

Research

Vanishing islands in the sky? A comparison of correlation- and mechanism-based forecasts of range dynamics for montane salamanders under climate change

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Forecasting the effects of climate change on species and populations is a fundamental goal of conservation biology, especially for montane endemics which seemingly are under the greatest threat of extinction given their association with cool, high elevation habitats. Species distribution models (also known as niche models) predict where on the landscape there is suitable habitat for a species of interest. Correlative niche modeling, the most commonly employed approach to predict species' distributions, relies on correlations between species' localities and current environmental data. This type of model could spuriously forecast less future suitable habitat because species' current distributions may not adequately represent their thermal tolerance, and future climate conditions may not be analogous to current conditions. We compared the predicted distributions for three montane species of *Plethodon* salamanders in the southern Appalachian Mountains of North America using a correlative modeling approach and a mechanistic model. The mechanistic model incorporates species-specific physiology, morphology and behavior to predict an annual energy budget on the landscape. Both modeling approaches performed well at predicting the species' current distributions and predicted that all species could persist in habitats at higher elevation through 2085. The mechanistic model predicted more future suitable habitat than the correlative model. We attribute these differences to the mechanistic approach being able to model shifts in key range-limiting biological processes (changes in surface activity time and energy costs) that the correlative approach cannot. Choice of global circulation model (GCM) contributed significantly to distribution predictions, with a tenfold difference in future suitability based on GCM, indicating that GCM variability should be either directly included in models of species distributions or, indirectly, through the use of multi-model ensemble averages. Our results indicate that correlative models are over-predicting habitat loss for montane species, suggesting a critical need to incorporate mechanisms into forecasts of species' range dynamics.

Keywords: amphibians, climate change, niche model



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Introduction

Anthropogenic climate change poses a major threat to biodiversity, especially in montane regions (Parmesan 2006, Thuiller et al. 2008, La Sorte and Jetz 2010, Gottfried et al. 2012). Some montane species have seemingly already responded to contemporary warming by contracting their ranges upslope (Parmesan and Yohe 2003, Wilson et al. 2005, Moritz et al. 2008, Raxworthy et al. 2008, Rovito et al. 2009, Chen et al. 2011, Feeley et al. 2013, Freeman and Class Freeman 2014). Given that mountains are centers of endemism and species richness for many groups of plants and animals (Myers et al. 2000, Körner and Spehn 2002, Graham et al. 2014), the erosion of the geographic distributions of montane taxa is particularly alarming. Moreover, recent studies suggest that species inhabiting montane regions may have a limited capacity to adapt to changes in climate, even over evolutionary timescales (Smith et al. 2007, Li et al. 2009, Kozak and Wiens 2010a). Consequently, predicting the fates of species that make up montane biodiversity hotspots has emerged as a major challenge for biologists.

Correlative niche models have become the primary tool for forecasting the range dynamics of species under climate change (Thuiller et al. 2008). This class of models uses two types of data, species' occurrence records and GIS-based maps of environmental variation (e.g. climate), to build statistical models describing the association between the contemporary environmental conditions and the presence of a species (Elith and Leathwick 2009). These models are then projected onto maps of future environmental conditions to predict whether the geographic distribution of suitable habitat for a species will shift, contract or remain stable (Peterson et al. 2002, Williams et al. 2003). Correlative niche models often predict extensive loss of climatically suitable habitats to the point of extinction, especially for species inhabiting montane regions (Williams et al. 2003, Thuiller et al. 2005, Milanovich et al. 2010).

Correlative models make at least two important assumptions in the context of predicting species' range dynamics in response to climate change. First, they assume that a species' documented geographic distribution encompasses the full range of environmental conditions habitable by that species (Araújo and Peterson 2012). Second, they assume that correlations between environmental variables and the processes setting range limits remain fixed across space and time (Pearson and Dawson 2003). These correlative approaches may then do a poor job extrapolating into new, future environments where climatic variable values and combinations are different from the current variable values used to train the model (Fitzpatrick and Hargrove 2009). Given that factors other than abiotic conditions can limit the distributions of species (e.g. species interactions) and that correlations among environmental variables and range-limiting processes may change over time, some authors have argued that the range dynamics of species cannot be predicted from current climate and species' distribution data (Kearney and Porter 2004, 2009, Williams and Jackson 2007). Mechanistic niche modeling

is a potentially powerful alternative that does not use species' realized geographic ranges to forecast future distributions. The mechanistic approach links functional-trait and climatic data to model spatial variation in parameters that determine whether a species can persist in a given location (e.g. energetics, development time, population size, species interactions). Because they focus on range-limiting biological processes, well-parameterized mechanistic models (i.e. those that include important mechanisms that limit species' ranges) may provide more accurate predictions of species' responses to climate change than correlative models (Kearney and Porter 2009, Buckley et al. 2010).

Do existing correlation-based forecasts signal the impending collapse of montane faunas and floras? Alternatively, can limitations associated with projecting correlative models beyond current environmental conditions explain the predicted drastic loss of suitable climates for montane endemics? These questions are critical to conservation efforts aimed at sustaining montane diversity in the face of climate change. Researchers have begun to compare the range dynamics that are predicted by correlative and mechanistic models (Hijmans and Graham 2006, Morin and Thuiller 2009, Buckley et al. 2010, Kearney et al. 2010) and have incorporated mechanistic variables into correlative approaches (Mathewson et al. 2016). However, no comparative studies of correlative and mechanistic forecasts exist for narrow ranging montane endemics, which are predicted by correlative models to be under threat of extinction as a result of climate change (Milanovich et al. 2010).

Here, we compare the range predictions of correlative and mechanistic niche models for three salamander species of the genus *Plethodon* that are restricted to the Appalachian Mountains of eastern North America (Fig. 1). These species (*P. jordani*, *P. montanus* and *P. metcalfei*) are mountaintop endemics that have restricted elevational and climatic distributions (Highton and Peabody 2000, Kozak and Wiens 2006), making them ideal species for studying the sensitivities of forecasting future suitable habitat. *Plethodon jordani* is only found within the Great Smoky Mountains National Park at elevations >1200 m, making it the most geographically-restricted species used in this study. *Plethodon montanus* and *P. metcalfei* have wider geographic distributions, together spanning the states of Virginia, Georgia, South Carolina and North Carolina. However, both of these species are restricted in elevation, generally occupying forested habitats above >1000 m. The climatic niches of *Plethodon* species have been conserved, resulting in allopatric speciation as populations have tracked suitable climates during periods of environmental change since the Miocene (Kozak and Wiens 2006). Climatic niche conservatism has also seemingly restricted many species in the clade from colonizing lowland climates (Kozak and Wiens 2010b, 2012).

In this study, we forecast and compare range dynamics predicted by a widely-used correlative method (Maxent, Phillips et al. 2006) and a mechanistic model based on the climatic sensitivity of metabolism, surface activity and digestive efficiency. Previous work using correlative models to

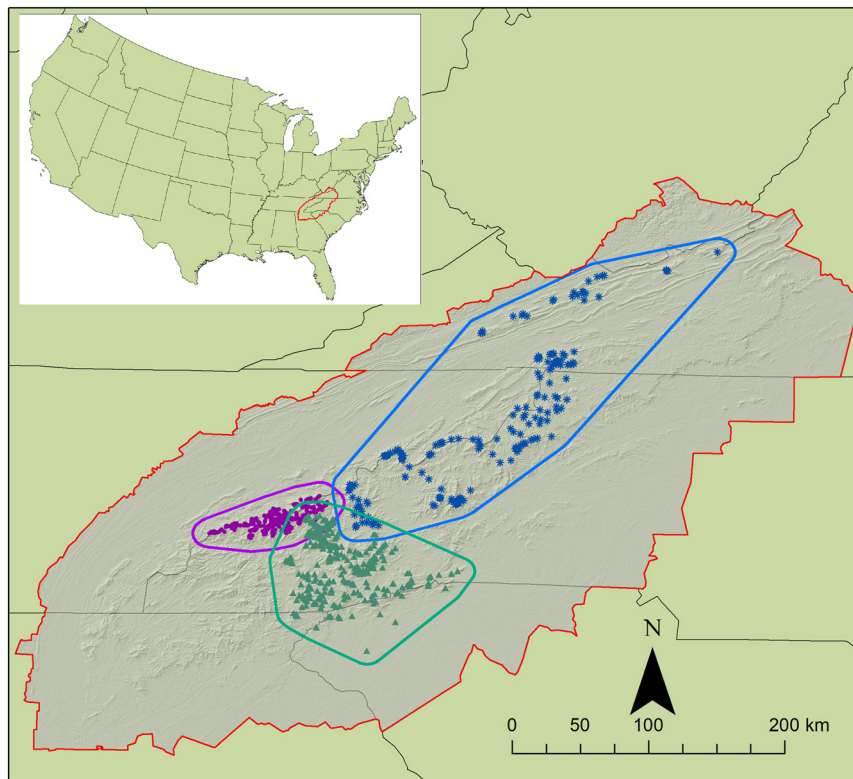


Figure 1. Salamander distributions in the southern Appalachians. Species ranges depicted by a 10-km buffered convex hull polygon based on localities obtained from US Natl Museum of Natural History used in niche model training and projecting, *Plethodon jordani* (purple, circles), *Plethodon metcalfi* (green, triangles) and *Plethodon montanus* (blue, asterisks).

forecast future suitable habitat predicts extensive range contractions and local extinctions of salamanders that inhabit the southern Appalachian Mountains (Milanovich et al. 2010). We hypothesize that these dire predictions arise from correlative models, parameterized using climatic variables that are good indicators of species present-day occurrence, needing to extrapolate beyond the training data to non-analog future climates. In contrast, given that our mechanistic model quantifies organism-specific monthly energy gains and expenditures related to environmental temperature, we hypothesize that it will be able to 1) incorporate suitable future climates not currently represented by species present-day distributions; and 2) identify temporal shifts in temperature variation that are relevant to organismal activity and occurrence. Both of these are predicted to result in more future suitable habitat. First, we test how well each model predicts present distributions. We then project the niche models into future environmental conditions and quantify the amount of area predicted to remain suitable in 2050–2060 and 2080–2090. We inspect some of the underlying reasons for discrepancies between our modeling approaches, investigating the potential for correlative models to have issues extrapolating to non-analog climate and incorporating shifts in activity time. Finally, we examine how methodological choices of future environmental data in the form of global circulation models (GCMs) contribute to differences in predicted distributional extent.

Methods

Ground temperature

We generated high-resolution (90-m) layers of monthly maximum and minimum forest floor temperature estimates for present and future time periods using a model developed by Fridley (2009) for the Great Smoky Mountains National Park. All three species inhabit forested habitats within or in close proximity to the Great Smoky Mountains National Park, which allowed us to generate new temperature layers for present day and future climates. Because of variability between GCMs, we created future temperature layers for fifteen different GCMs and one GCM ensemble mean covering two time periods (2050–2060 and 2080–2090) resulting in 32 future climate ground temperature layers. This method estimates near-ground temperatures (~1-m) for the densely vegetated forest using data on incoming solar radiation, topographic shading, slope, aspect and soil moisture, along with model coefficients based on data gathered from ground level data loggers over the course of two years (Fridley 2009). The ground temperature model built by Fridley (2009) incorporates air temperature through the use of lapse rates (degree temperature change per meter elevation change) calculated from the elevation and average monthly maximum and minimum temperatures recorded at weather stations within the park.

We calculated lapse rates for present and future climates from random points placed at a density of 1 per 80 km² within a 10-km buffered polygon of the species' current range. Climate data were then extracted to points using the ClimateNA ver. 5.21 software package (<<http://tinyurl.com/ClimateNA>>) based on methodology described by Wang et al. (2016). All other inputs were generated using methodology described by Fridley (2009) and are detailed in the supplementary material (Supplementary material Appendix 2). We assumed that the other values used in the Fridley models would not change in the two future time periods. Precipitation in the southern Appalachians is not predicted to change drastically in the near future (Jiang et al. 2016), and other values, including radiative heating, stream location and topographic convergence index, are dependent on the topology and location, which should remain relatively constant.

Climate models

Creating future climate layers requires researchers to choose both a greenhouse gas scenario or representative concentration pathway (RCP) and a global circulation model (GCM). The choice of RCP is based on predictions for how individuals and governments will attempt to mitigate warming and curb greenhouse gas emissions (IPCC 2014). We used RCP4.5, which assumes greenhouse gas emissions peak in 2040 and then decline (IPCC 2014). We were primarily interested in how the correlative and mechanistic niche models differ in their projections in response to forecasts from different GCMs, therefore we chose an RCP that represents an intermediate future greenhouse gas scenario. Many meteorological research centers have developed GCMs that simulate climatic responses to increased greenhouse gas emissions. Because of large uncertainties in the interplay of physical processes, feedback processes and parameterization, there is substantial variation in the predicted temperatures for different GCMs under the same RCP for a given future date (Buisson et al. 2010, Wright et al. 2014). We ran both the correlative and mechanistic models for 15 GCMs (Supplementary material Appendix 1 Table A1.2). These 15 models represent major clusters of similar GCMs identified by Knutti et al. (2013) using hierarchical clustering from a distance matrix of monthly climate projections, which were locally downscaled by Wang et al. (2016) using the delta method. Compared to the scale at which the global processes simulated by each GCM operate, the southern Appalachians is a small region and inter-model variability between GCMs is therefore likely to be high. Ensemble-averaging using multiple GCMs has been suggested as a method to overcome some of the issues relating to inter-model variability (Fordham et al. 2011), so we also included a GCM ensemble mean projection of the same 15 GCMs.

Mechanistic model

We modeled spatial variation in energetics to predict the potential geographic distribution of the three *Plethodon*

species and their future range dynamics under climate change. Our mechanistic model was based on models developed by Kearney and Porter (2004) and Buckley and Roughgarden (2005, 2006), and was modified to incorporate hydric constraints on salamander surface activity (Gifford and Kozak 2012). This mechanistic model is based on the premise that viable populations cannot persist in locations where energetic costs exceed energetic inputs. For every 90-m grid cell within our 10-km buffer of each species range, we computed annual energy budget as the sum of monthly budgets based on energetic inputs through potential foraging time, prey availability and digestive efficiency. Energetic costs are calculated from temperature-dependent metabolism and the cost of annual reproduction. Many of these inputs and outputs directly relate to the temperature on the landscape. For example, potential foraging time is computed as the time when salamanders can be surface-active based on preferred body temperature (which results from modeled ground temperatures) and assumes animals forage until 10% of their body mass is lost through evaporative water loss (also related to modeled ground temperature). These computations were done using the R package *biophys* (Peterman 2014), which was developed based on the model used in Gifford and Kozak (2012) for *P. jordani*, although it is broadly applicable to organisms with available species-specific physiological, behavioral and ecological parameters. We used species-specific metabolic rates measured previously in our laboratory, while other parameters relating to reproductive expenditures and digestive efficiency were based on prior work on related species of *Plethodon*. To parameterize the environmental variables in the mechanistic model, we used the high-resolution (90-m) model of temperature variation described above, and empirically-derived estimates of wind speed and 95% humidity. For more details of the mechanistic model, please refer to the supplementary information (Supplementary material Appendix 1 Fig. A1.1, Appendix 2).

To assess whether differences in the future suitable habitat forecast by the mechanistic model resulted from changes in the time of year when the salamanders could be surface-active, we compared the monthly potential foraging time (PFT) for *P. jordani* under current conditions and two future GCMs (HadGEM2-ES and CNRM-CM5). We chose to focus on these two GCMs as examples because the correlative model using HadGEM2-ES had the lowest predicted range retention and the predictions using CNRM-CM5 had the largest difference in suitable habitat between the correlative and mechanistic models. We ran the model for each GCM and month separately and extracted monthly PFT values for current known localities of *P. jordani* (n = 357 obtained from U.S. National Museum of Natural History).

A common criticism of mechanistic models is that the large number of parameters and uncertainty around parameter values is poorly understood and not well represented in model outputs (Peterman and Gade 2017). We assessed the effects of parameter uncertainty by performing a one factor at a time (OFAT) sensitivity analysis, where we altered a single parameter while leaving the others at the default

values (Supplementary material Appendix 2). A more ideal approach (when uncertainty around all parameters has been experimentally quantified) is to conduct global sensitivity analyses to address how simultaneously varying multiple parameters effects model predictions (Fordham et al. 2016). For the present study, implementation and interpretation of such an analysis is complicated by a lack of knowledge of biologically-realistic bounds in which to vary all the parameters in the mechanistic model. Therefore, we restricted our sensitivity analysis to evaluating how changing snout-vent length by 10% and changing minimum and maximum foraging temperature by 10% of the temperature range influences our model outputs for *P. jordani* under current and future conditions. We also analyzed the effect of using the metabolic rates of *P. metcalfi* and *P. montanus* on *P. jordani* distribution predictions, since this was the species-specific parameter included in the model. Using the metabolic rate equations for the other montane-endemic species allowed us to quantify the influence of species-specific metabolic differences and vary the metabolic rate equation parameters while retaining biologically realistic values. Of the species used in this study, *P. jordani* has the most well documented distribution and natural history; by focusing on this species for a sensitivity analysis we were better able to interpret the output of our model and compare our results with prior research (Peterman and Gade 2017).

Correlative model

We used Maxent ver. 3.3.3 (Phillips et al. 2006) to quantify the correlation between climate and georeferenced occurrence locations (obtained from the US Natl Museum of Natural History; *P. jordani* n=357, *P. metcalfi* n=283, *P. montanus* n=188, after the removal of any points that were in the same 90-m grid cell as another occurrence). Maxent is an approach for characterizing the probability that habitat is suitable at a given raster cell from incomplete information. In the context of modeling a species' geographic range, it computes a probability distribution that describes the relative suitability of each grid cell as a function of the environmental variables at the known occurrence locations for the species (Phillips et al. 2006). To facilitate direct comparison of the mechanistic and correlative models, while also avoiding over-fitting our correlative model (Phillips et al. 2006), we used the same ground temperature monthly maximum and minimum environmental layers at a 90-m spatial resolution to construct bioclimatic variables (annual mean temperature, maximum temperature of the warmest quarter, and minimum temperature of the coldest quarter). By using the results of the ground temperature model, we were able to work at a finer resolution than is available with other open-source bioclimatic data. We focus on these three bioclimatic variables because 1) they most closely parallel the variables used to generate surface activity time in the mechanistic model; and 2) they are the temperature variables that have been used in other studies to model *Plethodon* distributions (Cunningham et al. 2009).

As with most correlative modeling studies, we were restricted to running presence only models based on the data available. In this study, we did have a set of locality points for other salamander species that we used as absence points for analyzing model performance. We used a presence only model because these absence points were sparse and studies rarely have access to absence points. The three species of *Plethodon* that we focused on have robust locality data based on four decades of fieldwork by R. Highton. Present and future niches were modeled within a 10-km buffer of a convex hull based on current locality information. We randomly selected 75% of the occurrence locations for model construction; the remaining 25% were set aside to test the model. Models were calibrated using default features, 10 000 randomly generated background points, 500 iterations, and a convergence threshold of 0.0001. Each model was run ten times using subsampling; thus a different 25% subset of points were set aside to test the model over 10 different runs and we used the average threshold and average log likelihood values across these runs. We investigated the impact of choice of regularization parameter on the resulting estimates of suitable habitat for *P. jordani* with all GCMs using the regularization values of 1, 3 and 5; results were not significantly different (ANOVA, $F_{2,87}=0.17$, $p=0.98$) so we used the default regularization of 1 for all Maxent models.

To evaluate to what degree the models were extrapolating in future scenarios, we plotted multivariate environmental similarity surfaces (MESS), which quantify the similarity between any given location in the future projection dataset and the training dataset (Elith et al. 2010). MESS output is in the form of a map, where negative raster values represent localities where at least one future variable in the projection is outside the range of variables used in the training dataset. We quantified the percentage of area within the convex hull of each species' current distribution that had a negative MESS value, indicating extrapolation in at least one variable. We also visually checked where those areas of extrapolation were on the landscape.

Model performance

To examine the extent to which the mechanistic and correlative models discriminated among presence and absence localities, we used the sensitivity and specificity indices of Manel et al. (2001). The sensitivity index measures the proportion of true presences that were correctly predicted. The specificity index measures the proportion of absences that were correctly predicted. We also calculated the proportion of all locations that were correctly predicted and the true skills statistic (TSS), which has been shown to measure model performance while avoiding potential statistical artifacts relating to prevalence (Allouche et al. 2006). To avoid using the same presence points to calibrate and validate the correlative Maxent model, we used 75% of the data to calibrate the model, while the remaining 25% of the data was used to validate the model. Absences were defined using localities

from the Natl Museum of Natural History where R. Highton recorded occurrences of species of *Plethodon*, but not the species of interest. Because of the thoroughness and protracted time period over which Highton conducted his surveys of plethodontid salamanders, we are confident that these points represent true absences (number of absence points not occurring in the same 90-m grid cell *P. jordani* n = 50, *P. metcalfi* n = 27, *P. montanus* n = 96).

Implementation of these validation metrics required a threshold to transform probabilistic predictions of habitat suitability into binary predictions of species presence and absence. For the mechanistic model, we considered any grid-cell with a discretionary energy value ≤ 0 unsuitable. We used Maxent to generate threshold values according to eleven metrics. The four threshold techniques that were able to correctly predict on average at least 85% of current presences and absences for the three species were the 10th percentile training presence, fixed cumulative value 10, maximum training sensitivity plus specificity, and maximum testing sensitivity plus specificity. The amount of suitable future habitat was not sensitive to the differences between these four thresholds, therefore we used the 10th percentile of training presence. This is the suitability threshold associated with the top 90% of the training presence records averaged across 10 replicate runs.

Model differences

We projected the modeled ecological niche onto future climatic conditions using both niche modeling approaches. For each model type, we calculated the habitat suitability in the form of binary presence-absence predictions for each species at two climate snapshots (focused on 2055 and 2085) for 15 GCMs and the GCM ensemble mean. We used a generalized linear model to explore the influence of modeling approach (correlative versus mechanistic), future time period (2055 or 2085) and global circulation model (15 used in this study) on the percentage of suitable habitat retained between present and future forecasts. We compared and ranked models including all combinations of these three predictors using Akaike's information criterion with small sample size bias adjustment (AICc) in the R package MuMIn (Barton 2019).

Results

The mechanistic and correlative models produced highly congruent predictions of the contemporary range of each species. We found little difference in the extent to which the present-day climatic niche is over- or under-predicted based on the contemporary range. Table 1 shows that both the correlative and mechanistic models had high overall prediction success (78–98%), high percentages of true positives correctly predicted (sensitivity 74–99%) and high percentages of true negatives correctly predicted (specificity 75–100%). The mechanistic model for *Plethodon montanus* produced the lowest values across all metrics.

AICc for each species supported a generalized linear model for change in suitable area that includes niche model (correlative versus mechanistic), GCM, and year (Supplementary material Appendix 1 Table A1.5–A1.6). For most GCMs, the mechanistic model predicted that more of the currently suitable habitat would remain suitable in the future (Fig. 2). The mechanistic model predicted significantly more future suitable habitat compared with the future suitable habitat predicted using a Maxent/correlative approach. Whereas the correlative model predicted that *P. jordani* would persist on average in 19% of its current habitat across the 15 GCMs (16% using the GCM ensemble mean) by 2055, the mechanistic model predicted it would persist in 51% of its current habitat (49% using the GCM ensemble mean) (Fig. 3). For *P. metcalfi* the mechanistic model predicted its persistence in 34% of its current habitat across the 15 GCMs (25% for the GCM ensemble mean) in 2055, whereas the correlative predicted 26% (21% from the GCM ensemble mean) in 2055. *Plethodon metcalfi* currently occupies some moist microhabitats at lower elevation, so the model in Maxent included habitat suitability correlations for more sites, projecting less range contraction than for the other two species. For *P. montanus*, using Maxent we predicted that this species would lose all but 7% (4% from the GCM ensemble mean) of its suitable habitat by 2055, with the mechanistic model predicting an average retention of 20% of its currently suitable habitat (9% from the GCM ensemble mean). We note that some GCMs still predicted a loss of almost 100% of suitable habitat even

Table 1. Model performance metrics for two niche modeling approaches. Data comparing the ability of the correlative and mechanistic models to predict known presence (sensitivity) and known absence (specificity), overall performance and true skill statistic (specificity + sensitivity⁻¹) for three species of *Plethodon* salamanders. Overall performance is the number of presence and absence points correctly identified divided by the total number of points.

Model	Sensitivity (% Correct +)	Specificity (% Correct –)	Performance (% Correct+ and –)	True skill statistic (TSS)
<i>Plethodon jordani</i>				
correlative	88%	98%	92%	0.86
mechanistic	99%	90%	98%	0.89
<i>Plethodon metcalfi</i>				
correlative	87%	93%	88%	0.80
mechanistic	81%	100%	83%	0.81
<i>Plethodon montanus</i>				
correlative	92%	75%	81%	0.67
mechanistic	74%	85%	78%	0.60

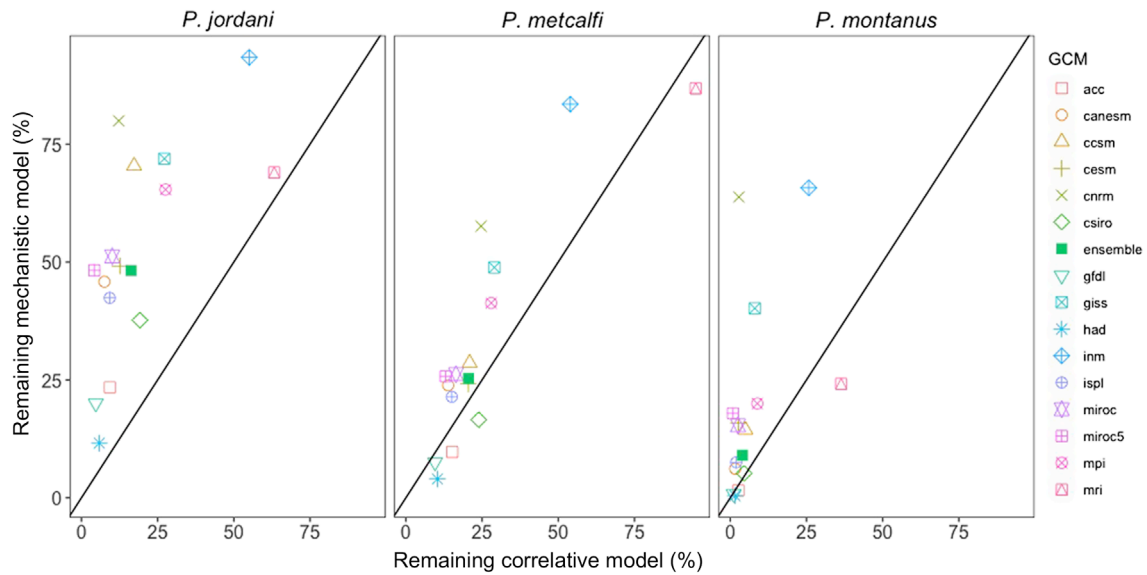


Figure 2. Comparison of predicted suitable habitat retention under correlative and mechanistic models for 15 GCMs for 2050–2060. Points represent global circulation models, colored by model, line for $y = x$. Points above the line represent instances where the mechanistic model predicted more suitable habitat than the correlative model.

using a mechanistic model (Fig. 2, Supplementary material Appendix 1 Table A1.4). For maps of predicted suitable area using GCM ensemble mean (Fig. 4). Supplementary material Appendix 1 Fig. A1.2 for average suitable area across GCMs.

We tested how sensitive our mechanistic model results were to the parameter values that we used. Though we found that small changes in the input values for animal size and activity temperature range resulted in differences in the

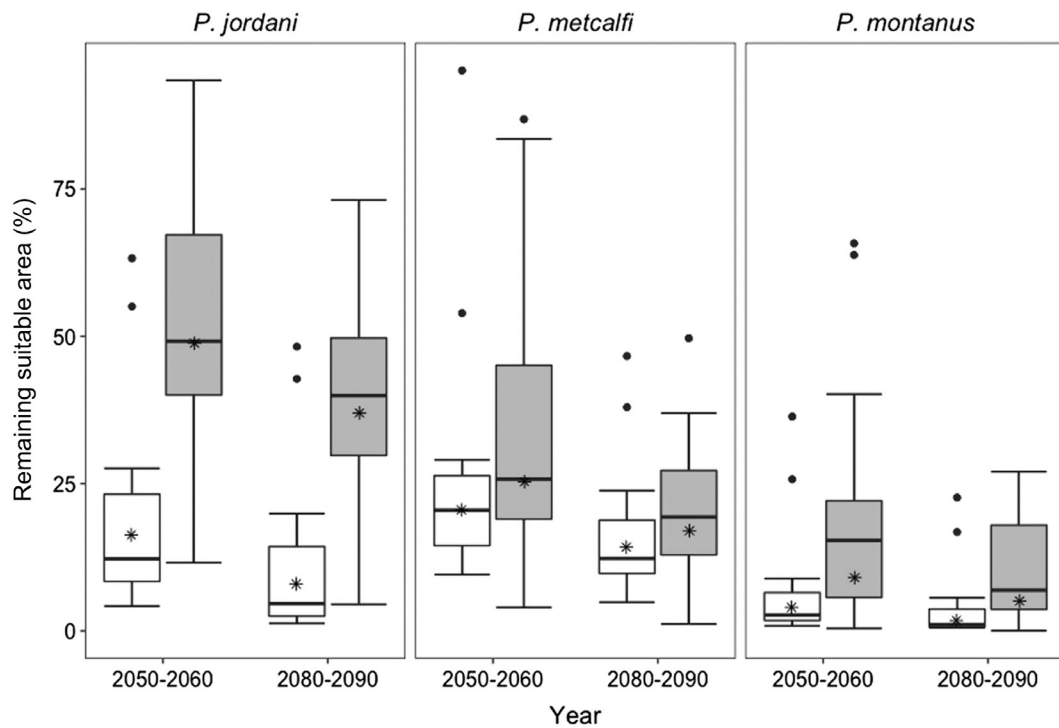


Figure 3. Proportion of total area predicted to remain suitable in 2050–2060 and 2080–2090. Variation represents differences between projected suitable area under 15 different global circulation models. Correlative model results in white and mechanistic model results in grey. Proportion remaining suitable based on GCM ensemble mean represented by asterisks. AICc for each species supports a generalized linear model for change in suitable area that includes niche model (correlative versus mechanistic), GCM and year (Supplementary material Appendix 1 Table A1.5, A1.6).

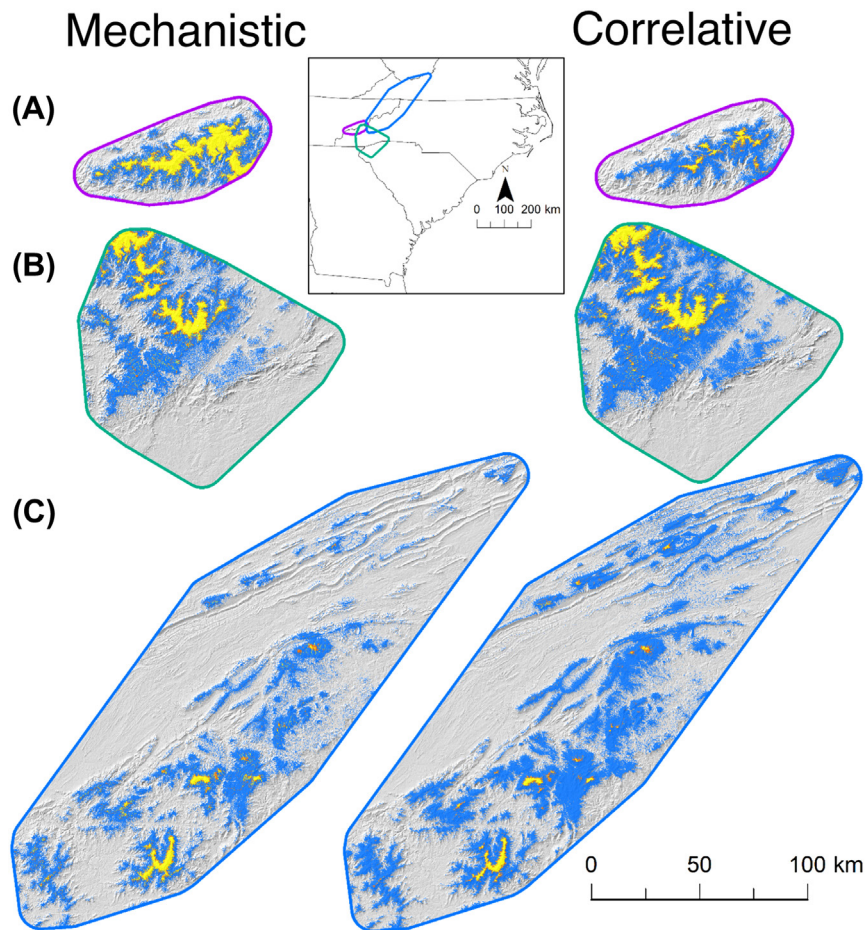


Figure 4. Maps predicting suitable area based on current temperature data and future temperature data from the GCM ensemble mean. Inset map shows study region geographic extent with colored polygons of study area for each species. (A) *P. jordani* outlined in purple, (B) *P. metcalfi* outlined in green and (C) *P. montanus* outlined in blue. Grid cells are classified as unsuitable (grey), current distribution lost by 2055 (blue), suitable area lost between 2055 and 2085 (orange) and area still suitable in 2085 (yellow).

amount of predicted suitable habitat, the result we were most interested in quantifying, percent change in suitable area between present and future climate, had low sensitivity to changes in parameter values. The mechanistic model using the default parameters and the GCM ensemble mean for *P. jordani* predicted 49% retention of suitable habitat in 2055. Changing the snout–vent length parameter by 10% resulted in the largest deviation in predicted suitable habitat retention among the parameters we tested (33% habitat retention with a reduction in animal length and 57% habitat retention with increasing the animal length parameter) (Supplementary material Appendix 1 Table A1.7).

To address why the two niche modeling approaches resulted in somewhat different future estimates of suitable habitat, we examined the extent to which the correlative approach was extrapolating to novel environmental conditions, and for *P. jordani* whether the mechanistic model incorporated a shift in the time of year when salamanders were able to be surface-active. When using the correlative model, we found that GCMs that predicted less future suitable habitat had a larger area with negative (extrapolated)

raster cells in the multivariate environmental similarity surface (MESS) maps (Supplementary material Appendix 1 Fig. A1.3). This relationship could indicate that the high predicted loss of suitable habitat under these GCMs resulted from extrapolating beyond the training data. However, based on the Maxent MESS output maps for the three species, all areas of extrapolation appear to be in low elevation areas (Supplementary material Appendix 1 Fig. A1.4). These low elevation areas are not currently inhabited by our focal species because they are climatically unsuitable, and therefore potential issues of extrapolation based on these low elevation areas do not affect our quantification of range loss in higher elevation areas. The response curves further indicated that the current warmer training temperatures for the three environmental variables are already associated with unsuitable habitat (Supplementary material Appendix 1 Fig. A1.5).

We analyzed whether the mechanistic model incorporated temporal shifts in the time of year when one of our focal species, *P. jordani*, was able to forage to offset annual energy costs by comparing current monthly foraging predictions for

two GCMs for 2055. Potential foraging time (PFT) did shift temporally, with more PFT in March for the Hadley model and in November for the CNRM model compared to current predicted activity patterns (Fig. 5).

For each modeling approach and future time period, the predicted suitable habitat varied by at least an order of magnitude based on the GCM that was used (Supplementary material Appendix 1 Table A1.4). While the mean values for predicted range retention across the tested GCMs were consistently higher for the mechanistic niche model, there was also more variation in the predicted suitable area among GCMs with the mechanistic model (Fig. 3). Overall, GCMs that predicted low or high future habitat retention in correlative models also predicted low or high retention of suitable habitat in the mechanistic model (Fig. 2, Supplementary material Appendix 1 Table A1.4).

Discussion

Many montane species appear to be living near the upper thermal limits of their niches, making climate change one of the leading threats to montane floras and faunas (La Sorte and Jetz 2010). Correlative niche models predict that upslope migration of species will continue throughout the 21st century, pushing many montane species to the brink of extinction (Williams et al. 2003, Thuiller et al. 2005, Milanovich et al. 2010). We compared the forecasts from a widely used correlative model (Maxent), to forecasts from a mechanistic model that incorporates processes limiting species' ranges. As predicted by other studies (Milanovich et al. 2010, Moskwik 2014), both Maxent and the mechanistic model forecasted that the ranges of all three species will contract upslope in

response to warming. However, in this study we found that correlative models are likely to over-predict the amount of habitat that montane species will lose under climate change.

Correlative model under-prediction

Why does the correlative model, especially for *Plethodon jordani*, seemingly fail to predict many of the future locations that the mechanistic model forecasts as climatically suitable? Correlative models are restricted to finding correlations between present environmental variables and occurrence data, which may not represent the processes that actually limit a species' range (Fitzpatrick and Hargrove 2009, Elith et al. 2010, Araújo and Peterson 2012). Although the temperature variables used to construct the correlative model are associated with the range limit, they do not strictly reflect the underlying process that constrains the range (i.e. limits and costs to surface activity calculated in the mechanistic model). Two grid cells could have similar mean temperatures, yet differ in the overall length of time that they are thermally suitable for surface activity and foraging, resulting in different forecasts of range dynamics between the modeling approaches. Put another way, the mechanistic model is seemingly able to detect subtle temporal shifts in relevant climatic conditions throughout the year that the correlative model cannot.

Overall, our comparisons demonstrate that correlative models may overestimate range loss because of mismatches between bioclimatic variables (e.g. mean annual temperature, maximum temperature of the warmest month) and range-limiting biological processes. Conversely, our results do not suggest that the correlative model forecasts less suitable habitat in the future because of extrapolation to non-analogous

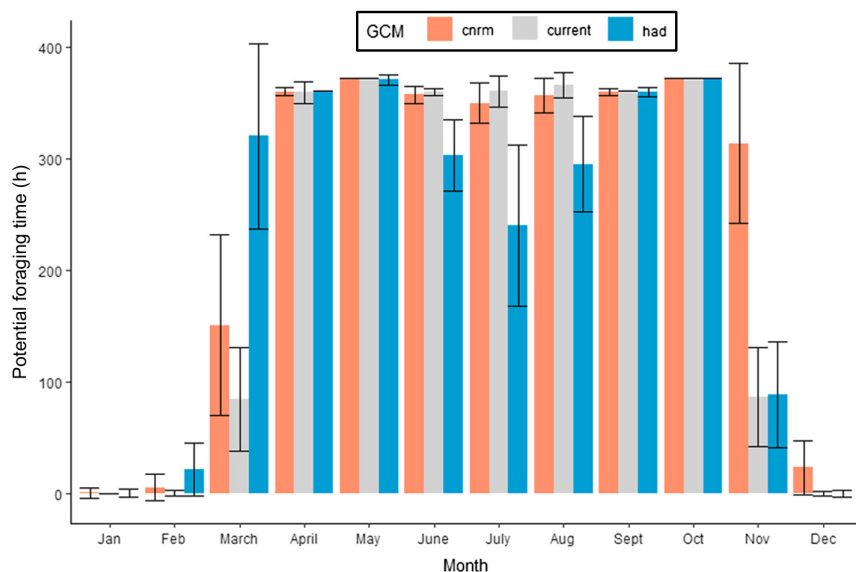


Figure 5. Shifts in foraging time for *P. jordani* under two global circulation models. Average estimated monthly foraging time in hours for *P. jordani* at current localities for three climate scenarios: current temperatures (grey), predicted temperatures based on HadGEM2-ES ('had' in orange) and CNRM-CM5 ('cnrm' in blue). Maximum number of hours in a 30 day month is 360 and 31 day month is 372. Error bars represent the standard deviation of values across localities.

climates (Briscoe et al. 2019). We found that areas identified by Maxent as having future temperatures ranges outside of the training conditions occur at lower elevations, areas that are not currently inhabited, or expected to be inhabited in the future. The current climate conditions used to train the correlative model already encompass the upper limit of temperature tolerated by all three species.

Prior work using paleoclimatic modeling on *P. jordani*'s distribution supports the idea that the mechanistic model used in our study may forecast more realistic distributions when projected across different time periods. Luxbacher (2014) used the mechanistic model from Gifford and Kozak (2012) and Maxent to produce niche models for *P. jordani* within the Great Smoky Mountains National Park during the LGM. As with our future forecast, the hindcast of the correlative model predicted significantly less suitable area at the LGM with little overlap with the current distribution. Both the mechanistic model and the genetic data demonstrated that populations across the range of this species were large and stable in size during the LGM (Highton and Peabody 2000, Weisrock and Larson 2006, Luxbacher 2014). However, the correlative model failed to predict suitable habitat across most of this species' range suggesting that the ability of the correlative model to predict future distributions in novel future habitats may be unreliable as well (Luxbacher 2014).

Mechanistic model sensitivity

By doing a local OFAT sensitivity analysis, we were able to quantify how small changes in key parameters affected our results. The main focus of our study was to compare differences in the percentage of habitat predicted to remain suitable by the correlative and mechanistic models under future conditions, which overall were not very sensitive to changes in parameter values. However, the amount of predicted suitable area under current and future conditions was sensitive to changes in parameter values. For example, lowering the minimum activity temperature resulted in a large decrease in suitable habitat for both current and future time periods. Intriguingly, even though this change increases the window of temperature in which salamanders could be surface-active, it results in a decrease in the annual energy budget (at temperatures below 5°C our model predicts inefficiency in food intake, resulting in a greater net expenditure of energy). Increasing the maximum activity temperature increases foraging time and prey intake (particularly at lower elevations), but it also increases energy consumption because of the greater metabolic cost of activity at higher temperatures. The greater cost of foraging at warm temperatures is more pronounced in a future, warmer climate, which is why the percentage of loss goes up slightly with increasing the maximum foraging temperature, and the percentage of loss decreases with decreasing the maximum foraging temperature.

We restricted our sensitivity analysis to varying a single parameter at a time, focusing on parameters that we believe are most biologically relevant to predicting habitat suitability.

Using an OFAT approach, however, meant we were unable to quantify how simultaneously considering uncertainty in a wide-range of parameters influenced loss of habitat suitability. One possible shortcoming of this approach is that by accounting for uncertainty simultaneously across parameters the differences in habitat loss predicted by the mechanistic approach compared to the correlative approach could become less pronounced (Fordham et al. 2016). Nevertheless, recent studies on the ecophysiology of montane plethodontids suggest that our results are likely to be robust. For example, montane plethodontids exhibit metabolic depression in response to warm temperatures (Markle and Kozak 2018), especially at the range edge (Bernardo and Spotila 2006), which could actually interact with the temperature window for surface activity by reducing metabolic costs, thereby resulting in even less habitat loss in the future than we predict here. Similarly, intraspecific clinal variation and plasticity in water loss rates along elevational gradients seemingly allows at least some montane plethodontids to persist in warmer and drier conditions at the range edge (Riddell et al. 2018). Such plasticity could also interact with the temperature window for surface activity and allow salamanders to remain surface-active for longer periods of time before having to retreat because of dehydration stress at higher temperatures.

Future work on this system will benefit from global sensitivity analyses that quantify how simultaneously considering variation around multiple parameters influences the predictions of the mechanistic model (Fordham et al. 2016, Peterman and Gade 2017). This type of global sensitivity analysis could also identify which parameters are most important to the outcome of our model and be used to guide experimental studies to generate more precise, species-specific parameter estimates.

Environmental data

In addition to the niche modeling approach, the environmental input data played a large role in the predicted future distributions. Prior studies have found that GCMs induce as much variation in model results as RCPs (Wright et al. 2014), but without following a predictable outcome. As others have previously found (McKenney et al. 2011, Tuanmu 2012, Thorne et al. 2013, Wright et al. 2014, Goberville et al. 2015), the choice of GCM had over a 10-fold impact on predicted range loss. Variation between predictions using different GCMs was more pronounced when employing the mechanistic model, which is likely explained by the finer temporal scale of environmental data necessary for the mechanistic model. For each species, there was at least one GCM-mechanistic model combination that resulted in almost a complete loss of suitable habitat; some GCMs predict substantially more warming in the southern Appalachians. The degree of warming predicted by these circulation models is most likely intolerable for small montane *Plethodon*. However, with the mechanistic models there were many more instances with substantial range retention in comparison to the correlative niche model for the same GCM.

Some GCMs consistently predicted more future suitable habitat (INM-CM4 and MRI-CGCM3), while others consistently predicted more future loss across species and niche modeling approach (HadGEM2-ES and GFDL-CM3). Employing a multi-GCM ensemble averaged forecast is a potential method for creating predictions that are likely to perform better than employing a single or few GCMs (Fordham et al. 2011), particularly for small regions such as our study region. These ensemble forecasts are already available on multiple platforms (see Wang et al. 2016 used in this study, or Fordham et al. 2012 for a more flexible framework). However, there is still much uncertainty in how the climate will change in the coming decades; it is important to capture and represent the range of predicted outcomes to incorporate climate uncertainty in conservation planning, especially when using global climate models to predict regional environmental change.

Improving mechanistic models

Our goal was to employ a simple mechanistic model to forecast suitable habitat now and in the future. Given the availability of high-resolution ground-temperature data (Fridley 2009), and that elevational variation in temperature is strongly associated with the lower elevational range limit for *P. jordani* (Gifford and Kozak 2012, Lyons et al. 2016), we focused on this aspect of climate. However, we note that precipitation also influences surface-activity patterns (Connette and Semlitsch 2015), and likely shapes the range limits of montane *Plethodon* species. Thus, our model may oversimplify the role of soil moisture and time since precipitation on surface activity (Peterman and Gade 2017). Recent work also suggests that there is room to improve parameters related to water-loss rate, which has been shown to be more plastic than previously assumed (Riddell and Sears 2015, Riddell et al. 2016). Finally, some of the parameters used in our model are based on related species and simplified biological phenomena; these are areas in which our mechanistic model could be improved with experimental species-specific information. Nevertheless, our mechanistic model performed as well as the correlative model at predicting current distributions. The flexibility of mechanistic models means they can be modified to model more complex biological processes as more species-specific data and new environmental layers become available.

Conclusion

In this study, we have demonstrated how taking a mechanistic approach can alter the projected range dynamics of narrow-ranging montane endemics. We found that a mechanistic approach that incorporates species-specific biology predicts a less dire future for mountaintop salamanders in the southern Appalachians, especially for the most narrow ranging montane endemic we studied, *P. jordani*. In our study, future climates appear to present a challenge for correlative niche modeling because this approach does not identify subtle temporal shifts

in climate that affect species activity times. We recognize that for many species building mechanistic models may not be feasible because of the whole-system understanding that is required. A hybrid approach using environmental layers built on a mechanistic understanding of species-specific biology that does not rely on correlations between simple climate variables and species distributions provides a promising avenue for forecasting future distributions (Bateman et al. 2012, Mathewson et al. 2016, Methorst et al. 2017).

Species must be managed as dynamic entities in the context of climate change. Knowledge of where climatically suitable habitats will be retained and lost, along with the size of those habitats, will be critical to the development of conservation plans that can preserve narrow-ranging montane endemics and the population processes that sustain them. The differences in predicted range loss between a correlative and a mechanistic model that we report here suggest a critical need to incorporate mechanisms into forecasts of species range dynamics, especially for montane salamanders.

Data availability statement

Data are available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.qz612jm9b>> (Lyons and Kozak 2019).

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Supplementary material (available online as Appendix ecog-04282 at <www.ecography.org/appendix/ecog-04282>). Appendix 1–2.