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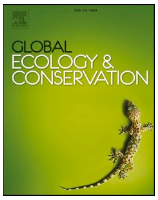

Climatic and landscape vulnerability of the eastern Hellbender salamander (*Cryptobranchus alleganiensis alleganiensis)*

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ABSTRACT

Developing strategies to protect biodiversity is an overriding goal of conservation biology. Amphibians represent a taxon under decline due to the collective impacts of anthropogenic land use, emerging pathogens, pollution, and climate change. One salamander species that is currently in decline throughout its range is the eastern Hellbender (*Cryptobranchus alleganiensis alleganiensis*). Population declines of this fully aquatic species are driven by a combination of anthropogenic stressors, yet, a landscape scale vulnerability analysis has not been conducted. We analyzed the spatially-explicit vulnerability of eastern Hellbenders as a combined measure of threats from current land use, future climate change, and paucity of formally protected habitat. Overall, we found that projected loss of climatic suitability and relative lack of habitats with formal protection were the primary drivers of vulnerability. Of the ecoregions that accounted for greater than 1% of the predicted suitable habitat for the eastern Hellbender, the Northern Allegheny Plateau, Erie Drift Plains, Interior Plateau, and Interior River Valleys and Hills ecoregions were predicted as most vulnerable. As 35.6% of the total predicted suitable habitat for the eastern Hellbender occurs in these ecoregions, it is imperative that conservation efforts are implemented in these landscapes to reduce vulnerability. Establishment of permanent conservation areas, continued conservation and monitoring of currently protected habitats, increasing stream connectivity, and restoration of targeted stream ecosystems are the most attainable strategies to decrease vulnerability for the eastern Hellbender.

1. Introduction

Concerns for the conservation of biodiversity have increased given global trends of human-influenced species declines and extinctions (Butchart et al., 2010), with current rates of extinction estimated as significantly greater than accepted background rates (De Vos et al., 2014). The primary drivers of these declines are various and include overharvesting, habitat destruction and degradation, pollution, emerging pathogens, and climate change (Johnson et al., 2017). One of the goals of conservation biology is to identify vulnerable ecosystems and develop strategies to protect biodiversity that occurs within these habitats. However, the synergistic impacts of landscape alteration and climate change increases the difficulties of establishing long-term strategies to conserve biodiversity and the landscapes they inhabit (Oliver et al., 2016; Northrup et al., 2019), especially for species with large or under-surveyed

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geographic ranges.

Species Distribution Models (SDMs) have become increasingly important tools to better delineate species distributions and quantify climate and land-use patterns, which are all effective for conservation planning at the landscape scale (e.g., Arbuckle and Downing,

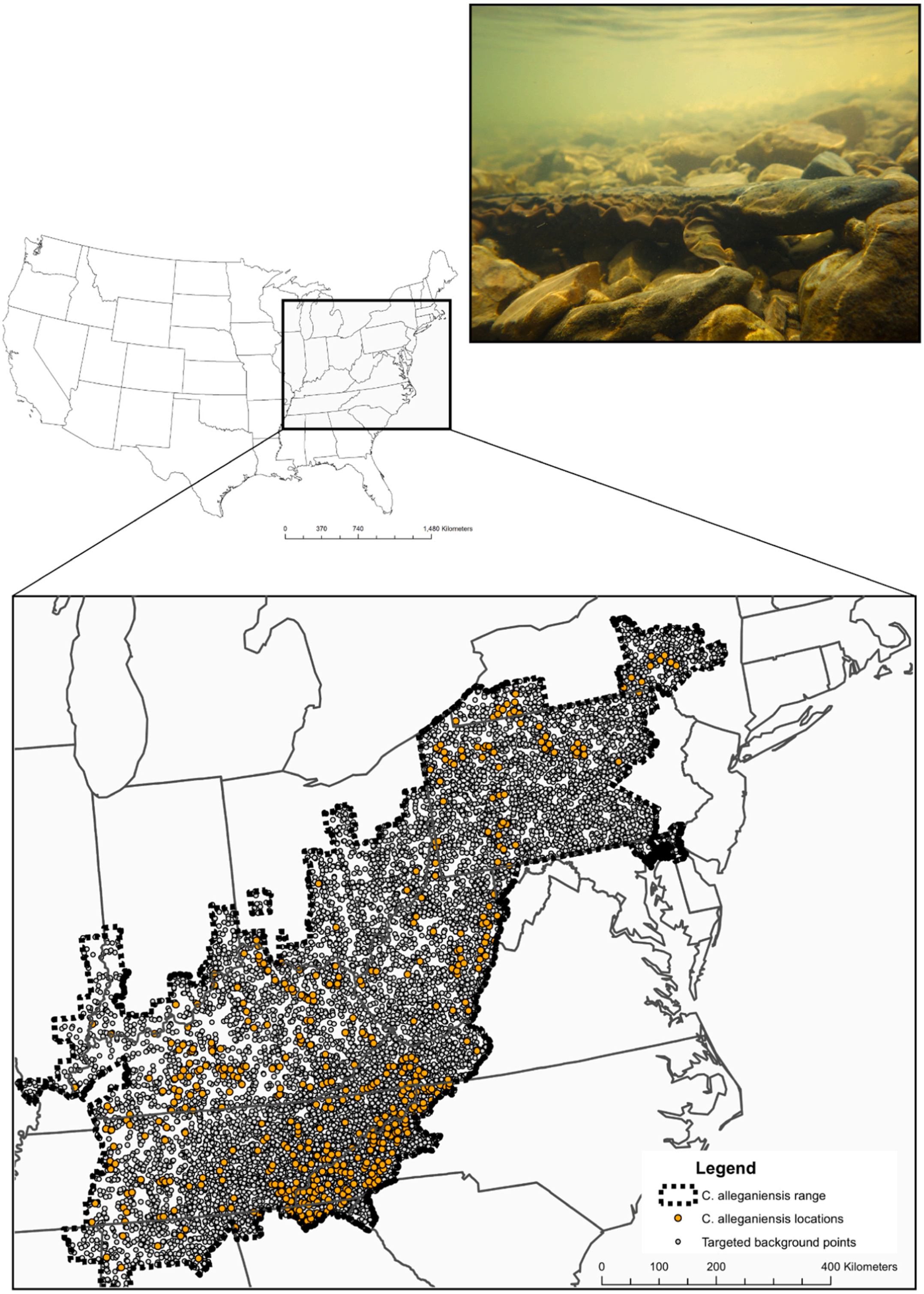

Fig. 1. Eastern Hellbender presence localities (orange points) and background localities (grey points) of sympatric salamander species used to create the bias file. Top right: Adult eastern Hellbender (photograph credit: WBS).

2002). Briefly, SDMs combine species locality data and georeferenced environmental data to predict geographic areas that contain suitable conditions for taxa of interest (Costa et al., 2010). Additionally, SDMs allow for the prediction of habitat suitability in the future through incorporation of climate and land use change models (e.g., Milanovich et al., 2010; Gifford and Kozak, 2012). Previous work has suggested that under climate change, climatically suitable habitat may shift into areas with less protection (Araújo et al., 2004; Hannah et al., 2007), highlighting the importance of incorporating these models into conservation planning. This concept is especially important for species with relatively low vagility (e.g., Della Rocca and Milanesi, 2020), which decreases the ability of the organism to migrate to suitable habitats in the face of habitat and climate change.

Although a majority of native biodiversity is predicted to be impacted by anthropogenic climate and land use change, amphibians represent a taxon in particularly rapid decline (Houlahan et al., 2000; Semlitsch, 2003), with at least a third of the more than 6000 currently recognized species threatened with extinction (Wake and Vredenburg, 2008). Amphibians are threatened simultaneously on multiple spatial scales, both regionally (e.g., climate change, pathogens) and locally (e.g., habitat destruction, fragmentation, invasive species). Global climate change represents a broad-scale phenomenon that impacts many biological communities and their associated habitats. Ectotherms are believed to be particularly at risk (Paaijmans et al., 2013), and large changes in climatic suitability has been projected for many species (Milanovich et al., 2010; Sutton et al., 2015). In addition, habitat loss via anthropogenic disturbance, including urbanization, deforestation, and agricultural land uses presents another primary threat to amphibian populations (Barrett and Guyer, 2008; Cordier, 2021). These cumulative effects reduce and often isolate populations across an increasingly fragmented landscape (Dodd and Smith, 2003).

Among the growing list of amphibian species currently at risk of decline is the Hellbender (*Cryptobranchus alleganiensis*), which is currently differentiated as two subspecies, including the eastern Hellbender (*Cryptobranchus alleganiensis alleganiensis*) and the federally-Endangered Ozark Hellbender (*C. a. bishop*i; Sabatino and Routman, 2009). Hellbenders are aquatic, long-lived habitat specialists that utilize cool, clear, rocky rivers, and streams (Wheeler et al., 2003). The range of *C. a. alleganiensis* encompasses much of the Southern and Central Appalachians, a global biodiversity and salamander diversity hotspot (Petranka, 1998; Buckley and Jetz, 2007). In addition, these regions are predicted as vulnerable to the effects of climate change (Milanovich et al., 2010; Sutton et al., 2015), as well as land use change (Terando et al., 2014). Hellbender population declines are caused by multiple factors, including riparian habitat degradation, habitat fragmentation, and aquatic sedimentation (Wheeler et al., 2003; Foster et al., 2009; Graham et al., 2011; Freake et al., 2017). As a result of these declines, *C. a. alleganiensis* (eastern Hellbender, hereafter) is state listed as protected or in need of management throughout most of its range (and listed as a Federally Endangered Distinct Population Segment in Missouri (U.S. Fish and Wildlife Service, 2021)). Although potential sources of decline have been identified for eastern Hellbenders (e.g., U.S. Fish and Wildlife Service, 2018), a range-wide quantitative assessment of the collective landscape and climatic stressors has not been conducted.

The central aims of this research were to: 1) identify vulnerable populations of this species, 2) identify the primary causes of vulnerability, and 3) develop strategic conservation recommendations to reduce long-term vulnerability. Based on previous work on climate change assessments on salamanders (e.g., Sutton et al., 2015) and current land-use trends, we predicted that populations within the Western Allegheny Plateau, Central Appalachians, and Interior Plateau ecoregions will have greatest vulnerability due to current land-use trends and predicted impacts of future climate change, whereas the Blue Ridge and Northern Allegheny Plateau ecoregions will have comparably lower vulnerability estimates due to existing protected lands and variability in climatic niche space due to greater elevation variation in these ecoregions.

2. Materials and Methods

2.1. Habitat suitability

The geographic range of the eastern Hellbender spans 15 states and extends from south-central New York State southwest to extreme northeastern Mississippi, with isolated populations in central Missouri (Powell et al., 2016). However, as the published geographic range maps for the eastern Hellbender are over-predictive and include substantial areas of non-aquatic habitat (e.g., Lannoo, 2005; Powell et al., 2016), we first estimated lotic habitat suitability for the species using the Maxiumum Entropy (MaxENT) and Random Forest (RF) SDM algorithms. We acquired eastern Hellbender occurrence data from the Global Biodiversity Information Facility (GBIF [Table S1]; www.gbif.org), Biodiversity Information Serving Our Nation (BISON), VertNet (www.vertnet.org), and state Natural Heritage databases, and only included data points from the years 1970 to present to better correspond with contemporary land use and climate data. We inspected locality data for outliers, duplicate records, and those with insufficient specificity (records with less than four decimal places for both latitude and longitude at each locality (e.g., Barrett et al., 2014; Sutton et al., 2015). We removed several outlier localities, which were defined as records that occurred outside of the known geographic extent for the species. Prior to any further analysis, we snapped all eastern Hellbender presence points to the Horizon Systems Corporation National Hydrography Dataset (NHD) Version 2 https://nhdplus.com/NHDPlus/; accessed 06/10/2022) flowlines that corresponded with the capture location. Overall, data curation resulted in 357 presence points for the eastern Hellbender (Fig. 1).

We used the MaxEnt algorithm (Phillips et al., 2006) within the R package dismo (Hijmans et al., 2020), as well as the RF algorithm within the R package randomForest (Liaw and Wiener, 2002) to estimate lotic habitat suitability for the eastern Hellbender. MaxENT and RF are two frequently used machine learning methods that perform better than other widely used regression methods for ecological niche modeling (Elith et al., 2006). MaxENT is a correlative SDM that uses species occurrences in combination with environmental covariates to estimate the geographic distribution of a species (Phillips et al., 2006; Baldwin, 2009) and is generally favored among SDM algorithms due to its compatibility with ArcGIS and robustness and accuracy of model predictions (Baldwin, 2009;

Elith and Graham, 2009). The RF approach uses a bootstrap aggregation method to average the output of regression trees to predict a species geographic distribution (Liaw and Wiener, 2002). Previous work has suggested that RF models provide robust estimates of species distributions from relatively few data points, and generally perform better than other machine learning methods at extrapolating to under-sampled geographic areas (Mi et al., 2017).

We generated a bias file to select background locations while removing sampling bias (e.g., Phillips et al., 2009; Syfert et al., 2013), rather than using a random allocation of background samples to estimate suitable habitat for the eastern Hellbender. The bias file approach is useful when sampling bias is expected in the presence file, which is usually the case with occurrence data acquired from state monitoring and museum databases (Phillips et al., 2009). To develop the bias file, we used the GBIF, VertNet, and BISON databases to acquire locations for all salamander species that occur within the geographic range of the eastern Hellbender (Table S2). We used publicly-available range maps through both NatureServe (www.natureserve.org) and the International Union for the Conservation of Nature (IUCN) Redlist (www.iucn.org) to determine which salamander species occur within the geographic range of the eastern Hellbender. We used the resulting bias file to select 10,000 sampling points along the NHD flowlines (Fig. 1), which permitted the generation of a sampling effort layer for salamander occurrence data throughout the study area. Use of a sampling bias grid to select background points for distribution modeling can improve model performance and reduce the influence of sampling bias on resulting model predictions (Phillips et al., 2009; Syfert et al., 2013).

We filtered the eastern Hellbender presence file by 5 km to remove duplicate samples and limit spatial bias due to oversampling at well-known and accessible sampling locations (e.g., biological research stations, national parks, sites near roads) as recommended in Kramer-Schadt et al. (2013). We limited background point selection to within 1 km of the NHD flowline shapefile that was clipped to the known geographic extent of the eastern Hellbender. The number of background points used has the potential to influence model accuracy and the relationship between model fit, and the ratio of background:presence points is algorithm specific (Barbet-Massin et al., 2012). Specifically, model fit was greatest for RF models when the number of background points was equal to the number of presence points, whereas for MaxENT, the greatest model fit occurred with the inclusion of 10,000 background points (Barbet-Massin et al., 2012). Therefore, we used the bias file to allocate 10,000 background points for the MaxENT model and 357 background points for RF models within the NHD stream flowline layer throughout the range of the eastern Hellbender.

We acquired geospatial data from the NHD Version 2 (https://nhdplus.com/NHDPlus/; accessed 06/10/2022) dataset. We appended stream covariate data from the NHDPlusV2 Extended Feature Class and Tables dataset to the NHD flowline feature data set via the Common ID (COMID) using the Spatial Join Function in ArcGIS v. 10.5 as conducted in McGarvey et al. (2021). From this dataset, we used eight NHD variables similar to Leonard et al. (2015) to develop the eastern Hellbender stream habitat suitability model, which included stream order (Strahler, 1957), flow, velocity, maximum elevation, minimum elevation, slope, precipitation, and stream level. Prior to further analysis, we converted each of the stream flowline variables to raster datasets with a minimum data grain of 1 km^2. We conducted this analysis across the conterminous range of the eastern Hellbender, which did not include the isolated portion of the eastern Hellbender range in Missouri, as we lacked adequate locality data to model suitability for this portion of the range. In addition, we did not include land use data in the habitat suitability model as these data were evaluated in the evaluation of vulnerability as described below.

We evaluated model fit for the MaxENT and RF models using Area Under the Curve (AUC) estimates determined through cross-validation of five sub-sampled replicates. While the use of AUC as an indicator of model support has been called into question (Lobo et al., 2007), we avoided errors associated with the use of AUC by restricting the modeled area to the NHD flowlines that occurred within the geographic extent of the eastern Hellbender (Lobo et al., 2007). We created an ensembled habitat suitability SDM by averaging the logistic MaxENT and RF outputs. We thresholded the ensembled SDM via a single value averaged across the maximum sensitivity and specificity (MSS), fixed 10 cumulative (f10), and minimum training presence (MTP) threshold values, which represents a series of conservative to liberal threshold approaches to generate a binary (1 – suitable, 0 – unsuitable) habitat suitability raster.

2.2. Climatic Suitabilityniche estimation

We used the MaxEnt and RF algorithms to model the current and projected climatic suitability of the eastern Hellbender. We used similar methods described in the habitat suitability portion of the manuscript, except we used the modeled habitat suitability layer (buffered by 5 km) as the climatic footprint to model current and projected climatic suitability. After we estimated current climatic suitability, we projected this distribution on 12 projected Global Climatic Models (GCMs; Table S3). We incorporated output from multiple GCMs to increase the accuracy of estimated projections (Overland et al., 2011). Due to the similarity of GCM predictions, Knutti et al. (2013) generated a hierarchical clustering of models from a distance matrix of monthly climate projections, with each cluster representing groups of similar GCMs. We selected 12 models that represented each distinct cluster of similar models to incorporate the diversity of GCM predictions. Each model was selected at random from within a cluster of similar models following Lyons and Kozak (2020). To account for uncertainty in climatic projections, we estimated change under two Representative Concentration Pathways (RCPs), including the RCP 4.5 and RCP 8.5 greenhouse gas scenarios. The RCPs represent a range of projected greenhouse gas emission scenarios into the year 2100 (based on radiative forcing) to pre-industrial values (van Vuuren et al., 2011). We evaluated the RCP 4.5 and 8.5 scenarios to estimate climate change based on moderate and extreme levels of future greenhouse gas emissions as conducted in Sutton et al. (2015).

We acquired current and projected climatic data that were publicly available from the Worldclim database (http://www.worldclim.org) at the 30-second resolution. These data represent 19 bioclimatic variables derived from global temperature and precipitation grids (Hijmans et al., 2005). Prior to analysis, we removed 12 highly correlated ($>$ 0.75) bioclimatic variables and maintained seven bioclimatic variables (http://www.worldclim.org/bioclim) for current and projected climate scenarios (Table S4). We created a climatic ensemble (Araújo and New, 2006) for the eastern Hellbender to indicate areas of climate refugia for both the RCP 4.5 and RCP 8.5 scenarios at both 2050 and 2070 by averaging each of the 12 distributions within a particular RCP scenario/year combination. We averaged these four models into a single layer for downstream analyses using the raster package in R (v.3.4–10; Hijmans et al., 2015).

2.3. Landscape threats

In addition to examining potential threats of climate change on eastern Hellbenders, we evaluated land use trends throughout the range of the species to estimate the potential impacts of additional landscape stressors. We used the habitat suitability SDM that we developed for the eastern Hellbender to clip the climatic suitability, land-use integrity, protected areas, and land use raster datasets.

We used three data sources to assess land use threats, including the 2011 Land Use Land Cover (LULC) dataset (Homer et al., 2015), the 2006 Landscape Integrity Index (LII; Theobold, 2013), and the Protected Areas Dataset of the United States (PADUS; U.S. Geological Survey [USGS], Gap Analysis Program [GAP], 2018). Prior to analysis, we reclassified the LULC layer to provide the following data: 1 – Open Water (LULC category 11), 2 – Urbanization (LULC categories 21, 22, 23, and 24), 3 – Barren (LULC category 31), 4 – Forested (LULC categories 41, 42, and 43), Shrub/Scrub (LULC category 52), Grassland/Herbaceous (LULC category 71), Agriculture (LULC categories 81 and 82), and Wetlands (LULC category 90 and 95). As the LULC dataset provides only a thematic representation of land use, we utilized the LII to obtain a quantitative estimate of landscape condition on a scale of 0 – 1, where 0 represents a fully intact landscape and 1 represents a highly-compromised and non-functional landscape (Theobold, 2013).

We utilized the PADUS dataset, and specifically, the GAP Status Code to assess the extent of landscape protection throughout the study area. Briefly, the GAP Status Code is a measure of management intent to conserve biodiversity (U.S. Geological Survey (USGS) Gap Analysis Project (GAP), 2018). The GAP Status Codes (SCs) are defined as follows: SC 1 – an area having permanent protection from conversion of natural land cover and a mandated management plan in operation to maintain a natural state within which disturbance events are allowed to proceed without interference or are mimicked through management; SC 2 – an area having permanent protection from conversion of natural land cover and a mandated management plan to maintain a primarily natural state, but which may receive uses or management practices that degrade the quality of existing natural communities, including suppression of natural disturbance; SC 3 – an area having permanent protection from conversion of natural land cover for the majority of the area, but subject to extractive uses of either a broad, low-intensity type or localized intense type; and SC 4 – no known public or private institutional mandates or legally recognized easements or deed restrictions held by the managing entity to prevent conversion of natural habitat types to anthropogenic habitat types (U.S. Geological Survey (USGS) Gap Analysis Project (GAP), 2018). Our primary aim was to evaluate the contributions of PADUS lands for potentially mitigating the impacts of climate and land use change on eastern Hellbenders. Although it is likely that the degree of landscape protection does not scale linearly with the effect of protection within a given PADUS landscape, our primary aim was to evaluate landscapes based on the benefits of maintaining protection, while scoring the variable in a manner that accounted for the amount of anthropogenic disturbance permitted on these landscapes. Our assumption was that PADUS landscapes that were protected in perpetuity and permitted occurrence of disturbances in-line with the historical disturbance regime would provide greater adaptive capacity than PADUS lands that have protections, but permitted anthropogenic disturbances that were not in-line with a natural disturbance regime.

2.4. Vulnerability calculation

We assessed the range-wide vulnerability of the eastern Hellbender to climate and land use change via a framework similar to Magness et al. (2011). We defined vulnerability as the degree to which an ecosystem is susceptible to and the potential for system

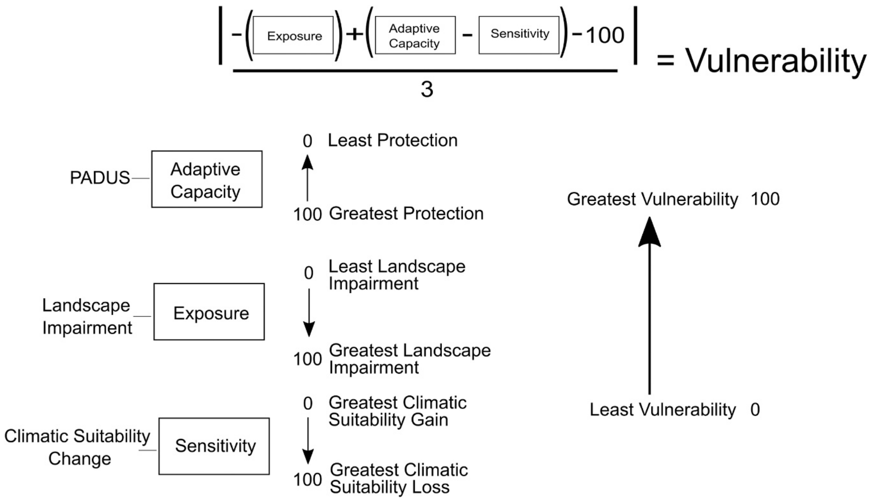

Fig. 2. Workflow diagram describing the calculation of vulnerability based on adaptive capacity, exposure, and sensitivity.

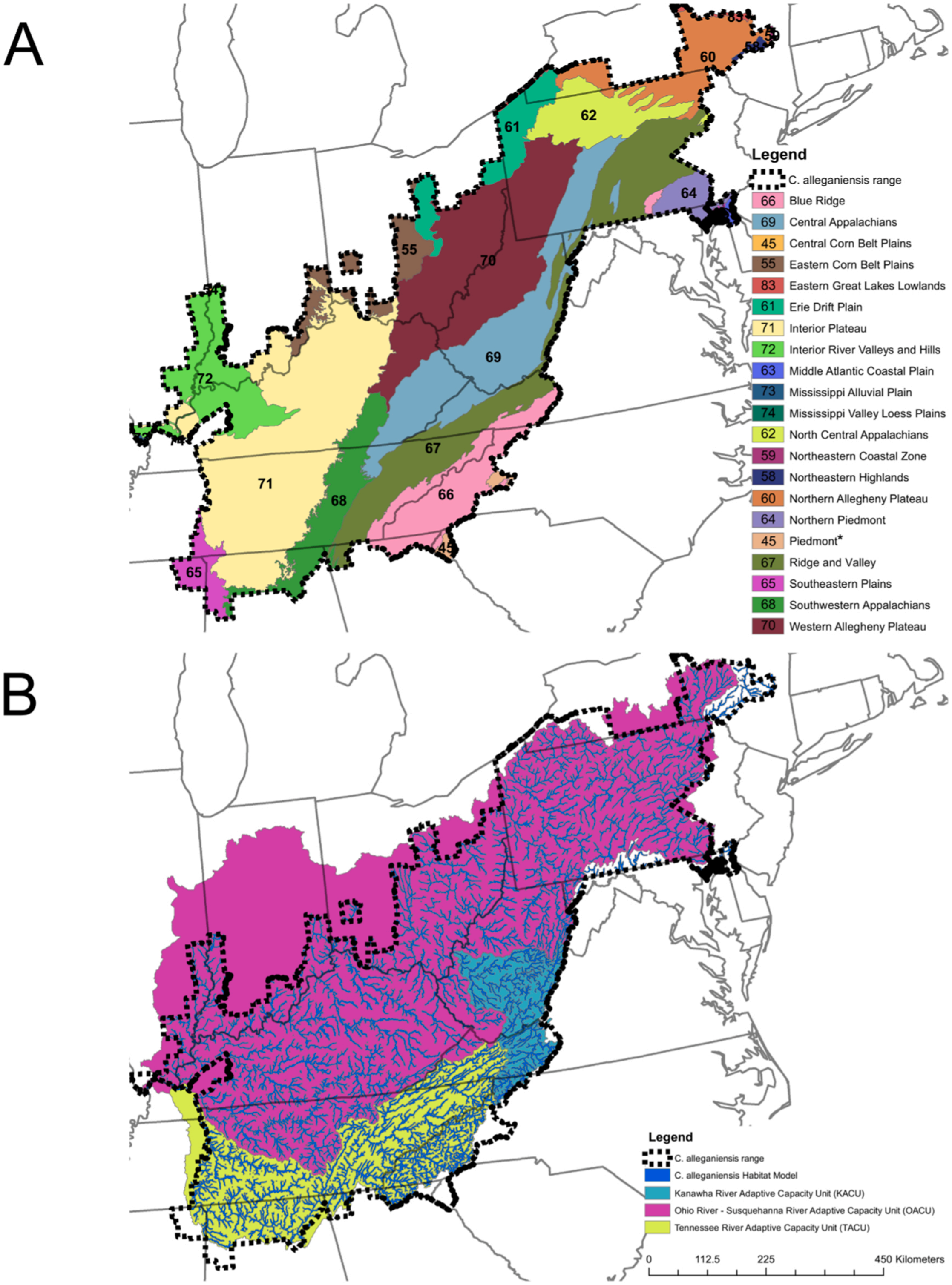

Fig. 3. A). Geographic distribution of the eastern Hellbender in reference to EPA Level III Ecoregions. An asterisk denotes an ecoregion removed from analyses due to lack of suitable habitat, B) habitat suitability SDM generated for the eastern Hellbender in reference to the geographic range and Adaptive Capacity Units (ACUs).

transformation when confronted with a stressor (Gallopín, 2006). We evaluated vulnerability by incorporating exposure (e.g., extent of an environmental stressor), sensitivity (e.g., degree in which a species or landscape experiences a stressor), and adaptive capacity (e.g., capacity of a species or landscape to cope with a stressor) throughout the conterminous range of the eastern Hellbender (Fig. 2). We used a direct index approach to calculate vulnerability, which permitted a geospatial representation of exposure, sensitivity, adaptive capacity, and vulnerability, rather than a nested threshold-based approach used in Magness et al. (2011).

We evaluated exposure by scaling the LII from 0 to 100, where 100 represented landscapes with the greatest anthropogenic impairment (Fig. 2). Land use change represents one of the greatest threats to amphibian populations (Cordier et al., 2021) and is identified as a primary threat to eastern Hellbender populations, especially when habitat change results in increased sedimentation and decreased water quality in impacted riparian zones (Jachowski and Hopkins, 2018).

To assess sensitivity, we determined change in climatic suitability based on current and predicted climate projections throughout the conterminous geographic range of the eastern Hellbender. Global climate change represents a conservation threat for many amphibians (e.g., Wake, 2007; Cohen et al., 2019) and is predicted to negatively impact eastern Hellbenders via increased water temperatures and by increasing irregularity of droughts and large rainfall events (U.S. Fish and Wildlife Service, 2018). We estimated climatic suitability change by subtracting the raster cell values for the RCP 4.5 and 8.5 scenario at years 2050 and 2070 from the current climatic suitability raster. We then averaged the four RCP/year combinations to determine mean gains and losses in climatic suitability. These values were relativized on a scale of 0 to 100, with 0 representing the greatest gain in climatic suitability and100 representing the greatest loss in climatic suitability (Fig. 2).

We estimated adaptive capacity by reclassifying the PADUS polygon layer to a raster based on the GAP Status Code via the Polygon to Raster function in ArcGIS v. 10.5. We reclassified this raster on a scale from 0 to 4, where categories 1 – 4 were inverted to correspond with the GAP Status Codes and 0 corresponded with landscapes that have no formal protection as identified via the PADUS layer. We used this raster to determine the amount of PADUS lands (direct protection) that occurred in the eastern Hellbender habitat suiability prediction. We then performed a 3 × 3 cell moving window analysis, which is an iterative spatial analysis that occurs in a pre-determined geospatial window across the entire raster dataset via the Cell Statistics Tool in ArcGIS v. 10.5. We conducted this analysis to form a gradient of mean habitat protection for habitats adjacent to borders of protected areas (indirect protection) to account for conservation benefits that protected lands provide for adjacent private lands (Naughton-Treves et al., 2005). We then relativized the direct protection raster on a scale of 0 – 100, where 0 represented no formal landscape protection and 100 represented landscapes with the greatest landscape protection (Fig. 2), which corresponded with GAP status code 1. Although amphibian populations are under-represented under current global protected areas (Nori et al., 2015), protected areas with formal habitat protection are invaluable for eastern Hellbender conservation (Freake and DePerno, 2017).

For the respective components used to derive vulnerability, we used the LII score (range: 0 – 100) to represent exposure, change in climatic suitability of the eastern Hellbender (range: 0 – 100) to represent sensitivity, and percent of protected lands (range: 0 – 100) to represent adaptive capacity (Fig. 2). We determined vulnerability within each raster cell of the predicted eastern Hellbender habitat suitability layer by subtracting 100 (a constant) from the sum of exposure and resiliency, the latter of which is defined as adaptive capacity – sensitivity. We multiplied this total by 1/3 and took the absolute value of the product to provide a vulnerability estimate between 0 and 100, where 100 represented greatest vulnerability (Fig. 2).

As previous evaluations of habitat suitability on eastern Hellbender occupancy found that ecoregion was important for predicting occupancy (e.g., da Silva Neto et al., 2020), we summarized land use and climatic stressors within each EPA Level III ecoregion (U.S. Environmental Protection Agency, 2006) that occurred within the conterminous range of the eastern Hellbender (Fig. 3). Ecoregions represent areas of similar ecosystem characteristics (Omernik, 1987) that provide a framework for relating impacts of land use on biodiversity patterns (Bryce et al., 1999; Yaffee, 1999; Turnock, 2002; Gallant et al., 2004) and are effective conservation units (Olson and Dinerstein, 1998). However, as Hellbenders are fully aquatic organisms, it is important to evaluate land use patterns and primary conservation threats at a watershed spatial scale. Therefore, we used the Adaptive Capacity Units (ACUs; Fig. 3) as identified in U.S. Fish and Wildlife Service (2018) to further evaluate land use and climatic stressors. These ACUs were derived based on genetic relationships within the eastern Hellbender range and represent evolutionary distinct lineages as identified by Hime (2017) at a large watershed scale.

We used R (v. 4.1.0; R Core Team, 2021) to calculate mean (± S.E.) values of current and projected climatic suitability, landscape protection, and landscape impairment, and the proportion of each LULC category of suitable eastern Hellbender habitat within each Level III ecoregion and ACU. We also generated mean exposure, sensitivity, adaptive capacity, and vulnerability scores of suitable eastern Hellbender habitat within each Level III ecoregion and ACU. To account for the influence of Level III Ecoregion and ACU area, we multiplied the mean vulnerability score by the percent of the suitable eastern Hellbender range within a given Level III ecoregion or ACU.

3. Results

The habitat suitability SDM (Fig. 3) for the eastern Hellbender was well supported, with a mean AUC estimate of 0.83 ± 0.03 (MaxENT: 0.81 ± 0.02; RF: 0.85 ± 0.02). Within both modeling algorithms, the Flow variable had the greatest percent contribution to the habitat suitability prediction (MaxENT [80.6], RF [31.2]), whereas the Velocity (MaxENT [1.5], RF [20.7]), Stream Order (MaxENT [5.8], RF [19.3]), Minimum Elevation (MaxENT [6.5], RF [12.8]), and Maximum Elevation (MaxENT [1.2], RF [12.0]) variables were of secondary importance in terms of percent contribution for both SDM approaches. The Precipitation (MaxENT [1.0], RF [11.0]) and Stream Level (MaxENT [1.0], RF [2.0]) variables had the lowest percent contribution for habitat suitability predictions.

Based on the eastern Hellbender habitat suitability SDM, 23.3% of the predicted suitable habitat occurred in the Interior Plateau

(29,802.4 km^2), Western Allegheny Plateau (14.4% of range; 18,381.3 km^2), Ridge and Valley (13.7% of range; 17,468.6 km^2), and Central Appalachians (12.2% of range; 15,648.2 km^2, Table 1) ecoregions. The Blue Ridge, Interior River Valleys and Hills, Southwestern Appalachians, North Central Appalachians, and Northern Allegheny Plateau ecoregions accounted for 9.1% (11,642.2 km^2), 6.0% (7733.7 km^2), 5.0% (6434.1 km^2), 4.1% (5282.4 km^2), and 3.7% (4688.7 km^2), respectively (Table 1). The remaining ecoregions (Erie Drift Plains, Eastern Corn Belt Plains, Northern Piedmont, Southeastern Plains, Northeastern Highlands, Middle Atlantic Coastal Plain, Eastern Great Lakes Lowlands, Northeastern Coastal Zone, Mississippi Alluvial Plain, Central Corn Belt Plains, and Mississippi Valley Loess Plains accounted for the remaining 8.3% (10,675.4 km^2) of the suitable habitat (Table 1). Within the proposed geographic range of the eastern Hellbender, approximately 66.4% (82,497.6 km^2) of the suitable habitat occurred in the Ohio River-Susquehanna River Adaptive Capacity Unit (OACU), 25.6% occurred in the Tennessee River Adaptive Capacity Unit (TACU; 31,779.9 km^2), and 8.0% occurred in the Kanawha River Adaptive Capacity Unit (KACU; 9954.2 km^2; Table 1).

3.1. *Land use*

Within the predicted suitable habitat, forest cover was greatest in the Northeastern Highlands (84.7%; Table 2), Central Appalachians (79.7%), and North Central Appalachians (78.6%). Forest cover was least in the Mississippi Alluvial Plains (1.1%) and Middle Atlantic Coastal Plains (8.5%). Land cover converted to agriculture was greatest in the Interior River Valley and Hills (50.0%), the Eastern Great Lakes Lowlands (42.2%), and the Eastern Corn Belt Plains (40.6%). Urbanization was most extensive within the Middle Atlantic Coastal Plains (38.8%), the Eastern Corn Belt Plains (23.6%), and the Mississippi Valley Loess Plains (23.3%). Within the ACUs, forest cover was greatest in the KACU (73.1%), and least in the Ohio River-Susquehanna River ACU (53.1%; Table 2). The greatest proportion of land converted to agriculture occurred in the OACU (26.4%). In addition, urbanized habitats were also most extensive in the OACU (11.6%). Mean landscape impairment (LII) was greatest (most disturbance) in the Mississippi Valley Loess Plains (69.8) and the Mississippi Alluvial Plains ecoregions (65.7; Table 2). The Northeastern Highlands had the lowest LII value (33.1). Within ACUs, the greatest LII value (most disturbance) occurred in the OACU (49.2), whereas the lowest landscape LII value occurred in the KACU (44.2).

3.2. *Climatic suitability change*

The test area-under-the-curve (AUC) estimate for the climatic suitability SDM was 0.68 ± 0.02 for MaxENT and 0.71 ± 0.02 for the RF algorithm. Based on the MaxENT model, the Mean Diurnal Range (bio 2) and Annual Precipitation (bio 12) variables had the greatest percent contribution values of 70.4 and 8.4, respectively. For the RF model, the Annual Precipitation (bio 12) and mean Diurnal Range (bio 2) variables had the greatest contribution values of 29.9 and 28.8, respectively. The ecoregion projected to

Table 1

Area (km^2) of protected lands (all protected areas defned in the PADUS dataset) based on eastern Hellbender habitat suitability among Adaptive Capacity Units (ACUs) and EPA Level III Ecoregions. Areas identified as directly protected are rivers within protected lands, whereas areas identified as indirectly were determined through a moving window analysis to account for protection conferred on rivers adjacent to protected lands. Values in parentheses represent percentages of the total range (area km^2 column) and percentage of area protected within the ecoregion (Area indirectly protected km^2 and Area directly protected km^2 columns).

Adaptive Capacity Unit / Ecoregion	Area km^2	Area indirectly protected km^2	Area directly protected km^2
Adaptive Capacity Unit			
TACU	31,779.9 (25.6%)	23,016.7 (72.4%)	6178.6 (19.4%)
OACU	82,497.6 (66.4%)	53,217.9 (64.5%)	11,176.5 (13.5%)
KACU	9954.2 (8.0%)	6691.5 (67.2%)	1620.8 (16.3%)
Ecoregion			
Blue Ridge	11,642.2 (9.1%)	10,711.3 (92%)	3875.9 (33.3%)
Central Appalachians	15,648.2 (12.2%)	9155.65 (58.5%)	2651.2 (16.9%)
Central Corn Belt Plains	10.6 (0.01%)	6.0 (56.3%)	0 (0%)
Eastern Corn Belt Plains	3182.7 (2.5%)	2332.4 (73.3%)	443.4 (13.9%)
Eastern Great Lakes Lowlands	178.2 (0.1%)	97.9 (55.0%)	1.9 (1.1%)
Erie Drift Plain	3352.3 (2.6%)	2576.1 (76.8%)	372.7 (11.1%)
Interior Plateau	29,802.4 (23.3%)	15,947.41 (53.5%)	2989.2 (10.0%)
Interior River Valleys and Hills	7733.7 (6.0%)	4238.8 (54.8%)	526.7 (6.8%)
Middle Atlantic Coastal Plain	184.9 (0.1%)	184.9 (100%)	53.7 (29.1%)
Mississippi Alluvial Plain	35.0 (0.02%)	35.0 (100%)	0.7 (2.0%)
Mississippi Valley Loess Plains	6.2 (0.001%)	4.8 (77.8%)	0 (0%)
North Central Appalachians	5282.4 (4.1%)	4770.6 (90.3%)	2371.5 (44.9%)
Northeastern Coastal Zone	149.5 (0.1%)	136.1 (91.1%)	19.1 (12.8%)
Northeastern Highlands	237.8 (0.2%)	237.8 (100%)	62.5 (26.3%)
Northern Allegheny Plateau	4688.7 (3.7%)	3355.4 (71.6%)	258.8 (5.5%)
Northern Piedmont	1803.3 (1.4%)	1722.4 (95.5%)	232.4 (12.9%)
Ridge and Valley	17,468.6 (13.7%)	13,595.6 (77.8%)	2240.2 (12.8%)
Southeastern Plains	1535.2 (1.2%)	1049.6 (68.4%)	181.9 (11.8%)
Southwestern Appalachians	6434.1 (5.0%)	4774.9 (74.2%)	1554.2 (24.2%)
Western Allegheny Plateau	18,381.3 (14.4%)	11,069.3 (60.2%)	1795.4 (9.8%)

Table 2
Percent land-use composition based on eastern Hellbender habitat suitability within Adaptive Capacity Units (ACUs) and EPA Level III Ecoregions. Greater scores for landscape integrity indicate greater landscape impairment.

Adaptive Capacity Unit / Ecoregion	Urbanization	Barren	Forest	Shrub/ Scrub	Grassland	Agriculture	Wetlands	Landscape Integrity
Adaptive Capacity Unit								
TACU	11.2	0.2	54.9	1.1	1.1	22.3	2.7	46.4
OACU	11.6	0.3	53.1	0.8	0.8	26.4	2.8	49.2
KACU	8.9	0.2	73.1	1.6	1.1	13.1	0.5	44.2
Ecoregion								
Blue Ridge	11.5	0.1	73.9	0.9	0.7	10.8	0.2	45.3
Central Appalachians	8.4	0.4	79.7	1.7	1.5	6.1	0.8	43.8
Central Corn Belt Plains	6.5	0.2	52.7	0.1	1.1	39.1	0.1	39.7
Eastern Corn Belt Plains	23.6	0.5	28.5	0.2	0.6	40.6	2.0	59.1
Eastern Great Lakes Lowlands	12.7	0.8	31.4	0.6	0.9	42.2	5.7	64.6
Erie Drift Plain	15.4	0.2	37.1	0.3	0.5	30.5	11.1	57.5
Interior Plateau	9.8	0.2	43.2	0.6	0.7	36.6	2.6	47.4
Interior River Valleys and Hills	5.9	0.2	24.7	0.3	0.5	50.0	10.9	45.5
Middle Atlantic Coastal Plain	38.8	0.3	8.5	0.5	0.9	11.7	29.6	65.5
Mississippi Alluvial Plain	18.2	0.1	1.1	0.0	0.2	29.4	16.1	65.7
Mississippi Valley Loess Plains	23.3	0.1	30.5	0.4	0.1	17.8	14.4	69.8
North Central Appalachians	6.9	0.1	78.6	1.2	0.4	6.4	4.0	38.1
Northeastern Coastal Zone	13.5	0.5	41.0	0.4	0.7	7.6	10.9	62.8
Northeastern Highlands	6.7	0.1	84.7	0.3	0.5	4.0	2.5	33.1
Northern Allegheny Plateau	11.2	0.3	54.8	0.7	0.5	24.8	4.7	56.3
Northern Piedmont	19.9	0.3	30.2	1.0	0.3	39.2	2.0	59.5
Ridge and Valley	14.3	0.3	49.0	0.8	1.1	27.6	1.1	53.0
Southeastern Plains	6.3	0.3	42.5	2.9	1.2	22.2	13.5	37.2
Southwestern Appalachians	6.0	0.3	70.1	1.7	1.6	14.4	1.3	37.8
Western Allegheny Plateau	14.8	0.2	61.2	0.8	0.8	17.4	0.9	51.9

experience the greatest loss in average climatic suitability was the North Central Appalachians, which saw a 15.6% reduction (Table 3). Additionally, the Mississippi Valley Loess Plains and Interior Plateau ecoregions were projected to experience 13.2% and 12.1% decreases in average climatic suitability, respectively (Table 3). Conversely, some ecoregions were projected to increase in average suitability, with the Northern Piedmont (27.1%), and the Central Corn Belt Plains (26.1%) projected to experience an increase in

Table 3
Projected climatic suitability (% suitability ± S.E.) within Adaptive Capacity Units (ACUs) and EPA Level III ecoregions for the eastern Hellbender based on averaged 2050 and 2070 projected climatic scenarios (12 GCM models) and two Representative Concentration Pathways (RCP 4.5 and 8.5). The last column represents relative percent change in climatic suitability (± S.E.). Positive values in the average change column correspond with an increase in climatic suitability, whereas negative values correspond with a decrease in climatic suitability.

Adaptive Capacity Unit / Ecoregion	Current Climate	RCP 4.5 2050	RCP 4.5 2070	RCP 8.5 2050	RCP 8.5 2070	Predicted Mean	Average Change
Adaptive Capacity Unit							
TACU	62.6 ± 25.3	56.1 ± 19.2	55.0 ± 18.1	53.1 ± 17.8	53.0 ± 17.6	54.3 ± 17.8	–5.8 ± 2.9
OACU	45.1 ± 27.9	43.2 ± 21.9	44.2 ± 21.6	43.7 ± 21.1	42.9 ± 21.3	43.5 ± 20.9	–1.6 ± 1.2
KACU	50.9 ± 21.5	58.0 ± 16.0	60.4 ± 15.6	59.4 ± 16.1	62.2 ± 16.3	60.0 ± 15.6	9.1 ± 6.4
Ecoregion							
Blue Ridge	72.3 ± 30.6	64.7 ± 20.6	62.3 ± 17.9	60.7 ± 16.9	60.9 ± 15.9	34.4 ± 0.7	–10.2 ± 6.5
Central Appalachians	52.4 ± 26.5	55.2 ± 22.5	57.6 ± 21.5	55.8 ± 21.6	56.7 ± 20.9	32.1 ± 8.3	3.9 ± 2.7
Central Corn Belt Plains	8.3 ± 0.6	38.2 ± 1.0	30.7 ± 0.4	38.7 ± 1.4	29.9 ± 0.7	22.4 ± 5.0	26.0 ± 0.0
Eastern Corn Belt Plains	24.2 ± 19.9	31.1 ± 10.5	31.2 ± 9.4	33.9 ± 10.4	32.1 ± 7.1	45.0 ± 4.6	7.9 ± 5.8
Eastern Great Lakes Lowlands	30.9 ± 6.6	21.1 ± 2.4	23.3 ± 3.7	24.4 ± 3.1	26.9 ± 3.5	26.7 ± 11.0	–6.9 ± 1.8
Erie Drift Plain	30.1 ± 23.4	26.6 ± 12.5	30.8 ± 12.1	33.2 ± 13.4	36.8 ± 10.1	31.8 ± 11.8	1.8 ± 5.8
Interior Plateau	57,0 ± 23.4	46.1 ± 13.6	46.0 ± 12.9	44.5 ± 12.4	43.0 ± 11.6	33.3 ± 13.2	–12.1 ± 5.7
Interior River Valleys and Hills	36.7 ± 25.4	34.2 ± 8.6	33.7 ± 7.7	33.2 ± 7.7	31.4 ± 8.0	40.4 ± 5.4	–3.6 ± 8.8
Middle Atlantic Coastal Plain	27.2 ± 20.0	43.4 ± 5.6	40.3 ± 4.6	40.1 ± 6.5	38.1 ± 5.6	41.3 ± 6.4	13.2 ± 7.3
Mississippi Alluvial Plain	33.6 ± 2.0	26.6 ± 0.7	27.1 ± 0.7	26.3 ± 0.6	25.2 ± 0.9	46.5 ± 4.5	–7.3 ± 0.7
Mississippi Valley Loess Plains	46.7 ± 4.3	34.5 ± 0.4	34.1 ± 0.3	33.1 ± 0.2	32.6 ± 0.4	62.1 ± 17.5	–13.2 ± 2.0
North Central Appalachians	48.9 ± 26.4	30.6 ± 12.7	33.7 ± 14.2	32.8 ± 13.2	36.2 ± 13.9	51.3 ± 19.6	–15.6 ± 6.6
Northeastern Coastal Zone	35.9 ± 3.9	40.3 ± 4.9	45.9 ± 4.1	43.9 ± 5.8	49.8 ± 5.2	44.2 ± 14.0	9.1 ± 0.4
Northeastern Highlands	21.9 ± 16.9	22.0 ± 4.5	22.7 ± 5.5	21.5 ± 5.9	23.5 ± 5.1	56.3 ± 21.1	1.0 ± 5.9
Northern Allegheny Plateau	36.9 ± 23.6	23.0 ± 10.1	26.4 ± 12.1	26.5 ± 10.5	30.9 ± 13.2	52.9 ± 16.9	–10.2 ± 6.3
Northern Piedmont	14.2 ± 23.8	41.3 ± 7.2	40.1 ± 6.2	42.8 ± 7.4	41.1 ± 8.5	44.9 ± 12.1	27.1 ± 8.7
Ridge and Valley	45.4 ± 28.1	51.1 ± 21.9	51.4 ± 19.7	50.8 ± 20.0	51.8 ± 19.3	33.1 ± 7.8	5.8 ± 4.3
Southeastern Plains	51.3 ± 19.6	45.3 ± 4.9	47.3 ± 5.3	47.3 ± 4.2	45.9 ± 4.6	26.3 ± 0.7	–4.8 ± 7.5
Southwestern Appalachians	48.7 ± 18.6	46.7 ± 15.5	45.0 ± 14.1	43.0 ± 14.2	42.1 ± 12.3	33.6 ± 0.3	–4.5 ± 2.3
Western Allegheny Plateau	46.1 ± 25.0	52.9 ± 19.1	54.3 ± 17.7	53.6 ± 17.6	50.9 ± 15.8	23.9 ± 2.9	6.9 ± 4.1

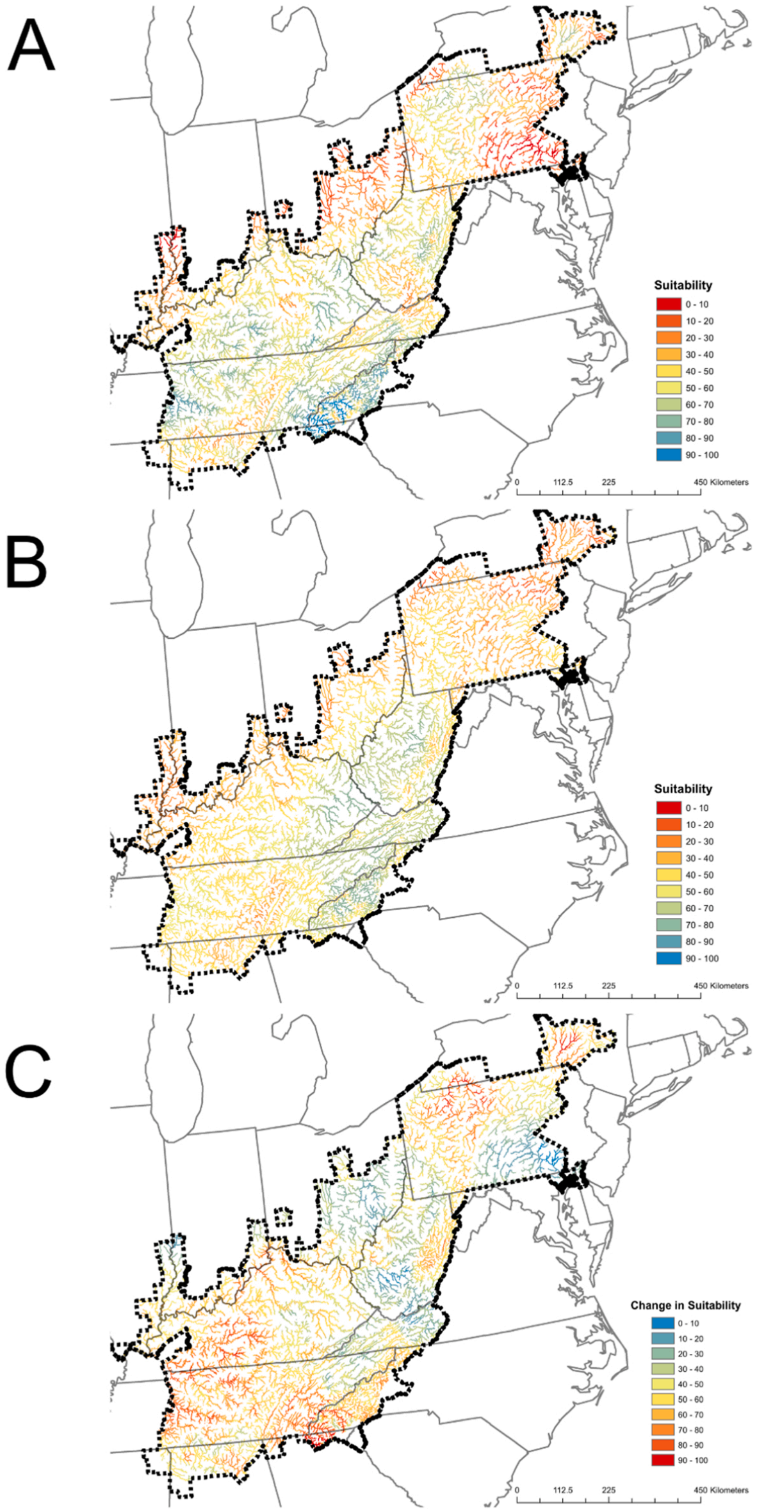

Fig. 4. A) Current climatic suitability for the eastern Hellbender determined through ensembling models built with the MaxENT and RF SDMs (MaxENT AUC = 0.68 ± 0.02, RF AUC= 0.71 ± 0.02). Areas in blue represent high predicted suitability whereas areas in red represent predicted low suitability. B) Predicted climatic suitability for the eastern Hellbender. The climatic suitability prediction was based on 12 Global Circulation Models and two Representative Concentration Pathway (RCP) trajectories (RCP 4.5 and 8.5) for 2050 and 2070. C) Relative change in climatic suitability was determined by subtracting the current climatic suitability raster (A), from the predicted climatic suitability raster (B).

average suitability of greater than 25% (Table 3; Fig. 4). The OACU was projected as relatively stable with a 1.6% decrease in average suitability. Conversely, the TACU was predicted to decrease in average climatic suitability by 5.8%.

3.3. Current Protection and Vulnerability

Analysis of the geographic range of the eastern Hellbender by land protection status (i.e., lands in some form of conservation ownership) indicated that populations residing in the Interior Plateau and Interior River and Valleys were least secure with 46.5% and 45.2% of suitable habitat within these ecoregions receiving no direct or indirect protection (Table 1; Fig. 5A). However, when looking only at direct protection, populations within the Central Corn Belt Plains and the Mississippi Valley Loess Plains ecoregions were least secure with 0% of suitable habitat receiving direct protection (Table 1; Fig. 5A). Populations within the Middle Atlantic Coastal Plains, the Mississippi Alluvial Plains, and the Northeastern Highlands were afforded the most indirect protection (100% of suitable habitat in each). Populations in the North Central Appalachians and the Blue Ridge were afforded the most direct protection (44.9% and 33.3% respectively). Populations within the Tennessee River ACU were offered the most direct protection (19.4%) followed by the Kanawha River ACU (16.3%), as well as greatest indirect protection (72.4% and 67.2%, respectively).

Within-ecoregion vulnerability was greatest for eastern Hellbender populations in the Mississippi Valley Loess Plains, Mississippi Alluvial Plains, Eastern Great Lakes Lowlands, North Allegheny Plateau, and Interior Plateau ecoregions, with vulnerability estimates of 77.5, 74.4, 73.7, 71.1, and 69.2, respectively (Table 4; Fig. 5D; Fig. 6). After adjusting vulnerability by the percent of the total suitable eastern Hellbender habitat within each ecoregion, the Interior Plateau, Western Allegheny Plateau, Ridge and Valley, and Central Appalachians had the greatest predicted vulnerability, with relativized estimates of 16.1, 9.0, 8.5, and 7.2, respectively (Table 4; Fig. 5D). The Interior Plateau ecoregion was most vulnerable due to relatively high exposure (47.4), high sensitivity (63.5),

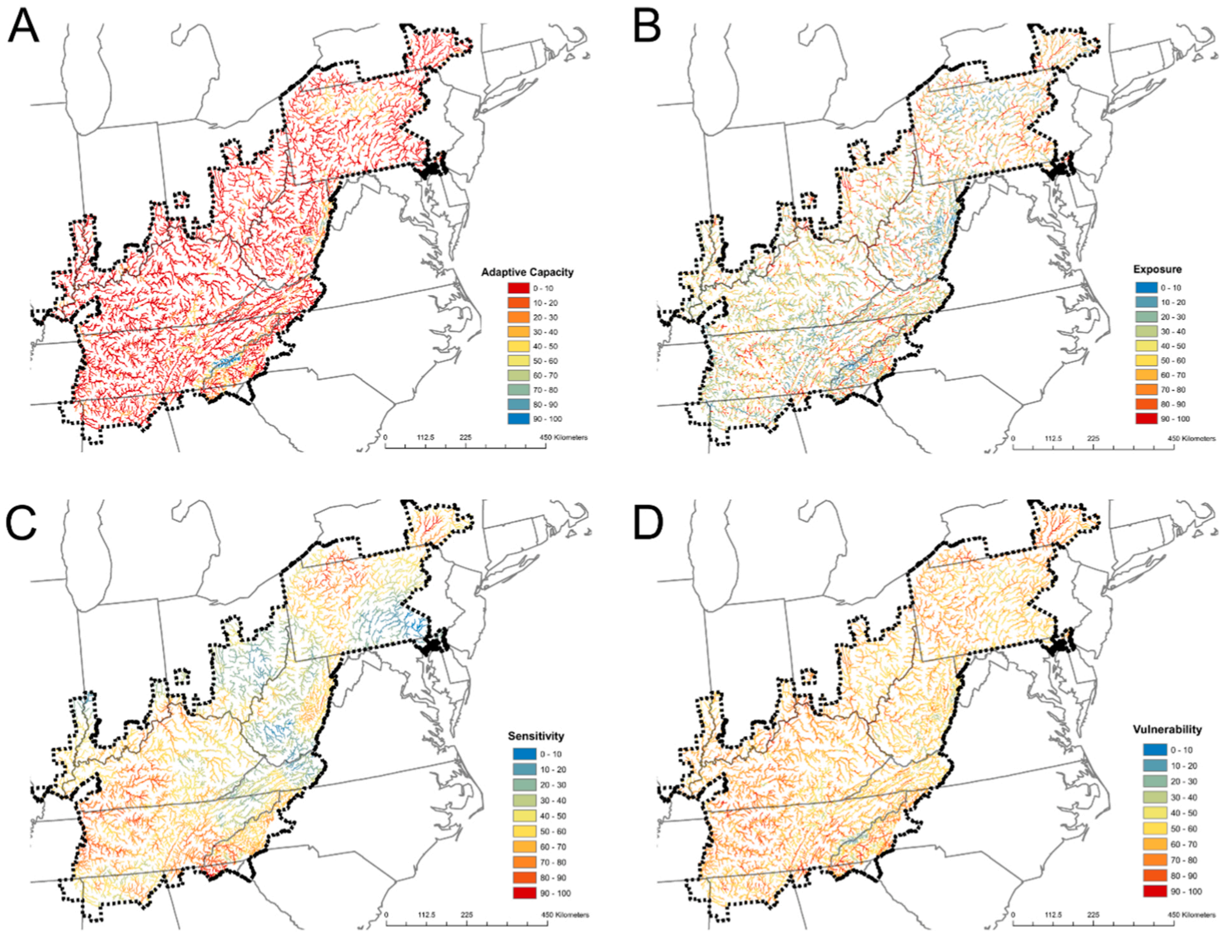

Fig. 5. Vulnerability analysis for the eastern Hellbender, where adaptive capacity (A) was determined as the relativized amount of protected lands (range: 0 – 100), where red indicates low/no protection and blue indicates the highest level of protection; exposure (B) was determined as the relativized landscape integrity index score (range 0 – 100), with a value of 100 (red) representing complete impairment, and value of 0 representing areas of no impairment (blue); sensitivity (C) was determined as the relativized change in the climatic suitability (0 100) - areas with high sensitivity, or the largest decrease in climatic suitability, are represented in red; and vulnerability (D) was estimated between 0 and 100, where areas in red represent greatest vulnerability.

and low adaptive capacity (10.0) (Table 4). Of the ACUs, the TACU and OACU had greatest vulnerability, with estimates of 64.6 and 64.7, respectively (Table 4; Fig. 6). After correcting for the amount of suitable habitat within each ACU, the OACU had greatest vulnerability (Table 4). The relatively high vulnerability of the OACU was due primarily to high exposure (49.2).

4. Discussion

Our study demonstrates the development of a multi-metric vulnerability modeling approach for the eastern Hellbender by incorporating habitat suitability predictions, along with the inclusion of multiple spatially-explicit datasets that permit the estimation of exposure, sensitivity, and adaptive capacity. Our analysis predicts that portions of the eastern Hellbender geographic range in the Northern Allegheny Plateau, Mississippi Valley Loess Plains, Eastern Great Lakes Lowlands, Mississippi Alluvial Plain, and Interior Plateau ecoregions had the greatest estimated vulnerability. After accounting for the suitable habitat area within each ecoregion, the Interior Plateau was supported as most vulnerable, whereas the Northern Alleghany Plateau scored relatively high vulnerability prior to accounting for ecoregion size. The other vulnerable ecoregions before accounting for the amount of suitable habitat (e.g., Mississippi Valley Loess Plains, Southeastern Plains, Erie Drift Plains) are located on the periphery of the eastern Hellbender geographic range and harbor far fewer eastern Hellbender populations compared to the core portions of the range. This is a promising finding, however, peripheral populations are often more tolerant to environmental variation and therefore represent important populations for future dispersal, particularly in the face of climate change (Gibson et al., 2009). Of the most vulnerable ecoregions, the Interior Plateau and Northern Allegheny Plateau compose nearly 27.0% (34,490.9 km^2) of the estimated suitable habitat for the eastern Hellbender, and represent two ecoregions within two genetically distinct ACUs that harbor eastern Hellbender populations, but are vulnerable from anthropogenic land-uses, projected climatic stressors, and relative lack of habitat protections. The least vulnerable populations occurred within the Central Appalachians, Southwestern Appalachians, Blue Ridge, and Western Allegheny Plateau ecoregions. This result is somewhat fortunate as one of the least vulnerable ecoregions (Blue Ridge) contains three (French Broad, Hiwassee, and Ocoee) of four (Holston) genetically distinct watersheds that were previously identified based on mitochondrial gene variability (Freake et al., 2018).

At the larger ACU watershed scale, the OACU was predicted to have greatest vulnerability, which suggests this genetically distinct portion of the eastern Hellbender range is under the greatest threats from landscape and climatic stressors. In particular, the OACU had the greatest amount of agricultural land use and overall landscape impairment compared to the other ACUs. Watersheds with relatively large anthropogenic impacts, such as agriculture, urbanization, and mining tend to have greater specific conductivity (Dow and Zampella, 2000), along with other water quality issues. The negative interactions of anthropogenic disturbance and conductivity on assemblage richness have been observed for several organisms including fish (Vieira and Tejerina-Garro, 2020), amphibians (Harmer and Parris, 2011), and macroinvertebrates (Kasangaki et al., 2006). Additionally, studies have shown that eastern Hellbender site occupancy is inversely related to stream specific conductivity (Keitzer et al., 2013; Jachowski and Hopkins, 2018), and within

Table 4

Estimates of exposure, sensitivity, adaptive capacity, and vulnerability by Adaptive Capcity Unit (ACU) and Level III ecoregion within suitable habitat of the eastern Hellbender. The area corrected estimate of vulnerability is presented on a relative scale based on the original vulnerability score multiplied by the proportion of suitable habitat within each ACU and level III Ecoregion.

Adaptive Capacity Unit / Ecoregion	Exposure	Adaptive Capacity	Sensitivity	Vulnerability	Area Corrected Vulnerability (Vulnerability × % Suitable Range)
Adaptive Capacity Unit					
TACU	46.4	11.3	58.4	64.6	16.5
OACU	49.2	6.3	50.5	64.4	42.7
KACU	44.2	9.9	37.0	56.9	4.6
Ecoregion					
Blue Ridge	45.3	21.4	61.1	61.5	5.6
Central Appalachians	43.8	9.6	43.5	59.1	7.2
Central Corn Belt Plains	39.7	0.4	15.9	52.0	0.01
Eastern Corn Belt Plains	59.1	2.9	38.5	65.1	1.6
Eastern Great Lakes Lowlands	64.6	0.7	57.1	73.7	0.1
Erie Drift Plain	57.5	3.1	46.2	66.8	1.7
Interior Plateau	47.4	3.4	63.5	69.2	16.1
Interior River Valleys and Hills	45.5	3.6	52.9	65.0	3.9
Middle Atlantic Coastal Plain	65.5	11.9	31.3	62.5	0.1
Mississippi Alluvial Plain	65.7	4.3	57.5	74.4	0.01
Mississippi Valley Loess Plains	69.8	1.2	64.9	77.5	0.01
North Central Appalachians	38.1	24.0	67.9	60.4	2.5
Northeastern Coastal Zone	62.8	5.0	37.0	65.3	0.07
Northeastern Highlands	33.1	26.1	47.7	51.7	0.09
Northern Allegheny Plateau	56.3	3.3	61.2	71.1	2.6
Northern Piedmont	59.5	4.4	14.5	56.6	0.8
Ridge and Valley	53.0	7.7	41.1	62.1	8.5
Southeastern Plains	37.2	6.0	54.5	61.8	0.7
Southwestern Appalachians	37.8	11.3	54.0	60.1	3.0
Western Allegheny Plateau	51.9	4.4	39.8	62.3	9.0

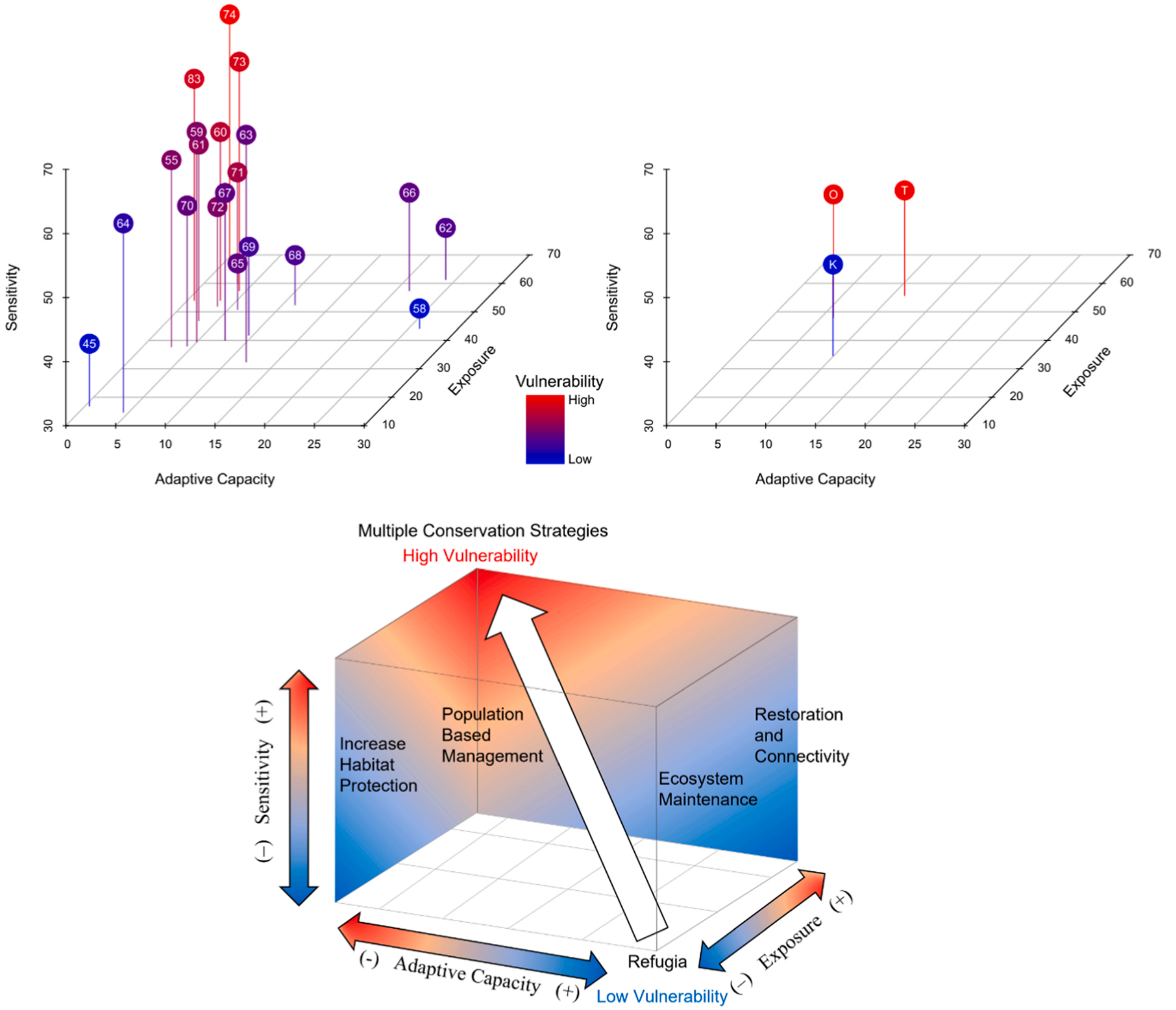

Fig. 6. Lollipop graphical representation of exposure, sensitivity, adaptive capacity, and vulnerability for each Level III Ecoregion (top left) and Adaptive Capacity Units (ACUs; top right) within the predicted suitable habitat for the eastern Hellbender. Relative position within the plots indicates the primary drivers of vulnerability. Relative height of bars, along with color (Blue – Red) indicate progressively greater vulnerability. Labels within the circles correspond with Level III Ecoregions and ACUs (O [OACU], T [TACU], and K [KACU]) in Fig. 3. The bottom figure provides context on the influence of exposure, sensitivity, and adaptive capacity on vulnerability. Example conservation and management actions for the eastern Hellbender are provided along each axis of the figure that correspond with patterns in exposure, sensitivity, adaptive capacity, and vulnerability.

ecoregions that have a relatively greater history of anthropogenic disturbance at the landscape scale (Bodinof Jachowski et al., 2016; Neto et al., 2020).

The relative amount of landscape protection was considerably different among ecoregions. Of the ecoregions that composed greater than 1% of the eastern Hellbender geographic range, the Northern Allegheny Plateau (5.5%) and Interior River Valleys and Hills (6.8%) ecoregions had the least direct protection; however, if indirect protection is included, the Interior Plateau and Interior River Valleys and Hills ecoregions are the least secure with 53.5% and 54.8%, respectively of their land area receiving no direct, or indirect protection from adjacent protected landscapes. In addition to providing important habitat for the conservation of biodiversity, protected areas play important roles for preventing conversion of habitats (Andam et al., 2008) and may be the only natural or semi-natural landscapes that remain in some portions of the globe (Stolton et al., 2015). In this study, for ecoregions that composed $>$ 1% of the eastern Hellbender range, the greatest proportion of land area that was protected (both directly and indirectly) occurred in the North Central Appalachians (Direct: 44.9%; Indirect: 90.3%) and Blue Ridge (Direct: 33.3%; Indirect: 92.0%) ecoregions. Joppa and Pfaff (2009) found that protected area networks are biased towards landscapes that are not likely to face land conversion even without protection. However, in many areas of the eastern Hellbender geographic range, protected areas provide key habitat for Hellbender populations (Freake and DePerno, 2017). In addition, protected areas also serve as climate refugia for biodiversity (Haight and Hammill, 2020), and zones of species range expansions in landscapes with novel climatic conditions (Thomas et al., 2012).

Although designation and maintenance of protected habitats and biological reserves represents a highly effective conservation strategy, additional conservation and management decisions will depend on the primary causes of elevated vulnerability. For example, in protected area landscapes that are isolated by anthropogenic disturbances (i.e., high adaptive capacity, moderate exposure), managers may need to conduct stream restoration practices that increase stream connectivity to permit animal migration and gene flow among populations. For example, obsolete low-head dams represent barriers to migration for aquatic species (e.g., Reid et al., 2008), and in these instances, dam removals may represent a direct conservation action that can result in restored population connectivity. In landscapes where stream connectivity cannot be restored, assisted migration may be necessary to encourage gene flow in fragmented eastern Hellbender populations (Nissen et al., 2023; Kraus et al., 2017). In general, eastern Hellbenders have high site fidelity and relatively small (10 – 511 m^2) annual home ranges (Peterson and Wilkinson, 1996; Humphries and Pauley, 2005). However, long distance migrations of $>$ 2.5 km have been documented in wild populations (Nissen et al., 2023), which suggests that some individuals can move long distances and have the potential to emigrate to suitable habitat patches.

Maintenance of stream connectivity is of particular importance for landscapes that are at additional vulnerability due to loss of climatic suitability (e.g., high sensitivity). In the face of landscape stressors such as climate change, habitat protection and restoration of habitat connectivity likely serves as one of the most effective measures for mitigating the impacts of climate change, especially for watersheds that possess a variety of climatic gradients. For example, Troia et al. (2019) found that species-specific traits, along with aquatic connectivity, are important for providing adaptation potential in the face of climate change within watersheds. In habitats that lack landscape protection and also exist in a landscape matrix with landscape impairment (i.e., low adaptive capacity, moderate exposure), managers may need to focus efforts towards population-based management, which may include maintenance and provisioning of microhabitat features, such as Hellbender nest boxes (e.g., Button et al., 2020) and small-scale stream restoration to provide life-stage specific stream microhabitats (e.g., da Silva Neto et al., 2019; Hecht et al., 2019). In addition, translocation of zoo-raised animals (Bodinof et al., 2012) may be used as a strategy to bolster declining populations and increase genetic diversity in isolated populations.

Direct impacts of climate change on wildlife populations are often difficult to document. Primary climate change impacts often manifest as shifting phenological patterns, which may result in mismatches in organismal interactions (e.g., pollinators and flowering rates) and shifting distributional patterns that correlate with shifts in the climatic niche (Parmesan and Yohe, 2003; Tingley et al., 2009). In reference to amphibian populations, drought has been documented as a causative agent for amphibian declines in several instances (Corn and Fogleman, 1984; Pounds et al., 1999; Li et al., 2013). While there have been few studies directly measuring the impact of climate change on eastern Hellbenders, previous work has shown that growth and immune function declined at warmer temperatures consistent with climate change predictions (Terrell et al., 2021). In addition, warmer temperatures will likely decrease the dissolved oxygen content of streams (U.S. Fish and Wildlife Service, 2018), which could negatively impact habitat suitability during hot and dry periods. Unpredictability of precipitation patterns will likely result in the occurrence of flash droughts and floods, which will both likely impact stream habitat suitability for benthic organisms.

As reported in previous analyses of climatic suitability change of salamanders (e.g., Milanovich et al., 2010; Barrett et al., 2014; Sutton et al., 2015), the modeling algorithm(s) used in these studies (and the current study) is/are correlative and assume(s) that the limits of climatic suitability for the target species are known. This assumption is a limitation, as salamanders have the capacity to adapt to elevational and moisture gradients (Riddell and Sears, 2015). In addition, our models are not parameterized with laboratory measurements of physiological limits (e.g., Gifford and Kozak, 2012) and are unable to estimate the physiological mechanisms that determine an organisms' vulnerability to climate change (see Troia, 2022). Lastly, the relatively large spatial scale of most climate data makes it difficult to translate the predicted change in climatic suitability to population-level impacts. For example, the spatial scale of the climate data used during this study was 1 km^2, which is inadequate to incorporate the climate mitigating effects of microhabitats, especially for organisms with high site fidelity, such as eastern Hellbenders. For the purposes of this analysis, our results should only be used to compare relative vulnerability, exposure, sensitivity, and adaptive capacity of eastern Hellbender populations among Level III Ecoregions and ACUs throughout the conterminous geographic range.

Understanding the collective impacts of anthropogenic change on organismal distributions is important for future protection of global biodiversity (Butchart et al., 2010). Rarely do stressors impact ecosystems singularly, but rather synergistically. For example, Hof et al. (2011) found that regions of the globe with greatest amphibian richness were more likely to be impacted by multiple stressors (e.g., climate change, pathogens), and the synergistic nature of these stressors is predicted to further exacerbate amphibian declines. Furthermore, small-scale experiments have shown that moderate climate change coupled with other stressors such as altered moisture regimes and pollution via pesticides operate synergistically to alter amphibian behaviors (e.g., foraging), which can lead to loss of individual body mass and potentially population declines (Rohr et al., 2013). These findings do not suggest that all stressors impact organisms equally and at the same spatial scale. Therefore, estimates of ecosystem vulnerability need to be evaluated to understand the relative contribution of sources of exposure, sensitivity, and adaptive capacity.

Foden et al. (2013) suggested that amphibians are among the most vulnerable taxa to global change. Therefore, our vulnerability estimates provide an initial and valuable estimate of eastern Hellbender populations vulnerable to future climate and landscape change. Based on our estimates of vulnerability, protection of natural landscapes via private land conservation programs (e.g., conservation easements), further acquisition and expansion of state and federally protected lands, and restoring stream connectivity likely serve as the best strategies for management and conservation of eastern Hellbenders in the face of climate change. Specifically, we suggest expanded land protection efforts in portions of the eastern Hellbender range with known populations that currently lack land protection efforts. An example landscape would include the Lower Duck River watershed in the Interior Plateau ecoregion of Tennessee. This area is an example of a landscape that harbors eastern Hellbender populations, but is impacted by anthropogenic land-use (e.g., agriculture), is projected to experience an overall loss of current climatic suitability, and generally lacks state, federal, or private land protections. Our vulnerability analysis combined with the knowledge of extant eastern Hellbender populations can be used to target landscapes for further conservation and management activities that will increase the resiliency of these populations to future global change.

Declaration of Competing Interest

The authors declare no competing interests.

Data Availability

Data will be made available on request.

Acknowledgments

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02554.

References

Andam, K.S., Feraro, P.J., Pfaff, A., Sanchez-Azofeifa, G.A., Robalino, J.A., 2008. Measuring the effectiveness of protected area networks in reducing deforestation. Proc. Natl. Acad. Sci. USA 105, 16089–16094.

Araújo, M.B., New, M., 2006. Ensemble forecasting of species distributions. Trends Ecol. Evol. 22, 42–47.

Araújo, M.B., Cabeza, M., Thuiller, W., Hannah, L., Williams, P.H., 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. Glob. Change Biol. 10, 1618–1626.

Arbuckle, K.E., Downing, J.A., 2002. Freshwater mussel abundance and species richness: GIS relationships with watershed land use and geology. Can. J. Fish. Aquat. Sci. 59, 310–316.

Baldwin, R.A., 2009. Use of maximum entropy modeling in wildlife research. Entropy 11, 854–866.

Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: how, where and how many? Methods Ecol. Evol. 3, 327–338.

Barrett, K., Guyer, C., 2008. Differential responses of amphibians and reptiles in riparian and stream habitats to land use disturbances in western Georgia, USA. Biol. Conserv. 141, 2290–2300.

Barrett, K., Nibbelink, N.P., Maerz, J.C., 2014. Identifying priority species and conservation opportunities under future climate scenarios: amphibians in a biodiversity hotspot. J. Fish Wildl. Manag. 5, 282–297.

Bodinof, C.M., Briggler, J.T., Junge, R.E., Mong, T., Beringer, J., Wanner, M.D., Schuette, C.D., Ettling, J., Millspaugh, J.J., 2012. Survival and body condition of captive-reared juvenile Ozark hellbenders (*Cryptobranchus alleganiensis bishopi*) following translocation to the wild. Copeia 2012, 150–159.

Bodinof Jachowski, C.M., Millspaugh, J.J., Hopkins, W.A., 2016. Current land use is a poor predictor of hellbender occurrence: why assumptions matter when predicting distributions of data-deficient species. Divers. Distrib. 22, 865–880.

Bryce, S.A., Omernik, J.M., Larsen, D.P., 1999. Ecoregions: a geographic framework to guide risk characterization and ecosystem management. Environ. Pract. 1, 141–155.

Buckley, L.B., Jetz, W., 2007. Environmental and historical constraints on global patterns of amphibian richness. Proc. R. Soc. B 274, 1167–1173.

Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., et al., 2010. Global biodiversity: indicators of recent declines. Science 328, 1164–1168.

Button, S.T., Bodinof Jachowski, C.M., Case, B.F., Groffen, J., Hopkins, W.A., 2020. The influence of multiscale habitat variables and population density on artificial shelter use by hellbenders (*Cryptobranchus alleganiensis*). Herpetologica 76, 355–365.

Cohen, J.M., Civitello, D.J., Venesky, M.D., McMahon, T.A., Rohr, J.R., 2019. An interaction between climate change and infectious disease drove widespread amphibian declines. Glob. Change Biol. 25, 927–937.

Cordier, J.M., Aguilar, R., Lescano, J.N., Leynaud, G.C., Bonino, A., Miloch, D., Loyola, R., Nori, J., 2021. A global assessment of amphibian and reptile responses to land-use changes. Biol. Conserv. 253, 108863.

Corn, P.S., Fogleman, J.C., 1984. Extinction of montane populations of the northern leopard frog (*Rana pipiens*) in Colorado. J. Herpetol. 18, 147–152.

Costa, G.C., Nogueira, C., Machado, R.B., Colli, G.R., 2010. Sampling bias and the use of ecological niche modeling in conservation planning: a field evaluation in a biodiversity hotspot. Biodivers. Conserv. 19, 883–899.

da Silva Neto, J.G., Sutton, W.B., Freake, M.J., 2019. Life-stage differences in microhabitat use by hellbenders (*Cryptobranchus alleganiensis*). Herpetologica 75, 21–29.

De Vos, J.M., Joppa, L.N., Gittleman, J.L., Stephens, P.R., Pimm, S.L., 2014. Estimating the normal background rate of species extinction. Conserv. Biol. 29, 452–462.

Della Rocca, F., Milanesi, P., 2020. Combining climate, land use change and dispersal to predict the distribution of endangered species with limited vagility. J. Biogeogr. 47, 1427–1438.

Dodd Jr, C.K., Smith, L.L., 2003. Habitat destruction and alteration: historical trends and future prospects for amphibians. In: Semlitsch, R.D. (Ed.), Pp 94-112 *In* Amphibian conservation. Smithsonian Institution Press, Washington D.C., USA.

Dow, C.L., Zampella, R.A., 2000. Specific conductance and pH as indicators of watershed disturbance in streams of the New Jersey pinelands, USA. Environ. Manag. 26, 437–445.

Elith, J., Graham, C.H., 2009. Do they? How do they? Why do they differ? On finding reasons for differing performances of species distribution models. Ecography 32, 66–77.

Elith, J., Graham, C.H., Anderson, R.P., Dudık, M., Ferrier, S., Guisan, A., et al., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129–151.

Foden, W.B., Butchart, S.H.M., Stuart, S.N., Vié, J., Akçakaya, H.R., Angulo, A., et al., 2013. Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. PLoS ONe 8, e65427.

Foster, R.L., McMillan, A.M., Roblee, K.J., 2009. Population status of hellbender salamanders (*Cryptobranchus alleganiensis*) in the Allegheny River drainage of New York State. J. Herpetol. 43, 579–588.

Freake, M., O'Neill, E., Unger, S., Spear, S., Routman, E., 2018. Conservation genetics of eastern hellbenders *Cryptobranchus alleganiensis alleganiensis* in the Tennessee Valley. Conserv. Genet. 19, 571–585.

Freake, M.J., DePerno, C.S., 2017. Importance of demographic surveys and public lands for the conservation of eastern hellbenders *Cryptobranchus alleganiensis alleganiensis* in southeast USA. PLoS One 12, e0179153.

Gallant, A.L., Loveland, T.R., Sohl, T.L., Napton, D.E., 2004. Using an ecoregion framework to analyze land-cover and land-use dynamics. Environ. Manag. 34, S89–S110.

Gallopín, G.C., 2006. Linkages between vulnerabililty, resilience, and adaptive capacity. Glob. Environ. Chang 16, 293–303.

Gibson, S.Y., Van der Marel, R.C., Starzomski, B.M., 2009. Climate change and conservation of leading-edge peripheral populations. Conserv. Biol. 23, 1369–1373.

Gifford, M.E., Kozak, K.H., 2012. Islands in the sky or squeezed at the top? Ecological causes of elevational range limits in montane salamanders. Ecography 35, 193–203.

Graham, S.P., Soehren, E.C., Cline, G.R., Schmidt, C.M., Sutton, W.B., Rayburn, J.R., et al., 2011. Conservation status of hellbenders (*Cryptobranchus alleganiensis*) in Alabama, USA. Herpetol. Conserv. Biol. 6, 242–249.

Haight, J., Hammill, E., 2020. Protected areas as potential refugia for biodiversity under climate change. Biol. Cons. 241, 108258.

Hannah, L., Midgley, G., Andelman, S., Araújo, M., Hughes, G., Martinez-Meyer, E., Pearson, R., Williams, P., 2007. Protected area needs in a changing climate. Front. Ecol. Environ. 5, 131–138.

Harmer, A.J., Parris, K.M., 2011. Local and landscape determinants of amphibian communities in urban ponds. Ecol. Appl. 21, 378–390.

Hecht, K.A., Freake, M.J., Nickerson, M.A., Colclough, P., 2019. Hellbender salamanders (*Cryptobranchus alleganiensis*) exhibit an ontogenetic shift in microhabitat use in a Blue Ridge physiographic region stream. Copeia 107, 152–159.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.

Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J., 2020. Dismo:Species distribution modeling. R Package Version 1, 3–3.

Hijmans, R.J., J. Van Etten, J. Cheng, M. Mattiuzzi, M. Sumner, J.A. Greenberg, O.P. et al. 2015. Package 'raster'. R package, 734.

Hime, P.M., 2017. Genomic perspectives on amphibian evolution across multiple phylogenetic scales. Theses Diss. –Biol. 45. ⟨https://uknowledge.uky.edu/biology_etds/45⟩.

Hof, C., Araújo, M.B., Jetz, W., Rahbek, C., 2011. Additive threats from pathogens, climate and land-use change for global amphibian diversity. Nature 480, 22–29.

Homer, C.G., Dewitz, J.A., Yang, L., Jin, S., Danielson, P., Xian, G., et al., 2015. Completion of the 2011 national land cover database for the conterminous United States – representing a decade of land cover change information. Photogramm. Eng. Remote Sens. 81, 345–354.

Houlahan, J.E., Findlay, S.C., Schmidt, B.R., Meyer, A.H., Kuzmin, S.L., 2000. Quantitative evidence for global amphibian population declines. Nature 404, 752–755.

Humphries, W.J., Pauley, T.K., 2005. Life history of the hellbender, *Cryptobranchus alleganiensis*, in a West Virginia stream. Am. Midl. Nat. 154, 135–142.

Jachowski, C.M.B., Hopkins, W.A., 2018. Loss of catchment-wide riparian forest cover is associated with reduced recruitment in a long-lived amphibian. Biol. Conserv. 220, 215–227.

Johnson, C.N., Balmford, A., Brook, B.W., Buettel, J.C., Galetti, M., Lei, G.C., Wilmshurst, J.M., 2017. Biodiversity losses and conservation responses in the Anthropocene. Science 356, 270–274.

Joppa, L.N., Pfaff, A., 2009. High and far: biases in the location of protected areas. PLoS One 4, e8273.

Kasangaki, A., Babaasa, D., Efutre, J., McNeilage, A., Bitariho, R., 2006. Links between anthropogenic perturbations and benthic macroinvertebrate assemblages in Afromontane forest streams in Uganda. Hydrobiologica 563, 231–245.

Keitzer, S.C., Pauley, T.K., Burcher, C.L., 2013. Stream characteristics associated with site occupancy by the eastern hellbender, *Cryptobranchus alleganiensis alleganiensis*, in southern West Virginia. Northeast Nat. 20, 666–677.

Knutti, R., Masson, D., Gettelman, A., 2013. Climate model genealogy: Generation CMIP5 and how we got there. Geophys. Res. Lett. 40, 1194–1199.

Kramer-Schadt, S., Niedballa, J., Pilgrim, N.J., Schröder, B., Lindenborn, J., Reinfelder, V., et al., 2013. The importance of correcting for sampling bias in MaxEnt species distribution models. Divers. Distrib. 2013, 1366–1379.

Kraus, B.T., McCallen, E.B., Williams, R.N., 2017. Evaluating the survival of translocated adult and captive-reared, juvenile eastern hellbenders (*Cryptobranchus alleganiensis alleganiensis*). Herpetologica 73, 271–276.

, 2005Lannoo, M.J. ed., 2005. Amphibian declines: the conservation status of United States species. Univ of California Press.

Leonard, P., Baldwin, R., Kanno, Y., Jachowski, D., Powell, R., Nelson, A., Ogletree, S., 2015. Interactive conservation planning and design phase I for the Appalachian Landscape Conservation Cooperative. Final Report. 123.

Li, Y., Cohen, J.M., Rohr, J.R., 2013. Review and synthesis of the effects of climate change on amphibians. Integr. Zool. 8, 145–161.

Liaw, A., Wiener, M., 2002. Classification and regression by randomForest. *R. N.* 2 3, 18–22.

Lobo, J.M., Jiménez-Valverde, A., Real, R., 2007. AUC: A misleading measure of the performance of predictive distribution models. Glob. Ecol. Biogeogr. 17, 145–151.

Lyons, M.P., Kozak, K.H., 2020. Vanishing islands in the sky? A comparison of correlation-and mechanism-based forecasts of range dynamics for montane salamanders under climate change. Ecography 43, 481–493.

Magness, D.R., Morton, J.M., Huettmann, F., Chapin, F.A., McGuire, A.D., 2011. A climate-change adaptation framework to reduce continental-scale vulnerability across conservation reserves. Ecosphere 2, 1–23.

McGarvey, D.J., Brown, A.L., Chen, E.B., Viverette, C.B., Tuley, P.A., Latham, O.C., Gibbs, et al., 2021. Do fishes enjoy the view? A MaxEnt assessment of fish habitat suitability within scenic rivers. Biol. Conserv. 263, 109357.

Mi, C., Huettmann, F., Guo, Y., Han, X., Wen, L., 2017. Why choose Random Forest to predict rare species distribution with few samples in large undersampled areas? Three Asian crane species models provide supporting evidence. PeerJ 5, e2849.

Milanovich, J.R., Peterman, W.E., Nibbelink, N.P., Maerz, J.C., 2010. Projected loss of a salamander diversity hotspot as a consequence of projected global climate change. PLoS One 5, e12189.

Naughton-Treves, L., Holland, M.B., Brandon, K., 2005. The role of protected areas in conserving and sustaining local livelihoods. Annu. Rev. Environ. Resour. 30, 219–252.

Neto, J.G.D.S., Sutton, W.B., Spear, S.F., Freake, M.J., Kéry, M., Schmidt, B.R., 2020. Integrating species distribution and occupancy modeling to study hellbender (*Cryptobranchus alleganiensis*) occurrence based on eDNA surveys. Biol. Conserv. 251, 108787.

Nissen, B.D., Freake, M.J., Nolan, E., Hardman, R.H., Sutton, W.B., 2023. Evaluating translocation success of wild eastern hellbenders (*Cryptobranchus alleganiensis alleganiensis*) in Blue Ridge Ecoregion streams using pre-and post-translocation home range sizes and movement metrics. Plos one 18, e0283377.

Nori, J., Lemes, P., Urbina-Cardona, N., Baldo, D., Lescano, J., Loyola, R., 2015. Amphibian conservation, land-use changes and protected areas: a global overview. Biol. Cons. 191, 367–374.

Northrup, J.M., Rivers, J.W., Yang, Z., Betts, M.G., 2019. Synergistic effects of climate and land-use change influence broad-scale avian population declines. Glob. Change Biol. 25, 1561–1575.

Oliver, I., Dorrough, J., Doherty, H., Andrew, N.R., 2016. Additive and synergistic effects of land cover, land use and climate on insect biodiversity. Landsc. Ecol. 31, 2415–2431.

Olson, D.M., Dinerstein, E., 1998. The Global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. Conserv Biol. 13, 502–512.

Omernik, J.M., 1987. Ecoregions of the conterminous United States. Map (scale 1:7,500,000). Ann. Assoc. Am. Geogr. 77, 118–125.

Overland, J.E., Wang, M., Bond, N.A., Walsh, J.E., Kattsov, V.M., Chapman, W.L., 2011. Considerations in the selection of global climate models for regional climate projections: the Arctic as a case study. J. Climate 24, 1583–1597.

Paaijmans, K.P., Heinig, R.L., Seliga, R.A., Blanford, J.I., Blanford S, S., Murdock, C.C., Thomas, M.B., 2013. Temperature variation makes ectotherms more sensitive to climate change. Glob. Change Biol. 19, 2373–2380.

Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42.

Peterson, C.L., Wilkinson, R.E., 1996. Home range size of the hellbender *Cryptobranchus alleganiensis* in Missouri. Herpetol. Rev. 27, 12.

Petranka, J.W., 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington D.C., USA.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model 190, 231–259.

Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models: Implications for background and pseudo-absence data. Ecol. Appl. 19, 181–197.

Pounds, J.A., Fogden, M.P.L., Campbell, J.H., 1999. Biological response to climate change on a tropical mountain. Nature 398, 611–614.

Powell, R., R. Conant, and J.T. Collins. 2016. Peterson Field Guide to Reptiles and Amphibians of Eastern and Central North America, 4th ed. Houghton Mifflin Harcourt Publishing Company, 215 Park Avenue South, New York, New York 10003. 494 pp.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Reid, S.M., Wilson, C.C., Mandrak, N.E., Carl, L.M., 2008. Population structure and genetic diversity of black redhorse (*Moxostoma duquesnei*) in a highly fragmented watershed. Conserv. Genet. 9, 531–546.

Riddell, E.A., Sears, M.W., 2015. Geographic variation of resistance to water loss within two species of lungless salamanders: implications for activity. Ecosphere 6, 1–16.

Rohr, J.R., Palmer, B.D., 2013. Climate change, multiple stressors, and the decline of ectotherms. Conserv. Biol. 27, 74–751.

Sabatino, S.J., Routman, E.J., 2009. Phylogeography and conservation genetics of the hellbender salamander (*Cryptobranchus alleganiensis*). Conserv Genet 10 (1235), 1246.

Semlitsch, R.D., 2003. Introduction: general threats to amphibians. In: Semlitsch, R.D. (Ed.), Pp 1–12 *In* Amphibian Conservation. Smithsonian Institution Press, Washington D.C., USA.

Stolton, S., Dudley, N., Avcıoğlu Çokçalışkan, B., Hunter, D., Ivanić, K.Z., Kanga, E., et al., 2015. Values and benefits of protected areas. In: Worboys, G.L., Lockwood, M., Kothari, A., Feary, S., Pulsford, I. (Eds.), Protected Area Governance and Management. ANU Press, Canberra, Australia, pp. 145–168.

Strahler, A.N., 1957. Quantitative analysis of watershed geomorphology. Eos Trans. Am. Geophys. Union 38, 913–920.

Sutton, W.B., Barrett, K., Moody, A.T., Loftin, C.S., deMaynadier, P.G., Nanjappa, P., 2015. Predicted changes in climatic niche and climate refugia of conservation priority salamander species in the northeastern United States. Forests 6, 1–26.

Syfert, M.M., Smith, M.J., Coomes, D.A., 2013. The effects of sampling bias and model complexity on the predictive performance of maxent species distribution models. PLoS One. https://doi.org/10.1371/journal.pone.0055158.

Terando, A.J., Costanza, J., Belyea, C., Dunn, R.R., McKerrow, A., Collazo, J.A., 2014. The Southern Megalopolis: using the past to predict the future of urban sprawl in the Southeastern United States. PLoS One 9, e102261.

Terrell, K.A., Quintero, R.P., Glicia, V.A., Bronikowski, E., Evans, M., Kleopfer, J.D., et al., 2021. Physiological impacts of temperature variability and climate warming in hellbenders (*Cryptobranchus alleganiensis*). Conserv. Pysiol. 79.

Theobold, D.M., 2013. A general model to quantify ecological integrity for landscape assessments and US application. Landsc. Ecol. 28, 1859–1874.

Thomas, C.D., Gillingham, P.K., Bradbury, R.B., Roy, D.B., Anderson, B.J., Baxter, J.M., Bourne, N.A.D., et al., 2012. Protected areas facilitate species range expansions. Proc. Natl. Acad. Sci. USA 109, 14063–14068.

Tingley, M.W., Monohan, W.B., Beissinger, S.R., Moritz, C.G., 2009. Birds track their Grinellian niche through a century of climate change. Proc. Natl. Acad. Sci. USA 106, 19637–19643.

Troia, M.J. 2022. Magnitude-duration relationships of physiological sensitivity and environmental exposure improve climate change vulnerability assessments. Ecography p.e06217.

Troia, M.J., A.L. Kaz, J.C. Niemeyer, and X. Giam. 2019. Species traits and reduced habitat suitability limit efficacy of climate change refugia in streams. Nat Ecol Evol 3:1321–1330.

Turnock, D., 2002. Ecoregion-based conservation in the Carpathians and the land-use implications. Land Use Policy 19, 47–63.

U.S. Environmental Protection Agency. 2006. Level III Ecoregions of the Continental United States. National Health and Environmental Effects Resource Lab, Corvalis, OR. Map M-1.

U.S. Fish and Wildlife Service, 2021. Endangered and threatened wildlife and plants; endangered species status for the Missouri distinct population segment of eastern hellbender. 50 CFR 17, 13465–13475, 86 FR.

U.S. Fish and Wildlife Service Species Status Assess. Rep. East. Hellbender (*Cryptobranchus alleganiensis alleganiensis*). 2018 104.

U.S. Geological Survey (USGS) Gap Analysis Project (GAP). 2018. Protected AreasDatabase of the United States (PAD-US): U.S. Geological Survey Data Release, version1.4.doi: https://doi.org/10.5066/P955KPLE.

van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., et al., 2011. The representative concentration pathways: an overview. Clim. Change 109, 5–31.

Vieira, T.B., Tejerina-Garro, F.L., 2020. Relationships between environmental conditions and fish assemblages in tropical savanna headwater streams. Sci. Rep. 10, 2174.

Wake, D.B., 2007. Climate change implicated in amphibian and lizard declines. Proc. Natl. Acad. Sci. USA 104, 8201–8202.

Wake, D.B., Vredenburg, V.T., 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. P Natl. Acad. Sci. USA 105, 11466–11473.

Wheeler, B.A., Prosen, E., Mathis, A., Wilkinson, R.F., 2003. Population declines of a long-lived salamander: A 20+-year study of hellbenders, *Cryptobranchus alleganiensis*. Biol. Conserv. 109, 151–156.

Yaffee, S.L., 1999. Three faces of ecosystem management. Conserv. Biol. 13, 713–725.