

**THE VULNERABILITY OF EASTERN NORTH AMERICAN
PLETHODONTIDAE SALAMANDERS TO CLIMATIC CHANGE**

An Undergraduate Research Scholars Thesis

by

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ABSTRACT

The Vulnerability of Eastern North American Plethodontidae Salamanders to Climatic Change.
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Many biologists rely on environmental niche modeling to predict where species will migrate upon imminent climate changes. These coarse-scale approaches base species' movements on variables such as temperature, habitat, and rainfall in their current ecosystems. The model, however, does not consider the animals' metabolic rates, thermal range limits, niche competition, or other intrinsic physiological capabilities to tolerate changing climate. Environmental niche modeling also fails to consider the importance of microclimate acting as a buffer against regional climate change. This project entails the construction of a species' traits-based matrix for Eastern North American Plethodontidae salamanders. Each species within this family is critically analyzed by elevation, latitude and longitude, critical thermal maximum, metabolic capacity, overall range area, and numerous other criteria. Based on the data collected from literature and Dr. Bernardo's field research over the past several years, each animal will be scored and given an overall vulnerability assessment. By evaluating variables based on both species' physiological limits and local environmental factors, the risk of endangerment as well as future range contractions can be more accurately predicted and managed.

CHAPTER I

INTRODUCTION

The most pervasive threat to global species diversity is anthropogenic climate change. Biologists have been struggling to identify vulnerable species and regions in order to understand how ecosystems will change and what actions must be taken to preserve the biodiversity (1). Initially, many prognoses of species' range contractions (e.g. (2)) have been accrued through environmental niche modeling which analyzes and maps current climatic properties of its habitat such as precipitation, temperature, and altitude (3). Environmental niche models (ENMs) are convenient because they permit analysis of both community-level extinction estimates and individual species risk (2, 4). However, these models require no knowledge of organismal resiliency or sensitivity to climate change, making assumptions about future range contractions based solely on climate data and current species localities (4).

This top-down, phenomenological approach is problematic. First, ENMs assumes that most species have been evenly sampled across their geographic ranges. Reviews of these models have found that most species collection data are biased in geographic sampling and statistically insufficient (5, 6).

Second, many localities, identifications, and elevations found in online databases have error rates greater than twenty-five percent (6).

Third, these models assume that macroclimatic data accurately characterizes the operative environments of the organisms. Different species experience distinct microclimates (e.g. an oak tree and a soil arthropod) within one macroclimate (7). Significant differences in ambient air temperatures below ground vs above, shading by vegetation or topography, variation of soil type and moisture level, etc. all affect the microclimate the organism actually experiences (8-11). Dispersal of a species in such a climatically heterogeneous landscape is also influenced by behavioral traits, such as butterflies laying eggs on cooler northward facing leaves or amphibians remaining close to water (7, 12). One review studying dispersal behavior in microclimates found that amphibians operate well below their critical thermal maximum temperatures by seeking shade, burrowing, and maintaining skin moisture (9). By studying the body temperature instead of modeling against air temperature, it can be inferred that organisms use microclimates to modulate their operative temperature (9). Applying such detailed, local variables also elucidates the reasoning behind the climatic migration lag observed in many species; their microclimates act as a buffer to regional climate change, thus obviating the need to move (8). Current models have a spatial mismatch in the scale of climatic data of approximately four orders in animals and three orders in plants (13).

Fourth, ENMs attempt to estimate an organism's fundamental range from its realized range, ignoring biotic interactions and physiographic limitations. For instance, in Connell's classic study of barnacle intertidal distribution, *Chthamalus* barnacles were excluded from the lower tidal zone by *Balanus* barnacles, even though physiologically *Chthamalus* thrives in the lower tidal zone (14). Ecology has recognized for over a half century that species fundamental and

realized niches are discordant, but environmental niche modeling has consistently ignored the fact.

Fifth, an organism's response is a joint function of climatic change and intrinsic sensitivity, but environmental niche modeling disregards species traits as moderators of exposure (4, 15).

Species' physiological, behavioral, and morphological traits (e.g. (9)) determine an organism's sensitivity to environmental change and thus these traits could either exacerbate or ameliorate how climate change affects the organism (16). Some organisms may acclimatize to shifting climates and alter their thermal performance curve, still other species lacking the genetic capability to evolve or appropriate physiological traits of tolerance may decline (17). Species' traits will determine the outcome of their vulnerability.

The IUCN Red List is a widely used method for gauging species susceptibility to endangerment and extinction. This list contains five categories of criteria, with subcategories, that define the thresholds of vulnerability to extinction; it can be applied to any organism even when minimal knowledge is available (18). Numerous field studies have been undertaken to accumulate data to apply the criteria, including that for the Global Amphibian Assessment, all of which have aided in understanding patterns of species endangerment (19). These criteria were developed long before climate change was a primary concern, so it is uncertain whether these criteria capture climate change vulnerability. Again, the IUCN model only accounts for ecological factors such as range size, habitat loss, and population size. It was not designed with climate change in mind so we must look for additional criteria that could also influence vulnerability.

Here, we examine a range of new criteria that attempt to identify species traits that relate to climate change responsiveness. There are three ways for an organism to respond to climate change: one is to migrate somewhere else, the second is to tolerate these new conditions, and third is to evolve the capacity to tolerate the novel environment or migrate (16). While utilizing the criteria already provided by the IUCN, new variables have been added to this model to include physiological traits as important influencers of dispersal. The new criteria are developed and applied in the context of the IUCN framework (20).

In this paper, we apply this traits-based model to thirty species of lungless salamanders of eastern North America and contrast our findings with those of ENM of the same species (1). To apply these new criteria we will extract relevant data from primary literature in physiological ecology, population genetics, evolutionary biology, biophysical ecology, and climate models to evaluate Plethodontidae salamanders' risk to extinction (3, 4). This species' traits-based model addresses the fact that species' susceptibility is shaped by both the degree of warming in the environment and the biology of the organism, with larger increases in temperature expected in higher latitudes (15, 16). Mechanistic modeling also allows us to identify limiting factors affecting species vulnerability (3). However, the disadvantage to computing such a detailed range is the enormous compilation of data needed and the numerous calculations performed (5). Conclusions drawn about salamander vulnerability from this model are expected to be decisively different from that of the IUCN.

North American Eastern Plethodontidae salamanders are key constituents of forest ecosystems and can serve as models of vulnerability to climate change. The Appalachian Mountains harbor

the richest diversity of salamander species in the world with seven of the nine families found in these highlands (1). Populations were initially thought to be small, but recent surveys have found that large numbers of salamanders spend their time underground and constitute a significant amount of the biomass in ecosystems (21, 22). Plethodontid salamanders play crucial roles as predators of invertebrates, prey for small mammals and birds, in influencing soil structure, and also allowing the flow of energy between terrestrial and aquatic ecosystems (21, 22). Concentrations of salamander species are higher in regions with aspects related to their role in the ecosystem (21). With the eastern United States as the global hotspot for Plethodontidae diversity, it is clear these organisms are ecologically important to maintaining natural energy balances (1, 22). We will assess the resiliency or susceptibility of these salamanders by a mechanistic model using climatic data and species traits.

CHAPTER II

METHODS

For this paper, I am analyzing the salamander fauna east of the Mississippi River and west to Ohio, extending from Florida to Maine. I used insights from published and unpublished phylogeographic analyses to define cryptic species (unnamed, genetically distinctive lineages, 23). This exercise resulted in a salamander fauna comprising 123 species representing 18 genera and seven families. Here I examined a subset of 30 species whose anticipated responses to climate change were studied by Milanovich et al. using environmental niche modeling (1).

To analyze the vulnerability of Plethodontidae salamanders to global climate change a traits-based matrix was constructed. In addition to the IUCN Red List criteria which are ecological properties (species distributions, population size and trends), several new categories of criteria were included that account for the three main avenues of response to climate change (tolerance, dispersal ability, and evolutionary potential). Each of these variables outlines specific thresholds that define the species as highly vulnerable (1), vulnerable (0, denoted z in Table 2), or not vulnerable (-1) (Table 1).

I relied heavily on recent phylogenetic studies showing that some nominal species were more than one (*Desmognathus*, *Aneides*). The type species will be referred to as “sensu stricto” (s.s.) with other lineages renamed accordingly.

I used the data that Dr. Bernardo, the primary literature, secondary literature (IUCN database), and museum specimens provided on latitudes, elevations, location coordinates, and species traits. The data was ranked according to the table generated by Dr. Bernardo and his colleagues (Table 1).

In order to calculate the geographic ranges and area of occupancy, I used the software ArcGIS to map the collected coordinates of each species. The range was found by applying elevation maps to the ArcGIS program and using the measuring tool to draw lines encompassing the total area of all the data points. Area of occupancy was calculated by measuring the area each individual data point occupied and then multiplying by the number of locations the organism was found. I also utilized Google Earth to estimate coordinate values when only the names of the location were provided.

Additional data was sought by reading through primary and secondary literature describing life history traits, ecological relationships, dispersal, genetic diversity, and other descriptors. Once obtained, the physiological data will be the key criteria in assessing species' vulnerabilities.

Table 1- Endangerment Criteria and Thresholds			
	Vulnerability Score		
Criterion	Highly vulnerable (1)	Vulnerable (0)	Not vulnerable (-1)
I.A. Reduction in population size based on number of mature individuals	Decline of 70% over 10 years or 3 generations	Decline of 50% over 10 years or 3 generations	No population reduction
I.B.1. Geographic range: extent of occurrence	<5,000 km ²	<20,000 km ²	>20,000 km ²
I.B.2. Geographic range: area of occupancy	<500 km ²	<2000 km ²	>2000 km ²
I.C. Small population size and decline	20% decline or N<2500	10% decline or N<10,000	No evidence of decline
I.D. Very small or restricted population	<250 individuals	<1,000 individuals	Not restricted
I.E. Quantitative analysis showing probability of extinction in the wild is at a defined threshold in defined timeframe	Loss of 20% in 20 years or 5 generations	Loss of 10% in 100 years	No evidence for probability of extinction
I.F. Latitude	<1°	1-5°	>5°
I.G. Altitude	<1000m	1000-2000m	>2000m
I.H. Ecological Dependency on other species	extreme specialist, obligate or single host	narrow specialist, facultative or several hosts	generalist or no dependency
II.A. Tolerance breadth	<6°C	>6 to 13	>13°C
II.B. Long-term thermal functional threshold (pejus) surpassed	regularly	occasionally	rarely
II.C. Short-term exposure to ambient extremes	regularly	occasionally	rarely
II.D. Plasticity of long term and critical thresholds	0 to 1°C	1 to 3°C	>3°C

Table 1- Continued			
Criterion	Highly vulnerable (1)	Vulnerable (0)	Not vulnerable (-1)
II.E.1. Safety margin (long-term)	Ambient is 0 to 1°C below upper pejus T	Ambient is 2 to 3° below upper pejus T	Ambient is >3°C below upper pejus T
II.E.2. Safety margin (short-term)	Ambient is 0 to 1°C below upper CT _{max}	Ambient is 2 to 5°C below upper CT _{max}	Ambient is >5°C below upper CT _{max}
II.F. Performance optimum mismatch	Ambient T close to optimum T	Ambient T slightly (3°C) below optimum	Ambient T >5°C below optimum
II.G. Magnitude of environmental change	large	medium	small
II.H. Behavioral / phenological response	Sedentary / no phenological shift	Hibernator / aestivator / incomplete phenological shift	Microsite selection Migratory/ phenological tracking
II.I. Metabolic capacity (if aerobic)	low	medium	high
III.A.1 Indirect measures of dispersal	Strong significant IBD, high phylogeographic structure throughout range as evidenced by many haplogroups, low Nm , high Φ_{ST} or F_{ST}	Some significant IBD, some phylogeographic structure, few haplogroups, medium Nm , medium Φ_{ST} or F_{ST}	No significant IBD, little phylogeographic structure, 1 or 2 haplogroups, high Nm , low Φ_{ST} or F_{ST}
III.A.2 Direct measures of dispersal	highly philopatric or not vagile	can and do get around to some extent	plenty of movement, over large parts of range
IV.A.1 Overall genetic diversity across the species	low estimates of H_d , π , Θ , H_o or H_e	medium estimates of H_d , π , Θ , H_o or H_e	high estimates of H_d , π , Θ , H_o or H_e

Table 1- Continued			
Criterion	Highly vulnerable (1)	Vulnerable (0)	Not vulnerable (-1)
IV.A.2 Genetic diversity partitioned within species	presence of many locally restricted haplotypes, low numbers of alleles and haplotypes	some locally restricted haplotypes, medium numbers of alleles and haplotypes	vast majority of genetic diversity over most of the populations with very few locally restricted haplotypes
IV.B. Genetic erosion	huge decline in recent diversity from historical ($\pi \ll \Theta$), skyline plot shows drastic decrease from historical to present	some decline in recent diversity from historical, or a decrease in genetic diversity across parts of range ($\pi < \Theta$), skyline plot shows moderate decrease from historical to present	no evidence of decline or some evidence of increase ($\pi = \Theta$ or $\pi > \Theta$), skyline plot shows no decrease or some growth from historical to present
IV.C.1 Overall quantitative genetic diversity across the species	low h^2 (< 0.05) or V_A , and/or evidence of severe evolutionary constraints from multivariate studies	moderate h^2 ($0.05-0.30$) or V_A , and/or evidence of minimal evolutionary constraints	high h^2 (> 0.30) or V_A , and/or evidence of no evolutionary constraints
IV.C.2 Quantitative genetic diversity partitioned within species	High Q_{ST}	Moderate Q_{ST}	Low Q_{ST}
IV.D. Life history	Long generation times, small effective population sizes, low fecundity	medium generation times, medium effective population sizes, medium fecundity	short generation times, large effective population sizes, high fecundity

CHAPTER III

RESULTS

To date, most of the data collected pertained to aspects of geographic distribution of each species. These included geographic range, area of occupancy, latitudinal breadth, altitudinal breadth, and population size and trends (Criteria I.A-H, Table 2). We are still extracting data from the primary literature pertaining to obtain physiological and evolutionary criteria. Therefore, I focus only on the ecological criteria.

In criterion I.A., it shows that most species have not experienced any population reductions over the past ten years or three generations (Table 2). Populations appear to be stable. However, exceptions are *D. marmoratus s.s.*, *D. ocoee s.s.*, *P. chatahoochee*, and *P. chlorobryonis*. These species we do not yet have data for or are otherwise calculating directly from the primary literature. *D. conanti s.s.* is the only species observed exhibiting a reduction of 50% over the past ten years and thus labeled vulnerable for this criterion.

Criterion I.B. captures two dimensions of geographic range area. Sub-criterion I.B.1., extent of occurrence, (Table 2) shows most species are not vulnerable because their range of occurrence exceeds 20,000 km². Several species (*D. imitator*, *D. marmoratus s.s.*, *D. santeetlah*, *D. wrighti*, and *P. chatahoochee*) are vulnerable with ranges less than 20,000 km². *P. jordani s.s.* occupies a range area of less than 5,000 km² making it highly vulnerable. All of the vulnerable species except *P. chatahoochee* are mountain endemic species.

The other sub-criterion, area of occupancy (I.B.2.), is currently a work in progress with little data, but it has provided some interesting results (Table 2). For instance, *P. jordani s.s.*, scored highly vulnerable in the previous criterion, its area of occupancy within this range is over 2,000 km² and not vulnerable. Other species with high areas of occupancy (i.e. low vulnerability) are *D. fuscus s.s.*, *D. imitator*, *D. monticola*, *D. ochrophaeus*, and *D. quadramaculatus s.s.*. Thus far, only *D. wrighti* occupies an area less than 2,000 km² and is vulnerable.

The results for I.C. have found that *D. conanti s.s.* exhibits both a small population and a decline of 20% (Table 2). Carrying over to criteria I.D. this population is very restricted with less than 250 individuals (Table 2). Both of these scored highly vulnerable. The data available for the other species in the subset show no evidence of decline and unrestricted populations.

Problematic areas with respect to the salamanders include both altitudinal breadth and latitudinal breadth (Table 2: I. F-G). Most species occupy latitudinal ranges of less than five degrees which raises concern on their ability to tolerate a wider range of climates. Altitudinal range typically falls between 1000 to 2000 meters with a few species showing critical values of less than 1000 meters. Small altitudinal range breadths are generally thought to be indicative of narrow climatic tolerances, but there are relatively few studies that show this supposed relationship empirically (16).

Criterion I.H. is meant to capture strong ecological dependencies such as symbioses or specialists ecological strategies. Because all of the species in this subset show generalist characteristics, none of them are vulnerable under this criterion.

Observations in criterion II H in Table 2 show that most plethodontids are capable of microclimatic selection. For instance, salamanders exposed to a range of temperatures in the lab showed a preferential response to certain temperatures. This ability to seek out suitable microclimates should provide a buffer to short term climatic variability within present day geographic ranges. However, we must still consider microclimatic selection by each species and its buffering effect against regional climate change (7-11). If the current geographic range becomes too physiologically stressful, do salamanders have the ability to move across the landscape to new ranges? A species may have the behavioral ability to migrate, but be limited by geographical and ecological barriers.

Table 2- Matrix of Vulnerability Criteria and Species' Traits with Subset Species and Completed Assessments. See color legend at bottom.

<i>Genus species</i>	<i>Desmognathus aeneus</i>	<i>Desmognathus carolinensis</i>	<i>Desmognathus conanti</i> s.s.	<i>Desmognathus fuscus</i> s.s.	<i>Desmognathus initiator</i>	<i>Desmognathus marmoratus</i> s.s.	<i>Desmognathus monticola</i>	<i>Desmognathus ochrophaeus</i>	<i>Desmognathus ocoee</i> s.s.	<i>Desmognathus quadramaculatus</i> s.s.	<i>Desmognathus santeedii</i>	<i>Desmognathus wrighti</i>	<i>Hemidactylium scutatum</i>	<i>Eurycea wilderae</i>	<i>Eurycea bislineata</i>	<i>Eurycea longicauda</i>	<i>Eurycea guttolineata</i>	<i>Eurycea cirrigera</i>	<i>Plethodon chatahoochee</i>	<i>Plethodon chlorobryonis</i>	<i>Plethodon cinereus</i>	<i>Plethodon cylindraceus</i>	<i>Plethodon dorsalis</i>	<i>Plethodon electromorphus</i>	<i>Plethodon glutinosus</i>	<i>Plethodon hoffmani</i>	<i>Plethodon jordani</i> s.s.	<i>Plethodon kentucki</i>	<i>Plethodon montanus</i>	<i>Plethodon taylorae</i>
I.A. Reduction in population size based on number of mature individuals.																														
I.B.1. Geographic range: extent of occurrence																														
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I.H. Known or suspected critical ecological dependency on another species																														
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II.B. Long term thermal functional threshold (pejus) surpassed																														
II.C. Short term exposure to ambient extremes																														

Table 2- Continued

<i>Genus species</i>	Desmognathus aeneus	Desmognathus carolinensis	Desmognathus conanti s.s.	Desmognathus fuscus s.s.	Desmognathus imitator	Desmognathus marmoratus s.s.	Desmognathus monticola	Desmognathus ochrophaeus	Desmognathus ocoee s.s.	Desmognathus quadramaculatus s.s.	Desmognathus santeetlah	Desmognathus wrighti	Hemidactylium scutatum	Eurycea wilderae	Eurycea bislineata	Eurycea longicauda	Eurycea guttolineata	Eurycea cirrigera	Plethodon chatahochee	Plethodon chlorobryonis	Plethodon cinereus	Plethodon cylindraceus	Plethodon dorsalis	Plethodon electromorphus	Plethodon glutinosus	Plethodon hoffmani	Plethodon jordani s.s.	Plethodon kentucki	Plethodon montanus	Plethodon taylorae
II.E.1. Safety margin (long-term)																														
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III.A.1. Indirect measures of dispersal (genetic)																														
III.A.2. Direct measures of dispersal (non-genetic)																														
IV.A.1 Overall Genetic diversity																														
IV.A.2 Genetic diversity partitioned within species																														
IV.B. Genetic erosion (historical to recent times)																														
IV.C.1 Overall Quantitative Genetic Diversity Across the Species																														
IV.C.2 Quantitative Genetic Diversity Partitioned Within Species																														
IV.D. Life history patterns																														
"1"																														
"2"																														
"-1"																														
we will calculate directly																														

CHAPTER IV

CONCLUSION

Using species-traits analysis, the results show that each of the plethodontid species exhibited differential vulnerabilities to climate change. Endangerment levels varied across this species subset, as opposed to the findings in Milanovich et al. which claim that all of the species are endangered and will face extinction (*I*).

These findings, especially with completed physiological criteria, will give us insight into how the species and their habitats need to be managed. Individual, instead of broad-scale, management techniques will need to be implemented to cater to the independent endangerment risk of each species. Individualized management of a few species will also aid in saving time and resources.

However, contrary to popular notion, many long term temperature trend studies have found the Southeast is actually experiencing a cooling trend and an increase in precipitation by 3-5mm each day (24-28). The minimum monthly temperature has increased by almost 1.646°C per century with the maximum monthly temperature decreasing by -0.468°C per century (25, 26). Since most of the salamanders in this subset of interest reside in the southern Appalachians and across the Southeast, the climate may actually become more suitable. Still, other anthropogenic factors such as habitat destruction and pollution will require management plans for affected species.

Variables of environmental niche modeling are too coarse-scaled to give an accurate assessment of species vulnerability to climate change. They ignore microclimatic selection, species' physiologies, biotic interactions, and physiographic limitations that may ameliorate or exacerbate species' survival. The species-traits approach provides a much finer scale of analysis that illustrates notable differences in vulnerability across plethodontid species. Future vulnerability assessments need to include species-traits in their analyses.

Work is ongoing to evaluate the remaining criteria which include physiological variables and evolutionary potential. Once completed this data should provide a clearer picture on the current state of salamander endangerment. One possibility is that I may find that species showing vulnerabilities through their habitats are none the less resilient in their physiologies which enable them to survive climate change. Still, others may reflect the fact that generalists can be vulnerable to endangerment as well, no matter how great their range and population. Physiological analysis will be the defining feature of this study to give us conclusive evidence of species endangerment levels.

Our long term goal is to contrast our results with the phenomenological approach. This goal will provide a multi-dimensional analysis.

REFERENCES

1. Milanovich, J.R., et al., *Projected loss of a salamander diversity hotspot as a consequence of projected global climate change*. PLoS One, 2010. **5**(8): p. e12189.
2. Thomas, C.D., et al., *Extinction risk from climate change*. Nature, 2004. **427**(6970): p. 145-148.
3. Kearney, M., et al., *Integrating biophysical models and evolutionary theory to predict climatic impacts on species' ranges: the dengue mosquito Aedes aegypti in Australia*. Functional Ecology, 2009. **23**(3): p. 528-538.
4. Bernardo, J., *Biologically grounded predictions of species resistance and resilience to climate change*. Proceedings of the National Academy of Sciences, USA, 2014. **111**: p. 5450-5451.
5. Botkin, D.B., et al., *Forecasting the effects of global warming on biodiversity*. Bioscience, 2007. **57**(3): p. 227-236.
6. Mesibov, R., *A specialist's audit of aggregated occurrence records*. ZooKeys, 2013. **293**(0): p. 1-18.
7. Suggitt, A.J., et al., *Habitat microclimates drive fine-scale variation in extreme temperatures*. Oikos, 2010. **120**: p. 1-8.
8. De Frenne, P., et al., *Microclimate moderates plant responses to macroclimate warming*. Proceedings of the National Academy of Sciences, 2013. **110**(46): p. 18561-18565.
9. Sunday, J.M., et al., *Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation*. Proceedings of the National Academy of Sciences, 2014. **111**(15): p. 5610-5615.
10. Kearney, M.R., et al., *Microclimate modelling at macro scales: a test of a general microclimate model integrated with gridded continental-scale soil and weather data*. Methods in Ecology and Evolution, 2014. **5**(3): p. 273-286.
11. Kearney, M.R., A.P. Isaac, and W.P. Porter, *microclim: Global estimates of hourly microclimate based on long-term monthly climate averages*. Scientific Data, 2014. **1**.
12. Storlie, C., et al., *Stepping inside the niche: microclimate data are critical for accurate assessment of species' vulnerability to climate change*. Biology Letters, 2014. **10**(9).

13. Potter, K.A., H. Arthur Woods, and S. Pincebourde, *Microclimatic challenges in global change biology*. *Global Change Biology*, 2013. **19**(10): p. 2932-2939.
14. Connell, J.H., *The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus*. *Ecology*, 1961. **42**(4): p. 710-723.
15. Deutsch, C.A., et al., *Impacts of climate warming on terrestrial ectotherms across latitude*. *Proceedings of the National Academy of Sciences*, 2008. **105**(18): p. 6668-6672.
16. Bernardo, J., et al., *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*, 2007. **3**(6): p. 695-699.
17. Huey, R.B., et al., *Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation*. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 2012. **367**(1596): p. 1665-1679.
18. IUCN, *Guidelines for Using the IUCN Red List Categories and Criteria. Version 9.0*, S.a.P. Subcommittee, Editor 2011.
19. Stuart, S.N., et al., *Status and trends of amphibian declines and extinctions worldwide*. *Science*, 2004. **306**: p. 1783.
20. Bernardo, J., et al., *Expanding IUCN Red List Criteria in response to climate change: An operational framework integrating species traits from physiology, phylogeography and evolution into biodiversity vulnerability assessment*. *Science*, 201?: p. to be submitted.
21. Semlitsch, R.D., K.M. O'ÄöDonnell, and F.R. Thompson, *Abundance, biomass production, nutrient content, and the possible role of terrestrial salamanders in Missouri Ozark forest ecosystems*. *Canadian Journal of Zoology*, 2014: p. 997-1004.
22. Davic, R.D. and H.H. Welsh, *On the ecological roles of salamanders*. *Annual Review of Ecology, Evolution, and Systematics*, 2004. **35**(1): p. 405-434.
23. Bernardo, J. 2011 A critical appraisal of the meaning and diagnosability of cryptic evolutionary diversity, and its implications for conservation in the face of climate change. In *Climate Change, Ecology and Systematics* (eds. T. Hodkinson, M. Jones, S. Waldren & J. Parnell), pp. 380-438. Cambridge, Cambridge University Press.
24. Mulholland, P.J., et al., *Effects of climate change on freshwater ecosystems of the southeastern United States and the Gulf Coast of Mexico*. *Hydrological Processes*, 1997. **11**(8): p. 949-970.

25. Portmann, R.W., S. Solomon, and G.C. Hegerl, *Spatial and seasonal patterns in climate change, temperatures, and precipitation across the United States*. Proceedings of the National Academy of Sciences, 2009. **106**(18): p. 7324-7329.
26. Lee, J., S. Li, and R. Lund, *Trends in extreme U.S. temperatures*. Journal of Climate, 2014. **27**(11): p. 4209-4225.
27. Brown, P.J. and A.T. DeGaetano, *Trends in U.S. surface humidity, 1930-2010*. Journal of Applied Meteorology and Climatology, 2012. **52**(1): p. 147-163.
28. Lu, Q.Q., R. Lund, and L. Seymour, *An update of U.S. temperature trends*. Journal of Climate, 2005. **18**(22): p. 4906-4914.