Received: 26 April 2024 | Accepted: 9 July 2024

DOI: 10.1002/ajb2.16394

ON THE NATURE OF THINGS

American Journal of Botany

Living collections: Biodiversity cultivated at public gardens has the power to connect ecological questions and evolutionary context

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KEYWORDS
botanical garden, common garden, microevolution, phylogeny

Combining ecological questions with evolutionary context generates novel insight into both ecology and evolution. However, our ability to draw broad inferences can be limited by the taxonomic diversity present within and across species at a site. Public gardens (including botanical gardens and arboreta) may focus solely on aesthetics in developing their gardens, but some public gardens include scientific inquiry and conservation at the core of their missions (Hohn, 2022). These scientifically oriented public gardens follow community standards of excellence (Hohn, 2022) to provide unique access to curated plant collections specifically designed to gather high levels of biodiversity, both among and within species, at a single geographic location. These research-grade collections include long-lived species cared for over many decades. Such public gardens have long histories of conducting and supporting research harnessing the power inherent in these diverse collections, including explorations of systematics, ecophysiology, and ecology. By bringing together species, as well as individuals within species, from across broad spatial ranges into a single site, these collections offer living repositories of diversity ripe for scientific exploration as de facto common gardens (Dosmann, 2006; Dosmann and Groover, 2012; Primack et al., 2021).

PHYLOGENETIC APPROACHES

The biodiversity curated by public gardens can offer a unique context for addressing questions at the intersection of ecology and evolution, such as *how does phylogenetic history shape plant trait evolution?* For example, Mason et al. (2020) explored seasonal trait shifts across 25 species of *Cornus* at the Arnold Arboretum (Boston, Massachusetts, USA) to ask whether there are tradeoffs among ecophysiological traits and how those traits correlate with home environment. They measured traits such as leaf chlorophyll content and leaf water content. By measuring plant traits across many species, they answered questions about ecophysiological trait evolution within a comparative phylogenetic framework. By doing so in a common garden, they controlled for much of the environmental variation that would otherwise confound a study across so many species, that occur in different habitats and locations in their native ranges. Their new analytical approaches simultaneously incorporated phylogenetic methods and within-species variation over time (Mason et al., 2020). With this comparison, they demonstrated that traditional phylogenetic comparative approaches, which analyze a single trait mean per species, might come to erroneous conclusions about trait–trait correlations. For example, leaf nitrogen mostly declines through the growing season in *Cornus*, leading to changes in sign of correlations across the season (Mason et al., 2020).

Plant–soil interactions are another growing area of research that stands to benefit from the diverse woody plant collections maintained by public gardens. The longevity of plants within public gardens gives them the time to drive changes in the soil microbial community within their rhizosphere. This creates an opportunity to use public gardens as a source for soils that have been influenced by plants (e.g., Liu et al., 2021; Figure 1), in the vein of plant–soil feedback experiments (Bever et al., 2010). Furthermore, the diversity of species within a single site uniquely allows for comparisons of microbiomes across plant species and phylogeny (Medeiros et al., 2022), addressing the question of whether close relatives share similar microbiomes. Botanical gardens can allow researchers to ask *are close relatives similar in their interactions with soil pathogens?* Liu et al. (2021) used 14 species of *Rhododendron* from the Holden Arboretum (Kirtland, Ohio, USA) to ask whether soil microbial communities modify pathogen effects. They found that live soil biota collected from the Holden Arboretum suppress plant biomass, but enhance survival in the presence of a soil pathogen (Figure 1) in a factorial greenhouse experiment. Thus, ecological benefits of soil microbes occurred across multiple evolutionary lineages.

WITHIN-SPECIES VARIATION

Natural selection acts on within-species trait variation, and understanding evolutionary dynamics has become increasingly important as climates shift. As such, data on within-species trait variation are critical for answering questions such as *how variable is the niche within species? And does local adaptation influence success in a novel range?* At public gardens that prioritize scientific and conservation use of collections, within-species variation has long been actively

FIGURE 1 (A) *Rhododendron calendulaceum* at Holden Arboretum (Kirtland, Ohio, USA) with pollination bags on flower buds, as well as (B) Noah Clayton hand pollinating these flowers. This technique uses genotypes from the gardens to create species-true seeds for experimentation (e.g., Liu et al. 2021). (C) Plants and (D) flower of *Primula nutans* ssp. *finmarchica* planted into common garden experiments across five botanical gardens (Hällfors et al., 2020). Photo credits: (A, B), Jean H. Burns, (C, D) Maria Hällfors.

prioritized in collections planning for ex situ conservation (Griffith et al., 2015). Scientifically minded public gardens also record plant provenance, or the origin of individuals within the collections, and intentionally house replicates for each species and/or population. Replicates are also often shared across public gardens, allowing researchers to take advantage of multiple representatives of the same species, or even the same genotype, growing under different climate conditions. While many research studies may acquire commercially procured plants and seed, which typically lack such detail on origin and dedicated access to within-species diversity, within-species diversity can be key to addressing pressing ecological questions. For example, studies of the niche are critical to predicting future ranges, but there can be considerable within-species variation in the niche. Climate models at the provenance (within-species) scale better-predicted plant survival than species-level climatic models, calculated from an average across the native range (Thomas et al., 2022), for a data set from the Missouri Botanical Garden (St. Louis, Missouri, USA). In other words, taking species level averages can be inadequate to answer many research questions such as predicting future species ranges, because of within-species variation due to local adaptation.

Replication within species is key to understanding local adaptation and niche evolution but is especially difficult to achieve in long-lived woody species. This is where public gardens excel. Considerable genotypic replication, both within gardens and across gardens, is often in place, or might be added to experimental plantings within the garden. Working with public garden curators to obtain their collections policy and understand the strengths of their collections, as well as engaging in discussions to determine which species and/or collections will best align with research needs, is key because gardens have information about site-level variation within their gardens and can guide researchers toward species, plantings, or even other gardens that are most appropriate for the research question.

Planting location can be considered a complicating factor across public gardens, but as in other types of planting arrays, sampling design and statistical techniques can be used to control for variation because of environmental covariates, location, or individual. For example, for research on phenology, Panchen et al. (2014) used a mathematical approach to account for planting location by calculating an adjusted leaf-out date for each species, such that all sites had the same mean leaf-out date. They demonstrated that site influenced the average time of leaf out, but that the rank order among species was generally the same across sites (Panchen et al., 2014). Some studies have also examined individual plants over time, replicated across species, or controlled for individual using the differences over time calculated on a per individual basis (Miller-Rushing et al., 2009). This allowed them to address effects of shifting climate on plant physiology across 100 years, demonstrating that intrinsic water use efficiency did not change over time for individual trees, although stomatal density declined and guard cell length increased (Miller-Rushing et al., 2009).

Employing random effects in statistical models is also valuable, if underutilized, in the context of public garden studies. For example, stratified random sampling can account for standing variation (Arnab, 2017): garden beds and species can be defined as strata to structure allocation of species evenly across garden beds, followed by use of a random number generator to choose individual plants within beds for experimental replicates (Medeiros et al., 2022). In another example, Hällfors et al. (2020) tested for local adaptation by planting within-species replicates at five botanical gardens and compared models with and without random plot effects within gardens (Figure 1). Their common garden approach across multiple gardens demonstrated maladaptation to current climate conditions, likely to be exacerbated by climate change (Hällfors et al., 2020). Because public gardens often include plantings outside the natural range, they are critical in such situations, where climate change might lead to maladaptation to local climate.

CONCLUSIONS

Plant collections at public gardens are uniquely suited to exploring questions at the intersection of ecology and evolution, and calls to use botanical gardens more extensively for research date back decades (e.g., Dosmann, 2006). The historical focus of public gardens on clade-based sampling provides unprecedented collections of biodiversity within related groups of species (e.g., Cycads at Montgomery Botanical Center, Coral Gables, Florida, USA [Griffith et al., 2015]). More research is needed to address questions such as (1) how could *ex situ* conservation be more optimally designed to capture genetic diversity within species and ensure species persistence (Hoban et al., 2020), and (2) how has evolutionary history (phylogeny) shaped among-species variation in conservation status? Additionally, collections with provenance information within species can be used to characterize local adaptation (Thomas et al., 2022). Using materials such as seeds and cuttings from public garden collections can make use of provenance information in manipulative experiments. Collections housed within public gardens provide a valuable resource to help answer questions such as *how has evolution shaped species ability to respond to novel future climates, pathogens, or other factors?*

AUTHOR CONTRIBUTIONS

The authors contributed equally to conceptualizing, writing, and editing the manuscript.

ACKNOWLEDGMENTS

The authors thank the National Science Foundation for funding provided to J.H.B. during the writing of this paper (DEB 2217714). The authors also thank two anonymous reviewers and Pamela Diggle for constructive comments on the manuscript.

DATA AVAILABILITY STATEMENT

No new data were generated for this essay.

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How to cite this article: Burns J. H., K. L.Stuble, and J. S. Medeiros. 2024. Living collections: Biodiversity cultivated at public gardens has the power to connect ecological questions and evolutionary context. *American Journal of Botany* 111(9): e16394. https://doi.org/10.1002/ajb2.16394