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Surveys

Identifying Priority Species and Conservation Opportunities Under Future Climate Scenarios: Amphibians in a Biodiversity Hotspot

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Abstract

Climate change is driving shifts in the distribution of plants and animals, and prioritizing management actions for such shifts is a necessary but technically difficult challenge. We worked with state agencies in the southeastern United States to identify high-priority amphibian species, to model the vulnerabilities of those species to regional climate change, and to identify long-term climatic refugia within the context of existing conservation lands. Directly interfacing with state natural resource experts ensured that 1) species prioritization schemes extend beyond political boundaries and 2) our models resulted in conservation-relevant applications. We used a correlative model to project midcentury distributions of suitable climate for priority species and to evaluate each species' vulnerability to climate change. Using spatially explicit projected climate distributions, we ranked existing protected areas relative to their ability to provide climatic refugia for priority species in 2050. We identified 21 species as regional high-priority species. Fifteen of the 21 species are forecast to lose more than 85% of their climatically suitable habitat. Regions in the Appalachian Mountains, the Florida Panhandle, and the north-central region of Alabama are projected to lose the most climatic habitat for priority amphibian species. We identified many existing protected areas as midcentury climatic refugia in the Appalachians; however, our projections indicated refugia in the Southeast Coastal Plain to be exceedingly scarce. Although the topographic relief present in the Appalachians appears to provide future conservation opportunities via climatic refugia, the Coastal Plain affords fewer such opportunities and conservation of amphibians in that region is likely to be more challenging. The approach outlined here could be applied across a broad range of taxa and regions.

Keywords: Appalachian Mountains; climatic niche; Coastal Plain; frog; salamander

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Introduction

Anthropogenic threats to native biodiversity such as land use change, invasive species, and disease represent serious challenges to plant and wildlife conservation (Czech 1997). Based on the vulnerability of species to these threats, researchers have developed promising conservation tools to help preserve native diversity (Sarkar et al. 2006; Watts et al. 2010). Climate change

represents yet another threat to species, and the current and future effects of climate change are likely to exacerbate existing stressors (Pressey et al. 2007; Hof et al. 2011). Furthermore, abundant evidence for recent climate-related shifts in species distributions and phenologies indicates that future climate change scenarios will be useful when incorporated into current management decisions and conservation plans (Parmesan and Yohe 2003). Limited resources require prioritization of



management activities; therefore, it is important to evaluate which species are most vulnerable to climate shifts, whether current locations for management efforts will remain suitable for target species, where future areas for conservation should be targeted, and whether species will need assistance migrating between current and future management areas.

All of the above issues represent management and conservation problems that are complex because of the number of factors that interact to yield the response of any one species to climate change. For example, some species will have dispersal capabilities that allow them to track shifting climate envelopes, whereas others will experience range contractions as parts of their range no longer exhibit climatic patterns suitable for the species to maintain stable or increasing population growth (Parmesan et al. 1999). Furthermore, populations are likely to differ in their overall sensitivity to changing climatic conditions, or in their ability to change phenotypes or gene frequencies in a way that allows for adjustment to a novel environment. In an analysis of recently collected and historical data, Davis et al. (2010) found that although closely related plants respond to climate change in similar ways, the response of birds often lacked a phylogenetic signal. That is, knowing something about the response of one species of bird may (or may not) be informative when it comes to forecasting the response of a closely related species. Because of the complexities associated with understanding species response to climate change, a strong interest in climate change vulnerability assessments has developed among scientists and managers. For example, a Web of Science search for "climate change and vulnerability assessment" reveals 165 references published from 2010 to 2014; however, only nine articles on the topic were published from 2000 to 2004.

Many species-based climate change vulnerability assessments do not have a direct link to on-the-ground species management and conservation, even when they contribute to our understanding of how climate change will affect species (Lawler et al. 2010; Primack and Miller-Rushing 2012). In many cases, published assessments combine coarse estimates of climate change exposure with information on species traits to generate an overall measure of vulnerability for each of the species in the assessment (Thomas et al. 2011). Such approaches can aid species prioritization schemes, but do not provide specifics on *places* where species conservation efforts will be most effective. Other efforts to understand the effect of climate change on species do offer a spatial component to the analysis; however, the spatial resolution of the analysis is too large to inform management at scales relevant to individual management areas or parks (Lawler et al. 2010; Schloss et al. 2012), or the vulnerable areas are not made explicit in the analysis (Ohlemüller et al. 2006). Managers urgently need models developed at smaller scales (i.e., square kilometers) that can inform climate change-related decision making. Managers especially need such information in areas of high biodiversity where many species-specific decisions are likely to be made by a wide variety of stakeholders.

The southeastern United States represents a global hotspot of amphibian diversity, with nearly 200 species in the region, over 50 of which are regional endemics (Duellman 1999). There is ample evidence for the strong relationship between climate and the distribution of amphibians and patterns of amphibian diversity at global, regional, and local scales (Bernardo et al. 2007; Buckley and Jetz 2007; Kozak and Wiens 2010). Because of the strong relationship between climate and amphibian distributions, there has been considerable concern among researchers over the potential impacts of global climate change on amphibians in the region (Milanovich et al. 2010). For example, a recent analysis of potential climate change effects on Plethodontid salamanders in the Appalachian Mountains predicts that amphibian species with small, more southerly distributions will experience more significant loss of suitable climatic range than northern-distributed species with larger ranges (Milanovich et al. 2010). Nevertheless, there is little information that directly links amphibian declines to climate-based causes for the decline (Li et al. 2013). In addition, few studies are available to guide specific management and monitoring schemes for particular species beyond basic predictions about the impacts of climate change on regional diversity.

To provide information on amphibian vulnerability to climate change that will inform future research and management efforts, we developed a process for identifying species that state agency biologists consider to be conservation-priority species within the southeastern United States, with respect to climate change. We then used spatially explicit niche models to assess vulnerability to climate change for these species and places. As part of this process, we have identified existing public lands likely to remain climatically suitable for these priority species. Our approach demonstrates the benefits of incorporating expert opinion and local priorities with regional modeling and conservation planning, and we believe this approach would be applicable to a wide variety of taxa.

Methods

Determination of regional priority amphibian species

We determined priority amphibian species for an eight-state region collectively representing the southeastern United States (Alabama, Florida, Georgia, Kentucky, Mississippi, North Carolina, South Carolina, and Tennessee), a region that is a recognized global diversity hotspot for amphibians (Duellman 1999). We began with each state's State Wildlife Action Plan (Association of Fish & Wildlife Agencies 2011) to generate a list of all amphibian species listed in at least one state as a "species of greatest conservation need." Next, we eliminated species that were only listed by one state, and had a range that overlapped many other states. This refined list resulted in 44 species total, with the number of species within any given state ranging from 11 (Kentucky and Mississippi) to 26 (North Carolina). We then contacted state agency personnel tasked with



managing or identifying herpetofauna of conservation concern, and asked them to indicate which of the amphibian species on the list were the five highest priorities for their state in the face of changing climates. Because we wanted to address conservation needs at a regional scale, rather than solely within a state, we asked each state to consider not including a species if it was a priority within their state boundaries, but common throughout the rest of its range. This approach allowed for the selection of species that were endemic to a single state or species that had broad ranges, but were listed throughout much of the range.

Species distribution modeling

We constructed climatic niche models for all of the species identified by state agency personnel. We used the inductive, presence-only modeling approach Maxent (Phillips et al. 2006), using only climatic variables, to model species' climatic distributions. Although several tools are available for constructing these types of correlative distribution models, we selected Maxent because it is known to perform as well as or better than many alternative algorithms (Elith et al. 2006). Because of its strong performance, the tool has been extensively vetted in the literature, resulting in a robust understanding of the method's strengths and weaknesses (Graham et al. 2008; Elith and Graham 2009; Elith and Leathwick 2009; Phillips et al. 2009; VanDerWal et al. 2009a; Veloz 2009; Elith et al. 2011).

We accomplished the first step of collecting locality data on each species through the publically accessible museum database portal HerpNet (2011). We set a goal of obtaining 30 locality records (latitude and longitude coordinates) for each modeled species. Nearly half of our 21 species fell short of that goal after searching the public databases (Table S1). For these species we addressed data shortages by appealing directly to state inventories for additional locality records. State data were requested and obtained from all Southeast states. These additional data allowed us to represent the broadest possible climatic niche for each species. For several species, many locality points were clustered closely together. Locality clusters likely represented areas that were sampled more frequently, and not necessarily areas of high climatic suitability for the species of interest. This kind of data distribution can bias model results (Veloz 2009; Kramer-Schadt et al. 2013); therefore, we haphazardly selected a single point among clusters of points that were within 5 km of one another, and removed the remaining nearby localities. Our choice of a 5-km filter size was somewhat arbitrary; however, we felt it was likely to remove most samples that were collected as the result of repeated visits to a single sampling area (i.e., sites near an easy access point or near a university). After removing clusters and other uncertain point locality data, we were able to meet our goal of 30 locality records for 13 of the 21 species, and for an additional four species we had at least 20 records. The remaining species had only 12–14 records each. Although this sample size is lower than we would have preferred, Maxent has proven more effective at generating useful models with

low numbers of presence points than other distribution modeling algorithms (Hernandez et al. 2006).

To assess current and projected climate envelopes for species we selected 11 biologically relevant climate measurements (BIO 1–3, 7–9, and 15–19; Table 1) from among 19 temperature and rainfall variables (Worldclim 2010). These variables were synthesized from long-term monthly averages (1950–2000) and projected at a scale of approximately 1 km². We selected these variables based on a previous analysis that identified them as exhibiting low pairwise correlations and having relevance to amphibian biology (Rissler and Apodaca 2007). We then intersected these climate variables with locality data for each species as well as background points to allow the Maxent algorithm to compare occupied environments to background environments. We generated background points by randomly placing 10,000 points within a 50-km buffered range of the species (range maps were acquired from the International Union for Conservation of Nature's spatial data download page [IUCN 2011]). We used software (Maxent, Version 3.3.3a) that relies on principles of maximum entropy to determine the joint distribution of climatic conditions correlating with presence records of each species (Phillips et al. 2006). The approach estimates climatic suitability by comparing the values of environmental variables in places where the species is known to occur (locality records) to the same data at background point localities. We evaluated model fit based on area under the curve (AUC) values obtained from a test data set (a random selection of 20% of all locality points). Although some have argued that AUC is a poor measure of quality for species distribution models, we avoided one of the most serious pitfalls associated with this metric by restricting our modeled area to the known range of the species in question (Lobo et al. 2007).

After Maxent estimates preferred climates, it maximizes the entropy in the probability distribution of suitability across all areas of the distribution where empirical observations are lacking. We then projected climatic preferences onto statistically downscaled projections of climate change for the 11 climate variables based on two different CO₂ emissions scenarios (the B2a "medium" and A2a "high" scenarios) as generated by two different general circulation models (GCMs; Met Office's Hadley Centre and the Canadian Centre for Climate Modelling and Analysis). We selected the two climate scenarios as a way to bracket potential future CO₂ emissions (note that even our "high" scenario is a slight underestimation of current emissions), and selected the GCMs to match those used in a recently published analysis of Appalachian salamander response to climate change (Milanovich et al. 2010). We statistically downscaled all current climate averages and the projected climate changes at approximately 1 km² (30 arc seconds). The output from the species distribution models provides a continuous surface from 0–1 that represents low to high probability that the climate is suitable for the modeled species. For analyses where a binary model of suitability is required, we evaluated three different thresholds for identifying whether or not a particular climate is suitable. These thresholds represented a range from conservative to

Table 1. List of bioclimatic variables (www.worldclim.org/bioclim) used in all species distribution models (accessed in 2010).

Variable	Definition
BIO 1	Annual mean temperature
BIO 2	Mean diurnal range (mean of monthly (max temp - min temp))
BIO 3	Isothermality (BIO 2/ BIO 7) × 100
BIO 7	Temperature annual range (max temp of warmest month – max temp of coldest month)
BIO 8	Mean temperature of wettest quarter
BIO 9	Mean temperature of driest quarter
BIO 15	Precipitation seasonality (coefficient of variation)
BIO 16	Precipitation of wettest quarter
BIO 17	Precipitation of driest quarter
BIO 18	Precipitation of warmest quarter
BIO 19	Precipitation of coldest quarter

liberal estimates of what might be deemed suitable habitat (i.e., some were more inclusive of a broader range of climate zones than others). The thresholds that we evaluated were “fixed cumulative value 10” (the threshold that results in a 10% omission rate of training data), “minimum training presence” (the minimum value for which all presence localities are correctly predicted), and “maximum training sensitivity + specificity.” The two CO₂ futures crossed with two GCMs and three thresholds yielded a total of 12 binary models evaluated for each of the species. After the models were generated, we clipped the resulting prediction map to a 50-km buffer of the currently suspected range for each species. This is a very generous estimate of the ability of most amphibians to track their respective climate envelopes via dispersal (Semlitsch 2008).

Data analysis and reporting

We report on species-specific output, as well as collective output from all modeled species. We reported species-specific distribution model results from the ensemble of two GCMs, each of which was examined across three thresholds. This resulted in six possible outcomes for a given CO₂ emissions scenario. Each CO₂ scenario is reported separately, because the climate outcomes under each represent distinct (nonoverlapping) future outcomes. We evaluated the variables that contributed the most explanatory power to each species-based model using the permutation importance metric that is produced as part of Maxent model output. Specifically, we used training gain, or the ability of the model to differentiate presence points from the background, as the measure of explanatory power when evaluating variable importance. In addition to the spatially explicit depiction of shifts in climatic suitability, we ranked protected areas within states based on the amount of climatically suitable habitat the protected area is projected to have by 2050 for a given species. We did calculations in a weighted manner, such that areas projected to remain climatically suitable by more than one model were weighted more heavily than those areas appearing as suitable in only one model projection. Specifically, for a given species, we calculated protected area value by the following formula:

$$\frac{\sum_{n=1}^6 (Sn_i)}{6N}, \quad (1)$$

where S = the number of cells within the protected area deemed climatically suitable, n_{1-6} indicates the number of models that are in agreement regarding climatic suitability, and N = the total number of cells present within the protected area. The denominator is multiplied by 6 in order to scale the potential result from 0 to 1, where 0 indicates no suitable climatic areas under any scenario, and 1 would indicate that 100% of the cells in the protected area were climatically suitable under all six model scenarios. Once we identified a value for all species, we then summed the values across species for each protected area in the southeast (1,520 units). The summed values will increase as a function of both species richness and species-specific climatic suitability in the region. The maximum value is set by the number of species present within the protected area (i.e., because the values for an individual species range from zero to one, a protected area with habitat climatically suitable for six species has a maximum value of six). We did these calculations for the A2a and B2a greenhouse gas emissions scenarios separately. We used a similar approach to rank protected areas based on their current climatic suitability. Because current data are downscaled from direct observation as opposed to GCMs, there were only three model scenarios derived from the range of species distribution thresholds. Substituting a “3” for the “6” in Equation 1 allowed us to calculate the current value of protected areas for each species. We obtained protected areas from the Protected Areas Database of the United States, hosted by the U.S. Geological Survey Gap Analysis Program (www.protectedlands.net/padus/). These areas do not necessarily confer protection upon a given species, but rather these 1,520 areas within the focal southeastern states are zones of public land ownership, management, and conservation lands. The database also includes voluntarily provided privately protected areas. Finally, we ranked climatic sensitivity across species by examining the average amount of climatic suitability projected to be lost across all model scenarios.

To identify areas within the southeast that are likely to lose climatic suitability for a large number of species of concern, we combined individual species models and examined areas of change between current and projected models. We began by estimating the number of priority species with overlapping ranges (per 1-km² grid cell), defined here as the number of overlapping species models from a given threshold (as listed above). We then estimated the number of overlapping ranges per cell for 2050 across all 12 scenarios (two GCMs × two CO₂ futures × three thresholds), and calculated the difference between future and current values. This calculation resulted in 12 estimates of change in species number between now and 2050 for each 1-km² grid cell in the focal southeastern states. These 12 estimates were averaged to allow for a depiction of mean loss across all models. We also calculated the standard deviation across the 12 estimates to facilitate a spatial evaluation of the areas with the greatest uncertainty in projected loss of suitable climatic habitat. In sum, these analyses allow for a large-scale assessment of areas projected to be most sensitive (or most resistant) to climate change with respect to the priority species evaluated in our study.

Results

Species selection

We identified 21 species representing 12 genera among the eight states as regionally high-priority amphibian species (Table 2). Fifteen of the species were salamanders, and six were frogs. We identified 10 of the species as one of the top-five species of concern (with respect to climate change) by more than one state in the Southeast. The green salamander (*Aneides aeneus*) was the most frequently identified species of concern (listed by five states). Five species occurred in more than one ecoregion; however, among the remaining 19 species, 6 species were predominantly located within the Appalachian Mountains, 2 species occur predominantly in the Piedmont, and 8 species occur predominantly in the Coastal Plain. Two species, the tiger salamander (*Ambystoma tigrinum*) and the wood frog (*Lithobates sylvaticus*), stand out as being relatively widespread beyond the Southeast. Although the selection of these species by a state was inconsistent with our requested criteria (see “Methods”), we included them because of their perceived priority status by at least one state.

We did not require that state experts justify the species they selected as state priorities. Nevertheless, we did receive specific rationale from some states and in other cases general trends emerged based on species that were selected. Alabama, Florida, and Georgia made selections for some species that were deemed to be sensitive to shifting precipitation patterns (i.e., amphibians breeding in ephemeral wetlands). Many states within the Appalachian geography identified high-altitude endemics as a priority (i.e., Georgia, Kentucky, North Carolina, and Tennessee). Finally, almost all states identified at least some species that had very patchy or limited distributions within the state as priorities.

Table 2. Species selected in 2010 through state fish and wildlife agency cooperation for a southeastern U.S. climate change vulnerability analysis. Values in parentheses indicate the species was identified as a priority by more than one state. Superscripts indicate species that are closely (but not exclusively) affiliated with either the Coastal Plain (CP) or Appalachian ecoregion (APP).

Salamanders	
<i>Ambystoma cingulatum</i>	^{CP} (2)
<i>Ambystoma tigrinum</i>	
<i>Amphiuma pholeter</i>	
<i>Aneides aeneus</i>	(5)
<i>Cryptobranchus alleganiensis</i>	(3)
<i>Desmognathus aeneus</i>	^{APP} (3)
<i>Desmognathus welteri</i>	^{APP}
<i>Desmognathus wrighti</i>	^{APP}
<i>Hemidactylium scutatum</i>	(2)
<i>Necturus alabamensis</i>	^{APP}
<i>Notophthalmus perstriatus</i>	^{CP} (2)
<i>Plethodon ventralis</i>	^{APP}
<i>Plethodon websteri</i>	(2)
<i>Plethodon wehrlei</i>	^{APP} (2)
<i>Plethodon welleri</i>	^{APP}
Frogs	
<i>Hyla andersonii</i>	^{CP} (2)
<i>Pseudacris brachyphona</i>	^{APP}
<i>Pseudacris ornata</i>	^{CP}
<i>Lithobates capito</i>	^{CP} (3)
<i>Lithobates okaloosae</i>	^{CP}
<i>Lithobates sylvaticus</i>	

Species-specific results

All species, with the exception of the four-toed salamander (*Hemidactylium scutatum*) are, on average, predicted to lose climatically suitable habitat across all scenarios examined (Table 3, Figure 1, Figures S1–S60). The list of species losing the most climatically suitable habitat by 2050 (≥95%) is dominated by species from the Coastal Plain (five out of the eight species examined in this study), and also includes two species from the Appalachian Mountains and one species from the Piedmont (Table 3). Among all species examined, BIO 1 (mean annual temperature) had the highest mean variable importance value (23.2%, range = 0.7–65.1%), and this variable also contributed most when we examined species closely associated with either the Appalachian Mountains or Coastal Plain separately (Figure 2). The next most important variables, as assessed across all species, were three precipitation and temperature variables assessed seasonally (BIOs 8, 15, and 19). These variables represented a mean 10% contribution each for all species, but varied in their importance to species associated with the Appalachian Mountains or Coastal Plain when we evaluated those species separately (Figure 2a). When we evaluated frogs

Table 3. Proportion of each priority amphibian species' current climatic range that is projected to be climatically unsuitable by 2050 (as modeled in 2011). The number of localities used to build the model (*N*) appears in column 2, and test area under the curve (AUC) represents a measure of model quality (see "Individual Species Results" for more detail). Cells with "none" indicate 100% of climatically suitable habitat is projected to be lost. Species are ranked in order of the mean loss across model types (negative values indicate gains in climatic suitability for a species). All modeled scenarios and thresholds are depicted below. Scenario A2a represents a future with relatively high CO2 emissions, while B2a represents a climate driven by more moderate emissions. Threshold abbreviations: MTP = minimum training presence, F10 = fixed cumulative value 10, MTP = maximum training sensitivity plus specificity. See "Methods" for threshold definitions. Negative values indicate the species is projected to gain habitat under a given scenario.

Species	<i>N</i>	Test AUC	Hadley						Canadian						Mean loss	
			A2a			B2a			A2a			B2a				
			MTP	F10	MTR	MTP	F10	MTR	MTP	F10	MTR	MTP	F10	MTR		
<i>Ambystoma cingulatum</i> , Frosted flatwood salamander	24	0.69	None	None	None	None	None	None	None	None	None	None	None	None	None	1.00
<i>Lithobates okaloosae</i> , Florida bog frog	48	0.93	None	None	None	None	None	None	None	None	None	None	None	None	None	1.00
<i>Necturus alabamensis</i> , Alabama waterdog	17	0.84	None	None	None	None	None	None	None	None	None	None	None	None	None	1.00
<i>Notophthalmus perstriatus</i> , Striped newt	41	0.76	None	None	None	None	None	None	None	None	None	None	None	None	None	1.00
<i>Plethodon websteri</i> , Webster's salamander	24	0.83	None	None	None	0.98	0.98	None	None	None	None	None	None	None	None	1.00
<i>Plethodon ventralis</i> , Southern zigzag salamander	32	0.70	0.97	0.98	0.98	0.97	0.98	0.98	0.97	0.98	None	None	None	None	None	0.98
<i>Lithobates capito</i> , Gopher frog	152	0.85	0.92	None	None	0.94	0.99	None	0.92	None	None	0.90	0.98	None	None	0.97
<i>Desmognathus welteri</i> , Black Mountain salamander	25	0.83	0.91	0.91	0.90	0.90	0.90	0.87	None	None	None	0.97	0.98	None	None	0.95
<i>Desmognathus aeneus</i> , Seepage salamander	22	0.98	0.98	0.97	0.91	0.98	0.97	0.94	0.95	0.92	0.80	0.97	0.96	0.88	0.94	0.94
<i>Aneides aeneus</i> , Green salamander	62	0.72	0.92	0.93	0.92	0.92	0.93	0.94	0.89	0.92	0.90	0.95	0.95	0.95	0.95	0.93
<i>Plethodon wehrlei</i> , Wehrle's salamander	93	0.73	0.91	0.93	0.95	0.89	0.94	0.98	0.95	0.98	None	0.80	0.90	0.95	0.93	0.93
<i>Hyla andersonii</i> , Pine Barrens treefrog	52	0.82	0.86	0.84	0.82	0.90	0.95	0.95	0.90	0.94	0.97	0.90	0.92	0.93	0.91	0.91
<i>Desmognathus wrighti</i> , Pygmy salamander	30	0.98	0.92	0.94	0.94	0.87	0.93	0.91	0.89	0.91	0.90	0.89	0.88	0.87	0.90	0.90
<i>Plethodon welleri</i> , Weller's salamander	14	0.94	0.78	0.77	0.82	0.78	0.82	0.80	0.97	0.97	0.98	0.90	0.87	0.92	0.87	0.87
<i>Pseudacris brachyphona</i> , Mountain chorus frog	53	0.80	0.85	0.85	0.93	0.80	0.80	0.83	0.88	0.88	0.96	0.84	0.83	0.88	0.86	0.86
<i>Amphiuma pholeter</i> ^a , One-toed amphiuma	14	0.37	None	None	None	None	None	None	0.82	0.80	-1.56	0.99	0.99	0.89	0.75	0.75
<i>Cryptobranchus alleganiensis</i> , Eastern hellbender	83	0.91	0.84	0.96	0.99	0.78	0.97	0.98	0.47	0.52	0.51	0.40	0.59	0.66	0.72	0.72
<i>Pseudacris ornata</i> ^a , Ornate chorus frog	12	0.62	0.85	0.88	0.60	0.90	0.92	0.74	0.72	0.77	0.11	0.69	0.74	0.28	0.68	0.68
<i>Ambystoma tigrinum</i> , Tiger salamander	32	0.82	0.30	0.31	0.29	0.37	0.44	0.59	0.23	0.16	0.86	0.30	0.24	0.87	0.41	0.41
<i>Lithobates sylvaticus</i> , Wood frog	451	0.94	-0.04	0.42	0.57	-0.03	0.35	0.46	-0.15	0.11	0.25	-0.09	0.02	0.17	0.17	0.17
<i>Hemidactylum scutatum</i> , Four-toed salamander	197	0.84	0.33	-0.22	0.96	0.25	-1.62	0.92	-6.47	-5.88	0.40	-7.32	-7.50	0.18	-2.16	-2.16

^a Low test AUC values that indicate poor model quality for these species.

and salamanders independent of one another, BIO 1 again appeared as most important for both groups; however, the second most important variable was BIO 15 for frogs and BIO 8 for salamander (Figure 2b).

For all species except flatwoods salamander (*Ambystoma cingulatum*), Florida bog frog (*Lithobates okaloosae*), and Alabama waterdog (*Necturus alabamensis*) we identified at least two protected areas projected to contain

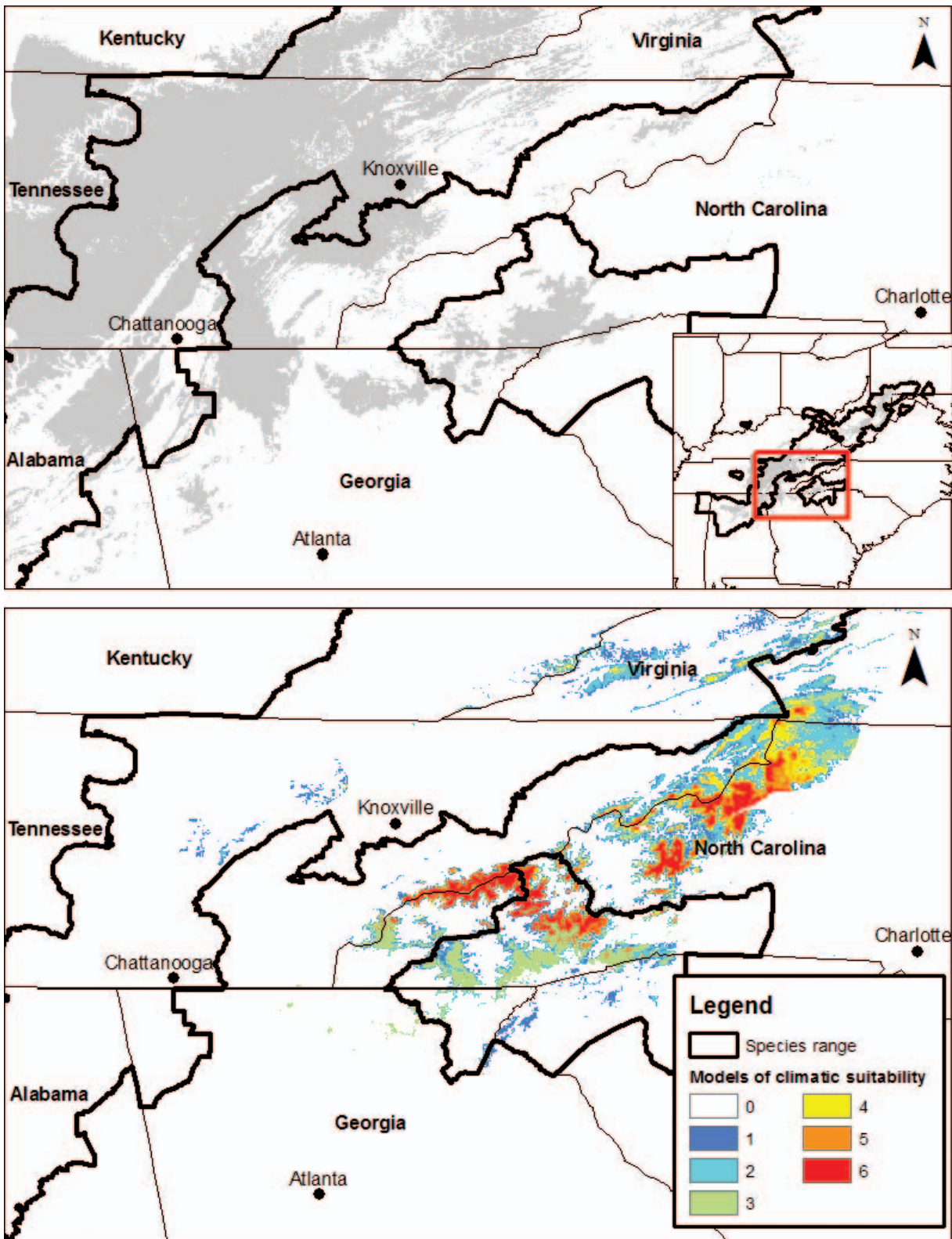


Figure 1. An example of species-specific climatic niche shift projections (here, for the green salamander [*Aneides aeneus*]). All species-specific model results appear in the Supplementary Material. The inset in the top panel shows the entire range of the green salamander (bold black polygon) and the species' current climatic niche throughout that range (based on a single model threshold represented by the gray area). The red rectangle in the inset corresponds to the enlarged area shown in the main top panel. The lower panel represents an ensemble climatic suitability map produced from two downscaled climate data sets × three species thresholds for 2050. Warmer colors indicate greater overlap among the six possible model outcomes (i.e., warmer colors suggest more models identify an area as climatically suitable for the species in 2050). This approach was used for each species to generate the datasets shown in Tables 2 and 3.

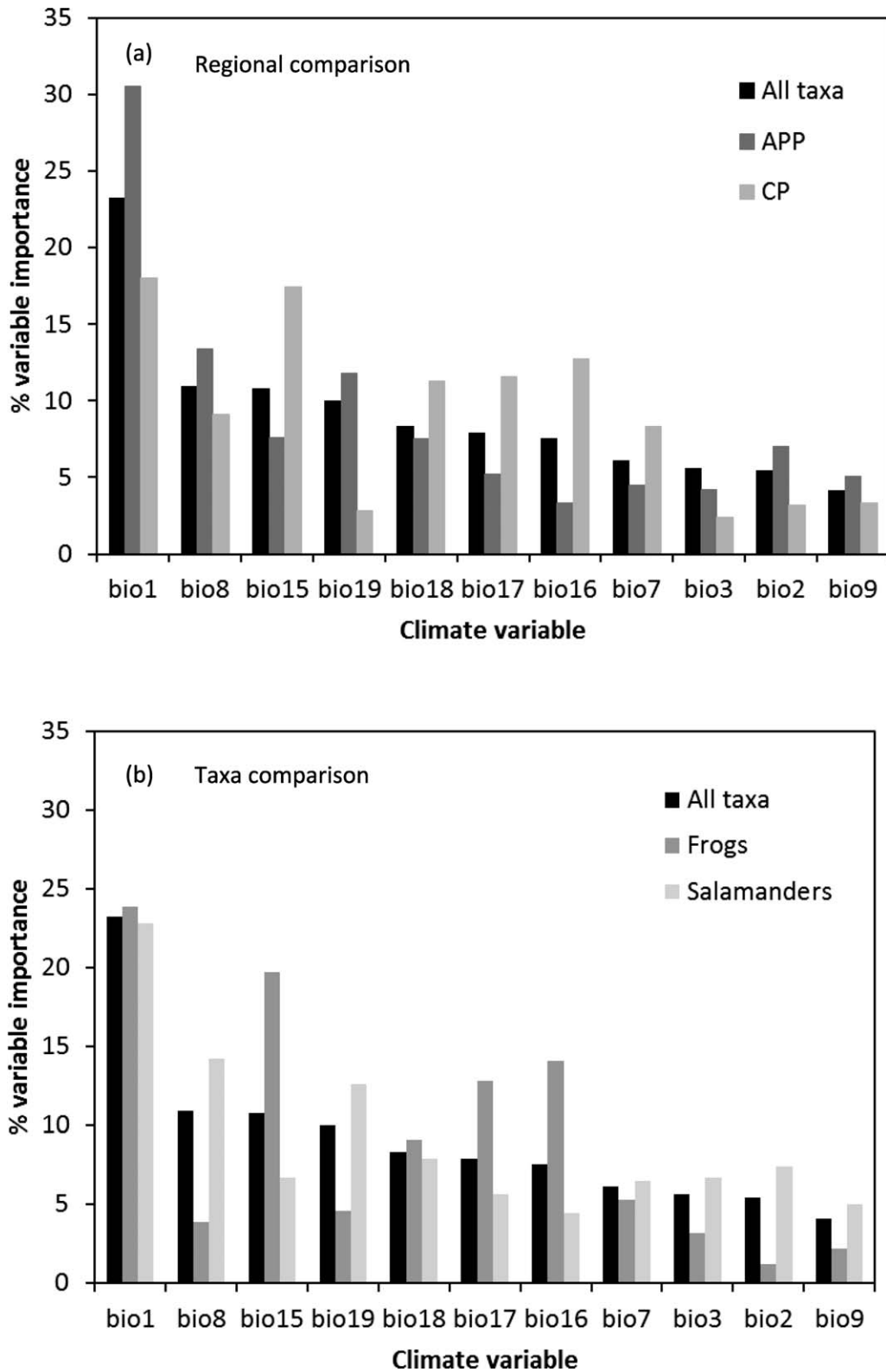


Figure 2. Mean variable importance for climatic models as assessed across all species and for (a) Appalachian (APP) and Coastal Plain (CP) species separately and (b) frog and salamander species separately. Variables are in descending order of average importance across all species. BIO 1 = annual mean temperature, BIO 2 = mean diurnal temperature range, BIO 3 = isothermality (BIO 2/BIO 7) × 100, BIO 7 = temperature annual range, BIO 8 = mean temperature of wettest quarter, BIO 9 = mean temperature of driest quarter, BIO 15 = precipitation seasonality (CV), BIO 16 = precipitation of wettest quarter, BIO 17 = precipitation of driest quarter, BIO 18 = precipitation of warmest quarter, BIO 19 = precipitation of coldest quarter.

climatically suitable habitat by 2050 under some scenario (median = 40, range = 2–660; Tables S2–S19). The sum of protected areas for each species with at least some protected habitat had a median value of 640,202 ha, with the smallest sum (3,281 ha) associated with projections for Webster's salamander (*Plethodon websteri*) and the largest (13,189,000 ha) with the tiger salamander, *tigrinum*. Of the 1,520 currently protected areas in our focal southeastern states, we have projected 866 (57%) (by at least one model) to maintain some climatically suitable habitat for priority amphibians. When we ranked protected areas based on the A2a weighted score of value as a long-term refugia (see "Data Analysis and Reporting" for details), the top 5% of the 866 units (Table 4) primarily included protected areas in the Appalachian and Cumberland Plateau regions of the southeast. We identified only one unit, Florida Caverns State Park, in the Coastal Plain region. The majority of the protected areas that we projected to be high-priority climatic refugia in 2050 were also identified as being of high climatic suitability to a large number of species currently (i.e., within the upper 25th percentile of sites as ranked by current climatic suitability; Table 4). Nevertheless, three units that ranked relatively low based on current estimates (lower 75th percentile), appear within the high-priority climatic refugia list for 2050.

Overlap in species projections

The increase or decrease in overlap of climatically suitable habitat for priority species between current and future climate projections ranged between mean values (for a given 1-km² cell) of two additional to seven fewer species (Figure 3). We project the vast majority of land within the southeast to either maintain current climatic suitability for the same number of priority species as currently seen, or to lose climatic suitability for at least one or more species. The only regions in the Southeast that we projected to show an increase in priority species richness by 2050 are a few scattered cells in the Appalachian Mountains located in Swain and Haywood counties, North Carolina, and in Sevier County, Tennessee. Because these regions are collectively so small (totaling 210 km²), it would be difficult to imagine these sites representing critical future habitat that can sustain populations of priority species over the long term. Three regions, the Florida Panhandle, the Appalachian Plateaus of north-central Alabama and northwestern Georgia, and the Ridge and Valley Appalachian regions of Tennessee, contained the areas with at least a mean of four species lost between current estimates and 2050 projections (Figure 3). Two of these regions (the Florida Panhandle and the Appalachian Plateaus of north-central Alabama) were also regions with greater variance around the mean of the 12 scenarios (Figure 4). Although it is not unusual for parameters with a higher mean to also have higher variance, this correlation was not exhibited in all regions found to have high mean loss of climatically suitable habitat (e.g., the South Atlantic Coast exhibited high loss but low variance). Areas noted to be highly vulnerable and exhibiting high uncertainty are likely to be strong

candidates to target during species and assemblage monitoring plans.

Discussion

Because species' ranges generally transcend political boundaries, and because climate change will alter species' distributions, managing wildlife in the context of climate change requires regional cooperation and tools for informing management actions. We illustrate a process by which regional priority species can be identified by managers, and climate model projections for those priority taxa can be used to select the most vulnerable species and current areas of importance for future management. Traditionally, species prioritization efforts consider only specific management areas or the interests of a state. By using existing state species of greatest conservation need lists and polling state agency personnel within the southeastern region, we were able to generate a regional list of priority amphibian species. A key aspect of this effort was asking personnel to consider a species' status outside their own state in ranking priority species. Next, we used niche models to rank the vulnerability of priority species to a range of climate change scenarios. We found that species within the Coastal Plain of the southeastern United States were particularly vulnerable to loss of climatic niche, but that 15 of the 21 species are projected to lose 85% or more of climatically suitable habitat within the range of those species. It is important to note that we were not forecasting whether species will go extinct. Rather, we quantified where all or most climate models project 2050 temperature and precipitation patterns will no longer match recent climate (1950–2000) within a species' current range (Table 3). We did not examine climatic suitability in areas beyond 50 km of the current range map for a species. Although these areas may be of interest in discussions of managed relocations, we view that complex issue as beyond the scope of our analysis.

In addition to the ranking of species vulnerability to climate change, we identified areas within the range of each priority species where climatic suitability is projected to be maintained under future climate scenarios (Figure 1). Identification of areas within existing species' ranges that are likely to remain climatically suitable will be essential to conservation in the face of climate change. Local managers can build upon our climate suitability projections to determine which currently protected areas contain necessary habitat features for priority species, and whether specific habitat management will be necessary to ensure that a particular location could serve as a climate refugium. For example, given the knowledge that temperature and precipitation patterns conducive to the persistence of a particular pond-breeding frog will be maintained in the near future, managers may decide that efforts to increase wetland density across the landscape would be warranted. Alternatively, those sites identified as climate refugia that are also protected from stressors such as habitat fragmentation, may be candidates for very little management (Magness et al. 2011), which would free up

Table 4. Protected areas in the southeastern United States that are in the top 5% of those projected to have at least some climatically suitable habitat for priority species. Ranking is based on a weighted average of the amount of climatically suitable habitat available for each priority species within the protected area, using the higher greenhouse gas emissions scenario (A2a; however, the weighted score for the more moderate greenhouse gas emissions scenario (B2a) is also shown. Model runs were completed in 2011.

Type of protected area	Name	State	Area (ha)	A2a weighted ^a	B2a weighted ^a	2050 species ^b	Current species ^c	Current rank ^d
National forest (USFS) ^e	Roan Mountain	Tennessee	1,866	3.32	3.52	7	7	60
State game land	Elk Knob State Game Land	North Carolina	295	3.27	4.08	7	8	7
Scenic area (USFS)	Rogers Ridge Scenic Area	Tennessee	2,257	3.24	3.49	9	9	4
National parkway (NPS)	Blue Ridge Parkway	North Carolina	20,242	3.19	2.80	10	11	14
State game land	Three Top Mountain State Game Land	North Carolina	1,186	3.07	3.85	8	9	3
State natural area	Elk Knob State Natural Area	North Carolina	936	3.03	3.90	8	8	8
Wilderness area (USFS)	Shining Rock Wilderness	North Carolina	7,656	3.02	2.52	6	6	251
National forest (USFS)	Appalachian National Scenic Trail	Tennessee	14,624	3.00	2.97	8	9	16
State natural area	Mount Jefferson State Natural Area	North Carolina	278	3.00	3.57	8	9	10
Wilderness area (USFS)	Unaka Mountain Wilderness	Tennessee	1,808	2.91	2.89	8	8	18
Scenic area (USFS)	Stoney Creek Scenic Area	Tennessee	1,053	2.91	3.11	7	8	17
Wilderness area (USFS)	Southern Nantahala Wilderness Area	Georgia/North Carolina	9,364	2.90	2.42	7	6	69
National park (NPS)	Great Smoky Mountains National Park	North Carolina/Tennessee	208,142	2.85	2.71	8	8	21
State game land	Cherokee State Game Land	North Carolina	137	2.83	3.75	7	9	9
Scenic area (USFS)	Unaka Mountain Scenic Area	Tennessee	285	2.79	2.49	7	7	36
Wilderness area (USFS)	Middle Prong Wilderness	North Carolina	3,061	2.75	2.27	6	5	244
State natural area	Hampton Creek Cove State Natural Area	Tennessee	278	2.69	2.64	7	7	38
National forest (USFS)	Big Laurel Branch Addition	Tennessee	1,995	2.58	2.61	7	8	46
State game land	Cold Mountain State Game Land	North Carolina	1,343	2.56	2.36	6	8	279
Nature Conservancy fee land	Rainbow Springs Preserve	North Carolina	751	2.54	2.13	5	4	92
State park	Roane Mountain State Park	Tennessee	820	2.46	2.27	6	7	82
Wilderness area (USFS)	Joyce Kilmer-Slickrock Wilderness	North Carolina/Tennessee	7,422	2.40	2.37	7	8	5
Conservancy easement (The Nature Conservancy)	Grandfather Mountain Preserve	North Carolina	475	2.37	2.71	5	5	167
State park	Mount Mitchell State Park	North Carolina	655	2.29	2.57	4	5	346
State forest	Gill State Forest	North Carolina	187	2.28	2.28	5	7	78
Wilderness area (USFS)	Pond Mountain Wilderness	Tennessee	2,832	2.24	2.26	7	8	29
National forest (USFS)	Pisgah National Forest	North Carolina	203,220	2.24	2.45	9	10	125
Scenic area (USFS)	Doe River Gorge Scenic Area	Tennessee	1,094	2.21	1.89	7	8	30

Table 4. Continued.

Type of protected area	Name	State	Area (ha)	A2a weighted ^a	B2a weighted ^a	2050 species ^b	Current species ^c	Current rank ^d
National forest (USFS)	Nantahala National Forest	North Carolina	196,940	2.14	1.96	8	9	45
Wilderness area (USFS)	Big Laurel Branch Wilderness	Tennessee	2,573	2.07	1.82	7	8	46
Wilderness area (USFS)	Citico Creek Wilderness	Tennessee	6,526	2.06	1.92	7	9	12
National forest (USFS)	Nolichucky River	Tennessee	147	2.06	1.61	4	6	151
Scenic area (USFS)	Bald Mountain Ridge Scenic Area	Tennessee	3,516	2.05	1.89	6	6	105
Wilderness area (USFS)	Linville Gorge Wilderness	North Carolina	4,766	2.01	1.67	6	8	179
National forest (USFS)	Cherokee National Forest	Tennessee	196,040	1.99	1.89	11	12	1
Experimental forest (USFS)	Coweeta Hydrologic Laboratory	North Carolina	2,198	1.87	1.77	5	6	200
Historical area (USFS)	Wasp Community Cultural Heritage Area	Tennessee	149	1.78	1.64	3	4	272
Wilderness area (USFS)	Sampson Mountain Wilderness	Tennessee	3,224	1.72	1.43	4	7	123
State park	Florida Caverns State Park	Florida	518	1.71	0.00	4	5	591
State natural area	Bays Mountain State Natural Area	Tennessee	1,233	1.69	1.19	6	8	13
State forest	Dupont State Forest	North Carolina	4,161	1.67	1.59	4	5	798
Wilderness area (USFS)	Tray Mountain Wilderness Area	Georgia	4,262	1.66	1.36	5	6	216
State natural area	Frozen Head State Park State Natural Area	Tennessee	4,673	1.65	1.54	5	9	23

^a Weighted averages for the A2a and B2a scenarios were generated by first calculating a weighted score of climatic suitability for each species per protected area (as in Equation 1). We then summed those scores to get an overall value for any given protected area. Zero represents the minimum value and the maximum possible value is set by the number of species for which climatically suitable habitat exists (see "Methods: Data Analysis and Reporting" for additional detail).

^b The number of species projected to have at least some climatically suitable habitat in the protected area, as assessed by multiple models of the A2a greenhouse gas emissions scenario.

^c The number of species projected to currently have climatically suitable habitat in the protected area, as assessed by climatic niche only. This number may not reflect the number of species actually present in the protected area. In general, species from 2050 were a subset of those from current models.

^d The rank of the protected area based on the amount of climatically suitable habitat currently available to priority species. Scores were assigned for current climatic suitability in the same manner that weighted averages were determined for the A2a and B2a emissions scenarios, then protected areas were ranked in descending order based on these values.

^e USFS = U.S. Forest Service, NPS = National Park Service.

resources for more vulnerable landscape patches. We advocate that it will be the management of local habitat within areas of the most suitable climate that will maximize the likelihood that priority species can persist within their current ranges. Even in this context, conservation practitioners will need to consider the response of species not currently considered priority by our process or others, as these species may not be captured by current conservation planning processes, yet they may exhibit vulnerability to climate change (Summers et al. 2012).

Our ensemble approach provides a mechanism for conservation practitioners to incorporate the uncertainty of future climate projections into management decisions. Projected shifts in temperature and precipitation are accompanied by a large amount of uncertainty (Christensen et al. 2007). Uncertainty about future climates is

compounded by the fact that our niche models are correlative rather than mechanistic. Though mechanistic niche models are potentially more realistic than correlative models (Buckley et al. 2010), data sufficient to generate mechanistic models are lacking for most species. We have addressed uncertainty by bracketing a suite of climate projections (two greenhouse gas emissions scenarios × two GCMs) and by varying the strictness with which a species distribution is predicted by climate (three thresholds). Although we cannot provide information on the relative likelihood of different model projections, we have provided a range of scenarios containing future conditions that are likely to be conservative estimates of the amount of change over the next 35 y. As a result, we provided a way for managers to explicitly incorporate some elements of uncertainty and some measure of consensus into any on-

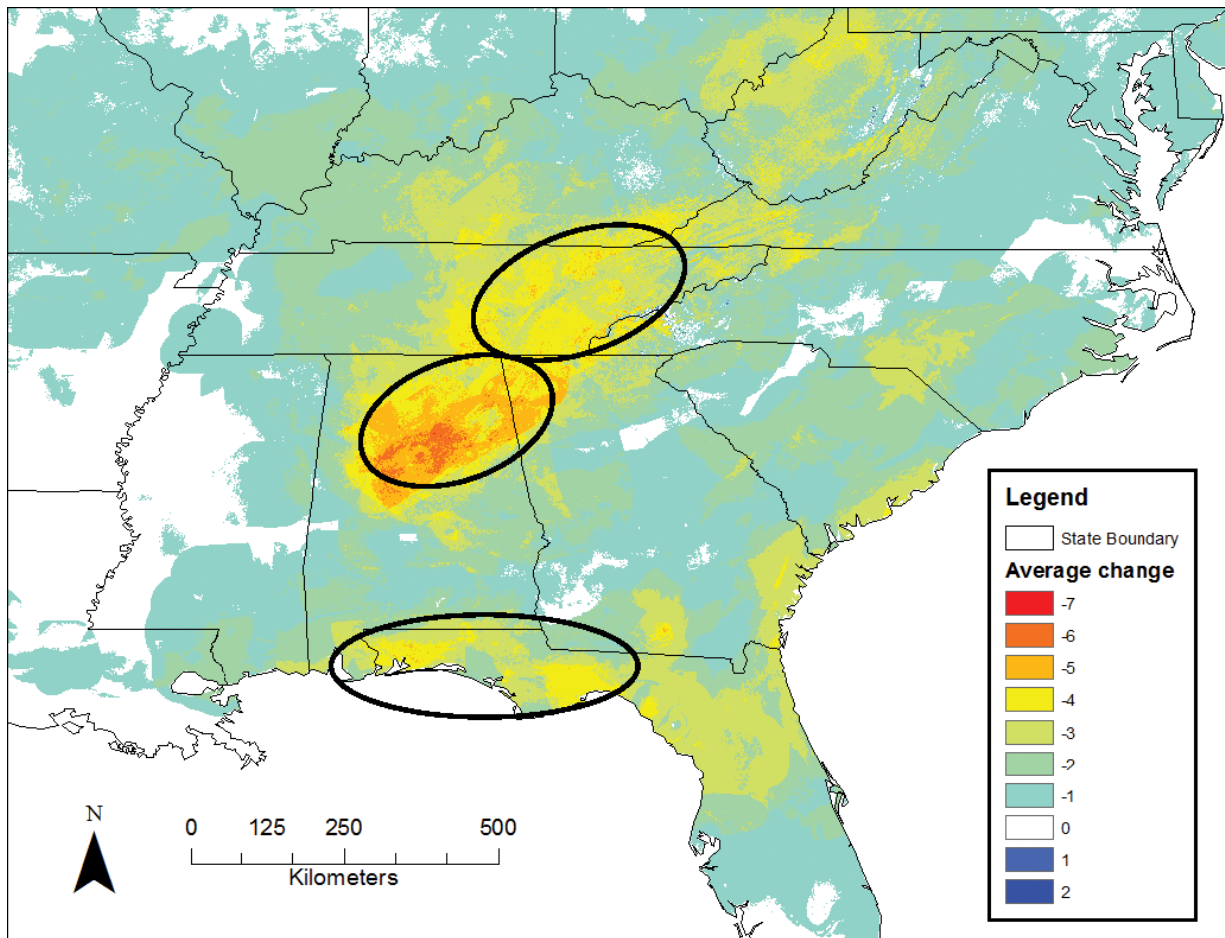


Figure 3. Mean change in the number of overlapping priority species (based on climatic suitability) as calculated from 12 different change scenarios between current estimates and 2050 projections (as available in 2011). The areas within ovals represent large regions with climatic habitat project to be lost for at least four species, on average. These areas are, from south to north, the Florida Panhandle, the Appalachian Plateau, and the Ridge and Valley plus the Blue Ridge of the Appalachians. See “Methods” for detail on the generation of future projections.

the-ground decisions involving these results. Additionally, we have modeled at a spatial scale fine enough (1 km²) such that the chance of overestimating climatically suitable habitat is reduced (Seo et al. 2009). It is noteworthy that mean annual temperature emerged, on average, as the most important variable in our species-based models (as measured by contribution to increase in model AUC). Although we do not discount the importance of precipitation in setting amphibian distributions, our data suggest that a coarse-scale temperature measure offers important insight into the vulnerability of many amphibian species. This is a valuable result for conservation planning given the greater agreement among GCMs with respect to mid-century changes in temperature relative to changes forecast for precipitation across the southeastern United States (Hawkins and Sutton 2011; Sobolowski and Pavelsky 2012; van Oldenborgh et al. 2013).

Uncertainty in species distribution models also arises because factors besides climate can strongly influence the distribution and abundance of species. Although

biotic factors can act in conjunction with climate to determine a species’ realized distribution, models that do not incorporate biotic variables still exhibit strong predictive performance relative to models that attempt to incorporate species interactions (Godsoe and Harmon 2012). We believe that empirical relationships between climate and species distributions among amphibians make our climate-based models a robust starting point for informing species’ vulnerabilities to climate change. The precision of our projections could be refined with the integration of species-specific performance data related to climate (Buckley et al. 2011). An additional limit to the utility of our projections is that we cannot yet link indices of climatic suitability with population abundance or individual performance. VanDerWal et al. (2009b) have argued that models of environmental suitability do at least allow us to identify areas where the upper limit of local abundance may be achieved (i.e., areas of high environmental suitability). Nevertheless, the relationship VanDerWal et al. (2009b) describe is wedge-shaped, with low variation in abundance where environ-

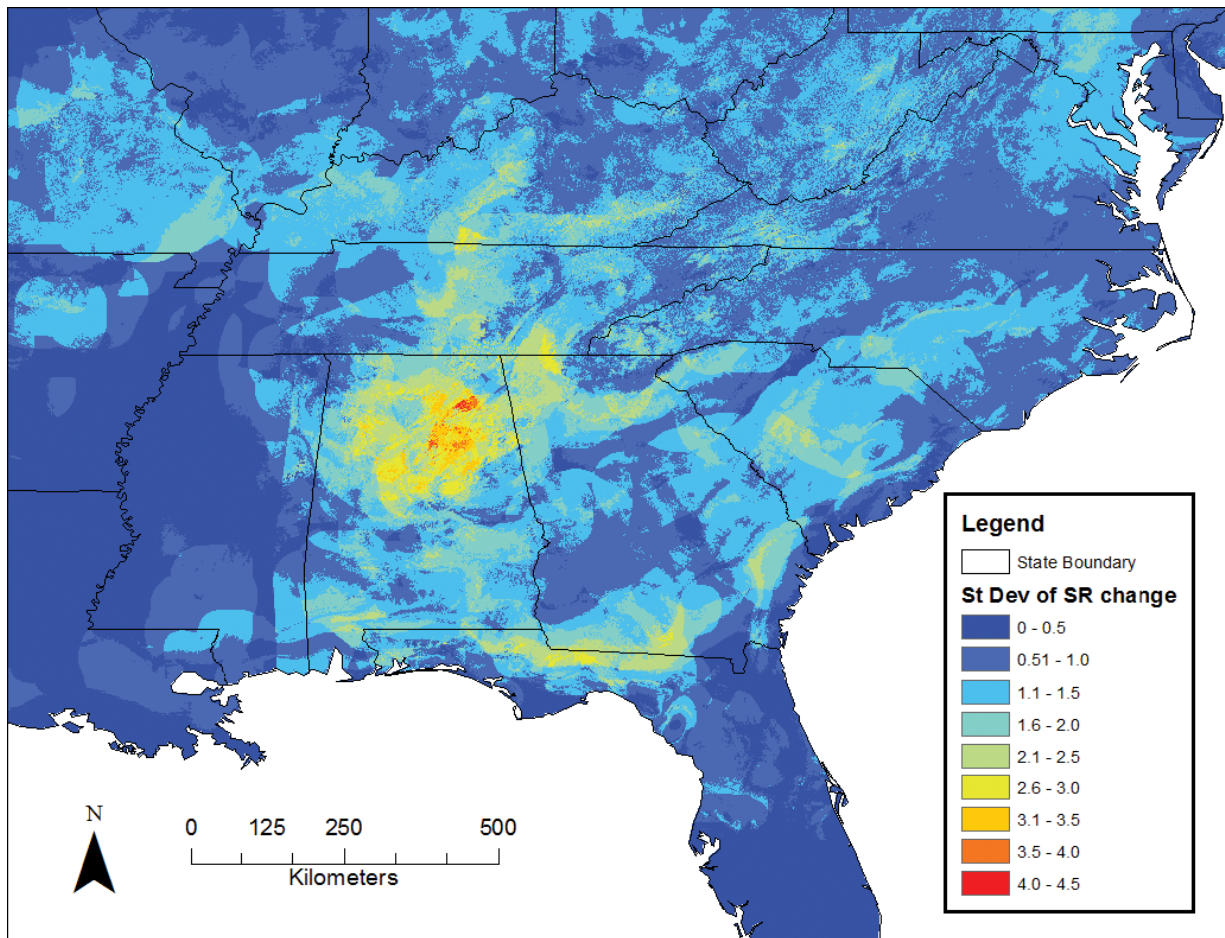


Figure 4. The spatial distribution of standard deviation values resulting from 12 different change scenarios in priority species overlap (based on climatic suitability) between current estimates and 2050 projections (as available in 2011). Readers must use caution when interpreting this map, as low standard error values might result from agreement across all models or from low estimates of total species overlap. As a result, this figure is best interpreted with reference to Figure 3. See “Methods” for detail on the generation of future projections.

mental suitability is low, but high variation in abundance where environmental suitability is also thought to be high. This shape implies that even at the highest levels of environmental suitability some unaccounted for factors are influencing abundance.

The immediate utility of models that attempt to forecast species vulnerability to climate change includes, but is not limited to, 1) model relevance to the types of decisions conservation planners are making, 2) the timeline of the projections relative to the timeline of management decisions, and 3) the ability of the model to incorporate and convey uncertainty. Our approach to ensure relevance to conservation decision making was to involve decision makers in the process from the very beginning. We then focused on midcentury projections, where uncertainty in the climate future is less, and we synthesized the uncertainty that is present so that it becomes easier to integrate into the decision-making process. There are many well-founded concerns with projections based on climate niche alone (Fitzpatrick and Hargrove 2009; Lavergne et al. 2010), yet these models

provide a starting point for species and landscape prioritization schemes. Future work should begin to address approaches that help us understand and enhance the adaptive capacity of species. For example, our assessment of climatic vulnerability focuses on the future exposure of species to temperature and precipitation shifts. Such an assessment may be refined by further considering the historical exposure species have faced by examining phylogeographic origins of specific lineages (Kozak and Wiens 2010; Scoble and Lowe 2010). Additionally, where data are available, more complex models that couple population dynamics to climate change can offer specific management solutions (Conlisk et al. 2013).

Supplemental Material

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Table S1. Amphibian records obtained from species-specific searches of the HerpNet database March 2010–December 2011. Latitude and longitude values of selected individuals were used to generate presence-only models of climatic niche (see “Methods” for details).

Found at DOI: <http://dx.doi.org/10.3996/022014-JFWM-015.S1>. (1295 KB XLS)

Tables S2–S19. Protected areas that contain climatically suitable habitat in 2050 within a 50 km buffer of the currently known range for priority species identified by state agency biologists in the southeastern United States.

Found at DOI: <http://dx.doi.org/10.3996/022014-JFWM-015.S2> (6,676 KB PDF)

Text S1. A guide for interpreting species-specific figures (Figures S1–S60) and tables (Tables S2–S19).

Found at DOI: <http://dx.doi.org/10.3996/022014-JFWM-015.S2> (6,676 KB PDF)

Text S2. A guide to interpreting plots of model quality.

Found at DOI: <http://dx.doi.org/10.3996/022014-JFWM-015.S2> (6,676 KB PDF)

Figures S1–S60. Figures detailing model quality, current climatic suitability models, and 2050 climatic suitability models for each of the priority species identified by state agency biologists in the southeastern United States.

Found at DOI: <http://dx.doi.org/10.3996/022014-JFWM-015.S2> (6,676 KB PDF)

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References

- Association of Fish & Wildlife Agencies. Teaming with wildlife: a natural investment. Available: www.teaming.com/state-wildlife-action-plans-swaps. Accessed 13 March 2011.
- Bernardo J, Ossola RJ, Spotila J, Crandall KA. 2007. Interspecies physiological variation as a tool for cross-species assessments of global warming-induced endangerment: validation of an intrinsic determinant of macroecological and phylogeographic structure. *Biology Letters* 3:695–698.
- Buckley LB, Jetz W. 2007. Environmental and historical constraints on global patterns of amphibian richness. *Proceedings of the Royal Society B: Biological Sciences* 274:1167–1173.
- Buckley LB, Urban MC, Angilletta MJ, Crozier LG, Rissler LJ, Sears MW. 2010. Can mechanism inform species' distribution models? *Ecology Letters* 13:1041–1054.
- Buckley LB, Waaser SA, MacLean HJ, Fox R. 2011. Does including physiology improve species distribution model predictions of responses to recent climate change? *Ecology* 92:2214–2221.
- Christensen JH, Hewitson B, Busuioc A, Chen A, Gao X, Held I, Jones RC, Kolli RK, Kwon W-T, Laprise R, and others. 2007. 2007: Regional climate projections. Pages 847–940 in Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL, editors. *Climate change 2007: the physical science basis contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, United Kingdom and New York: Cambridge University Press.
- Conlisk E, Syphard AD, Franklin J, Flint L, Flint A, Regan H. 2013. Uncertainty in assessing the impacts of global change with coupled dynamic species distribution and population models. *Global Change Biology* 19:858–869.
- Czech B. 1997. Distribution and causation of species endangerment in the United States. *Science* 277:1116.
- Davis CC, Willis CG, Primack RB, Miller-Rushing AJ. 2010. The importance of phylogeny to the study of phenological response to global climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:3201–3213.
- Duellman WE. 1999. Global distribution of amphibians: patterns, conservation, and future challenges. Pages 1–31 in Duellman WE, editor. *Patterns of distribution of amphibians*. Baltimore, Maryland: John Hopkins University Press.
- Elith J, Graham CH. 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 CH, Anderson RP, Dudik M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, and others. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129–151.

- Elith J, Leathwick JR. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* 40:677–697.
- Elith J, Phillips SJ, Hastie T, Dudik M, Chee YE, Yates CJ. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17:43–57.
- Fitzpatrick M, Hargrove W. 2009. The projection of species distribution models and the problem of non-analog climate. *Biodiversity and Conservation* 18:2255–2261.
- Godsoe W, Harmon LJ. 2012. How do species interactions affect species distribution models? *Ecography* 35:811–820.
- Graham CH, Elith J, Hijmans RJ, Guisan A, Peterson AT, Loiselle BA, Gro NPSW. 2008. The influence of spatial errors in species occurrence data used in distribution models. *Journal of Applied Ecology* 45:239–247.
- Hawkins E, Sutton R. 2011. The potential to narrow uncertainty in projections of regional precipitation change. *Climate Dynamics* 37:407–418.
- Hernandez PA, Graham CH, Master LL, Albert DL. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29:773–785.
- Herpnet [Internet]. n.d [cited 2011 March 13]. Available from: <http://www.herpnet.org>.
- Hof C, Araujo MB, Jetz W, Rahbek C. 2011. Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature* 480:516–519.
- [IUCN] International Union for Conservation of Nature. n.d. [cited 2012 June 20]. Red List spatial data. Available: <http://www.iucnredlist.org/technical-documents/spatial-data#amphibians>.
- Kozak KH, Wiens JJ. 2010. Niche conservatism drives elevational diversity patterns in Appalachian salamanders. *American Naturalist* 176:40–54.
- Kramer-Schadt S, Niedballa J, Pilgrim JD, Schröder B, Lindenborn J, Reinfelder V, Stillfried M, Heckmann I, Scharf AK, Augeri DM, and others. 2013. The importance of correcting for sampling bias in MaxEnt species distribution models. *Diversity and Distributions* 19:1366–1379.
- Lavergne S, Mouquet N, Thuiller W, Ronce O. 2010. Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. *Annual Review of Ecology, Evolution, and Systematics* 41:321–350.
- Lawler JJ, Shafer SL, Blaustein AR. 2010. Projected climate impacts for the amphibians of the Western Hemisphere. *Conservation Biology* 24:38–50.
- Li Y, Cohen JM, Rohr JR. 2013. Review and synthesis of the effects of climate change on amphibians. *Integrative Zoology* 8:145–161.
- Lobo JM, Jiménez-Valverde A, Real R. 2007. AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography* 17:145–151.
- Magness DR, Morton JM, Huettmann F, Chapin FS III, McGuire AD. 2011. A climate-change adaptation framework to reduce continental-scale vulnerability across conservation reserves. *Ecosphere* 2:112.
- Milanovich JR, Peterman WE, Nibbelink NP, Maerz JC. 2010. Projected loss of a salamander diversity hotspot as a consequence of projected global climate change. *Plos One* 5:e12189.
- Ohlemüller R, Gritti ES, Sykes MT, Thomas CD. 2006. Quantifying components of risk for European woody species under climate change. *Global Change Biology* 12:1788–1799.
- Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399:579–583.
- Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231–259.
- Phillips SJ, Dudik M, Elith J, Graham CH, Lehmann A, Leathwick J, Ferrier S. 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications* 19:181–197.
- Pressey RL, Cabeza M, Watts ME, Cowling RM, Wilson KA. 2007. Conservation planning in a changing world. *Trends in Ecology & Evolution* 22:583–592.
- Primack RB, Miller-Rushing AJ. 2012. Uncovering, collecting, and analyzing records to investigate the ecological impacts of climate change: a template from Thoreau's Concord. *Bioscience* 62:170–181.
- Rissler LJ, Apodaca JJ. 2007. Adding more ecology into species delimitation: ecological niche models and phylogeography help define cryptic species in the black salamander (*Aneides flavipunctatus*). *Systematic Biology* 56:924–942.
- Sarkar S, Pressey RL, Faith DP, Margules CR, Fuller T, Stoms DM, Moffett A, Wilson KA, Williams KJ, Williams PH. 2006. Biodiversity conservation planning tools: present status and challenges for the future. *Annual Review of Environment and Resources* 31:123–159.
- Schloss CA, Nuñez TA, Lawler JJ. 2012. Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proceedings of the National Academy of Sciences of the United States of America* 109:8606–8611.
- Scoble J, Lowe AJ. 2010. A case for incorporating phylogeography and landscape genetics into species distribution modelling approaches to improve climate adaptation and conservation planning. *Diversity and Distributions* 16:343–353.
- Semlitsch RD. 2008. Differentiating migration and dispersal processes for pond-breeding amphibians. *The Journal of Wildlife Management* 72:260–267.
- Seo C, Thorne JH, Hannah L, Thuiller W. 2009. Scale effects in species distribution models: implications for

- conservation planning under climate change. *Biology Letters* 5:39–43.
- Sobolowski S, Pavelsky T. 2012. Evaluation of present and future North American Regional Climate Change Assessment Program (NARCCAP) regional climate simulations over the southeast United States. *Journal of Geophysical Research-Atmospheres* 117. doi: 10.1029/2011JD016430
- Summers DM, Bryan BA, Crossman ND, Meyer WS. 2012. Species vulnerability to climate change: impacts on spatial conservation priorities and species representation. *Global Change Biology* 18:2335–2348.
- Thomas CD, Hill JK, Anderson BJ, Bailey S, Beale CM, Bradbury RB, Bulman CR, Crick HQP, Eigenbrod F, Griffiths HM and others. 2011. A framework for assessing threats and benefits to species responding to climate change. *Methods in Ecology and Evolution* 2:125–142.
- VanDerWal J, Shoo LP, Graham C, Williams SE. 2009a. Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? *Ecological Modelling* 220:589–594.
- VanDerWal J, Shoo LP, Johnson CN, Williams SE. 2009b. Abundance and the environmental niche: environmental suitability estimated from niche models predicts the upper limit of local abundance. *American Naturalist* 174:282–291.
- van Oldenborgh GJ, Reyes FJD, Drijfhout SS, Hawkins E. 2013. Reliability of regional climate model trends. *Environmental Research Letters* 8. doi: 10.1088/1748-9326/8/1/014055
- Veloz SD. 2009. Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. *Journal of Biogeography* 36:2290–2299.
- Watts K, Eycott A, Handley P, Ray D, Humphrey J, Quine C. 2010. Targeting and evaluating biodiversity conservation action within fragmented landscapes: an approach based on generic focal species and least-cost networks. *Landscape Ecology* 25:1305–1318.
- Worldclim – Global Climate Data. Bioclim. [Internet]. n.d. [2010 November 14]. Available: www.worldclim.org/bioclim