Too Hot to Handle: Climate Change and Adaptive Evolution in Vertebrates

Jaime J. Coon¹ Wiline M. Pangle²

ABSTRACT

Adaptability is crucial to life on earth, providing an avenue for populations to change when environments change. Anthropomorphic disturbance, including climate change, is altering and often destroying habitats at a faster rate than ever before. However, evolution may be a potential mitigating factor in these scenarios. Can microevolution respond to human-caused climate change? My review of the scientific literature in this area has shown that while an evolutionary approach to conservation biology is warranted, scientists do not agree on how to evaluate conservation concerns from an evolutionary perspective. Further, evolutionary principles have not often been incorporated into conservation research or policy. Few concrete examples exist of adaptive evolution at work in organisms impacted by climate-change. Disentangling the sometimes contradicting effects of climate change in addition to differentiating the roles of adaptive evolution and phenotypic plasticity on populations is currently a major struggle for evolutionary biologists. As a future conservation biologist interested in ecological restoration, it is important that I learn how to integrate evolutionary perspectives into my work, potentially harnessing evolutionary resilience as a management tool while continuing to explore the boundaries and intersections between ecological, phenotypic, and evolutionary responses.

KEYWORDS

Climate Change, Phenotypic Plasticity, Adaptive Evolution, Conservation Biology

Scientists agree that the climate is rapidly changing. What we do not yet know is how exactly this change will alter the Earth's natural systems and

AUTHOR NOTE: Please direct correspondence to Jaime J. Coon, Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, 1102 S. Goodwin Ave., W-411 Turner Hall, E-mail: jicoon2@illinois.edu

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¹Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign

²Department of Biology, Central Michigan University

processes, such as evolution by natural selection (Berg et al. 2009; Lavergne et al. 2010). Adaptability is crucial to life on earth, providing an avenue for populations to change when environments change. However, anthropomorphic disturbance, including climate change, is altering and often destroying habitats at a faster rate than ever before. The question has yet to be answered: can microevolution respond to human-caused climate change? My review of the scientific literature in this area reveals that while an evolutionary approach to conservation biology is warranted, scientists do not agree on how to evaluate conservation concerns from an evolutionary perspective. I sought examples of species that are evolving in response to human environmental disturbance, specifically examining how ecological changes related to climate change have influenced evolutionary dynamics in vertebrate species that have recently adapted to climate change. I will examine this evolutionary approach to climate change, the role of climate change as a potential selection pressure, and particular evolutionary strengths and weaknesses of certain vertebrate species groups to the changing climate. Lastly, I will explore both the limits of the literature and the importance of integrating this evolutionary approach into conservation management decisions.

AN EVOLUTIONARY APPROACH TO CLIMATE CHANGE RESEARCH

Conservation biology examines the impact of human disturbance on populations of organisms. Because speciation and adaptation can be in reaction to changing environments due to human actions, evolutionary biology is a critically important discipline to integrate into conservation research (Lavergne et al. 2010; Hendry et al. 2010). Evolution can help scientists trace and understand the causes of diversification, whether it's humans or other natural sources that may be causing the changes in gene frequencies (Hendry et al. 2010). However, evolutionary principles have not often been incorporated into either conservation policy or biodiversity research (Hendry et al. 2010). A community ecology and multi-species approach to evolutionary conservation biology can provide significant insight into the impact of human actions on ecosystems (Berg et al. 2010).

It is interesting that evolution is not commonly integrated into conservation science given that the ecological basis for many conservation initiatives is maintaining biodiversity, which is by definition an evolutionary term. This lack of integration may be due to the large difference in time scales being examined: human environmental impacts (such as climate change) are accruing quickly, whereas evolution is usually examined over millennia (Gienapp et al. 2007). For example, Ganzhorn et al. (2014) explain Madagascar's biodiversity using evolutionary processes, describing the process of speciation in response to climatic or geologic events. This is an important line of evolutionary inquiry that can be described as having conservation implications for Madagascar, but it is not necessarily practical on a shorter conservation time scale. Additionally, Ganzhorn et al. (2014) argue that decisions are often based on individual initiatives or charismatic species instead of evolutionary science-based approaches. A contributing factor to this problem could be that ecologists (or policymakers, for that matter) working on conservation issues may not see evolution as a practical matter that can effectively inform conservation decision-making. I argue that a more helpful

approach to integrating evolution into conservation research is to focus on the distinction between phenotypic plasticity and microevolution in response to human alterations to ecosystems in order to utilize evolutionary insights on a more usable time scale.

CLIMATE CHANGE AS A SELECTION PRESSURE: GENES OR PHENOTYPE?

Climate change is a general term that can refer to a multitude of deviations from the usual climates, microclimates, and weather on a global scale due to human carbon dioxide pollution and the resulting greenhouse gas effect. There is a dramatic warming trend overall that is melting the icecaps, raising the ocean level, acidifying major bodies of water, and altering biological communities. Warming winter temperatures are leading to longer growing seasons, increased disease prevalence, decreased net primary productivity, earlier arrival of spring, and shifting species distributions (Hoegh-Guldberg and Bruno 2010; Bradshaw et al. 2008). The worst-case scenario for biodiversity is a projected 43 percent loss within biodiversity hotspots, but evolution is a potential mitigating factor for this loss and must be considered (Skelly et al. 2007). Gienapp et al. (2008) identifies three possible responses to climate change: (1) Dispersal to more suitable habitats; (2) Staying and responding phenotypically; and (3) Adaptation. Clearly, events and changes are imposing strong, directional selection pressures on traits that are important for fitness. A central debate I have identified in the evolutionary literature centers around the following question: Can evolution respond in time to climate change?

Marine, freshwater, and terrestrial plants and animals have exhibited changes in distribution, phenology, and resource use in response to climate change, but specific vertebrate examples are difficult to find in the literature (Parmesan 2006; Teplitsky et al. 2008). While microevolutionary responses "should be detectable in principle," there are few examples in the biological world, and even fewer in vertebrate organisms (Gienapp et al. 2008). There are three widely cited examples identified by Bradshaw and Holzapfel (2008). First, there is genetic evidence of change in response to climate in the Yukon red squirrel in Canada (Tamiascurus hudsonicus) in terms of seasonal reproduction. Secondly, the European Great Tit, a bird species, have recently declined due to earlier caterpillar emergence as a result of untimely spring climate, but genetic diversity surrounding egg-laying date has allowed some of these individuals to increase their fitness. However, the overall fitness of the population is still declining. Lastly, Bearhop et al. (2005) identified genetically based migration differences for European black cap birds (Slyvia atricapilla) in overwintering strategies that likely improve fitness in response to climate change. However, none of these studies have direct evidence that climate alone is causing these genetic changes (Bradshaw and Holzapfel 2008).

Complicating this further, the multifaceted problems caused by climate change may affect organisms in contradictory ways, and so detection of natural selection becomes even more difficult. For example, Crozier et al. (2008) showed that Chinook (*Oncorhynchus tshawtscha*) and sockeye (*Oncorhynchus nerka*) salmon had multiple climate stressors at different life stages, such as accelerated growth and stress signals from higher temperatures at various times in their lives. Their models predicted the fish would need a combination of disease resistance,

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adaptive behaviors to avoid heat, and migration changes in order to combat the negative fitness effects of climate change, a trifecta that is unlikely to be simultaneously selected for during a short time frame.

Anthropomorphic climate change is happening at a rate faster than previous climatic events in geologic history. Many scientists believe that organisms can adapt quickly enough to respond to the selection pressures of climate change (Gienapp et al. 2008; Réale et al. 2006). Some scientists believe that microevolution can happen as quickly as over the period of a decade (Réale et al. 2006). Visser (2008) postulates that there is an acceptable rate for climate change—the maximum rate of microevolution is the fastest acceptable rate the climate can change without losing biodiversity. However, there is no clear data on the rate of microevolution, so there is no way to accurately predict an "acceptable" rate of climate change (Visser 2008).

Some in the scientific community believe that microevolution via genetic changes will not be able to conserve biodiversity under climate change. Instead, phenotypic plasticity may have greater potential for preserving biodiversity. Charmantier et al. (2008) argue that phenotypic plasticity will allow organisms to quickly and effectively respond to the changing climate. They support this claim using the Great Tit example again, showing how the bird from the United Kingdom was able to individually adjust behavior and survive in response to environmental changes (Charmantier et al. 2008). Refsnider and Janzen (2012) also found that behavioral plasticity allowed an organism, in this case the long-lived turtle Chrysemys picta, to respond effectively to climate change. Turtles experience Temperature Dependent Sex Determination (TDSD), and the turtle Chrysemys picta was able to alter nest depth under different temperature regimes, and therefore was able to avoid changes in sex ratios (Charmantier et al. 2008). Scientists who believe that phenotypic plasticity will be more effective than genetic adaptive evolution in stopping biodiversity loss theorize that genetic and ecological constraints may limit a population's ability to adapt, which allows for phenotypic plasticity to take the lead (Merila 2012).

However, Visser (2008) believes that phenotypic plasticity cannot respond as effectively as microevolution to climate change. First, Visser argues that phenotypic plasticity in the form of learning cannot be passed down through generations and that maternal effects may not be adaptive in light of climate change. Secondly, phenotypic plasticity does not occur in a vacuum. Responses to climate change that are plastic may in turn trigger an evolutionary response. For example, when an organism immigrates to a new location (phenotypic plasticity) they may adapt to components of their new habitat (adaptive evolution). Teplitsky et al. (2008) found that red-billed gulls had a reduction in body size in response to climate change, and the researchers theorized that microevolution and phenotypic plasticity might be at work in this situation. Separating microevolutionary and phenotypic responses is extremely difficult, but it is important to remember that the two sources of change often may not be mutually exclusive (Teplitsky et al. 2008).

ADAPTING TO A WARMING PLANET: STRENGTHS AND VULNERABILITIES

Certain groups of species are better equipped to respond to the changes associated with climate change. Populations of animals with shorter life spans may be able to respond adaptively to climate change in a very small time frame (Bronson 2009). In general, organisms with complex life history traits that are tied to climate, especially those surrounding reproduction, are predicted to be the least adaptable to the warming associated with climate change (Bronson 2009; Moore and Huntington 2008). Adding further complexity, adaptive evolution in response to climate change is predicted through modeling to be ecologically constrained from both higher and lower trophic levels with no clear trends for certain groups, and these trends differ greatly depending on the specific organism or predator/prey status (Both et al. 2009).

Differences at the molecular level in vertebrate organisms' physiological tolerance limits may impact their ability to adapt to changing climates as well. To examine acclimatization at a cellular level, scientists ask: how much change in a DNA sequence is enough to stabilize a protein under higher temperatures? Certain species may have protein coding genes or regulatory mechanisms that could facilitate the changes in a sequence needed for microevolution to respond to climate change (Somero 2009). Conversely, molecular stress levels in some organisms are correlated to climate. For example, tropical lizards are responding to summer warming with increased stress levels (Huey et al. 2009). This may decrease the overall fitness of individuals and threaten species longevity.

Because climate change disproportionately affects certain ecosystems, populations in those ecosystems have the strongest selection pressures and highest extinction risk. Arctic and polar species are the species hardest hit by climate change. In Arctic environments, the melting ice, seasonally uncharacteristic weather patterns, and early or late season shifts have exerted a heavy selection pressure on the species that live in Arctic regions. This group of vertebrates has been the first to experience drastic range contractions and the ultimate evolutionary dead end: extinctions (Parmesan 2006). The North American red squirrel in the Yukon has exhibited changes in response to climate change within decades of the climatic changes. Because the selection pressure in these environments is so strong, some animals have experienced potential microevolutionary responses in very short time spans (Réale et al. 2003).

Many populations are unable to respond to the ecological problems caused by climate change in the current rapid time frame due to inherent vulnerabilities. In this quickly changing global environment, previous adaptations often become maladaptive (Parmesan 2006). In species where predator-prey coevolutionary relationships are very specific or strong, the potential decoupling of these interactions can have negative effects on the species' ability to adapt. Often, genetic shifts in response to climate change mitigate negative effects only at the local level and species-level responses cannot develop quickly enough (Visser and Holleman 2001). Species that migrate are also at risk: climate change often alters triggers seasonal shifts that then negatively impact migration routes (Robinson et al. 2009; Visser et al. 2009). Reptiles that depend on thermoregulation regimes that have evolved over millions of years are maladaptive in a warming planet. Temperature dependent sex determination puts some reptile species at risk for extinction

because warming temperatures may lead to unequal sex ratios if the species is not able to adapt (Telemeco et al. 2009).

LIMITS OF LITERATURE AND FUTURE DIRECTIONS

The difficulty in this evolutionary conservation approach to climate change research lies in disentangling the root causes for a potentially adaptive change. Scientists have to tease apart whether genetic or environmental causes are determining the change. Gienapp et al. (2008) found that most studies examining microevolution in response to climate change were not based on genetic research but instead completely on phenotypic data, and Merila (2012) found that phenotypic plasticity and genetic responses are often being confused in these studies.

Much of the work on climate change and vertebrate communities was ecological in nature, and while I was interested in examining the ecological-evolutionary dynamics surrounding climate change adaptations in vertebrates, there are few actual examples of evolutionary responses to climate change for vertebrate species. Frustrated that my specific literature searches were not providing enough information, I broadened my search terms and began going through articles by one by one. My broadest searches in Google Scholar provided nine hundred thousand results for "evolutionary impact of climate change," versus two million for "ecological impact of climate change." Delving further, most of the evolution and climate change papers I was able to find were very ecological and short term in nature and often did not deal directly with evolution, much less specific adaptations, which made this project very difficult.

Evolution is a difficult topic to study in this context because it is often a long-term process over broad time scales, and it is especially difficult to examine when short-term changes are involved. In my opinion, in a few decades scientists will find that the major evolutionary force at work in response to climate change is not microevolution or phenotypic plasticity, but extinction. Controlled studies or those that directly examine genetic changes were virtually nonexistent in the literature as of this writing. While there are many theoretical, modeling, and prediction-based papers on the topic of evolution in response to climate change, future studies that examine genetic changes in vertebrate organisms could add legitimacy to the evolutionary-ecological approach to climate change. In addition, as pointed out in Lavergne et al. (2010), many ecological and evolutionary forces may be at work simultaneously, especially in terms of events such as dispersal, so it is important to consider both disciplines.

As a future conservation biologist interested in ecological restoration, it is vitally important that I learn how to integrate evolutionary perspectives into my work. If the field of conservation neglects evolution, or if evolution neglects conservation, scientists such as myself will be missing huge swaths of the biodiversity crises' context. By applying this evolution-conservation approach directly to my future career, there is potential for harnessing evolutionary resilience as a management tool while continuing to explore the boundaries and intersections between ecological, phenotypic, and evolutionary responses and the overlapping areas between these responses (Srgo et al. 2010).

The climate change crisis is a call to action for scientists, legislators, and the public. As human degradation of the environment and increased carbon dioxide deposition continue to contribute to global climate change, we may not know if the rate of warming is faster than the rate of adaptation, and for many species it may be too late already. It is important that we do not depend on organisms' ability to adapt, but rather we must learn to adapt ourselves to better suit the environment we are destined to share with biological communities.

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