

#### GLOBAL BIOLOGICAL CHANGE

## BOTANY AND A CHANGING WORLD: INTRODUCTION TO THE SPECIAL ISSUE ON GLOBAL BIOLOGICAL CHANGE<sup>1</sup>

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• The impacts of global change have heightened the need to understand how organisms respond to and influence these changes. Can we forecast how change at the global scale may lead to biological change? Can we identify systems, processes, and organisms that are most vulnerable to global changes? Can we use this understanding to enhance resilience to global changes? This special issue on global biological change emphasizes the integration of botanical information at different biological levels to gain perspective on the direct and indirect effects of global change. Contributions span a range of spatial scales and include both ecological and evolutionary timescales and highlight work across levels of organization, including cellular and physiological processes, individuals, populations, and ecosystems. Integrative botanical approaches to global change are critical for the ecological and evolutionary insights they provide and for the implications these studies have for species conservation and ecosystem management.

**Key words:** community dynamics; flowering phenology; functional traits; global biological change; invasive species; land-use patterns; plant-microbial interactions; species interactions.

The impacts of global change, including increased carbon dioxide and its effect on climate, changes in biogeochemical cycles, changes in land use and habitat fragmentation, patterns of harvesting, introductions of alien species, and other human use of resources, continue to increase with the growth of the human population to over seven billion people. Concern that these changes may lead to rapid and irreversible changes in the global ecosystem (Barnosky et al., 2012; Marcott et al., 2013) has heightened the need to understand how organisms respond to and influence these processes. Can we forecast how change at the global scale may lead to biological change? Can we identify systems, processes, and organisms that are most vulnerable to global changes? Can we use this understanding to enhance resilience to global changes?

Responding to this call to better understand biological responses to global change is no simple matter. Direct and indirect effects on the Earth's biota occur at all biological levels and affect cellular and physiological processes, population sizes and distributions, the evolution of species, community-level interactions, and ecosystem processes. Responses can occur at both ecological and evolutionary timescales and may include phenotypic changes within the lifetime of long-lived organisms, evolutionary changes in populations that affect range limits, hybridization that affects the integrity of species, and interactions among species that affect abundance and precipitate species loss. For us to tackle such complex challenges, scientific

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perspectives need to span spatial and temporal scales, as well as integrate across biological levels of organization.

This special issue was assembled to advance a view of global biological change that includes diverse botanical approaches and disciplines essential for understanding how terrestrial plants at all levels of organization are both responding to, and affecting, environmental change. We hope this special issue provides an expanded view of global biological change by emphasizing the integration of botanical information using traditional and multidisciplinary fields as well as a diversity of approaches including experiments, observations, and reviews to gain perspective on this rapidly developing area. We also hope that the diversity of papers highlighted in this collection will stimulate readers to make new methodological and conceptual connections among these many approaches and will lead to a greater understanding of global biological change.

### INTEGRATION OVER TIME: LOOKING BACKWARD TO LOOK FORWARD

Past changes provide insights into the rate at which current communities may be able to respond to rapid changes in climate and other environmental changes. Using the rich fossil record of the Bighorn Basin in Wyoming at the Paleocene-Eocene Thermal Maximum, Wing and Currano (2013) discuss rates of change in species distributions. They demonstrate a remarkable shift in the mesophytic flora over a 200 000-yr period of warming. At this time scale, evolutionary responses to climate change seem likely and may explain the persistence of those species that immigrated into the Big Horn Basin during the Thermal Maximum and remained following a return to lower temperatures. These species may have evolved in response to cooling temperatures, although in most cases the species that returned to the region were typical of cooler, more

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mesic conditions. Future shifts in vegetation are likely to be far greater and occur at a faster pace than those that took place during the Paleocene-Eocene Thermal Maximum. These future changes are unlikely to keep pace with climatic changes that occur too rapidly for ecological equilibrium to develop or for adaptive evolutionary responses. The potential complexity of these changes is illustrated by Ordonez's (2013) study of pollen records from the late Pleistocene, examining changes in the geographical ranges of 20 taxa. His work indicates a disequilibrium between species ranges and changes in the climate. Although realized temperature niches of species changed during this period of climatic warming, they did so at a slower rate than the shift in temperatures. Responses varied by individual species, suggesting that future community assemblages in response to climate change may be quite different than those existing at present. Many factors, including the occurrence of future climates that have no current analog, differences in migration capacity, and unanticipated ecological interactions will influence the nature of communities in the future. Understanding the capacity of species to shift their climate niches may permit a better understanding of these communities of the future and aid in their management.

The idea of vegetation in disequilibrium is more generally reviewed by Svenning and Sandel (2013). For long-lived species, the leading edge of the range of a species is characterized by lags in migration, slow population growth, or even extinction of species that are slow to respond to changes. At the trailing edge of distributions, disequilibrium dynamics may obscure the effects of climate change because long-lived species persist but are no longer capable of reproducing. In contrast, short-lived species may be able to respond to environmental changes with more rapid evolutionary responses. As Svenning and Sandel note, many additional changes, including biological invasions, fragmentation, and modified disturbance regimes also will impact the extent of disequilibrium dynamics at the leading and trailing edges of species ranges.

Both habitat fragmentation and biological invasions have had significant impacts on vegetation dynamics. Deliberate or accidental introductions mediated by humans have greatly increased the migratory ability of species, leading to major impacts on the equilibrium of ecosystems. Using online and literature surveys, Lehan et al. (2013) focus on the importance of invasive plant species that arrive through accidental introductions in the continental United States and how these patterns have changed through time. Accidental introductions are often contaminants of seeds used in management of agricultural and rangeland areas and thus are more likely to be forbs and grasses in the western United States. Understanding the shifts in modes of introduction of potentially invasive species may help to better regulate and control future introductions. Vellend et al. (2013) examine the possibilities and limitations of using unconventional data (data that were not collected as part of long-term ecological studies) to detect the effects of climate warming and land-use changes. These data include historical vegetation surveys, maps, photos, and herbarium specimens and may reveal bias that is otherwise hard to detect. For example, remnant communities are now often found in habitats that were unusual for these communities before land use change, and conclusions about past distributions based on current distributions of communities might lead to erroneous interpretations. Historical data on fragmentation are especially useful for relating the magnitude of changes in landscapes relative to changes in the environment, particularly with respect to delays in extinction following

fragmentation, and the slow pace of recolonization of newly created habitats. These more recent patterns also provide evidence for the disequilibrium dynamics shown during other periods of climate change (as shown in this issue by Svenning and Sandel, 2013; Ordonez, 2013; Wing and Currano, 2013). Major challenges in the use of unconventional historical data are inferring causation, the evaluation of alternative hypotheses, and careful consideration of processes that vary spatially or occur at different time scales (Vellend et al., 2013 in this issue).

# INTEGRATION ACROSS FUNCTION: USING TRAITS TO SPAN ECOLOGICAL AND EVOLUTIONARY RESPONSES

Thinking about species in terms of their function—in addition to their taxonomic classification—is an exciting new avenue of research that may allow for increased generalization across species at many scales. Plant functional traits have been defined as any plant attribute that may significantly influence establishment, survival, and fitness of plants (Reich et al., 2003) and often include morphological and physiological traits that affect the ability to acquire, use, and conserve resources. Plant functional traits and their importance to global environmental change have been studied at many levels, including the response of individual species to drought and rising temperatures, their impact on mutualistic and competitive interactions among native and invasive species, and their effect on the assembly of communities. These studies are often driven by a desire for a mechanistic understanding of how selection acts to change range limits and other patterns of biological change associated with global change.

Phylogenetic approaches may reveal how the past evolutionary history of functional traits may predict the ability to adapt to future changes in climate. In a study of highly diverse South African Pelargonium species (Jones et al., 2013), leaf traits in three clades showed different patterns of integration related to climate. Jones et al. (2013) argue that conditions prevailing at the time each of these clades evolved have determined the nature of leaf adaptations in each clade as well as their likely response to future climate change. Consideration of the integration of traits is critical because mean trait values alone would lead to different predictions about which clades might persist in hotter, drier climates. More widespread application of this phylogenetically based approach may lead to greater understanding of how climate change will affect future shifts in community composition or the response of species to climate change (see Mazer et al., 2013 in this issue). Campbell and Wendlandt (2013) also examine a single lineage but take an experimental approach to examine how functional traits may influence the consequences of hybridization associated with climate-related shifts in the distribution of two species of Ipomopsis. With reduced precipitation, hybrids were favored within the range of *I. aggregata* due to increased water-use efficiency. The authors also point out the potential influence of climate on prezygotic isolating mechanisms mediated through pollinators. These complexities illustrate how climate change can impact the fitness of organisms directly through fitness differences associated with functional traits, and indirectly through community-level interactions.

Fonti et al. (2013) use a 312-yr chronology of tree rings of *Larix siberica* (Pinaceae) to demonstrate how a long-lived tree species may adapt to climate change through phenotypic plasticity of the

cell morphology of the xylem in long-lived individuals. For this cold-limited species, climate warming has been associated with formation of xylem with wider cell lumen and increased water conduction, favoring greater photosynthetic capacity. Increased cell walls of latewood increase the level of mechanical support as trees reach greater size. The complex response of individuals of a single species to climate change indicates the difficulty in predicting how entire communities will respond to climate change. In a study of range shifts over a 100-yr period in three conifer species, Ettinger and HilleRisLambers (2013) examine traits that reflect climatic factors and competition at different life stages. For two species that reach treeline, growth was limited by low temperatures and heavy snowpacks, suggesting that as climate warms, the ranges of these species will shift upwards, moving treeline to higher elevations. In contrast, at the lower limits of these species, growth was less strongly affected by climate. Competition, often assumed to have the primary role determining lower range limits, showed no consistent pattern over the range of these species, but for two of the species, competition was important at the upper range limits where climate also has its greatest impact. Upper and lower limits of range distributions may be controlled by different functional traits related to climate as well as competition.

Changes in land use may result in community types that differ in plant functional traits. If these traits can be identified, the trajectory of community change may be anticipated more readily, increasing the likelihood that viable conservation measures can be identified. Mayfield et al. (2013) conducted a meta-analysis across 15 forest communities using seven functional traits, including both morphological traits as well as traits indicating potential ecological interactions (e.g., pollination syndrome, seed dispersal). Land use patterns included different levels of disturbance, ranging from natural (relatively undisturbed) forests to pastures and old-growth fields, and forests undergoing secondary succession following logging. Changes in land use and site productivity (NPP) were not good predictors of changes in functional traits for forest systems (Mayfield et al., 2013), although differences in trait variation did occur between the forest understory and forest canopy with different land use conversions. These results suggest that broad generalizations may be difficult as we grapple with the effects of global biological change at the landscape level.

Huxman et al. (2013) use functional traits affecting ecophysiology, plant life history, and species interactions to investigate shifts in the community composition of Sonoran Desert annuals in response to climate change. In this ecosystem, climate change has been characterized by gradual warming and the occurrence of precipitation later in the winter season. Tradeoffs between relative growth rate and water-use efficiency may contribute to species coexistence in this desert ecosystem, as observations of permanent plots indicate long-term species coexistence. A striking result from this study is a relative increase in species that germinate later in the winter season and are more cold-adapted. One goal of this research is to predict the features of these communities as the effects of climate change accelerate and desert ecosystems become increasing invaded by alien species.

### INTEGRATION ACROSS SEASONS: TRACKING HOW TRAITS TRACK CLIMATE CHANGES

Changes in plant phenology, particularly changes in the time of flowering, are one of the most conspicuous consequences of global warming. Mazer et al. (2013) use a phylogenetic perspective to

determine whether taxonomic affinity can be employed to predict phenological responses of seasonal temperate-zone species that have not yet been studied. Using temperate species distributed in 119 plant families, seven sites, and species observed for 8-37 yr, Mazer et al. (2013) find that family membership predicts the response of first flowering date to temperature for individual species. With warmer temperatures, families with early flowering means are more likely to advance their first flowering date than families with late-flowering means. This change may reflect a greater sensitivity to temperature and greater phenotypic plasticity in flowering time of species in the early flowering families, which could be adaptive when early season conditions are highly variable among years. Consistent changes in the date of first flowering were not associated with changes in precipitation. Mazer et al. (2013) conclude that for the seasonal temperate communities examined, family membership can be used to identify taxa that will be sensitive to temperature changes. Interannual variation in phenology may make it difficult to see longer-term trends. Using four decades of flowering records from Colorado and Greenland, Iler et al. (2013) demonstrate that despite an overall pattern of earlier flowering at both sites, in Colorado snowmelt was a strong predictor of flowering time, and flowering was delayed during some of the 10-yr periods. Iler et al. (2013) suggest that in Greenland, consistent earlier flowering for all 10-yr periods is related to the far greater rate of global warming at high latitudes. At the Colorado site, earlier-flowering species tended to advance more in flowering time than later-flowering species, while in Greenland, the reverse was true, probably because later-flowering species at that site occur in snow banks, which are more common at that site. Despite the potential for evolutionary responses in phenology associated with climate change (Hancock et al., 2011; Anderson et al., 2012), in Colorado, the relatively short-term variation in the direction of changes in flowering phenology with environmental predictors indicates that these changes are probably the result of phenotypic plasticity. In view of work by Mazer et al. (2013, this issue), exploring the importance of phylogenetic relationships with respect to patterns of phenological shifts at these sites may be of particular interest.

Changes in first flowering date with climate change can also change community dynamics. Wolkovich et al. (2013) find that alien species may be successful invaders because they are more phenologically flexible than native species and track climate change more closely. Either phenotypic plasticity or genetically based local adaptation may contribute to phenological flexibility. These species may use empty niches that may appear as a warming climate lengthens growing seasons. Alien species tend to have earlier mean annual flowering times than native species and are more sensitive than native species to temperature at three mesic sites, suggesting support for both the empty niche model and increased phenological sensitivity. At two grassland sites, precipitation and soil moisture appear to be more important than temperature in determining responses of alien and native species. Grassland sites had nearly identical flowering times for native and alien species. Wolkovich et al. (2013) used a phylogenetically corrected data set, but further consideration of the proportion of alien species within families as well as information on the general phenology of flowering of the families (see Mazer et al., 2013 in this issue) might help to better understand this pattern.

Gornish and Tylianakis (2013) address the dependency on scale of environmental effects on plant communities. In their literature synthesis on effects of global change on plant communities, they identify patterns in abiotic or biotic pathways underpinning these changes, as well as whether these pathways may change at different scales of inference. Several important points emerge from their synthesis. First, large-scale studies more consistently identify composition and diversity changes, while local studies are more context-dependent. This conclusion suggests that a push is needed in botanical work to link studies at a local/site level to patterns at larger scales for generalization. Second, Gornish and Tylianakis (2013) find that these changes to plant communities, as a result of shifts in phenology, foliar quality from the perspective of potential herbivores, and species abundance, affect plantinsect interactions and higher trophic levels.

### INTEGRATION ACROSS TAXA: THINKING ABOUT PLANTS IN A LARGER BIOLOGICAL CONTEXT

Interactions of plants with microbes are likely to have a pervasive influence in mediating the effects of global change. The importance of interactions between fungal endophytes and terrestrial plants in prevention of plant water loss over a steep precipitation gradient was experimentally tested by Giauque and Hawkes (2013). Fungal endophytes isolated from plants at the drier end of the gradient were more effective at preventing water loss for plants grown in the greenhouse, although the taxonomic identity of the endophyte was more important than geographic origin in determining the response of the plant to moisture limitation. The plasticity of plant traits with respect to varying moisture was far greater if endophytes were present, although the effects of individual endophyte species were again also highly variable. To the extent that endophytes exhibit local adaptation, they could buffer plants against climate change and contribute to a lagged response of plants to these changes. The complexity of interactions between endophytes and plants, including the possibility that endophytes may be commensals in living plants and decomposers in senescent tissues, or even parasites, contributes to the difficulty in predicting the extent of symbiosis and localized adaptation of fungal endophytes. The role of fungal symbionts in plant responses to global change was examined more broadly through a meta-analysis by Kivlin et al. (2013). Of the four global change factors analyzed independently (enriched CO<sub>2</sub>, drought, nitrogen deposition, and warming), all except elevated CO<sub>2</sub> changed plant responses to global change scenarios. Fungal symbioses ameliorated the effects of drought and warming, but an increase in nitrogen decreased the benefits of symbioses. Interactions among these four global change factors are likely, leading to unanticipated responses under more realistic situations. Additionally, specific combinations of fungal symbionts may be nonadditive in their effects. Few studies have investigated these interactions, particularly in the context of global biological change, suggesting that much remains to be learned before predictions of the effects of these changes can be formulated. Kivlin et al. (2013) provide a framework for the kinds of studies that will help to understand how fungal symbioses will mediate the effects of global biological change.

Community-level effects of one aspect of global biological change, increased nitrogen deposition, were investigated by Farrer et al. (2013). Plants may be affected directly through modification of competitive interactions for nitrogen or indirectly influence the relative abundance of plants by modifying soil microbial communities. Despite substantial worldwide increases in nitrogen deposition and subsequent modifications of

plant communities usually leading to a loss of diversity, there have been only a few studies and little empirical support to suggest that competition is the primary mechanism for the loss in diversity under these conditions (Farrer et al., 2013, in this issue). Following nitrogen additions in an alpine community, microbial communities in association with two plant species changed significantly, but the effects on plant growth differed between the species. Thus, in contrast to the focus on changes in plant—plant competition, results point to the importance of changes in plant—microbial interactions and constraints at the organismal level in determining responses to drivers of global change.

#### LOOKING FORWARD

Global biological change encompasses a broad and rich research area, both in terms of the disciplines involved (from molecular biology to ecosystem ecology) and in terms of the diversity of types of interactions and processes that it embodies. The broad sweep of papers included in this special issue illustrates the breadth and depth—as well as the integrative possibilities—that can be achieved by looking at traditional topics in botany from a global change perspective. By gathering together contributions emphasizing global change at many levels of organization, we believe that new insights will be gained into how plants are affected by global change and how plants are themselves influencing global change. We hope that readers will be inspired to tackle these and additional questions from a variety of disciplines and perspectives.

While quite diverse, we can identify some general themes arising from these papers. This special issue highlights how a myriad of research approaches can be used to inform our understanding of biological changes—from observations using a wide range of information sources, both past and present, to experiments set in greenhouses or in the field, and to data syntheses. We are only beginning to think about how to integrate across data sources or experimental approaches. For a start, integration of both ecological and evolutionary responses and syntheses at multiple sites, of multiple species, and of multiple types of interactions are critical. In a complex world where interactions may depend on scale, we need to integrate research approaches, temporal and spatial scales, and levels of biological organization more explicitly. Integrative botanical approaches to global change are critical not only for the ecological and evolutionary insights possible, but because of the potentially profound implications our studies may have for species conservation and ecosystem management.

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