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Studying plant–pollinator interactions facing climate change and changing environments[1]

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Plant–pollinator interactions are essential for successful plant reproduction in both natural and agricultural systems. These interactions are negatively impacted by recent large-scale alterations of the environments, particularly climate change. The responses of plants and pollinators to changing abiotic conditions that vary seasonally and geographically are often uncoordinated, potentially leading to the breakdown of this interaction. The complexity of the responses of plants and pollinators to our changing climate necessitates creative approaches. The six articles in this special issue directly address this need by providing a variety of key methods and reviews of current methodology. The articles include: DNA barcoding methods for use on pollen collected from visiting bees; methods for assessment of plant attraction traits (nectar and review of floral volatiles methods); a field sampling method for ground nesting bees; a review of using spatial and temporal transplants for addressing changing dynamics of plant–pollinator interactions; and a review of approaches used to assess potential shifts in phenology of plants and pollinators. Collectively, these articles illustrate some of the breadth of approaches needed to address the changing dynamics of plant–pollinator interactions.

Key words: climate change; DNA barcoding; floral traits; phenology; plant–pollinator interactions; transplants.

Plant–pollinator interactions are not only essential for successful reproduction of many native plant species (Vanbergen and Insect Pollinators Initiative, 2013), they are also fundamental to the resilience of many ecosystems in which plant communities are connected by their pollinators (Kearns et al., 1998; Berenbaum et al., 2007; Ollerton et al., 2011; Bartomeus et al., 2013; Bascompte and Olesen, 2015). Additionally, pollinators' importance cannot be overstated for many agricultural plants whose crop yield relies entirely on adequate pollinator services (Berenbaum et al., 2007; Klein et al., 2007; Hoehn et al., 2008). Hence, understanding the mutualistic interactions between plants and their pollinators is important for ecological and evolutionary biology as well as for agricultural applications.

These interactions are currently under threat due to multiple environmental impacts including invasive species, habitat loss and fragmentation, and broad-scale changes in global climate (González-Varo et al., 2013; Kiers et al., 2015). The current and future environmental changes associated with climate change (i.e., global warming) are imposing unique challenges for the spatial and temporal dynamics of these interactions (Diez et al., 2012; González-Varo et al., 2013; Ovaskainen et al., 2013). Facing these challenges, assessment of all the actors involved in these interactions requires creative and diverse approaches. This motivated the symposium Studying Plant–Pollinator Interactions in Changing Environments: Approaches, Lessons, and Future Directions at Botany 2016, the annual meeting of the Botanical Society of America, held in Savannah, Georgia, USA. This special issue focusing on plant–pollinator interactions facing climate change is a result of that symposium along with invited submissions from other authors.

Climate change is likely to have significant and unpredictable impacts on the dynamics of most natural systems, which will translate into unique challenges for assessment and predictions of future interactions in an altered environment (Scheffers et al., 2016). There are several reasons why it is particularly complex to assess the effects of climate change on plant–pollinator interactions. First, changes in abiotic factors caused by climate change may not affect both plants and pollinators. For example, increased carbon dioxide, one of the main causes for climate change, can delay flowering (Ward et al., 2012), but does not, to our knowledge, directly impact phenology of pollinators. In alpine habitats, flowering phenology is associated with snowmelt, while bee emergence is associated with temperature (Kudo and Ida, 2013), illustrating their response to different cues that are both independently varying with climate change. Second, even when both plants and pollinators do respond to the same type of environmental cues, how the plant and pollinator assess the cue may differ. For example, plants typically respond to a longer mean seasonal temperature as a cue for flowering, while pollinators use a shorter interval of temperature for emerging (Doi et al., 2008). As a result, changes in the environmental cues could

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lead to phenological mismatching between plants and pollinators through their differential responses to these cues.

Finally, specific aspects of climate change may differ on both spatial and temporal scales. Geographically, warming is greater in the Arctic followed by northern regions of North America, Europe, and Asia (IPCC, 2014), making plant–pollinator mutualisms in these regions more vulnerable to disruption. Seasonally, winters are warming faster than other seasons in regions such as Northern Europe, potentially leading to reduced flowering due to a lack of sufficient vernalization in these regions (Kreyling, 2010). With shorter and warmer winters, pollinators in these regions are responding with shortened or no diapause. These changes in diapause could result in increased exposure to temperatures that are lower than the insects' tolerable range, due to the increased frequency of extreme frosts (associated with climate change). Because the bees are no longer in diapause, this can result in increased mortality (Owen et al., 2013).

In addition to changes in the timing of events such as earlier emergence or flowering, species may also respond to the environmental changes via altering their spatial distribution. When the partners of a mutualistic relationship differ in their responses either spatially and/or temporally, the interactions can break down (Pyke et al., 2016). Breakdown of these interactions may have cascading effects in the pollination network as well as broader community impacts (Olesen et al., 2007; Schewieger et al., 2010; Tylianakis et al., 2010; Palmer et al., 2015).

Considering the temporal and spatial effects that climate change may pose on plant–pollinator mutualisms, novel and encompassing methodologies are needed for accurate and timely assessment of any changes in the association and functionality of the interactions between plants and their pollinators.

The first paper in this issue addresses how to effectively identify the plant community diversity of pollen collected by bees. Numerous studies of pollination networks (i.e., all plant–pollinator interactions in an area) from different habitats have provided comprehensive views of how the entire community of flowering plants and their coexisting pollinators may interact (Olesen et al., 2007; Burkle et al., 2013). Typically, pollination networks are constructed with visitation data obtained via observations. Extensive time and effort are required to collect observational data, and missing connections can be common (Chacoff et al., 2012). Bell and colleagues (2017) here outline a recently developed alternative approach that uses DNA barcoding to complement observational data. This approach provides not only taxonomic identities but also the diversity and relative quantity of pollen grains carried by flower visitors. It has the potential to enhance both the speed and accuracy with which plant species interacting with a particular pollinator are identified.

While the changes in phenology, particularly of plants, are well studied, the impacts of climate change on traits associated with pollinator attraction are less studied. It will be increasingly important to quantify these traits, as competition for pollinators is likely to increase as a result of climate changes and other environmental disruptions, such as the potential for mismatching, weakening or loss of links in plant–pollinator networks, and declining pollinator diversity with a greater proportion of generalists. Two of the papers in this issue present field methods for assessment of nectar (Arnold and Michaels, 2017) or floral volatiles (Burkle and Runyon, 2017). These traits are important for pollinator attraction, and evidence from a few studies indicates that they are impacted by climate changes (Burkle and Runyon, 2015; Mu et al., 2015; Takkis et al., 2015). Both to assess how these key resources linking plants and pollinators are being impacted by the changing climate and to support restoration efforts within the community, more frequent assessment of these traits is essential.

Nectar is a common reward for pollinators but is often difficult to study quantitatively, particularly in species that produce a very small amount per flower. The study by Arnold and Michaels (2017) outlines a relatively low-cost procedure that allows rapid extraction of nectar for sugar and amino acids analysis.

Floral volatiles are often understudied in field ecology; in part, this may be attributed to a lack of feasible approaches for the novice. Therefore, the contribution of Burkle and Runyon (2017) will be particularly useful to anyone interested in quantifying floral volatiles. In their review on measuring floral scent, they provide a historical perspective, applications of current field methods to quantifying floral scent in climate change studies, many practical details for field applications, and further directions in floral scent field measurements.

Assessment of the abundance of bees' activity at flowers may be time-consuming but is fairly straightforward. However, quantifying only the activity of pollinators at plants does not directly quantify their phenology, and methods to accurately assess their emergence at their nests are needed. Approaches for quantifying emergence and suitable habitat for ground nesting bees are less straightforward than observation at flowers. In their contribution, Pane and Harmon-Threatt (2017) outline an inexpensive approach using short-term sampling with emergence tents, which can be used in a diversity of habitat types.

The temporal and spatial variations associated with abiotic changes and biotic responses require studies in multiple dimensions. Morton and Rafferty (2017) review the use of transplant experiments across space and time to explore how these different dimensions have been experimentally tested. These types of approaches are where future studies are needed.

A comprehensive assessment of the impact of climate change on plant–pollinator interactions is difficult in part because of the temporal and spatial dimensions of the abiotic changes and biotic responses. This may necessitate multiple approaches ranging from use of herbarium specimens to experimental transplant studies. Byers (2017) reviews the diversity of current approaches assessing phenological changes in particular species to plant–pollinator networks. In this broad review, she discusses the advantages and limitations of the available approaches, as well as research needs in some understudied areas.

As the effects of climate change and other human-induced changes continue to alter our environment, it is increasingly important to develop and share new and improved approaches to study how these critical ecological interactions are being affected. We see this special issue and the associated symposium as the start of a conversation that will continue here and elsewhere.

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