TOWARD THE METACOLLECTION:
Coordinating conservation collections to safeguard plant diversity

Botanic gardens hold amazing plant diversity, such as these palms at Montgomery Botanical Center – connecting and coordinating living collections together finds new benefits for conservation.

THE LARGEST FORCE FOR PLANT CONSERVATION

Worldwide, over 3,000 botanic gardens maintain at least one-third of all known plant diversity. The collective conservation power of botanic gardens is essential to stop plant extinction. Networks allow gardens to coordinate efforts to save endangered plants. The global web of botanic gardens is the world's largest force for plant conservation – as long as it is well coordinated!

A single plant grown at a garden can contribute to conservation, but it takes many plants to capture sufficient genetic diversity and thus truly safeguard species for the long term. So, gardens might ask, "Which plants should I grow, and how many?"

Garden conservation science applied to real-world scenarios shows how vital our garden networks are to safeguarding plant biodiversity. A close look at the genetics of collections of exceptional plant species[1] – and how they are networked among multiple botanic gardens – brings new insight into how gardens are doing at present and how they can do better in the future.

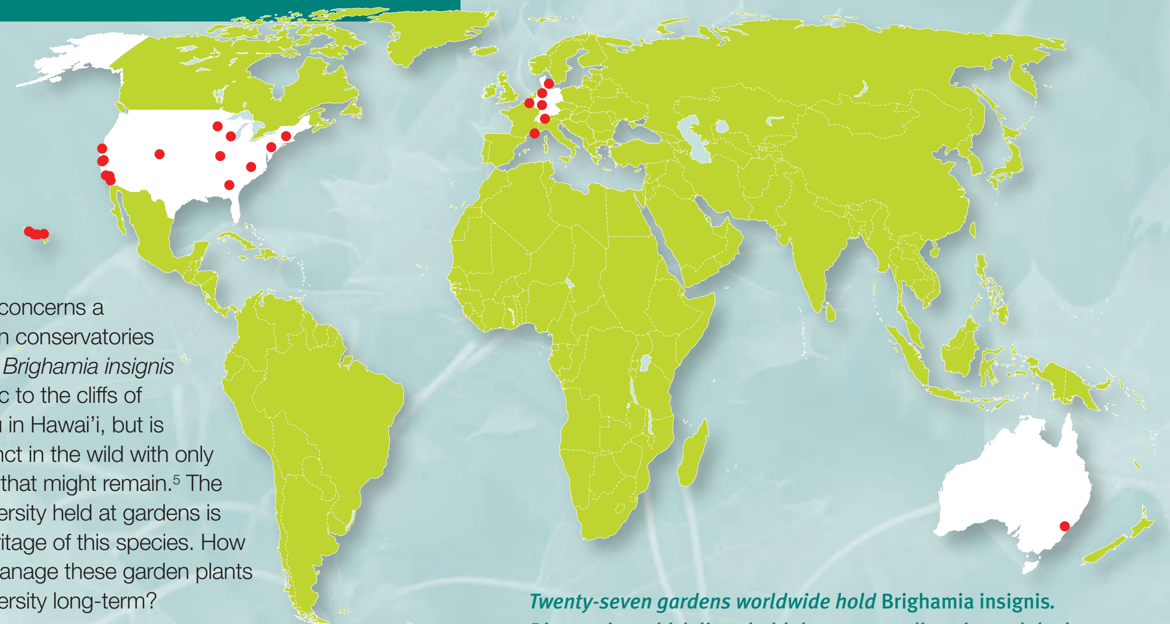
Here we present recent discoveries and recommendations for capturing and maintaining diversity in a plant collection, and describe how to leverage a network of such collections to advance conservation. We introduce and illustrate the METACOLLECTION concept, with examples at different scales, provide an overview of sampling strategy for capturing diversity, and provide examples of how gardens can leverage methods developed by the zoo community to collectively manage conservation collections.

GARDENS: WORK TOGETHER!

Holding a critical plant collection at a single garden is no longer the best practice. As per the old adage, ***the best way to keep a plant is to give it away*** – hence gardens distribute risk by distributing plants. Something as minor as an irrigation break or a change in management puts garden plants at risk, not to mention the havoc a wildfire or hurricane can bring! Keeping those plants at multiple locations reduces the likelihood of loss. Thus, the metacollection is the best way forward for conservation collections. Metacollections assure necessary redundancy, but also maintain diversity, minimize genetic drift from random losses, and reduce inbreeding.

METACOLLECTION (n.). The combined holdings of a group of collections. For gardens, metacollections are envisioned as common resources held by separate institutions but stewarded collaboratively for research and conservation purposes. Networking multiple collections into a single metacollection increases potential coverage within a group, allows broader access to greater diversity, dilutes risk of loss, and can reduce maintenance costs. The American Public Gardens Association's Multisite Collections[2], BGCI's Global Conservation Consortia[3] and the CPC National Collection[4] are established examples of metacollections. Like any collection, a metacollection can be of any scope or taxonomic level.

Example: *Brighamia insignis*



Twenty-seven gardens worldwide hold Brighamia insignis. *Discovering which lines hold the greatest diversity and the best potential to sustain diversity allows these gardens to carefully choose which plants to propagate and exchange.*

Our first example concerns a beloved treasure in conservatories around the world: *Brighamia insignis* was once endemic to the cliffs of Kaua'i and Ni'ihau in Hawai'i, but is now possibly extinct in the wild with only a single individual that might remain.[5] The extant genetic diversity held at gardens is now the entire heritage of this species. How should we best manage these garden plants to sustain that diversity long-term?

Review of collections found the species was kept at 27 gardens in Hawai'i, the mainland U.S., Europe, and Australia. Careful study of the extant diversity from both genetic and pedigree perspectives provided curators at these botanic gardens an informed view of which lines to propagate, exchange, and cross among collections, and which lines may be overrepresented. For example, a particular maternal line may need to be propagated more than others in order to balance genetic diversity across collections.

Brighamia insignis *requires expert horticultural care to survive, as it is pollinator-dependent, self-incompatible and natural pollinators have never been documented.[6] Decisions about which plants to breed are informed by new applications adapted from the zoo community.*

Lesson learned: Leverage the shared heritage of all collections to advance conservation! While many gardens held *B. insignis* for a variety of purposes, genetic data allowed gardens to contribute to better conservation planning for survival of the species. Coordination across the metacollection of *B. insignis* is essential to its conservation.

Seana Walsh/National Tropical Botanical Garden

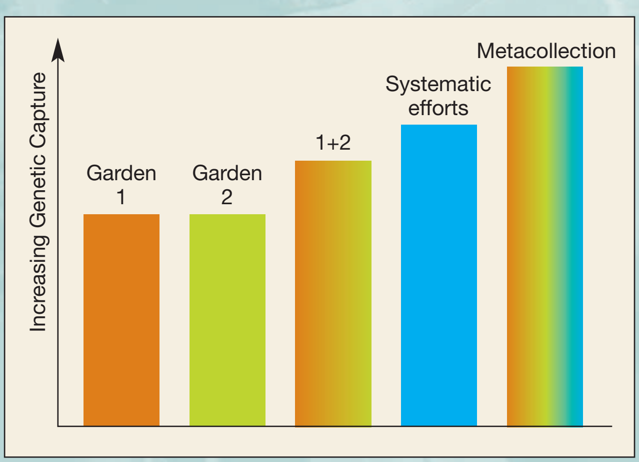
Example: *Pseudophoenix ekmanii*

This endangered palm is limited to a very small area of southwestern Dominican Republic, in Parque Nacional Jaragua. Sought by poachers, the conservation plan for this slow-growing charismatic icon includes off-site reserves – *ex situ* collections – to augment the declining wild diversity.[7] The largest botanic garden collections were located and contacted, and provided access for genetic study. A collaborative, systematic collecting effort was further coordinated to augment these legacy collections with new material from the wild population.

Comparing the genetics of these collections with the genetic diversity of remaining wild palms shows the value of metacollections: (1) On their own, legacy collections from Jardin Nacional Rafael Moscoso and Montgomery Botanical Center capture a significant, but incomplete amount of genetic diversity. (2) Combining these two collections improves the conservation value. (3) A systematic, collaborative effort by both gardens to capture genetic diversity through deliberate field collections performed better than both legacy collections together. (4) The best genetic capture comes from the global international metacollection: all collections combined into a single pool.

Pseudophoenix ekmanii is critically threatened by sap poachers, which cut the growing meristem to extract sap before the palm has a chance to flower. This Guardabosques sees much evidence for this illegal and lethal exploitation.

Lesson learned: The whole is greater than the sum of its parts! Even two gardens working together is more effective than going it alone. Drawing from both legacy collections, augmenting these with additional field collections, and combining all of these into a single metacollection best serve the conservation needs of *Pseudophoenix ekmanii*.



Capture of Pseudophoenix ekmanii genetic diversity by collection cohort. Combining efforts of multiple collections and using deliberately structured collecting protocols produces the best capture of genetic diversity.

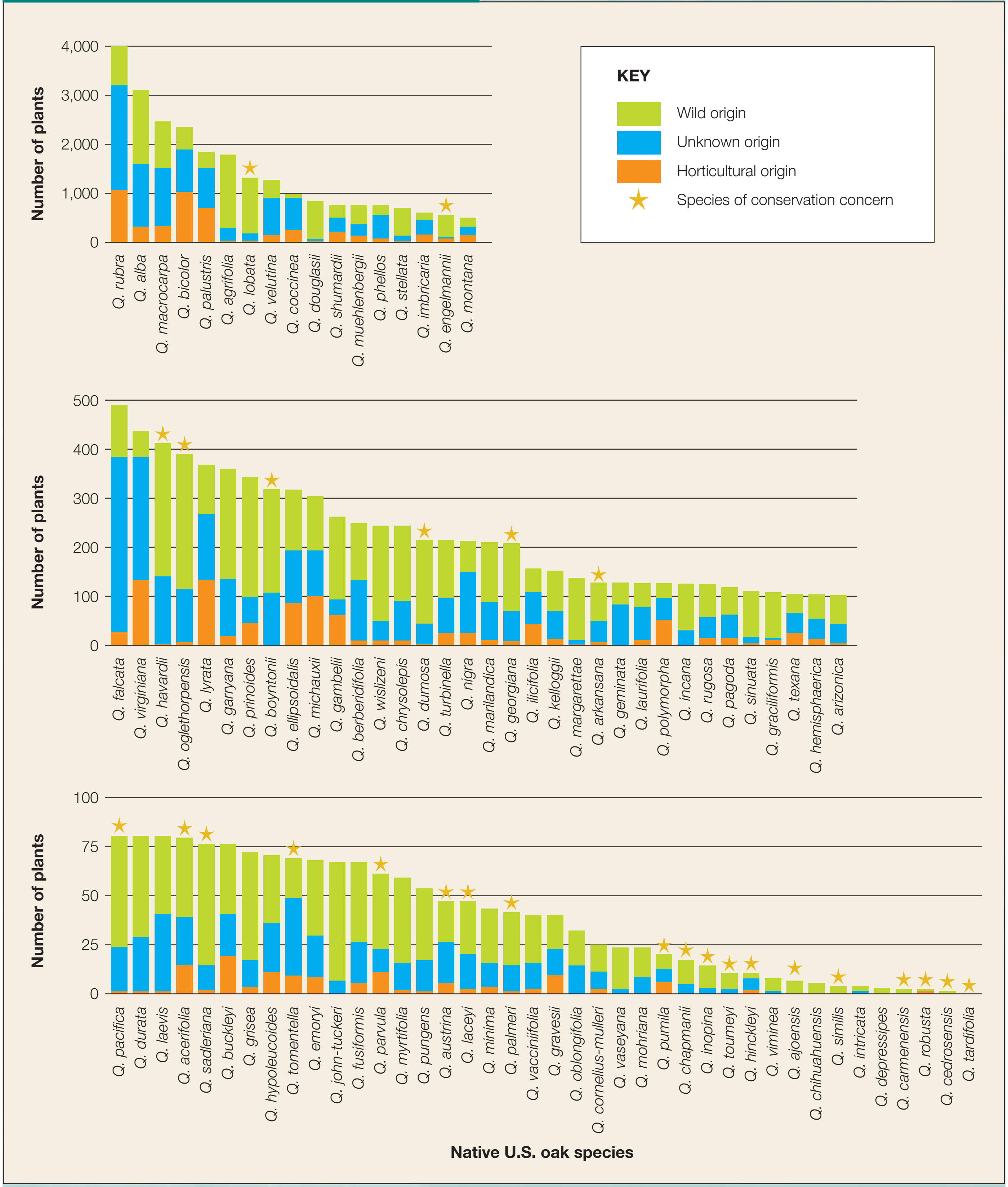
Example: *Quercus*

The two previous examples highlighted areas where metacollections advance conservation objectives for a single species. Moving the frame out to a genus, recent study of botanic garden holdings of US oaks – *Quercus* – highlights additional benefits of the metacollection approach.[8] Survey and analysis of the combined *Quercus* holdings of 162 gardens worldwide demonstrated areas of greatest need.

Of the 91 species of native US oaks, only one was not in protective cultivation (see next page). But, species of greatest conservation concern had the fewest plants at the fewest gardens, showing a clear path forward for future collections development: focus on the most threatened species. Note that 25 oak species have fewer than 50 trees in collections (a recognized minimum conservation collection size) and 14 of these species are of conservation concern. There is a long way to go to ensure the most threatened tree species are maintained in viable, genetically-diverse garden metacollections. Considering the global holdings of *Quercus* as a single metacollection allows insight on priorities for securing species of conservation concern.

Lesson learned: Connecting global collection resources provides insight on local conservation priorities. The pooled metacollection inventory highlighted which rare local species require additional representation in gardens. A clear path forward can be found through broad assessment with a metacollection approach.

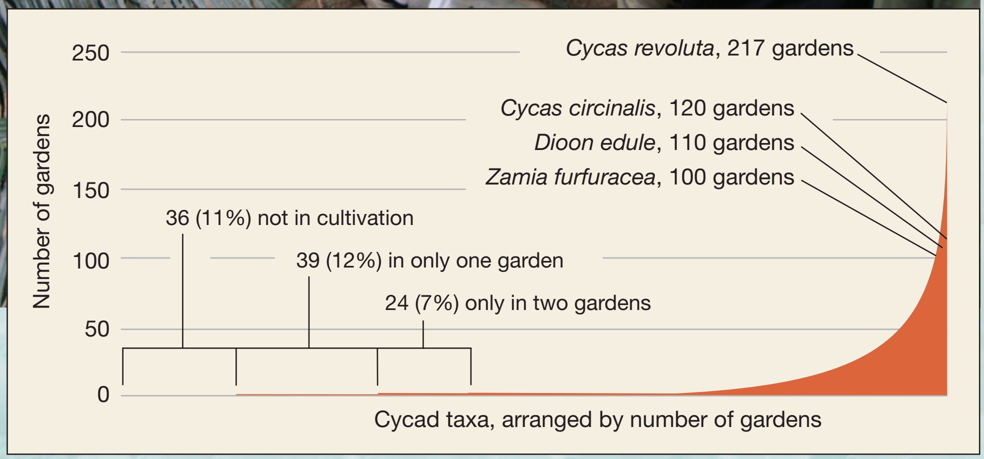
Example: ***Quercus*** **(continued)**



Considering global garden holdings of US oaks as a pooled resource gave insight for planning future conservation measures, by showing a correlation between conservation concern and lack of ex situ *collections – note the large difference in vertical scale between panels.*[8]

Example: **Cycads**

Shenzhen Fairylake Botanical Garden, home of the Chinese National Cycad Conservation Center, joined with an international group of cycad collections to found the Botanic Gardens Cycad Collections Consortium.



Clear direction for conservation collections development resulted from a metacollection analysis of cycad holdings. Bringing underrepresented species into garden collections is a clear priority.[9]

The previous oak example shows the value of organizing at the generic scale. At an even broader taxonomic framework are cycads, a paleo-order of plants with more extinct than extant species. Comprising ten ancient genera, these are the most imperiled group of plants worldwide. The international scope and breadth of these concerns necessitate a collaborative approach to maintaining conservation collections.

A group of five leading cycad collections gathered to negotiate coordinating these holdings to advance the common good, creating the *Botanic Gardens Cycad Collections Consortium*.[9] Theft is a real issue with cycad collections so concerns about balancing data-sharing with security led this group to leverage the established resources of BGCI's PlantSearch,[10] a central database that makes collective holdings discoverable, while giving curators the option to vet requests for access. As in the oak example above, a global gap analysis of cycad holdings provided clear direction for future development, under the auspices of the IUCN SSC Cycad Specialist Group. Some taxa such as *Cycas revoluta* are secure, with very redundant collections, yet over 10% of cycad species are not held in any protective cultivation.

The Plant Collections Network Multisite Cycad Collection[11] was able to combine inventories, allowing for better planning within the US. Within this single national metacollection, holdings are much less broad than at the global level, but data sharing allows planning for specific exchanges to broaden coverage and lessen risk. Specific advances include discovery of matched male and female plants at different gardens, allowing propagation of endangered taxa such as *Zamia restrepoi* – a species still imperiled despite *in situ*, 'inter situ' and *ex situ* efforts.

Lesson learned: Even under constraints, there are still great benefits from coordinating collections. Specific challenges associated with security from theft can be addressed by selectively sharing data, which allows a global analysis of conservation priorities for cycad collections without jeopardizing existing holdings. Where data can be shared among members of a metacollection, specific exchanges can be prioritized to advance conservation objectives.

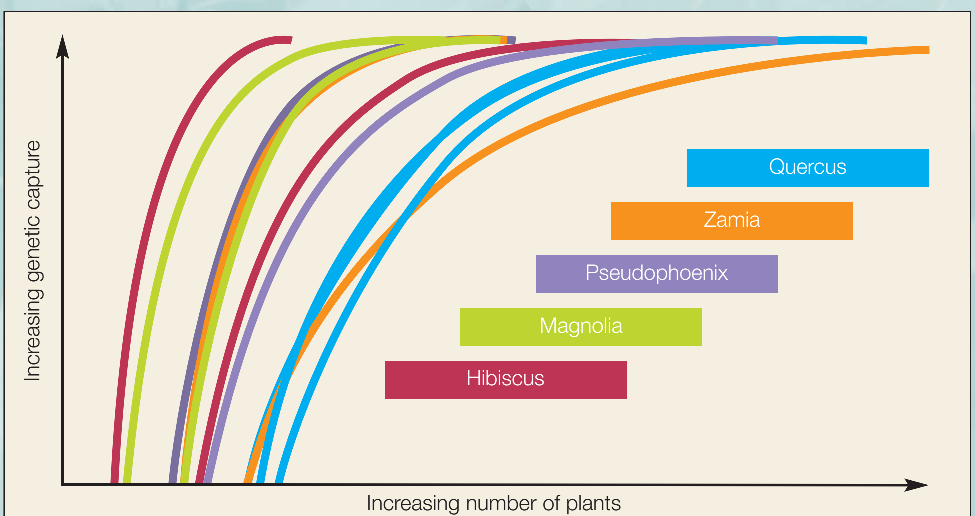
PAY ATTENTION TO BIOLOGY AT ALL SCALES

Great variety and diversity draws us to the plant world. And the variation in life histories and reproductive strategies of plants affects how we should care for and manage them in collections. As the name suggests, exceptional species need exceptions to thrive; and usual models for capturing and sustaining diversity may not always apply. This section illustrates how biological factors can influence the genetic diversity of collections at different scales.

Example: **Broad comparisons across the plant kingdom**

There are nearly 400,000 species of vascular plants, such as these beautiful collections at Block Botanical Gardens. A broad comparison of distant relatives provides insight into what general methods can be applied to the genetic conservation of exceptional species, even when plants may vary due to biology.

We compared 11 exceptional species from five genera across the plant kingdom – from gymnosperms to oaks, and from monocots to mallows – to determine whether natural history and biology influences how well wild diversity can be captured in collections using a standard approach. Two general rules emerged from the study. First, more plants capture more diversity, but for all species you eventually reach a point of reduced efficiency (i.e., the law of diminishing returns). Great variation is the other rule: each species varies in the rate of their "capture curve" and threshold for number of plants needed. This shows the value of generalized models for conserving species in collections, but also shows how specific factors can affect how well a generalized protocol can capture genetic diversity.



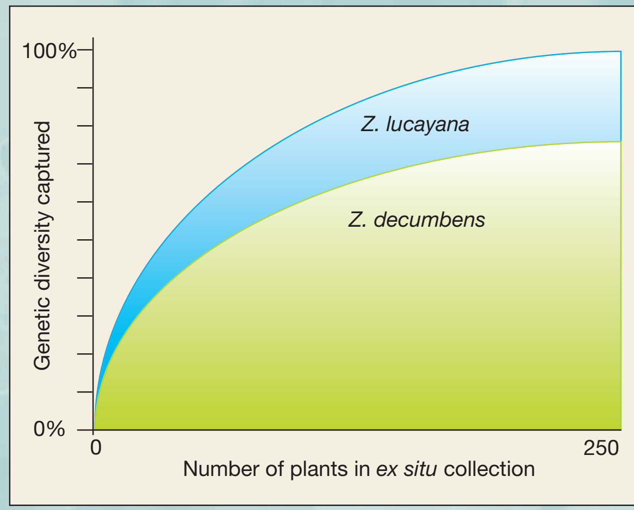
A broad look at plants – from gymnosperms to mallows – shows the general pattern of rapid increase in genetic capture with a tapering off point. The rate of capture differs across all species, showing that a standardized sample size protocol may not serve the conservation needs of all plants.

Lesson learned:
Every plant benefits from broader sampling to capture diversity – but a single protocol for capturing collections can lead to different results, depending on the species. A common sampling protocol may work very predictably for some groups (e.g., oaks) but not others (e.g., cycads).

Example: **Very close comparisons within one genus**

Let us take a closer look at just one of those genera featured above. Cycads, including *Zamia*, have separate male and female plants and limited wild distributions. Cycads are known for slow growth, but some mature in just a few years! Systematic comparison of two closely related cycads provides insight into how biology influences *ex situ* conservation. Collections of the fast-growing, abundantly coning, beach cycad (*Zamia lucayana*) capture sufficient diversity with far fewer plants than its close relative, the sinkhole cycad (*Zamia decumbens*) – which cones very infrequently and much later in life. These differences in life history evidently require changes to the collecting protocols used to capture sufficient diversity.

Lesson learned: Wild plants do not conform to models! Not every plant flowers or cones every year. Methods for sampling wild diversity for garden collections should consider the specific biology of those plants; biology informs strategy.



Even closely related species can differ with regard to how well collections can capture genetic diversity. The differences shown here are likely due to generation time and frequency of coning.[12]

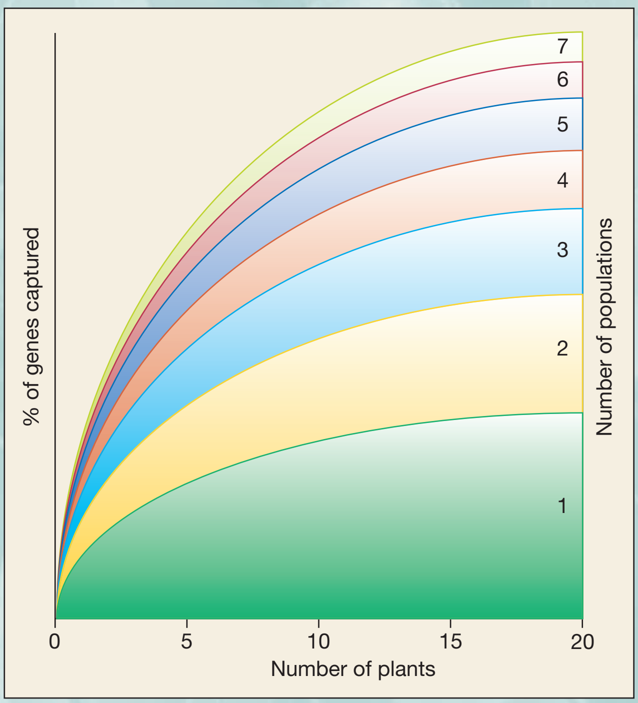
Tracy Magellan/Montgomery Botanical Center

Zamia lucayana *is notable among cycads for its fast growth and reproduction. This biological difference informs best practices for* ex situ *collections.*

Example: **Population-scale collections of *Quercus oglethorpensis***

Taking the taxonomic scale even lower – below the species level – highlights critical factors in capturing diversity. The Oglethorp oak is an endangered species that occurs in multiple populations across five states, requiring significant logistics to visit. Balancing the need for genetic capture with the funding, space, time and effort to collect and maintain collections is an important consideration: no garden has infinite resources. What are the tradeoffs when considering sufficient versus efficient capture of genetic diversity? Sufficient here would be defined by the needs of the collection manager: perhaps a certain minimum percent of alleles captured, or a certain number of genotypes maintained. Efficient genetic capture also considers the resources used to reach the targeted level of genetic capture, and also includes a chosen stopping point when resources have been used cost-effectively.

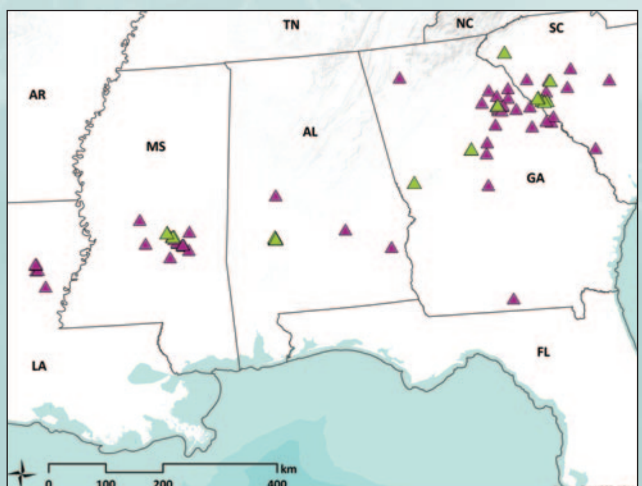
The genetic capture curves for *Q. oglethorpensis* illustrate these considerations. In all cases, maintaining large numbers of plants increases genetic capture, but collecting these from multiple populations further increases genetic capture, as well as important adaptive genetics localized to certain sites. This is straightforward for efficiency in the collection or metacollection: given space for a limited number of trees, maintaining trees from as many populations as possible maximizes genetic capture (sufficiency). However, this must be balanced against the significant cost of visiting multiple sites (efficiency).



For a given number of trees, a collection comprised of multiple populations will more efficiently capture the genetic diversity of this species. However, the incremental gains from increasing sampling from one to two populations are much greater than moving from six to seven populations. These considerations are important, given limited resources.

Quercus oglethorpensis *occurs in scattered populations across the Southeastern US, requiring significant logistics to access, visit, and collect from. Balancing investment in fieldwork against expected genetic capture requires careful consideration.*

Lesson learned: Think carefully about "which plants and how many?" More is always better with genetic capture, but returns diminish. Consider the best use of the limited space and resources at a garden and go for effective over ideal.



Provenance of Quercus oglethorpensis *trees held in the metacollection (green triangles) does not represent the species' full documented geographic range (purple triangles). Seeds from uncollected populations could represent new genetic lines for the metacollection.*

LEARN FROM ZOOS

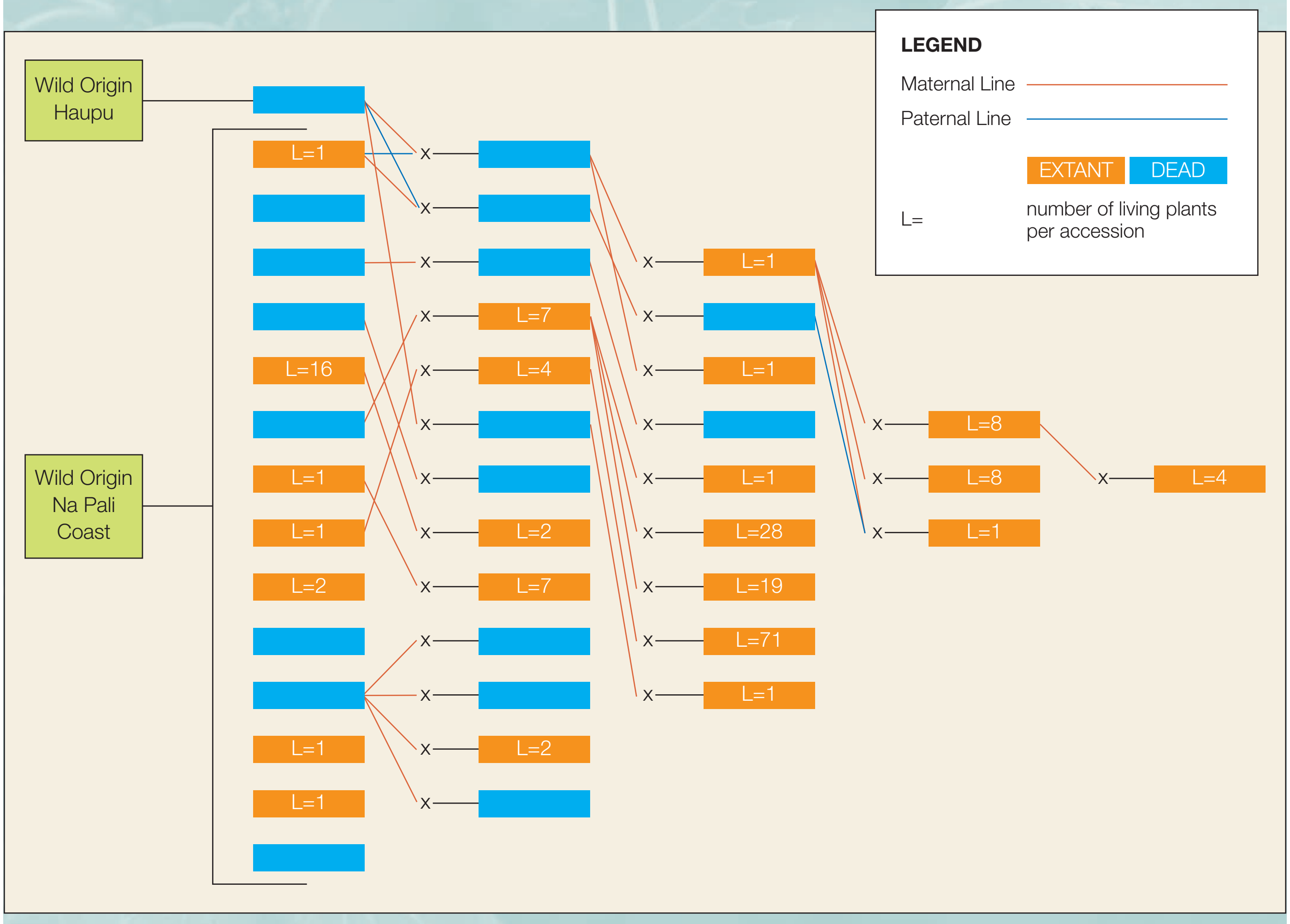
The metacollection approach is a strategy adopted by zoos over 40 years ago and is now embodied in the successful species management programs for zoo animals. Given that the investment of space and resources needed for large megafauna limit the numbers sustainable at any one zoo, the large numbers needed to conserve viable diversity called for a networked approach to achieve genetic conservation. Gardens have been less formalized in networking plant genetic resources, but adapting zoo methods for plant collections yields some important advances.[13] Here, examples of these adapted crossover methods illustrate how animal breeding strategies can help plant collections.

Example: Pedigree analysis guides propagation

Lesson learned: Don't depend on the most productive plants! The ones with the most seed, best germination, and fastest growth are unconsciously selected for at botanic gardens.[14] Work to ensure that all lines are represented.

Brighamia insignis, as previously described, is limited to what is in gardens today – wild collections are no longer possible. Thus, pollinated and cloned propagations are vital to the survival of this species, which takes us back to the original question: "Which plants should I grow," or more specifically, "Which plants should I breed?" This is important in order to avoid inbreeding and eventual demise of the *ex situ* metacollection.

One approach used by zoos to answer this question is to track the history of propagations, or crosses between individual plants, through a pedigree, or a record of descent. Underrepresented lines can be prioritized for future husbandry to ensure they do not leave the metacollection. This is especially important when some lines are easier to breed than others; the famous example of the golden lion tamarin shows a narrowing of pedigree from reliance on the more fecund lineages. Pedigree analysis of *B. insignis* (as of 2018) showed a similar imbalance in propagations – some founding lines were easier to propagate than others. However for genetic diversity conservation, an emphasis on these less-common lines for future propagations is vital to making sure all remaining genetic diversity is maintained in the metacollection.



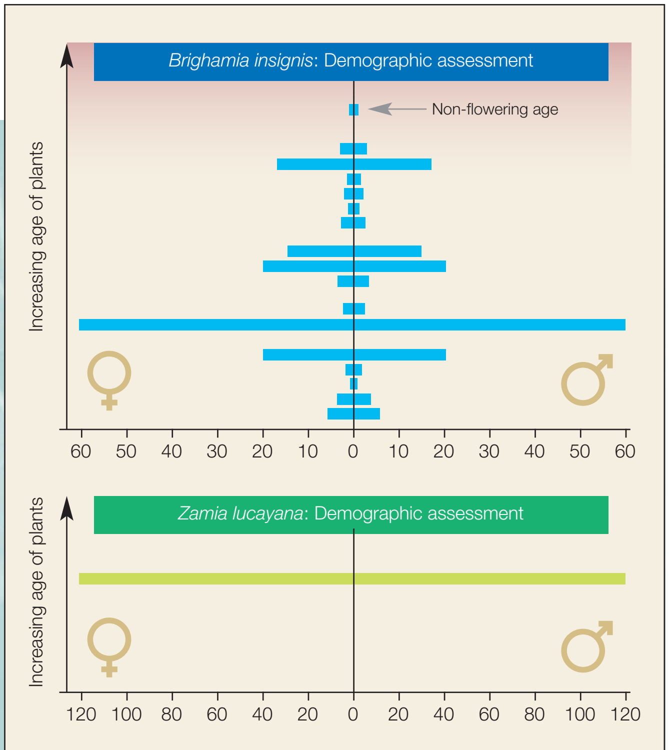
Tracking the pedigree of Brighamia insignis *collections at the National Tropical Botanical Garden reveals overrepresented and underrepresented lines, and lets collection managers best decide how to manage future propagations.*

Example: Demographic depth ensures sustainability

The pedigree example above shows relatedness within a plant collection, but does not directly track age. Zoos work to keep enough breeding-age animals on hand, via a demographic reserve of younger animals to replace aging stock. Gardens have sometimes mistakenly viewed long-lived perennial trees as more or less "immortal" given long lives and sustained flowering. But trees in fact do senesce, decline and die with great age, and often long before their natural lifespan.[15] In fact, the rates of loss in collections are much higher than perceived.[16] How do we ensure demographic depth?

Comparison of a *Brighamia* and a *Zamia* collection illustrate these issues. While both collections could use additional propagation of new stock to ensure future sustainability, the *Z. lucayana* collection shows a total – and alarming – lack of demographic depth. This single-age collection emphasized broad and deep genetic capture of wild genotypes in the *Zamia* collection in a single year, rather than ensuring stock for future replacement.

Thus, considering the purpose of a collection can guide emphasis on demography: a rescue operation seeking to bring genetic diversity into cultivation would be less concerned with demography than an assurance colony, or an extant collection of an extirpated lineage. Were the wild population of *Zamia lucayana* to suddenly be extirpated, propagation of this single-age collection would be vital. This has parallels with concerns over even-age tree stands at established gardens.



***Brighamia insignis* plants in this collection are of multiple ages. Note the oldest plants are now past breeding age. Demographic depth of younger generations ensures continued availability for plants to replace aging and dying stock. For the *Zamia*, all extant plants are the same age, from the same field collection event. If these plants reach a senescent age without reproducing, the collection will not be sustainable.**

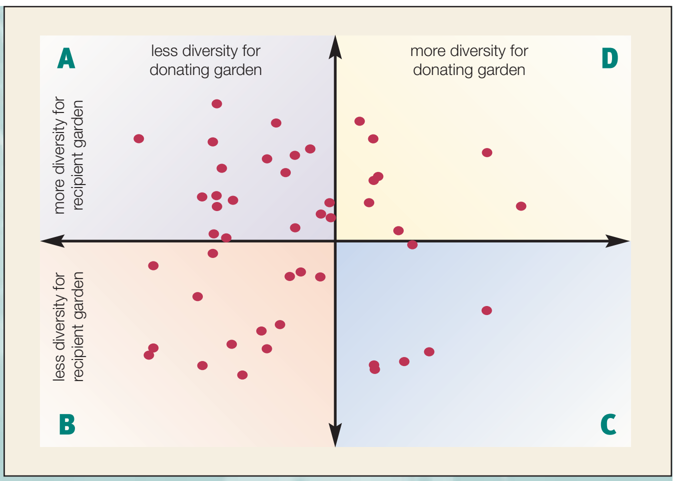
Lesson learned: Even-age collections are risky! To plan for future propagation needs, demographic depth is essential.

Example: Genetic diversity guides exchanges

To manage metacollections, zoos use population management software (PMx), which guides decisions on which animals to breed or exchange between collections to best sustain genetic diversity.[17] The software makes recommendations based on relatedness between individuals. Can this tool and these methods be used for plants?

Analysis of *B. insignis* collections provides insight on which are the best candidate plants to breed and move between gardens, or for reintroduction back into threatened wild populations. Plants at a particular garden with unique genotypes in the metacollection are good candidates for exchange, whereas plants with redundant genotypes are better suited for reintroductions or other higher-risk uses – those plants are more expendable. These decisions can be balanced against the need for appropriate local variation for reintroductions, and in fact PMx software allows subdivision of a global metacollection into management groups that can be used to maintain locally adapted ecotypes.

Lesson learned: Maximize diversity by sharing plants carefully. Which plants should I grow? The best candidates for exchange can be determined by comparing genetic or pedigree information, which ensures sustained diversity over time. Plants with redundant genotypes are perfect for higher-risk uses such as testing reintroduction practices.



Moving an individual from a garden collection to a reintroduced population can change the diversity of both groups. Quadrant A outplants an under-represented genetic line, which benefits the reintroduced population but reduces diversity held in the collection. Quadrant B reintroduces lineages rare in the collection but common in wild, and thus has limited benefit to both. Quadrant C introduces plants over-represented in both ex-situ collections and in the wild, and is of marginal value for diversity. Quadrant D outplants a lineage redundant in collections but rare in the wild, thus benefitting both.

TOWARD THE METACOLLECTION!

What emerges from these studies of collections genetics?

Gardens need to work together to sustain these living treasures. Bringing our collective resources and expertise to bear on the problem of plant conservation is the best way forward – curators and researchers integrating plants and genetic data provides the best path forward. This can be done at large global scales and broad taxonomic levels, or organized around a single local species. Whatever the scale or scope of the issue, these examples all point in one direction: pooling collection resources advances the common good.

Onward to the metacollection!

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Notes and References

1. Exceptional species are plant species that: 1) do not produce seeds that can be stored using traditional seed banking techniques (i.e., has recalcitrant seeds), 2) do not produce seeds, or 3) produce seeds that are not available (e.g., plants located in difficult-to-access locations, seed is predated before collection, etc.) Living plant collections are often the only way to conserve exceptional species. Focusing on exceptional species for living plant collections will provide the greatest conservation benefit. See Pence, V.C. (2014). Tissue Cryopreservation for Plant Conservation: Potential and Challenges. International Journal of Plant Sciences 175:40-45.
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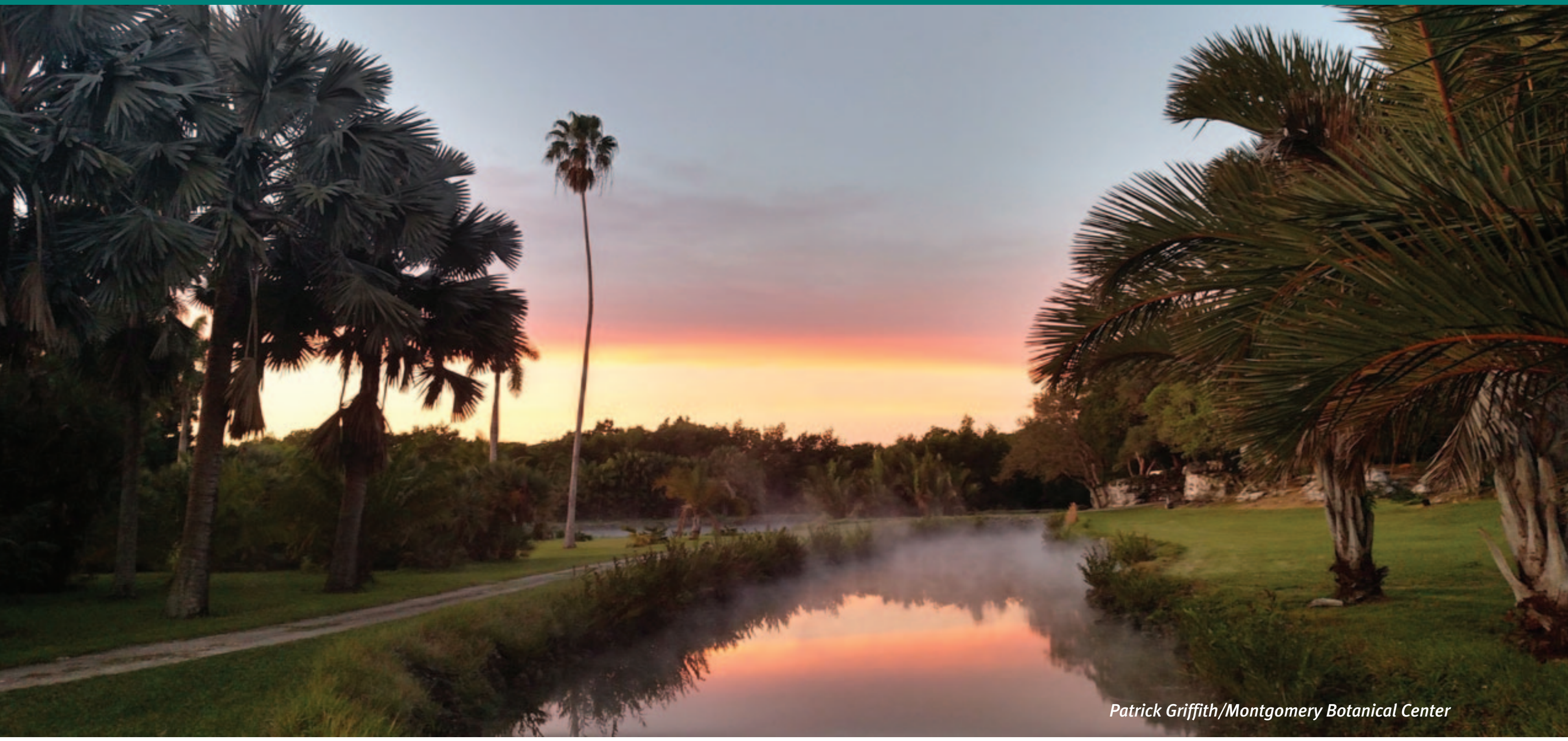

Patrick Griffith/Montgomery Botanical Center

For more information contact:

M. Patrick Griffith, Ph.D.
Montgomery Botanical Center
patrick@montgomerybotanical.org

Botanic Gardens Conservation International, U.S.
1151 Oxford Road
San Marino, CA 91108
www.bgci.org