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Mechanistic variables can enhance predictive models of endotherm distributions: the American pika under current, past, and future climates

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Title: Mechanistic variables can enhance predictive models of endotherm distributions: the American pika under current, past, and future climates.

Running Head: Improving endotherm SDMs with mechanism

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ABSTRACT

How climate constrains species' distributions through time and space is an important question in the context of conservation planning for climate change. Despite increasing awareness of the need to incorporate mechanism into species distribution models (SDMs), mechanistic modelling of endotherm distributions remains limited in the current literature. Using the American pika (*Ochotona princeps*) as an example, we present a framework whereby mechanism can be incorporated into endotherm SDMs. Pika distribution has repeatedly been found to be constrained by warm temperatures, so we used Niche Mapper, a mechanistic heat-balance model, to convert macroclimate data to pika-specific surface-activity time in summer across the western United States. We then explored the difference between using a macroclimate predictor (summer temperature) and using a mechanistic predictor (predicted surface-activity time) in SDMs. Both approaches accurately predicted pika presences in current and past climate regimes. However, the activity models predicted 8-19% less habitat loss in response to annual temperature increases of ~3-5°C predicted in the region by 2070, suggesting that pikas may be able to buffer some climate-change effects through behavioral thermoregulation that can be captured by mechanistic modeling. Incorporating mechanism added value to the modeling by providing increased confidence in areas where different modeling approaches agreed and providing a range of outcomes in areas of disagreement. It also provided a more proximate variable relating animal distribution to climate, allowing investigations into how unique habitat characteristics and intraspecific phenotypic variation may allow pikas to exist in areas outside those predicted by generic SDMs. Only a small number of easily obtainable data are required to parameterize this mechanistic model for any endotherm, and its use can improve SDM predictions by explicitly modeling a widely applicable direct physiological effect: climate-imposed restrictions on activity. This more complete understanding is necessary to inform climate-adaptation actions, management strategies, and conservation plans.

INTRODUCTION

The pervasive effects of global climate change on biodiversity are well documented (e.g., Parmesan & Yohe, 2003; Thomas, 2010; Bellard *et al.*, 2012), and threats due to climate change are playing a more prominent role in species assessments for conservation purposes (Staudinger et al, 2013). Predicting the impacts of climate change on species is therefore an important conservation challenge (e.g., McGuire & Davis, 2013). Species distribution models (SDMs), which combine spatial environmental data with information about a focal species to predict areas likely to support the species, are a primary tool used to address this challenge, as evidenced by the rapid increase in their use over the past decade (Franklin, 2010; Guisan *et al.*, 2013). SDMs can play valuable roles in informing conservation actions, including: 1) identifying potential future range contractions or shifts due to climate change to inform conservation status assessments; 2) prioritizing habitat reserves, corridors, and essential microrefugia for conservation; and 3) informing decisions about when and to where species may need to be translocated (e.g., Schwartz, 2012; Guisan & Thuiller, 2005; Guisan *et al.*, 2013; Araújo *et al.*, 2011)

At one end of the modeling spectrum are correlative SDMs, which statistically relate species occurrence data to environmental variables (Elith & Leathwick, 2009). Variables thought to constrain a species' distribution are selected for use in the model, but the process(es) by which the variable(s) limit the species' distribution remain implicit. On the other end of the spectrum, mechanistic models explicitly model processes thought to limit a species' distribution (Kearney & Porter, 2009). Mechanistic approaches model the consequences of interactions between a species' functional traits (morphology, physiology and behavior) and its environment on the species' energetics, development and reproduction (Dormann *et al.*, 2012). Purely mechanistic models do not rely on known species distributions; rather, the predicted distributions are an emergent property of the process being modeled (Meineri *et al.*, 2015).

To date, most SDM efforts have used a correlative approach, due to their relative ease of use and wider availability, fewer and more easily met data requirements, and the range of biotic and abiotic interactions that they can (implicitly) capture (see reviews by, e.g., Elith & Leathwick, 2009; Kearney & Porter, 2009; Evans *et al.*, 2015). However, when it comes to predicting the impact of climate change on a species, purely correlative models provide little insight into *why* a decline is predicted, limiting their ability to inform conservation responses. Such omission has important implications for policy-makers, natural-resource managers, and other conservation practitioners, because without such insight, climate-adaptation actions in response to species declines are relegated to trial and error (Beever *et al.*, 2010; Evans *et al.*, 2015).

Furthermore, by relying on correlations rather than a process, transferring correlative models into novel environmental conditions risks erroneous extrapolation, a key issue for many studies of climate-change effects (Kearney & Porter, 2009; Veloz *et al.*, 2012). Mechanistic models, in contrast, do not require extrapolation when transferred into novel environmental conditions, and therefore may provide more accurate predictions regarding future shifts in suitable habitat due to climate change (Kearney & Porter, 2009; Rawson *et al.*, 2011; Tomlinson *et al.*, 2014). However, mechanistic models can be data-intensive and may require difficult-to-obtain or time-consuming information, limiting wider use of these models (Dormann *et al.*, 2012; Meineri *et al.*, 2015).

Using the two approaches in tandem may allow studies to take advantage of the respective strengths of each approach while counteracting the respective weaknesses, thereby increasing confidence in predictions (e.g., Buckley *et al.*, 2010; Kearney *et al.*, 2010; Dormann *et al.*, 2012; Meineri *et al.*, 2015; Briscoe *et al.*, 2016). One possibility is the integration of the two approaches by using mechanistic model outputs as inputs to a correlative model (Elith *et al.*, 2010). For example, mechanistic models can produce spatial layers representing how macroclimate variables (e.g., temperature) and habitat features (e.g., shade availability) affect a species' energy requirements or activity time across a heterogeneous landscape. These mechanistic output layers, which may be more proximate drivers of species persistence than the climate variable itself, can then be used as inputs for a correlative model (Kearney & Porter, 2009; Buckley *et al.*, 2010; Cahill *et al.*, 2013).

Mechanistic modelling of endotherms is particularly underrepresented in the existing literature as compared to ectotherms (Boyles *et al.*, 2011; Oswald & Arnold, 2012; La Sorte & Jetz, 2013). Although endotherms are better able to buffer themselves against changing thermal conditions than ectotherms, such buffering has costs and limits. Endotherms facing heat stress may sweat or pant to increase evaporative heat loss, or avoid heat if local refugia exist. Conversely, endotherms facing cold stress may shiver or metabolize fat stores to produce body heat. These coping mechanisms require time and resources that could otherwise be used for growth and reproduction, thus imposing limits on the species' distribution (Buckley *et al.*, 2012; du Plessis *et al.*, 2012; Oswald & Arnold, 2012). Therefore, a model that predicts such thermoregulatory costs can provide valuable information about the processes by which climate limits distributions and how distributions may shift in a changing climate (Briscoe *et al.*, 2016).

Here, we show how a mechanistic model can be incorporated into distribution predictions of a heat-sensitive endotherm. Niche Mapper^{TM} uses heat-transfer principles to calculate an animal's heat balance in its local microclimate (Porter & Mitchell, 2006). Informed by morphological, physiological, and behavioral information about an animal, the model calculates the necessary (in cold temperatures) or allowable (in warm temperatures) metabolic rate that will enable an animal to maintain its body temperature within a tolerable range. Niche Mapper can thus compare relative levels of heat stress (e.g., reduced activity) or cold stress (e.g., increased food requirements) across the landscape. This approach also allows us to better distinguish direct (e.g., energy deficits and activity reductions) from indirect (e.g., changes to species interactions and habitat structure; *sensu* Thomas 2010) effects of climate change.

The American pika (*Ochotona princeps* Richardson) is a small mammal typically found in relatively cool and moist, montane habitats (Hafner & Smith, 2010 but see, e.g., Shinderman, 2015; Ray *et al.*, 2016; and Varner & Dearing, 2014 for examples of populations occurring outside this general niche: all these examples are facilitated by fine-scale habitat complexity decoupling refugial conditions from coarse-scale climatic conditions). Pikas maintain a high resting body temperature (40.1°C) that is close to their upper lethal temperature (43.1°C), have high metabolic requirements, and thick fur, which limits their ability to dissipate heat (Smith & Weston, 1990; Beever *et al.*, 2013). Consequently, individuals that are unable to behaviorally thermoregulate are prone to death from heat exposure in moderate temperatures (25.5-29.4°C) (MacArthur & Wang, 1973, 1974; Smith, 1974). Studies investigating pika distribution at ecoregional to continental scales have found warming temperatures to be the primary driver of distributional change over time (Grayson, 2005; Galbreath *et al.*, 2009) and chronic heat stress to be a leading predictor of pika persistence under recent climate conditions (Beever *et al.*, 2003, 2010, 2011, 2013; Wilkening *et al.*, 2011; Calkins *et al.*, 2012). At more local scales, the influence of warm temperatures on pika distributions is not as straightforward: while warm temperatures have been found to be a primary determinant of pika distributions in some locations (e.g., Moritz *et al.*, 2008; Stewart *et al.*, 2015), other aspects of climate and habitat characteristics have been identified as more important in other locations (e.g., Erb *et al.*, 2011; Yandow *et al.*, 2015; Schwalm *et al.*, 2016).

Despite the evidence of broad distributional changes being related to warm temperatures, it is unclear exactly *how* temperatures operate to limit pika distribution. Warm temperatures could influence pikas directly (e.g., through exceeding thermal limits or limiting time available to forage) or indirectly (e.g., through increased disease transmission, facilitation of competitors, changes in vegetation affecting food availability and quality, or reduced insulating snowpack layer in the winter). Pikas cope with heat stress by retreating to thermal refugia in the interstices of their rocky habitat (MacArthur & Wang, 1974; Smith, 1974; Moyer-Horner *et al.*, 2015). During the summer, pikas must be surface-active to feed, find mates, and defend territory. Furthermore, across most of their range, pikas must also build up food caches (“haying”) to survive the winter months because they do not hibernate (Smith, 1974; Dearing, 1987). Collectively, these observations support a hypothesis that increased temperatures may limit pika distributions by restricting the amount of time available for foraging and haying activities.

Activity windows have been identified as a promising and widely applicable physiological process to incorporate into SDMs in order to better understand how warm temperatures affect distributions (Evans *et al.*, 2015), in contrast to other physiological processes like upper thermal tolerance, which has been found to poorly predict biogeography (e.g., Cahill *et al.*, 2013). Here, we use Niche Mapper to explicitly model this mechanism and test whether potential summer activity time is a robust predictor of pika distribution. We compare distributions of pikas in the United States predicted by 1) a correlative model using only macroclimate predictors vs. 2) a model that incorporates mechanism in the form of summer thermal environments converted to pika-specific allowable surface-activity time. We show how using the correlative and mechanistic approaches in tandem can help overcome the shortcomings of both approaches to provide more confident predictions of, and insights into, climate-change effects. Although we use the pika as a model organism to illustrate the framework, the general modeling approach can be used on any species whose distribution is constrained by thermoregulatory pressures. It therefore can help fill the existing knowledge gap regarding predicting the direct physiological effects of climate change on endotherms and thus facilitate better-informed conservation and management actions.

MATERIALS AND METHODS

Niche Mapper Predictions of Surface-Activity Hours

Niche Mapper is a coupled microclimate and animal heat- and mass-balance model that has been previously described in detail (e.g., Porter *et al.*, 2000; Porter & Mitchell, 2006). It has been shown to accurately predict metabolic heat production, habitat use, or landscape distributions of a variety of animals, including mammals ranging in size from mice (*Mus* spp.) and gliding possum (*Petauroides volans*) to elk (*Cervus canadensis*) and polar bears (*Ursus maritimus*) (e.g., Porter *et al.*, 1994; Kearney *et al.*, 2010; Mathewson & Porter, 2013; Long *et* *al.*, 2014). Specific to pikas, Moyer-Horner *et al.* (2015) demonstrated that Niche Mapper can accurately predict both pika metabolic rate as a function of temperature and pika activity reductions in Glacier National Park, USA. We note that prior uses of Niche Mapper to predict habitat use and landscape distributions were purely mechanistic and thus required detailed information about the focal animal's physiology and diet properties. Here, we are exploring a methodology that only uses the heat balance aspect of Niche Mapper, minimizing the number of required inputs needed in order to make it easily adaptable to other species.

Briefly, Niche Mapper consists of two sub-models: 1) a microclimate model that calculates environmental conditions at animal height, and 2) a biophysical/behavioral/morphological animal model (Fig. 1). The microclimate model calculates hourly profiles of air temperature, wind speed, relative humidity, and solar and long-wavelength thermal radiation that an animal experiences (Fuentes & Porter, 2013; Kearney *et al.*, 2014). The animal model then solves a heat balance equation (Eq. 1) wherein the animal's metabolic heat generation (Q_{gen}) must equal heat transfer through its fur (Q_{fur}) and the net heat flux with its microenvironment [radiative (Q_{rad}), convective (Q_{conv}), solar (Q_{sol}), and evaporative (respiratory, Q_{resp}, and cutaneous, Q_{evap})], in order for the animal to maintain its core temperature during each hour of the day:

$$Q_{gen} - Q_{resp} - Q_{evap} = Q_{fur} = Q_{rad} + Q_{conv} - Q_{sol} \qquad (1)$$

Niche Mapper was used to predict the number of hours pikas could be active at 2x basal metabolic rate (a conservative field metabolic rate; Karasov, 1992) while still maintaining a heat balance during crepuscular and diurnal hours in the summer months (defined here as June-September) across the western United States. For each month, an "average" day was modeled, using the mean monthly maximum and minimum temperature, and the model day's allowable activity hours were multiplied by the number of days in that month (See Appendix S1 for more details about Niche Mapper operation).

Activity-hour predictions were made for current, past, and future climate conditions. Current climate data came from 1981-2010 climate normals from the PRISM Climate Group at 800 m resolution (http://www.prism.oregonstate.edu/; Daly *et al.*, 2008). Climate data for the Last Glacial Maximum ("LGM"; ~22,000 years b.p; 4 km resolution) and the mid-Holocene ("MH" ~6,000 years b.p; 800 m resolution) were obtained from the WorldClim database (http://www.worldclim.org; Hijmans *et al.*, 2005). For future climate, we used predictions for

2070 climate conditions from global circulation models (GCMs) used in the IPCC Fifth Assessment (IPCC, 2013) that predicted conservative (MRI-CGCM3, RCP2.6), moderate (NorESM1-M, RCP4.5), and largest magnitude (MIROC-ESM-CHEM, RCP8.5) climate-change scenarios in the western United States. GCM data were obtained from the WorldClim database at 800 m resolution (See Appendix S1 for additional information on spatial data acquisition). Activity predictions were also made assuming uniform maximum and minimum temperature increases of 3°C and 5°C in order to illustrate more simply how the two modeling approaches differ in their predictions of pika response to warming temperatures, without the confounding effect of spatially varying temperature changes.

Pika bodies were modeled as single ellipsoids with the properties listed in Table S1. Pikas are not known to pant or sweat, so the only thermoregulatory options allowed were for the core temperature to rise and for flesh thermal conductivity to increase (simulating vasodilation). For sensitivity analyses and other pika model-building details, see Moyer-Horner *et al.* (2015). Pikas inhabit talus and talus-like substrates (Tyser, 1980), but national land cover datasets have limited ability to identify such specific substrates at broad spatial scales (Moyer-Horner *et al*. in review; EAB, pers. obs.). Thus, we assumed that every pixel contained suitable rocky habitat and all substrate inputs for the microclimate submodel were for a rocky surface (Table S2). We assumed that no above-talus shade was available, because pikas are typically found in open, rocky areas. We assumed clear skies for all simulations in order to develop a model applicable to climate scenarios that lack cloud-cover data. A sensitivity analysis showed that incorporating cloud cover affected the absolute number of activity hours, but did not substantially affect relative amounts of activity across the pika’s range in the United States, resulting in very similar predicted distributions with and without cloud cover (Fig. S1).

Species Distribution Models

There is no known minimum amount of surface activity during summer needed for pika survival, so one option to build a distribution model based on activity time is to use the activity-hour threshold that separates extant from extirpated sites (e.g., Sinervo *et al.*, 2010). Such persistence/extirpation data are available for pikas in the United States from 39 sites in the hydrographic Great Basin. However, this approach assumes that the threshold identified at these sites is applicable throughout the species’ range. Furthermore, similar presence/absence data are not available for many species, limiting wide use. Therefore, to provide a generally applicable methodology to convert activity hours into a predicted distribution, we used activity hours as a predictor within a correlative modelling framework (Fig. 1). We fit correlative models using Maxent, because this model is widely used, has been found to perform well compared to other models, and was developed for presence-only data (Elith *et al.*, 2006; Phillips *et al.*, 2006).

Presence data for the range-wide Maxent models were obtained from online zoological record databases and from prior pika studies to fill in known gaps in the database records. To minimize the effect of sampling bias on model predictions, we used the target-group background approach (Phillips *et al.*, 2009), using terrestrial mammal records to select background points (see Appendix S1 for additional details on presence- and background point selection). Presence and background points were filtered to remove duplicate points in each 800-m pixel. Models were built using only hinge and product features in order to smooth the response curves and avoid overfitting (Elith *et al.*, 2010), while allowing for potential interactions. Models were evaluated using 10-fold cross-validation. Other model settings were set to default values, including the use of clamping when extrapolating, which treats variables outside the training range as if they were at the limit of the training range.

Baseline models to predict pika distributions were first built using only either mean temperature of the warmest quarter or summer activity predicted by Niche Mapper. This allowed for the most direct comparison between using the macroclimate predictor (summer temperature) and a mechanistic explanatory variable (summer activity). These models are referred to hereafter as the “temperature baseline model” and the “activity baseline model” (Fig. 1).

Precipitation and winter cold have been identified as important determinants of pika persistence in addition to summer temperatures, particularly at more localized scales (Beever *et al.*, 2010; Millar & Westfall, 2010; Erb *et al.*, 2011; Jeffress *et al.*, 2013; Schwalm *et al.*, 2016). The relative importance of summer activity time likely varies in response to these other variables across the pika’s range. In areas with high plant productivity and/or shorter winters, fewer summer activity hours may be required because foraging is likely more efficient and/or smaller food caches are sufficient to survive the winter. To account for these potential interactions, we explored adding additional climate layers to the baseline models: minimum temperature of the coldest month (abbreviated here as “winter cold;” proxy for acute cold stress and winter duration; less correlated with the baseline inputs than mean temperature of the coldest quarter or growing-season duration), growing-season precipitation (calculated as the sum of the precipitation in months where the mean temperature is >5°C), and snowpack potential (calculated as the sum of the precipitation in months where the minimum temperature is < 0°C).

Models were built using current climate and pika distribution data, and then used to predict habitat suitability under past and future climate scenarios. We identified areas where the SDMs would require extrapolation under past and future climate scenarios using multivariate environmental similarity surfaces (MESS maps; Elith *et al.*, 2010). To facilitate easier comparisons between predictions made by the different modeling approaches and evaluate the degree to which the approach influences estimates of percent range change, we converted Maxent's continuous output into a binary suitable/unsuitable output using the threshold that maximized training sensitivity plus specificity ("MSS"), as suggested for use with presence-only data by Liu *et al.* (2005, 2013).

Model Evaluation

To test whether summer activity hours predicted by Niche Mapper could distinguish between suitable and unsuitable habitat, we examined predicted activity at 39 long-term pika monitoring sites in the Great Basin (Beever *et al.*, 2003, 2008, *in review;* Wilkening *et al.*, 2011; EAB, *unpublished data*). We compared the average activity hours predicted by Niche Mapper for all pixels within a 3-km radius (matching the extent of field surveys around each historical record) at sites with persistent populations in 2015 (n=25) to the hours available within 3 km of sites that have been extirpated in the last century (n=14; hereafter, "recently-extirpated sites").

To evaluate model performance, we used area under the receiver-operator curve (AUC) and True Skill Statistic (TSS; Allouche *et al.*, 2006). TSS statistics were evaluated for both the 39 Great Basin pika sites (true presence/absence data) and for the 616 pika locations and 10,000 background (pseudoabsence) points used in the Maxent modeling (Additional details on these tests are found in Appendix S1). To account for the fact that pikas may be observed in an "unsuitable" pixel if that pixel is in close proximity to suitable habitat due to the metapopulation dynamics the species exhibits, we also calculated the number of known pika locations within 3 km of the nearest suitable habitat pixel. We used 3 km because it is an estimated limit of pika dispersal in most habitat types (Beever *et al.*, 2003; 2011) and is the average (range: 1.1-4.5 km) genetic neighborhood distance found by Schwalm *et al.* (2016) at eight US National Park Service units in the western United States.

To evaluate the models' transferability to different climatic conditions, we used 48 fossil pika locations from the Quaternary period (Hafner, 1993; Grayson, 2005; Galbreath *et al.*, 2009) to test the models' ability to predict pika range retractions from the LGM (colder and drier than present) to the MH (drier and similar summertime temperatures in the Northern Hemisphere than present in some areas). In tests to quantify the models' abilities to track this observed range retraction, we assumed that in the mid-Holocene all MH and late Holocene (LH) fossil locations would be within 3 km from predicted thermally-suitable habitat and all LGM and early Holocene (EH) fossil locations will be more than 3 km from any predicted thermally-suitable habitat. Finally, we assumed that all recently-extirpated and current pika locations must be within 10-20 km (estimated maximum pika dispersal distance over millenia; Hafner, 1994; Hafner & Sullivan, 1995) of areas with predicted suitable habitat in the MH.

RESULTS

Niche Mapper Activity Predictions

Summer activity levels predicted by Niche Mapper corresponded well with the known distribution of *O. princeps* (Fig. S2). In the Great Basin, pika-extant sites averaged 19% more predicted surface activity time during summer than did pika-extirpated sites (1410 vs. 1159 hours) (Mann-Whitney U = 32, $p<0.001$; Fig. 2; Table S3). A threshold value of 1132 hours (53% of diurnal and crepuscular hours for the period) separated the extant site with the lowest predicted activity hours from all but four of the 14 extirpated sites (chi-square test of association $\chi^2 = 24.01$, $p<0.001$).

Species Distribution Model Results: 1981-2010 Climate Conditions

Model response curves to the inputs were reasonable and expected: suitability declined with increasing summer temperature and decreasing available activity time (Figs. S3, S4). The two baseline models predicted similar raw (i.e., no threshold applied) habitat suitability scores for pixels within 3 km of the 616 pika presence locations (Table 1, paired t-test, $t=-1.38$, $p=0.17$).

When using the MSS threshold to delineate suitable and unsuitable habitat, baseline model predictions for suitable habitat using summer temperatures and summer activity agreed for 76% of all pixels in the western United States predicted as suitable by either model. The activity baseline model predicted 19% more suitable habitat across the western United States than did the temperature baseline model, mostly in the northern and eastern portions of study area (Table 2;

Fig. 3). The temperature baseline model predicted additional suitable habitat along the western coast and in the lower elevations of the Cascade Range.

For both baseline models, more than 95% of all pika records were within 3 km of suitable (defined using the MSS threshold) habitat (Table 1). When comparing predictions at the 39 Great Basin monitoring sites, both models accurately distinguish pika-extirpated sites from extant sites (χ^2 test of association $p< 0.01$ for each; Table S4, Fig. S5). The activity baseline model identified all extant sites as suitable (the temperature model had two false negatives), but had three more false positives than did the temperature model (5 vs. 2).

When adding any combination of additional inputs, the mean-summer-temperature or summer-activity input consistently remained the most important factor, contributing >70% to every model. AUC values did not change appreciably (range: 0.889-0.920 in the Great Basin and 0.923-0.938 across the western United States), and all combinations of variables indicated good to excellent model fit (Swets, 1988). Thus, the TSS metric was primarily used to compare model performance.

Adding growing-season precipitation to both baseline models improved model performance across the western United States by capturing additional presence locations in the Cascade Range, an area with a high density of presence points, but performed worse in the drier Great Basin where there are true presence/absence data (Table S4). Similarly, adding potential snow accumulation improved model performance across the western United States by capturing more presence sites in the Cascade Range at the expense of decreased performance in the Great Basin (Table S4).

Adding minimum temperature of the coldest month to both baseline models increased model performance both in the entire western United States and in the Great Basin (Table S4). Specifically, adding winter cold to the models expanded predicted suitable habitat in the lower elevations of the Cascade Range (moderate winter cold; encompassing pika presence sites not identified as suitable by the baseline models) and decreased predicted suitability in lower-elevation areas in the Rocky Mountains (colder minimum winter temperatures; eliminating areas where no pikas have been documented) (Fig. S6).

Adding either or both of the precipitation variables did not improve model performance above the baseline + winter-cold models, so additional analyses only considered the baseline (to most simply compare the effect of using summer-activity time or summer temperatures) and baseline + winter cold models (the best overall model).

Species Distribution Model Results: Hindcasting

MESS maps (Elith *et al.*, 2010) indicated that there was considerable extrapolation in the LGM, and to a lesser degree, the MH due to lower minimum temperatures (winter cold) than captured in the training data (Fig. S7). Both baseline models predicted extensive suitable habitat throughout the western United States during the LGM (Fig. S8). All recently-extirpated and current sites, and all but three fossil pika locations (Corn Creek [NV], Mescal/Antelope Creek [CA], and Kokoweef Cave [CA]) were within 4.5 km (the approximate resolution of the LGM climate data at these latitudes) of predicted suitable habitat (Table S5).

The baseline models predicted substantial reductions in suitable habitat in the mid-Holocene (Fig. S9). Both models predicted habitat loss at most of the LGM and EH fossil locations, yet still predicted habitat within 3 km of the MH and LH fossil locations, with the exception of Pintwater Cave, NV (Table 3). All recently-extirpated and current pika records were within 20 km of suitable habitat predicted in the MH by both models (Table 3).

Adding minimum winter temperatures contracted habitat suitability predicted by both models in the LGM in the southern latitudes, causing additional fossil pika sites to be missed (Fig. 4; Table S5). Suitable habitat contracted more in the summer activity model than it did the summer temperature model, due to a stronger interaction between activity hours and winter cold than between summer temperatures and winter cold.

Pintwater Cave was still the only MH or LH fossil site missed by >3km by both the baseline + winter cold models hindcasting to the MH (Table 3). The summer temperature + winter cold model also missed an additional Holocene fossil site (Horned Owl Cave, WY). Adding winter cold resulted in a small number of current or recently-extirpated locations to be missed in the MH predictions, exclusively lava-flow sites and low-elevation sites in the northwest Great Basin portions of Nevada, Oregon, and California (Table 3).

Species Distribution Model Results: Future Climate Warming

There was some extrapolation beyond the range of environmental data captured in the training dataset when predicting to the more severe climate-change scenarios, with respect to mean summer temperatures and, to a lesser degree, winter cold (Fig. S7). Both baseline models predicted substantial reductions in thermally-suitable habitat throughout the western United

States under the moderate- and warmest-magnitude climate change scenarios and <5% loss under the conservative scenario (Fig. 5, Table 2). The modeling approaches predicted differing magnitudes of declines in suitable habitat as temperatures increased, with the activity baseline model predicting >13-15% less habitat loss (absolute difference) under the moderate- and warmest-climate change scenarios (Table 2). When limiting the area of analysis to within 3 km of the pika presence locations used in the modeling rather than using the whole western United States, the activity model still predicted less future habitat loss (Table 1). Under the warmest scenario, the activity baseline model predicted >100 more pika presence sites to still be within 3 km of thermally-suitable habitat compared to the temperature model.

Adding winter cold to the baseline models increased habitat loss predictions in the conservative and moderate scenarios. These scenarios predicted that there will be areas where minimum winter temperatures will get colder and summer temperatures are expected to increase or remain the same (Table 2). As with the baseline models, the summer activity + winter cold model predicted less habitat loss with warming temperatures: 8% less in under the moderate scenario and 17% less under the warmest scenario (Table 2, Fig. 5). The difference in predicted habitat loss between summer temperature and summer activity models was even more pronounced when we assumed uniform temperature increases (Fig. 5).

DISCUSSION

Comparing Model Predictions

We aimed to explore how incorporating mechanism into a species distribution model affected model predictions. We found broad agreement between models using summer temperatures and models using summer surface-activity time with respect to both: 1) predicting suitable habitat at or near current pika locations, and 2) general patterns of habitat expansions and contractions under past- and future-climate scenarios. However, the models predicted different magnitudes of future range contraction, with the activity models predicting 8-19% less habitat loss than the temperature models, range-wide. Modeling a more proximate relationship between an animal and its environment enabled a better understanding of how climate limits pika distribution, how pikas persist in areas outside of their typical climate envelope, and how they might be able to buffer future climate-change effects.

The observed differences in predicted response to climate change are similar to prior comparisons of correlative and mechanistic modeling approaches (Morin & Thuiller, 2009; Buckley *et al.*, 2010, Buckley *et al.*, 2011). These results are also consistent with Araújo *et al.* (2011), who noted that SDMs can be good tools for identifying the direction of range shifts, but they are more uncertain when it comes to predicting the magnitude of the change. In contrast to the more opaque relationship between pika presence and temperatures, the more easily interpretable mechanistic input of activity time allows insight into the reason for differences in model predictions, both for the present and the future.

Under current climate conditions, the summer activity baseline model predicted more suitable habitat in the inland regions of the study area than did the summer temperature model (Fig. 3). In contrast, the summer temperature model predicted additional suitable habitat beyond that predicted by the summer activity model along the Pacific coast and in the Cascade Range. A potential explanation for these differences is that the areas where summer activity predicts additional suitable habitat have a more continental climate with a wider range of daily temperatures. The mean summer temperature in these areas is relatively high, rendering them unsuitable by the temperature model. However, given the wide daily temperature range, there are enough hours in a day where Niche Mapper predicts activity is possible, resulting in these areas being considered suitable by the activity model. Conversely, the Pacific coastline and lower elevations of the Cascade Range have a more moderate climate, buffered by proximity to the ocean. The mean temperatures are not as high (allowing these areas to be considered suitable by the temperature model), but the reduced daily temperature range does not provide enough hours where Niche Mapper predicts surface activity is possible for these areas to be considered suitable by the activity model.

Similarly, for predictions under future climates, model divergences become more pronounced in the northern latitudes of the study area. For example, under the moderate-warming scenario, the activity + winter cold model predicted 2,150 km^2 less suitable habitat than the temperature + winter cold model below 40° latitude, but 19,376 km^2 more habitat above 40° latitude. Under the warmest future scenario, the activity + winter cold model predicted 2,446 km^2 more suitable habitat below 40° latitude but 43,195 km^2 more habitat above 40° latitude. At higher latitudes, longer day lengths in summer allow pikas to make up for activity time lost due to thermoregulatory retreats below the surface during the hottest part of the day; these longer day lengths thereby provide adequate time for foraging and haying. Thus, in terms of a pika's ability to be active, not all locations with the same mean summer temperature are functionally equivalent, and the effect of warmer maximum temperatures in the future may be buffered through behavioral thermoregulation. This is a concept that becomes evident and is captured using mechanistic modeling but would be harder to detect using a purely correlative approach.

Hindcasting suggests niche conservatism and instills confidence in future predictions

In an important model-validation step not taken in many SDM studies, we show that the models built under current climatic conditions can be used to predict distributions under different climatic conditions through hindcasting. In contrast to Martínez-Meyer *et al.* (2004), who found that ecological niche models built using present-day pika locations poorly predicted LGM fossil locations, but similar to Galbreath *et al*. (2009), we found evidence of niche conservatism when hindcasting models to the LGM. The models missed only three to five of 49 fossil locations in the LGM. We note that across the entire study area, the models perhaps overpredict actual suitability. There was substantial extrapolation with respect to the winter cold input in the northern portion of the study area (Fig. S7), and we used Maxent's clamping option; thus, cold temperatures may have limited pika distributions in the LGM more than the coldest conditions in the current climate do. Indeed, Galbreath *et al*. (2009) used a full suite of bioclimatic variables in their hindcasting and did not predict the same extent of suitability in the LGM. However, Galbreath *et al*. (2009) appear to have missed a number of fossil locations that our models do predict as suitable. Furthermore, for the purposes of this work, which is focused on warm temperatures as the key driver of pika distributions, the most-informative regions of the LGM hindcasting are along the southern edges of predicted distributions. These are the areas where warm temperatures are limiting habitat suitability, and our models are in fact discriminating in these areas.

The models also accurately predicted range contraction from the LGM to the MH. Among the MH fossil locations, Pintwater Cave was the only MH/LH fossil location that no model predicted suitable habitat within 3 km during the MH. We note that Grayson (2005) questioned pika persistence at this site in the Holocene, and these modeling results also suggest that these fossils might be erroneously dated. The ability of these models to be accurately applied to both current climate conditions and two past climate scenarios provides increased confidence in their ability to predict the effects of future climate warming, assuming that future climate change will not lead to no-analog niche dynamics (e.g., Veloz *et al*., 2012).

Benefits of combining modeling approaches

These results illustrate the value of using multiple modeling approaches when predicting species distributions. Mechanistically modeling a direct effect of warmer temperatures on organisms is theoretically more reliable than relying solely on climate correlations when extrapolating to novel conditions (Kearney & Porter, 2009; Elith *et al.*, 2010; Franklin, 2013). However, we were unable to test whether a mechanistic model is in fact more reliable when predicting pika distribution changes in response to climates markedly warmer than today. We do not have locations for pikas under such conditions and thus no way to evaluate whether one model performed better. Nonetheless, utilizing two modeling approaches can help to corroborate predicted trends and bracket the magnitude of potential habitat losses. Here, there is increased confidence in the large areas of habitat loss predicted by both models (Kearney *et al.*, 2010; Meineri *et al.*, 2015; Briscoe *et al.*, 2016). Meanwhile, the mechanistic model predictions identified additional areas that may remain suitable under warmer conditions, areas that should be considered in management planning (e.g., for identifying habitats to conserve in order to protect current populations or as translocation sites).

Integration with a correlative approach also improved interpretation of Niche Mapper's mechanistic predictions. Maxent's statistical framework allowed a mechanistic output with no known threshold value (activity hours) to be converted into an index of habitat suitability without the need for a presence/absence data set. Furthermore, the importance of summer activity as a limiting process likely varies across the pika's range. Activity model predictions were improved by adding a winter-cold variable, which modified the importance of summer activity, expanding and contracting suitability predictions in logical ways. Areas where pikas currently exist with summer activity times slightly below the suitability threshold and milder winters were predicted as unsuitable by the activity baseline model, but suitable by the activity + winter cold model. This suggests that lower summer activity may be sufficient to facilitate pika persistence where winters are milder, potentially due to a longer growing season or reduced energetic costs in the winter (*sensu* Varner & Dearing, 2014, who found that haypile size correlated with winter duration). In contrast, areas with summer activity levels just above the threshold and with colder winters where pikas are not found were predicted as suitable by the activity baseline model, but unsuitable by the activity + winter cold model

We recognize that the baseline + winter cold models performed slightly worse in the hindcasting tests than the baseline models. However, that performance needs to be balanced against the uncertainty and reduced resolution of climate reconstructions for past epochs and the superior performance of these models under current climate conditions where there is less uncertainty regarding the climate data. Given these considerations, we do not believe the modest decline in performance in the hindcasting is reason to conclude that these models are worse than the baseline models.

Lastly, incorporating a mechanistic model also allows investigations of outlying areas that do not fit general distribution patterns found at the landscape level. For example, no model predicted suitable habitat in low-elevation lava-flow landscapes where pikas are known to exist (e.g., Craters of the Moon and Lava Beds National Monuments, Newberry National Volcanic Monument; Jeffress *et al.*, 2013; Shinderman 2015; Ray *et al.*, 2016). One possible explanation is that surface connections to subsurface reservoirs of cool air and ice found in the lava tubes creates cooler surface microclimates around these connections than predicted using macroclimate data (Shinderman, 2015; Ray *et al.*, 2016). Another possible explanation is that these populations may have different morphological characteristics. Hall & Bowlus (1938) report that pikas in Craters of the Moon are smaller than neighboring mountain populations, and Moyer-Horner *et al.* (2015) illustrated the importance of body size and fur properties to a model pika's ability to maintain activity levels in warm temperatures. Indeed, if pikas are modeled with 10-20% reductions in body size and/or fur thickness, summer activity in areas of Craters of the Moon and Lava Beds National Monuments where pikas are found are predicted to be above the 1132-hour threshold identified for persistence at Great Basin sites (Fig. S10). Clearly, more detailed and comprehensive comparative measurements would be required to fully evaluate this idea. Nonetheless, this example illustrates how biophysical models like Niche Mapper can incorporate intraspecific phenotypic variation into species distribution models, an important contribution that mechanistic models can provide (Buckley, 2008; Kolbe *et al.*, 2010; Boyles *et al.*, 2011).

Another area where the models did not predict suitable habitat but where pikas are known to exist was at the very bottom of the Columbia River Gorge. This is a unique habitat with abundant shade on the talus and moss covering the talus, providing thermal buffering of surface microclimate temperatures (Varner & Dearing, 2014). For simplicity, the activity model assumed a bare rock surface and no shade, which is characteristic of the majority of pika habitat elsewhere in the species' range. However, when the substrate is changed in Niche Mapper's microclimate model to assume a shaded, moss-covered surface and region-specific cloud cover is considered, predicted activity hours at Gorge locations of pika detection increased by up to 40% (Fig. S11) and results in more areas being classified as suitable habitat (Fig. S12). This ability to investigate the thermal buffering effects of specific microhabitats has important implications for incorporating the synergistic relationship of habitat alteration and climate change into predictions of species distribution changes (*sensu* Kearney, 2013).

Broad applicability and relevance

Whether, and how accurately, SDMs can be used to make accurate predictions of species responses under future climate conditions are topics of extensive debate and research. One way forward is to compare different modelling approaches to better understand the reliability of predictions under different conditions. We recognize that interspecific interactions and non-climatic, abiotic factors such as habitat quality and connectivity are also important to predicting current occupancy and future persistence (e.g., Schwalm *et al.*, 2016). However, climate remains a principal driver in many SDMs, and the primary goal of this work is to present a generally-applicable approach to endotherm SDM development through mechanistic modeling of a more proximal relationship between climate and species distribution.

For mechanistic models to be more widely used conservation tools, they must be able to be easily and quickly tailored for a range of species (Evans *et al.*, 2015). Heat-balance biophysical models like Niche Mapper are based on heat-transfer principles and thermodynamic laws that apply to any species. When being used to predict the impacts of chronic heat stress (e.g., activity restriction) or cold stress (e.g., increased food requirements), such models only require a few and easily obtainable inputs beyond those required for a purely correlative model to be tailored for specific species: animal size and body-part dimensions, fur properties, resting metabolic rate, and body temperature. This information can often be found in the existing literature or estimated from well-established allometric equations. Thus, while we use pikas as an example, this modeling approach is broadly applicable to other species. In fact, its ability to investigate the effects of trait variation and habitat characteristics on animal performance may make the approach more valuable for focal species with greater intraspecific phenotypic variation or that are more habitat generalists than pikas. As illustrated by this work, incorporation of mechanism with other environmental variables and distribution data helps to provide a more complete understanding of how species may be limited by climate, an understanding that is necessary to inform climate-adaptation actions, management strategies, and conservation plans.

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FIGURE LEGENDS

Figure 1. Flow diagram illustrating the how the two baseline models were developed and key input data. The baseline temperature model is a purely correlative model, relating macroclimate conditions to presence locations in order to predict distribution. The baseline activity model incorporates mechanism into distribution predictions by first translating the macroclimate data to a biologically-relevant mechanistic output (time available to be surface active). Additional climate predictors that potentially modify how summer temperatures or activity time limit distributions are added to these baseline models (see text) as an input to the Maxent model building process (i.e., entering the Maxent box along with summer temperatures or surface activity time.

Figure 2. Comparison of predicted summer time activity hours at extant and extirpated historic monitoring sites in the Great Basin, USA. The outlying extirpated site is Duffer Peak, NV, which was recommended as a potential recipient site should pika translocations be considered (Beever *et al*., 2016).

Figure 3. Baseline model predictions of climatically suitable habitat for pikas under 1981-2010 climate conditions. Summer activity time predicted by Niche Mapper was the only input to the activity baseline model, and mean summer temperature was the only input to the temperature baseline model. The current pika locations used to build the model are shown along with fossil pika locations reported by Mead (1987), Hafner (1993), Grayson (2005), Galbreath *et al.* (2009) in order to show sensitivity of the model to different climate conditions. Current pika locations do not include the recently-extirpated sites from the Great Basin.

Figure 4. Hindcasting the summer temperature (ST) or summer activity (SA) baseline + winter cold models to the Last Glacial Maximum (~22,000 years before present), showing increased areas of predicted suitable habitat. A detailed view of the southern edge of predicted suitable

habitat is shown in the inset. Average summer temperatures in the western United States were ~13°C cooler than present. Three fossil locations (indicated as “No Date”) were not assigned to a specific epoch. The approximate southern edge of glacial ice sheets is represented by the dashed red line.

Figure 5. Habitat suitability predictions for various future climate scenarios using baseline models and with the baseline + winter cold models. The baseline models used either the mean temperature of the warmest quarter or summer activity predicted by Niche Mapper to predict habitat suitability. Minimum temperature of the coldest month was added to the two baseline models. Mean changes in mean summer/minimum winter temperatures in the western United States predicted by the global circulation models: conservative (+0.31/-0.08°C); moderate (+2.59/+0.83°C); warmest (+5.73/+4.05 °C). With the exception of the conservative GCM scenario, the summer activity models predicted less habitat loss than the summer temperature models.

SUPPORTING INFORMATION

Appendix S1. Additional details on modeling methodology, data acquisition, and model evaluation.

Figure S1. Maps with results from sensitivity analysis of the clear-skies assumption made in activity-time modeling.

Figure S2. The number of summer (June – September) activity hours predicted by Niche Mapper for pikas in the summer across the western United States based on 1981-2010 average monthly maximum and minimum temperatures.

Figure S3. Maxent model response curves to individual variables used in the final distribution models.

Figure S4. Plots showing the combined effect of winter cold and summer temperature (a) or summer activity (b) on habitat suitability predicted by Maxent.

Figure S5. Detailed map of habitat predicted as suitable long-term pika-research sites in the Hydrographic Great Basin, USA.

Figure S6. Map comparing an activity-only model to an activity + winter cold model.

Figure S7. Multivariate Environment Similarity Surfaces that show how similar the climate conditions in each climate scenario are to the values used in the model training under current climate conditions.

Figure S8. Hindcasting the baseline models to the Last Glacial Maximum (~22,000 years before present), showing increased areas of predicted thermally-suitable habitat from present.

Figure S9. Hindcasting the baseline models to the Mid-Holocene (~6,000 years before present), showing substantial reductions of predicted thermally-suitable habitat from the Last Glacial Maximum.

Figure S10. Maps showing how predicted surface-activity time in Craters of the Moon and Lava Beds National Monuments changes with different assumptions of pika body size and/or fur depth.

Figure S11. The effects of including site-specific habitat characteristics on Niche Mapper summer activity predictions at four pika locations in the Columbia River Gorge, OR.

Figure S12. Map showing how habitat suitability predictions in the Columbia River Gorge change when site-specific habitat characteristics are used by Niche Mapper when predicting surface-activity time.

Table S1. Animal submodel inputs used to model American pikas.

Table S2. Microclimate submodel input table used to model typical pika habitat.

Table S3. Total summer (June – September) activity hours predicted by Niche Mapper at long-term pika research sites in the Hydrographic Great Basin, USA.

Table S4. Evaluation metrics for model performance under current (1981-2010) climate conditions.

Table S5. Distance from nearest predicted suitable habitat for fossil pika locations not identified as suitable habitat in the Last Glacial Maximum.

Table 1. Average habitat suitability score for all pixels within 3 km of the known pika locations (n=616) used in the species distribution modeling for models built using summer temperature (ST), summer activity (SA), summer temperature plus winter cold (ST+WC), summer activity plus winter cold (SA+WC). The number of locations within 3 km of suitable habitat is noted in parentheses. Suitability was determined by using a threshold that maximizes specificity + sensitivity. All models predicted high mean suitability across known pika locations and predicted a strong decrease in suitability under climate change scenarios, however declines in habitat suitability were stronger for models that included summer temperature compared to models that included summer activity.

Climate Scenario		Model			
		ST	**SA**	**ST+WC**	**SA+WC**
1981-2010 Climate Conditions		0.502 (586)	0.501 (589)	0.506 (597)	0.509 (597)
Global Circulation Model Predictions for 2070	MRI-CGCM3 (Conservative change)	0.512 (588)	0.486 (596)	0.501 (592)	0.479 (589)
	NorESM1-M (Moderate change)	0.358 (541)	0.346 (565)	0.332 (547)	0.349 (563)
	MIROC-ESM-CHEM (Largest magnitude change)	0.155 (300)	0.188 (432)	0.150 (319)	0.216 (431)
Uniform Temperature Increases	+3°C	0.277 (463)	0.300 (508)	0.285 (482)	0.345 (528)
	+5°C	0.147 (308)	0.184 (440)	0.157 (329)	0.235 (457)

Table 2. Area of suitable habitat (km^2) predicted by Maxent species distribution models using either mean summer temperature or predicted summer activity under different climate change scenarios. Percent change from current climate conditions is noted in parentheses. Model abbreviations: SA (summer activity); ST (summer temperatures); WC (winter cold).

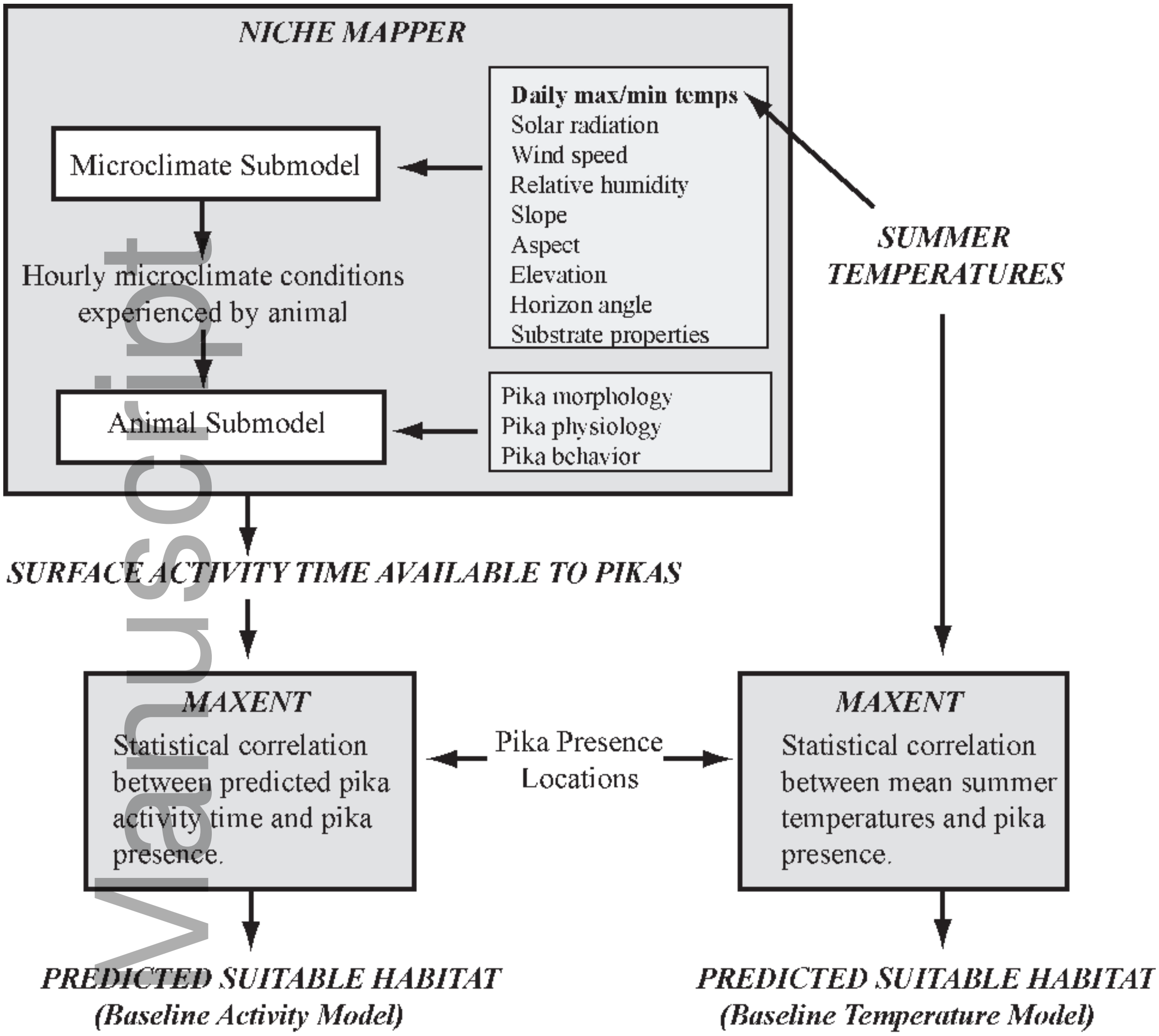
Climate Scenario	Model			
	ST	**SA**	**ST+WC**	**SA+WC**

1981-2010 Climate Conditions		414,355	494,540	366,000	344,193
Global Circulation Model Predictions for 2070	MRI-CGCM3 (Conservative change)	407,958 (-2%)	479,405 (-3%)	345,707 (-6%)	303,128 (-12%)
	NorESM1-M (Moderate change)	184,227 (-56%)	283,609 (-43%)	136,700 (-63%)	156,502 (-55%)
	MIROC-ESM-CHEM (Largest magnitude change)	52,911 (-87%)	139,713 (-72%)	44,462 (-88%)	98,412 (-71%)
Uniform Temperature Increases	+3°C	118,401 (-71%)	224,232 (-55%)	110,357 (-70%)	170,239 (-51%)
	+5°C	34,218 (-92%)	139,713 (-78%)	34,579 (-91%)	87,368 (-75%)

Table 3. Evaluation of model hindcasting to the mid-Holocene (MH) showing the number of sites misclassified by the models based on assumptions that 1) all Last Glacial Maximum (LGM) and early Holocene (EH) sites were unsuitable in the MH while all mid- and late Holocene (LH) sites were suitable in the MH and 2) that all recently-extirpated and current locations are within 10-20 km of suitable habitat in the MH. The former assumption was statistically evaluated with a chi square test of association. Model abbreviations: SA (summer activity); ST (summer temperatures); WC (winter cold).

Model	No. of LGM and EH sites < 3 km from predicted suitable habitat (n=39)	No. of MH and LH sites > 3 km from predicted suitable habitat (n=9)	Recently-extirpated/Current Locations (n= 629)	
			No habitat <10 km	No habitat <20km
ST	15	1^a	10	0
SA	16	1^a	3	0
ST+WC	7	2^b	16	9
SA+WC	9	1^b	17	9

^{a}Chi square test of association $p<0.05$; ^{b} Chi square test of association $p<0.001$



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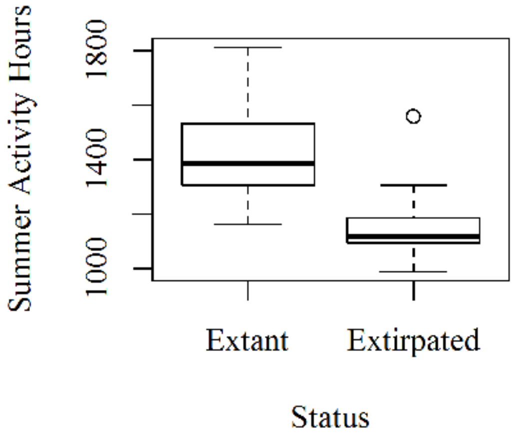

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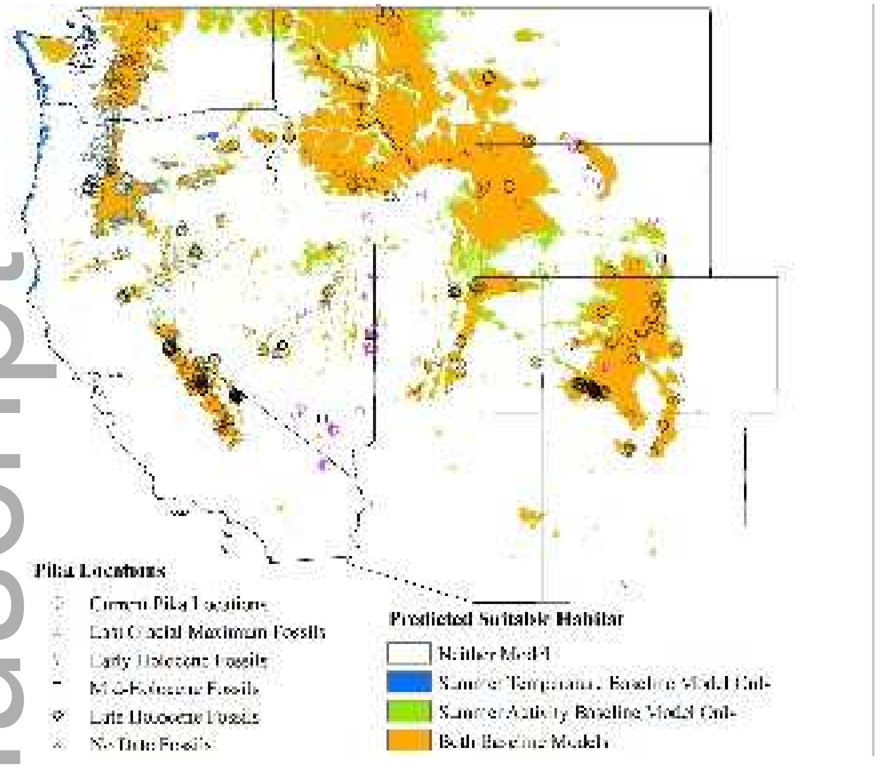

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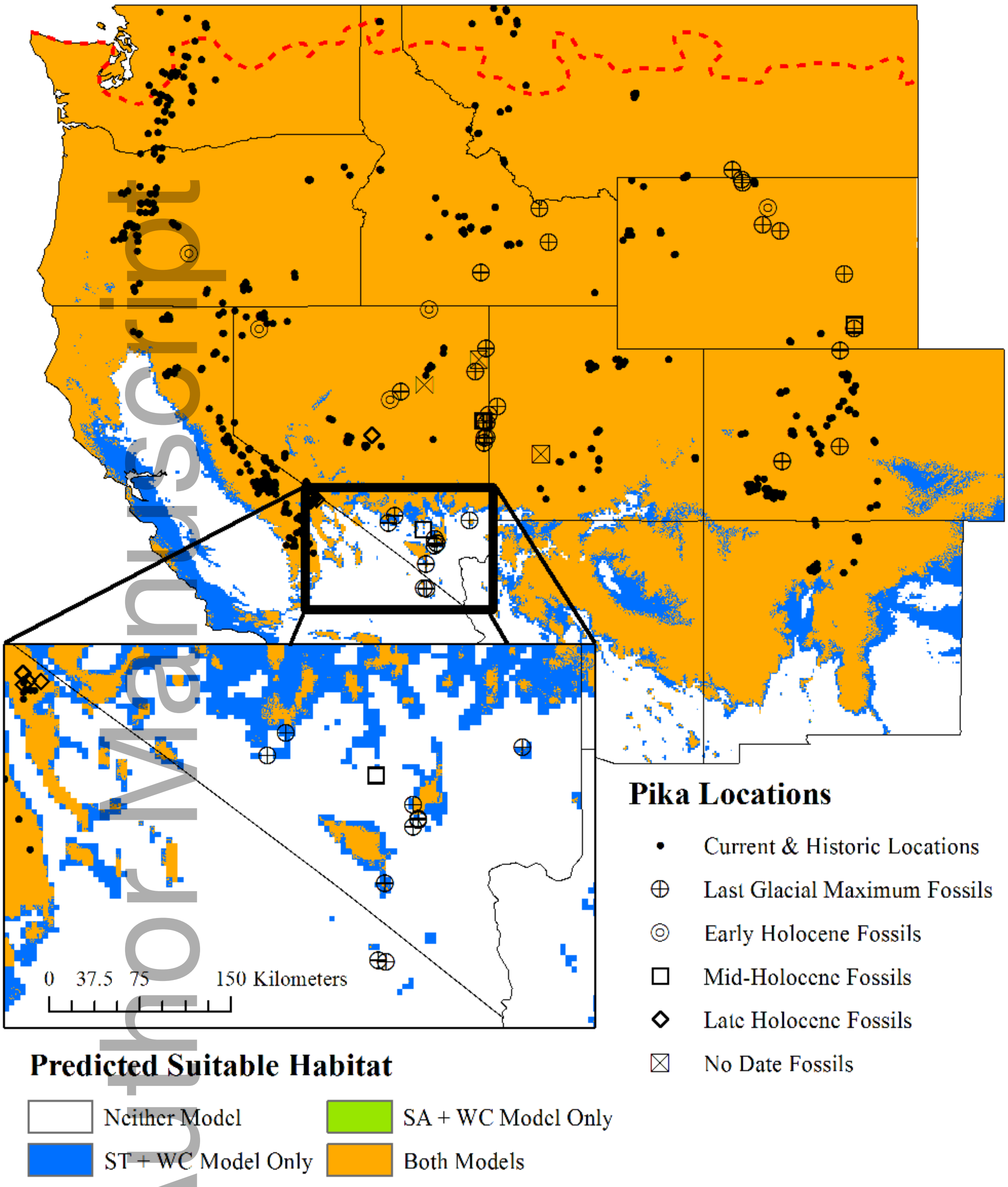

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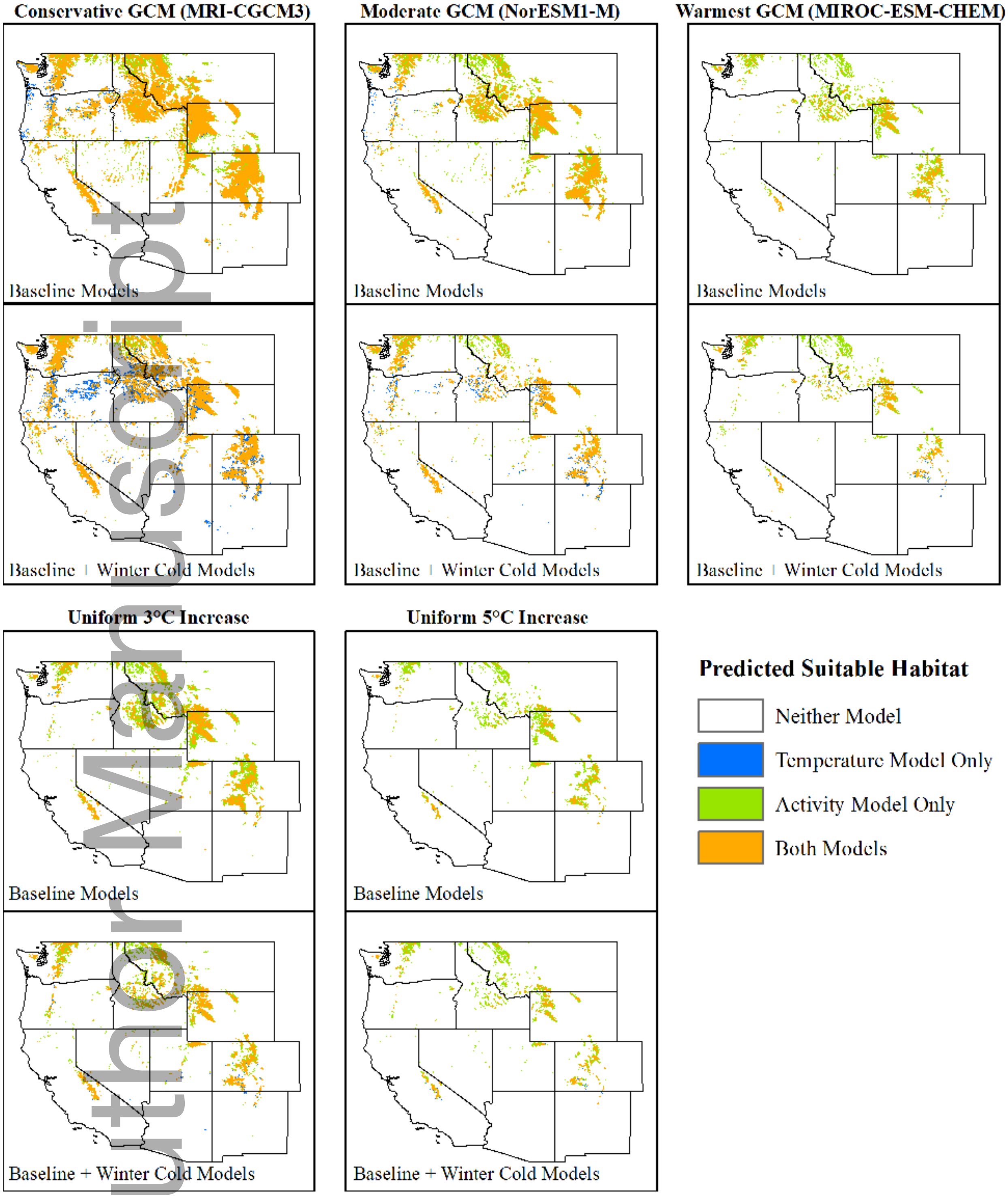

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