New Phytologist

Review

Tansley review

The growing and vital role of botanical gardens in climate change research

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Received: *7 December 2020*
Accepted: *25 February 2021*

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New Phytologist (2021) **231:** 917–932
doi: 10.1111/nph.17410

Key words: botanical gardens, climate change, conservation, herbarium specimens, phenology, phylogenetics, physiology, public engagement.

Summary

Botanical gardens make unique contributions to climate change research, conservation, and public engagement. They host unique resources, including diverse collections of plant species growing in natural conditions, historical records, and expert staff, and attract large numbers of visitors and volunteers. Networks of botanical gardens spanning biomes and continents can expand the value of these resources. Over the past decade, research at botanical gardens has advanced our understanding of climate change impacts on plant phenology, physiology, anatomy, and conservation. For example, researchers have utilized botanical garden networks to assess anatomical and functional traits associated with phenological responses to climate change. New methods have enhanced the pace and impact of this research, including phylogenetic and comparative methods, and online databases of herbarium specimens and photographs that allow studies to expand geographically, temporally, and taxonomically in scope. Botanical gardens have grown their community and citizen science programs, informing the public about climate change and monitoring plants more intensively than is possible with garden staff alone. Despite these advances, botanical gardens are still underutilized in climate change research. To address this, we review recent progress and describe promising future directions for research and public engagement at botanical gardens.

I. Introduction

Over the past 20 years, the scientific community has described a range of ways that climate change affects plants – influencing phenology, physiology, anatomy, and other aspects of plant ecology and evolution (Parmesan & Yohe, 2003; Wolkovich *et al.*, 2012). The timing of plant leaf out, flowering, fruiting, and senescence are changing, as are plant functional traits and carbon budgets (Menzel *et al.*, 2006; Gallinat *et al.*, 2015). Climate change is also influencing plant conservation, with biologists taking actions to identify and preserve plant species most threatened by changing environmental conditions (Salguero-Gómez *et al.*, 2012). As part of these efforts, scientists and educators are increasingly engaging the public in botany and plant ecology, including through community and citizen science initiatives aimed at tracking plant responses to climate change (Ellwood *et al.*, 2017). (We use community and citizen science to refer to projects in which the public participates in research and data collection, sometimes as a part of projects designed by community members and sometimes as a part of projects designed by scientists.) With the vast botanical resources they house and the visitors they draw, botanical gardens are uniquely suited to timely climate change research, conservation, and public engagement (Krishnan & Novy, 2016).

In 2009, we published a *New Phytologist* Tansley Review (Primack & Miller-Rushing, 2009) that highlighted the underutilized capacity of botanical gardens – gardens that specialize in the display, scientific study, and utilization of plant diversity – to advance climate change research. In the decade since, botanical gardens have indeed advanced climate change research, often through the use of new or improved tools that allow researchers to leverage the living, historical, and specimen collections of botanical gardens. At the same time, new scientific, conservation, and public engagement challenges have arisen that botanical gardens are uniquely positioned to address.

Several features of botanical gardens allow researchers to answer questions they could not elsewhere. Botanical gardens are located around the world (Fig. 1) and have large living collections of plants representing both diverse taxa and historical biogeographies growing in shared conditions. As such, botanical gardens can be used as common gardens, where researchers can conduct unmatched comparative studies of plant physiology, anatomy, and responses to climate change (Donaldson, 2009; Sellmann & Bogner, 2013; Chen & Sun, 2018). Many botanical gardens also house unique historical records – such as herbarium specimens, photographs, and field observations – that document plant responses to climate change over decades or centuries. Sometimes these specimens and records are linked to individual plants with known histories growing on garden grounds, again providing data that are difficult to find elsewhere (Primack *et al.*, 2004; Miller-Rushing *et al.*, 2006; Heywood, 2017; Lang *et al.*, 2019). Many botanical gardens monitor, and have historical records describing, abiotic conditions, such as weather and air quality, which can be used to examine plants' responses to climate change over long periods. Botanical gardens also facilitate connections among botanists, ecologists, students, and volunteers investigating plants, through place-based research networks. And by attracting millions of visitors each year and through their connections with local communities, botanical gardens serve as a point of outreach and exchange with the public, providing opportunities for people to learn about the impacts of climate change on plants and to participate in real research through community and citizen science.

Despite the advantages of botanical gardens, we believe they continue to be underutilized for climate change research. There is great untapped potential for researchers and science communicators to better partner with and use the resources that botanical gardens provide, and to communicate and engage the public in the work taking place at botanical gardens. Much of the climate change research during the past decade at botanical gardens has focused on woody plant collections, often at arboreta, in temperate regions. As a result, there are great opportunities for climate change research focusing on herbaceous species and at botanical gardens located in tropical and polar regions.

Here we review advances in climate change research at botanical gardens around the world, take stock of novel resources and techniques, and describe promising future directions. We focus on research that takes advantage of the special features of botanical gardens – for example, diverse living collections, often with substantial related records such as herbarium specimens and photographs, and documentation of where source material was collected – rather than studies that could easily have occurred at other locations, such as studies of single species. Our goals are to unify the climate change-related work of botanical garden researchers and encourage new researchers to use botanical gardens as places to study and communicate the critical questions about the impacts of climate change on plants. We argue that botanical gardens and researchers working at them have the resources and expertise to address the following important questions: How do populations and species vary in their responses to climate change? How have individual plants responded to climate change over long periods of time? How will plants respond to future climate change? How can we best protect plant species threatened by climate change? And how can we effectively communicate these ideas to the public and increase their engagement with climate change science? Research at botanical gardens has already generated valuable insights that will help us to answer these questions, and these efforts are poised to offer more in the coming years and decades.

II. New methods and resources

1. New phylogenetic and comparative methods

Studies at botanical gardens can include dozens or even hundreds of species. Examining and accounting for the evolutionary history of those species can provide more information about why plants differ in their responses to climate change. Recent advances in phylogenetic tools and trait databases have provided new opportunities for researchers to leverage the diverse living collections and herbaria at botanical gardens. Advances include the open-access release of high-resolution plant phylogenies (Zanne *et al.*, 2014; Qian & Jin, 2016), tools researchers can use to generate phylogenies (e.g. Smith & Walker, 2019), and new eco-phylogenetic statistical approaches for estimating and accounting for the ways species' relatedness

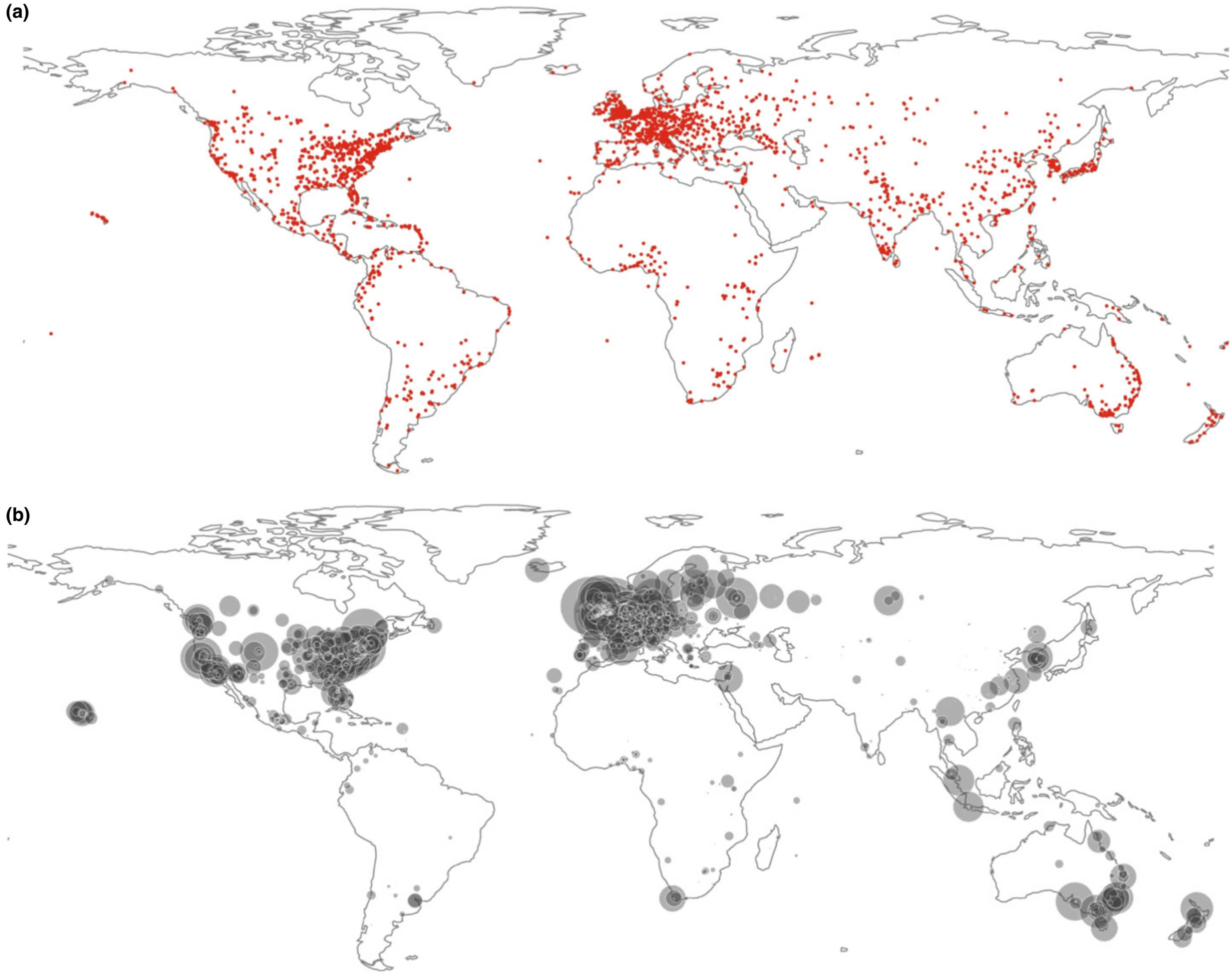

Fig. 1 (a) Thousands of botanical gardens are distributed throughout the world. (b) Concentrations of species are found in botanical gardens, particularly in Europe, North America, Eastern Asia, and Eastern Australia (from Mounce *et al*., 2017).

affects their comparative ecology (e.g. Orme *et al*., 2012; Pearse *et al*., 2015). For example, prior to our review in 2009, researchers often treated species as independent data points, despite different levels of relatedness among those species. However, many plant traits, including their responses to climate change, are phylogenetically conserved, with close relatives sharing more similar traits than would be expected by chance (Webb *et al*., 2002; Davies *et al*., 2013). Modern phylogenetic analysis can estimate the phylogenetic patterns among species' traits, indicating the strength of evolutionary constraint on those traits and allowing for more accurate comparisons among groups, such as deciduous and evergreen species, different growth forms, and provenances.

The recent development of global plant trait databases, including the TRY (Kattge *et al*., 2011, 2020) and BIEN (Enquist *et al*., 2016; Maitner *et al*., 2018) databases, has further enabled researchers to examine the ways in which functional traits and their evolutionary history mediate relationships between plants and their environments. For instance, the TRY database now houses over 11 million trait records for over 250 000 plant taxa which are available to researchers upon request. Botanical gardens have contributed information to these databases. For understudied species, like many tropical species, botanical gardens may be among the best places to collect trait data, particularly for understudied traits (Perez *et al*., 2018). Studies at botanical gardens have also made use of these data, often in concert with phylogenetic tools, to better understand the effects of climate change on plants (Panchen *et al*., 2014; Smith *et al*., 2019).

Many of the examples we discuss in the following sections of this paper use these phylogenetic and comparative methods, tools, and databases to advance climate change research and address questions that would be difficult or impossible to address elsewhere.

2. Growing botanical garden networks

The power of comparative analyses at single botanical gardens is magnified by connections across gardens. Networks of botanical gardens allow researchers to study the same species growing in different locations under different present-day climate conditions. In our previous review (Primack & Miller-Rushing, 2009) we described the pioneering efforts and valuable long-term records kept by the International Phenological Gardens (IPG) network, which was founded in 1957 and spans approx. 90 locations across Europe (Chmielewski *et al.*, 2013). The IPG provided some of the best early data describing plant phenological responses to climate change and described broad patterns of variation across regions, phenophases, taxa, and growth forms – for example, the spring phenology of plants (leaf out, flowering) is generally more sensitive to warming than autumn phenology (leaf senescence) (Menzel, 2000; Menzel *et al.*, 2006; Chmielewski *et al.*, 2013; Gallinat *et al.*, 2015). Recently, the network's data have been incorporated into larger data sets – for example, the Pan European Phenological database (Templ *et al.*, 2018) – and have supported a number of larger scale studies, including those assessing nonlinear changes in phenology, examining nonintuitive shifts in autumn phenology, and using remote sensing to examine phenology across large landscapes or countries (Jochner *et al.*, 2016; Donnelly *et al.*, 2018; Zani *et al.*, 2020). Newer networks and programs in the USA also link observations across botanical gardens and other research sites – for example, the National Phenology Network (www.usa-npn.org), Project Budburst (www.budburst.org), and iNaturalist (www.inaturalist.org).

Networks of botanical gardens have further expanded in the past decade to include a network of researchers at gardens around the world. In 2012, a network of eight botanical gardens in North America, Europe, and Asia began a long-term collaboration to monitor the timing of spring leaf out, summer fruiting, and autumn leaf senescence of more than 1000 woody plant species (see section III, Phenology, below). The research team has been able to study multiple seasonal events for a large number of diverse species at locations across three continents – research that would be very difficult to achieve without botanical gardens (Panchen *et al.*, 2014, 2015; Gallinat *et al.*, 2018).

3. Improved access to herbarium specimens, photographs, and other historical records

Access to herbarium specimens, photographs, and historic observations is dramatically improving and researchers are identifying new ways to use them to provide data critical to climate change research, often at botanical gardens (Zohner & Renner, 2014; Willis *et al.*, 2017; Younis *et al.*, 2018; Pearson *et al.*, 2020). In the past, researchers had to visit herbaria in person to examine large numbers of herbarium specimens covering broad regions. Now, tens of millions of herbarium specimens, collected from all around the world, have been imaged and are available online (Blagoderov *et al.*, 2012; Soltis, 2017), including through the Global Biodiversity Information Facility (Heberling *et al.*, 2021). This facilitates the combining of detailed observations and experiments from botanical gardens with the broad geographical perspectives supplied by herbarium specimens collected across regions, continents, and the world. Over the past decade researchers have continued to use herbarium specimens, photographs, and field observations to provide insights into plant responses to climate change (Panchen *et al.*, 2012; Rawal *et al.*, 2015), even in remote areas such as the Himalayas, where it is difficult to collect long-term observations (Hart *et al.*, 2014). Additional specialized collections of preserved wood, seed, and pollen collections collected and stored at particular gardens provide further under-explored research opportunities.

III. Phenology

Shifts in phenology – the timing of seasonal events like leafing out, flowering, fruiting, and leaf senescence – are among the most immediate and easily observed impacts of climate change on plants. However, many basic features of these shifts in plants remain unknown, including how species vary in their phenological sensitivity to environmental factors like temperature and precipitation, the extent to which evolution and environment constrain phenology, and which traits mediate interactions between plants and their environments. It has become increasingly common for botanical gardens to record the phenology of their living collections (Fig. 2), and such monitoring is often matched with a renewed appreciation for, and rediscovery of, past records of phenological monitoring at these gardens. This has resulted in a number of publications demonstrating that plants at botanical gardens in temperate regions are now flowering and leafing out earlier in the spring than in the past as a result of warming temperatures (Tooke & Battery, 2010; Sparks *et al.*, 2011; Du *et al.*, 2017).

In recent decades, researchers at botanical gardens have made progress by comparing the phenology of species across seasons and across gardens, identifying how phylogeny and functional traits constrain phenology, and connecting botanical garden phenology data to additional data sources for more integrative comparisons.

1. The complex relationship between climate and plant phenology

The responses of plant phenology to changes in climate are complex and vary substantially across species, locations, and seasons (Piao *et al.*, 2019). Depending on these factors, plant phenology may respond to changes in temperature, precipitation, snowmelt, or daylength – and plants may respond to cues differently in different seasons (Basler & Körner, 2012; Lenz *et al.*, 2013; Flynn & Wolkovich, 2018). For example, a study examined 10 295 *Rhododendron* herbarium specimens collected between 1894 and 2009 in the Himalayas and stored at a number of botanical gardens and other herbaria (Hart *et al.*, 2014). Their analysis showed that over the full study period plants tended to flower earlier as a result of warming springs, but that flowering phenology has not advanced over the past 45 years because of the offsetting influence of warmer springs, which tended to advance flowering, and warmer autumns, which tended to delay flowering (Hart *et al.*, 2014). Another recent study, partially based on botanical garden data, found that growing-season productivity largely regulates tree leaf senescence phenology across Europe, suggesting that leaf senescence will occur earlier in the year as conditions continue to warm, rather than later in the year as previous models had suggested (Zani *et al.*, 2020).

Fig. 2 Phenological studies at botanical gardens now often cover the full range of major plant phenophases, including (clockwise from top left) flowering, fruiting, leaf senescence, leaf out, and leaf senescence.

2. Explaining variation in phenological responses to climate change

A major challenge in plant phenology research is to disentangle the complexity of climate–phenology relationships by examining how and why phenological sensitivities vary across species, locations, and seasons. A new network of eight botanical gardens studied leaf phenology of 1597 tree, shrub and vine species, and fruit phenology for over 400 species, growing at gardens in North America, Europe, and Asia (Panchen *et al.*, 2014, 2015; Gallinat *et al.*, 2018). This research is unusual for the large number of species monitored at multiple botanical gardens using a standard protocol. The design allowed researchers to assess factors that drive variation in species responses to climate change, resulting in five key findings.

First, the studies reveal that the timing of phenological events varies substantially across species. For example, plant species vary by as much as three months in their leafing out times at individual botanical gardens, with some species leafing out in early March and others leafing out in early June. This finding suggests that the onset of carbon sequestration and other ecological processes associated with leaf out also vary dramatically among species.

Second, these studies collectively show that leaf-out and fruit phenology are constrained across species – that is, species tend to leaf out and fruit in the same sequence in different years and at different botanical gardens. By contrast, leaf senescence phenology (defined as the date when 50% of leaves had changed color or had fallen) is much more flexible and is not correlated across botanical gardens. This result suggests that leaf senescence may respond to a more varied set of environmental cues, including local site conditions, or may be a more plastic trait compared to leaf-out and fruit phenology. This greater complexity of leaf senescence compared to leaf out is supported by other studies from the individual to canopy scale (Menzel *et al.*, 2006; Gallinat *et al.*, 2015; Zani *et al.*, 2020). Botanical garden collections have provided a unique contribution to this area of research by expanding the taxonomic breadth, which is essential to understand the complexity of responses.

Third, in the study of leaf out, the researchers found that species with diffuse and semi-ring porous stem anatomy tended to leaf out earlier than ring porous species, and species with smaller diameter xylem vessels leafed out earlier than species with larger diameter vessels (Panchen *et al.*, 2014). This result is consistent with the greater freezing tolerance of smaller vessels, which allows them to move water to leaves earlier in the spring (Lechowicz, 1984). Deciduous species tend to leaf out before evergreen species, both across large taxonomic groupings, such as angiosperms vs gymnosperms, and within particular genera, such as *Rhododendron*, which include deciduous and evergreen species. This research informs predictions of which species will be better able to adapt to changing climate conditions, as field studies suggest that plant species with the ability to adjust their phenology are more likely to persist in a changing climate (Willis *et al.*, 2008).

Fourth, the studies found that leaf out and fruiting exhibit moderate to strong phylogenetic signals, while leaf senescence does not (Panchen *et al.*, 2014, 2015; Gallinat *et al.*, 2015). In other words, closely related species tend to leaf out and fruit at similar times to one another, but this is not the case for leaf senescence. For example, phylogenetic analysis demonstrated that certain clades tend to leaf out early (such as the Rosaceae and the Dipsacales, including *Lonicera* and *Viburnum*) and other clades tend to leaf out late (such as the Ericaceae and the Fagales, including *Fagus* and *Quercus*; Fig. 3; Panchen *et al.*, 2014). A separate study at the Forest Botanical Garden of Heilongjiang Province, China also found that the responses of flowering and leaf-out phenology are also strongly phylogenetically conserved among 52 woody species (Du *et al.*, 2017). Together, these results suggest that there are evolutionary constraints on flowering, leaf-out, and fruiting times, which may limit the extent to which phenology shifts under climate change.

Fifth, researchers have found that biogeography of species explains some of the variation in phenology. Within particular genera and families, species of eastern North America tend to leaf out later in the spring than species from Europe and East Asia (Zohner & Renner, 2017), which may reflect the fact that the more variable weather of eastern North America, and greater possibility of late-spring frosts, has selected for greater winter chilling and spring forcing requirements to help plants avoid damage. A further study at the Munich Botanical Garden showed that species of eastern North America were more likely to display red coloration in their leaves during senescence compared to species of Europe (Renner & Zohner, 2019), perhaps due to the photoprotective function of these pigments during the bright and cold autumn season of eastern North America (though see Pena-Novas & Archetti, 2020). Related research from botanical gardens and the wild shows that flowering phenologies of nonnative species were more responsive to temperature than were those of native species (Du *et al.*, 2017), supporting the idea that some nonnative invasive species may increase their competitive advantage under climate change by shifting their phenology earlier in spring (Willis *et al.*, 2008; Wolkovich & Cleland, 2011).

3. Contributing to descriptions of regional changes in phenology

Because phenological gardens have become hubs for phenology data, researchers are increasingly using them to anchor studies of phenological change across regions. For example, Donnelly *et al.* (2018) used observations of leaf color and leaf fall phenology at four botanical gardens in Ireland to assess the ability of satellite-based remote sensing to capture autumn plant phenology across rural and urban locations in the country. They found that remote sensing was relatively good at capturing autumn plant phenology across large homogenous landscapes compared to more heterogenous landscapes.

IV. Physiology and anatomy

In addition to seasonal vegetative and reproductive timing, plants may exhibit climate-driven changes in other functional traits. Many anatomical and physiological plant traits vary along environmental gradients, suggesting that they may respond to climate change and allow plants to tolerate changing conditions around the world (Guittar *et al.*, 2016). The diversity of living collections and specimens at botanical gardens can help researchers document the plasticity and role of plant functional traits in climate responses within and across species. Plant physiology and anatomy play key roles in regulating how plants tolerate heat waves and drought stress, how changing phenology influences vulnerability to frost, and how plant growth and water use efficiency respond to increasing levels of carbon dioxide in the atmosphere, longer growing seasons, warmer winters, and reduced snowpack (Becklin *et al.*, 2016; Crous, 2019; Aparecido *et al.*, 2021). In this section we discuss examples of studies that have used botanical gardens to investigate these physiological and anatomical attributes.

1. Water use efficiency and stomata

Increasing atmospheric CO_2 concentrations around the world are pushing plants to adapt their anatomy and physiology. Over the past 100 yr, atmospheric CO_2 concentrations in Massachusetts, USA have increased by over 100 parts per million and temperatures have increased by 1.8°C. A study at the Arnold Arboretum of Harvard University in Boston, Massachusetts investigated whether plant physiology and anatomy, specifically water use efficiency and stomata, changed over that same period (Miller-Rushing *et al.*, 2009). The team expected that water use efficiency would decline over time as the concentration of atmospheric CO_2 increased. Using herbarium specimens collected from trees of 24 different taxa of *Acer* (maples), *Quercus* (oaks), and *Carpinus* (hornbeams) growing on the arboretum grounds, the researchers compared leaves from contemporary specimens with those collected decades

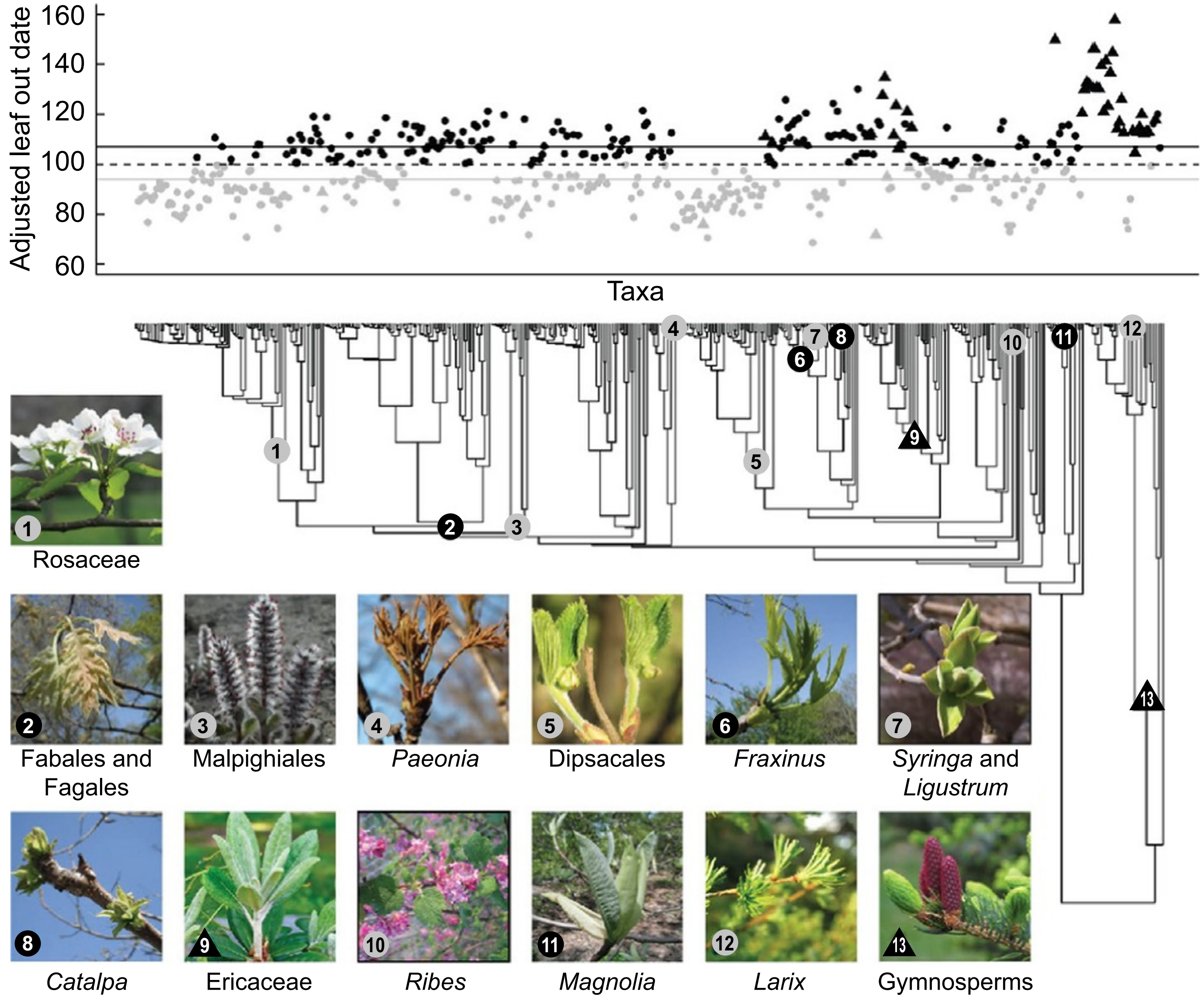

Fig. 3 Spring leaf-out times are phylogenetically conserved, meaning closely related species tend to leaf out at similar times. The dotted line shows the mean date of leaf emergence for all species in this evolutionary tree. The solid black line indicates the date after which species leaf out significantly later than the average; the gray line indicates the date before which species leaf out significantly earlier. Black and gray dots represent species that leaf out late or early, respectively. Circles are deciduous species; triangles are evergreen. The numbers set within the shapes correspond to pictured clades; for example, species above the '1' in the grey circle are Rosaceae species that are primarily deciduous and leaf out early, and the species above the '13' in the black triangle are Gymnosperms that are primarily evergreen and leaf out late. (from Panchen *et al*., 2014).

ago or even a century ago from the same individual trees. Surprisingly, they found that water use efficiency did not change over time. Stomatal density declined over time but was compensated for by a tendency for stomates to increase in size, leading to no net change in stomatal conductance and water use efficiency (Miller-Rushing *et al*., 2009). This study highlights one of many innovative ways studies can combine analyses of living collections and herbaria to investigate plant responses to climate change. However, this study did require destructive sampling of herbarium specimens for stable isotope analysis. Such destructive sampling requires careful consideration of the amount of plant tissue available and required, and the comparative value of using specimens for research now or maintaining more complete specimens for the future. In this study, the researchers used only specimens with numerous leaves, and only removed one small leaf fragment per specimen.

2. Frost damage and stem anatomy

One of the greatest challenges faced by temperate deciduous plants in adapting to a changing climate is the trade-off between leafing out early enough to obtain the greatest carbon gain and maintain a competitive advantage, and avoiding leafing out so early as to incur tissue damage from late-season frosts. Late frosts can damage delicate young leaves and flowers, and while plants might be able to produce a new flush of leaves to replace those damaged by frost, they will consume important carbon resources in the process, detracting from future growth and reproduction (Polgar & Primack, 2011; Lenz *et al.*, 2013). Similarly, plants will generally not replace flowers damaged by late frosts and will lose fitness. Using data from botanical gardens and other locations and herbarium specimens, Zohner *et al.* (2020) and Park *et al.* (2020) examined that risk of late-season frost to young leaves and flowers in scenarios of future climate, finding that risk is increasing in Europe and Asia but is declining in North America.

A research team at the Longenecker Horticultural Garden at the University of Wisconsin-Madison Arboretum documented the sensitivity of different woody species to unusual periods of winter warming associated with climate change (Ladwig *et al.*, 2019). Following 6 d of exceptionally warm weather in February 2017, they found that 45 of the 101 species they studied showed evidence of budbreak, exposing them to greater risk of frost. March frosts are common at that site and throughout the Midwest and Northeast of the United States. Many of the precocious plants in this study belonged to closely related species in Rosaceae and the genera *Fraxinus* and *Acer* (Ladwig *et al.*, 2019). In future studies, it would be useful to determine whether these more responsive species are more frost-tolerant than less responsive species.

3. Environmental triggers for the onset of spring and autumn activity

Spring leaf and flower phenology of many temperate plant species is regulated through a combination of winter chilling, spring warming, and daylength. Many plants have advanced their spring phenology with warming temperatures, but recent research suggests that these advances are beginning to decrease in strength, possibly due to unmet chilling and photoperiod requirements (Fu *et al.*, 2015). Botanical gardens provide excellent sites to investigate when, where, and for which species chilling requirements and other factors will limit plants' phenological responses to climate, and how this might affect ecological relationships within and across taxa.

For example, researchers have cut dormant twigs from plants in the living collections at some botanical gardens and brought them into the lab to examine the relative importance of factors determining spring leaf out (Fig. 4). Researchers cut the twigs at different times during the winter and early spring, placed the twigs in water in the lab, and exposed them to different conditions, such as different temperatures and light environments (Miller-Rushing & Primack, 2008; Basler & Körner, 2013; Lenz *et al.*, 2013; Laube *et al.*, 2014; Polgar *et al.*, 2014; Primack *et al.*, 2015; Flynn & Wolkovich, 2018). Using this technique, researchers have found that species vary considerably in their winter chilling requirements and the length of time needed to respond to spring forcing. These studies suggest that photoperiod requirements may be less important than winter chilling and spring forcing requirements for many species. Photoperiod requirements have been most extensively studied in *Fagus sylvatica* (European beech), a species with a relatively strong photoperiodic requirement (Zohner & Renner, 2015). Future studies at botanical gardens can explicitly test the importance of photoperiod relative to other factors for a wide variety of species.

The timing of autumn leaf senescence is difficult to study using cuttings and is regulated by a more complex set of factors than spring leaf out and flowering, but botanical gardens can still contribute to these studies. A recent study by Zani *et al.* (2020) used historical data from botanical gardens and other locations in Europe, along with shading experiments (also done at a botanical garden) and climate chamber experiments, to explore factors that regulate autumn senescence in European trees. Surprisingly, they found that plant productivity was the primary driver of leaf senescence phenology in the trees they studied, rather than temperature or other factors (Zani *et al.*, 2020). It is difficult to know how general their findings are, but botanical gardens provide ideal locations for repeating variations of their study to further investigate factors driving leaf senescence.

V. Conservation

1. Preserving rare species and genetic variation in living collections and seed banks

As the climate changes, botanical gardens play a key role in preserving living collections and seed banks to store and maintain rare plants, for later use in restorations and recovery in the wild (Schulman & Lehvävirta, 2011; Smith *et al.*, 2019; Knapp *et al.*, 2021). At an international level, these activities are coordinated by Botanic Gardens Conservation International (www.bgci.org). ArbNet similarly coordinates activities among arboreta, botanical gardens specializing in trees, shrubs, and vines (http://www.arbnet.org/). It is estimated that the world's 3000 botanical gardens protect 30% of all plant diversity and over 41% of known threatened species, including around 500 species thought to be regionally or globally extinct in the wild (Mounce *et al.*, 2017; O'Donnell & Sharrock, 2018). Roughly 350 botanic gardens maintain seed collections, which together contain 57 000 taxa (O'Donnell & Sharrock, 2018). These plants and seeds can provide material for use in restoration and reintroductions when appropriate. The value of this material is enhanced when collections include detailed records of where the parent material was collected (i.e. provenance) to ensure that there is a good match between the genotype and site conditions. This important conservation role of botanical gardens in growing and preserving rare and endangered plants will increase as more species are threatened by climate change.

Botanical garden seed collections also have special importance in facilitating the adaptation of agricultural crops to a changing climate (Smith *et al.*, 2019). Seed collectors often target wild populations of cultivated species and wild species that are closely related to cultivated species. When plants grown from these wild seeds are hybridized with crop plants, genes for traits that promote resilience to climate change, such as drought tolerance or insect resistance, may be transferred to cultivated crops, and may increase crop yields under future environmental change.

2. Ecology of rare species

Botanical gardens offer the opportunity to investigate the responses of rare species to climate change by measuring their

Fig. 4 Dormant twigs can be used for laboratory experiments to test the environmental determinants of plant phenology. (a) Dormant twigs being collected for an experiment. (b) Dormant twigs in controlled conditions. (c) Dormant twigs in a lab setting with natural and supplemental lighting. (d) Extended day length led to earlier leaf out in American beech.

performance in different climates across networks of botanical gardens. For example, one research team planted 35 plant species at five botanical gardens located at different altitudes and climates in Switzerland (Vincent *et al.*, 2020). Of these species, 24 were locally distributed and rare in Switzerland, while the other 11 species were common. The team found that rare species had lower probabilities of surviving and lower production of biomass in comparison with common species. Survival of rare species was diminished at botanical gardens with climates that were the most different from the climates where the species naturally occur. This study demonstrates that rare species may be more susceptible to the damaging effects of a changing climate than common species.

3. Managed relocation

Similar experiments can inform the potential use of managed relocation (also known as assisted migration or assisted colonization), in which individuals of rare and endangered species are introduced outside their current range in response to a changing climate (Vitt *et al.*, 2010; Ali & Trevedi, 2011). This may be necessary because most plant species are not able to migrate fast enough to track the pace of the changing climate. Smith *et al.* (2014) proposed a plan in which botanical gardens could 'chaperone' plants as a part of managed relocation efforts by moving species outside their historic ranges, testing new locations where they may be able to persist, developing methods to help species survive translocation, and screening species for potential invasiveness, pests, diseases, and hybridization. Some gardens are already doing this (Van der Veken *et al.*, 2008). For example, a network of gardens in Finland, Norway, and Estonia tested translocations of northern and southern varieties of Siberian primrose (*Primula nutans* ssp. *Finmarchica*) (Hällfors *et al.*, 2020), a species protected in Europe. They found that climate change is already harming the performance in the species' current habitats (especially northern varieties), that plants performed best at northern locations, and that managed relocation may be a necessary and appropriate strategy to help the species persist.

Botanical gardens, such as the Royal Botanic Gardens Victoria, Australia, are incorporating managed relocation-type methods into their landscape plans – that is, they are planning to transition their living collections to species that are likely to succeed in future climate conditions (Royal Botanic Gardens Board Victoria, 2016; Kendal & Farrar, 2017). In 2018, a group of botanical gardens formed the Climate Change Alliance of Botanic Gardens to promote collective preparedness for climate change in living botanical collections (CCABC, 2018). As a part of these efforts, botanical gardens might consider starting or modifying plant breeding programs for rare and endangered species to help them adapt to climate change as part of managed relocation programs.

4. Changes in nonplant species and abiotic conditions

Botanical gardens have also played a central role in the past for producing other types of biological data which can be used to investigate the impacts of climate change on conservation. For example, at the Munich Botanical Garden in Germany, researchers have studied the bee fauna over a 20-yr period (Hofmann *et al.*, 2018). Among the new species recorded over time at the garden, most were warm-adapted species, suggesting that climate change is impacting the bee fauna at this site. It is likely that other botanical gardens are collecting similar data describing changes in insects, fungi, and soil conditions. Botanical gardens have a special role to play as early warning systems to detect emerging plant pests and diseases, many of which are shifting their range to due climate change (Smith *et al.*, 2019).

VI. Public engagement

Together, botanical gardens attract more than 500 million visitors each year and have thousands of dedicated volunteers (Miller *et al.*, 2020). Visitors are attracted to gardens because of their beauty, and also because people want to learn about plants (Williams *et al.*, 2015). Thus, one of the most important roles of botanical gardens is to promote learning and engagement related to the value of plants and the need to conserve biological diversity (Miller *et al.*, 2020). Climate change is a critical part of that learning and engagement, given its influence on plant ecology and conservation and on the operations of botanical gardens.

1. Public education programs and inclusion

Botanical gardens engage visitors in free-choice learning and host student groups during field trips. Evidence shows that botanical gardens have positive impacts on knowledge and environmental attitudes in student groups and visitors, including on topics specifically related to plants and climate change (Sellmann & Bogner, 2013; Sellmann, 2014; Williams *et al.*, 2015; Eberbach & Crowley, 2017). Botanical gardens are making efforts to grow and improve these education programs and to engage groups that have been previously underserved by their environmental education programs (Dodd & Jones, 2010; Suárez-López & Eugenio, 2018). These efforts include, for example, engaging such audiences in projects related to climate change, biodiversity conservation, edible gardening, enhancing food security, and sharing personal stories about the value of trees to local communities (Vergou & Willison, 2013, 2016).

2. Community and citizen science

In recent years, botanical gardens have increased their engagement of the public in monitoring the effects of climate change on plants in their living collections as a part of community and citizen science projects (Miller & Derewnicka, 2019; Fig. 5). Most of these projects focus on phenology and encourage volunteers to record stages of plant life cycles that can be seen throughout the growing season, including leaf out, flowering, fruiting, and leaf senescence (Chmielewski *et al.*, 2013; Havens & Henderson, 2013). Some gardens tie these observations to past records to help people see how phenology has changed over time. In most cases, these observations follow established protocols, which allow data from different gardens (and other locations) to be combined, informing studies of phenological events over broad geographic areas (e.g. Chmielewski *et al.*, 2013; Denny *et al.*, 2014). The availability of smartphone apps – like Nature's Notebook, iNaturalist, and custom apps for specific gardens – has made it easier for many people to participate in these programs.

In addition to phenology, botanical gardens are engaging the public in studies of the impacts of climate change on pollination, monitoring rare plant populations, the digitization of herbarium specimens used in climate change research, and the documentation of traits in digitized specimens (Havens *et al.*, 2012; Willis *et al.*, 2017).

3. Communicating and engaging the public in climate change adaptation

On a practical level botanical gardens are adjusting their operations and the management of their collections to the changing climate conditions at the gardens (Royal Botanic Gardens Board Victoria, 2016; CCABC, 2018). These changes provide an excellent opportunity to communicate local stories of climate change adaptation to the public and to engage the public in helping to

Fig. 5 Methods for monitoring phenology, clockwise from top left: a drone being launched to monitor leaf-out phenology at the Arnold Arboretum; volunteers at the Royal Botanical Garden Edinburgh evaluating plant phenology; students planting a phenology garden at their school, with support from the Chicago Botanical Garden; students learning to monitor phenology at the Chicago Botanical Garden.

implement some of the changes (Royal Botanic Gardens Board Victoria, 2016; Miller *et al.*, 2020). These stories might involve how winter conditions are now mild enough to grow certain species that were formerly killed by deep freezing, or how other species that used to be hardy are now harmed by summer heat waves and drought.

VII. Recommendations for future research and engagement

1. Broaden geographic distribution of climate change research and engagement

Climate change research in botanical gardens has been disproportionately concentrated in Europe and North America. Indeed, botanical gardens are disproportionately concentrated on these two continents (Fig. 1). Broadening the geographic distribution of climate change research at gardens will improve our understanding of how a greater diversity of species respond to a greater variety of climate conditions. We are still gaining appreciation for geographic variation even in relatively well-studied Europe and North America (e.g. Renner & Zohner, 2018). The variation is likely to be much greater as we study species from tropical rain forests, tropical dry forests, savannahs, deserts, and other ecosystems that have been understudied in terms of their responses to climate change.

We suggest that research at botanical gardens in the Global South should be better highlighted in the literature – for example, by recruiting representation into leadership of relevant organizations and by journals recruiting more diverse key staff and researchers from these institutions as editors, reviewers, and authors, and by organizing special issues (Primack *et al.*, 2019; Maas *et al.*, 2021; Pettorelli *et al.*, 2021). Botanical gardens in the Global North could also partner with gardens in the Global South to encourage and support the establishment of climate change research in regions that are understudied, underfunded, and disproportionately impacted by climate change. Networks of botanical gardens could also make additional efforts to include gardens from underrepresented regions.

2. Continued monitoring of phenology and other traits and digitization of historical records

Long-term monitoring of plants in botanical gardens – for example phenology, anatomy, and other traits – and the collection of herbarium specimens from plants in living collections have added critical insights into our understanding of plant responses to climate change (e.g. Panchen *et al.*, 2015; Zohner & Renner, 2017; Gallinat *et al.*, 2018; Hällfors *et al.*, 2020; Zohner *et al.*, 2020). Some of these monitoring approaches require little technology and can be carried out with modest but consistent effort. Many simply require observers to walk around gardens' grounds and record observations on paper data sheets, in field books, or on smartphone apps. Some observations can be made once a year, whereas phenology is generally best recorded once or twice per week. In some cases, increased efforts can help capture additional measures of plant performance, such as flowering intensity, production of fruits and seed, and growth rate. We strongly urge botanical gardens to continue to expand these programs to include more species, a wider range of traits, and a greater number and diversity of observers. For example, coring living trees and collecting wood samples could complement historical trait information held in herbarium specimens, which generally focus on leaves and flowers. New observations in extreme climate conditions – including heat waves, drought, flooding, and lack of winter snowpack – will likely yield more important insights. We also recommend that botanical gardens continue to digitize their past records, including records of when plants were planted and died, and make their records available online so that they can be used in larger regional and international comparisons (Blagoderov *et al.*, 2012; Soltis, 2017; Willis *et al.*, 2017; Younis *et al.*, 2018; Pearson *et al.*, 2020).

3. More comprehensive and integrated studies of phenology

Previous studies have focused primarily on one phenological stage at a time. However, successive phenological stages are linked through anatomical, physiological and developmental processes (Primack, 1987; Ettinger *et al.*, 2018; Gougherty & Gougherty, 2018; Diggle & Mulder, 2019). As climate changes, it will be valuable to collect new phenology data on multiple phenophases in the same plants and to re-analyze existing data sets to determine how these linkages will change, and if particular phenological stages will respond differently to climate change. For example, if flowering times are more responsive to climate change than fruiting times, then there will be a longer time available for fruit development, with implications for physiological ecology and plant–herbivore interactions. Earlier leaf-out times might be linked to earlier leaf senescence times if leaves have finite lifetimes (Keenan & Richardson, 2015).

When expanding phenology monitoring, leaf out, flowering, and fruit maturation are straightforward to assess in the field. Leaf senescence is more difficult, because of variability among species. However, gardens have developed standard methods, such as recording leaf senescence when approximately half of the leaves on the plant have either fallen off or changed color (Panchen *et al.*, 2015). Such visual evaluations of color change correspond very closely to measurements done with a Chl meter (Gallinat *et al.*, 2013).

Additionally, we recommend that botanical gardens expand their phenology research to include more herbaceous plants. Most phenology studies at botanical gardens have examined woody plants. There is a surprising paucity of studies on the leaf-out, leaf senescence, and fruiting times of herbaceous species at botanical gardens, even though they represent the greatest diversity of vascular plants in terrestrial ecosystems and are crucial for providing food for insects and other species. The newly launched PhenObs network of botanical gardens, based in Germany, aims to close this gap in our knowledge and provide standard methods for monitoring phenology (e.g. first leaf out, which can be difficult) of herbaceous plants in botanical gardens (Nordt *et al.*, 2021). The Botanical Garden at Charles University in Prague has shown the way forward in this field, demonstrating that differences among herbaceous species in light levels and mature plant heights influence plant growth phenology (Huang *et al.*, 2018; Schnablová *et al.*, 2020).

4. Assess frost tolerance across a variety of species

Frost damage can limit species ranges (native and nonnative) and can severely harm crop and horticultural species. Studies have shown that the risk of frost is changing differently in different locations – declining in North America, but increasing in Europe and Asia – as a result of climate change (Park *et al.*, 2020; Zohner *et al.*, 2020). However, these results are based only on trends in phenology and the dates of last frost in the spring; they lack data on frost tolerance for different species that is important for assessing frost risk. Monitoring of frost damage to plants growing at botanical gardens, where plants are often growing in conditions beyond their native ranges, could give insights into traits associated with different frost tolerances, informing estimates of risk and potential shifts in species ranges as climate conditions change.

For example, recent experimental research has suggested that woody species of the Swiss Alps that leaf out earlier in the spring have greater ability to tolerate mild frost events than species that leaf out later (Lenz *et al.*, 2013). Plant species with smaller vessel elements and diffuse porous stem anatomy tend to leaf out earlier than species with larger vessel elements and with ring porous stem anatomy (Panchen *et al.*, 2014), presumably because species with smaller vessel elements are more resistant to freeze–thaw cycles (Miller-Rushing & Primack, 2008).

There are several ways researchers can examine the frost tolerance of young growth of plants at botanical gardens, all of which can take advantage of the concentration of diverse plant species growing at gardens. One method is to examine frost damage to young leaves or flowers after an early, warm spring followed by a late, hard frost (as in Augspurger, 2013). This method has the advantage of reflecting natural conditions, but researchers are unable to predict when these conditions will occur, nor can they control the ambient freezing temperature, which would allow comparisons of frost severity at different temperatures. Monitoring frost damage at several botanical gardens in different climate conditions can help alleviate some of these challenges because freezing temperatures and the time between budburst and frost would naturally vary across locations. A second method involves collecting newly leafed-out twigs from plants in a botanical garden or cutting dormant twigs and forcing leaf-out in the lab. Researchers can then experimentally expose the young leaves to different freezing temperatures and record the extent of the damage, either by observing visible damage or by recording the leakage of cellular fluids into solution (Lenz *et al*., 2013; Primack *et al*., 2015). However, it is unknown whether young leaves on cut twigs will have the same freezing properties as young leaves growing on intact plants outside.

5. Carbon budgets, photosynthesis, and the light environment

New studies suggest that climate change-driven shifts in phenology are significantly altering the light environments and carbon budgets of understory wildflowers and shrubs, which rely on periods of high light and favorable conditions for photosynthesis when trees have few or no leaves (Fridley, 2012; Heberling *et al*., 2019). Similarly, plants show differing growth responses to rising levels of CO_2 and nitrogen deposition (Dukes & Mooney, 1999; Luo *et al*., 2004). These studies have used historical observations and experimental gardens set up at field locations. Using such approaches at botanical gardens could dramatically improve our understanding of these phenomena. For example, Fridley (2012) grew 43 native shrub and vine species alongside 30 nonnative invasive shrub and vine species in an experimental garden in Syracuse, NY, USA. The species were matched so that the native and invasive species were in the same families and genera. Nonnative species retained their leaves on average four weeks later in the autumn than did native species. This increased autumn carbon budget is a likely a key factor in the competitive success of these invasive species. Further experiments of this type could be conducted at botanical gardens, making use of their diverse living collections, common growing conditions, and range of species' geographic origins. Coordinated experiments across networks of botanical gardens could allow researchers to investigate species growing under a range of climatic conditions.

6. Drones and fixed cameras

Drones and fixed digital cameras have the potential to contribute to monitoring and research at botanical gardens. Drones allow operators to survey individual trees growing in open areas (Scher *et al*., 2019), and have the potential to record when each plant is leafing out and flowering, and to monitor the structure, photosynthetic rate, and temperature of trees (Fig. 5a). In just a few hours, a drone could fly over hundreds or thousands of plants and take detailed digital images of all of the plants. Using images from successive days and weeks, it might be possible to determine the detailed phenology of all of the plants in a collection, though matching plants from one flight to the next remains a significant challenge. Similarly, fixed digital cameras have the potential to automate observations of flowering and leafing out (Brown *et al*., 2016), though each camera records only a single view.

7. Increased communication and public outreach

We recommend that botanical gardens continue to communicate their efforts to preserve species threatened by climate change and actions they are taking to adapt their gardens as climate conditions change. For example, gardens could prominently display species that are threatened by climate change in the wild. Additionally, they could collect and display species that are not currently hardy in their climate zones but will likely be hardy in coming years as the climate continues to warm (Friedman *et al*., 2016). For example, in Boston, camellias (*Camellia* sp.), crepe myrtles (*Lagerstroemia* sp.) and fig trees (*Ficus carica*) are not generally hardy, but will likely be in coming decades. Botanical gardens could feature such species on their grounds, using them to highlight the effects of climate change, and noting when they survive winters, or are killed by cold weather. Botanical gardens could take such displays one step further by growing cold tolerant and cold intolerant varieties of these species next to each other, to further demonstrate different tolerances to cold. Similarly, botanical gardens could have displays of plants that are not doing well or have died due to heat waves and droughts (Hultine *et al*., 2016).

In recent years, botanical gardens have increased the extent to which they invest in engaging underserved audiences (Dodd & Jones, 2010). It is increasingly recognized that diversity, equity, and inclusion are critical for climate change science, engagement, and action (Patz *et al*., 2005; Fischer, 2009; Mason & Rigg, 2019). Botanical gardens are situated to engage with underserved audiences – including children, low-income groups, and racial and ethnic minorities – in meaningful discussions and actions (including science) related to climate change that are relevant to these communities (Vergou & Willison, 2016). Some gardens, such as the Chicago Botanic Garden, have long-running and successful programs addressing climate change by working with existing community groups and leaders (Hatchett *et al*., 2015; http://www.connectcca.org/). These efforts should continue to grow and advance climate change science and engagement.

VIII. Conclusion

Climate change has emerged as one of the greatest challenges faced by human society, and the urgency of this challenge continues to grow as the climate continues to warm. Botanical gardens have a special role to play in investigating climate change because they have large collections of living plants that can be used for scientific investigations, they have botanical expertise, and they are places where the public comes to learn about plants. Their impacts on climate change research and climate change have already been substantial. New technologies and initiatives at botanical gardens around the world are providing new research opportunities. We encourage botanical garden staff, researchers, and science communicators to continue to work together to advance climate change-related science, conservation, and public engagement.

Acknowledgements

Kayri Havens, Chuck Cannon, Mason Heberling, Tara Miller, and four anonymous reviewers provided helpful comments. Funding was provided by a grant from the OPUS program of the U.S. National Science Foundation (NSF DEB 1950447). The findings and conclusions presented in this paper are those of the authors and do not necessarily reflect those of the US Government or the US Department of the Interior.

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