DR. MEGAN FITZPATRICK (Orcid ID : 0000-0002-8332-6465)

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Title: Future winters present a complex energetic landscape of decreased costs and reduced risk for a freeze-tolerant amphibian, the Wood Frog (*Lithobates sylvaticus*)

Running title: Future winter energetic landscape for Wood Frog

Authors:

Megan J. Fitzpatrick^{1,4,5,6}, Warren P. Porter⁴, Jonathan N. Pauli¹, Michael R. Kearney², Michael Notaro³, Benjamin Zuckerberg¹

¹Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, Wisconsin USA

²School of BioSciences, The University of Melbourne, Parkville, Victoria 3010 Australia

³Nelson Institute Center for Climatic Research, University of Wisconsin-Madison, Madison, Wisconsin USA

⁴Department of Integrative Biology, University of Wisconsin-Madison, Madison, Wisconsin USA

⁵Current affiliation: Wetland Wildlife Population and Research Group, Minnesota Department of Natural Resources, Bemidji, Minnesota USA

⁶megan.fitzpatrick@state.mn.us, (218) 308-2284

Abstract

Winter climate warming is rapidly leading to changes in snow depth and soil temperatures across mid- and high-latitude ecosystems, with important implications for survival and distribution of species that overwinter beneath the snow. Amphibians are a particularly vulnerable group to winter climate change because of the tight coupling between their body temperature and metabolic rate. Here, we used a mechanistic microclimate model coupled to an animal

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biophysics model to predict the spatially-explicit effects of future climate change on the wintering energetics of a freeze-tolerant amphibian, the Wood Frog (*Lithobates sylvaticus*), across its distributional range in the eastern United States. Our below-the-snow microclimate simulations were driven by dynamically downscaled climate projections from a regional climate model coupled to a one-dimensional model of the Laurentian Great Lakes. We found that warming soil temperatures and decreasing winter length has opposing effects on Wood Frog winter energy requirements, leading to geographically heterogeneous implications for Wood Frogs. While energy expenditures and peak body ice content were predicted to decline in Wood Frogs across most of our study region, we identified an area of heightened energetic risk in the northwestern part of the Great Lakes region where energy requirements were predicted to increase. Because Wood Frogs rely on body stores acquired in fall to fuel winter survival and spring breeding, increased winter energy requirements have the potential to impact local survival and reproduction. Given the geographically variable and intertwined drivers of future under-snow conditions (e.g. declining snow depths, rising air temperatures, shortening winters), spatially-explicit assessments of species energetics and risk will be important to understanding the vulnerability of subnivium-adapted species.

Keywords

climate change, mechanistic model, microclimate, Niche Mapper, NicheMapR, *Rana sylvatica*, subnivium, Wood Frog

Introduction

Current rates of diminishing snow and ice — including glaciers, ice fields and seasonal snow cover — portend important changes in the ecology and distribution of winter-adapted species (Williams et al. 2015) and a looming threat for mid-and high-latitude ecosystems (Contosta et al. 2019). A critical, yet understudied, consequence of climate change on winter environments is the sudden loss (Thompson et al. in 2018) of an extensive microhabitat underneath the snow, the subnivium, where the majority of biodiversity in northern temperate areas spends the winter (Pauli et al. 2013). The subnivium exists at the soil-snow interface and acts as a stable thermal environment sheltering plants and small animals attempting to survive a period of resource deprivation and inclement weather to emerge in the spring and begin their annual reproductive processes (Pauli et al. 2013). A wide-ranging microhabitat, the subnivium extends throughout much of the cryosphere, but winter warming and diminishing snow cover threaten the extent,

61 timing, and stability of the subnivium and its dependent species (Thompson et al. 2018,
62 Zuckerberg and Pauli 2018). Decreases in snow cover extent, duration, and thermal insulation
63 capacity (arising from reduced depth and increased density), disrupt a diversity of ecological
64 processes ranging from nutrient cycling and hydrology to community composition and biotic
65 interactions (Campbell et al. 2005; Kreyling et al. 2012; Martz et al. 2016; Contosta et al. 2017).

66 The subnivium provides cover and stable temperatures for a suite of winter-adapted
67 animals ranging from invertebrates to small mammals and herptiles (Williams et al. 2015; Pauli
68 et al. 2013). For ectotherms like herptiles, body temperature is tightly tied to environmental
69 temperature, with consequences for both energy requirements (metabolic rates) and risk of lethal
70 freezing. While rising temperatures may increase winter energy demands, reduced snow
71 insulation may expose organisms to extreme cold temperatures at intervals (Williams et al.
72 2015). Terrestrial ectotherms typically survive low winter temperatures via supercooling (freeze-
73 avoidance) or adaptations to regulate and survive freezing of body tissues (freeze-tolerance)
74 (Costanzo and Lee 2013). Future risks of lethal cold exposure will vary depending on reliance on
75 freeze-tolerance versus freeze avoidance, species-specific temperature tolerances, typical
76 hibernaculum choice (e.g. burrow depth), and region-specific changes in subnivium conditions.

77 The Wood Frog (*Lithobates sylvaticus*) is a freeze-tolerant amphibian with a broad
78 distribution over North America, extending from the boreal forest in the north to the southern
79 Appalachians, with extensive research on the physiological aspects of whole-body freezing (e.g.
80 Storey and Storey 1984, Layne and Lee 1987, Costanzo et al. 1991, Sinclair et al. 2013, Larson
81 et al. 2014). Wood Frogs appear to be particularly vulnerable to the effects of warming
82 temperatures brought on by climate change with clear climate-demographic linkages that could
83 lead to population changes and range contraction (Fitzpatrick et al. 2019, Amburgey et al. 2018).
84 Shallow soil temperatures are most sensitive to changing snow insulation, and shallow-
85 burrowing animals like Wood Frogs will be among the first subnivium-dwellers to experience
86 the consequences of reducing snow insulation. Further, freeze-tolerant animals may face
87 particularly heightened energy demands with more variable subnivium temperatures due to
88 increasing frequency of freeze-thaw events (Sinclair et al. 2013).

89 During the onset of winter, as a Wood Frog's body temperature declines to
90 approximately -2 °C in its shallow-soil hibernaculum, nucleating agents in the blood initialize
91 formation of extracellular ice (Wolanczyk et al. 1990). This ice formation triggers rapid

conversion of glycogen stores into circulating glucose (Storey and Storey 1986), which is taken up by cells to prevent freezing damage (Carpenter and Crowe 1988) and osmotic water loss (Storey and Storey 1987). Later in winter, as temperatures rise above freezing, circulation is restored and glucose is recovered (Costanzo et al. 1997) and converted back into glycogen for storage. Wood Frogs may undergo numerous freeze-thaw cycles throughout the winter as soil temperatures rise and fall (Sinclair et al. 2013), especially at the beginning and end of the winter season (Larson et al. 2014). The process of glucose mobilization and recovery is energetically costly, inducing increases in metabolic rate with each freeze-thaw cycle (Sinclair et al. 2013). Without the stability of the subnivium, temperature fluctuations can incur large energetic costs, deplete energy and cryoprotectant (glucose) stores, and increase the risk of reaching lethal ice content levels ($>2/3$ body water frozen) (Sinclair et al. 2013; Layne and Lee 1987, Costanzo and Lee 2013). Heightened energy use has the potential to be particularly problematic for Wood Frogs because they rely entirely on body reserves (lipid and glycogen) acquired in fall to fuel both winter survival and spring reproduction. Risk of ice nucleation in the gut, inhibition of digestion by cold temperatures, and absence of their insect prey prevent feeding during midwinter or prior to their early spring breeding season (Costanzo and Lee 2013, Wells and Bevier 1997, Sinclair et al. 2013).

Given projected changes in the winter environment, characterized by reduced snow cover (Notaro et al. 2014, Notaro et al. 2015) and loss of the subnivium, freeze-tolerant amphibians are at risk of elevated energetic costs and exposure to increased climate variability (Sinclair et al. 2013). Many of these projected changes are strongly regional due to differences in snow cover regimes across latitudinal gradients and proximity to water bodies which mediate local weather patterns (Notaro et al. 2013, Notaro et al. 2015), creating the potential for regional differences in future Wood Frog winter microclimates. Further, the buffering impact of snow on soil microclimate involves non-linear and interacting influences of various weather components (e.g. humidity, wind speed, solar radiation, air temperature) (Kearney, 2020). Although winter climate change poses a significant threat for cold-adapted species, effective modeling of the physiological and energetic costs of rising and more variable winter temperatures on subnivium-dependent species is difficult. To address this knowledge gap, we recently developed a general mechanistic model of frog energetics and ice dynamics operating within the subnivium (Fitzpatrick et al. 2019). Our model, integrated with the Niche MapperTM/NicheMapR modeling

suite (Mathewson et al. 2017, Kearney and Porter 2020), was directly linked to variability in winter microenvironments (both above and below the snow) and is capable of mapping energetic landscapes across geographic scales.

Our goal in this study was to use the coupled microclimate and frog mechanistic models to predict the future effects of climate change on the energetics, survival and distribution of Wood Frogs under different warming scenarios across the Great Lakes region. We hypothesized that future winter air temperature warming and corresponding declines in snow cover would influence the amount of energy required to survive the winter and the physiological risk of Wood Frogs reaching critical ice content levels. Specifically, we predicted that warming winter temperatures would lead to warmer soil temperatures (Sinha and Cherkauer 2010, Henry 2008) and increased winter energy requirements via increased metabolic rates. We further predicted that increased variability in soil temperatures – as result of a loss of snow cover and a degrading subnivium (Zhu et al. 2017, 2019) – would heighten the risk of reaching critical ice content levels (via lower minimum soil temperatures). Variability in soil temperatures could also increase energy expenditure via increased number of freeze-thaw cycles and Jensen’s inequality (i.e., higher variation in body temperature around a given mean temperature over a given period of time results in higher total energy expenditure) (Sinclair et al. 2013, Ruel and Ayres 1999). Finally, we predicted that these physiological consequences would be geographically complex due to the heterogeneous nature of climate change and variability in snow cover regimes, but that high-latitude regions and lake effect zones could serve as critical winter refugia for Wood Frogs in the future.

Materials and Methods

Model description

We simulated future microclimates and Wood Frog biology using the Niche Mapper/NicheMapR program suite (Fitzpatrick et al., 2019; Kearney & Porter, 2017; US Patent No. 7155377, 2006), which consists of a microclimate model coupled to a biophysical animal model. In short, the microclimate model simulates hourly conditions at a series of heights above ground and depths below the snow or soil surface by applying physics- and meteorology-based equations to user-input daily climate conditions: daily minimum and maximum air temperature, wind speed, cloud cover, and humidity; and daily total precipitation and other characteristics of

local terrain (e.g. elevation, slope, aspect, soil properties, shade conditions). The biophysical model uses hourly microclimate conditions specific to Wood Frog height/depth to simulate body temperature, metabolic rate, and percent of body water that is frozen (per-mass basis).

Microclimate simulations

We simulated future microclimate conditions using daily weather conditions dynamically downscaled from Coupled Model Intercomparison Project Phase Five (CMIP5) global climate models (GCMs) to 25-km grid spacing for three 20-year time periods: late 20th century (1980-1999), mid-21st century (2040-2059), and late-21st century (2080-2099) (Notaro et al., 2016). Notaro (2016) downscaled the output from six GCMs according to the representative concentration pathway 8.5 (RCP 8.5) using the Abdus Salam International Centre for Theoretical Physics Region Climate Model version four (RegCM4) interactively coupled to a one-dimensional model of the Great Lakes with a lake ice sub-model. The inclusion of a lake model helps the regional climate model capture lake-effect snow events occurring downwind of the Great Lakes, which is important for simulating subnivium conditions in our study region. Notaro (2016) debiased the downscaled data, both in terms of daily mean and daily interannual standard deviation, against gridded observational meteorological data for 1984-2013.

We simulated each grid cell's hourly microclimate conditions for each 20-year period using the downscaled, debiased data from four GCMs. We chose these GCMs to bound the range of changes in climate conditions affecting Wood Frog wintering biology. Specifically, the models projecting the least amount of change in air temperatures and snow in the eastern and Midwestern United States were the Meteorological Research Institute Coupled Global Climate Model Version Three (MRI-CGCM3; hereafter MRI) and the National Oceanic and Atmospheric Administration Geophysical Fluid Dynamics Laboratory model (GFDL-ESM2M; hereafter GFDL), and the models predicting the most change were the Model for Interdisciplinary Research on Climate Version Five (MIROC5) and the Centre for Australian Weather and Climate Research, Australia GCM (ACCESS1-0; hereafter ACCESS) (Notaro et al., 2016) (Table 1). We simulated microclimate conditions using the debiased, dynamically downscaled daily minimum and maximum air temperature, daily total precipitation, and daily average wind speed, and humidity, as inputs to the NicheMapR microclimate model (Fitzpatrick et al., 2019). We also used dynamically downscaled values of average daily downward shortwave radiation divided by Niche Mapper-generated values for clear sky on each day of year to estimate daily

average fraction of clear sky and subtracted this value from 1.0 to get the fractional cloud cover. Microclimate was simulated from July of the first year of the downscaled dataset to July of the last year to only incorporate winters with a complete weather dataset (19 winters total).

We used the National Elevation Dataset (United States Geological Survey) aggregated to 25 km resolution and resampled to the center of each grid cell. Given the 25-km resolution, we treated each grid cell as flat ground (no slope, average elevation). We obtained location- and depth-specific soil bulk density and soil texture classes (silt, loam, etc.) from CONUS-soil grids (Miller & White, 1998). We resampled (bilinear interpolation) and aggregated (mean values) bulk density to match our 25-km grid cells. We resampled (nearest neighbor) and aggregated (majority rules) soil texture classes to match our 25-km grids. We obtained values of air entry potential, the “b” exponent, and saturated hydraulic conductivity for each soil texture class from Campbell & Norman (1998, Table 9.2) and volumetric water content at saturation from Cosby, et al. (1984, Table 3). Above these soil layers, we simulated a 5-cm organic layer and a 5-cm leaf litter layer (Fitzpatrick et al., 2019; Kearney et al., 2014), and used snow model parameters described in Fitzpatrick et al. (2019). Based on Wood Frog habitat preferences, we simulated microclimate conditions using the shade, wind speed, and snow interception conditions of deciduous forest (Fitzpatrick et al., 2019).

Wood Frog simulations

We used the Niche Mapper ectotherm biophysics model to simulate wintering Wood Frogs [previously described in Fitzpatrick et al. (2019)]. In short, Wood Frogs were simulated under the microclimate conditions of 5-cm soil depth (below the leaf litter layer). The model calculates Wood Frog core temperature and ice content (percent of body water frozen) by solving a transient heat balance equation, incorporating a stored heat term, between the animal and the soil on an hourly basis. Stored heat is directed to hourly changes in frog body temperature or ice content based on the frog’s core temperature during the previous hour and the user-input osmolality of its body fluids. Hourly energy expenditure is calculated from core temperature via an empirical temperature-respiration equation for Wood Frogs (Sinclair et al., 2013). Threshold energy costs of cooling below 1 °C, ice nucleation, and thawing (Sinclair et al., 2013) were simulated as described in Fitzpatrick et al. (2019). We assumed that frogs used glycogen to fuel non-threshold energy costs while frozen, fat to fuel non-threshold energy costs when not frozen,

and glycogen to fuel all threshold costs (Fitzpatrick et al., 2019). We modeled frogs using morphological and physiological parameters from Fitzpatrick et al. (2019) (Table S1).

We defined winter as the period during which frogs are restricted to hibernacula, based on either the presence of snowpack and/or ice in the frog's body. Each modelled winter started during the first hour that the frog developed ice in its body or the first hour when snowpack occurred on ground. (The microclimate model simulated a minimum snowpack depth of 1 cm.) Modelled winter ended when the following conditions were met: (1) the frog was completely thawed, (2) the frog would not freeze again until the following winter, (3) there was no simulated snowpack on the ground, (4) there would be no simulated snowpack on the ground until the following winter. Thus, winter was longer in years when cold temperatures and/or snow occurred over a longer period of days. The model summed total frog energy expenditure (J) over each winter for each grid cell simulated by the microclimate model. Microclimate and ectotherm model outputs were averaged across the 19 winters. These outputs were average winter soil temperature at hibernaculum depth, winter length, total number of freeze-thaw cycles, peak body ice content (where >67% body water frozen is considered lethal; Layne and Lee 1987, Costanzo and Lee 2013), and total frog energy expenditure. We converted the 19-yr averages to rasters and assessed geographic patterns using ArcMap (ArcGIS Desktop 10.5.1; Environmental Systems Research Institute, Redlands, California, USA).

Results

Late 20th-century simulations of winter climate characteristics (winter length, snow depth, soil temperature) (Fig. 1a-c, Fig. S1a,d,g,j-S3 a,d,g,j) were similar across models. Across the study region (33-49°N, 67-98°W), winter length varied from 22 days in southerly areas to 210 days in northerly areas (Fig. 1a). Late 20th century winter soil temperatures showed a similar latitudinal difference with average soil temperatures ranging from -5.1 °C in the northwest to 2.8 °C in the south (Fig. 1c). Snow depth was greatest in the northeast and declined from north to south (Fig. 1b).

Despite these strong latitudinal differences in winter climate, there was little overall change in Wood Frog energy expenditure across latitudinal gradients due to the opposing influences of winter length and soil temperatures (Fig. 1e). While winter length was shorter in the south (lowering total energy expenditure), soil temperatures were higher in the south, raising

daily metabolic rates (increasing total winter energy expenditure). For example, grid cells with energy expenditure values in the 10th percentile and below were distributed primarily in two disjunct regions: along the southern/eastern border of the Wood Frog's range, and in the far northwest of our study region (northwestern Minnesota), where cold soil temperatures — driven by colder air temperatures and low snow depths — offset the effects of longer winters. Similarly, grid cells with energy expenditures in the 90th percentile and above occurred in latitudinally disjunct regions: high elevation areas with long winters (Appalachian and Adirondack Mountains) and zones of lake-effect snow (primarily downwind - south and east - of the Great Lakes), which drove longer winters and higher soil temperatures. Overall, the highest total winter energy expenditures (22,025 J/y) occurred in the southern Appalachian Mountains, whereas the lowest energy expenditures (3,353 J/y) occurred along the southern boundary of the Wood Frog range. Assuming energy density of 39.94 kJ/g for lipids and 17.58 kJ/g for carbohydrates, the 18,672 J/y geographic range in energy expenditure corresponds to 1.06 grams of carbohydrate reserves (9.2% body mass) or 0.47 grams of lipid reserves (4.0% body mass) required to fuel the fasting Wood Frog's metabolic requirements.

Contemporary patterns in Wood Frog ice content generally tracked gradients in soil temperatures (Fig. 1f). Ice content was higher at northerly latitudes, and especially in the northwest and at higher elevations; ice content was typically lower in lake effect snow zones and southerly latitudes. Lethal ice contents occurred primarily in the northwest region of the study region (northern Minnesota), with scattered areas throughout the central part of the study region.

Predicted changes in Wood Frog energy expenditure into the mid- and late-21st century were driven by the opposing forces of shortening winter seasons and increasing soil temperatures. Except for a few isolated locations with decreased soil temperatures (magnitude < 0.4°C), 20-year-average winter soil temperatures warmed across the study region (Fig. 2, Fig. S3). Overall, soil temperatures were predicted to warm by up to 2.1 °C by the mid-21st century and up to 3.3 °C by the late 21st century, driving increases in Wood Frog metabolic rates. On the other hand, winter length (Fig. 3, Fig. S1) decreased at all but a few isolated locations by mid-21st century (maximum decrease of 62 days) and decreased at all sites by late 21st century in all models (minimum decrease 10 days, maximum decrease 93 days), decreasing energy expenditure.

The opposing forces of increasing soil temperature and declining winter length resulted in total energy expenditure decreasing in some geographical areas and increasing in others (Fig. 4, Fig. S5, S7). The greatest declines in energy expenditure occurred toward the southern border of the Wood Frog's range, with regions of increasing expenditure occurring farther north and in high elevation regions. In locations along the southern border, Wood Frog energy expenditure dropped below the range of values experienced anywhere in the study area in the late 20th century (Fig. 5). Because heightened values did not occur in areas of highest 20th century energy expenditure, future values remained below the maximum value modeled in our study area for the late 20th century. Regions of increased energy expenditure shrank between the mid- and late 21st century but were particularly persistent in the northwest. Overall, however, maximum increases in energy expenditure (3.3 kJ/y; MRI in mid-21st century) were an order of magnitude smaller than maximum decreases (-10.4 kJ/y; ACCESS in late 21st century). Changes in total winter energy expenditure from the late 20th to mid-21st century corresponded to percent changes ranging from -82% to 35%, but most were smaller in magnitude (median decrease of 6-7%, median increase 4-5%). Changes in total winter energy expenditure from the late 20th to the late 21st century corresponded to percent changes ranging from -142% to 38%, but most changes were smaller in magnitude (median decrease 14-15%, median increase 6-7%).

Predicted changes in Wood Frog peak winter ice content (Fig. 6, Fig. S6) and freeze-thaw cycles (Fig. S4) were complex, but generally decreased by the end of the century. For the mid-21st century, site-specific changes in Wood Frog ice content ranged from -43% to +20% ice compared to the late 20th century. For the late 21st century, change in peak ice values ranged from -63% to +23% ice. In only a small number of northerly sites, small increases in ice content changed peak ice values from non-lethal to lethal levels between the late 20th and mid-21st century, and these values declined back to non-lethal levels at all but 5 sites in the MRI late-21st century predictions (Fig. 6). At most sites, number of freeze thaw cycles decreased by mid-21st century and decreased further by late 21st century, with a maximum decrease of 10.6 freeze-thaw cycles. Some increases (up to 4.3 cycles) occurred in the northeast (Pennsylvania to Maine) and northwest (Michigan to Minnesota) of the study region by the mid-21st century, but these shrank by the late 21st century (Fig. S4).

Discussion

With mechanistic niche modelling, we estimated and projected the energetic landscape of wintering Wood Frogs across the eastern United States. Our findings supported our broader hypotheses that future changes in winter temperatures and snow cover would alter energy expenditure and the risk of reaching critical ice content levels. Projected winter energy expenditure and peak ice content for Wood Frogs was geographically complex due to the opposing forces of warming soil temperatures and shorter winters. As expected, soil temperatures were projected to increase across our study region, but these changes only led to increased winter energy expenditure in the northwest portion of our study region. Total winter energy expenditure decreased across most of the study region, particularly by the late 21st century. This decrease in energy expenditure occurred because shortening winters offset the effects of warming soil temperatures on Wood Frog metabolic rates. The number of freeze-thaw cycles also declined across most the winter range, despite the loss of snow cover, as air and soil temperatures rose and induced fewer whole-body freezing events. Overall, the reduction in freeze-thaw cycles and warming soil temperatures led to declining peak ice content in Wood Frogs over the majority of the study region.

Geographic patterns in late 20th century Wood Frog energy expenditure and ice content

By simulating geographic patterns in Wood Frog energy expenditure and ice content under recent (late 20th century) conditions, we found a wide range in energy expenditure (approximately 19,000 J/y) across our study region, corresponding to a difference in 1.06 g of carbohydrate reserves (9.2% body mass for the simulated 11.6 g frog) or 0.47 g of lipid reserves (4.0% body mass) required to fuel the metabolic requirements of a fasting Wood Frog. The biggest geographic differences in energy expenditure were driven not by latitudinal differences in climate conditions, but by more regional differences in temperature and snow conditions, including elevation and lake-effect snow.

Fitzpatrick et al. (2019) simulated winter energy expenditure for Wood Frogs across a smaller area of the eastern United States under early 21st century climate conditions. They found similar geographic patterns in energy expenditure. However, by including the southern Appalachian Mountains and extending the southern range boundary, we found a relatively larger range in energy expenditure (approximately 5,000 – 20,000 J/winter versus 3,000-22,000 J/winter). Heightened energy expenditures in lake-effect snow zones downwind of the Great

Lakes, where moderate winter air temperatures and deep snow drove long winters with warmer under-snow soil temperatures (higher Wood Frog metabolic rates; Fitzpatrick et al. 2019), were also apparent in this study. Low total winter energy expenditures were most common in northwestern Minnesota, where relatively low snow depths combined with the broader latitudinal pattern of cold northern air temperatures to reduce soil temperatures. The impact of low soil temperatures on Wood Frog metabolic rate offset the impacts of longer winter length with latitude. This region remains one of the lowest in terms of energy expenditure even when simulations are extended to the southern border of the Wood Frog's range.

Peak winter ice contents in this study were higher than those simulated in Fitzpatrick et al. (2019), where Wood Frogs did not freeze in a portion of the Upper Midwest and Great Lakes Basin study area. Fitzpatrick et al. (2019) suggested that peak ice contents may have been underestimated because they used averaged daily climate data for the 10-year study period to simulate a 365-day "average year". This may have lessened the influence of extreme cold events, which are unlikely to occur on the same Julian days year to year. The current study made use of high throughput computing resources to simulate microclimate conditions and Wood Frog ice dynamics based on daily data over a 19-year period (i.e., 6,935 days simulated), better accounting for variability in daily weather conditions.

Simulated Wood Frog ice contents are sensitive to body concentrations of colligative cryoprotectants (e.g. glucose and urea; Fitzpatrick et al. 2019) that may vary locally. Costanzo et al. (2013) found that cryoprotectant concentrations were higher in Wood Frogs from Alaska compared to Ohio, even when they were acclimatized to the same conditions. However, to our knowledge, total osmolality of frog plasma (including urea) of other populations has not been measured. We simulated frog cryoprotectant concentrations based on measured values from Ottawa, Canada and Ohio (Storey and Storey 1986; Costanzo et al. 2013). Cryoprotectant concentrations may differ in some regions, such as the area where lethal ice contents were predicted in northern Minnesota.

Inter-population differences in hibernaculum depth exist in our study region. For example, our simulated hibernaculum depth at the soil-leaf litter interface was based on depths reported in Connecticut (maximum of 3 cm below leaf litter; O'Connor and Rittenhouse 2016). However, in montane Maine, where winter temperatures are more similar to those in northern Minnesota, Wood Frogs wintered as deep as 12 cm below leaf litter (Groff et al. 2016). Further,

intra-population differences in Wood Frog hibernaculum depth impact winter mortality rates (O'Connor and Rittenhouse 2016). Fitzpatrick et al. (2019) found that simulated Wood Frog ice content and energy expenditure were sensitive to hibernaculum depth changes of only 5 cm, and the ideal depth to balance the risk of lethal ice content (shallower depths, colder soil temperatures) versus higher energy expenditures (deeper depths, warmer soil temperatures) may differ between geographic regions. To better incorporate local adaptations, future studies of Wood Frog wintering physiology and behavior are required, including assessments of the plasticity of burrowing behavior and of cryoprotectant concentrations throughout the geographic range.

Future climate impacts on Wood Frogs

Our models projected that a significantly shorter winter season characterized by high soil temperatures could produce a diversity of effects on Wood Frog energetics by the end of the century. Despite decreasing energy expenditure over much of the study region (median 14-15% change), we found strong regional heterogeneity. Indeed, energy expenditures were projected to increase through the end of the century in the northwest (northern Wisconsin and Minnesota; median 6-7% increase). In the GFDL and ACCESS models (Fig. 4), median change values were approximately -2000 J/winter for grid cells where energy expenditure decreased, and approximately +650 J/winter for grid cells where energy expenditure increased (-1,663 and +693 J/winter GFDL; -2,582 and +606 J/winter ACCESS). These median values correspond to approximately 0.114 g less of glycogen reserves or 0.05 g less of lipid reserves required to survive winter in grid cells where energy expenditure was projected to decrease; and 0.037 g more glycogen or 0.016 g more lipid to survive winter in grid cells where energy expenditure was projected to increase in the future. The greatest declines in energy expenditure occurred along the southern range boundary, such that Wood Frogs in the far south were projected to experience energy demands lower than any simulated for the late 20th century in our study region. Between reduced energy expenditure in the south and increased energy expenditure in the northwest, our simulations projected a shifting energetic landscape for Wood Frogs.

Wood Frogs from different populations (Ohio and Alaska) store different amounts of fat and glycogen reserves prior to winter (Costanzo et al. 2013), with frogs from Ohio storing more coelomic lipids but substantially less liver glycogen than frogs from Alaska (which require

higher levels of glucose cryoprotectant and overall greater energy stores to survive longer, colder winters). Simulated changes can be compared to measured values. If the same percent body fat and glycogen from Costanzo et al. (2013) is assumed on a per-mass basis, an 11.6 g frog would contain ~0.01 g fat and 0.10 g glycogen if from Ohio or ~0.002 g fat and 0.34 g glycogen if from Alaska (Fitzpatrick 2019). Our median change values corresponded to substantial percentages of these measured values: e.g., a savings corresponding to 33% (Alaska) or 114% (Ohio) mass of glycogen reserves available; or an increased use corresponding to 11% (Alaska) or 37% (Ohio) mass of glycogen reserves available. However, given Costanzo et al.'s (2013) evidence of local adaptation in mass of body reserves stored, percent change between time periods for frogs simulated in the same geographic location is likely a more relevant estimate of the magnitude of climate change impacts on Wood Frogs (i.e. -14-15%; +6-7%).

Because Wood Frogs rely on fall-acquired body reserves to fuel both winter survival and spring reproduction, the projected changes in total overwinter energy expenditure (which correspond directly to use of energy reserves) have the potential to directly influence reproductive output. For example, energetically-costly calling behavior in males is fueled by glycogen stores, and depletion of trunk muscle glycogen reserves may be an important constraint on the length of the breeding season (Wells and Bevier 1997). For females, Benard (2015) found a correlation between fecundity and winter temperature, with Wood Frogs in southeastern Michigan producing 3.3% fewer eggs for each 1°C increase in average winter air temperature. This pattern is consistent with increased energy reserve use during warmer winters (Benard 2015). However, as in many amphibians, larval survival in Wood Frogs is density dependent (Berven 1990; but see Berven 1995), such that changes in average numbers of eggs produced may not ultimately affect number of metamorphosing juveniles (Vonesh and De la Cruz 2002; Biek et al. 2002). Additional density dependent effects operate in juvenile and adult stages, possibly due to limited food availability or summer or winter refugia (Berven 2009). On the other hand, there may be a limit beyond which decreasing egg production reduces larval survival. Bernard (2015) suggested that winter temperature-correlated variation in clutch size observed under recent conditions has the potential to affect adult population size under some realistic scenarios. We also note that climate change-driven changes in amphibian phenology during aquatic stages (e.g. timing of hatch relative to competing species, larval growth rates, intraspecific hatching synchrony) may influence population vital rates (Rasmussen and Rudolf

2015, Rudolf and Singh 2013). Consequently, climate-induced changes in reproductive output over the next century have the potential to produce complex population-level effects through, e.g., density-induced changes in average size at metamorphosis, which may impact size, survival, and reproductive output at later life stages (Berven 1990).

Integrating our microclimate-biophysical model with a demographic model (e.g., Karraker 2008) and incorporating dynamic energy budgets (e.g., Mueller et al. 2012) would allow assessment of winter climate change on Wood Frog population sizes, given regionally-specific projected changes in subnivium conditions. However, there are several challenges in doing so. First, future mechanistic-demographic models should incorporate differing life stages (e.g. juvenile versus adult). Previous work found that peak Wood Frog ice contents were minimally sensitive to body size, because even large Wood Frogs have little thermal inertia (Fitzpatrick et al. 2019), but juveniles may acquire proportionally fewer nutrient reserves in fall. Second, we bounded our study region by the limits of our dynamically-downscaled future climate dataset, but the Wood Frog range extends much farther to the north and west. For a full assessment of population-level impacts, future modeling should explore projected climate impacts to Wood Frogs deeper into Canada and more northerly regions.

We predicted that warming winters would lead to heightened risk of experiencing lethal ice content in Wood Frogs, due to reduced snow insulation and more variable subnivium temperatures. However, our results suggest that shorter winters and warmer soil temperatures — especially by the end of the century — will reduce the likelihood of critical ice levels in Wood Frogs. Indeed, our model predicts that Wood Frogs will no longer undergo freeze-thaw cycles in some regions along the southern border of their range by the late 21st century, opening the possibility of loss of freeze-tolerance in southern populations in the long term. Given that availability of winter hibernacula sites may be a limiting factor in terrestrial life stages (Berven 2009), the reduced risk of Wood Frogs reaching critical ice levels may have demographic benefits, but Wood Frogs may remain vulnerable to climate change impacts in other seasons and aquatic life stages (Amburgey et al. 2018, Davenport et al. 2017).

Conclusions

Based on our mechanistic model and the incorporation of below-the-snow microclimates, Wood Frog populations across most of the eastern United States are projected to experience

reduced energy expenditure and lower risk of reaching critical ice contents due to shortening of the winter season and rapidly increasing soil temperatures. These findings suggest neutral to positive outcomes of warming winters for Wood Frog populations, pending density-dependent population parameters. However, climate change may impose negative consequences in other seasons and earlier life stages (Amburgey et al. 2018, Davenport et al. 2017). We demonstrate that Wood Frogs within the northwest region of our study area (northern Minnesota and Wisconsin) should experience increased energy expenditures. Integrating this type of mechanistic microclimate-biophysics model with a demographic model incorporating density-dependent effects would provide a better assessment of whether changes in energy stores remaining at the end of winter will impact population sizes. Similarly, incorporating local adaptation and plasticity in wintering behavior (burrow depth) and physiology (cryoprotectant concentration), especially in the region where energy expenditure is expected to increase, would improve predictions of how Wood Frogs will respond to climate change. Additional modeling beyond the northwestern border of our study region may reveal additional regional risks to Wood Frogs. Overall, our study shows the advantages of using a mechanistic model to assess spatially-explicit effects of climate change on a species's winter biology. We were able to incorporate complex, interrelated aspects of climate on microclimate conditions (e.g. impacts of warming air temperatures on soil temperatures confounded by reduced snow insulation) and organism biology (e.g. shortening length of winter dormancy versus increased winter metabolic rates), along with a dynamically-downscaled projected climate dataset accounting for effects of the Great Lakes. In doing so, we identified geographically-variable impacts of climate change on wintering Wood Frogs. Future studies should consider such complex, landscape-level variation when predicting impacts of climate change on subnivium-dwelling organisms.

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Conflict of Interest Statement: WPP is a co-founder and CEO of Niche Mapper, LLC.

Data Availability Statement: The data that support the findings of this study are available from the corresponding author upon request.

References

- Amburgey, S.M., Miller, D.A., Campbell Grant, E.H., Rittenhouse, T.A., Benard, M.F., Richardson, J.L., . . . Davis, C.J. (2018). Range position and climate sensitivity: The structure of among-population demographic responses to climatic variation. *Global Change Biology*, 24, 439-454.
- Benard, M.F. (2015). Warmer winters reduce frog fecundity and shift breeding phenology, which consequently alters larval development and metamorphic timing. *Global Change Biology*, 21, 1058-1065. doi: 10.1111/gcb.12720
- Berven, K. A. (1990). Factors affecting population fluctuations in larval and adult stages of the Wood Frog (*Rana sylvatica*). *Ecology*, 71, 1599-1608.
- Berven, K. A. (1995). 2nd World Congress of Herpetology: Population regulation in the Wood Frog, *Rana sylvatica*, from three diverse geographic localities. *Australian Journal of Ecology*, 20, 385-392.
- Berven, K. A. (2009). Density Dependence in the Terrestrial Stage of Wood Frogs: Evidence from a 21-Year Population Study. *Copeia*, 2009, 328-338. doi:10.1643/CH-08-052
- Biek, R., Funk, W. C., Maxell, B. A., & Mills, L. S. (2002). What is missing in amphibian decline research: insights from ecological sensitivity analysis. *Conservation Biology*, 16, 728-734.
- Campbell, G.S., & Norman, J.M. (1998). *An Introduction to Environmental Biophysics* (2nd ed.). New York, NY: Springer-Verlag.
- Campbell, J.L., Mitchell, M.J., Groffman, P.M., Christenson, L.M., & Hardy, J.P. (2005). Winter in northeastern North America: a critical period for ecological processes. *Frontiers in Ecology and the Environment*, 3, 314-322.
- Carpenter, J.F., & Crowe, J.H. (1988). The mechanism of cryoprotection of proteins by solutes. *Cryobiology*, 25, 244-255.

524 Chen, X., Liang, S., & Cao, Y. (2016). Satellite observed changes in the Northern Hemisphere
 525 snow cover phenology and the associated radiative forcing and feedback between 1982
 526 and 2013. *Environmental Research Letters*, 11, 084002. doi:10.1088/1748-
 527 9326/11/8/084002

528 Contosta, A.R., Adolph, A., Burchsted, D., Burakowski, E., Green., M., Guerra, D., . . .
 529 Wollheim, W. (2017). A longer vernal window: the role of winter coldness and snowpack
 530 in driving spring transitions and lags. *Global Change Biology*, 23, 1610-1625.

531 Contosta, A.R., Casson, N.J., Garlick, S., Nelson, S.J., Ayres, M.P., Burakowski, E.A., . . .
 532 Thornbrugh, C. (2019). Northern forest winters have lost cold, snowy conditions that are
 533 important for ecosystems and human communities. *Ecological Applications* 29, e01974.
 534 doi: 10.1002/eap.1974

535 Cosby, B., Hornberger, G., Clapp, R., & Ginn, T. (1984). A statistical exploration of the
 536 relationships of soil moisture characteristics to the physical properties of soils. *Water*
 537 *Resources Research*, 20, 682-690.

538 Costanzo, J. P., do Amaral, M. C. F., Rosendale, A. J., & Lee, R. E. (2013). Hibernation
 539 physiology, freezing adaptation and extreme freeze tolerance in a northern population of
 540 the Wood Frog. *The Journal of Experimental Biology*, 216, 3461-3473.
 541 doi:10.1242/jeb.089342

542 Costanzo, J.P., & Lee, R.E. (2013). Avoidance and tolerance of freezing in ectothermic
 543 vertebrates. *The Journal of Experimental Biology*, 216, 1961-1967.
 544 doi:10.1242/jeb.070268

545 Costanzo, J.P., Lee, R.E., & Wright, M.F. (1991). Effect of cooling rate on the survival of frozen
 546 Wood Frogs, *Rana sylvatica*. *Journal of Comparative Physiology B*, 161, 225-229.
 547 doi:10.1007/bf00262302

548 Costanzo, J.P., P.A. Callahan, R.E. Lee, M.F. Wright. (1997). Frogs reabsorb glucose from
 549 urinary bladder. *Nature*, 389, 343-344.

550 Davenport, J.M., Hossack, B.R., & Fishback, L. (2017). Additive impacts of experimental
 551 climate change increase risk to an ectotherm at the Arctic's edge. *Global Change*
 552 *Biology*, 23, 2262-2271. doi: 10.1111/gcb.13543

- Fitzpatrick, M.J., Zuckerberg, B., Pauli, J.N., Kearney, M.R., Thompson, K.L., Werner, L.C., & Porter, W.P. (2019). Modeling the distribution of niche space and risk for a freeze-tolerant ectotherm, *Lithobates sylvaticus*. *Ecosphere*, 10, e02788.
- Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., ... Winne, C.T. (2000). The global decline of reptiles, déjà vu amphibians. *BioScience*, 50, 653-666.
- Groff, L. A., Calhoun, A. J. K., & Loftin, C. S. (2016). Hibernation habitat selection by Wood Frogs (*Lithobates sylvaticus*) in a northern New England montane landscape. *Journal of Herpetology*, 50, 559-569. doi:10.1670/15-131R1
- Henry, H.A.L. (2008). Climate change and soil freezing dynamics: historical trends and projected changes. *Climate Change*, 87, 421-434.
- Hoving, C.L., Lee, Y.M., Badra, P.J., & Klatt, B.J. (2013). Changing climate, changing wildlife: a vulnerability assessment of 400 species of greatest conservation need and game species in Michigan (Michigan Department of Natural Resources Wildlife Division Report No. 3564). Lansing, MI: Michigan Department of Natural Resources.
- Karraker, N. E., Gibbs, J. P., & Vonesh, J. R. (2008). Impacts of road deicing salt on the demography of vernal pool-breeding amphibians. *Ecological Applications*, 18, 724-734.
- Kearney, M.R., & Porter, W.P. (2017). NicheMapR—an R package for biophysical modelling: the microclimate model. *Ecography*, 39, 664-674.
- Kearney, M.R., Shamakh, A., Tingley, R., Karoly, D.J., Hoffmann, A.A., Briggs, P.R., & Porter, W.P. (2014). Microclimate modelling at macro scales: a test of a general microclimate model integrated with gridded continental-scale soil and weather data. *Methods in Ecology and Evolution*, 5, 273-286.
- Kearney, M.R., & Porter, W.P. (2020). NicheMapR – an R package for biophysical modelling: the ectotherm and dynamic energy budget models. *Ecography*, 43, 85-96. doi: 0.1111/ecog.04680
- Kearney, M.R. (2020). How will snow alter exposure of organisms to cold stress under climate warming? *Global Ecology and Biogeography*, 29, 1246-1256. <https://doi.org/10.1111/geb.13100>
- Kodra, E., Steinhäuser, K., & Ganguly, A.R. (2011). Persisting cold extremes under 21st-century warming scenarios. *Geophysical Research Letters*, 38. doi: 10.1029/2011GL047103

- Kreyling, J., Haei, M., Laudon, H. (2012). Absence of snow cover reduces understory plant cover and alters plant community composition in boreal forests. *Oecologia*, 168, 577-587.
- Larson, D.J., Middle, L., Vu, H., Zhang, W., Serianni, A.S., Duman, J., & Barnes, B.M. (2014). Wood Frog adaptations to overwintering in Alaska: new limits to freezing tolerance. *The Journal of Experimental Biology*, 217, 2193-2200. doi:10.1242/jeb.101931
- Layne J.R., & Lee, R.E. (1987). Freeze tolerance and the dynamics of ice formation in Wood Frogs (*Rana sylvatica*) from southern Ohio. *Canadian Journal of Zoology*, 65, 2062-2065.
- Martz, F., Vuosku, J., Ovaskainen, A., Stark, S., & Rautio, P. (2016). The snow must go on: ground ice encasement, snow compaction and absence of snow differently cause soil hypoxia, CO₂ accumulation and tree seedling damage in boreal forest. *Plos One*, 11, e0156620. doi:10.1371/journal.pone.015662
- Mathewson, P.D., Moyer-Horner, L., Beever, E.A., Briscoe, N.J., Kearney, M., Yahn, J.M., & Porter, W.P. (2017). Mechanistic models can enhance predictive models of endotherm distributions: the American pika under current, past, and future climates. *Global Change Biology*, 23, 1048-1064. doi: 10.1111/gcb.13454
- Miller, D., & White, R. (1998). A conterminous United States multi-layer soil characteristics data set for regional climate and hydrology modeling. *Earth Interactions*, 2, 1-26.
- Mueller, C. A., Augustine, S., Kooijman, S. A., Kearney, M. R., & Seymour, R. S. (2012). The trade-off between maturation and growth during accelerated development in frogs. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 163, 95-102.
- Notaro, M., Holman, K., Zarrin, A., Fluck, E., Vavrus, S., & Bennington, V. (2013). Influence of the Laurentian Great Lakes on regional climate. *Journal of Climate*, 26, 789-804. doi: 10.1175/JCLI-D-12-00140.1
- Notaro, M., Lorenz, D., Hoving, C., Schummer, M. (2014). Twenty-first-century projections of snowfall and winter severity across central-eastern North America. *Journal of Climate* 27, 6526-6550. doi: 10.1175/JCLI-D-13-00520.1
- Notaro, M., Bennington, V., & Vavrus, S. (2015). Dynamically downscaled projections of lake-effect snow in the Great Lakes Basin. *Journal of Climatology*, 28, 1661-1684.

- Notaro, M., Schummer, M., Zhong, Y., Vavrus, S., Van Den Elsen, L., Coluccy, J., & Hoving, C. (2016). Projected influences of changes in weather severity on autumn-winter distributions of dabbling ducks in the Mississippi and Atlantic flyways during the twenty-first century. *PloS One*, *11*, e0167506.
- O'Connor, J. H., & Rittenhouse, T. A. (2016). Snow cover and late fall movement influence Wood Frog survival during an unusually cold winter. *Oecologia*, *181*, 635-644.
- Pauli, J.N., Zuckerberg, B., Whiteman, J.P., & Porter, W. (2013). The subnivium: a deteriorating seasonal refugium. *Frontiers in Ecology and the Environment*, *11*, 260-267.
- Rasmussen, N.L., & Rudolf, V.H.W. (2015). Phenological synchronization drives demographic rates of populations. *Ecology*, *97*, 1754-1760.
- Rudolf, V.H.W., & Singh, M. (2013). Disentangling climate change effects on species interactions: effects of temperature, phenological shifts, and body size. *Oecologia*, *173*, 1043-1052.
- Ruel, J.J., & Ayres, M.P. (1999). Jensen's inequality predicts effects of environmental variation. *Trends Ecol. Evol.*, *14*, 361-366.
- Sarady, M., & Sahlin, E.A.U. (2016). The influence of snow cover on ground freeze-thaw frequency, intensity, and duration: An experimental study conducted in coastal northern Sweden. *Norsk Geografisk Tidsskrift*, *70*, 82-94.
- Sinclair, B.J., Stinziano, J.R., Williams, C.M., MacMillan, H.A., Marshall, K.E., & Storey, K.B. (2013). Real-time measurement of metabolic rate during freezing and thawing of the Wood Frog, *Rana sylvatica*: implications for overwinter energy use. *Journal of Experimental Biology*, *216*, 292-302.
- Sinha, T., & Cherkauer, K. (2010). Impacts of future climate change on soil frost in the midwestern United States. *Journal of Geophysical Research: Atmospheres*, *115*, D08105 doi: 10.1029/2009JD012188.
- Storey, K.B. & J.M. Storey. (1987). Persistence of freeze tolerance in terrestrially hibernating frogs after spring emergence. *Copeia*, *1987*, 720-726.
- Storey, K.B., & Storey, J.M. (1984). Biochemical adaption for freezing tolerance in the Wood Frog, *Rana sylvatica*. *Journal of Comparative Physiology B*, *155*, 29-36. doi:10.1007/bf00688788

- Storey, K.B., & Storey, J.M. (1986). Freeze tolerant frogs: cryoprotectants and tissue metabolism during freeze-thaw cycles. *Canadian Journal of Zoology* 64, 49-56.
- Thompson, K., Zuckerberg, B., Porter, W., & Pauli, J. (2018). The phenology of the subnivium. *Environmental Research Letters*, 13, 064037. doi:10.1088/1748-9326/aac670
- US Patent No. 7155377. 2006. Porter, W.P., & Mitchell, J.W. Retrieved from <https://www.warf.org/technologies/information-technology/software/summary/system-for-calculating-the-spatial-temporal-effects-of-environmental-conditions-on-animals-p01251us.cmsx>
- Vonesh, J. R., & De la Cruz, O. (2002). Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. *Oecologia*, 133, 325-333.
- Wake, D.B. (2007). Climate change implicated in amphibian and lizard declines. *Proceedings of the National Academy of Sciences*, 104, 8201-8202.
- Wells, K.D., & Bevier, C.R. (1997). Contrasting patterns of energy substrate use in two species of frogs that breed in cold weather. *Herpetologica*, 53, 70-80.
- Williams, C.M., Henry, H.A.L., & Sinclair, B.J. (2015). Cold truths: how winter drives responses of terrestrial organisms to climate change. *Biological Reviews*, 90, 214-235. doi:10.1111/brv.12105
- Wolanczyk, J.P., Storey, K.B., & Baust, J.G. (1990). Ice nucleating activity in the blood of the freeze-tolerant frog, *Rana sylvatica*. *Cryobiology*, 27, 328-335.
- Zhu, L., Ives, A.R., Zhang, C., Guo, Y., & Radeloff, V.C. (2019) Climate change causes functionally colder winters for snow cover-dependent organisms. *Nature Climate Change*, 9, 886-893.
- Zhu, L., Radeloff, V.C., & Ives, A.R. (2017). Characterizing global patterns of frozen ground with and without snow cover using microwave and MODIS satellite data products. *Remote Sensing of the Environment*, 191, 168-178.
- Zuckerberg, B., & Pauli, J.N. (2018). Conserving and managing the subnivium. *Conservation Biology*, 32, 774-781.

Tables:

Table 1. Dynamically downscaled climate models predicting the greatest and least change in air temperature and snow conditions in the Great Lakes region of the United States (Notaro et al., 2016).

Parameter	Least change by mid-21 st century	Least change by late-21 st century	Most change by mid-21 st century	Most change by late-21 st century
Increase in winter air temperatures	GFDL	MRI	MIROC5	MIROC5
Decrease in lake effect snowstorms	GFDL	GFDL	ACCESS	ACCESS
Decrease in snow cover duration	GFDL	GFDL	ACCESS	MIROC5

Figures Legends

Figure 1. Model-averaged values of (a) winter length, (b) snow depth, (c) average 5-cm depth winter soil temperature, (d) number of freeze-thaw cycles per winter, (e) total winter energy expenditure, and (f) maximum ice content (percent body water frozen) for Wood Frogs in the late 20th century. Values are averages across a 19-winter period and across six global climate models. Winter was defined as the period when simulated frogs were restricted to hibernacula due to snow and/or frozen body fluids.

Figure 2. Modeled change in average 5cm-depth winter soil temperature from the late 20th century to the mid-21st and late 21st century for the two global climate models generating the least (GFDL) and most (MIROC5) change. Values are averages across a 19-winter period. Panels show change in average winter soil temperature from the late 20th century to the (a) mid-21st century under GFDL, (b) late-21st century under GFDL, (c) mid-21st century under MIROC5, (d) late-21st century under MIROC5. Note that the negative scale (cool colors) is shorter than the positive scale (warm colors).

699

700 Figure 3. Modeled change in average winter length from the late 20th century to the mid-21st and
701 late 21st century for the two global climate models generating the least (GFDL) and most
702 (MIROC5) change. Values are averages across a 19-winter period. Panels show change in
703 average winter length from the late 20th century to the (a) mid-21st century under GFDL, (b) late-
704 21st century under GFDL, (c) mid-21st century under MIROC5, (d) late-21st century under
705 MIROC5. Note that the range in warm colors is shorter than the range in cool colors.

706

707 Figure 4. Modeled change in total winter energy expenditure from the late 20th century to the
708 mid-21st and late 21st century for the two global climate models generating the least (GFDL) and
709 most (ACCESS) change. Values are averages across a 19-winter period. Panels show change in
710 average winter length from the late 20th century to the (a) mid-21st century under GFDL, (b) late-
711 21st century under GFDL, (c) mid-21st century under ACCESS, (d) late-21st century under
712 ACCESS. Note that the range in warm colors is shorter than the range in cool colors.

713

714 Figure 5. Modeled future total winter energy expenditure from the late 20th century to the mid-
715 21st and late 21st century for the two global climate models generating the least (GFDL) and most
716 (ACCESS) change. Values are averages across a 19-winter period. Panels show total winter
717 energy expenditure for the (a) mid-21st century under GFDL, (b) late-21st century under GFDL,
718 (c) mid-21st century under ACCESS, (d) late-21st century under ACCESS. Black color shows
719 areas where total winter energy expenditure is lower than the lowest value in the study area
720 under 20th century conditions (3,143 J/y under ACCESS and 2,609 J/y under GFDL), i.e. novel
721 conditions for Wood Frogs in our study region.

722

723 Figure 6. Modeled change in peak Wood Frog body ice content from the late 20th century to the
724 mid-21st and late 21st century for the two global climate models generating the least (GFDL) and
725 most (MIROC5) change. Values are averages across a 19-winter period. Units are percentage of
726 body water frozen (per-mass basis). Panels show change in ice content from the late 20th century
727 to the (a) mid-21st century under GFDL, (b) late-21st century under GFDL, (c) mid-21st century
728 under MIROC5, (d) late-21st century under MIROC5. Note that the range in warm colors is

729 shorter than the change in cool colors. Black represents sites where ice was non-lethal ($<67\%$
730 body water mass frozen) in the late 20th century and lethal ($>67\%$) in future projections.

Author Manuscript

GFDL

(a)

(b)

MIROC5

(c)

(d)

MRI

(a)

(b)

MIROC5

(c)

(d)

GFDL

(a)

(b)

ACCESS

(c)

(d)

GFDL

ACCESS

mid-21st century

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late 21st century

GFDL

(a)

(b)

MIROC5

(c)

(d)

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Author/s:

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