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Editorial: Arthropod Interactions and Responses to Disturbance in a Changing World

Shannon M. Murphy[1]*, *Lora A. Richards*[2] *and Gina M. Wimp*[3]

[1] Department of Biological Sciences, University of Denver, Denver, CO, United States, [2] Department of Biology, University of Nevada, Reno, NV, United States, [3] Department of Biology, Georgetown University, Washington, DC, United States

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Editorial on the Research Topic

Arthropod Interactions and Responses to Disturbance in a Changing World

INTRODUCTION

Global environmental change is affecting insect communities worldwide. Recently there has been a debate in the literature about whether insect populations are declining precipitously as an "insect apocalypse" (Hallmann et al., 2017; Lister and Garcia, 2018; Sanchez-Bayo and Wyckhuys, 2019; Salcido et al., 2020). However, some have argued that the insect apocalypse is an overstatement, since supporting research has been restricted to specific sites and/or does not account for other disturbances (e.g., Thomas et al., 2019; Willig et al., 2019). In order to understand whether and how insect populations are changing over time, we need to understand the mechanistic drivers of declining insect diversity. Each of the articles in this issue examines how species interactions, diversity, and community composition are changing as a result of anthropogenic disturbance. Understanding the impacts of global change on population dynamics, ecological communities, biodiversity, and ecosystem processes thus requires a multi-trophic perspective.

LAND-USE CHANGE

Natural vegetation on every continent except Antarctica has been removed by human activities, leaving fragmented patches of suitable habitat across the landscape (Saunders et al., 1991). While human activities are negatively impacting biodiversity via multiple mechanisms, habitat fragmentation is widely considered to be the primary factor leading to species extinction worldwide (Wilson, 2002). Notably, habitat change is thought to be the primary driver of what some authors describe as the "insect apocalypse" (e.g., Sanchez-Bayo and Wyckhuys, 2019). Species that are dependent on natural habitats may be impacted not only by the size of habitat fragments, but also by increasing isolation among patches and altered species interactions along habitat edges (Debinski and Holt, 2000; Fahrig, 2003; Ewers and Didham, 2006; Murphy et al., 2016). While the focus of land use change has primarily been on species in natural habitats, managed habitats constitute roughly 34% of total land mass (Ramankutty et al., 2008). More importantly, ∼45% of insect species losses are thought to be the result of intensified agriculture, deforestation, and urbanization, while practices associated with agriculture, such as pesticide and fertilizer use, are thought to account for another ∼23% of insect species losses (Sanchez-Bayo and Wyckhuys, 2019). Thus, managed habitats and the practices associated with such management could account for two-thirds of insect declines. It is therefore essential that we understand how different land use practices may impact biodiversity and ecosystem services.

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Dennis Murray,
Trent University, Canada

****Correspondence:***
Shannon M. Murphy
shannon.m.murphy@du.edu

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Organisms at higher trophic levels often display higher sensitivity to land use change. While habitat modifications are known to be a primary driver of species losses, fragmentation differentially impacts species with different life histories, trophic strategies, and levels of resource specialization. Organisms at higher trophic levels are often more susceptible to resource fragmentation because they are dependent on dynamics at lower trophic levels (Holt et al., 1999), however the level of susceptibility can be dependent on diet breadth. Anderson et al. found that while caterpillars were not affected by the size of a forest patch, resource specialization in the caterpillar prey affected higher trophic levels. In fragmented habitats, parasitism on specialist caterpillars decreased, but the authors found no change in parasitism on generalist caterpillars. Thus, resource specialization leads to stronger responses to habitat fragmentation in prey, with subsequent effects on their predators and parasites. Not only does habitat alteration affect herbivore natural enemies, but it can also affect native pollinator communities, with consequences for pollination services. While agricultural intensification can reduce the resources necessary for native pollinators, Kremen et al. found that the creation of native-plant hedgerows may mitigate these impacts on native pollinators. Kremen et al. found that native, perennial hedgerows provide floral and nesting resources necessary to native pollinators, particularly as the hedgerows age. While agricultural intensification can lead to the loss of beneficial species such as natural enemies and pollinators, such intensification can also lead to herbivore outbreaks. Such outbreaks have long been associated with extensive monocultures used in farming, but Le Gall et al. present compelling evidence that locust swarming is exacerbated by grazing practices, not cropland practices.

Even when habitats are not directly modified, nutrient runoff and pollution from agriculture and urbanization can alter natural communities. For example, Wimp et al. found nutrient subsidies at a landscape-level alter the trophic structure of the arthropod community by changing the relative abundances of various feeding groups. Herbivores had a negative response to increasing plant nitrogen density; specialist predators tracked their herbivore prey and thus also responded negatively to nitrogen density. However, generalists were not negatively affected by nitrogen density and indeed some generalist predators responded positively to nitrogen density. Such inputs of nutrients from agricultural and urban habitats into nearby natural systems are increasing, and differential responses by organisms with different feeding strategies and diet breadth can alter community composition.

While urbanization can affect organisms in nearby natural systems, arthropods living within cities are directly affected by human activities. The review by Miles et al. highlights the numerous abiotic factors that are altered in urban habitats (e.g., urban heat island effects, chemical and light pollution, and water availability), which in turn affect plant resources and herbivores. For example, salt is used for road deicing in the winter at northern latitudes, but soil salinization can decrease the ability of plants to take-up water from the soil. Bouraoui et al. found that salt pollution negatively impacted the growth and physiology of lime trees growing in urban greenspaces, which in turn negatively impacted arthropod biodiversity. Herbivores are thus directly affected by altered abiotic conditions in urban habitats, and indirectly via changes in their host plant. According to Miles et al., such alterations to critical resources not only affect herbivore population dynamics, but also interactions with predators. Because abiotic conditions and biotic interactions may be altered in urban habitats, Jamieson et al. argue the large number of bee samples collected near universities may lead to a distorted view of worldwide pollinator resources and biodiversity patterns. Such biased sampling may also affect our overall view of human impacts on arthropod biodiversity.

WILDFIRE

Climate change is known to be altering global fire regimes, primarily because of changes in precipitation regimes. However, how these increasingly frequent and severe fires are affecting species interactions and eco-evolutionary processes is not well-understood and there is a clear need for experimental work (Koltz et al., 2018). Further, there are entire taxa for which we know very little about how they respond to altered fire regimes, such as native bees, particularly because fire could impact resources they use for nesting or plants they pollinate. Burkle et al. addressed these critical knowledge gaps by studying the abundance and diversity of native bees, their floral and nesting resources, solitary bee nesting success, and traits of bees and plants in burned and unburned areas of three separate wildfires in Montana, USA. Their study is unique as they simultaneously measured not only the abundance and diversity of two interacting trophic levels important for pollination services, but also bee nesting success and trait variation, which are critical for understanding plant-pollinator interactions after wildfire. Burkle et al. found higher density and diversity of native bees and floral resources in burned areas, including areas that burned with high-severity wildfires, for two of the three wildfires that they studied. Notably, they found that nesting resources, such as bare ground and coarse woody debris, were higher in burned areas, and nesting success of solitary bees was also higher in burned areas. The results from Burkle et al. demonstrate that even large, high-severity wildfires can create conditions that support native bees and the resources they need to thrive, but unburned areas help maintain critical trait variation. Thus, having a landscape that is a mosaic of burned and unburned areas helps to conserve biodiversity of native bees.

Dell et al. used empirical metrics to quantify redundancy and resiliency in the fire-dependent longleaf pine ecosystem through measures of interaction diversity pre and post-fire to support the idea of response diversity (sensu, Elmqvist et al., 2003). While the concept of interaction diversity has been discussed for decades, especially in the context of conservation and global change, Dell et al. are the first to use empirical data to quantify interaction diversity at ecologically relevant scales to examine its role in resiliency. This was accomplished by recording interaction diversity parameters across a time since fire gradient as well as at hierarchical spatial scales. They found that local scale patterns of interaction diversity are associated with short-term resilience and broader scale patterns confer longer-term resilience. These findings are important, because they demonstrate that fire not only maintains species diversity but it also maintains the important interactions that contribute to ecosystem function and services, such as biological control. As global change continues to alter disturbance cycles as well as species richness, these relationships between disturbance and diversity are important to understand. Murphy et al. focused specifically on how fire severity affects insect-plant interactions, which are key drivers of forest ecosystem dynamics. Using wild forest fires of variable severity in Colorado, USA, they investigated how fire severity affects herbivore damage and plant quality. Murphy et al.. found that increasing fire severity decreased herbivore damage and altered plant quality by lowering water content, increasing C:N ratio, and increasing toughness. Interestingly, they found that the direct effect of fire was stronger than the plant-mediated effect on herbivore damage. The results from Murphy et al.. demonstrate that fire severity can have profound impacts on interactions between herbivores and their host plants with severity significantly affecting host plant quality. Understanding the outcomes of these complex interactions will be critical in order to predict the effects of increasing fire severity and frequency on communities in response to global climate change.

TEMPERATURE AND PRECIPITATION

Long term deviations in temperature and precipitation from historical patterns is the most direct effect of climate change on arthropods. Recent attention to insect declines has highlighted the negative consequences of increasing temperature and precipitation anomalies on insect species richness as well as the associated multitrophic interactions (Salcido et al., 2020). Arthropod life cycles and community composition are closely timed with seasonal climate patterns, leading to high susceptibility of arthropod populations changes in these patterns. Through long term continuous data collections, we are beginning to understand the underpinnings of climate variability on arthropod populations. Marquis et al. combined 20 years of caterpillar data on oak trees in southeastern Missouri to find that spring frosts and summer droughts caused a 62–99% decrease in caterpillar abundance. The magnitude of the effect varied according to caterpillar body size, feeding guild, and the type of weather event. However, the strength of these findings lie in their ability to monitor insect recovery after the extreme weather event, with most populations recovering in 1–5 years. This insight will increase our ability to make predictions on population resilience under future climate change models. Similar to oak tree caterpillar communities, Abarca et al. found that the timing of extreme weather events, in this case heatwaves, can have devastating effect on the populations of the Baltimore Checkerspot (*Euphydryas phaeton phaeton*). While summer heatwaves, which often reach an organism's critical thermal maximum, would intuitively have detrimental effects on the populations, surprisingly winter heatwaves during the overwintering life stage were the most damaging, with 75–100% mortality. Interestingly, larvae feeding on a native host plant had greater body mass and were better able to survive summer heatwaves compared to larvae feeding on an introduced host. As the frequency of extreme weather events are predicted to increase, long term data, and mechanistic life stage specific experiments have become increasingly important in our understanding of the consequences of climate change on insect diversity and abundance. Beyond weather anomalies, changes in the timing and duration of seasons can alter the phenological timing of arthropod emergence and potentially create an asynchrony with food availability (Visser and Gienapp, 2019). For pollinators, asynchrony and arthropod declines can cascade through the ecosystem as they provide fundamental services to their community. With this in mind, Slominski and Burkle combined field and lab based approaches to determine how temperature and season length influence mortality, phenology, and body condition of two solitary bee species. Their results suggest that the adult-wintering species may suffer higher mortality and reduced fitness under climate change due to earlier spring onset. Additionally, differences in sex-specific responses may alter sex ratios further contributing to population declines.

Changes in temperature and precipitation can have far reaching effects on the interactions between individuals, within species and across trophic levels. Macchiano et al. investigated sex-specific thermal responses in courtship activity of two sympatric species of treehoppers. They found both species-specific and sex-specific differences. For one species, male and female courtship activity changed similarly with temperature with females more likely to signal. In the other species, male and female activity responded differently, with females more likely to display signaling at very lowest and highest temperatures and males signaling more at mid temperatures. These results suggest that mating may be constrained in response to changing temperatures. Climate effects on the interactions between species, such as between hosts and parasitoid, have expanded our understanding of the consequences of altering population control mechanisms (e.g., Stireman et al., 2005). However, very little is known about these interactions in the Arctic, which is rapidly warming. Koltz et al. leveraged 18 years of data found in museum samples to investigate wolf spider egg sac parasitism in the Arctic. They found that parasitism was common in the southern site and not found in the northern site. In the south, the highest parasitism frequency was during the peak of the growing season, suggesting that the timing and window of vulnerability may shift as the Arctic warms. Trophic interactions also make understanding species responses to climate change more complex. In their review, Szczepaniec and Finke summarize the role of drought on a tripartite interaction between plants, pathogens, and insect vectors. Increasing incidence of droughts can increase a plant's susceptibility to pathogens due to cross talk between the signaling pathway of salicylic acid and the hormone abscisic acid, with some exceptions. Although there was no overall pattern in sap feeding insect performance on plants with a water deficit, changes in feeding behavior had indirect effects on pathogen transmission. More studies are needed that combine molecular, behavioral, and ecological techniques to further understand the mechanisms and consequences of drought on plant-pathogen-insect vector interactions and the implications for agroecosystems and pest outbreaks.

RANGE EXPANSIONS AND INVASIONS

Since Margaret Davis' pioneering work on North American plant range shifts after the last glaciation (e.g., Davis, 1981; Davis and Shaw, 2001), we have known that species can move in response to changing climatic conditions. However, the rate at which species are shifting their ranges currently and the rate at which climate envelopes are predicted to change in the near future is unprecedented (IPCC, 2014). Many species are shifting their ranges poleward (e.g., Parmesan et al., 1999) or upwards in elevation (e.g., Parmesan and Yohe, 2003), but novel species interactions may constrain range shifts (e.g., Jankowski et al., 2010). Further, not all species are moving poleward, but instead are shifting their ranges to maintain their climatic niche (e.g., VanDerWal et al., 2013). Further, range expansions propagated by human introductions of exotic species can significantly affect native ecological communities (Mooney and Hobbs, 2000).

Global change drivers that affect species range boundaries offer a new opportunity to study the evolution of species boundaries over rapid evolutionary timescales. This is particularly true for insects, whose geographic ranges, behaviors and life history traits are temperature dependent. Larson et al. review the potential for climate change to influence gene flow and species boundaries between closely related insect species, focusing on studies that have tracked changes in climate and insect distributions and/or have evaluated temperature dependent reproductive barriers between species. Manfredini et al. ask the question of why some social insects have become invasive species (e.g., fire ants and yellowjackets) while other social insects are in decline (e.g., bee pollinators). Why are some species thriving while others are on the brink of extinction? Social insects form highly cooperative colonies, characterized by different castes of individuals (such as queens and workers). These insects are renowned for their amazing flexibility in terms of their ability to produce different castes as well as adjust their behavior to meet colony needs. In their review, Manfredini et al. explore whether differences in their ability to flexibly adapt to their environments (termed phenotypic plasticity) can help to explain both the invasive nature and decline of different groups of social insects. Social insects are not the only introduced species with significant effects on ecosystems. Exotic plant species can have large impacts on ecological communities by altering plant-herbivore interactions. The study by Carper et al.. suggests that the impacts of novel host chemistry across larval development are likely complex and dependent on variation in host plant chemistry, and on stage-specific relationships between sequestration and defense. This research represents some of the first steps to understanding the mechanisms driving tradeoffs in defense strategies across caterpillar development, and how introduced hosts impact tritrophic interactions.

CONCLUSIONS

Collectively the papers in our Research Topic explore some of the many ways in which species interactions, diversity, and community composition are changing as a result of anthropogenic disturbance. One of our goals with our Research Topic was to highlight research from a diverse group of authors, and we feel that we have succeeded. Authors in our topic include not only professors across ranks from Assistant to Full, but also undergraduate students (7%), graduate students (18%), post-doctoral fellows (15%), and scientists not found in traditional academic positions (14%). Women in particular are often underrepresented in invited research forums (e.g., Nittrouer et al., 2018; Emma et al., 2019) and we are proud that the contributions to our Research Topic represent a balance between male and female contributing authors (55% of our authors identify as female and comprise 68% of our first authors and 53% of our last authors). While currently unusual, this kind of diversity and inclusion in STEM is imperative as we try to understand the new facets of how anthropogenic global change is affecting natural systems. Groups formed by diverse participants are effective at problem solving (Hong and Page, 2004) and thus the inclusion of a diverse pool of scientists will help us further our understanding of the possible impacts of global change. The publication of this volume will inform and hopefully stimulate more studies on how anthropogenic disturbances are changing arthropod interactions.

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All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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