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Climate change and an invasive, tropical milkweed: an ecological trap for monarch butterflies

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Abstract. While it is well established that climate change affects species distributions and abundances, the impacts of climate change on species interactions has not been extensively studied. This is particularly important for specialists whose interactions are tightly linked, such as between the monarch butterfly (*Danaus plexippus*) and the plant genus *Asclepias*, on which it depends. We used open-top chambers (OTCs) to increase temperatures in experimental plots and placed either nonnative *Asclepias curassavica* or native *A. incarnata* in each plot along with monarch larvae. We found, under current climatic conditions, adult monarchs had higher survival and mass when feeding on *A. curassavica*. However, under future conditions, monarchs fared much worse on *A. curassavica*. The decrease in adult survival and mass was associated with increasing cardenolide concentrations under warmer temperatures. Increased temperatures alone reduced monarch forewing length. Cardenolide concentrations in *A. curassavica* may have transitioned from beneficial to detrimental as temperature increased. Thus, the increasing cardenolide concentrations may have pushed the larvae over a tipping point into an ecological trap; whereby past environmental cues associated with increased fitness give misleading information. Given the ubiquity of specialist plant–herbivore interactions, the potential for such ecological traps to emerge as temperatures increase may have far-reaching consequences.

Key words: *Asclepias*; cardenolide; *Danaus plexippus*; global warming; Lepidoptera; plant defense.

Introduction

As global temperatures continue to rise, species may respond to climate change in a variety of ways. For instance, species may shift their distributions by migrating to unaffected or climatically similar areas (Parmesan and Yohe 2003, Moritz et al. 2008). Alternatively, species may undergo phenotypic change that ameliorates negative climate-induced impacts or takes advantage of potential positive effects (i.e., increase in population growth at higher latitudes; Schlaepfer et al. 2002, Deutsch et al. 2008, Angilletta 2009). Regardless of the mechanism, climate change research has often focused on the responses of single species to changes in global climate. While this research provides valuable insight into the effects of global warming on generalist consumers, the impacts of climate change on dietary specialists are not as readily apparent (Gough et al. 2015). Thus, it has become increasingly recognized that species interactions, especially interactions between tightly packed species, need to be considered when trying to understand the full impacts of climate change on ecological dynamics (O'Connor et al. 2012, Urban et al. 2013, Elderd and Reilly 2014).

Whenever rapid environmental change reduces the quality of an organism's habitat, including the quality of its diet, there is potential for the species to be caught in an ecological trap (Schlaepfer et al. 2002, Battin 2004). Ecological traps occur when organisms make maladaptive habitat choices and/or experience negative phenotypic responses based on environmental cues that once correlated positively with habitat quality and/or evolutionarily stable phenotypic traits (Schlaepfer et al. 2002, Robertson and Hutto 2006). In an altered environment, formerly reliable signals may no longer correspond to positive adaptive outcomes and the organism becomes "trapped" by their responses. This may result in a decline in fitness (Schlaepfer et al. 2002, Van Dyck et al. 2015). Ecological traps due to anthropogenic actions have become increasingly prevalent. For example, off the coast of Western Africa, climate-change-induced environmental variability and overfishing have created cool, chlorophyll dense waters, usually indicative of healthy fish populations, that are devoid of fish (Sherley et al. 2017). This has created an ecological trap for endangered African penguins, which use chlorophyll density as an indicator of good fishing grounds (Sherley et al. 2017). However, effects of climate change on species interactions that generate ecological traps represent a recognized but surprisingly little-studied problem (Urban et al. 2013). For herbivores, and particularly specialists, rapid changes in the quality of their plant hosts under

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environmental change ma generate ecological traps if the plants upon which the rel become unsuitable.

Man specialists feed either on a single plant species or multiple species within a single genus, and an herbivore's fitness ma var depending upon the t pe of species and qualit of the species being consumed (Ali and Agrawal 2012). For instance, the monarch butterfl (Danaus plexippus) feeds almost exclusivel on milkweed species within the genus Asclepias. Asclepias species var widel in their production of cardenolides, secondar chemical defenses that the monarch sequesters as an anti-predator (Brower et al. 1967) or an anti-parasite defense (de Roode et al. 2008). Furthermore, Asclepias species differ in latex production (Agrawal and Konno 2009), ph sical defenses, leaf morpholog (Agrawal et al. 2009a), and phenologies (Woodson 1954). Individual monarch fitness varies non-linearl with cardenolide production, where more toxic milkweeds confer a greater defense against predators, but can be too toxic to monarchs at high of concentrations, such that intermediate levels result in higher fitness (Malcolm 1994, Sternberg et al. 2012). Consequentl , an changes, either positive or negative, to milkweed chemistr due to global warming could have corresponding indirect effects on monarch performance.

Even if plant qualit is unaffected b increased temperatures, monarch ph siolog , development, and cardenolide metabolism ma change with different temperatures. Monat 28°C. The seeds were sown in a mixture of Sun Gro professional growing soil (Sun Gro, Seba Beach, AB, Canada), vermiculite, and Scotts 14-14-14 osmocote fertilizer (The Scotts Company, Marysville, OH, USA). At the time of the experiment, the individual milkweed plants were 4 months old.

Experimental setup

Experimental design.—We conducted a full factorial experiment to examine how increased temperature and milkweed species identity affect monarch growth and development. We crossed ambient vs. elevated temperature with the two milkweed species (A. incarnata and A. curassavica), and we established 10 replicates of each of the four treatments. To warm the experimental sites, we constructed open-top chambers (OTCs; Godfree et al. 2011, Elderd and Reilly 2014). OTCs were constructed with plexiglass plates (Solar Components Corporation, Manchester, New Hampshire, USA) that slant inward to focus solar energy within the plot (Godfree et al. 2011). A single, hexagonal OTC consisted of six trapezoidal sections attached with fencing brackets and PVC piping. Each trapezoidal section was supported by a thin, wooden skeleton spanning the outer edges, and was covered by the solar plexiglass. In the center ofbersapant the internal standard (digitoxin) and the estimated sample mass.

Statistical analysis

A. curassavica produced a five times greater variet of cardenolides than did A. incarnata (PerMANOVA, $F_{1,55} = 28.7645$, $P = 0.001$), with cardenolide composition changing significantl over time (PerMANOVA, $F_{1,55} = 21.7170$, $P = 0.001$). The temporal changes in cardenolide composition were more variable among individual A. incarnata breeding niches for monarch butterflies northward (Batalden et al. 2007), and current winter range ma become inadequate for monarchs due to increased cool weather precipitation (Oberhauser and Peterson 2003). Furthermore, predicted northward shifts of Asclepias sp. into Canada ma lead to northward shifts in monarch summer distributions (Lemoine 2015). Understanding changes in host plant distributions for tightl coupled, insect–plant interactions (e.g., the monarch–milkweed s stem) is crucial, but understanding changes in host resource qualit is equall important to consider. Other environmental drivers ma also influence these interactions, including water availabilit (Andrews and Hunter 2015), nutrient deposition, (Zehnder and Hunter 2008, Tao et al. 2014), and elevated atmospheric concentrations of carbon dioxide (Vannette and Hunter 2014). Biotic interactions with other species ma also need to be considered. For example, and improve sequestered defenses. Our experiments may have imposed a substantial stress on milkweeds, potentially inducing changes in foliar quality different from those that may accompany more gradual climate change. However, in addition to increases in average annual temperature, climate models predict concomitant increases in climatic variability, including a higher frequency of heat waves (Karl et al. 2009). Higher annual temperatures and more frequent heat waves may combine to intensify the ecological trap that results from elevated cardenolide concentrations in A. curassavica. Ultimately, the combination of direct and indirect effects of multiple drivers will determine the overall effects of environmental change on monarchs and their milkweed hosts. Nonetheless, warming alone appears sufficient to generate an ecological trap for the populations of monarchs feeding on A. curassavica.

In general, research continues to show the importance of indirect effects in determining how species respond to climate change (O'Connor et al. 2012, Elderd and Reilly 2014, Cerrato et al. 2016). The direction and the strength of such interactions may have important fitness consequences regardless of whether or not individual species are consigned to an ecological trap. However, there is generally a temperature optimum at which individual fitness is maximized (Angilletta 2009). If that optimum is surpassed as the Earth warms (Deutsch et al. 2008), the species may eventually fall into a trap. Given current trends in planting of A. curassavica to alleviate habitat loss, best gardening practices should be reevaluated to reinforce the notion that native milkweed species should be preferentially planted. Addi-