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Vulnerability of high-elevation endemic salamanders to climate change: A case study with the Cow Knob Salamander (*Plethodon punctatus*)

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ABSTRACT

Rapid contemporary climate change is a potential threat to long-term persistence of montane wildlife species because they often have narrow thermal tolerances and have limited potential to shift their distributions. The Appalachian Mountain region in the eastern United States is a global biodiversity hotspot for woodland salamanders (genus *Plethodon*), many of which are high-elevation endemic species. Robust assessments of the vulnerability of high-elevation endemic salamanders to climate change, including delineation of future potential climate refugia, are needed to guide climate change adaptations strategies. The Cow Knob Salamander (*Plethodon punctatus*) is a species of conservation concern found at high elevations in the Valley and Ridge Province of western Virginia and eastern West Virginia. We used habitat suitability models to examine relationships between landscape characteristics, climate variables, and *P. punctatus* occurrence, and estimated effects of future climate scenarios on the species' climatic niche. We found that elevation, slope, aspect, and hillshade were influential landscape predictors of species occurrence, and that mean annual temperature was the most influential climate variable. Future climate projections indicated this species will likely lose most of its climatic niche by mid-century, and that amount of suitable habitat will continue to decline through 2100. We identified several pockets of habitat that may represent climate change refugia for *P. punctatus* due to cooler microclimates from greater hillshade and aspects that receive less direct solar radiation; however, we found these refugia exist in small, isolated habitat patches. Our study provides quantitative estimates that support the general concern that high-elevation endemic salamanders are particularly vulnerable to climate change. Our models can be used by natural resource managers to guide current *P. punctatus* monitoring and habitat conservation efforts, as well as to identify focal areas that will likely serve as refugia for the species as the climate continues to change over this century.

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1. Introduction

Rapid climate changes are occurring at the global scale (IPCC, 2014), resulting in spatially and temporally novel abiotic and biotic conditions (Blois et al., 2013; Hayhoe et al., 2007). Many wildlife species are responding to climate changes by altering their latitudinal or altitudinal distributions (e.g., Chen et al., 2011; Moskwik, 2014; Zuckerberg et al., 2009). However, montane species are unable to respond to warming temperatures through dispersal to higher and cooler elevations, and thus there is concern that these species are particularly vulnerable to a warming climate (Elsen and Tingley, 2015; La Sorte and Jetz, 2010). In addition, some montane species have been shown to have a narrow thermal tolerance (e.g., Markle and Kozak, 2018). For these species, identifying and protecting areas within their current distribution that represent future climate refugia and corridors between them will be necessary to maximize their probability of persistence (Lembrechts et al., 2018; Nuñez et al., 2013).

The Appalachian Mountain region in the eastern United States is a global biodiversity hotspot for salamanders (Milanovich et al., 2010; Rissler and Smith, 2010), with many high-elevation endemic woodland salamanders (genus *Plethodon*) of conservation concern, such as the Shenandoah Salamander (*P. shenandoah*), Cheat Mountain Salamander (*P. nettingi*), Peaks of Otter Salamander (*P. hubrichti*), Weller's Salamander (*P. welleri*), and Cow Knob Salamander (*P. punctatus*). These species are lungless ectotherms that are dependent on both temperature and moisture for cutaneous respiration and activity patterns (Feder, 1983). While there are many biotic and abiotic factors that affect local-scale distributions of woodland salamander species, landscape-scale distributions are largely driven by climatic conditions (Kozak and Wiens, 2010). In particular, climate constraints on physiology set the lower elevation limits for many montane salamander species (Gifford and Kozak, 2012; Grant et al., 2018). Narrowly-distributed species are often specialists for their unique ecological niches and will have less plasticity in their response to climate change than more widely-distributed species (Markle and Kozak, 2018).

One woodland salamander that is potentially highly vulnerable to rapid contemporary climate change is *P. punctatus* (Fig. 1), a high-elevation species that is endemic to a small region (ca. 720 km^2) along the eastern and western border of West Virginia and Virginia, respectively. The majority of historically known-occupied locations are on Shenandoah Mountain in the George Washington National Forest, which occurs in the Valley and Ridge Province, the driest region in the central Appalachians (Lafon and Grissino-Mayer, 2007). The comparatively dry climate may limit the local distribution of the species, relegating it to the limited areas with cool, moist conditions (Flint and Harris, 2005). For example, Buhlmann et al. (1988) documented greater relative abundance of *P. punctatus* on north-facing slopes and at high elevations, presumably due to cooler and wetter conditions in these areas. In a laboratory study that investigated thermal tolerances of 16 species of

Fig. 1. A Cow Knob Salamander (*Plethodon punctatus*) in moss-covered talus habitat, George Washington National Forest, West Virginia, USA.

plethodontid salamanders, *P. punctatus* had the lowest capacity for acclimation to warmer temperatures, as well as one of the lowest critical thermal maxima (Markle and Kozak, 2018).

Two previous studies indicated that *P. punctatus* may be extremely vulnerable to climate change, as 100% of their climatic niche was projected to disappear by mid-century in both studies (Milanovich et al., 2010; Sutton et al., 2015). However, both were community-level studies, and thus did not explicitly focus on delineating the variables most influential for the occurrence of *P. punctatus*. Further, both studies used a small proportion of the known occurrence points for *P. punctatus* to train the models, and somewhat coarse-grained climate data (ca. 1 km^2). Given the potential for this species to be among the most vulnerable woodland salamanders to climate change, there is a need for a more robust assessment of its vulnerability, and for delineation of future potential climate refugia, to guide climate change adaptations strategies by natural resource managers (Bierbaum et al., 2013; Dawson et al., 2011; Fischman et al., 2014).

The purposes of this study were to 1) delineate important landscape-scale predictors of *P. punctatus* occurrence, 2) estimate fine-scale probability of occurrence under contemporary environmental conditions across the species' distribution 3) project fine-scale probability of occurrence under predicted future environmental conditions, and 4) assess the connectivity between habitat patches under contemporary and future climate scenarios. Results of this study can be used to enhance management of *P. punctatus* by guiding current monitoring and habitat conservation efforts, as well as identifying focal areas that will likely serve as refugia for the species as the climate changes.

2. Methods

2.1. Species occurrence data and study area

We compiled all known *P. punctatus* locations (n = 229, precise locations withheld due to conservation concerns) from federal and university researchers who have conducted surveys over the past three decades. We bounded our study area based on the distribution of the species and dispersal boundaries. First, we created a buffer of 30 km around observed locations on the periphery of the distribution to incorporate potentially occupied habitat that has not been surveyed. We then restricted the lower elevation study boundary to 500 m; all observed locations are above 625 m. Lastly, because this species has never been found west of Cowpasture River and the South Fork of the South Branch Potomac River, or east of the Shenandoah Valley, we considered these to be dispersal barriers and restricted our study area to these barriers. It is unlikely that *P. punctatus* can disperse from the defined study area because unsuitable, low elevation habitat surrounds the mountains, and plethodontid salamanders have limited long-distance dispersal capabilities (Gibbs, 1998). We gridded the study area into 24 m^2 cells (i.e., the resolution of the digital elevation model [DEM] we used), and used the observed locations to define known occurrence cells. We used the remaining cells to generate background habitat data.

2.2. Modeling overview

We used a habitat suitability model (HSM) approach to estimate relationships between environmental variables and species occurrence (Boyce et al., 1999; Guisan and Zimmermann, 2000). HSMs estimate spatially-explicit habitat quality based on correlations between species occurrence and environmental variables (Hirzel and Le Lay, 2008; Phillips et al., 2006). For this study, we created two HSMs to address our study objectives. First, we created a landscape model, with the goal of maximizing accuracy for the contemporary spatially-explicit probability of occurrence of *P. punctatus*. Second, we created a climatic niche model, with the goal of estimating how climate change will influence the distribution of this species. We included landscape variables that contribute to microclimate (i.e., heat load index (HLI) and hillshade) in our climatic niche models in order to identify areas of climate refugia.

We used the MaxLike HSM for this study (Royle et al., 2012). MaxLike uses species occurrence data coupled with background environmental data to model species-environment relationships. The function is a generalized linear model with a Bernoulli distribution and parameter value estimation using maximum likelihood (Royle et al., 2012). Although we acknowledge that presence-absence models are generally preferable to presence-only models (Brotons et al., 2004; Yackulic et al., 2013), a robust absence data set is not currently available for this species. In addition, false absences in species monitoring data can be prevalent when detection probability is low (Hirzel et al., 2002), as is the case for *P. punctatus* (Flint and Harris, 2005), potentially resulting in biased estimates from presence-absence models (Gu and Swihart, 2004; MacKenzie, 2006). We chose MaxLike over other presence-only models such as MaxEnt because previous research found that MaxLike tended to perform similarly (Merow and Silander, 2014), or better (Fitzpatrick et al., 2013). We created HSMs using the package 'maxlike' (version 0.1.7) in the statistical software R (version 3.5.1). We used the cloglog link function, rather than the default logit link function, because it resulted in a better model fit.

2.3. Landscape variables

We modeled the effects of several landscape variables that contribute to a cool and wet microclimate. We obtained a 1 arc second (ca. 24 m^2 at 39° North) resolution DEM through the USGS National Elevation Dataset. From this layer, we derived slope, HLI, topographical position index (TPI), and hillshade using ArcGIS (version 10.4). We standardized all variables by subtracting the mean and dividing by the standard deviation. HLI is a measurement of the potential heat and incident

radiation a site receives due to aspect and slope (McCune and Keon, 2002). This index assigns higher values for locations with a southwest aspect because they receive higher maximum temperatures from the afternoon sun. The following equation rescales aspect to a scale from 0 for cooler northeast-facing slopes, to 1 for warmer southwest-facing slopes:

$$Heat\ Load\ Index = \frac{1 - \cos(\theta - 45)}{2}$$

where θ = aspect in degrees east of north. TPI has been shown to be negatively correlated with woodland salamander abundance because areas with lower values (i.e., ravines and valleys) are wetter than areas with higher values (i.e., ridges; Peterman and Semlitsch, 2013). We calculated TPI as the slope position relative to the surrounding 600 m.

2.4. Climate variables

For contemporary climate normals, we used 30-year averages (1980–2010) of estimated monthly precipitation and temperature that were statistically downscaled to 550 m^2 resolution by CLIMsystems Ltd (Hamilton, New Zealand) using pattern scaling (Tebaldi and Arblaster, 2014). We resampled the layers to the resolution of the landscape variables. We initially examined the 19 bioclimatic variables from WorldClim (Himjans et al., 2005, Table 1), because they are widely used in climatic niche modeling. For highly correlated climatic variables ($r^2 > 0.75$), we retained the variables that were most biologically relevant based on woodland salamander ecology (Sutton et al., 2015). Our final analyses included 4 climatic variables: mean annual temperature, precipitation in the warmest quarter (i.e., June to August), precipitation in the wettest quarter (i.e., April to June), and temperature seasonality (i.e., the standard deviation in monthly temperature x 100). In addition to the climate variables, we included two topographical variables, HLI and hillshade, in our climatic niche models. Topographic variables that influence microclimate are often overlooked in climatic niche modeling (Title and Bemmles, 2018), and ignoring them may lead to an overestimation of extinction risk (Lembrechts et al., 2018).

The Intergovernmental Panel on Climate Change (IPCC) recommends using an ensemble of global climate models (GCMs) to account for variability in climate model projections and to buffer against unusually high or low projections from single models (IPCC, 2010). We extracted the median as well as the 10th and 90th percentile temperature scenarios from an ensemble of 31 global climate models using the 4.5 and 8.5 representative concentration pathways (RCPs) for the years 2050 and 2100. Each RCP represents a different greenhouse gas scenario. The RCP4.5 scenario represents a pathway where global greenhouse emissions gradually increase, followed by a decline after 2030. The RCP8.5 scenario represents a 'baseline' scenario pathway with no climate mitigation target and an increase in emissions throughout the century (Moss et al., 2010).

2.5. Model selection

We fit models using a forward stepwise approach based on Akaike's Information Criterion corrected for small sample size (AIC_c). Models with a lower score were ranked as more parsimonious. We calculated Akaike weights (w_i) to determine the weight of evidence for each model (Anderson and Burnham, 2002). For the best approximating landscape and climatic niche

Table 1
Variables considered (left) and used (right) for modeling the occurrence of the Cow Knob Salamander (*Plethodon punctatus*) across the species' distribution in eastern West Virginia and western Virginia, USA. All variables were standardized using a Z-score transformation prior to analyses.

Variable	Abbrev	Variable	Abbrev
Landscape Model			
Canopy Cover	CC	Elevation	Elev
Lithology	Lith	Heat load index	HLI
		Hillshade	Hill
		Slope	Slp
		Topographical position index	TPI
Climate niche model			
Mean diurnal range	Bio 2	Mean annual temperature	AT
Isothermality	Bio 3	Precipitation of wettest quarter	Pwet
Max temperature warmest month	Bio 5	Precipitation of warmest quarter	Pwarm
Min temperature coldest month	Bio 6	Temperature seasonality	TS
Annual temperature range	Bio 7	Heat load index	HLI
Mean temperature wettest quarter	Bio 8	Hillshade	Hill
Mean temperature driest quarter	Bio 9		
Mean temperature coldest quarter	Bio 11		
Annual precipitation	Bio 12		
Precipitation of wettest month	Bio 13		
Precipitation of driest month	Bio 14		
Precipitation seasonality	Bio 15		
Precipitation of driest quarter	Bio 17		
Precipitation of coldest quarter	Bio 19		

model, we performed model validation using the 'sdm' package (version 1.0–46) in program R. We ran 10 iterations of 10-fold cross-validation and considered models that had an area under the receiver operating characteristic curve (AUC) of 0.7–0.9 to be informative, and models with an AUC > 0.9 to be "very good" (Baldwin, 2009; Sutton et al., 2015).

2.6. Suitability thresholds

We used a threshold approach to create three probability of occurrence categories: not suitable, low occurrence probability, and high occurrence probability. Values above the ten fixed cumulative value (i.e., the value that results in 10% omission of training data) were considered to have a high occurrence probability. Low occurrence probability was determined by the minimum training presence threshold, where all known locations were correctly predicted by the model. Probability scores lower than the minimum training presence threshold were considered not suitable. The minimum training presence and 10% omission thresholds can be considered liberal and conservative approaches, respectively (Sutton et al., 2015). For our landscape model, we overlayed the high probability areas with areas where *P. punctatus* is protected by a conservation agreement between the United States Forest Service (USFS) and the United States Fish and Wildlife Service (USFWS; Mitchell, 1994).

2.7. Connectivity analysis

We analyzed connectivity between habitat patches based on our climate projections by applying the circuit theory approach (McRae et al., 2008) using Circuitscape v5. This method uses an underlying resistance map which represents the opposition of an animal's movement to a habitat type. For our connectivity analysis, we used our habitat suitability values as the inverse of resistance (i.e., conductance). We used the high probability threshold for our habitat patches because *Plethodon* salamanders have poor dispersal capabilities, so some level of habitat suitability would be needed between the patches for migration to occur. We identified a natural break in habitat patch size at ca. 3 ha and removed any habitat patches smaller than this. We analyzed the connectivity (i.e., current) between all patch pairs and generated a cumulative map of potential connectivity. For our climate niche models with no habitat patches remaining, we did not conduct a connectivity analysis. We overlayed our projected habitat patches and connectivity with areas managed under the USFS conservation agreement.

3. Results

3.1. Landscape model

Out of the 19 models fit, the elevation/HLI/hillshade/slope model was the best approximating model (Table 2). *Plethodon punctatus* occurrence was positively associated with elevation, slope, and hillshade, and negatively associated with HLI (Table 3). This model resulted in 40.9% not suitable, 42.1% low probability of occurrence, and 17.0% high probability of occurrence

Table 2
Model selection results to determine the optimal habitat suitability models for explaining the correlation between environmental variables and Cow Knob Salamander (*Plethodon punctatus*) occurrence across the species' distribution in eastern West Virginia and western Virginia, USA. The landscape models (left) consisted of topographic variables, while the climate niche models (right) consisted of climate and climate refugia variables. Variables included elevation (Elev), hillshade (Hill), heat load index (HLI), slope (Slp), topographical position index (TPI), mean annual temperature (AT), precipitation in the warmest quarter (Pwarm), precipitation in the wettest quarter (Pwet), and temperature seasonality (TS). Model selection was based on Akaike's Information Criterion corrected for small sample size (AIC_c).

Landscape Models				Climatic Niche Models			
Model	AIC_c	ΔAIC_c	w_i	Model	AIC_c	ΔAIC_c	w_i
Elev, HLI, Hill, Slp	6161.649	0	0.35	AT, Hill, HLI	6347.022	0	1
Elev, HLI, Hill, Slp, TPI	6162.413	0.764	0.239	AT, Hill, Pwarm	6390.543	43.521	0
Elev, HLI, Hill, TPI	6162.423	0.774	0.238	AT, HLI, Pwarm	6390.58	43.558	0
Elev, HLI, Hill	6163.046	1.397	0.174	AT, Hill	6391.465	44.443	0
Elev, Hill, Slp	6192.121	30.472	0	AT, HLI, TS	6391.755	44.733	0
Elev, Hill, Slp, TPI	6192.37	30.721	0	AT, HLI, Pwet	6393.561	46.539	0
Elev, Hill	6197.916	36.267	0	AT, HLI	6447.7	100.678	0
Elev, Hill, TPI	6199.521	37.872	0	AT, Pwarm	6507.522	160.5	0
Elev, HLI	6231.337	69.688	0	AT, TS	6507.56	160.538	0
Elev, HLI, TPI	6233.406	71.757	0	AT	6507.573	160.551	0
E, TPI, Slp	6274.762	113.113	0	AT, Pwet	6509.601	162.579	0
Elev	6277.338	115.689	0	Pwet	6907.564	560.542	0
Elev, TPI	6279.286	117.637	0	Pwarm	6932.333	585.311	0
Elev, HLI, Slp	6590.179	428.53	0	TS	7005.682	658.66	0
Hill	6965.741	804.092	0	Null model	7986.234	1639.212	0
TPI	6971.586	809.937	0				
HLI	7007.445	845.796	0				
Slp	7016.254	854.605	0				
Null model	7986.234	1823.821	0				

Table 3
Parameter estimates (β) and standard errors (SE) from the best approximating landscape model (left) and climate niche model (right) explaining the correlation between habitat variables and Cow Knob Salamander (*Plethodon punctatus*) occurrence across the species' distribution in eastern West Virginia and western Virginia, USA.

Landscape Model				Climatic Niche Model			
Variable	β	SE	P(>|z|)	Variable	β	SE	P (>|z|)
Intercept	−6.6840	0.5893	<0.001	Intercept	−5.702	0.7568	<0.001
Elev	1.5658	0.0835	<0.001	AT	−1.401	0.0871	<0.001
HLI	−0.3714	0.0690	<0.001	Hill	0.794	0.0937	<0.001
Slp	0.0906	0.0743	0.223	HLI	−0.437	0.0767	<0.001
Hill	0.6409	0.0873	<0.001				

habitat within the study area. Most of the high probability of occurrence habitat was located at high elevations on Shenandoah Mountain, with 40% occurring in areas managed under the USFS conservation agreement (Fig. 2). This model received an AUC of 0.936 (±0.017 SD). The second-best model, elevation/HLI/slope/hillshade/TPI, also received empirical support (Table 2). However, it is very similar to the top model, and TPI was not significantly correlated with *P. punctatus* presence.

3.2. Climate niche model

The best approximating climate niche model was the mean annual temperature/HLI/hillshade model (Table 2). *Plethodon punctatus* occurrence was positively associated with hillshade and negatively associated with HLI and mean annual temperature. Similar to the landscape model, most of the high probability of occurrence habitat was located on the ridgeline of Shenandoah Mountain. However, this model had a larger area of projected high probability of occurrence (Fig. 2). This model received an AUC score of 0.906 (±0.028 SD). No other climate niche model received strong empirical support.

Median projected increases in temperature for the study area ranged from 1.56 °C (2050, RCP4.5) to 5.14 °C (2100, RCP8.5; Table 4). Both projected increases in temperature resulted in a drastic reduction of suitable habitat for *P. punctatus*. The models projected 76–100% loss of high occurrence probability habitat and 31–100% loss of low occurrence probability habitat by 2050 (Table 4). The models projected an 85–100% loss in high occurrence probability habitat and 50–100% loss in low occurrence probability habitat by the year 2100 (Table 4).

In all of our future climate scenarios, we found that the large contiguous high probability habitat on the high elevations of Shenandoah Mountain became severely fragmented (Fig. 3). Our models identified potential climate refugia as areas that are high elevation, receive little direct solar radiation (i.e., low HLI and high hillshade), and are near the ridgeline of Shenandoah Mountain (Fig. 4). Most of our future projected habitat patches are protected by the USFS conservation agreement, with 92.8% of habitat patch area occurring in the area under the 2050 RCP4.5 scenario, and 100% under warmer scenarios (Fig. 3). However, these remaining habitat patches are small, severely fragmented, and isolated, compared to the current climatic niche model for *P. punctatus* (Fig. 3). Our connectivity analysis found connectivity lowered between habitat patches with each progressively warmer scenario (Fig. 3). We found that the high elevations near the ridgeline of Shenandoah Mountain could temporarily act as a corridor between habitat patches that are fragmented due to climate change.

4. Discussion

Our landscape HSM indicated that *P. punctatus* have limited suitable habitat under contemporary climate conditions, mostly at high elevations near the ridgeline of Shenandoah Mountain. While previous studies observed that *P. punctatus* occupancy and abundance was greater at higher elevations (i.e., Buhlmann et al., 1988; Downer, 2009), our research is the first to explicitly model the relationship between elevation and occurrence across the species' distribution. This model shows that *P. punctatus* are mostly relegated to areas with cool, moist conditions (i.e., high elevations and areas with little solar radiation).

The results of our climatic niche projections are consistent with the two previous studies (Milanovich et al., 2010; Sutton et al., 2015), and suggest that the *P. punctatus* will lose most its climatic niche, and therefore suitable habitat, by the year 2050, with further declines by the year 2100. The previous climatic niche studies showed a 100% loss in suitable habitat by 2050, whereas our study indicates there will likely be areas of climate refugia. Specifically, our climate niche model indicates that high elevation areas with a low HLI and high hillshade (i.e., areas that receive less solar radiation) will be important refugia as the climate warms. Thus, our study supports the importance of incorporating microrefugia in habitat suitability models (Lembrechts et al., 2018). Nevertheless, we found that the largest area of continuous habitat will be severely fragmented and connectivity between habitat patches will decrease, and it is unclear if *P. punctatus* could persist in these fragmented, isolated habitat patches.

The USFS conservation agreement aims to increase or maintain stable *P. punctatus* populations by protecting ca. 23,500 ha that contains vital current and future habitat, including most of our projected future climate refugia and areas of habitat connectivity (Fig. 3), by preventing the construction of new roads, timber production, and use of heavy equipment at elevations above 914 m. In addition to the protected areas, any locations in the George Washington National Forest where this

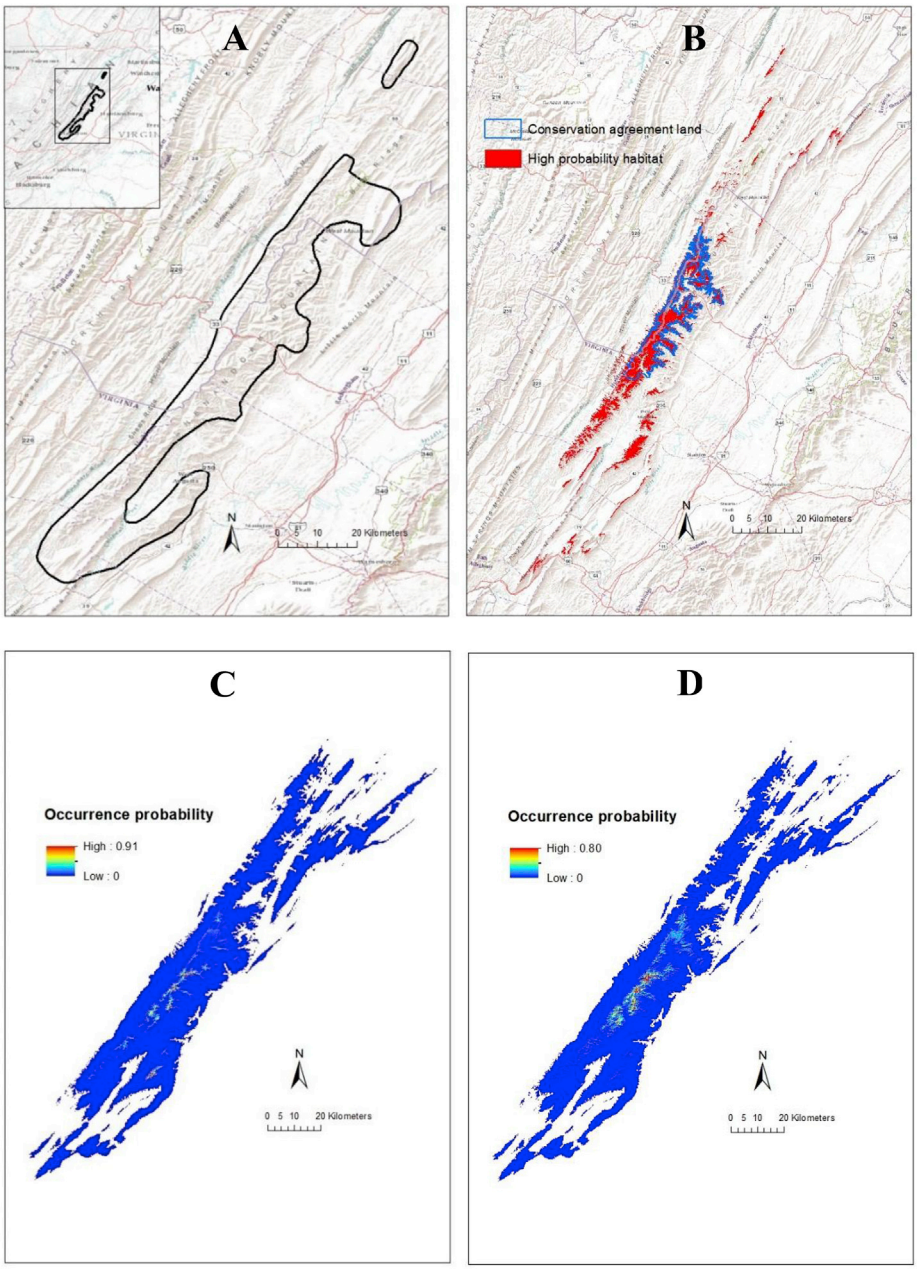

Fig. 2. A) General contemporary distribution map for the Cow Knob Salamander (*Plethodon punctatus*) along the West Virginia and Virginia border in the Valley and Ridge Province, USA. B) Projected contemporary occurrence probability for *P. punctatus* based on the top landscape model that used the additive effects elevation, heat load index (HLI), hillshade, and slope. C) Projected contemporary occurrence probability for *P. punctatus* based on the top climate niche model that used the additive effects of mean annual temperature, HLI, and hillshade.

species is known to occur is managed in the same manner (U.S. Forest Service, 2014). For our landscape model, our high probability habitat corresponded well with the 914 m elevation threshold in the agreement, though we found some high probability habitat below this elevation in areas with low HLI or high hillshade and areas above this elevation that are not high probability habitat due to greater solar exposure (Fig. 2), demonstrating the importance of considering these variables when assessing whether this species may be present. Our models indicate there are areas of high probability habitat outside the conservation agreement; most of these areas are lower in elevation and warmer, meaning *P. punctatus* populations may be most vulnerable here.

Table 4
Summary statistics for projected changes in mean annual temperature, and resulting percentage changes in species occurrence probability classes for the Cow Knob Salamander (*Plethodon punctatus*) across the species' distribution in eastern West Virginia and western Virginia, USA. Low occurrence probability habitat is defined by the minimum training presence threshold, where all known locations were correctly predicted by the model, while high occurrence probability habitat is defined by probability values that are above the 10 fixed cumulative (i.e., the value that results in a 10% omission in training data).

Climate condition	Mean temp increase °C	% Not suitable	% Low probability	% High probability
Baseline	NA	6.5	66.9	26.8
2050 RCP4.5				
median	1.56	74.3	23.7	2.1
(10th, 90th percentiles)	(0.99, 2.31)	(47.2, 91.2)	(46.4, 8.7)	(6.4, 0.2)
2050 RCP 8.5				
median	2.15	88.7	10.9	0.4
(10th, 90th percentiles)	(1.2, 3.18)	(66.4, 98.3)	(30.3, 1.7)	(3.3, 0.0)
2100 RCP 4.5				
median	2.07	86.9	12.5	0.5
(10th, 90th percentiles)	(1.31, 3.06)	(63.1, 97.6)	(33.0, 2.4)	(4.0, 0.0)
2100 RCP 8.5				
median	5.14	100	0.0	0.0
(10th, 90th percentiles)	(3.26, 7.60)	(98.5, 100)	(1.5, 0.0)	(0.0, 0.0)

Although our study indicates high vulnerability of *P. punctatus* populations to climate change across their distribution, we acknowledge that species occurrence-environment correlations under contemporary conditions may not extrapolate well to future novel environmental conditions (Gustafson, 2013). However, the vulnerability of *P. punctatus* to increasing temperature is supported by a recent laboratory study that found the metabolic rate of *P. punctatus* was more than 2.5 times greater when exposed to 25 °C temperatures compared to 15 °C (Markle and Kozak, 2018), indicating this species is physiologically stressed under warmer conditions, which could result in reduced fitness of individuals (Bernardo and Spotila, 2006). Thus, the mechanism underlying the apparent strong influence of mean annual temperature on habitat suitability could be related to temperature being a limiting factor for surface activity, or related to the influence of temperature on baseline energy expenditure. Specifically, *P. punctatus* spend the majority of time occupying deep subterranean talus habitat (Buhlmann et al., 1988; Flint and Harris, 2005), which generally reflects mean annual temperature conditions (Mammola and Leroy, 2018).

Another potential limitation of correlative climate niche models is they do not account for potential phenotypic plasticity, or behavioral and evolutionary responses to climate change (Luoto et al., 2005; Riddell et al., 2018). Temperatures are projected to warm at a much faster rate than previous climate adaptation rates for terrestrial vertebrates (Deutsch et al., 2008; Quintero and Wiens, 2013), and thus capacity to evolve in response to rapidly changing environmental conditions may be limited. However, terrestrial salamanders have behavioral adaptations that could allow them to survive in suboptimal environments. For example, salamanders can respond to shifts in weather such as drier conditions by climbing vegetation, which allows for them to be active on the surface longer (McEntire and Maerz, 2019). This thermoregulatory behavior appears to be employed by *P. punctatus*, as it frequently climbs woody vegetation (Jacobsen et al., 2019), indicating vertical structure may be an important component of climate refugia for this species. Additionally, warmer temperatures can cue phenotypic expressions by salamanders that provide physiological plasticity in response to changing environmental conditions. For example, Riddell et al. (2019) found that salamanders can regress and regenerate capillary beds in their skin, allowing for plasticity in desiccation resistance. In addition to influencing habitat suitability, climate change may affect interspecific competition between salamander species (Hoffacker et al., 2018). In our study area, the White-Spotted Slimy Salamander (*Plethodon cylindraceus*) is rarely found in the same high-elevation habitat as *P. punctatus* (Downer, 2009), but warmer temperatures could allow for it to expand into higher elevation habitat and potentially allow for interference competition; *P. cylindraceus* has been found to be more aggressive when exposed to warmer temperatures (Clay and Giffords, 2016). This competitive interference could be exacerbated if the increased metabolic rate for *P. punctatus* results in a smaller body size, which has been observed for several species in the region (Caruso et al., 2014).

We emphasize that our climate niche models project a loss of suitable habitat, not species extirpation. It is likely that *P. punctatus* will temporarily persist beyond the point when their habitat is no longer able to support stable population growth rates at dynamic equilibrium, referred to as extinction debt (Dullinger et al., 2012; Kuussaari et al., 2009). The landscape model we developed for this study is currently the most robust HSM for *P. punctatus*, and our model validation indicated it has high predictive accuracy. However, we were not able to find a variable that correlated strongly with the presence of talus habitat, which is positively correlated with local *P. punctatus* occupancy (Buhlmann et al., 1988), and we encourage future development of this habitat variable to improve model accuracy. We also did not include canopy cover in our models because this variable is dynamic, thus current coverage may not reflect canopy cover when the species was observed in that locality. Canopy cover is positively correlated with *P. punctatus* abundance (Jacobsen, 2019), and it is likely an important habitat component that would enhance climate refugia for this species.

In summary, our study supports the general concern that high-elevation endemic salamanders in the Appalachian region are particularly vulnerable to climate change, and provides useful information to enhance conservation of *P. punctatus*, a species of conservation concern. Our landscape model can be used by natural resource managers to guide current *P. punctatus*

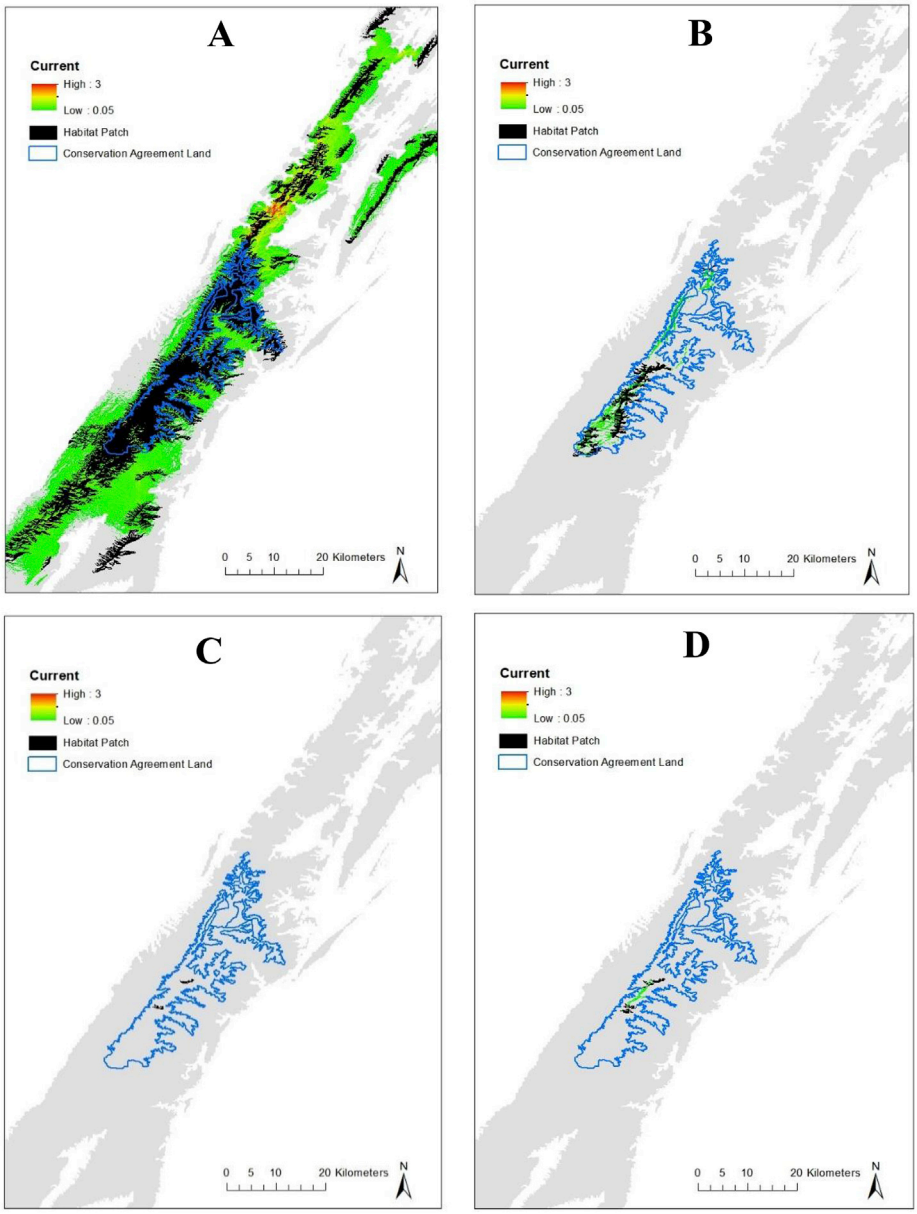

Fig. 3. Cumulative connectivity maps between high probability habitat patches (black) for the Cow Knob Salamander (*Plethodon punctatus*) shown in relation to land protected under a United States Forest Service conservation agreement (within blue lines) under A) baseline contemporary climate conditions, and future climate projections using the median of and ensemble of 31 climate models under the B) 2050 RCP 4.5, C) 2050 RCP 8.5, and D) 2100 RCP 4.5. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

habitat conservation efforts, as well as to direct future survey efforts that could facilitate the discovery of new *P. punctatus* populations, thus expanding our knowledge of the range-wide distribution of the species. Our climate niche models identify potential areas of refugia under warmer climate conditions, hence providing natural resource managers with defined areas to focus habitat and climate adaptation management efforts now.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

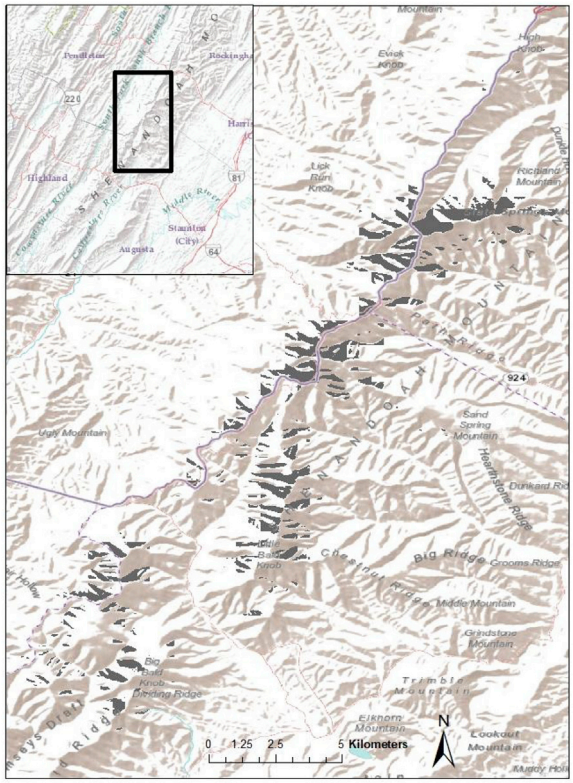

Fig. 4. Map of climate refugia (high occurrence probability habitat [dark shaded areas]) for the Cow Knob Salamander (*Plethodon punctatus*) in the year 2100 using the median of an ensemble of 31 climate models under the 4.5 representative concentration pathway (RCP) scenario that forces a gradual reduction in greenhouse gas emissions after the year 2030. This climatic niche model used the additive effects of mean annual temperature, HLI (heat load index), and hillshade.

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