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Research

Integrating physiology into correlative models can alter projections of habitat suitability under climate change for a threatened amphibian

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Rapid global change has increased interest in developing ways to identify suitable refugia for species of conservation concern. Correlative and mechanistic species distribution models (SDMs) represent two approaches to generate spatially-explicit estimates of climate vulnerability. Correlative SDMs generate distributions using statistical associations between environmental variables and species presence data. In contrast, mechanistic SDMs use physiological traits and tolerances to identify areas that meet the conditions required for growth, survival and reproduction. Correlative approaches assume modeled environmental variables influence species distributions directly or indirectly; however, the mechanisms underlying these associations are rarely verified empirically. We compared habitat suitability predictions between a correlative-only SDM, a mechanistic SDM and a correlative framework that incorporated mechanistic layers ('hybrid models'). Our comparison focused on green salamanders *Aneides aeneus*, a priority amphibian threatened by climate change throughout their disjunct range. We developed mechanistic SDMs using experiments to measure the thermal sensitivity of resistance to water loss (r_i) and metabolism. Under current climate conditions, correlative-only, hybrid and mechanistic SDMs predicted similar overlap in habitat suitability; however, mechanistic SDMs predicted habitat suitability to extend into regions without green salamanders but known to harbor many lungless salamanders. Under future warming scenarios, habitat suitability depended on climate scenario and SDM type. Correlative and hybrid models predicted a 42% reduction or 260% increase in area considered to be suitable depending on the climate scenario. In mechanistic SDMs, energetically suitable habitat declined with both climate scenarios and was driven by the thermal sensitivity of r_i. Our study indicates that correlative-only and hybrid approaches produce similar predictions of habitat suitability; however, discrepancies can arise for species that do not occupy their entire fundamental niche, which may hold consequences of conservation planning of threatened species.

Keywords: activity, *Aneides aeneus*, climate change, MaxEnt, mechanism, resistance to water loss

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Introduction

Climate change has been implicated in driving the five documented mass extinction events (Erwin 2001, Wake and Vredenburg 2008) and is currently associated with a potential sixth mass extinction event that is targeting amphibians (Pounds et al. 2006). Warming temperatures are linked to several threats that amphibians face, including more favorable conditions for emerging infectious diseases (Gray et al. 2009, Vasquez et al. 2009, Martel et al. 2013) and reductions in habitat suitability as climate warming and drying increase the likelihood of overheating and desiccation (Lertzman-Lepofsky et al. 2020). These threats are likely to cause further species extinctions due to the loss or rapid shifts of suitable habitat for herpetofauna with limited dispersal capacities (Araújo et al. 2006). Developing methods for ranking species' vulnerability to climate change is important for making more informed conservation and management decisions (Barrett et al. 2014).

A wide range of tools are available to forecast species response to climate change (Füssel and Klein 2006, Butchart et al. 2010, Sutton et al. 2015). Among the available tools, species distribution models (SDMs) provide spatially explicit predictions of vulnerability and resilience. While the maps produced from such models offer conservation practitioners guidance on where to exert efforts, there are important caveats associated with many of the distribution modeling approaches (Buckley et al. 2010, Barrett et al. 2014, Roach et al. 2017). Specifically, correlative models, which examine the association between climatic variables and species locality data (Kearney et al. 2010, Barrett et al. 2014), assume some underlying relationship between environmental conditions and the geographic distribution of the animal. Importantly, traits relevant to an organism's performance in nature are not explicitly incorporated. As a result, correlative models may poorly project habitat suitability in environments outside the range of the training data or in non-analogous climates (Fitzpatrick and Hargrove 2009, Elith et al. 2010, Milanovich et al. 2010). Mechanistic SDMs offer an alternative approach to distribution modeling. These models estimate animal performance (e.g. active foraging time or reproduction) across habitats using empirically-derived relationships between animal physiology and environmental conditions. Once these relationships are known, the distribution of an organism can be mapped onto a range of environmental conditions (Mathewson et al. 2017, Riddell et al. 2017). Despite the different philosophies between correlative and mechanistic models, they are not incompatible.

Research suggests that incorporating mechanism into correlative models can enhance predictions of climatically suitable habitat for a species (Mathewson et al. 2017). Specifically, correlative models can make use of both known species presences across the landscape and estimates of environmentally-sensitive performance. However, very few models that project the ecological impact of climate change consider any physiological, behavioral or life history mechanisms (Urban et al. 2016). The rarity of these models (relative to correlative approaches) may result from the expertise and data required to build them (i.e. experimentally-derived estimates of animal physiology under a range of environmental conditions). Nevertheless, mechanistic approaches are becoming more popular – especially for ectotherms (Buckley 2008, Buckley et al. 2010, Kolbe et al. 2010, Riddell and Sears 2015, 2020, Riddell et al. 2017). Hybrid models that inform correlative models with physiological mechanism have begun to address the ecological impact of climate change (Mathewson et al. 2017, Enriquez-Urzelai et al. 2019, Rodríguez et al. 2019), yet we still lack an understanding of how mechanistic variables contribute to hybrid models relative to climatic variables.

We used green salamanders, *Aneides aeneus* (Cope and Packard 1881), to assess the influence of adding physiological mechanisms to correlative SDMs. Green salamanders are a near threatened species that have experienced population declines in the Blue Ridge Escarpment (BRE) portion of their range (North Carolina, South Carolina and Georgia) beginning in the 1970s (Snyder 1983, Corser 2001). In addition to habitat loss, over-collection and disease, climate change has also been implicated as a threat to this species due to the direct effects of warmer, drier environments limiting their ability to forage and find mates (Corser 2001, Riddell et al. 2018). Several correlative models have been applied to green salamanders in all or parts of their range (Lipps 2005, Barrett et al. 2014, Hardman 2014). These correlative models evaluated habitat associations and helped researchers document new sites in states where green salamanders are vulnerable (Snyder 1983, Brodman 2004). Additionally, the mid-century and end-of-century predictions of habitat suitability from these models are likely to aid in conservation-based decisions.

Currently, we have little understanding of whether physiological constraints influence the geographic distribution of green salamanders, though several studies have shed light on their physiology. Green salamanders can withstand desiccating conditions longer than sympatric species of similar size (Gordon 1952). Further, multiple studies have demonstrated that green salamanders may prefer warmer, drier slopes of mountain ranges over more mesic slopes (Bruce 1968, Newman et al. 2018, Williams et al. 2020), suggesting that green salamanders might have evolved physiological adaptations for resisting the loss of water. For this study, we modeled the geographic range of green salamanders using the program MaxEnt (maximum entropy), a method for modeling species distributions using presence-only data (Phillips et al. 2006) and recently developed approaches in mechanistic species distribution modeling for terrestrial salamanders (Riddell et al. 2018). We modeled suitable climatic habitat for green salamanders throughout their disjunct range using both approaches, and then developed hybrid models by integrating mechanistic layers (e.g. durations of activity, energetics) into MaxEnt. In addition, we evaluated the sensitivity of hybrid models by running mechanistic models with average and thermally sensitive water loss rates measured from laboratory experiments. By combining these two methods,

our study offers a statistical framework to determine whether mechanistic layers are important predictors of salamander distributions, particularly when jointly modeled alongside climatic layers. In doing so, our approach develops a robust, quantitative approach informed by multiple perspectives for predicting the ecological impact of climate change on species of conservation concern.

Material and methods

Salamander care and collection

We conducted experiments on green salamanders to evaluate the thermal sensitivity of water loss rates and metabolic rates. We collected 2–6 green salamanders (avoiding nesting and gravid females as well as juveniles) from four sites in South Carolina (n = 19) at night from April to May 2017. Sites were located in Table Rock State Park and Nine Times Forest (precise locality withheld due to conservation concerns). We selected these sites because previous surveys suggested animal densities were high enough to provide sufficient captures for our trials without compromising the population. We transported salamanders in Ziploc® bags (with moist leaf litter) to Clemson University in Clemson, South Carolina and placed them in an incubator (15°C). Salamanders were acclimated in individual plastic containers (15.6 × 15.6 × 5.7 cm) without food on a wet paper towel for five days to ensure that physiological measurements occurred during a post-absorptive state (Riddell et al. 2018). As part of our animal care protocol, we estimated a baseline mass (to the nearest 0.001 g) at the beginning of the experiment to ensure that salamanders did not lose more than 10% of their baseline mass while in the laboratory. Salamanders that did not maintain a baseline mass were excluded from the experiment (below). After the acclimation period, we measured water loss rates and metabolic rates using a flow through system. All experiments were approved by the Institute for Animal Care and Use Committee at Clemson Univ. (AUP 2016-035), and approval for collections and experimentation were granted by the South Carolina State Park Service and the South Carolina Dept of Natural Resources. After the experimental trials, all collected animals were returned to capture sites.

Flow through system and physiological measurements

We measured the thermal sensitivity of water loss rates and metabolic rates using a flow through system. Our system continuously exposed salamanders to combinations of temperature and humidity while simultaneously measuring their physiology. We controlled the environmental temperature using a programmable incubator (Percival VL36). The flow through system pumped air beginning with a sub-sampler (SS-4; Sable Systems International (SSI)) to push air through a dewpoint generator (DG-4; SSI) controlling the vapor pressure deficit (VPD; the difference between the amount of moisture in the air and the amount of moisture the air can hold). A flow manifold (MF-8; SSI) was then used to divide the airstream into the individual cylindrical acrylic chambers and control flow rate (150 ml min^{-1}). The chambers (16 × 3.5 cm; volume ~ 153 ml) contained an individual green salamander placed on hardwire mesh to expose its surface to the airstream (simulating posture during activity). We cycled air between each chamber three times every ten minutes using a multiplexer (M8; SSI). The airstream was then sampled using a vapor analyzer (RH-300; SSI) which measured the change in water vapor pressure (kPa). Then, the air was scrubbed of water vapor and carbon dioxide using Drierite (W. A. Hammond Drierite Co. Ltd.) and soda lime, respectively. After scrubbing, we measured the partial pressure of oxygen using a dual channel, differential oxygen analyzer (Oxzilla SSI).

We moved the individual plastic containers to an environmental chamber set to a regulated experimental temperature (12, 18, 24°C) two hours prior to measuring water loss rates. These temperatures were chosen to reflect the temperatures that green salamanders would experience in nature during their active season (April–October; Gordon 1952). We calculated skin resistance to water loss of green salamanders using a combination of one of the three treatment temperatures (12, 18, 24°C) and a single VPD (0.5 kPA). This VPD was chosen because it is ecologically relevant for terrestrial salamanders (Riddell and Sears 2015, Riddell et al. 2017). We randomized the temperature treatments with respect to night of experiment to avoid acclimation effects. Physiological traits were measured between 19:00 and 01:00 hours to reduce influence of circadian rhythm of metabolism. Salamanders were allowed to acclimate to the flow through chambers for 30 min to adjust to their new surroundings. To ensure animals were resting, we did not include any measurements in our analyses with spikes or irregularities in vapor pressure that would be indicative of activity. We measured water loss rates and metabolic rates separately because metabolic rates were too low to detect using the flow rates from the water loss measurements.

Thermal sensitivity of metabolism

Energy balance for an ectotherm depends upon the temperatures that the organism experiences. We used the same flow through system in the laboratory to measure volume of oxygen consumption (VO_2) to estimate energy expenditure for the mechanistic distribution models. We reduced the flow rate to 50 ml min^{-1} allowing for increased resolution of the oxygen depletion curves during cooler temperature treatments when salamanders exhibit very low metabolic rates. We held VPD (0.5 kPa or 64–83% relative humidity) constant across temperature treatments. Using Oxzilla (SSI), we measured partial pressure of oxygen to measure volume of oxygen consumption at four experimental temperatures (6, 12, 18, 24°C) on different nights. We measured volume of oxygen consumption at a fourth, lower temperature treatment (6°C) that was not used in the water loss trials due to limitations with the equipment. We randomized the order of each experimental temperature to avoid acclimation

effects. We excluded two individuals from the metabolic trials because they failed to return to baseline mass after the water loss experiment. Partial pressures of gases were converted into meaningful physiological values using a series of established calculations (see following section).

Calculations for skin resistance to water loss and metabolic rate

We measured skin resistance to water loss using a suite of calculations presented in Riddell et al. (2017). First, we converted the water vapor pressure (e; kPa) to water vapor density (p_v; g ml^{-1}) using the following equation (eq. 1):

$$\rho_v = \frac{e}{\left(T \times R_v\right)} \quad (1)$$

where T is temperature in Kelvin (K) and R_v is the gas constant for water vapor (461.5 J K^{-1} kg^{-1}). We then converted the vapor density to evaporative water loss (EWL; g s^{-1}) using eq. 2:

$$\mathrm{EWL} = \rho_v \times \mathrm{FR} \times \frac{1}{60} \quad (2)$$

where FR is the flow rate of the air stream (ml min^{-1}) and 1/60 is a conversion factor to convert FR to ml s^{-1}. Next, we calculated cutaneous water loss (CWL; g s^{-1} cm^{-2}) by dividing the rate of water loss by the surface area of each salamander. The surface area (cm^2) was estimated by an empirically derived formula for the family Plethodontidae, where surface area = 8.42 × mass (g)$^{0.694}$ (Whitford and Hutchison 1967). We used CWL to calculate total resistance to water loss (r_T, s cm^{-1}) as follows (eq. 3):

$$r_T = \frac{\rho}{\mathrm{CWL}} \quad (3)$$

where ρ is the vapor density gradient (g cm^{-3}).

We then estimated the resistance of boundary layer assuming free convection conditions using a series of calculations in Riddell et al. (2017). Boundary layer resistance (r_b) is required to calculate skin resistance to water loss (r_i), and once we estimated r_b, we calculated skin resistance using eq. 4:

$$r_i = r_T - r_b \quad (4)$$

where r_T is the total resistance (s cm^{-1}) and r_b is the boundary layer resistance (s cm^{-1}). We then estimated volume of oxygen consumption (VO_2; µl h^{-1}) using eq. 5:

$$\mathrm{VO_2} = \mathrm{FR}_e\left(\mathrm{F_iO_2} - \mathrm{F''_eO_2}\right) / \left(1 - \mathrm{F_iO_2}\right) \quad (5)$$

where FR_e is the excurrent flow rate (ml), $\mathrm{F_iO_2}$ is the incurrent fractional concentration of oxygen (20.95%), and $\mathrm{F''_eO_2}$ is the excurrent fractional concentration of oxygen (Lighton 2008). We then integrated the thermal sensitivity of r_i and VO_2 into physiologically-structured species distribution models to estimate activity and energetics throughout the range of *A. aeneus*.

Estimation of environmental data for mechanistic species distribution model

Mechanistic models can predict activity, survival, growth and reproduction as a function of environmentally sensitive processes that influence energy and mass balance. Similar mechanistic SDMs have used *microclim* (Kearney et al. 2014) to estimate the relevant temperatures experienced by terrestrial salamanders; however, we used air temperatures from bioclimatic layers (Worldclim) for green salamanders (Fick and Hijmans 2017). Green salamanders are typically active at night on the surface of large boulders (Gordon 1952; see Supporting information for typical green salamander habitat); thus, the temperatures that they experience are likely closer to air temperature 1–2 m off the ground. Moreover, environmental temperatures near the surface are often very similar to air temperatures at night, especially in shaded habitats such as the southern Appalachians. To validate this assumption, we used *NicheMapR* (Kearney et al. 2014) to assess the relationship between air temperature and soil surface temperature. We used a randomly generated coordinate (35.23, −82.76) within the disjunct green salamander geographic range to model air and soil temperature assuming 90% shade on a typical loamy soil. We then assessed the correlation between air temperature and soil surface temperature at night (21:00–06:00) for each month of the year using the *micro_global* function in *NicheMapR*. The validation analysis indicates that air temperatures closely approximate soil surface temperatures at night with correlations near unity (Supporting information). To validate our assumptions in the field, we measured air temperatures every 40 min using iButtons (Maxim Integrated) encased in hardwire mesh containers placed on the leaf litter and the surface of a tree trunk roughly 1.5 m from the surface of the ground from 25 June 2016 to 9 October 2016. We collected 3412 measurements of temperature from the leaf litter and 1706 measurements from the tree trunk during nighttime hours (21:00–06:00). We then averaged the temperatures for each hour of the night and assessed the correlation between leaf litter temperature and tree trunk temperature as proxies of near soil temperature and air temperature, respectively. Consistent with the *NicheMapR* analysis, we found a close association between the two temperatures with correlations near unity (Supporting information), suggesting air temperatures provide a reasonable estimate of temperature for green salamanders. We caution, however, that this assumption will not be valid for many other organisms and is only reasonable given the unique behavior and natural history of our focal species. With the Worldclim layers, we estimated hourly variation in temperature from monthly minimum and maximum temperatures using equations 2.2 and 2.3 described in Campbell

and Norman (1998). Similar to previous mechanistic models, we estimated vapor pressure deficits under the established pattern that minimum nightly temperatures approach the dew point temperature (Riddell et al. 2017).

Mechanistic species distribution model

Our mechanistic species distribution model predicts activity and energy balance based upon thermal sensitivities of traits and the typical activity patterns of green salamanders. We used a custom script developed in Python (ver. 3.8.3), which is available online (<https://github.com/ecophysiology/salascape>). We simulated nightly activity for each location based upon the average hourly air temperature and humidity data over the entire year (Supporting information). Salamander activity was restricted to nighttime conditions (21:00–06:00 h), and activity only occurred when air temperatures were suitable (5–25°C) (as described in Spotila 1972). While active, we estimated body temperatures by accounting for the effect of evaporative cooling using humid operative temperatures (T_{eh}; Campbell and Norman 1998). We estimated T_{eh} using eq. 6:

$$T_{eh} = T_a + \frac{\gamma *}{s + \gamma *}\left(\frac{R_{\text{abs}} - \varepsilon_s \sigma T_a^4}{c_p g_{Hr}} - \frac{D}{\gamma * p_a}\right) \quad (6)$$

where T_a is ambient temperature, s is the slope of saturation mole fraction function, R_{abs} is the absorbed short- and long-wave radiation, γ^* is the apparent psychrometer constant, ε_s is the emissivity of the salamander (0.96), sigma is the Stefan–Boltzmann constant, c_p is the specific heat of air at constant pressure, g_{Hr} is the sum of boundary layer and radiative conductance, D is the vapor pressure deficit of the air and p_a is the atmospheric air pressure (Campbell and Norman 1998). For R_{abs}, we included long-wave radiation from the sky and ground (eq. 10.7 in Campbell and Norman (1998)), assuming the sky and ground were roughly the same temperature (see Supporting information for validation). We assumed emissivities of 1.0 for both the sky and the ground due to the near blackbody conditions (Campbell and Norman 1998). Direct and diffuse short-wave radiation were excluded because salamanders were only active at night. By assuming T_{eh} is equivalent to body temperature, we assume steady state thermal conditions, which is reasonable given the small body size of these salamanders and the limited temperature fluctuations that occur at night. In the field, we assumed the boundary layer resistance was a combination of free and forced convection at 0.1 m s^{-1} (Campbell and Norman 1998, Bird et al. 2002). We also compared estimates of body temperature from our simulations to estimates produced by *NicheMapR* for an ectotherm with a high r_i (1000 s cm^{-1}) and low r_i (6 s cm^{-1}) at a cool, wet site in the North Carolina mountains (35.00, −82.70) and a warm, dry site in the Mojave Desert (35.33, −115.308). Comparisons were nearly identical (Supporting information), with the exception of an ectotherm with very low r_i in a hot, dry environment in which we found up to a 20% difference at the hottest temperatures. Though animals with exceptionally low resistance in hot, arid regions are rare, the results suggest that calculations of T_{eh} might overestimate body temperatures when evaporative water loss greatly exceeds metabolic heat production (Campbell and Norman 1998). We then used body temperature to estimate energetic costs from volume of oxygen consumption while active for every hour. We calculated energetic costs based upon the thermal sensitivity of VO_2 measured from the laboratory experiments described above using the following equation (eq. 7):

$$\log \text{VO}_2 = \left(0.046 \times T\right) + \left(0.59 \times \log\left(\text{mass}\right)\right) + 0.86 \quad (7)$$

where VO_2 is volume of oxygen consumption (µl min^{-1}), T is body temperature (°C) and mass refers to the mass (g) of the green salamander. We then assumed a conversion factor of 20.1 J ml^{-1} to convert VO_2 to standardized units of energy. Energy intake was estimated from the thermal sensitivity of energy assimilation recently recorded in plethodontids (Clay and Gifford 2017). We estimated energy intake using eq. 8:

$$E_a = 0.003835 + \left(-0.002522\right) \times T + 0.0009089 \times T^2 + \left(-2.527 \times 10^{-5}\right) \times T^3 \quad (8)$$

where E_a is energy assimilated from prey (kJ g^{-1} day^{-1}), and T is body temperature (°C). The rate of energy assimilation was divided by 24 to estimate hourly energy assimilation at the given T_{eh}. Rates of energy consumption and assimilation are then summed together to estimate energy balance for each hour of the day. The model then tracks energy balance throughout the entire year to calculate annual energy balance for each geographic location. By using energy assimilation rates, the mechanistic model assumes that salamanders have unlimited access to prey – an assumption supported by both empirical and theoretical studies. Lungless salamanders are not limited by prey availability in nature (Hairston 1981), but instead by prevailing thermal and hydric conditions (Fraser 1976). Moreover, conclusions from mechanistic models are robust to variation in prey availability (Buckley and Roughgarden 2005, 2006), even for lungless salamanders (Gifford and Kozak 2012). Taken together, the assumption of high prey availability seems reasonable; however, our conclusions on future habitat suitability are likely to underestimate climate vulnerability in the event of future declines of insect prey. The model also included dietary water from prey based upon the average water content and energy content of typical insects (Riddell et al. 2017).

Salamanders frequently retreat to their microhabitat to avoid poor microclimatic conditions (Fraser 1976). While inactive, we assumed that salamanders retreated to 30 cm below the surface of granite boulders. We assumed this depth because it represents the minimum depth at which below-ground temperatures approach average air temperature for a given month (Campbell and Norman 1998). We estimated

temperatures within the granite using equation 2.4 from Campbell and Norman, and we used a damping depth of 17.0 based upon the typical properties of granite (Cho et al. 2009). We then use this temperature to approximate body temperatures that salamanders experience while inactive inside a granite boulder. By doing so, we assume that air temperatures approximate the surface temperature of the granite boulders, which is reasonable given that the boulders are found in heavily forested areas with very low amounts of direct solar radiation (Supporting information) (Shoo et al. 2010). We assumed that salamanders were not able to forage during times of inactivity. Salamanders were assumed to cease activity upon reaching their dehydration threshold, experiencing air temperatures beyond their preferred range, or during the daytime. We also incorporated variation using sensitivity analyses for parameter values in the mechanistic model. For instance, we selected a range of dehydration thresholds (5.0, 7.5 and 10%) at which salamanders ceased activity based upon empirically-observed values for plethodontids (Feder and Londos 1984). We also ran simulations across various body sizes reflected in our physiological experiments (2, 3, 4 g), humidity scenarios (+25% and −25% value of VPD), and skin resistance to water loss.

To determine the sensitivity of hybrid models to important physiological parameters, we ran simulations assuming an average r_i (6.0 s cm^{-1}) and a dynamic estimate of r_i, which was based on the thermal sensitivity of r_i measured from the experiments. For the average simulations, we used the average r_i between the 12 and 18°C treatments to assess the importance of ignoring physiological responses to warm temperatures. For the dynamic simulations, we used a quadratic function ($R^2 = 0.66$) to estimate r_i when body temperature fell between 12 and 24°C, which varied between 5.7 s cm^{-1} at 12°C to 11.2 s cm^{-1} at 24°C. We assumed r_i remained at 5.7 s cm^{-1} at body temperatures below 12°C and 11.19 s cm^{-1} above 24°C. We compared these simulations because mechanistic models are often parameterized with static values for resistance to water loss, and to our knowledge, studies have yet to incorporate the thermal sensitivity of resistance to water loss in mechanistic models. We ran our simulations for each combination of body size, dehydration threshold, humidity scenario and skin resistance to water loss to estimate activity budgets and energy balance throughout the year. We averaged estimates of activity and energy balance across all simulations that varied body size, dehydration threshold and humidity scenario for a particular r_i scenario (average and dynamic) to generate activity and energy balance layers to integrate into the statistical framework. We also predicted activity and energy balance using the same climate warming scenarios as the correlative approach (described below) to evaluate the sensitivity of hybrid models to climate scenario projections.

Correlative species distribution model

We used MaxEnt to assess correlations between climatic factors and presence data because it performed as well or better than other tools during a comprehensive model evaluation (Elith et al. 2006). It is also commonly used to generate distribution models of climate vulnerability (Pearson et al. 2007, Loarie et al. 2008, Puschendorf et al. 2009, Bradley et al. 2010). We focused on the disjunct population of green salamanders (North Carolina, South Carolina and Eastern Georgia), excluding the recently described Hickory Nut Gorge green salamander *Aneides caryaensis* (Patton et al. 2019), due to evidence of their recent population declines (Snyder 1983, Corser 2001). Genetic studies have revealed that this disjunct population is an evolutionarily significant unit from the mainland population (Patton et al. 2019). To create the spatial boundaries of our model, we used minimum bounding geometry in ArcGIS based on known locality points for the species. We created a 25-km buffer around this disjunct range. We extrapolated data on green salamander movement and predicted that green salamanders could potentially disperse ~15 km in 33 years if projecting to 2050 (Gordon 1952, Canterbury 1991; Supporting information). The remaining 10 km accounts for the possibility that the current range extends beyond currently cataloged localities.

We collected green salamander presence data from the South Carolina Dept of Natural Resources, Georgia Dept of Natural Resources, North Carolina Wildlife Resources Commission and publicly-accessible online databases (Price and Dorcas 2007, Cicero et al. 2010, USGS 2013). We also gathered new sites in South Carolina from a recent extensive habitat association survey (Newman et al. 2018). All points were uploaded into ArcMap ver. 10.3. We reduced clusters of points (and thus minimized potential sampling biases such as repeated sampling from easily accessible sites) by using a random point generator in ArcMap. Because the average north–south distance of rock outcrop of sites in South Carolina was 31 m (Newman et al. 2018), we randomly removed points in clusters that were less than 31 m apart.

We selected seven bioclimatic variables (BIO 1–2, 4, 8–9, 12, 15; Table 1), from a list of 19 (Hijmans et al. 2005) based on low pairwise correlations between variables. Though variables BIO1 and BIO15 exhibit a high pairwise correlation value (0.74), we included both of these variables to include an additional dimension of precipitation in the analysis. This pairwise comparison approach was first used by Rissler and Apodaca (2007) for a west coast congener species, *Aneides flavipunctatus* and has since been used several times to generate distribution models for amphibians (Milanovich et al. 2010, Barrett et al. 2014, Sutton et al. 2015). WorldClim derives these bioclimatic variables from a 30-year (1960–1990) dataset of monthly averages compiled of temperature and rainfall data at a spatial resolution of ~1 km^2 (Hijmans et al. 2005). Elevation was excluded because it had a high pairwise correlation with several bioclimatic variables. We intersected these climatic variables with both green salamander presence points and background points in ArcMap (ArcGIS ver. 10.3.1, ESRI). We generated background points by randomly placing ~2000 herpetofaunal presence points (*Plethodon yonhalosse*, *P. teyahalee*, *P. metcalfi*, *P. jordani*, *Terrapene carolina*, *Chrysemy picta*, *Pantherophis obsoletus*, *Diadophis punctatus*

Table 1. Predictor variables used in MaxEnt models for green salamander distribution models including bioclimatic variables (<www.worldclim.org/bioclim>; accessed in 2017) and mechanistic layers.

Variable	Definition
BIO1	Annual mean temperature
BIO2	Mean diurnal range (mean of monthly [max temp–min temp])
BIO4	Temperature seasonality (standard deviation × 100)
BIO8	Mean temperature of wettest quarter
BIO9	Mean temperature of driest quarter
BIO12	Annual precipitation
BIO15	Precipitation seasonality (coefficient of variation)
Activity	Annual average activity before an animal retreats to its microhabitat
Energy balance	The annual energetic expenditure

and *Storeria dekayi*) collectively distributed through the entire buffered disjunct range of the green salamander (Price and Dorcas 2007, Cicero et al. 2010, USGS 2013).

We used two different global climate models (GCM), with one representative concentration pathway (RCP) each. We downloaded two widely used GCMs from WorldClim: HadGEM2-CC (Hadley) and CCSM4. Model selection was based on hindcast accuracy in the northern hemisphere (Overland et al. 2011) and availability of projected data of the RCP 8.5 for 2050. We included two GCMs as the Hadley GCM tends to predict wetter future macroenvironmental conditions while the CCSM4 GCM tends to predict drier future macroenvironmental conditions (CIESIN 2000). We included the RCP 8.5 trajectory to provide a perspective representing rapid increase in greenhouse gas emission or the 'business-as-usual' climate scenario (Schwalm et al. 2020). MaxEnt produces species distribution models with probability of presence (ranging from 0 to 1 representing low to high habitat suitability). We used two thresholds (strict and moderate) to generate distributional range shifts in projected suitable habitat within the disjunct range of green salamanders. We used the fixed cumulative value 10 (F10; a moderate threshold resulting in 10% omission of training data), and the equal training sensitivity and specificity (ETSS; a relatively more restrictive threshold that balances the probability of missing suitable sites with the probability of assigning suitability to a site where the species is absent). Using default settings in MaxEnt can result in overly complex models (Moreno-Amat et al. 2015), and so we ran models using the linear and quadratic thresholds in MaxEnt based on suggestions from Merow et al. (2013).

Statistical analysis and model comparison

Statistical analyses for physiological experiments were conducted in R (ver. 4.0.2). We conducted linear mixed effects models for r_i and VO_2 separately using the *lme4* package. For each analysis, we included temperature as a factor and body mass as a covariate. For each model, we used the *lmerTest* package to calculate the predicted marginal means for each effect, using a Kenward–Roger approximation of the degrees of freedom (Kuznetsova et al. 2017). For analyses on VO_2, we log scaled body mass to meet the assumptions of homogeneity of variance. For each analysis, we also reported effect sizes (ω^2) for variables using the *sjstats* package (Olejnik and Algina 2003). For the habitat suitability models, we created a suite of climatic suitability models for green salamanders under current and future climatic conditions. Both correlative and mechanistic layers were used within an inductive, presence-only modeling approach MaxEnt (Phillips et al. 2006). Correlative-only models were built using only climatic variables, whereas our hybrid models contained climatic variables and two experimentally-derived mechanistic layers: activity and energy balance. Each of these mechanistic layers were also developed for average r_i and dynamic r_i to test the sensitivity of hybrid models. We compared the number of cells containing suitable habitat that were lost or gained after mechanistic predictors were added to the correlative model. In addition, we compared correlative only models to hybrid models that only contained mechanistic variables. Then we analyzed variable contribution among all models using two summary statistics, percent contribution and permutation importance. The percent contribution measures how much each variable contributed to the final model output, although it can change depending on the path the algorithm takes to arrive at a final solution (Phillips 2006). Permutation importance indicates the importance of a variable by randomly changing the value and measuring the change in training area under the curve. The results are normalized to percentages across all variables in the model (Phillips 2006). To assess model performance, we calculated the percentage of presence locations that fell within or outside suitable habitat under the current climate scenario predicted by the different modeling frameworks (correlative only, hybrid and overlap) within each model iteration (i.e. strict and moderate sensitivity thresholds, average and dynamic resistance to water loss assumptions). We also provided a minimum convex polygon with 2 km buffer to illustrate the general spatial distribution of presences for green salamanders. Lastly, we overlaid United States parks (including national, state, county, regional and local) with the climate model outputs of habitat suitability to determine the proportion of protected climate refugia in the green salamander's disjunct range under each climate scenario.

Results

Physiological experiments

Skin resistance to water loss varied significantly with temperature (Fig. 1a, $F = 112.9$, $p < 0.001$, $\omega^2 = 0.85$) and body mass (slope (β) $\pm$ standard error: 1.71 ± 0.32, $F = 35.2$, $p < 0.001$, $\omega^2 = 0.62$). Green salamanders exhibited the highest r_i under the warmest temperature treatment and the lowest r_i under the coolest temperature treatments (Fig. 1a). We also found that VO_2 increased with temperature (Fig. 1b, $F = 100.9$, $p < 0.001$, $\omega^2 = 0.85$) and body mass ($\beta = 123.2 \pm 22.9$, $F = 30.8$, $p < 0.001$, $\omega^2 = 0.62$).

Mechanistic-based habitat suitability

Under contemporary climate scenarios, the majority of green salamander presences were found in regions predicted to be in positive energy balance (69.2% with average r_i and 55.9% with dynamic r_i). Under future warming scenarios, fewer of these presence locations were associated with positive energy balance (Hadley: 2.4% with average r_i and 2.7% with dynamic r_i; CCSM4: 6.8% with average r_i and 6.8% with dynamic r_i). Estimates of energy balance under climate change scenarios were sensitive to using average or dynamic r_i (Fig. 2). In simulations with average r_i, the proportion of areas with positive energy balance (i.e. energetically suitable) declined by 6.2–9.3% under climate change scenarios, whereas in simulations with dynamic r_i, energetically suitable areas declined by 2.7–3.4%. Average energy balance (kJ) from models with dynamic r_i were also 18.5% higher relative to models with average r_i (Fig. 2). Overall, energy balance was 1.9–3.1-fold lower under climate change scenarios relative to contemporary climates. Under all climate change scenarios, mechanistic models predicted that regions associated with positive energy balance will shift northward into North Carolina (Fig. 2). Energy balance in South Carolina and Georgia was predicted to become primarily negative and thus energetically unsuitable (Fig. 2 and Supporting information).

Mechanistic models indicated that the duration of activity will decline under climate change scenarios, ranging from a 35.2 to 56.3% decline in activity (Supporting information). The greatest decline in activity occurred under the Hadley climate change scenarios (56.3% for average r_i and 35.2% for dynamic r_i), and activity declined by 47.6–50.4% under the CCSM scenario (Supporting information).

Hybrid species distribution models

Variable contribution analyses indicated the consistent importance of annual mean temperature, temperature seasonality and precipitation seasonality for predicting habitat suitability of green salamanders in all models. Upon adding mechanistic layers to correlative models, activity was also designated as a contributing variable (Table 2, Fig. 3). Response curves for annual mean temperature revealed an optimum for habitat suitability around 13°C (Fig. 3), and the predicted probability of suitable habitat increased with temperature seasonality and decreased with precipitation seasonality for all models (Fig. 3). The duration of activity also exhibited an optimum, with the greatest predicted probability of suitable habitat occurring at intermediate levels of activity (Fig. 3). Energy balance was not indicated as an important variable.

Under the current climate scenario, we found a high degree of overlap between models with and without mechanistic layers (Fig. 4). These patterns held whether hybrid models incorporated average or dynamic r_i (Fig. 4). Correlative-only models consistently predicted more suitable habitat than hybrid models, and this was especially apparent when the moderate threshold was applied to the dynamic r_i value. In the assessment of model performance, we found 74.5–92.3% of presence locations occurred within regions predicted to be suitable by both correlative and hybrid models (Supporting information), with more locations occurring in suitable

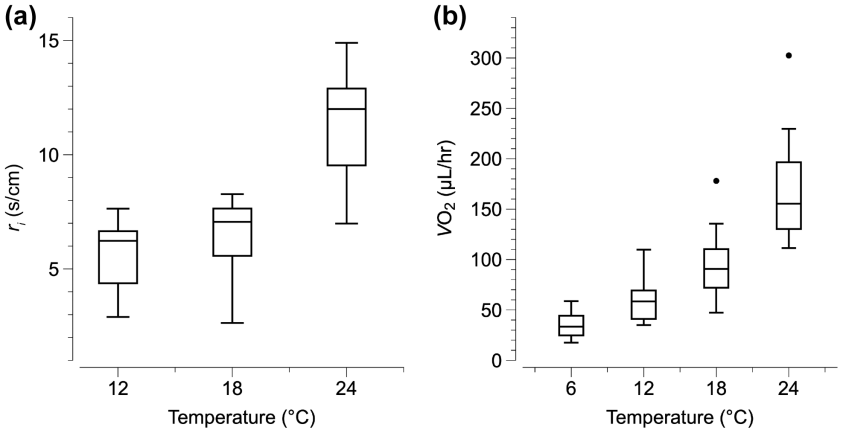

Figure 1. Thermal sensitivity of (a) skin resistance to water loss (r_i) and (b) volume of oxygen consumption (VO_2) for green salamanders. Experiments revealed that r_i increased substantially at the warmest temperature and VO_2 increased non-linearly with temperature. These experimental values were then used to parameterize the mechanistic species distribution model.

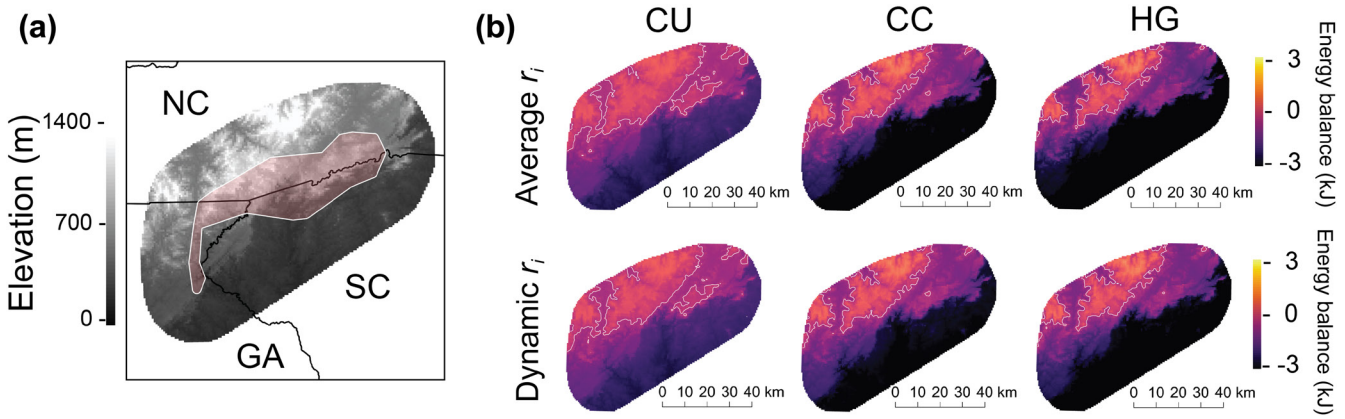

Figure 2. Projected energy balance from mechanistic species distribution model for green salamanders for three climatic scenarios. (a) The disjunct range of green salamanders located in North Carolina, South Carolina and Georgia, USA with minimum convex polygon (white outline) of green salamander presence locations. (b) Energy balance projections for current (CU), CCSM4 (CC) and Hadley (HG) GCMs with average r_i and thermally sensitive r_i (dynamic). White boundary surrounds regions with positive energy balance.

habitat in models that incorporated the thermal sensitivity of r_i with the moderate threshold.

Hybrid models that only incorporated mechanistic layers (i.e. no climate layers) exhibited a high degree of divergence from correlative-only models (Supporting information). In general, mechanism only models suggested suitable habitat was widespread, except for the most southern, low elevation regions. However, predictions were highly sensitive to the threshold (strict versus moderate), with the greatest divergence between models occurring with moderate thresholds. Under the moderate threshold, both correlative and mechanism-only models predicted 90.9% of presence locations to occur in suitable regions for average and dynamic r_i, respectively. Under the strict threshold, mechanism-only models predicted 63.9–68.2% of presence locations to occur in suitable regions for average and dynamic r_i, respectively, and correlative models predicted 75.7% of presence locations to occur in suitable regions for both average and dynamic r_i.

Habitat suitability under climate change

Correlative-only and hybrid models predicted similar patterns of habitat suitability across the disjunct range of green salamanders; however, there were some important differences.

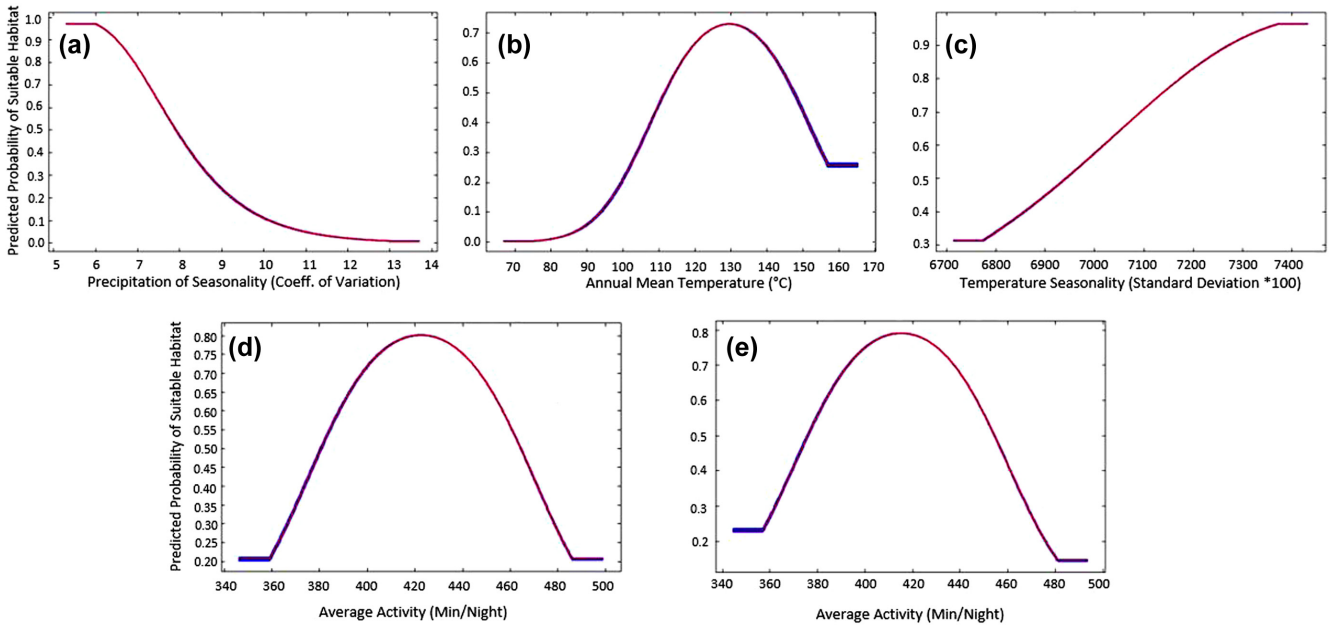

Figure 3. Response curves for contributing variables underlying green salamander distribution models. (a–e) Variables influencing models, regardless of scenario (a–c), included (a) mean annual temperature (BIO1), (b) temperature seasonality (BIO4) and (c) precipitation seasonality (BIO15). Variables influencing models when mechanistic layers were added (d–e), included (d) activity with average r_i and (e) activity with dynamic r_i.

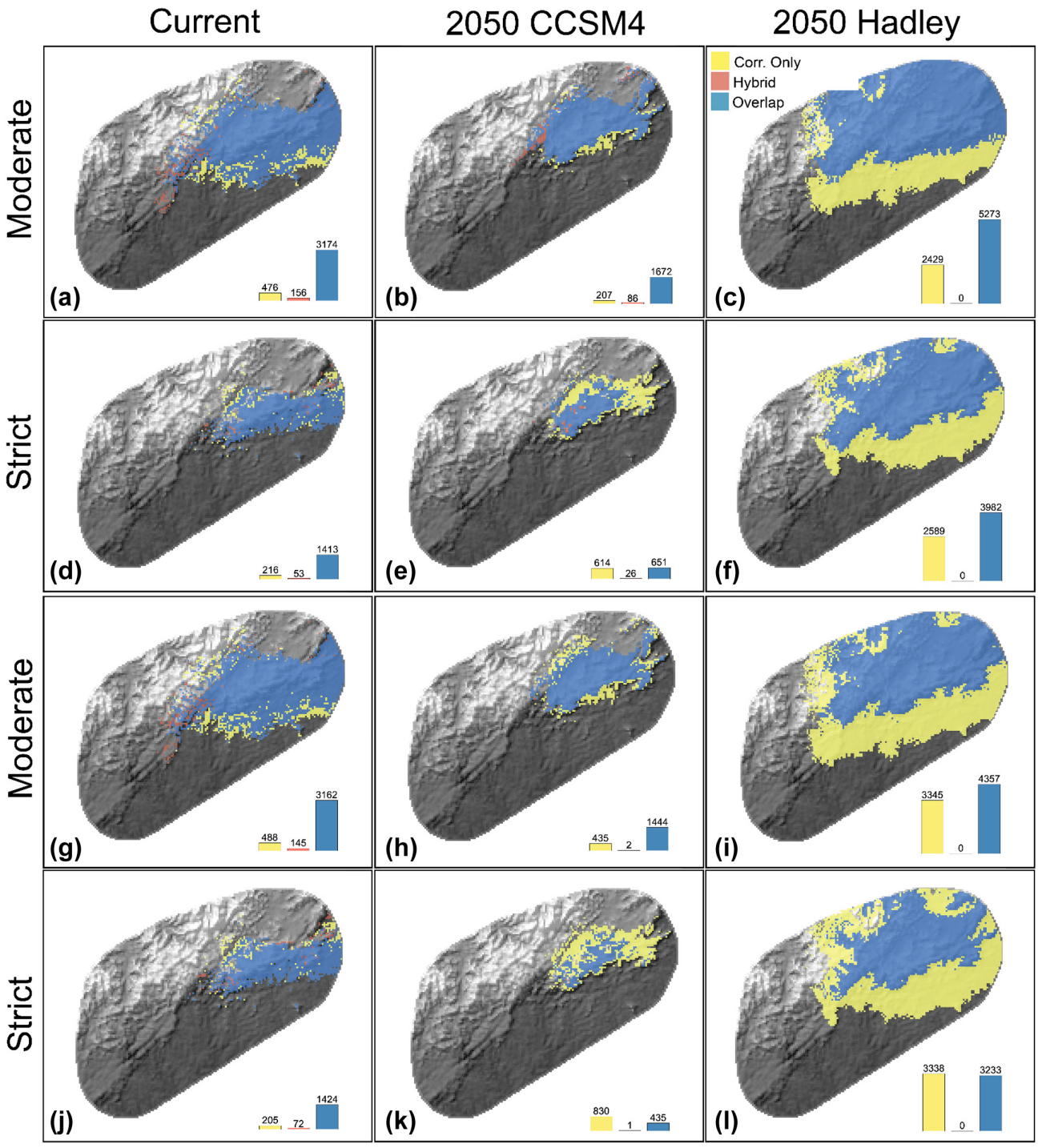

Figure 4. Projected suitable habitat from hybrid models for green salamanders throughout their disjunct range for current and 2050 climatic scenarios using average (panels a–f) and dynamic (panels g–l) skin resistance to water loss. Models for 2050 are derived from global circulation models (Hadley or CCSM4) representing Representative Concentration Pathway 8.5. Moderate (F10) or strict (ETSS) thresholds were applied to convert continuous predictions of suitability into binary categories of suitable/unsuitable. Modeled suitability is overlaid on a map of elevations (higher elevations appear as lighter shading). Bar graphs represent the number of cells of suitable habitat for green salamanders under each model type.

In the CCSM4 scenario, habitat suitability in hybrid models declined by 41.7% on average relative to contemporary climates (Fig. 4). In the Hadley climate change scenarios, however, habitat suitability increased by 2.6-fold relative to contemporary climates, and correlative-only models consistently extended habitat suitability further south relative to hybrid models (Fig. 4). In general, there were few suitable regions predicted by hybrid models alone, indicating hybrid

Table 2. Variable contributions within three Maxent models of habitat suitability for green salamanders in their disjunct range using percent contribution and permutation test. We used bioclimatic variables (Table 1) derived from two global circulation models (<www.worldclim.org/bioclim>) and experimentally-generated mechanistic variables. Percentages are in parentheses (see Methods for interpretation of the two approaches).

Model	Percent contribution	Permutation importance
Correlative	BIO15(58.1), BIO4(28.3)	BIO15(60.8), BIO1(31.8)
Hybrid [avg][1]	BIO15(55.3), BIO4(20.6), Activity(9.9)	BIO15(63.1), BIO1(24.8)
Hybrid [dyn][2]	BIO15(57.3), Activity(19.1), BIO4(11.5)	BIO15(63.1), BIO1(20.5)

[1]Average r_i used to predict mechanistic variables (duration of activity and annual energy balance).
[2]Dynamic r_i used to predict mechanistic variables (duration of activity and annual energy balance).

models were more conservative than correlative-only models. On average, models predicted 27.0% less suitable habitat under the strict threshold relative to the moderate. The hybrid models that only included mechanistic layers did not identify suitable habitat under the Hadley scenario and identified 0.3% of the region as suitable under the CCSM4 scenario.

Identification of conservation areas

By mapping suitable habitat with protected areas, we found that 78.3% of suitable habitat is unprotected under current scenarios and 58.7–76.3% of suitable habitat will remain unprotected under either future climate change scenario (Fig. 5). The lack of protection for suitable habitat was consistent between models that used average and dynamic r_i in the hybrid models (Fig. 5). We identified specific parks at the national, state and local level for conservation of green salamanders based on their overlap with areas of suitable habitat (Supporting information).

Discussion

Our study evaluated the predictions of habitat suitability using correlative, mechanistic and hybrid SDMs for a species of concern. The results suggest that the degree of overlap between approaches depends on the type of model used, climate change scenario and physiological parameterization. For instance, correlative-only and hybrid models projected a reduction in habitat suitability under the CCSM4 warming scenario, whereas they projected an increase in suitable habitat under the Hadley warming scenario (Fig. 4). The greatest divergence between correlative only and hybrid models occurred under the Hadley warming scenario (Fig. 4) or when hybrid models only contained mechanistic layers (i.e. no climate layers) (Supporting information). Despite the differences in energy balance between simulations with average and dynamic r_i, the effect of a dynamic r_i was very minimal on hybrid models (Fig. 4). Both correlative and hybrid models performed well at predicting the distribution of green salamander presences (Supporting information). The duration of activity was identified as informative by the hybrid framework, whereas energy balance was not (Table 2). The lack of support for energy balance and effect of activity on suitability highlights an important limitation of hybrid models.

Our analysis indicates that hybrid models should be interpreted cautiously for species that do not occupy their entire fundamental niche. Mechanistic SDMs estimate the fundamental niche (Kearney 2006, Kearney and Porter 2009) and

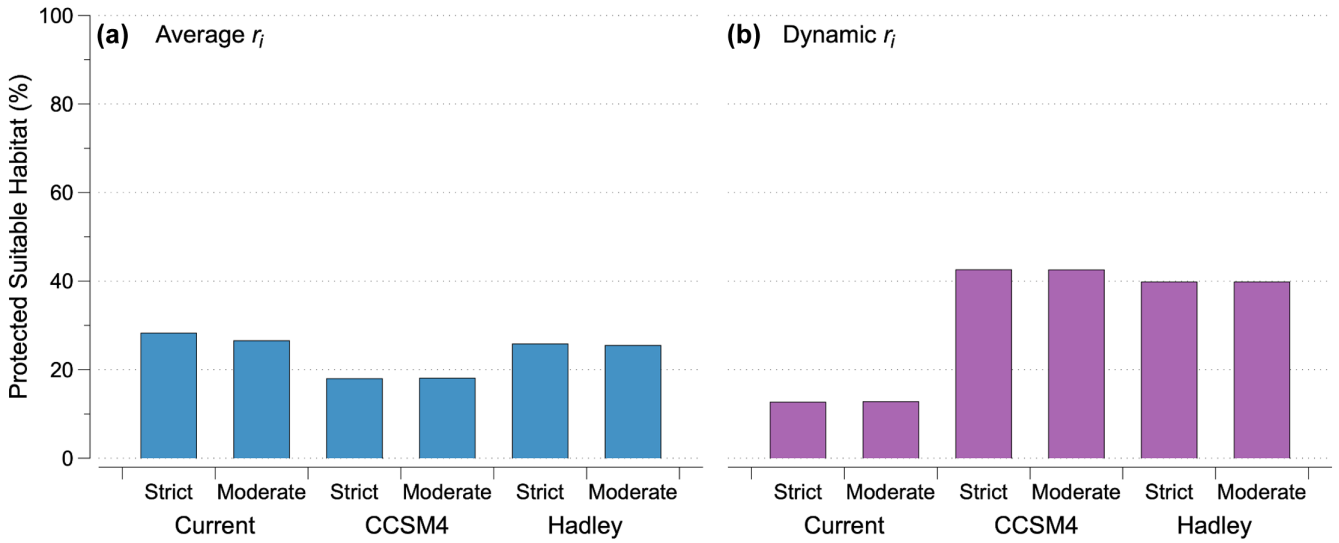

Figure 5. Proportion of suitable habitat for green salamanders protected by parks. Parks and protected areas protect the minority of suitable habitat, regardless of climate scenario or physiological parameters. Shown are the proportion of suitable habitat protected for all climate scenarios under strict and moderate thresholds with the two r_i simulations (a = average and b = dynamic).

therefore may identify regions as suitable even though the species does not occupy these regions for ecological reasons (i.e. competition, predation) or if the species range is not in equilibrium with climate (Araújo et al. 2005, Buckley et al. 2010). Our mechanistic SDMs predicted that the northern half of the disjunct range was energetically suitable and suitable for activity, despite green salamanders not occurring this far north (Fig. 2). Although green salamanders do not live there, this region is characterized by the highest density of salamander species in the world (Petranka 1998). Multiple lines of evidence suggest green salamanders may be sensitive to competitive interactions (Gordon 1952, Cliburn and Porter 1987), possibly explaining the lack of green salamanders in these regions and their more restricted realized niche (Fig. 2A). Salamanders in this area also exhibit similar metabolic rates and resistances to water loss (Riddell et al. 2018), providing evidence for a conserved fundamental niche among lungless, terrestrial salamanders (Kozak and Wiens 2006). These results indicate that the performance of hybrid models likely depends upon the extent to which species occupy their fundamental niche. The lack of support for energy balance as an informative predictor and the parabolic relationship between activity and suitability likely stems from the limited distribution of green salamanders. Similar studies that used hybrid approaches found activity (Mathewson et al. 2017) and energy balance (Briscoe et al. 2016) were important predictors of species' distributions. Whether these patterns are generalizable likely depends upon the species' traits and natural history. More specifically, hybrid models are likely to identify mechanistic layers as uninformative or to have unintuitive relationships with suitability if species do not occupy their entire fundamental niche. Understanding these important aspects of hybrid models may be important for interpreting hybrid models and predicting the resilience of species to climate change.

Range-wide correlative models show some resiliency in parts of the disjunct range of the green salamander (Barrett et al. 2014). Similarly, our hybrid models suggested some resiliency, although the regions of resiliency across models did not always overlap. Nevertheless, in all model runs, some suitable habitat is projected to remain for the species under future warming scenarios. However, not all plethodontids are likely to experience similar degrees of resiliency as green salamanders. Green salamanders may present a unique case for modeling suitable habitat because of their association with rock outcrops, a behavior not shared with most plethodontids (Gordon 1952, Jaeger 1971, Mount 1975). Green salamanders prefer moist crevices within rocky outcrops which may act as a buffer, allowing green salamanders to tolerate warmer and dryer temperatures of xeric slopes (Gordon 1952, Cho et al. 2009). Further, recent documented interspecific interactions between green salamanders and *Philomycus* slugs suggest that salamanders may utilize slugs for moisture within rock outcrops, eliminating the need for green salamanders to disperse long distances as much as other salamanders reliant on moist soil (Jaeger 1971, Cupp Jr. 2017, 2020). Therefore, green salamanders may be uniquely resilient to climate change given their behavior and natural history.

Our hybrid model projections indicate annual mean temperature and environmental seasonality (both temperature and precipitation) play a major role in shaping the green salamander distribution. Green salamanders are known to use and breed in moist rock crevices (Gordon 1952), and moisture appears to be a limiting factor in the distribution of other *Aneides* species (Rosenthal 1957, Spickler et al. 2006, Haan et al. 2007). Interestingly, both the CCSM4 and the Hadley GCMs predict a wetter future within the BRE (Supporting information), yet only the Hadley scenarios were associated with an increase in habitat suitability. The reliance of green salamanders on moist environments also likely explains why presence locations were associated with less seasonality in precipitation. The association with temperature seasonality is likely a reflection of inhabiting high elevations, where climatic conditions are more variable (Sømme and Block 1991, Ferguson and Messier 1996). Similarly, model selection curves also indicated a clear optimum average temperature (~13°C) associated with green salamander habitat suitability. Though green salamanders may not experience average annual temperatures frequently, the average annual temperature may be associated with more ecologically relevant temperatures experienced in granite outcrops that are important for maintaining positive energy balance or physiological performance. Exploring variation in optimum temperatures across species might also help to generate hypotheses on species-specific thermal performance or preferred temperatures that influence species' distributions.

The laboratory experiments demonstrated that green salamanders may exhibit similar resilience to climate change as other plethodontids due to the same physiological mechanisms. Green salamanders increased skin resistance to water loss when exposed to warm temperatures, shedding light on their tolerance to warm and dry conditions in laboratory studies (Gordon 1952, Canterbury 1991). Values of r_i and VO_2 in our study were comparable to measurements on other terrestrial plethodontids (Riddell et al. 2018), suggesting shared physiological traits may drive similar ecological responses to climate change. Long-term acclimation studies have revealed that plethodontid salamanders regulate water loss rates using combinations of perfusion, vascular regression and regulation of lipid composition in the skin (Riddell et al. 2019). Given that the green salamanders in our study only had a few hours to respond to the experimental temperature, we suggest that perfusion (i.e. the limiting of blood flow to the skin) represents the most likely regulatory mechanism, which has also been reported in similar species (Brown 1972). Despite sharing similar underlying mechanisms, green salamanders may struggle to track shifting climates in the absence of rock outcrops. Future studies that explicitly simulate these dispersal and habitat limitations might further improve predictions of habitat suitability.

Knowing when to use a particular distribution model can contribute to cost effective conservation. Under current climate conditions, several studies demonstrate that correlative

models can accurately predict species distribution and show minimal changes when mechanistic layers were incorporated (Buckley et al. 2010, Briscoe et al. 2016). We showed substantial overlap between models, suggesting correlative-only models are probably sufficient for many species under current climate conditions. Justification for a correlative-only approach is valuable given the data-intensive nature of mechanistic models. On the other hand, several studies have shown that mechanism-based forecasts diverge from those made when using correlative-based models (Briscoe et al. 2016, Mathewson et al. 2017). Mechanistic SDMs generated projections that were, in some cases, more optimistic than models based on correlative data. We recommend the use of such SDMs as stand alone approaches or layers in a correlative framework for projections assessing climate change vulnerability if resources are available. It is unclear whether mechanistic models are more accurate, so there may be an argument to use a more conservative (i.e. restrictive) threshold. Lastly, our models only evaluated climate data. In order to make management decisions about where to conserve green salamander habitat, it would be beneficial to incorporate landscape data (i.e. rocky outcrops) to make the most informed decisions.

Integrating these two approaches might also guide conservation efforts on species of conservation concern, such as the green salamander. Overlap in the approaches can specifically guide conservation practitioners to focus on specific areas for conservation planning. For instance, only one model scenario predicted suitable habitat on protected land in Georgia (Supporting information), and this information may help managers allocate time and resources more efficiently. According to our models, less than 50% of the suitable habitat for green salamanders will occur on protected land in 2050 under the most optimistic of scenarios (Fig. 5). Land acquisition in areas predicted to have suitable green salamander habitat (but are outside of public lands) will help conserve green salamanders should range shifts occur in the future. Additionally, periodic monitoring of occupied sites that are predicted to lose suitability may offer an early-warning signal related to climate vulnerability. Regardless of the conservation actions, our study demonstrates that integration of mechanistic and statistical approaches offer new insights for protecting species of concern.

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Author contributions

Jillian C. Newman: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Eric A. Riddell**: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Resources (equal); Software (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Lori A. Williams**: Data curation (equal); Resources (equal); Writing – review and editing (equal). **Michael W. Sears**: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Project administration (equal); Resources (equal); Software (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Kyle Barrett**: Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Methodology (equal); Project administration (equal); Resources (equal); Software (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Transparent peer review

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Data availability statement

Data are available from the Open Science Framework Repository: <https://osf.io/w6fek/> (Newman et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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