Retracing origins of exceptional cycads in botanical collections to increase conservation value

1 | INTRODUCTION

Living fossils, dinosaur food, survivors of ice ages, and asteroids. These are just some of the ways cycads are described in popular science. It’s no wonder cycads have long fascinated the public, collectors, and researchers alike and are among the most prized plants in the world (Croisiers & Malaisse, 1995; Kay et al., 2011). They represent the oldest extant lineage of seed plants originating ~300 million years ago, and remarkably persisted with little morphological change, hence their consideration as living fossils (Nagalingum et al., 2011). Cycads once had an almost worldwide distribution during their peak in the Mesozoic, 251 to 66 million years ago (Hermens et al., 2009; Nagalingum et al., 2011). Today, approximately 350 extant cycad species are known, with wild ranges in Africa, Australia, Southeast Asia, and the New World (Calonje et al., 2020).

Despite their incredibly long legacy on our planet, cycads are considered the most threatened lineage of plants in the world (Donaldson, 2003). Habitat destruction and harvesting of wild plants for horticulture and medicinal plant trade are among the top threats, and entire populations of some of the most highly threatened species have already been lost (Donaldson, 2003; IUCN, 2020). Ex situ conservation – keeping plants or plant propagules off-site where they can be used in conservation and restoration programs – is therefore deemed vital to cycads’ survival (BGCI, 2015; Donaldson, 2003). Cycads are considered “exceptional species” because they produce seeds that cannot be stored in seedbanks; thus, ex situ conservation for cycads is currently limited to keeping living plants off-site (Fant et al., 2016).

There is a growing movement led by members of Botanic Gardens Conservation International (BGCI) to engage botanic gardens in ex situ conservation and recovery of threatened plants, following what has been achieved by the zoo community including forming networks to manage metacollections of species that are genetically representative of remnant wild populations (Fant et al., 2016; Griffith et al., 2019; Hoban et al., 2020). Given their highly threatened status, cycads have been a model plant group to focus ex situ conservation measures on and have been featured in a number of recent studies (Griffith et al., 2015, 2017; Hoban et al., 2020). Proper record keeping and traceable provenance for living accessions are necessary components of an ex situ conservation strategy (Guerrant et al., 2006). However, provenance (particularly wild origins) for many of the cycads in botanic garden collections is unknown. Without knowledge of where a plant originates from means that it has little value for use in recovery programmes (Fant et al., 2016; Mounce et al., 2017).

2 | MILLENIAS IN THE WILD, CENTURIES IN BOTANIC GARDENS, AND NOW BACK TO THE WILD?

Referred to by early plant hunters as palms bearing cone-like structures, cycads were among the first plants brought back to Europe from botanical expeditions in the 18th century, transported as living plants and kept alive on ships for months as they made their way back to gardens in Europe (of course, at a time that predates the Convention on Biological Diversity [CBD] and the Convention on the International Trade of Endangered Species [CITES]). Botanic gardens in some cases have kept cycad plants alive for centuries after being brought back from historic plant collecting trips. Notable examples include Encephalartos caffra (Thunb.) Lehm (=Cycas caffra Thunb.) collected in South Africa by Carl Thunberg (1743–1828) and brought to Sweden in 1775, Dioon edule Lindl. collected in Mexico by Frederik Liebmann (1813–1856) and sailed back to Denmark in 1843 (Friis, 2015), and Encephalartos altensteinii Lehm.– designated as a living type (discussed below).

Cycads in botanic gardens originating from historical collections may represent unique genetic lineages and may also represent populations that are now extirpated. Furthermore, as is the case for many threatened plants, the wild collection of cycad seeds for ex situ conservation purposes poses certain challenges; entire populations have already been lost, remnant populations for many species are in remote and highly inaccessible regions, and plants are rarely found bearing mature cones during a single collecting trip. Thousands of cycads are maintained on display in botanic gardens around the world (BGCI, 2015). In fact, eighty-four percent (84%) of all the known cycad species are present in botanical collections – albeit often represented by a single botanic...
garden (BGCI, 2015; Griffith et al., 2015). Therefore, in addition to focusing ex situ conservation efforts on the collection of new, well-documented and genetically representative wild-collected plant accessions, retracing the provenance of plants already in cultivation deserves prioritization.

We discuss how population genomic methods can provide a solution to help retrace origins of such plants, and illustrate this with the tales of two charismatic cycads represented in botanical collections with connections to historical expeditions and for which poor provenance information exists.

### 3 | RETRACING THE ORIGINS OF CYCADS IN COLLECTIONS – A POPULATION GENOMICS APPROACH

When archival records fall short in retracing wild origins for a living accession, we propose that population genomics methods be a solution. Traditional DNA barcoding methods have been useful in identifying cycads in complex herbal mixtures and exposing the trafficking of threatened species, yet they do not provide sufficient genetic resolution to retrace origins (Little & Stevenson, 2007; Sass et al., 2007; Williamson et al., 2016). Microsatellite markers have been used extensively in conservation genetics to differentiate between and within populations of a number of cycads, but such methods are not universally applicable across all groups of cycad species (Aristizabal et al., 2018; Griffith et al., 2015; Hoban et al., 2020). Population genomics methods using short DNA reads from across a species’ genome have greater sensitivity and are more universally applicable to a wide range of cycads (Gutiérrez-Ortega et al., 2018; Clugston et al., 2019). Genomic barcodes can be developed that can assist in retracing origins to wild populations, and if wild populations are lacking to provide a suitable genomic reference, extant herbarium specimens can be used as a surrogate.

### 4 | *Encephalartos altensteinii*: THE CASE OF A LIVING TYPE

Herbaria are well-recognized as repositories of specimens from which botanists can base species descriptions on, and study evolutionary relationships and floristic changes over time and space. Living collections also have a legacy in helping botanists describe new species and can be designated as types. Just like herbarium specimens that have been stowed away in cabinets and have gone undescribed for a century or more (Bebber et al., 2010), many living plants brought back to European gardens from historic expeditions also went unnamed for years. One such example is the Eastern Cape giant cycad, *Encephalartos altensteinii*, collected by Kew Garden’s first plant hunter, Francis Masson (1741–1805). Living plants arrived at Kew Garden in London in 1775 after Kew’s first plant hunting trip to South Africa. The species however remained unnamed for decades; the German botanist Johan Georg Christian Lehmann (1792–1860) described the species in 1834 from a living plant at Hamburg Botanic Garden almost 60 years later (Figure 1). Plants collected by Masson still live on today at Kew. At 260 years, it is considered the world’s oldest potted plant (Figure 2). However, it is the plant that lives on at the Hamburg Botanic Garden that is designated as a living type. The plant in Hamburg was brought to the garden by the Danish plant collector Christian Friedrich Ecklon (1795–1868) in 1832, and remarkably survived damages incurred at the botanic garden during World War II. An off-shoot of the Hamburg plant was sent to Zurich Botanic Garden between 1843–1845 and is also still growing there today.

*Encephalartos altensteinii* is designated as vulnerable to extinction and 4000–10,000 individuals are estimated to remain in the wild (Donaldson, 2010; IUCN, 2020). Seventy-seven (77) different botanical gardens worldwide are listed as having at least one plant of this vulnerable species in their collections (BGCI Plant Search, 2020); however, in a recent survey of these gardens (only 12% of the gardens responded) only one of the gardens reported having provenance information for this species – aside from the oldest potted plant at Kew and the living type in Hamburg (Iwanycki Ahlstrand, unpublished data). Could the majority of the plants held in botanical collections have links to the very first collecting trip by European plant collectors? Or do the plants kept by botanical gardens represent differing genetic lineages, stemming from different collecting trips? Furthermore, are the historic living plants kept by botanical gardens still found in the wild today? Retracing where the *Encephalartos altensteinii* plants in living botanical collections come from using
population genomic methods could reveal how unique each accession is and would equip conservation scientists with the type of pedigree information needed to assist breeding and recovery work (Fant et al., 2016; Rae, 2011).

5 | Zamia acuminata: THE CASE OF A MYSTERY TYPE LOCALITY

Zamia acuminata Oerst. ex Thiselton-Dyer was first collected as a herbarium specimen by Danish botanist A.S. Ørsted (1816–1872) on his travels through Nicaragua and Costa Rica between 1845 and 1848. The specimen, which contained no reproductive structures, was brought back to Copenhagen and was eventually sent to British botanist William Thiselton-Dyer who described and named the species around 40 years later in 1884. The type specimen is maintained in Herbarium (C) at the Natural History Museum of Denmark, along with Ørsted’s unpublished field notes. A collection date and collection number are lacking for this specimen, and unfortunately the cycad is not mentioned in Ørsted’s field notes or in his publications (i.e. Ørsted, 1863). The collection locality is listed as “ad flumen S. Juan Nicaragua” (see Figure 3a). However, when we compared this label to those of other specimens collected by Ørsted from the same locality, the ink and penmanship differ, suggesting that the label for this specimen may have been written at a different time, or even by a different person. Furthermore, over the last 160 years plants resembling Ørsted’s type have never been collected in the vicinity of the San Juan River—either in Nicaragua or in neighboring Costa Rica, which the San Juan river divides.

In an attempt to piece together where Zamia acuminata was actually collected, modern day botanists retraced Ørsted’s footsteps...
and extensively reviewed cycad material in herbaria worldwide. Based on the type locality being at the San Juan River, assumptions were made that the species occurs in Costa Rica (reviewed in Lindström et al., 2013) but no cycads matching Ørsted’s type had been vouchered from the area. Lindström et al. (2013) provide convincing geographical and morphological data for specimens that do resemble Ørsted’s original collection – all which are concentrated in a small area off the Pacific Coast of Costa Rica and not in the vicinity of the San Juan River (Figure 3b). The collection locality on Ørsted’s type specimen is concluded to be erroneous. Species collected in Nicaragua and Panama, previously thought to be Z. acuminata, have subsequently been determined to be other Zamia species.

All evidence indicates that Ørsted’s Z. acuminata type must have been collected during his travels in Costa Rica – not Nicaragua. By reviewing Ørsted’s collection localities for his other type specimens and his travel itinerary and notes, the type specimen had to have been collected in Costa Rica in November 1846 or in April 1847 based on matching Ørsted’s travels to the populations of Z. acuminata determined by Lindström et al. (2013).

Zamia acuminata is designated as vulnerable (IUCN, 2020; Stevenson, 2010) and is listed as being in only nine botanical gardens (BGCI Plant Search, 2020). The case of the erroneous type locality is another example where population genomic methods could confirm the type locality and determine whether the plants cultivated at these nine gardens worldwide are true to type for Z. acuminata or perhaps represent examples of some of the reassigned species (see Lindström et al., 2013).

6 | CONCLUDING REMARKS

Cycads in living botanical collections are excellent models to connect people to the fascinating world of plants, evolution, conservation and human use; however, their role in conservation is currently underexploited and the lack of provenance data limits their use. By identifying where in the wild the cycads in our living collections come from, international ex situ conservation goals can be attained. Ex situ conservation is always considered secondary to the conservation of plants in situ. However, given that entire populations have already been lost due to overharvesting and habitat destruction, and the likely scenario that wild cycad populations will continue to dwindle as a result of these anthropogenic threats, the plants that are maintained in botanical gardens can serve as important sources for restoration and recovery programs.

KEYWORDS
botanic gardens, botanical collections, cycads, ex situ conservation, historical expeditions, retracing origins

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AUTHOR CONTRIBUTIONS
NIA developed the scope of the article and DWS provided species-specific cycad case studies. NIA wrote the manuscript with DWS.

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