	3.60	10.02	0.81	0.95	3.49	9.65	1.02
T_{soil} 20 cm (°C)	0.96	2.62	9.92	-0.11	0.96	2.54	9.91	0.00
T_{soil} 50 cm (°C)	0.92	2.57	13.47	0.07	0.89	2.81	15.18	0.27
T_{soil} 100 cm (°C)	0.67	4.26	21.91	1.27	0.58	4.57	24.4	1.35
M_{soil} 5 cm (%vol)	0.59	10.69	27.89	-6.55	0.59	7.99	19.96	-0.27
M_{soil} 10 cm (%vol)	0.61	8.71	24.58	-2.12	0.62	6.95	18.87	-0.35
M_{soil} 20 cm (%vol)	0.61	9.39	26.41	-2.20	0.61	7.2	20.68	-0.06
M_{soil} 50 cm (%vol)	0.56	9.92	29.32	-0.52	0.58	7.05	23.00	-0.49
M_{soil} 100 cm (%vol)	0.46	11.16	37.31	-2.74	0.45	9.47	32.91	-2.94

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Of the 590 SCAN/SNOTEL sites, 286 were simulated to have a mean annual snow depth of > 10 cm and these were clustered in the northwest (Fig. 2a) consistent with the empirical observations (Fig. S2a). The rate of warming of 2 m gridMET air temperatures exceeded 0.1 °C per decade at 87.1 % of sites and 0.5 °C per decade at 21.3 % of sites; over 75% of the latter sites were simulated to have > 10 cm mean annual snow depth per year (Fig. 2b, see Fig. S2b for local station observations and also Harpold & Brooks, 2018). Of the snow sites, 32 % showed linear declines in snow depth over the simulation period (R^2 > 0.1, slope < -0.3 cm/y) (Fig. 2c) and 12% showed linear declines in duration (Fig. 2d).

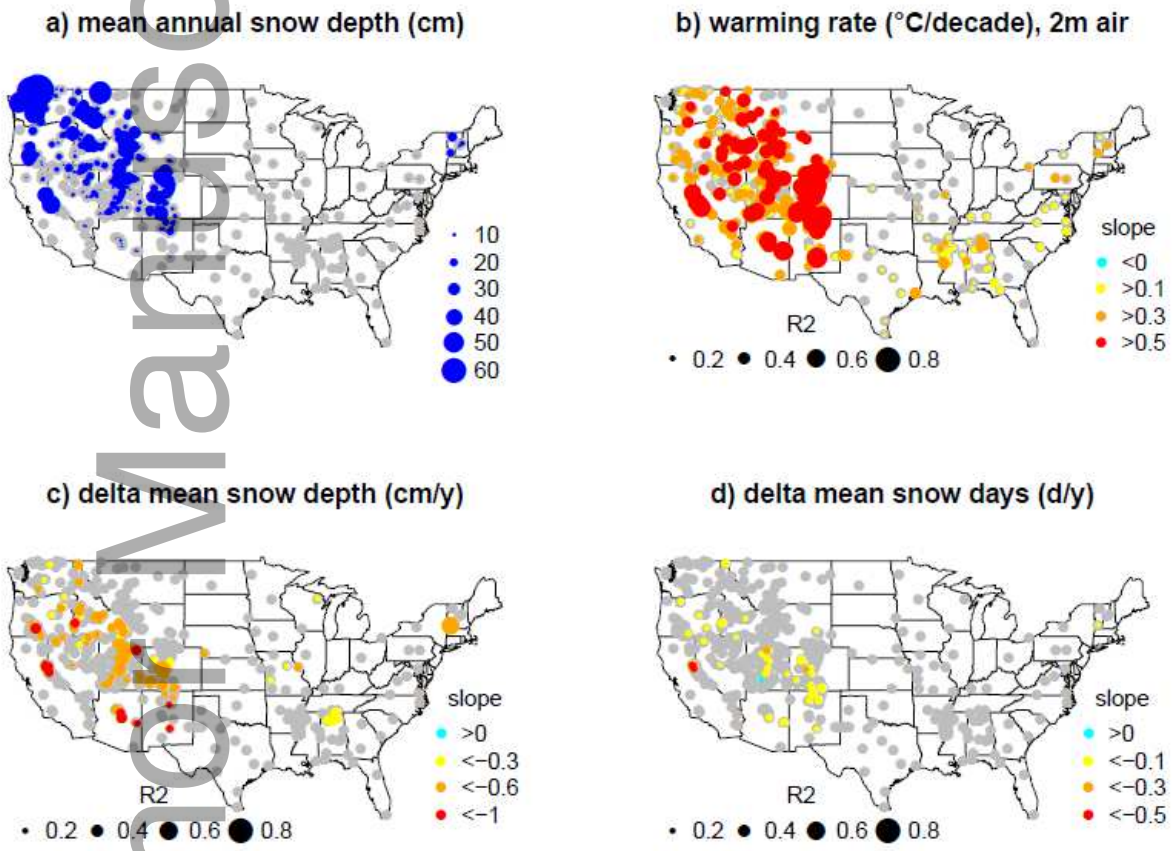

Figure 2. Simulation outputs (DefaultTest) of a) mean annual snow depth, b) annual warming rate of 2m air temperature, c) rate of change in mean annual snow depth and d) rate of change in mean annual snow duration across the USA between 1980 and 2017. Grey points indicate sites with magnitude zero. Figure S2 shows the equivalent figures for raw observational data.

The simulated 1 cm air temperature showed a similar pattern to the 2 m air temperature change with 21.5 % of sites exhibiting warming rates of > 0.5 °C (with an R^2 > 0.1 for the linear regression of warming on year, Fig. 3a). But in the soil at 5 cm depth, only 9.1 % sites showed warming rates > 0.5 °C (Fig. 3b). Similarly, the reduction in degree days of subzero 1 cm air temperatures was more than

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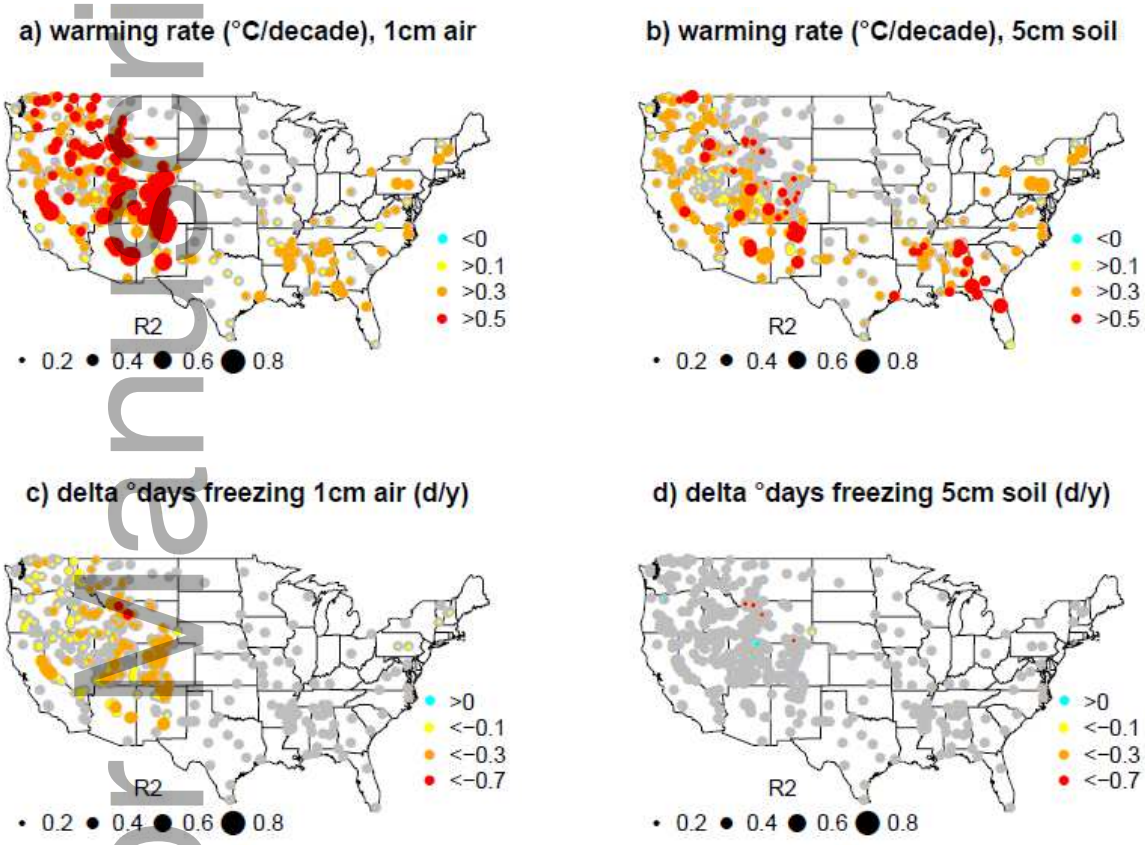
298 0.3 days per year at 50.7% of sites but for 5 cm soil this only occurred for 1.5 % of sites (Fig. 3c & d).
299 Comparison of these patterns with those when the snow model was turned off show that the
300 divergent responses of soil and air temperatures is attributable to the buffering effect of snow; i.e. in
301 the absence of snow for 5 cm soil, the proportion of sites with warming rates > 0.5 °C increased to
302 38.3 % and the number of sites with reductions in degree days of subzero exposure increased to
303 65.4 % (Fig. S3).
304



305
306 **Figure 3.** Simulated change in decadal warming rate of a) 1 cm air temperature and b) 5 cm soil
307 temperature as well as change in degree days below 0 °C of c) 1 cm air temperature and d) 5 cm soil
308 temperature across the USA between 1980 and 2017. Grey points indicate sites with magnitude
309 zero. Figure S3 shows the equivalent figures with the snow model turned off.
310
311 Biophysical simulations of a thermoregulating lizard experiencing conditions 1 cm above ground
312 show that historical warming has increased potential activity time across 57.4 % of sites, in some
313 cases by over 50 hours per decade (Fig. 4a), consistent with historical air temperature increases
314 (Figs. 2b & S2b). When the snow model was turned off, contemporary climate warming caused
315 substantial amelioration of cold stress exposure throughout the snow-affected regions (Fig. 4b) but
316 when snow effects were included there was little simulated change in cold stress exposure and, at

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some sites, increased cold stress exposure occurred (Fig. 4b). For the endotherm simulation, mean hibernation costs were greatest in the Southern Rocky Mountain Steppe ecoregion (Fig. S4) and it was in this region that strongest reductions in hibernation costs occurred in contemporary times (Fig. 4d). Simulated warming of 1, 2 and 3 °C resulted an overall reduction in cold stress (cold stress exposure for lizards, total hibernation energy requirements for endotherms) as warming increased relative to the baseline 1980-2017 condition, but there were always some sites exhibiting an increase in cold stress with warming (Fig. 5).

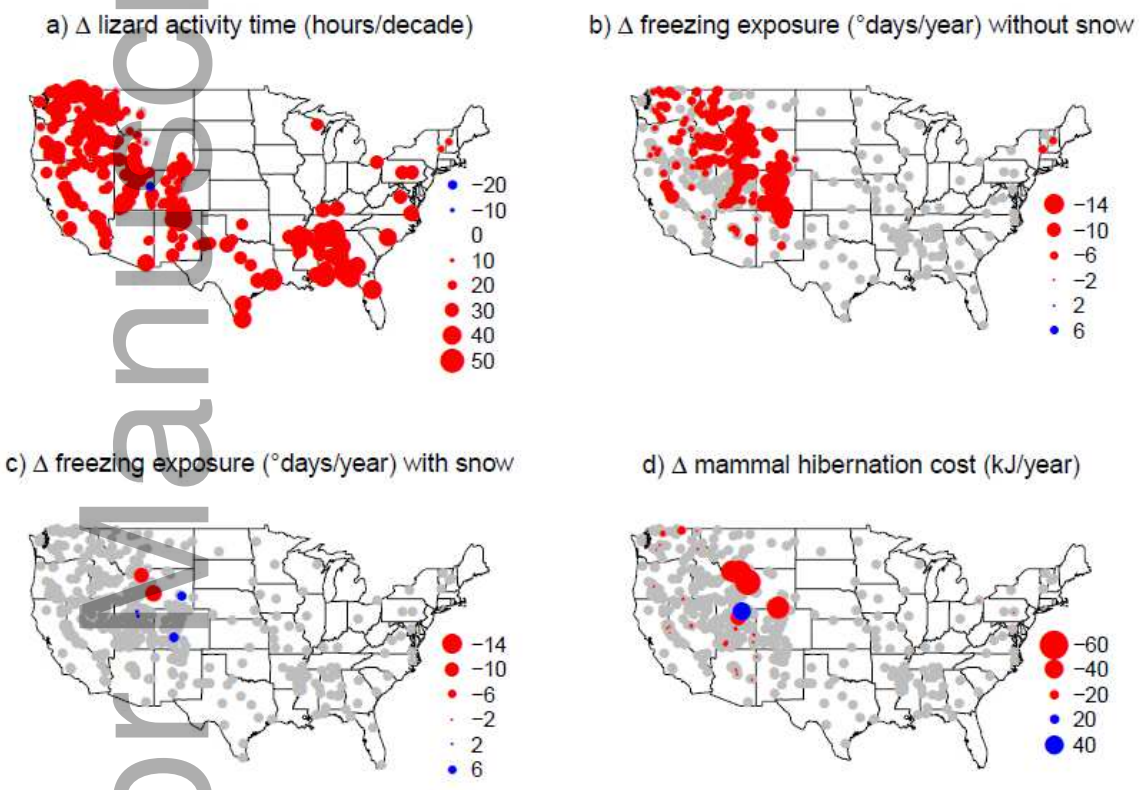

Figure 4. Simulated historical (1980-2017) changes in a) activity level, b) exposure to cold stress (< -0.63 °C if snow simulated to be absent c) or present, for a thermoregulating lizard retreating to 5 cm depth, and d) overwinter hibernation costs for an endotherm retreating to the same depth. Grey points indicate sites with magnitude zero.

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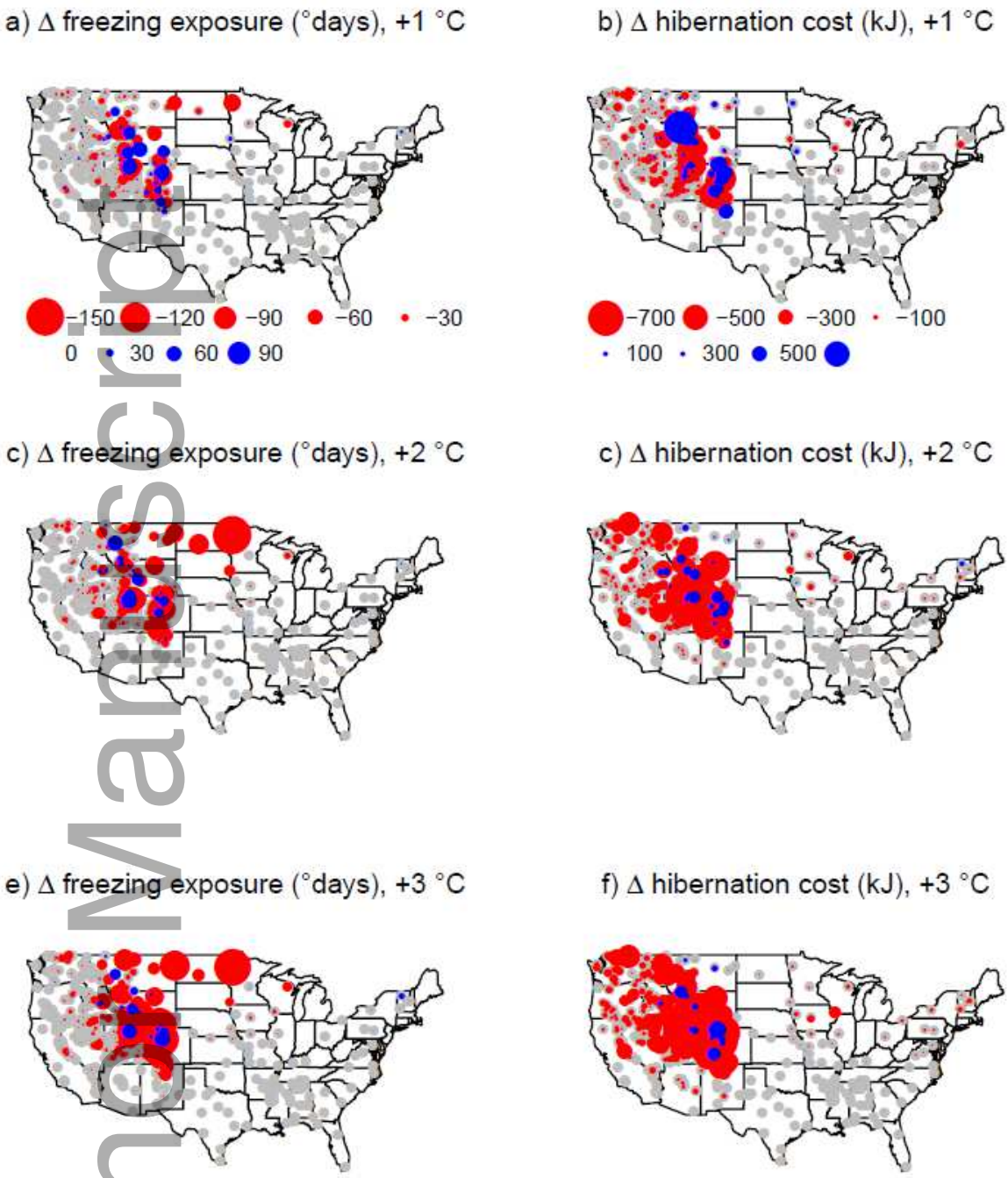

Figure 5. Simulated air temperature warming effects (+1, +2 and +3 °C) on changes in lizard cold stress (< -0.63 °C) exposure (a, c & e) and mammal hibernation costs (b, d & f) compared to base 1980-2017 environmental sequence for animals sheltering 5 cm underground. Red indicates a decrease in exposure to cold stress/energy requirements compared to baseline, blue an increase. Grey points indicate sites with magnitude zero.

Discussion

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The NicheMapR microclimate modelling system provided robust representation of snow accumulation and melting processes, and its feedbacks to soil temperature, across the USA. It was able to predict snow depth and soil temperatures to within 15% of the observed range (Table 1, Fig. 1), without any site-specific details other than those available from gridded environmental data. There is a wide range of snow models that vary in their representation of the environmental fluxes and vertical processes within the snowpack (see, e.g., Avanzi *et al.*, 2016 and references therein). The influence of snow on microclimates includes strong interactions and non-linearities, especially relating to humidity, wind speed and solar radiation effects (e.g. Harpold & Brooks, 2018). Thus fully-physical representations of the effect of snow on soil heat budgets should be more robust and generalisable to novel environmental conditions. The NicheMapR scheme neglects some details of the snow ripening process, such as water movement within the snowpack during freeze-thaw events, depth-specific changes in density, as well as vertical changes in snow structure and penetration of solar radiation. However, the present study shows that it can produce accurate microclimatic predictions at the temporal and spatial scales relevant to organisms under the influence of snow and can incorporate many terrain and landscape features that are important for species-specific microclimates (e.g. shade, slope, aspect, hill shade, soil thermal and hydraulic properties).

It was surprising that very little improvement was made on the predictions when site-specific details were included in the parameterisation, with only soil moisture showing substantial improvements (Table 1). However, there were some sites where soil temperature was clearly affected by shade, and in these cases the site-specific predictions were more accurate (e.g. SCAN site 2146, 5 cm *rmsdp* 9.1% with shade and 11.4% without shade). The use of photographs to estimate microclimatic conditions is of course not ideal and associated inaccuracies may have also contributed to the lack of improvement from site-specific parameters; ideally one would make on-site measurements of these parameters.

One of the main aims of this study was to generally quantify the effect of snow in decoupling soil temperature from climate warming. There is a strong air temperature warming signal in the gridMET dataset for the sites considered, especially those in the mountainous, inland snow-affected regions (Fig. 2b), as is borne out in analyses of the raw station data (see Fig. S2b and Harpold & Brooks, 2018). All else being equal, this warming should lead to general decreases in snow cover and duration (Isard *et al.*, 2007; Campbell *et al.*, 2010; Brown & DeGaetano, 2011), but such declines may be offset by increased precipitation or reduced solar radiation via cloud effects. The actual snow

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depth records are incomplete to various degrees, making it difficult to infer the degree of generality of warming effects on snow dynamics. However, the gridMET data captures the relevant climatic covariances and the simulation results predicted linear snow depth declines at almost one third of sites (Fig. 2c) with a less extensive effect on snow duration (Fig. 2d).

Theory and observation predict that snow cover reductions should generally result in a greater risk of exposure to freezing temperatures (e.g. Venn & Green, 2018). The simulated removal of snow (Fig. 1 and Fig. S1) reduced soil temperature in a manner consistent with experimental snow removal studies (Decker *et al.*, 2003; Wipf *et al.*, 2009; Chang *et al.*, 2014) and smaller-scale simulated removals (Xu & Spitler, 2014). The buffering effect of snow on minimum temperature was generally > 10 °C, in some places as high as 19 °C (Fig. S1). Accordingly, there was a strong decoupling between air temperature warming, whether at 2 m (Fig. 2b) or 1 cm (Fig. 3a), and soil temperature warming (Fig. 3b). The main effect was for the shallow soil temperature to warm at one third the rate of air temperature, and for the exposure to cold stress conditions to be indifferent to the air temperature warming. Few sites showed the paradoxical cooling effect of warming air temperature on shallow soils (Fig. 3d & 4c), at least with respect to exposure to freezing. Zhang et al. (2005) undertook a simulation study of a similar nature to the present study for Canada, using a monthly climatology as forcing data. They inferred a similar damping effect of snow on the historical rate of warming of soil when compared with air (0.6 °C and 1.0 °C, respectively, from 1900 to 1995) to that found in the present study, and Zhang et al.'s simulated air temperature warming, and cooling experiments showed a strong influence of feedbacks involving snow cover. In the present study, the decoupling between soil and air temperature persisted even with a 3.0 °C climate warming imposed on the historical air temperature data (as reflected in simulated lizard exposure to cold stress, Fig. 5), suggesting that this snow-mediated microclimatic effect will persist at least through the remainder of this century.

The decoupling of air and soil temperatures will have many important ecological consequences. Here I specifically investigated how it might influence ectothermic and endothermic animals, using a biophysical model to compute activity time and exposure to cold stress in a lizard and hibernation costs for a mammal over the study region and period. For the lizard, the contemporary warming evident in the gridMET data had the effect of substantially increasing activity time at the sites considered. This general beneficial effect of warming is contrary to previous work suggesting a general reduction in activity time (Sinervo *et al.*, 2010). However, the calculations here assume that shade is always available (Kearney *et al.*, 2009; see also Kearney, 2013; Walker *et al.*, 2015). Despite

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409 the substantial increases in air temperature over this period, the exposure to temperatures below
410 the freezing state of tissue (~ -0.6 °C, Lowe *et al.*, 1971) were ameliorated at only 2 % of all sites.
411 Moreover, cold exposure increased at 2% of sites (Fig. 4c), specifically in regions where snow depth
412 and/or duration were predicted to have declined (Fig. 2c & d). In contrast, when the simulation was
413 run with the snow model switched off, so that precipitation never fell as snow but still fell as rain,
414 there was a strong linear decline in cold stress exposure under historical warming in snow-affected
415 regions (Fig. 4b & Fig. 2a).
416 For the mammal, there was a generally positive effect of contemporary warming in the form of
417 reduced hibernation costs (see Fig. 1). The absolute costs of hibernation, which must be met by
418 stored energy, depend on both the duration of the hibernation period and the temperatures
419 experienced during hibernation. Hibernation costs are minimised when a mammal is in the
420 thermoneutral zone of its lowest tolerable body temperature (Geiser, 2004) and, for the present
421 simulation (hibernation T_b of 2 °C for a 20 g mammal), the optimal ambient temperature for
422 hibernation was ~1.6 °C (see example in SI Text). The positive effects of climate warming on
423 hibernation costs in the present study were a result of both a reduced snow period (e.g. shortened
424 hibernation periods Fig. 1) but also especially through the snow buffering the hibernaculum
425 temperature to near 0 °C due to the latent heat of fusion.
426
427 Under climate warming up to 3 °C, cold stress is reduced for both ectotherms and endotherms at
428 many sites, but some sites experienced increases in cold stress (Fig. 5). These latter sites cluster in
429 the Southern Rocky Mountains Steppe ecoregion (Bailey, 1998), an area of high elevation and
430 relative low precipitation that has experienced some of the highest rates of contemporary warming
431 (Fig. 2b). This ecoregion therefore stands out as worthy of future attention in studies of the
432 ecological effects of climate warming.
433
434 The example simulations presented here are clearly not exhaustive but are illustrative of the fact
435 that the direct effects of snow-mediated microclimate on organismal physiology are idiosyncratic
436 and must take account of species-specific factors (e.g. overwinter sites, metabolic systems, cold
437 tolerance mechanisms). The ecological consequences of such physiological effects are difficult to
438 predict; for instance, they may benefit cold-tolerant species through an increased growth season
439 without losing a competitive edge against warm-adapted competitors or hinder them through
440 inappropriate phenological responses. Thus, snow-mediated changes to the coupling of soil and air
441 temperature under climate warming, as presented here and reported an increasing number of
442 empirical and simulation studies around the world (Decker *et al.*, 2003; Zhang *et al.*, 2005; Wipf *et*

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al., 2009; Chang *et al.*, 2014; Xu & Spitler, 2014; Aalto *et al.*, 2018), will pose unique adaptive challenges. This will be especially the case for organisms spanning the soil/air interface physically (plants), behaviourally (e.g. underground retreats) or through ontogeny (e.g. eggs vs. adults). Ecologists studying snow-affected systems therefore need accessible tools to capture the underlying micrometeorological processes. The modelling framework developed here should provide an accessible means for ecologists to make accurate inferences of the microclimatic consequences of snow on biological processes in the USA and beyond (Kearney *et al.*, 2019).

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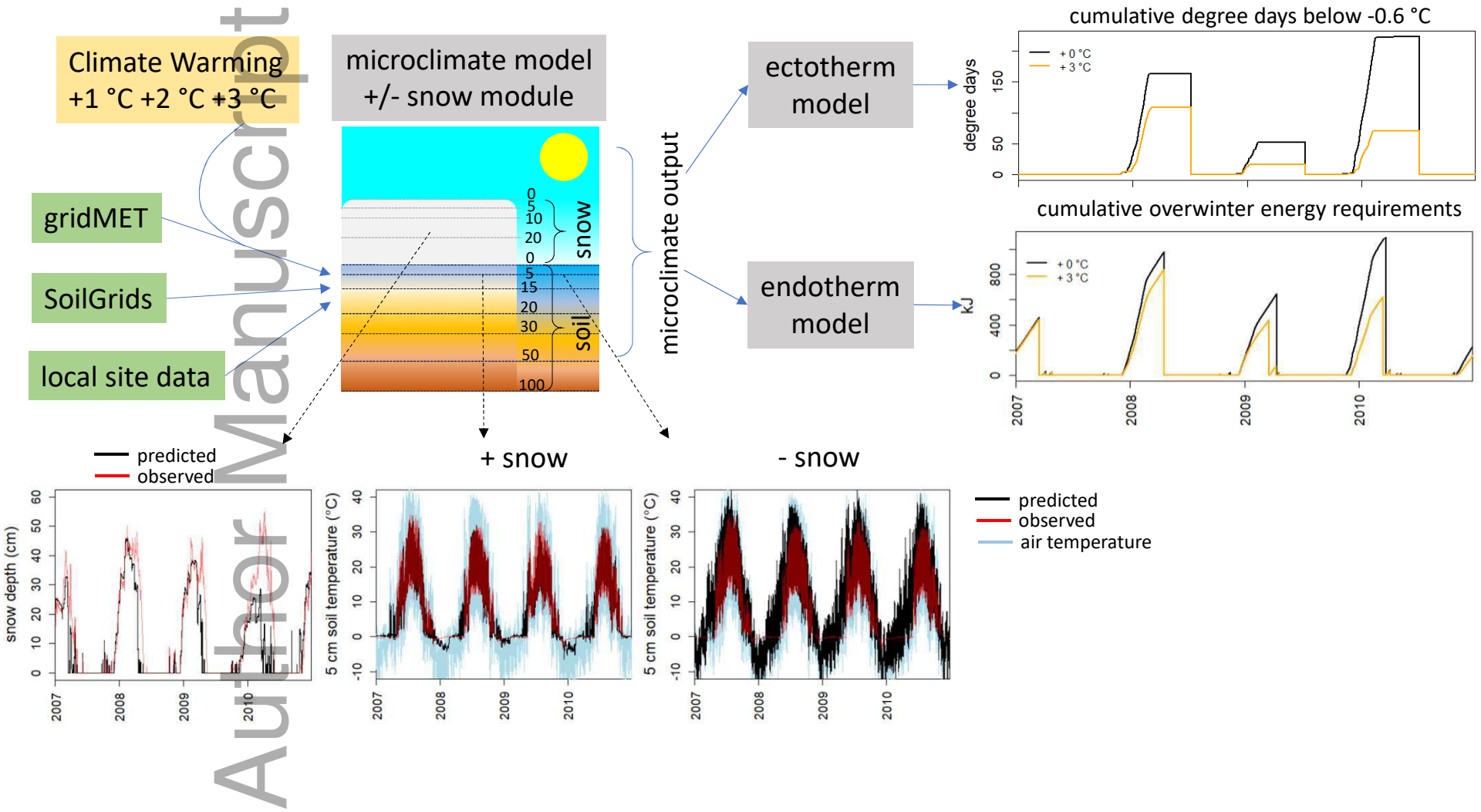

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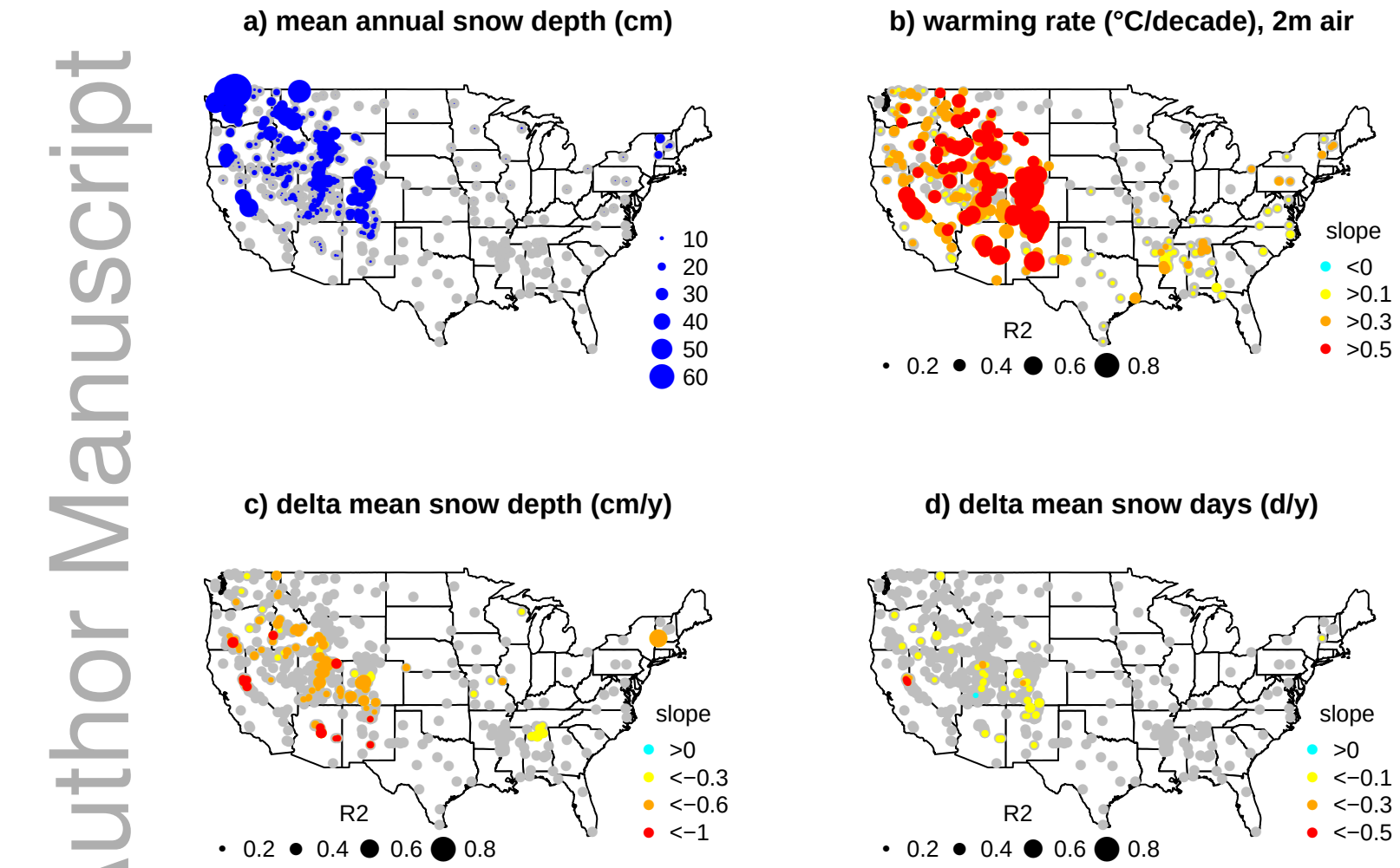

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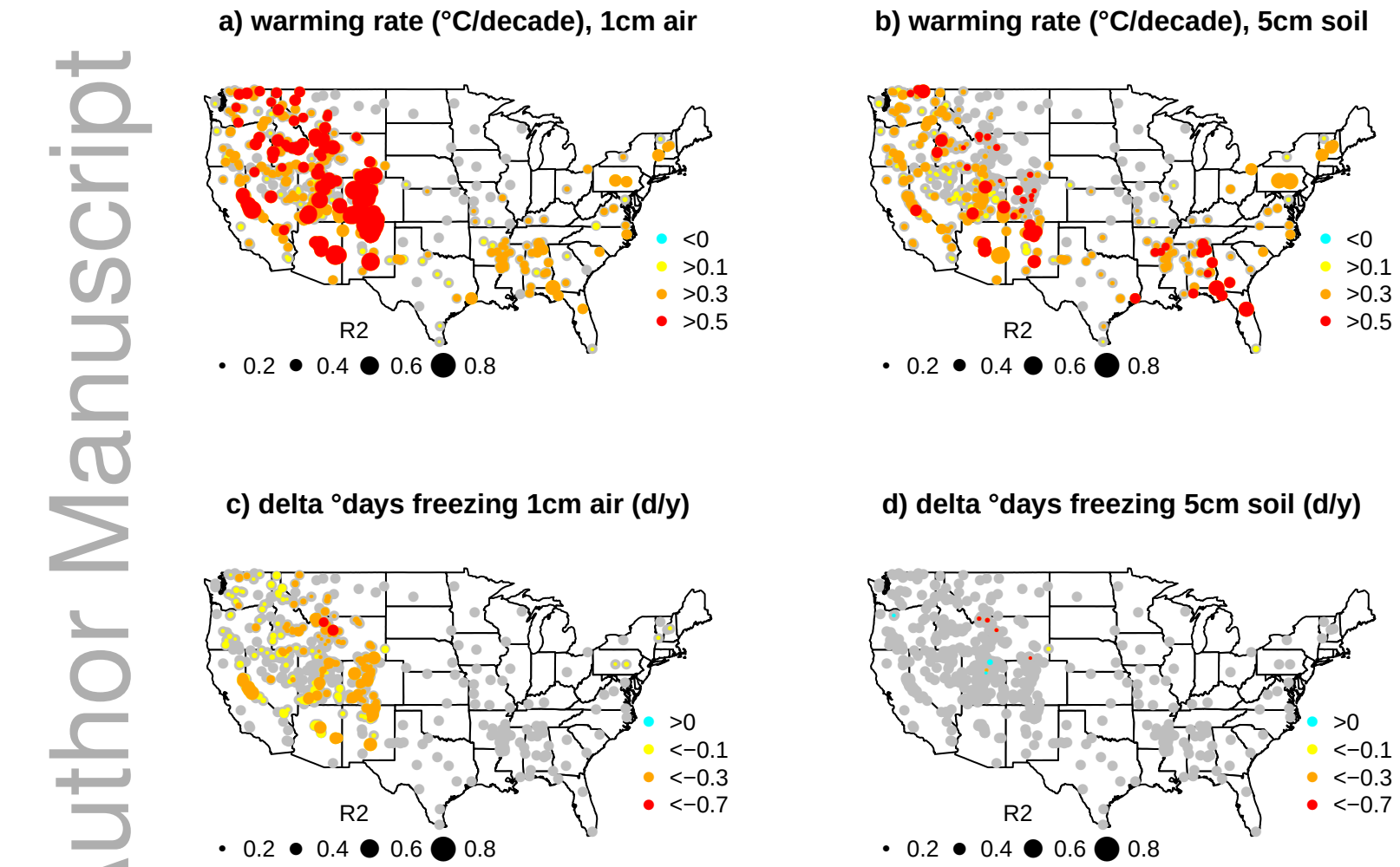

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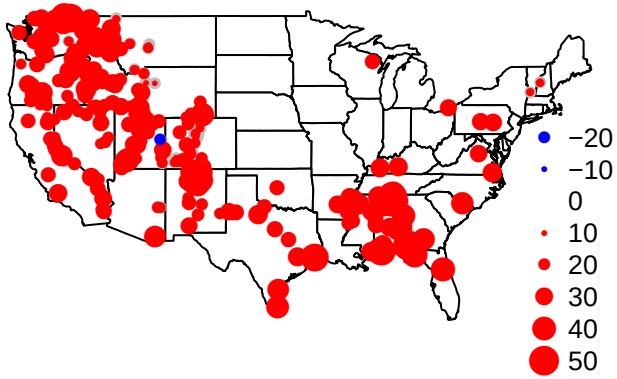
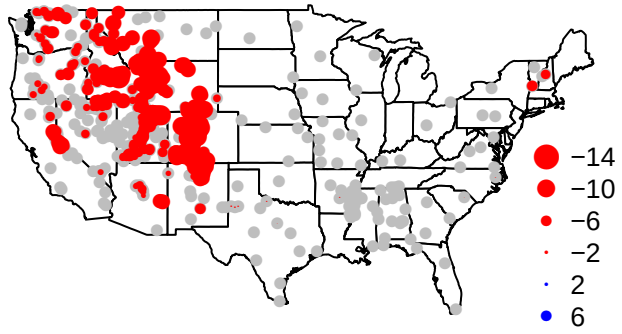
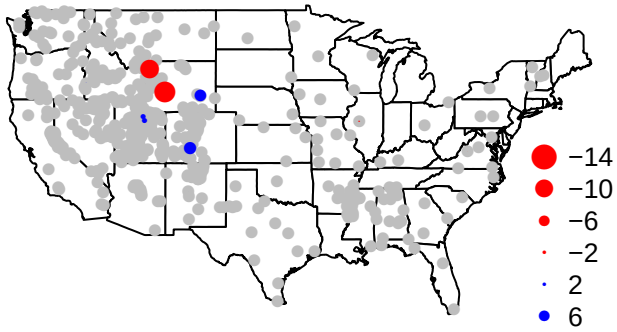
a) Δ lizard activity time (hours/decade)



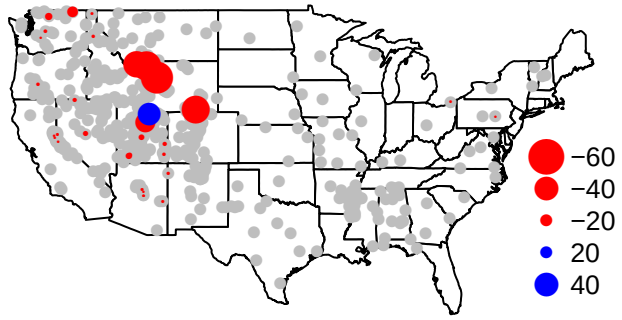
b) Δ freezing exposure (°days/year) without snow



c) Δ freezing exposure (°days/year) with snow



d) Δ mammal hibernation cost (kJ/year)



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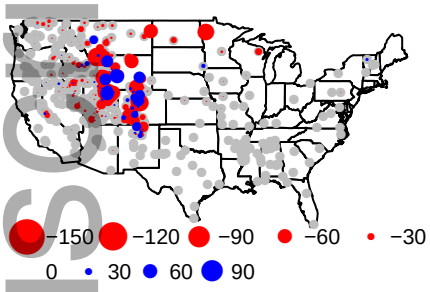
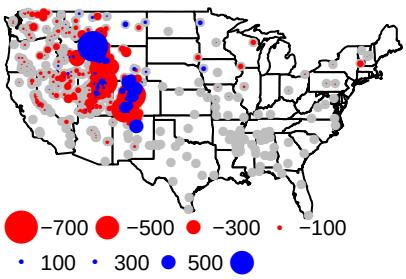
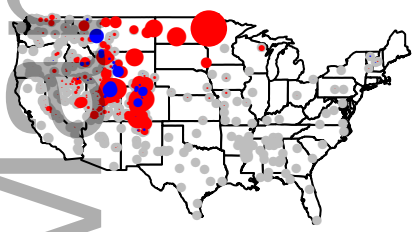
a) Δ freezing exposure (°days), +1 °C



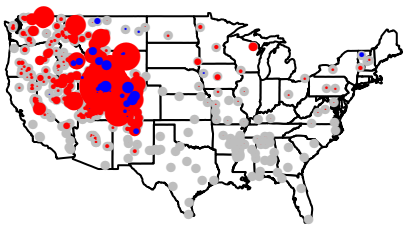
b) Δ hibernation cost (kJ), +1 °C



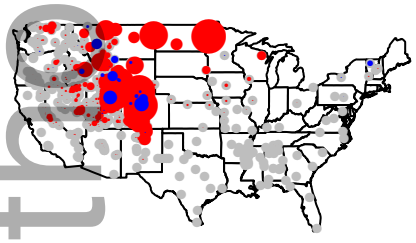
c) Δ freezing exposure (°days), +2 °C



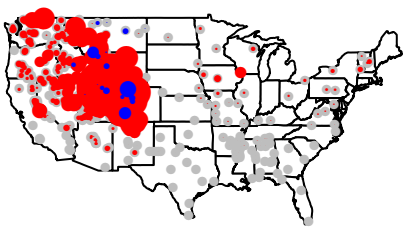
c) Δ hibernation cost (kJ), +2 °C



e) Δ freezing exposure (°days), +3 °C



f) Δ hibernation cost (kJ), +3 °C



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