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Projected future changes in the geographic distributions of the threatened *Plethodon nettingi* and a potential competitor

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ABSTRACT: The Central Appalachian region contains several high-elevation endemic woodland salamanders, which are thought to be particularly vulnerable to climate change due to their restricted distributions and low vagility. In West Virginia, there is a strong management focus on protection and recovery of the federally threatened Cheat Mountain salamander *Plethodon nettingi*. To support this focus, there is a need for improved understanding of the occurrence—habitat relationships and spatially explicit projections of fine-scale contemporary and potential future habitat quality to inform management actions. In addition, there is concern among natural resource managers that climate change may increase habitat quality at high elevations for potential competitors of *P. nettingi*, particularly the eastern red-backed salamander *P. cinereus*, potentially resulting in increased competition pressure for *P. nettingi*. To address these knowledge gaps concerning future habitat availability and competition, we created ecological niche models using the random forest classification algorithm and used the estimated occurrence—habitat relationships to assess ecological niche overlap between the species and project fine-scale contemporary and potential future habitat availability and quality. We estimated that the ecological niches of *P. nettingi* and *P. cinereus* were 80.5% similar. For *P. nettingi*, we estimated that the amount of high-quality habitat will be reduced by mid-century and potentially lost by end-of-century, but that moderate and low-quality habitat will persist. For *P. cinereus*, we estimated that the amount of high-quality habitat will increase through end-of-century, and that high elevations will become more suitable for this species, indicating that potential competition pressure for *P. nettingi* is likely to increase.

KEY WORDS: *Plethodon nettingi* · Climate change · Ecological niche model · Random forest

1. INTRODUCTION

The Central Appalachian region in the eastern USA is a global biodiversity hotspot for amphibians and contains several high-elevation endemic woodland salamanders (genus *Plethodon*) of conservation concern (Stuart et al. 2004, Rissler & Smith 2010). High biodiversity in the region is likely associated with wide variability in environmental conditions due to mountainous topography and lack of glaciation during the last glacial maximum (Stephenson 2013, Kozak & Wiens 2016). Climatic patterns in the Central Appalachians are changing, but there is high spatial variability in the direction of observed changes due to the complex topography (Stephenson 2013, Butler et al. 2015). Overall trends between 1906 and 2016 in West Virginia included increased minimum temperature, decreased maximum temperature, and increased annual precipitation, but directional patterns varied across weather stations (Kutta & Hubbart

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2018, 2019). Projections of future climate change in the region also indicate that directional patterns will vary spatially (Butler et al. 2015, Fernandez & Zegre 2019). The distributions of many wildlife species are shifting on the landscape in response to climatic changes (e.g. Root et al. 2003, Chen et al. 2011). However, woodland salamanders are generally restricted by low vagility and narrow ranges of thermal and hydrological tolerances (Markle & Kozak 2018). Home ranges for *Plethodon* species are typically small but can vary by species and sex, and most *Plethodon* species exhibit male-biased dispersion (Liebgold et al. 2011). For example, Muñoz et al. (2016) estimated that mean home range sizes substantially differed for male (47.9–76.3 m^2) and female (4.9–10.6 m^2) eastern red-backed salamanders *P. cinereus*. Salamanders restricted to montane habitats often have limited thermal and moisture tolerances and thus are particularly vulnerable to increases in temperature, as their restricted ranges reduce the availability of climatic refugia on the landscape (Elsen & Tingley 2015, Markle & Kozak 2018).

Several studies have suggested that climate changes in the eastern USA will negatively impact montane woodland salamanders due to impacts on climatic suitability. For example, Milanovich et al. (2010) projected substantial declines in habitat suitability for 41 salamander species in the southern and central Appalachians, and Sutton et al. (2015) projected 25 species of salamanders in the northeastern USA would lose between 3 and 100% of their climate niche within this century. In addition to direct impacts on habitat quality, climate change could result in increased competition pressure for montane salamanders as lower elevation salamanders increase their local distributions into higher elevations (Fraser 1976, Griffis & Jaeger 1998, Reichenbach & Kniowski 2009). For example, Kroschel et al. (2014) documented an increase in the occurrence probability of *P. cinereus* at mid- and high elevations in West Virginia between 1978 and 2011, and Moskwik (2014) documented shifts in the elevation distribution of several woodland salamanders in North Carolina. There is evidence that the lower elevational distributions of high-elevation endemic woodland salamanders are restricted by climate (Grant et al. 2018), and thus lower elevation limits could contract with projected climate change. Furthermore, it is unlikely that woodland salamanders with strict microclimate requirements would be able to extend their lower elevational limits (Spotila 1972, Gifford & Kozak 2012, Hocking et al. 2013, Farallo et al. 2020).

One species of high conservation concern in the Central Appalachian region is the federally threatened Cheat Mountain salamander *P. nettingi*, a high-elevation endemic woodland salamander that is restricted to the Allegheny Mountains of West Virginia (Pauley 2008a). The known distribution of this species includes 81 areas of observed presence across a latitudinal and longitudinal distance of approximately 31 and 84 km, respectively. This species is typically observed at elevations greater than 900 m, but one observed population has documented observations as low as 730 m above sea level (Pauley 2008a). The US Fish and Wildlife Service (2009) identified climate change and increased interspecific competition as factors that could potentially impact the long-term viability of the species. At least 7 species from the Plethodontidae family of salamanders occur in sympatry with *P. nettingi* (Pauley 2008b), with *P. cinereus* being the most frequently observed sympatric species (Pauley 2005). Previous research suggests *P. cinereus* could compete with *P. nettingi* for food resources and nesting sites (Pauley & Clovis 1980, Green & Pauley 1987, Pauley 2005). Furthermore, recent field studies have documented an increasing prevalence of *P. cinereus* at sites historically dominated by *P. nettingi* (Kroschel et al. 2014, Rucker et al. 2022).

There is a strong need to project the influence of climate changes on habitat quality for *P. nettingi* and *P. cinereus* to inform current *P. nettingi* recovery action planning and improve our understanding of the influence of climatic conditions on woodland salamander habitat quality. Projecting how changes in climate may impact the occurrence of species at a distribution-wide scale requires knowledge and quantification of the species' ecological niche (Broennimann et al. 2012). Several field and modeling studies have provided insights into the ecological niche of *P. nettingi* (e.g. Dillard et al. 2008a, Pauley 2008a, Brown et al. 2022); specifically, that the occurrence of this species is associated with high-elevation forests with a red spruce *Picea rubens* or eastern hemlock *Tsuga canadensis* component (Pauley 2007, 2008a, 2022), and lithological and topographical characteristics are important (Dillard et al. 2008a). Little research has been conducted on the climatic niche of *P. nettingi*, but several studies have suggested that *P. nettingi* appear to be associated with high-moisture environments (Brooks 1948, Pauley 2007, Dillard et al. 2008a, Brown et al. 2022).

P. cinereus is one of the most wide-ranging and well-studied woodland salamanders in eastern North America. Most studies have found that *P. cinereus* occurrence and density is positively associated with mature deciduous forests (e.g. DeGraaf & Rudis 1990, Brooks 2001, Beier et al. 2012), but the species has a

high tolerance for a wide range of environmental conditions (Brooks 2001, Riedel et al. 2008, Markle & Kozak 2018). Several studies have found that weather and climatic variability influence growth rate and body size in *P. cinereus* (e.g. Caruso et al. 2014, Biddle et al. 2017, McCarthy et al. 2017), but little research has focused on quantifying the species' climatic niche. However, field studies in the Central Appalachian region indicate that occupancy probability declines from mid- to high elevations (Kroschel et al. 2014, Grant et al. 2018), and that frequency of reproduction may be lower at high elevations (Takahashi & Pauley 2010).

The purpose of this study was to improve our understanding of the potential for climate change to influence habitat quality and interspecific competition pressure for *P. nettingi*. We used an ecological niche (EN) modeling approach, which is frequently used for terrestrial species to assess species–habitat relationships and predict the relative quality of habitat within a focal area (Warren & Seifert 2011, Sillero et al. 2021). We estimated the ecological niches for *P. nettingi* and *P. cinereus* (within the regional distribution of *P. nettingi*) based on historical occurrence data, projected their contemporary and potential future geographic distributions based on the modeled environmental relationships and climate projections, and quantified ecological niche overlap between the 2 species. To our knowledge, this is the first study to use an EN modeling approach for investigating potential impacts of climate change on interspecific competition pressure between woodland salamanders.

2. MATERIALS AND METHODS

2.1. Study area and occurrence data

To delineate the geographic distribution of *Plethodon nettingi*, we obtained all documented occurrence locations for the species (n = 702) from the West Virginia herpetofauna database, held by the West Virginia Division of Natural Resources. This data set is primarily the result of *P. nettingi* survey efforts from one of the authors (T. K. Pauley), who has searched >1300 locations since 1976 and documented locations of all salamander species found (Pauley 2022). We created a minimum convex polygon, which is the smallest polygon that contains all occurrence locations (Burgman & Fox 2003), around observed locations on the periphery of the known distribution. Within the geographic distribution, we restricted the lower elevation boundary to 700 m, as all presence locations of *P. nettingi* were above 730 m. The distribution of *P. nettingi* encompassed approximately 186 565 ha in the Allegheny Mountains of eastern West Virginia, primarily within the Monongahela National Forest (Fig. 1). To quantify the ecological niche of *P. cinereus* within the regional distribution of *P. nettingi*, we restricted our area of inference to within 30 km of the *P. nettingi* distribution (n = 1246 occurrence locations), thus allowing for environmental conditions outside of the *P. nettingi* distribution boundary to inform the *P. cinereus* model.

2.2. Initial candidate landscape variables

We identified 9 candidate landscape predictors based on a literature review for *P. nettingi* habitat associations, findings of previous ENMs for *P. nettingi* and other high-elevation salamanders, and expert opinion from the *P. nettingi* working group. We obtained a 30 m^2 resolution digital elevation model (DEM) through the US Geological Survey National Elevation Dataset (1 arc-second; USGS 2017) and used the DEM to calculate elevation, heat load index (HLI), and topographical position index (TPI). We included HLI as a candidate predictor because aspect is a geophysical characteristic correlated with *P. nettingi* occurrence (Green & Pauley 1987, Pauley 2008a, Kroschel et al. 2014). As temperatures are not symmetrical around the north–south axis, slopes with afternoon sun have greater maximum temperatures than slopes with morning sun (McCune & Keon 2002). The HLI allows us to account for this variation, providing an accurate representation of the influence of aspect on habitat quality while avoiding the circular nature of aspect measurements (McCune & Keon 2002). We included TPI as a candidate predictor, which is calculated from DEMs by comparing the elevation of raster cells to the mean elevation of neighboring cells. Positive TPI values signify locations that have a higher topographic position (i.e. ridges and rises), while negative values signify areas that have a lower topographic position than surrounding cells (i.e. depressions, drainages, and valleys; Vinod 2017).

The occurrence of *P. nettingi* is associated with the occurrence of red spruce *Picea rubens* and eastern hemlock *Tsuga canadensis* (Pauley 2022). We used the LANDFIRE 2016 Remap existing vegetation type database (https://landfire.gov/data/lf2016) (hereafter existing vegetation) to create 4 vegetation categories, including red spruce and eastern hemlock, deciduous forest, 'other' forest (e.g. pine forests), and non-forest (e.g. grassland, development). We also

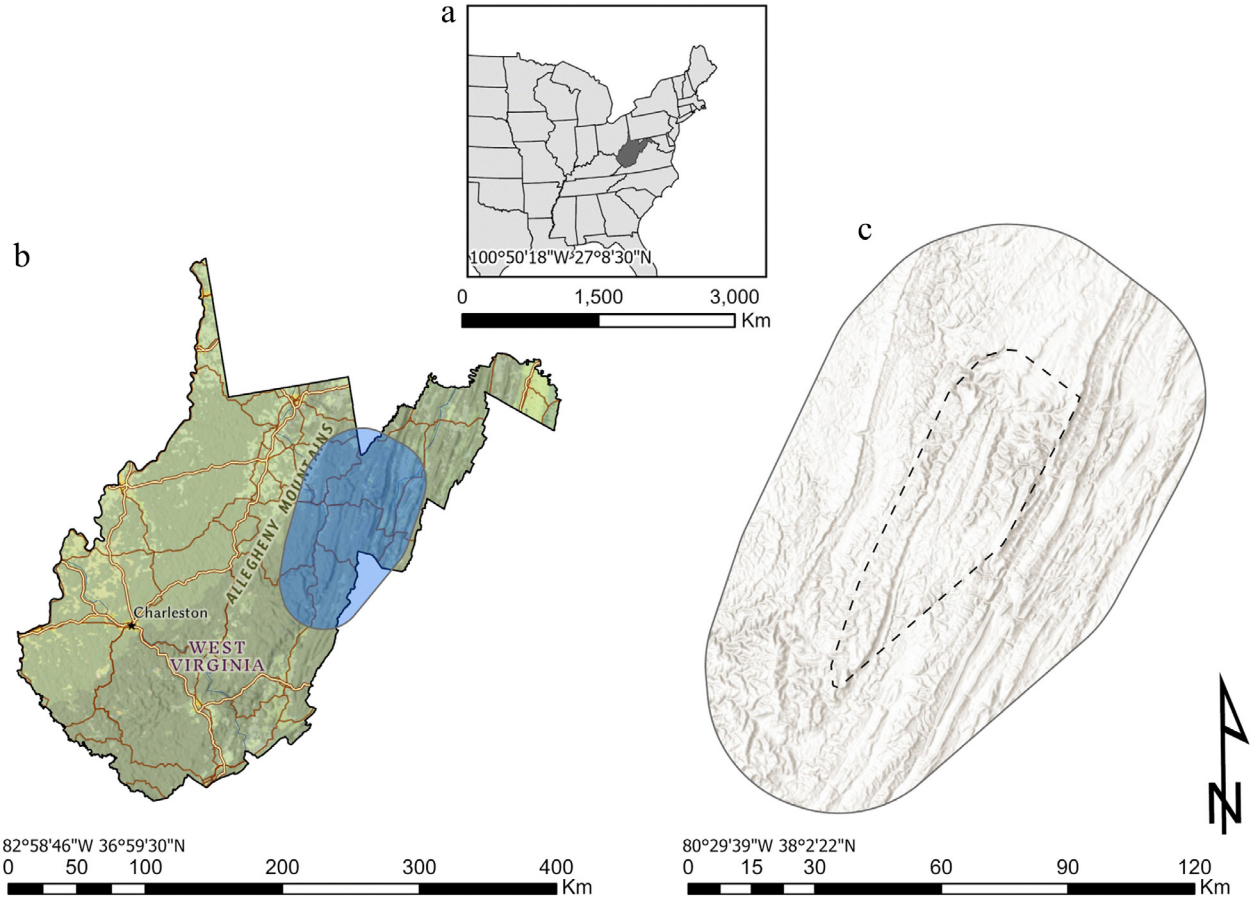

Fig. 1. (a) Geographic boundary for potential Cheat Mountain salamander *Plethodon nettingi* and eastern red-backed salamander *P. cinereus* habitat in the Allegheny Mountains of eastern West Virginia, USA. (b) The area of inference (blue shading) was delineated by creating a 30 km buffer around the periphery of observed *P. nettingi* locations and further restricted to elevations above 700 m for *P. nettingi*. (c) Known distribution of *P. nettingi* (dashed line) as defined by the periphery of observed locations. This area was used to estimate occurrence–habitat relationships and the potential influence of climate change on *P. nettingi* and to compare the environmental niches and habitat overlap of *P. nettingi* and *P. cinereus*

included canopy cover because woodland salamanders are typically associated with mature forests (Heatwole 1962, Petranka 1998, Means 2000, Blankers et al. 2012). We used the canopy cover layer created by Chazal et al. (2017), which was derived from the National Land Cover Database Tree Canopy Cover layer (Ruefenacht et al. 2015).

We included 4 candidate predictors representing soil and geological characteristics. Euclidean distance to rocky habitat was derived from the West Virginia Terrestrial Habitat Map, which was created by the West Virginia Division of Natural Resources based on the Northeast Terrestrial Habitat Map (NTHM; Ferree & Anderson 2013) with some revisions specific to West Virginia, including addition of completed habitat layers, reclassification of similar ecosystems, and corrections of known errors. The NTHM was developed from NatureServe's Ecological System Classification (Comer et al. 2003) and the National Vegetation Classification (FGDC 2008). Soil type was derived from the GSSURGO database (Soil Survey Staff 2014) and reclassified to represent the major soil orders associated with *P. nettingi* occurrence (Alfisols, Inceptisols, Spodosols, and Ultisols; all other categories reclassified as 'other') using the official soil description for each soil type located within the study area. Soil skeletal type was derived from the soil taxonomic class information. Rock type classification (surface geology) was created by the West Virginia Geological and Economic Survey and obtained from the West Virginia Division of Natural Resources. This layer was reclassified into 6 categories: alluvium, limestone, sandstone, shale, and siltstone (all other categories reclassified as 'other'). We created landscape variable layers using ArcGIS (v.10.7; Environmental Systems Research Institute).

2.3. Initial candidate climate variables

We used 30 yr averages (1981–2010) of estimated monthly precipitation and temperature to derive contemporary climate. Gridded climatic data from WorldCLIM (approximately 1 km^2 resolution) were statistically downscaled to approximately 0.5 km^2 by CLIMsystems. The cells were then clipped to the study area extent and resampled to the cell size of the ENM (30 m^2). We calculated 19 bioclimatic variables from the contemporary climate that are widely used in ENMs (Fick & Hijmans 2017). We derived the median, 10^{th} percentile, and 90^{th} percentile for projected future climatic conditions at mid-century (2050) and end-of-century (2100) using an ensemble of 31 climate models and used the 4.5 and 8.5 representative concentration pathways (RCPs) to account for multiple potential future emissions scenarios (Knutti et al. 2010). We created climate variable layers using R (v.4.2.1; R Core Team 2022) with the packages 'dismo' (v.1.3-9; Hijmans et al. 2022a) and 'raster' (v.3.5-15; Hijmans et al. 2022b).

2.4. Final candidate variables

We used a variance inflation factor (VIF) to assess correlations among the candidate landscape and climate predictors; predictors with VIF > 10 were considered to have high collinearity with other predictors (Hair et al. 1995). For highly correlated predictors, we retained the predictor with the highest explanatory power based on comparative single-variable logistic regressions with the *P. nettingi* data set (Marcoulides & Raykov 2019). Our final candidate predictors included 8 landscape variables and 3 climate variables (Table 1): existing vegetation, canopy cover, elevation, HLI, TPI, rock type, soil type, Euclidean distance to rocky habitat, annual mean temperature, temperature seasonality (i.e. the standard deviation of monthly temperature multiplied by 100), and precipitation in the warmest quarter (i.e. precipitation from June to August). Our final candidate predictors were assessed again with a VIF, and the highest VIF score returned was 1.30.

2.5. Ecological niche modeling

To estimate relationships between species occurrence and environmental variables for *P. nettingi* and *P. cinereus*, we used an EN modeling approach (Guisan & Zimmerman 2000). During preliminary analyses, we tested the performance of several models, including random forest (RF) with observed non-detection locations as absence points, RF with background locations as pseudo-absence points equal to the number of presence points for each species, logistic regression with the same pseudo-absence points as RF, and MaxLike with randomly generated pseudo-absence points equal to the number of presence points for each species. We found the RF model with pseudo-absence points had substantially higher explanatory power based on accuracy metrics (i.e. balanced accuracy, specificity error, and sensitivity error) than the other models, and we used this model for the final analyses.

RF is a machine learning model that uses bootstrap sampling to create multiple decision trees, with each decision tree grown with a subset of randomized predictors (Breiman 2001). Many uncorrelated trees operating as an ensemble typically outperforms the use of an individual tree approach (i.e. classification and regression trees [CART]) in predictive performance and minimizes the overfitting that commonly occurs in CART models (Prasad et al. 2006). RF ENMs have been found to perform well in predicting the distributions of many vegetation and wildlife species, including amphibians (e.g. Girardello et al. 2010, Murphy et al. 2010).

We created ENMs for the focal species and used the estimated environmental relationships to project contemporary and potential future changes in habitat quality. We withheld a random subset of 10% of the original data to create a validation data set, and the training control was created using a 10-fold cross-validation approach. We used the 'tuneRF' function

Table 1. Final landscape and climatic candidate predictors used for ecological niche modeling for the Cheat Mountain salamander *Plethodon nettingi* and eastern red-backed salamander *P. cinereus* in the Allegheny Mountains. All continuous variables were centered and scaled prior to analyses

Landscape covariates	References
Elevation	Pauley (2007), Dillard et al. (2008a)
Heat load index	Dillard et al. (2008a)
Existing vegetation type	Dillard et al. (2008a), Pauley (2008a,b)
Soil type	Expert opinion
Canopy cover	Margenau et al. (2020)
Rock type (surface geology)	Dillard et al. (2008b)
Topographical position index	Jacobsen et al. (2020)
Euclidean distance to rocky habitat	Expert opinion
Climate covariates	**References**
Mean annual precipitation	Sutton et al. (2015), Jacobsen et al. (2020)
Precipitation in warmest quarter	Sutton et al. (2015), Jacobsen et al. (2020)
Temperature seasonality	Sutton et al. (2015), Jacobsen et al. (2020)

to conduct a random search and generate accuracy estimates to select the most efficient tune length. We first created a global model containing all candidate predictors and then used backward selection (Speiser 2021) based on the mean decrease in accuracy to determine the importance of each predictor to the model. Through backward selection, variables were removed based on their importance until accuracy metrics (i.e. balanced accuracy, specificity error, and sensitivity error) did not improve. All models were optimized for the receiver operating classification curve (ROC), and the out-of-bag (OOB) error was calculated for each prediction model. After the most accurate model was selected, we predicted classes for the independent validation data set, and an area under the curve (AUC) score was calculated. We considered models with AUC > 0.70 to be informative and AUC > 0.90 to be highly informative (Guisan et al. 2017).

We used accumulated local effects (ALE) plots to calculate model-estimated covariate relationships (Molnar et al. 2018). These plots describe how each individual predictor influences the output prediction of RF models by isolating the changes in a prediction that results from the change in that predictor. ALE plots are an alternative to partial dependence plots, which can be difficult to interpret when there are many predictors in a model and some of those predictors are correlated with one another (Apley & Zhu 2020). We also quantified niche similarity between the 2 focal species within the current geographic distribution of *P. nettingi*. Using the contemporary ENM predictions within the *P. nettingi* distribution, we calculated the *I* statistic, which estimates the niche similarity of 2 ENMs on a scale of 0 (no niche overlap) to 1 (complete niche overlap; Warren et al. 2008). To compute this metric, we used the package 'spatialEco' (v.1.3-7; Evans 2021) in R.

We used the model-estimated covariate relationships to project spatially explicit contemporary habitat quality for *P. nettingi* and *P. cinereus*. We used the *P. cinereus* area of inference (i.e. *P. nettingi* distribution boundary + 30 km) for both projections to identify areas potentially suitable for *P. nettingi* that are outside of their known distribution. We created a mask from the DEM layer and loaded the final predictor covariate raster layers into a raster stack (i.e. collection of rasters with the same extent and resolution). Using the raster stack and the final model, we predicted the relative habitat quality value for each cell across the study area. The prediction raster was exported and used to create a visual representation of habitat quality for the study area with values that ranged from 0 (lowest quality) to 1 (highest quality; Rather et al. 2020). To maximize the value of this product for managers, we grouped quality scores into 4 categories: high-, moderate-, and low-quality cells, and non-suitable cells. The category thresholds were established by *P. nettingi* managers with the West Virginia Division of Natural Resources and US Fish and Wildlife Service West Virginia Ecological Field Office to reflect both regulatory and management needs. The low-quality threshold was delineated by extracting the quality scores in which specificity error was minimized (with an accepted false positive rate <5%). The moderate-quality threshold was delineated by extracting the quality scores in which sensitivity and specificity were balanced (with an accepted false negative rate of 5–15%). The high-quality threshold was delineated by extracting the quality scores in which sensitivity error was minimized (with an accepted false negative rate of <5%).

For both species, we used the best approximating model to project the potential influence of climate change on habitat availability and quality at the mid-century and end-of-century time periods (i.e. 2050 and 2100). We also quantified the change in the overlap of moderate- and high-quality habitat between the 2 focal species. We conducted this analysis in ArcMap (v.10.7-1) using the tabulate intersection geoprocessing tool. Model construction and plotting was conducted in R using the 'raster' (v.3.5-15; Hijmans et al. 2022b), 'rgdal' (v.1.5-28; Bivand et al. 2021), 'sp' (v.1.4-4; Pebesma & Bivand 2005, Bivand et al. 2013), 'caret' (v.6.0-93; Kuhn 2022), 'rpart' (v.4.1-15; Therneau & Atkinson 2019), 'randomForest' (v.4.6-14; Liaw & Wiener 2002), and 'iml' (v.0.10.1; Molnar et al. 2018) packages.

3. RESULTS

3.1. Ecological niches

The best approximating model for *Plethodon nettingi* included elevation, existing vegetation, HLI, canopy cover, soil type, rock type, Euclidean distance to rocky habitat, annual mean temperature, temperature seasonality, and precipitation in the warmest quarter. This model returned an OOB error of 11.37% and an AUC score of 0.96. The best approximating model for *P. cinereus* included elevation, HLI, canopy cover, rock type, Euclidean distance to rocky habitat, annual mean temperature, temperature seasonality, and precipitation in the warmest quarter. This model returned an OOB error of 11.53% and an AUC score of 0.94.

For the test of niche similarity, we found that the environmental niches of the 2 species were 80.5% similar based on the *I* metric. Based on mean decrease

in accuracy, the 4 most influential environmental variables for *P. nettingi* were elevation, rock type, precipitation in the warmest quarter, and annual mean temperature (Fig. 2); for *P. cinereus*, the most influential variables were precipitation in the warmest quarter, annual mean temperature, elevation, and temperature seasonality (Fig. 3). For *P. nettingi*, the ALE plots indicated that species presence was positively associated with elevation, canopy cover, presence of red spruce and eastern hemlock, presence of the sandstone rock type, presence of the Spodosol and Inceptisol soil types, temperature seasonality, and precipitation in the warmest quarter (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/n057p103_supp.pdf). The ALE plots indicated that *P. nettingi* presence was negatively associated with HLI, Euclidean distance to rocky habitat, and annual mean temperature (Fig. S1). For *P. cinereus*, the ALE plots indicated that species presence was positively associated with elevation, temperature seasonality, canopy cover, and presence of the sandstone rock type, and negatively associated with HLI, Euclidean distance to rocky habitat, annual mean temperature, and precipitation in the warmest quarter (Fig. S2).

3.2. Contemporary habitat availability and quality

The best approximating model for *P. nettingi* identified 6.6% (12 062 ha), 23.2% (42 316 ha), 12.4% (22 514 ha), and 57.8% (105 199 ha) of cells within the known *P. nettingi* distribution as high-quality habitat, moderate-quality habitat, low-quality habitat, and non-habitat, respectively (Fig. 4). Most (75%) of the high-quality habitat occurred within the high elevation regions of the Monongahela National Forest. The model identified an additional 8538 ha and 112 107 ha of high- and moderate-quality cells, respectively, within 30 km of the known geographic distribution (Fig. 4). The best approximating model for *P. cinereus* identified 84.3% (1 274 198 ha), 12.0% (181 267 ha), 3.3% (49 175 ha), and 0.5% (7606 ha) of the cells within the area of inference as high-quality habitat, moderate-quality habitat, low-quality habitat, and non-habitat, respectively (Fig. 4). Much of the high-quality *P. nettingi* habitat was classified as moderate- or low-quality habitat for *P. cinereus* (Fig. 4).

3.3. Future habitat availability and quality

For *P. nettingi*, the climate models projected a 10–46% decrease in high-quality habitat and 25% decrease to a 27% increase in moderate-quality habitat by 2050, and a 63–100% decrease in high-quality habitat and a 26% increase to 71% decrease in moderate-quality habitat, respectively, by 2100 (Table 2, Fig. 5). For *P. cinereus*, the median climate models projected a 10–19% increase in high-quality habitat and 43–100% decrease in moderate-quality habitat by 2050, and a 14–19% increase in high-quality habitat and 67–100% decrease in moderate-quality habitat by 2100 (Table 2, Fig. 6).

Within the geographic distribution of *P. nettingi*, the percentage overlap of high and moderate-quality habitat between *P. nettingi* and *P. cinereus* differed between the contemporary and projected future climatic conditions. Under contemporary climatic conditions, overlap in high-quality habitat was 23.0%, meaning that 23.0% of the area identified as high-quality habitat for *P. nettingi* was also high-quality habitat for *P. cinereus*. For the 2050 median climate change projections, overlap in high-quality habitat changed to 19.6–44.4%, although we note that very little high-quality habitat remained for *P. nettingi*. Since our model projected no high-quality habitat for *P. nettingi* in 2100 based on the median climate change projections, there was no overlap between the 2 species. Under contemporary climatic conditions, overlap in moderate-quality habitat was 49.2%. For the 2050 median climate change projections, overlap in moderate-quality habitat changed to 20.9–83.7%, and for the 2100 median climate change projections, overlap in moderate-quality habitat increased even further to 80.6–82.9%. Furthermore, the overlap in moderate-quality *P. nettingi* habitat with high-quality *P. cinereus* habitat in 2100 was 5.5–6.4%.

4. DISCUSSION

Our study suggests that climatic change could result in the majority of high-quality *Plethodon nettingi* habitat being lost this century. This finding is consistent with previous climate change response studies for high-elevation endemic salamanders in the Appalachian region (Milanovich et al. 2010, Sutton et al. 2015, Jacobsen et al. 2020). However, Sutton et al. (2015) projected that *P. nettingi* could lose 98% of their potential habitat by 2050. The more robust analysis we performed here resulted in more conservative projections of habitat loss by mid-century, but still indicates that Cheat Mountain salamander habitat availability and quality will decrease due to climate change. Additionally, our results suggest that *P. nettingi* has a restricted contemporary geographic

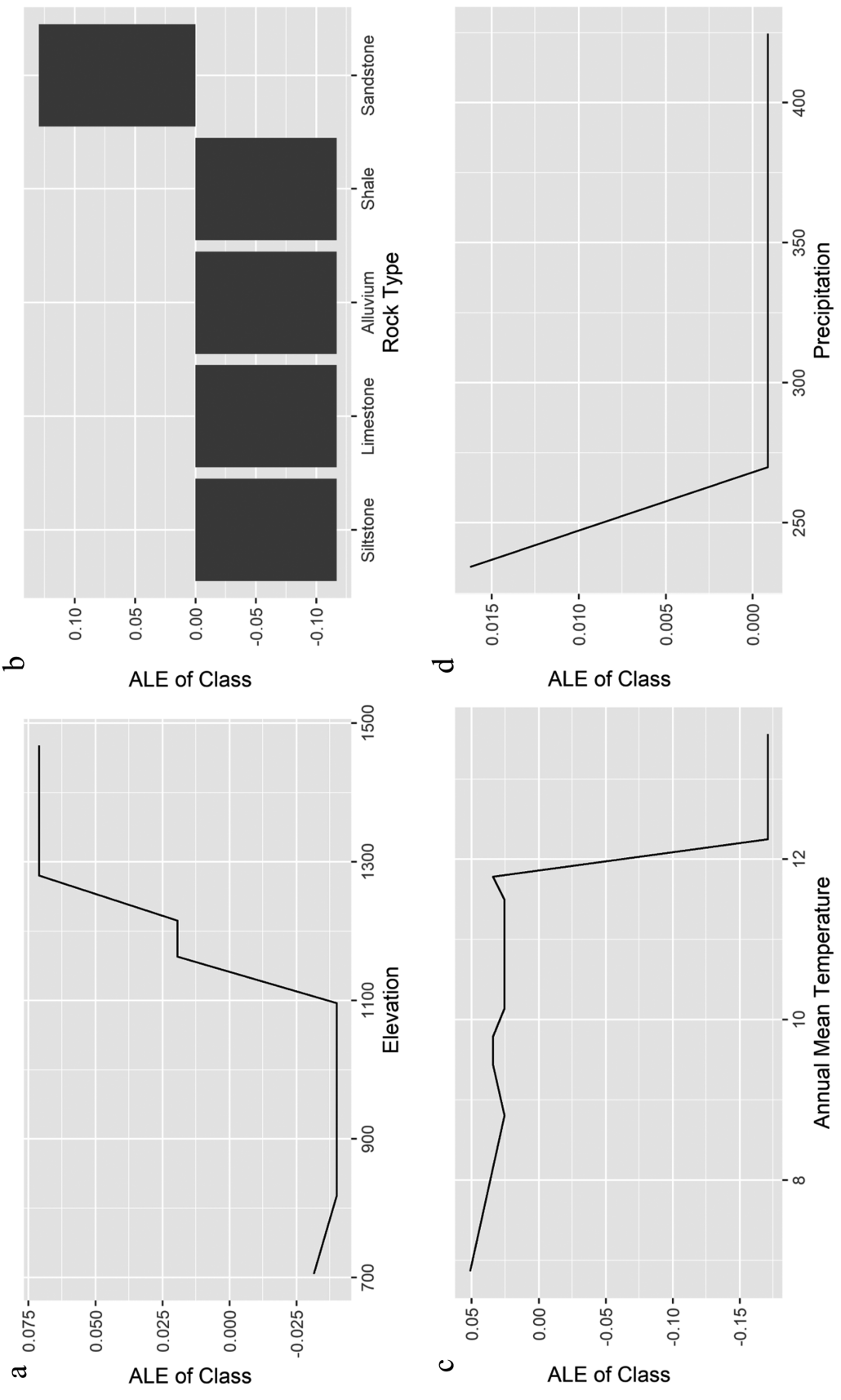

Fig. 2. Accumulated Local Effect (ALE) plots of the 4 most influential environmental variables for occurrence of Cheat Mountain salamanders *Plethodon nettingi* in the Allegheny Mountains. ALE plots represent the local effect of each predictor isolated from the other predictors. Seven continuous predictors and 3 categorical predictors were used to model habitat quality across the study area at 30 m^2 resolution. The most influential predictors were (a) elevation, (b) rock type, (c) temperature (annual mean; °C), and (d) precipitation (warmest quarter; mm). *Y*-axis: ALE values for species occurrence; *x*-axis: values of the predictor. See Fig. S1 for ALE plots of all environmental variables

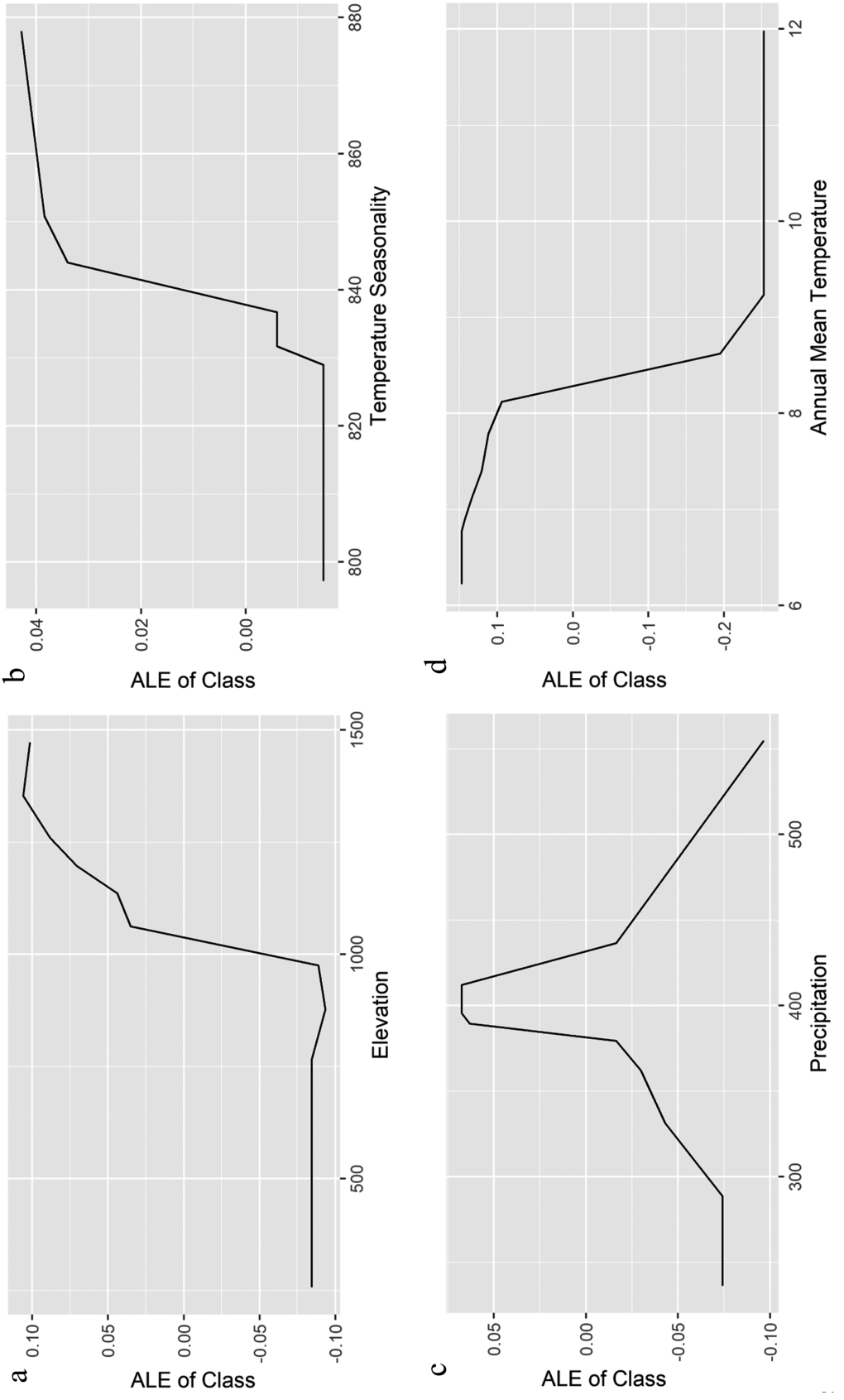

Fig. 3. Same as Fig. 2 but for eastern red-backed salamanders *Plethodon cinereus*. Seven continuous predictors and 2 categorical predictors were used to model habitat quality across the study area at 30 m^2 resolution. The most influential predictors were (a) elevation, (b) temperature seasonality (i.e. the standard deviation of monthly temperature multiplied by 100), (c) precipitation (warmest quarter; mm), and (d) temperature (annual mean; °C)

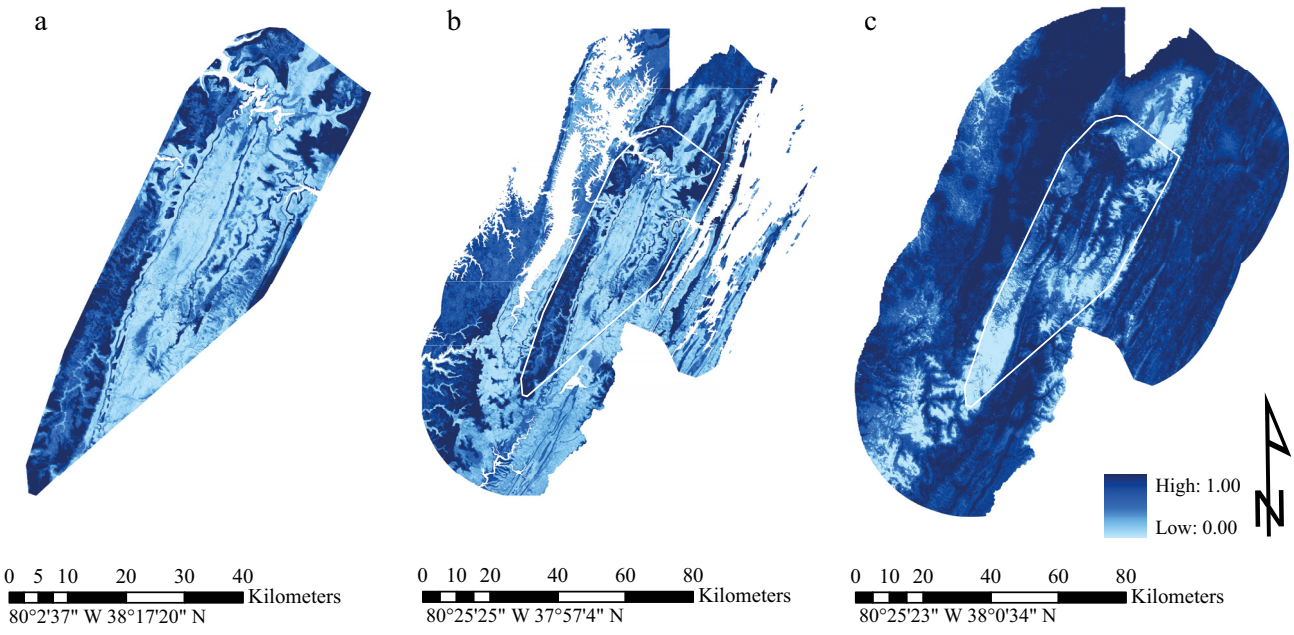

Fig. 4. Contemporary relative habitat quality derived from random forest ecological niche models (ENMs) for the Cheat Mountain salamander *Plethodon nettingi* and eastern red-backed salamander *P. cinereus* in the Allegheny Mountains, including habitat quality for *P. nettingi* within (a) the known geographic extent of the species and (b) the broader area of inference in eastern West Virginia, and (c) habitat quality for *P. cinereus*. Solid white line in (b,c): known geographic extent of *P. nettingi*. For *P. nettingi*, the model included 10 predictors: elevation, forest type (Landfire), canopy cover, soil type, heat load index, rock type classification, Euclidian distance to rocky habitat, annual mean temperature, temperature seasonality, and precipitation in the warmest quarter (out-of-bag error [OOB]: 11.37%; area under the curve [AUC]: 0.9268). For *P. cinereus*, the model included 8 predictors: elevation, Euclidian distance to rocky habitat, canopy cover, heat load index, rock type classification, annual mean temperature, temperature seasonality, and precipitation in the warmest quarter (OOB error: 14.72%; AUC: 0.9397)

distribution, consistent with previous modeling and field studies for this species (e.g. Dillard et al. 2008a, Pauley 2022). Based on our ENM, the majority of high-quality habitat occurs within the Monongahela National Forest, which is largely protected from development.

Our ENMs support and quantify previous empirically based inferences for *P. nettingi* habitat associations, particularly that the occurrence of the species is positively associated with red spruce, Spodosols, and rocky habitat (Pauley 2008a, Dillard et al. 2008b). Red spruce occurrence in West Virginia is associated with spodic soils, which are strongly acidic (Adams et al. 2019). Brown et al. (2022) speculated that *P. nettingi* may have a competitive advantage over *P. cinereus* in red spruce forests due to the lower tolerance of *P. cinereus* to acidic soils (Wyman & Hawksley-Lescault 1987, Sugalski & Claussen 1997). *P. nettingi* is one of several high-elevation endemic salamanders in the Appalachian region that are strongly associated with red spruce (e.g. Weller's salamander *Plethodon welleri*, pygmy salamander *Desmognathus wrighti*; Petranka 1998, Rossell et al. 2018), and thus are presumably adapted to acidic soil conditions. Pauley (2008b) suggested the strong association of *P. nettingi* with rocky habitat was likely a result of population loss in less rocky areas during historical landscape-scale clearcutting and wildfires in West Virginia.

Our projection that climatic changes will increase habitat quality at high elevations for *P. cinereus* is consistent with recent empirical research in the study area. Rucker et al. (2022) quantified climatic changes and estimated *P. cinereus* occupancy probability over a 34 yr period using 43 long-term monitoring plots in a high-elevation red spruce forest occupied by *P. nettingi* and found that minimum temperature at the site and *P. cinereus* plot occupancy increased over time. Kroschel et al. (2014) assessed changes in the occupancy probability of *P. cinereus* between 1978–1979 and 2011 along elevation gradients at 4 localities within the *P. nettingi* distribution and found that occupancy increased over time at sampling locations below 1300 m. *P. cinereus* is currently present at 89% of the known *P. nettingi* localities but relative prevalence of the 2 species is highly variable among sites (Pauley 2022). To date, no studies have been conducted on competition dynamics in the wild between these species, and thus additional research is needed to understand how increasing the density of *P. cinereus* could impact *P. nettingi* population viability.

Table 2. Percent change in habitat quality predictions for the Cheat Mountain salamander *Plethodon nettingi* and eastern red-backed salamander *P. cinereus* in the Allegheny Mountains based on the median, 10th percentile, and 90th percentile for projected future climatic conditions at mid-century (2050) and end-of-century (2100) using an ensemble of 31 climate models and RCP 4.5 and RCP 8.5. Percent change was calculated relative to estimated contemporary habitat quality. Dash values represent 'no data' as we did not calculate the 10th and 90th percentiles for contemporary climate. Zero values are 0 ha of the area of inference fell within that category

Climate model	Quality category	10th Area (ha)	50th Area (ha)	90th Area (ha)
Cheat Mountain salamander				
Contemporary	High quality	–	12062	–
	Moderate quality	–	42316	–
	Low quality	–	22514	–
	Non-suitable	–	104846	–
2050 RCP 4.5	High quality	10900	9680	10390
	Moderate quality	53407	50043	40915
	Low quality	27952	25090	24772
	Non-suitable	89479	96926	105660
2050 RCP 8.5	High quality	6545	8053	9905
	Moderate quality	57999	52615	31814
	Low quality	27050	20304	25589
	Non-suitable	90144	100767	114430
2100 RCP 4.5	High quality	7082	0	0
	Moderate quality	57555	52493	32839
	Low quality	27070	20694	25074
	Non-suitable	90032	108551	123825
2100 RCP 8.5	High quality	4468	0	0
	Moderate quality	66952	35208	12312
	Low quality	40670	40278	35010
	Non-suitable	69649	106253	134417
Eastern red-backed salamander				
Contemporary	High quality	–	1274198	–
	Moderate quality	–	181267	–
	Low quality	–	49175	–
	Non-suitable	–	7606	–
2050 RCP 4.5	High quality	1405796	1497105	1512441
	Moderate quality	103228	15416	81
	Low quality	4085	0	0
	Non-suitable	0	0	0
2050 RCP 8.5	High quality	1459456	1512498	1512511
	Moderate quality	53606	23	11
	Low quality	1	0	0
	Non-suitable	0	0	0
2100 RCP 4.5	High quality	1452788	1512401	1512506
	Moderate quality	59681	120	16
	Low quality	53	0	0
	Non-suitable	0	0	0
2100 RCP 8.5	High quality	1512521	1512521	1512521
	Moderate quality	0	0	0
	Low quality	0	0	0
	Non-suitable	0	0	0

However, these species are rarely found occupying the same cover object (Pauley 2022), indicating *P. cinereus* likely reduces microhabitat availability for *P. nettingi*. Furthermore, Brophy & Reichenbach (2020) found that removal of *P. cinereus* increased the relative abundance of another regional high-elevation endemic species, the Peaks of Otter salamander *P. hubrichti*.

Most additional studies assessing responses of high-elevation woodland salamanders to climate change indicate that these species may be a particularly vulnerable group of vertebrates (e.g. Milanovich et al. 2010, Barrett et al. 2014, Jacobsen et al. 2020). Recent research suggests that amphibians may have the physiological capacity to adapt to rapidly changing environmental conditions (Urban et al. 2014,

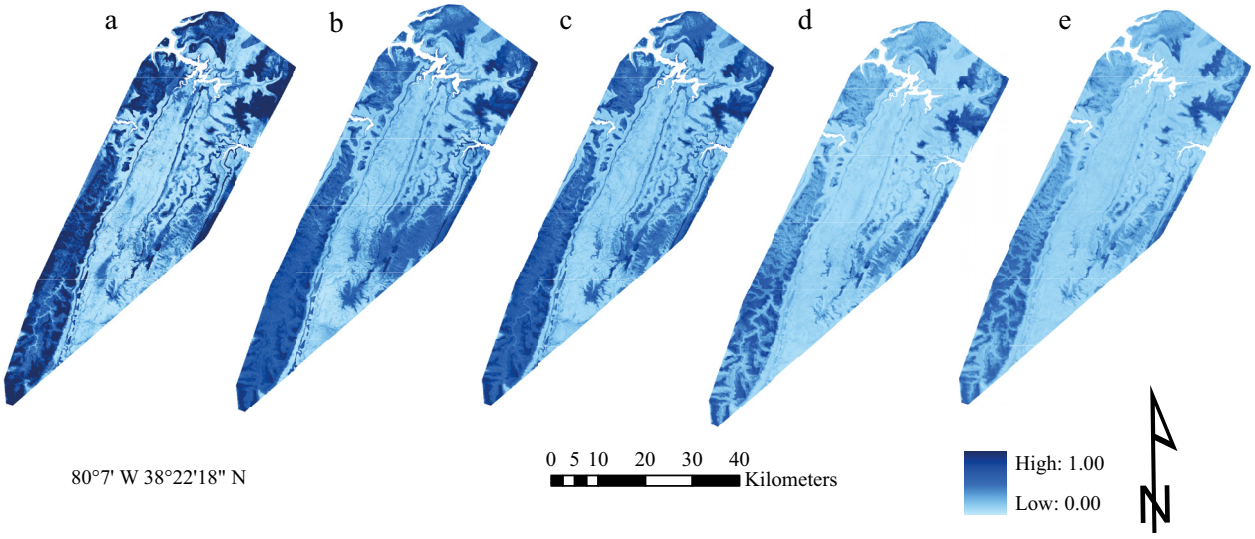

Fig. 5. Future relative habitat quality for the Cheat Mountain salamander *Plethodon nettingi* in the Allegheny Mountains derived from random forest ecological niche models (ENMs) and median future climate projections from a 31-model ensemble. The best approximating ENM was used to project mid-century and end-of-century (i.e. 2050 and 2100) habitat quality and availability based on representative concentration pathway (RCP) 4.5 and RCP 8.5. Projections include (a) contemporary ENM, (b) mid-century 4.5 RCP, (c) end-of-century 4.5 RCP, (d) mid-century 8.5 RCP, and (e) end-of-century 8.5 RCP

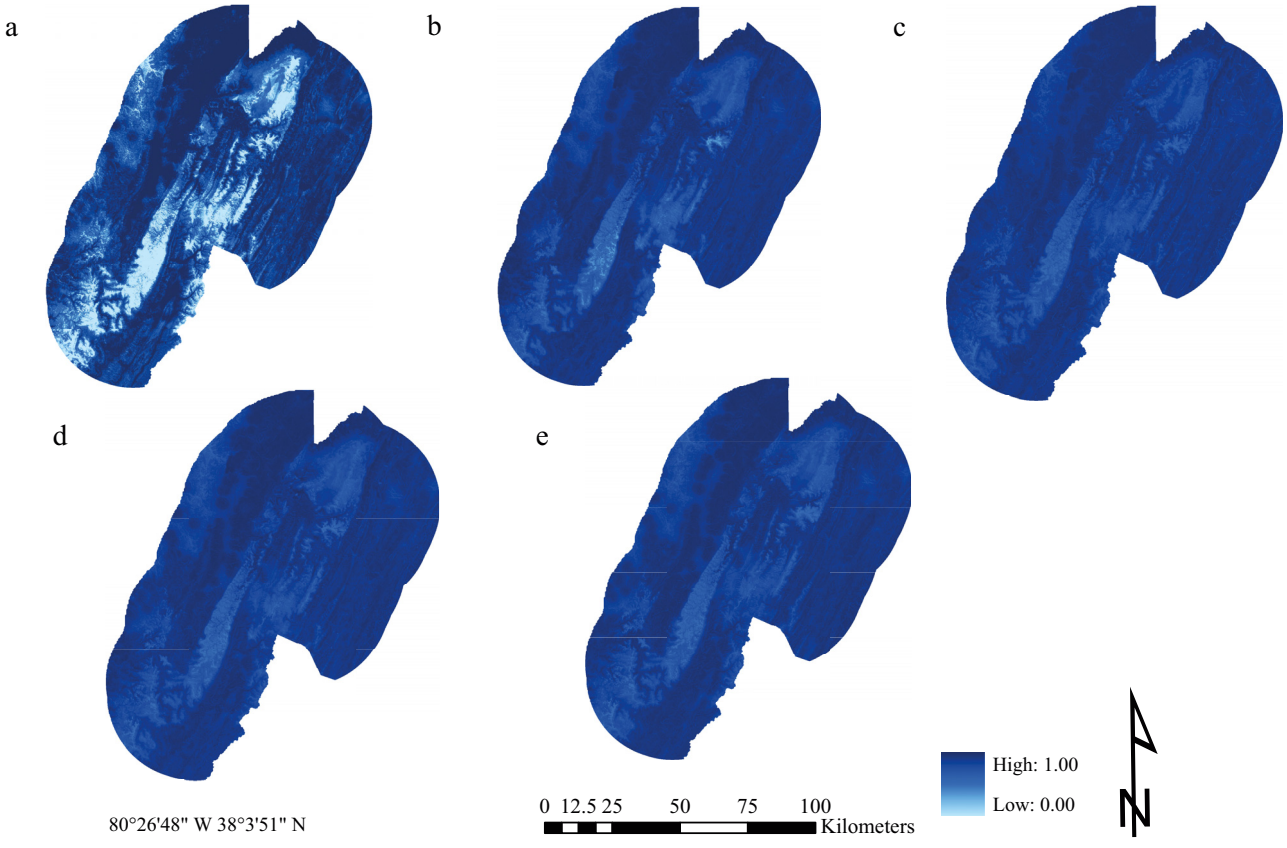

Fig. 6. Same as Fig. 5 but for the eastern red-backed salamander *Plethodon cinereus*. Projections include (a) contemporary ENM, (b) mid-century 4.5 RCP, (c) end-of-century 4.5 RCP, (d) mid-century 8.5 RCP, and (e) end-of-century 8.5 RCP

Lyons & Kozak 2020). However, the ability of salamanders to adapt to invasion of competing species is unclear. Additional research is needed to better understand the potential for high-elevation salamanders to adapt physiologically or behaviorally to warming environments, as well as invasion of potential competitors, as traditional ENMs do not consider that occurrence–climate relationships may change in the future, potentially overestimating climate change vulnerability.

Our study suggests that climate change will negatively impact habitat availability and quality for a high-elevation endemic salamander while increasing habitat quality for a generalist species. Our results can inform management strategies for *P. nettingi*, a federally threatened species. In particular, the contemporary ENM can be used to direct survey efforts that could result in the discovery of additional *P. nettingi* populations, as well as identify target areas for habitat restoration and management, and design experiments to address information gaps. The future projection models can be used to identify focal management areas to maximize the probability of persistence of this species as the climate changes.

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