

Applying the zoo model to conservation of threatened exceptional plant species

Jordan Wood, Chicago Botanic Garden and Northwestern University Plant Biology and Conservation Program

Jonathan D. Ballou, Smithsonian Conservation Biology Institute,

Taylor Callicrate, Species Conservation Toolkit Initiative

Jeremie B. Fant, Chicago Botanic Garden

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

Andrea T. Kramer, Chicago Botanic Garden

Robert C. Lacy, Species Conservation Toolkit Initiative

Abby Meyer, Botanic Gardens Conservation International

Sara Sullivan, Species Conservation Toolkit Initiative

Kathy Traylor-Holzer, IUCN SSC Conservation Planning Specialist Group

Seana K. Walsh, National Tropical Botanical Garden

Kayri Havens, Chicago Botanic Garden, khavens@chicagobotanic.org

Author for Correspondence:

Kayri Havens

Negaunee Institute for Plant Conservation Science and Action

Chicago Botanic Garden

1000 Lake Cook Road

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Glencoe, IL 60022

khavens@chicagobotanic.org

Running head: Zoo Model

Article Impact Statement: Using zoo-style studbooks and pedigree management will be transformative for the conservation of exceptional plants like *Brighamia insignis*.

Abstract:

Maintaining a living plant collection is the most common method of ex situ conservation for plant species that cannot be seed banked i.e. “exceptional” species. Viability of living collections, and their value for future conservation efforts, can be limited without coordinated efforts to track and manage individuals across institutions. The zoological community has established an inter-institutional infrastructure to support long-term viability of captive animal populations using a pedigree-focused approach. We assess the ability of this coordinated metacollection infrastructure to support conservation of four plant species curated in living collections at multiple botanic gardens around the world. Our results illustrate limitations in current practices in plant conservation and demonstrate how this framework can be used by the botanical community. We identified eight actions needed to improve the ex situ conservation of exceptional plant species. These actions include developing a central database to aggregate data and track unique individuals of priority threatened species among institutions, and adapting a pedigree-based population management tool that incorporates life history aspects unique to plants. We provide a framework for action that, if approached collaboratively across regional, national, and global scales, will be transformative for the ex situ conservation of threatened plant species.

Introduction

More than one million plant and animal species are threatened, prompting calls for transformative changes to reverse this trend and conserve species for the public good (IPBES 2019). For many species, ex situ collections are a key component of conservation efforts, and global guidelines describe when ex situ management is recommended and how it should be conducted (McGowan et al. 2017). When an ex situ collection’s purpose is extinction prevention or to support population reintroduction or augmentation, it must be managed for long-term viability by maintaining genetic diversity and demographic security (Guerrant et al. 2004). Currently, robust policy and management practices support ex situ conservation efforts to achieve these goals for captive animal populations (Ballou et al. 2010) and for plant species that can be seed banked (Guerrant et al. 2014). However, plant species that cannot be seed banked are at risk due to a gap in infrastructure and practice (Fant et al. 2016).

As many as half of threatened plant species are “exceptional,” either producing seeds that cannot tolerate traditional storage conditions (-18C, 15% RH), or producing few to no seeds (Pence 2013;

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Wyse et al. 2018). Consequently, for some plant taxa the primary long-term ex situ conservation method is to maintain them in living collections. Due to practical constraints, many botanic gardens curate only one or a few individuals of a species, particularly of large organisms, which greatly limits the total genetic diversity conserved (but see Griffith et al. 2015). Zoos face similar challenges, which led them to develop a robust system to manage ex situ collections as a metapopulation. For species maintained at multiple botanic gardens, total potential genetic diversity held ex situ can be higher (Griffith et al. 2020), but this is often not the case because many collections are derived from the same source, or are even clones of the same plants, and may represent a limited number of unique founders (Brütting et al. 2013). With so few founders and limited collection sizes, the long-term viability of many ex situ plant populations is questionable. This challenge of maintaining living plants in collections for conservation value is exacerbated by a lack of infrastructure to coordinate “metacollections” and manage them collaboratively across institutions (Griffith et al. 2020).

Unfortunately, there are currently few established best practices for maintaining viable plant populations in and across living collections, especially where the long-term maintenance of intraspecific diversity is the primary objective (Maunder et al. 2001). The genetic diversity of an ex situ population is largely determined by the population size and the relatedness of those individuals (Lacy 1994). The founding population represents the maximum genetic diversity of an ex situ collection, after which the loss of genetic diversity through drift is inevitable unless additional founders are added. The rate of loss in genetic diversity in collections or populations is directly related to management decisions (Ballou et al. 2010). Ex situ conservation in plants has been focused on species that can tolerate long-term storage in seed banks (Guerrant et al. 2014; Brütting et al. 2013), where the standing genetic diversity is preserved as long as seed remain viable. For species maintained as living collections, conservation practices are often focused on maintaining or maximizing the numbers of individuals, without consideration of how much of the original genetic diversity is being maintained (Ensslin et al. 2015). Consequently, collections comprised of few founding individuals, grown in managed landscapes for multiple generations, are at increased risk of experiencing genetic drift, inbreeding, hybridization, or selection to captivity (Havens 2004). In order to maintain genetic diversity within living plant collections for the long term, strategies are needed that can manage the risk of losses over multiple generations, track the diversity of founding individuals, maximize effective population size (N_e), mitigate genetic drift and inbreeding, and equalize family size to decrease the likelihood of artificial selection (Havens 2004; Lauterbach et al. 2012). In addition, institutions with large collections will need to ensure unintentional hybridization between related taxa is not occurring. This may involve isolating reproductive individuals, only collecting seed produced via hand pollination of bagged inflorescences, and weeding out any self-sown individuals with unknown genetic lineages (Maunder et al. 2004). Metacollections across multiple institutions can also serve to separate different genetic lineages, and as important backup collections for duplicate material.

Many in the botanical community recognize that the goal for living conservation collections, both in public displays and in specialized conservation collections, should shift to long-term population stability (Woodworth et al. 2002; Ballou et al. 2010). This is analogous to the challenges zoos faced more than three decades ago. Zoos recognized that most of their ex situ programs were not sustainable because they had too few animals, and even fewer genetically unique founders (Lees & Wilcken 2009). Because adding new wild founders to ex situ programs was increasingly difficult, the potential for inbreeding and loss of genetic diversity compromised the long-term viability of these captive populations (Willoughby et al. 2015). To address these challenges, zoos decided to track the pedigrees of all individuals held in ex situ collections and developed scientifically-based management (e.g. breeding and transfer) recommendations to collectively manage their animals. To achieve this, they leveraged a network of international (e.g. WAZA) and regional (e.g. AZA) organizations to build infrastructure for cooperative breeding programs. This included providing infrastructure and standardized protocols to coordinate multi-institution studbooks documenting pedigree and demographic data (Bingaman Lackey 2010) among institutions and to manage ex situ collections as a metapopulation (Table 1). With this infrastructure in place, population managers at zoos are able to: (1) trace lineages back to founders, (2) quantify each individual's genetic value relative to program goals, (3) identify and manage unequal representation of founder alleles, resulting from over-production of certain lineages, and (4) increase the genetic quality of exchange between institutions, minimizing inbreeding and distributing genetic variants among institutions.

Such an infrastructure is currently absent in the botanical community. To test the utility of this approach to plant conservation and to lay the foundation for future work, we created pedigrees to track founder lines of four exceptional plant species with different life histories held in living collections (Alula [*Brighamia insignis*], a Bahamian cycad [*Zamia lucayana*], Oglethorpe oak [*Quercus oglethorpensis*], and titan arum [*Amorphophallus titanum*]). We also analyzed these data in the zoological population management software (PMx; Lacy et al. 2012) to compare management recommendations based on pedigree to those from current botanical practices. PMx software uses pedigree data and genetic information to track founders and relatedness of the collection to provide breeding and transfer recommendations to minimize loss of genetic diversity and avoid inbreeding within the population (Lacy et al. 2012). From these examples we identified areas where the pedigree approach resulted in a shift in how management of collections was approached. From this work we developed eight actions necessary to increase long-term viability and conservation value of ex situ collections for threatened exceptional plant species. This work highlights how developing a "zoo-like" framework for the botanical community would improve long-term viability and conservation value of living plant collections.

Actions needed to improve living plant collections management

ACTION 1: Change how individual plants are tracked across generations. Tracking unique founders (maternal lines) is a critical aspect of developing pedigrees. Although this has been recommended within the plant conservation community (Guerrant et al. 2004), many botanic gardens maintain

plants by source (under a single accession), with little to no information of original founder or relative contribution of each founder line. This is further complicated when plants are maintained over multiple generations, and maternal or paternal (pollen) lines are not tracked. Although pedigree-based population management software, like PMx, can handle uncertainty about parentage, precision decreases as the number of possible parents increases. Without clear lineage documentation, unique or underrepresented founder alleles can easily be lost.

For example, *Brighamia insignis* was first cultivated for ex situ management in the 1970s, with additional collections from the 1980s and 1990s. Genetic and accession data suggest fewer than 27 founders were brought into cultivation (Wood 2018). Attempts were made to collect unique founders, but small source population sizes increased the likelihood that founders were closely related. Of the 13 original founders brought into the National Tropical Botanical Garden (NTBG) that we were able to assign to a pedigree, six (46%) were lost after 40 years. This loss in diversity cannot be replenished by collection from new wild founders because *B. insignis* is possibly extinct in the wild (Walsh 2016). Some of that lost diversity may persist in other collections, but the only way to assess that is through molecular genetic study, as details of relationship to original founders are largely absent.

ACTION 2: Create a centralized database to track pedigrees of current ex situ collections. The zoo community uses a mean kinship minimization management strategy to retain genetic diversity of founders over multiple generations and to predict the contribution of potential progeny to the overall genetic diversity of the captive population (Ballou et al. 2010; Ivy & Lacy 2010). This is possible because zoos maintain accurate records *across institutions* through studbooks, (e.g. ZIMS for Studbooks; Species360 2019). With these data they can use software (e.g. PMx; Lacy et al. 2012) that allows them to make management decisions that equalize the contribution of all founders. This requires maintaining up-to-date records, which is achieved through widespread participation in maintaining studbooks.

Although more than 1,500 gardens worldwide freely contribute taxon-level collections data to Botanic Gardens Conservation International's (BGCI) PlantSearch database, they currently do not include accession-level and plant-level data necessary for pedigree management. BGCI uses PlantSearch data as the foundation for reporting progress toward the ex situ-focused Target 8 of the *Global Strategy for Plant Conservation*. BGCI and partners are working to expand this widely-used tool to develop an optimal studbook-style resource to support pedigree management of living plant collections. They have explored potential pedigree data models, are working to develop an aggregation tool for pedigree and genetic data as part of the PlantSearch database for prioritized species of concern, and anticipate launching a functional pedigree module for these taxa soon.

ACTION 3: Prioritize conservation of the most genetically valuable individuals. To maintain genetic diversity over time, zoos use pedigrees to track descendants of all founding individuals, and thus representation of founder genes in the current living population. PMx uses this information to

identify the most genetically under-represented and over-represented individuals. For instance, of the 27 founders of *Brighamia insignis* we identified, three have no living descendants in the core conservation collection at NTBG. PMx identifies such under-represented individuals so that their propagation can be increased. Also, within NTBG's collection, at least 10% of individuals showed equal representation of similar founders and therefore could be removed from the population with minimal impact to the genetic diversity of the managed population. Similarly, in the case of *Zamia lucayana*, a dioecious species, the entire conservation collection at Montgomery Botanical Center (Miami, FL) was derived from seed collected from 16 maternal lines. Plants from one of three sub-populations were less representative of the species' genetic diversity (Griffith et al. 2017), suggesting that allocating resources to keeping the other two sub-populations would be most efficient.

Another important component of the pedigree approach is to identify over-representation of highly fecund individuals. A study of Golden Lion Tamarins (*Leontopithecus rosalia*) found that most of the captive population was derived from three overly-fecund individuals (Ballou et al. 2002), requiring a shift in breeding priorities. With plants, horticultural practices make it possible to produce many individuals from a few propagules. Although having larger numbers of plants may be desirable, if they are derived clonally or from few maternal lines, the genetic value of those plants declines. For example, ex situ collections of *Quercus oglethorpensis*, an oak species endemic to the southeastern United States, were comprised of only 46 individuals all from the eastern edge of its range. This number increased three-fold after recent expeditions to address gaps in sampling. Through these efforts, representation of genetic diversity within ex situ collections increased from 63% to 86% of the wild (source) populations. However, many new founders represent half-siblings and consequently some lineages are now over-represented (Wood 2018). Using a pedigree approach, we can quantify an individual's genetic value by the amount of unique genetic diversity they represent. Because any single institution's capacity to curate numerous trees is limited, this information can be useful in the selection of which seedlings to grow to maximize genetic diversity. The pedigree analysis also highlighted that, although highly fecund accessions might appear ideal candidates for plant exchanges between gardens, these individuals may be from the same maternal lines and offer little additional conservation value to the broader ex situ population. Nevertheless, they may still be important for research, education and play a role in secondary back-up, if resources allow.

ACTION 4: Limit inbreeding within the ex situ metacollection.

The pedigree management approach can guide breeding recommendations that will minimize the potential for inbreeding in the collection. Because many accessions are comprised of related plants, crosses within an institution may result in elevated inbreeding levels. Although this may have minimal short-term impact, long-term inbreeding can result in fitness declines. For *Amorphophallus titanum*, the rarity of bloom events, clonal nature of the species, and lack of information on plant lineages contribute to increased likelihood of inbreeding in collections. To date, inter-institutional pollen exchange has been driven by availability rather than genetic planning. Some institutions have early evidence of inbreeding depression, such as non-viable seed after hand-pollination (Havens,

pers. obs.). Similarly, a recent study of *Brighamia insignis* at NTBG has found that many plants are showing a drop in pollen viability, which may be evidence of inbreeding depression in this collection (Walsh et al. 2019).

ACTION 5: Identify the best candidates for ex situ transfers or wild reintroductions.

Most botanic garden transfers are made without evaluation of how this will impact an ex situ collection's or metacollection's "conservation value." Using a pedigree approach makes it possible to quantify how the selection of specimens for exchanges will impact genetic integrity of collections, while also allowing for the selection of individuals that would duplicate representation of unique founders in separate locations. For *Brighamia insignis*, we used PMx to identify the genetic pros and cons of moving plants into or out of the core conservation collection at NTBG. This PMx feature can help botanic gardens determine the impacts on net genetic diversity of moving an individual between institutions, with the ideal transfer increasing the average genetic diversity at both the receiving and the source garden (Fig. 1). Using PMx, we identify lineages of founders missing from the core collection at NTBG, and determined which individuals from the core collection could be transferred to the non-NTBG metacollection without lowering genetic diversity at NTBG. Finally, PMx identified three individuals that, if lost from NTBG, would lower the NTBG collection's genetic diversity. The zoo community often uses this type of analysis to identify the best candidates for inter-institutional transfer or for reintroduction. Likewise, the botanic garden community can use it to identify individuals that will optimize transfer of genetic diversity to the wild without compromising diversity of the core ex situ source collection.

ACTION 6: Use molecular genetic techniques to fill gaps in our knowledge. The pedigree approach traces all material back to the original founders to ensure that genetic diversity of those founders is maintained and represented equally throughout the metacollection. Tracking founders is difficult, especially if the species has been in collections for hundreds of years, and often requires a molecular genetic approach. The zoo community also employs genetic techniques when needed to both unravel uncertain pedigree history and resolve relationships among founders (Ivy & Lacy 2010; Hogg et al. 2019). Programs like PMx can use molecular data in place of or in concert with pedigrees to make accurate metacollection management recommendations (Norman et al. 2019). In developing a pedigree for the ex situ population of *Amorphophallus titanum*, it became clear that the origin of many plants is unknown. This charismatic plant has been in garden collections for more than 120 years. Seed was first collected in 1878 and shared with several institutions in Europe; ten years later the first inflorescence emerged at Royal Botanic Gardens, Kew (UK). Since the first expedition, there have been at least 20 documented introductions of new genetic material, subsequently distributed to 140 institutions (BGCI PlantSearch database). This history suggests potentially high genetic diversity within the botanical garden population, which could minimize the need for additional wild collection. Alternatively, most living plants could be descendants of only a few highly fecund individuals. Unfortunately, limited provenance information is available for most collections. Many

records of wild origin are unreliable, and genetic data will be required to identify unique lineages and generate a more accurate pedigree.

ACTION 7: Develop a pedigree management software for plants. Using the zoological community's population management software, PMx (Lacy et al. 2012), was challenging because of fundamental differences in the biology of plants, especially compared to vertebrate animals which are currently the main focus of the program (Table 2). For example, most vertebrate animals have discrete male and female individuals, while many plants can self-fertilize and their breeding systems vary widely. A recent version of PMx (Lacy 2012) was developed that dealt with some of these challenges (for example, providing genetic calculations for hermaphrodites), but some software features still cannot be applied to plants or species that are managed as groups (e.g. schools of fish). Currently the demographic component of PMx does not accommodate stage- or size-based classes commonly used in plant demography. A stage- or size-based model is more appropriate for plants because reproductive maturity is not necessarily related to age, and many plant taxa are able to produce pollen and set seed until death. The Species Conservation Toolkit Initiative (<https://scti.tools>) is developing a version of PMx with improved utility for plants called PMexceptional. This new version will also benefit many animal taxa with unusual life histories, unknown paternity, or those managed in groups or herds including corals, many invertebrates, some fishes and other vertebrates.

ACTION 8: Conduct outreach and provide education to the botanical garden community. Any major changes like the ones proposed here require outreach to stakeholders and ultimately their buy-in. We have already begun discussing this approach with the botanical garden community and have a mechanism to trial the approach with a group of "early adopter" gardens. A new initiative led by BGCI, the Global Conservation Consortia, is trialing this approach with four genera: Oaks, Maples, Magnolias, and Rhododendrons. Among these genera, the most threatened and exceptional species are being prioritized for this pedigree management approach, and we envision expanding this to a few hundred species over the next several years. This approach identifies a single institution to serve as the lead "Species Champion" (analogous to a studbook keeper in zoos) to maintain the pedigree and the core conservation collection. They are also responsible for working with Consortium "members" and "safe sites", a dedicated group of other gardens and partners that acquire additional unique and duplicate material, to ensure those individuals are incorporated into the metacollection's pedigree. This trial will allow us to test the new pedigree module in PlantSearch and PMexceptional, to modify them if needed, and to develop training materials to be rolled out to the larger community. This will also facilitate the development of a core set of ex situ collections standards and a set of priority data fields to support wild-collecting activities, plant records management, and ultimately, species conservation applications.

Not all exceptional species require this approach

The number of threatened, exceptional plant taxa that may benefit from this approach could surpass 50,000, presenting yet another challenge (Fig. 2). Identifying people and institutions to take responsibility for such a large number of pedigrees is daunting. For comparison, the zoo community manages approximately 1,000 studbooks worldwide (Oberwemmer et al. 2011). Careful prioritization is needed to roll out this approach in botanic gardens for taxa that will benefit most. We suggest concentrating on the threatened taxa most at risk, e.g. those critically endangered, those for which new collections from the wild are unlikely, and/or those in rapid decline. We also recommend focusing on species that can only be maintained as living collections, are shorter-lived (likely to need multiple generations ex situ), and amenable to cultivation. A multi-taxon assessment such as the Integrated Collection Assessment and Planning (ICAP) process can be used to further prioritize taxa if needed to maximize overall ex situ conservation benefit (Traylor-Holzer et al. 2019). The BGCI Global Conservation Consortia initiative is allowing us to test and fine-tune the approach with a limited number of taxa, increasing likelihood of success.

Conclusions

Here we make the case for considering pedigree-based management as a way to maximize the conservation value of living plant collections via studbook-style record keeping and population management software such as PMx. The genetic management focus of most zoo-based breeding programs has contributed to the long-term retention of gene diversity, helped to equalize the contributions of founders and minimized the mean kinship within scientifically-managed captive populations. To achieve this, managers use several tools to compile, share, and analyze captive population data (Flesness 2003), following practices developed to maximize genetic diversity and maintain demographic stability (Ballou et al. 2010). Pedigree management and analysis tools are widely used by regional zoo associations, and management decisions are increasingly integrated across the global zoo community (Penning et al. 2009), allowing genetic diversity to be managed under a unified program. An equivalent system does not yet exist for plants, but we have identified steps and infrastructure changes that can be adapted or expanded to support it, and therefore ensure long-term viability of ex situ collections of exceptional plant species.

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Table 1. Concordance between ex situ conservation infrastructure in zoos and botanic gardens.

| Zoological infrastructure | Infrastructure available for plants?* | Notes |
|---|---------------------------------------|--|
| Network of accredited institutions with conservation-focused missions and explicit, high standards of collections care and management (AZA, EAZA, ZAA) | +/- | Global network beginning to provide accreditation (BGCI), but not to same level as zoos. Regional networks with varying agreed conservation and collections standards (ANPC, CPC) |
| Policies and framework to bring individuals and organizations together to conserve species ex situ (e.g., Taxon Advisory Groups, Species Survival Plans ¹⁻⁵) | +/- | BGCI conducts taxon- and region-specific ex situ surveys ⁶ , PlantSearch ⁷ can locate institutions curating shared species, GardenSearch ⁸ can identify expertise in different locations |
| Guidance on selecting species and defining ex situ program purpose and goals (e.g., Integrated Collection Assessment and Planning (ICAP) process ⁹ , IUCN/SSC Guidelines ^{10,11}) | + | IUCN/SSC guidelines ^{10,11} and ICAP process ⁹ can be applied to plants |
| System to record and disseminate information about selected species and program goals (Regional Collection Plans ^{2,5,12}) | - | |
| Resources for Animal Program managers and participating institutions, including handbooks, program updates, online training modules, and contact information (AZA Animal Programs Database ¹³ ; EAZA Population Management Online Tutorial ¹⁴) | +/- | BGCI resources provide globally-accessible and relevant resources (PlantSearch ⁷ , GardenSearch ⁸), national programs (CPC) provide local resources. But none focus on curating exceptional species ex situ |
| Guidance on collecting new founders from wild if possible ^{3,5,15} | + | CPC guidelines ¹⁶ |
| Common studbook database (ZIMS for Studbooks ¹⁷) and data-sharing across institutions (standardized data entry guidelines and protocols ¹⁸⁻²¹) | - | PlantSearch pedigree module in development |
| Process to regularly evaluate genetic and demographic status of managed programs to determine if established goals are being met and to update breeding and transfer recommendations (PMx pedigree analysis software ²²) | - | PMx exceptional in development, but similar infrastructure missing except at local or national levels (individual gardens, CPC); potential for more capacity at BGCI |

| | | |
|-------------------------------------|--|--|
| assisted by various advisory groups | | |
|-------------------------------------|--|--|

* (+) = equivalent infrastructure available; (-) = equivalent infrastructure needed; (+/-) = some infrastructure available

Acronyms:

AZA – Association of Zoos and Aquariums

ANPC - Australian Network for Plant Conservation

BGCI – Botanic Gardens Conservation International

CPC – Center for Plant Conservation

EAZA – European Association of Zoos and Aquaria

IUCN – International Union for the Conservation of Nature, also known as World Conservation Union

SSC – Species Survival Commissions of IUCN

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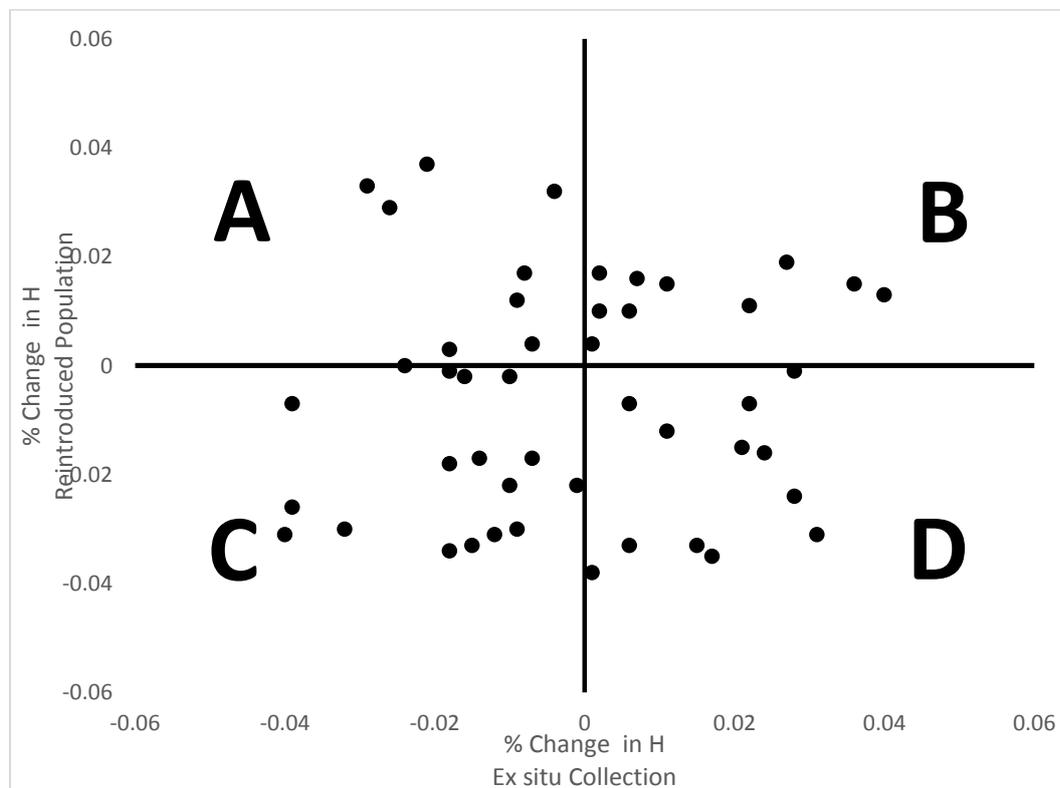
Table 2. Differences between animals (vertebrates) and (seed) plants that impact ex situ conservation practice; (+) = relatively likely, high, or easy; (-) = relatively unlikely, difficult, or low.

| Characteristics affecting conservation practice | Vertebrates | Seed Plants |
|--|----------------|---------------------------|
| Typical life history characteristics | | |
| Ability to assign taxon name confidently | + | - |
| Generation time | Medium | Short to very long |
| Number of offspring | Low-medium | Low to very high |
| Gender | Male/female | Many systems |
| Ploidy | Diploid | Haploid/Diploid/Polyploid |
| Logistical issues | | |
| Ability to move gametes | - (Some sperm) | + (Many pollen) |
| Ability to move adults | + | - (Size-dependent) |
| Ability to move embryos | - | + (Seeds) |
| Ability to clone | - | + |
| Current conservation protocols & investment | | |
| Existing pedigree | + | - |
| Provenance of ex situ individuals known | - | + |
| Parent determination | + | - |
| Long-term storage ability (embryos) | - | + (Orthodox seeds) |
| Reintroduction successes | Some | Several |
| Likelihood of hybridization in living collections | - | + |
| Conservation status assessed | + | - |

| | | |
|--------------------------------------|---|---|
| Cost of managing ex situ populations | + | - |
| Current conservation investment | + | - |

Figure Legends

Figure 1. Output from population management software PMx illustrating how moving an individual (represented by dots) from an ex situ collection to a reintroduced population (or recipient collection) can change the heterozygosity (H, a measure of genetic diversity) of the two groups. Individuals in Quadrant A represent transfer of a genetic line under-represented in both the ex situ collection and reintroduced population; transfer will benefit the reintroduced population (positive change in H) but reduce diversity in the ex situ collection (negative change). Individuals in Quadrant B represent common diversity in ex situ collections but rare in the reintroduced population so transfer benefits the reintroduction without harming the ex situ collection. Individuals in Quadrant C represent rare diversity in ex situ collections but common in the reintroduced population, therefore transfer from ex situ to the reintroduced population has a negative impact on both, as genes are moved from where they were valued to where they were not needed. Individuals in Quadrant D are over-represented genetic lines in both populations, hence transfer will not benefit the reintroduction but will benefit net genetic diversity of ex situ collections by improving balance of representation among genetic lineages there.



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Figure 2. Prioritization of plant species for a pedigree management approach.

