

# The role of botanical gardens in scientific research, conservation, and citizen science

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## ABSTRACT

Plant diversity is currently being lost at an unprecedented rate, resulting in an associated decrease in ecosystem services. About a third of the world's vascular plant species face the threat of extinction due to a variety of devastating activities, including, over-harvesting and over exploitation, destructive agricultural and forestry practices, urbanization, environmental pollution, land-use changes, exotic invasive species, global climate change, and more. We therefore need to increase our efforts to develop integrative conservation approaches for plant species conservation. Botanical gardens devote their resources to the study and conservation of plants, as well as making the world's plant species diversity known to the public. These gardens also play a central role in meeting human needs and providing well-being. In this minireview, a framework for the integrated missions of botanical gardens, including scientific research, *in/ex situ* conservation, plant resource utilization, and citizen science are cataloged. By reviewing the history of the development of Kunming Botanical Garden, we illustrate successful species conservation approaches (among others, projects involving *Camellia*, *Rhododendron*, *Magnolia*, *Begonia*, *Allium*, *Nepenthes*, medicinal plants, ornamental plants, and Plant Species with Extreme Small Populations), as well as citizen science, and scientific research at Kunming Botanical Garden over the past 80 years. We emphasize that Kunming Botanical Garden focuses largely on the *ex situ* conservation of plants from Southwest China, especially those endangered, endemic, and economically important plant species native to the Yunnan Plateau and the southern Hengduan Mountains. We also discuss the future challenges and responsibilities of botanical gardens in a changing world, including: the negative effects of outbreeding and/or inbreeding depression; promoting awareness, study, and conservation of plant species diversity; accelerating global access to information about plant diversity; increasing capacity building and training activities. We hope this minireview can promote understanding of the role of botanical gardens.

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## 1. Botanical gardens: a unique benefit for humans

Although the birth of the “garden” dates back to the Zhou dynasty in China, the modern concept of a botanical garden originated in Europe (Italy's Padova Botanic Garden was built in 1545). Today,

there are about 2500 botanical gardens in the world (Golding et al., 2010). Together, these botanical gardens cultivate more than 6 million accessions of living plants, representing around 80,000 taxa, or about one-quarter of the estimated number of vascular plant species in the world (Jackson, 2001; O'Donnell and Sharrock, 2017). These gardens thus play a central role in the *ex situ* conservation and exploration of global plant biodiversity (Mounce et al., 2017). Indeed, one of the targets of the Global Strategy for Plant Conservation (GSPC) is to have 70% of the world's threatened plant species conserved *ex situ* (Callmander et al., 2005; Sharrock and Jones, 2009; Huang, 2018). Botanical gardens also have an

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important role in the preservation of species necessary for human use and well-being (Waylen, 2006; Dunn, 2017), and this role is likely to become increasingly important as climate change becomes more severe (Donaldson, 2009; Primack and Miller-Rushing, 2009; Ren and Duan, 2017).

The range of scientific activities conducted by botanical gardens often includes conservation, propagation, horticulture, seed science, taxonomy, systematics, genetics, biotechnology, education, restoration ecology, public education, and much more ([http://www.bgci.org/garden\\_search.php](http://www.bgci.org/garden_search.php); Maunder et al., 2001; Donaldson, 2009). Plant diversity is currently being lost at an unprecedented rate, resulting in an associated decrease in ecosystem services. Currently about a third of the world's 300,000–450,000 vascular plant species face extinction due to a variety of devastating anthropogenic activities, including over-harvesting, over-exploitation through destructive agricultural and forestry practices, urbanization, environmental pollution, land-use changes, exotic invasive species, and global climate change (Pitman and Jørgensen, 2002; Ren and Duan, 2017). There is, therefore, an increased need to develop integrative conservation approaches for plants, particularly those threatened plant species in the wild (Li and Pritchard, 2009).

In this minireview, we introduce the scientific research, *in/ex situ* conservation and utilization, citizen science, education, and public communication taking place at Kunming Botanical Garden (KBG). Furthermore, to clarify the integrated functions of botanical gardens across the world, we introduce the future challenges and responsibilities these gardens face. Education, promoting awareness, and capacity building, involving both the public and staff at botanical gardens, are vital functions of modern botanical gardens (Blackmore et al., 2011). These functions provide unique opportunities for plant biodiversity research, horticulture, and conservation biology in popular public places. Raising public awareness of the problems facing our planet may be sufficient to bring about fundamental behavioral changes. Finally, we also want to emphasize specific work done at KBG to commemorate its 80<sup>th</sup> anniversary.

## 2. The functions of botanical gardens

### 2.1. Scientific research

Botanical gardens are good locations for many branches of scientific research. Botanical gardens not only serve as taxonomic and systematic research centers (Dosmann, 2006; Stevens, 2007), but they also play an important role as valuable sources of plant ecology data collection such as phenological indication of climate change, plant physiology and plant growth tactics, and plant–animal interactions (Coates and Dixon, 2007; Gratani et al., 2008; Dawson et al., 2009; Primack and Miller-Rushing, 2009; Wang et al., 2018). For plant functional characteristics, botanical gardens can provide a large set of species to study functional trade-offs between species traits and plant performance (Herben et al., 2012). The study of bamboos at Xishuangbanna Tropical Botanical Garden in Yunnan, China by Cao et al. (2012) revealed that the maximum height of grasses is determined by their roots. Another example is the monitoring of plant phenology varieties, which has a long tradition in some gardens and is regarded as one of the most sensitive indicators of climate impacts on vegetation in mid-latitude areas (Menzel et al., 2006). In fact, botanical gardens have contributed greatly to our understanding of the responses of plant species to global climate change (Primack and Miller-Rushing, 2009).

Additionally, botanical gardens are suitable locations for investigations into pollination ecology, seed dispersal, and other

interactions between plants and animals. For example, through the study of seed dispersal in an endangered species, *Taxus chinensis*, in an *ex situ* conservation population introduced into the Nanjing Botanical Garden in the 1950s, researchers were able to propose that any process for the conservation of these Chinese yews should comprise not only conservation of the trees, but also conservation of these tree's avian dispersers and habitats for seed germination and seedling growth (Lu et al., 2008; Li et al., 2014). Research at botanical gardens has also guided conservationists not to neglect the potential risks of hybridization in *ex situ* collection of threatened plant species. Specifically, spontaneous hybridization in *ex situ* facilities has been shown to undermine the genetic integrity of *ex situ* collections and may contaminate open-pollinated seeds or seedlings (Ye et al., 2006; Zhang et al., 2010). To effectively conserve and manage the *ex situ* population of endangered species in botanical gardens, pollination ecology, including breeding system, effective pollinators, and other factors should be recorded and monitored carefully (Norstog et al., 1986; Zhang and Ye, 2011; Chen et al., 2015a). Moreover, native pollinator biodiversity is related to successful naturalization of alien plants in botanical gardens (Razanajatovo et al., 2015). Moreover, successful naturalization of alien plants in botanical gardens also is related to native pollinator biodiversity (Razanajatovo et al., 2015).

Plant conservation genetics provides suitable tools to guide conservation and successful restoration, measure and monitor processes, and ultimately minimize extinction risk of threatened plant species in nature (Kramer and Havens, 2009). Over the past decades, conservation genetics has focused largely on the genetic consequences of small population size that may limit survival of populations and species. However, recent reviews on the genetic aspects of plant conservation have indicated that genetic erosion poses an increasing threat to the long-term survival of rare and common species (Desalle and Amato, 2004; Ouborg et al., 2006). For the purposes of scientific conservation, it is generally accepted that establishing a genetically representative *ex situ* collection requires that 50 populations per species be sampled, with 50 individuals per population (Brown et al., 1995). However, for very rare tree species already reduced to a handful of individuals in the wild, it is not possible to meet these guidelines. Bringing the species into cultivation and establishing *ex situ* collections must be an urgent priority and may represent the last chance against extinction in the wild (Oldfield et al., 2009).

### 2.2. *In/ex situ* conservation and utilization

Living plant collections are the main contribution of botanical gardens and Botanical Gardens Conservation International (BGCI) estimates that there are 6.13 million accessions in botanical gardens, comprising more than 80,000 species (<http://www.bgci.org/resources/1528>; Jackson, 2001). The conservation of living plants in botanical gardens, especially of species that are threatened in the wild, has a long tradition and has greatly contributed to our understanding of threatened species (Donaldson, 2009). The Convention on Biological Diversity defines *ex situ* conservation as the conservation of components of biological diversity outside their natural habitats. *Ex situ* conservation, which plays an important role in saving threatened plant species, is generally associated with botanical gardens. One of the major objectives of botanical gardens is to create and support collections of native taxa, and to build and maintain stocks of plants for *ex situ* conservation and sustainable utilization of plant resources in the world (Cibrian-Jaramillo et al., 2013).

A basic framework for integrated plant species conservation in a botanical garden includes identification and management of threats, long-term *ex situ* and/or *in situ* germplasm storage,

research and development information management, horticulture and living collections, conservation priorities, and environmental education (Blackmore et al., 2011). Botanical gardens often cultivate rare plant species for the purpose of *ex situ* conservation (Dosmann, 2006). As of 2013, botanical gardens of the Chinese Academy of Sciences (CAS) have collected about 20,000 vascular plant species for conservation, which accounts for approximately 90% of all plant species maintained by all Chinese botanical gardens. This demonstrates that CAS has conserved at least 60% of China's native flora and provided an important reserve of plant resources for sustainable economic development in China. Botanical gardens are also ideal places to integrate the study and conservation of trees species that are endangered in the wild (Newton and Oldfield, 2012). As an insurance policy against extinction, the cost of *ex situ* seed conservation is estimated to be as little as 1% of that of *in situ* conservation (Li and Pritchard, 2009).

Strategies for conserving living plants vary among and within garden collections (Farnsworth et al., 2006). The direct evaluation of the conservation value of an *ex situ* collection is difficult (Schal and Leverich, 2004). Understanding effective sampling structure to allow the capture of significant variation for living plant conservation collections is very important for *ex situ* botanical populations of endangered species. Botanical gardens cultivate many species introduced from different areas, but most cultivated taxa are held in only a small number of collections, and mostly only in small populations without sufficient genetic representation. Lack of genetic exchange and stochastic processes in small populations make them susceptible to detrimental genetic effects (Brütting et al., 2013). Therefore, both *in situ* ecosystem management and *in situ* conservation play important roles for the conservation of certain plant species in their native habitats. For example, Xishuangbanna Tropical Botanical Garden plays a leading conservation role because of more native species distributed in that area (Chen et al., 2009). The botanical garden conserves more than 10,000 plant species with living collections. Of course, the classic functions of a botanical garden, i.e., plant resource development and utilization, should not be neglected in modern botanical gardens.

### 2.3. Citizen science and popularization

In addition to scientific activities such as conservation and research, public education and garden displays are also important aims of botanical gardens in different countries (Maunder et al., 2001; Donaldson, 2009). Citizen science, the process whereby citizens engage in science as researchers (Kruger and Shannon, 2000), has long been associated with botanical gardens. Nowadays, the focus of modern citizen science is not "scientists using citizens as data collectors," but rather, "citizens as scientists" (Conrad and Hilchey, 2011). In fact, decision-makers and NGOs are enhancing their use of volunteers to increase their ability to monitor and control natural resources, assess at-risk species, and protect natural conservation areas (Silvertown, 2009). For instance, over the past 36 years, volunteers were able to provide evidence for dramatic declines in the numbers of monarch butterflies in western North America over the past 36 years (Schultz et al., 2017). Using a citizen science program to investigate the spread of invasive plant species by local resident may promote both knowledge and behavioral changes in local communities (Jordan and Ehrenfeld, 2011). In fact, developing and implementing public data-collection projects often yields both scientific and educational outcomes such as biological research, biodiversity monitoring, and science education (Raimondo et al., 2006; Bonney et al., 2009).

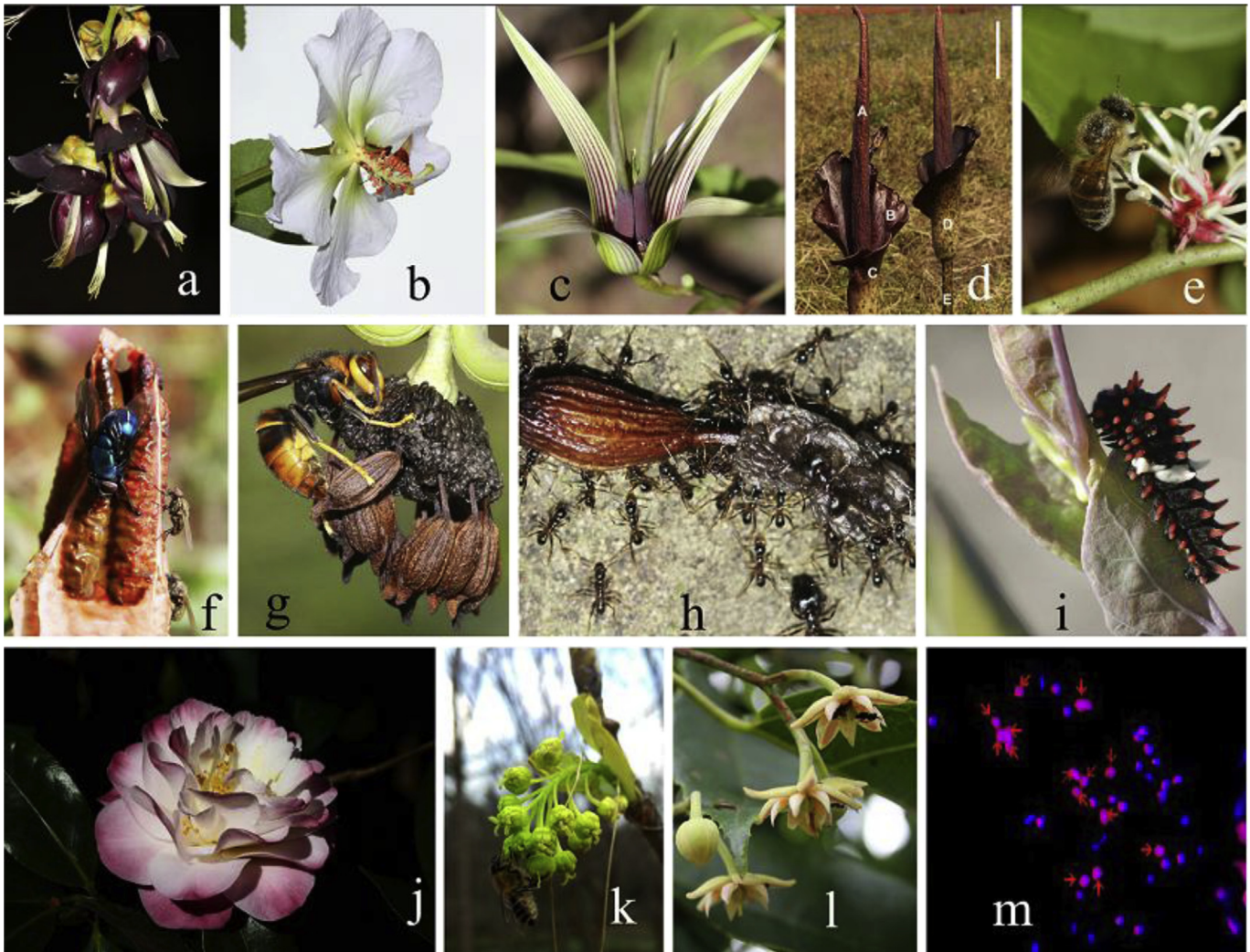
Cooperation between scientific researchers and volunteers from local communities have the potential to deepen the scope of research and increase the ability to collect scientific data (Close

et al., 2006; Fu et al., 2006; Aguraju et al., 2008). Local resident may contribute valuable information because they have more local knowledge from their communities (Cohn, 2008). Collection-based botanical gardens exhibit plant species and thus have a special connection with nature (Miller et al., 2004). Citizen science projects at botanical gardens include studies on demographics (Wagenius et al., 2007), reproduction (Donaldson et al., 2002; Wagenius, 2006), and ecological and genetic responses to habitat fragmentation (Neale et al., 2008). According to a recent study on the interactions between climate change and the functions of botanical gardens, environmental education or citizen science can affect the knowledge, attitudes, and beliefs of the people involved (Sellmann, 2014). For instance, by conducting pollination in botanical gardens, citizen scientists were able to help children make the transition from seeing the natural world to scientifically observing nature (Eberbach and Crowley, 2017).

### 3. A case study: Kunming Botanical Garden

KBG was founded in 1938 and it is affiliated with the Kunming Institute of Botany, Chinese Academy of Sciences. It is situated close to the Black Dragon Pool park in a quiet northern suburb of Kunming. The Garden is located at 25°07'04.9"–25°08'54.8"N, 102°44'15.2"–102°44'47.3"E at an elevation of 1914–1990 m above sea level, and has an annual average rainfall of 1006.5 mm, an annual average temperature of 14.7 °C and an annual average relative humidity of 73%. KBG focuses largely on the *ex situ* conservation of plants from Southwest China, especially endangered, endemic or economically important plant species native to the Yunnan Plateau or the southern Hengduan Mountains. The primary research of KBG is on the cultivation and domestication of resource plants and the biology and botany of *ex situ* conservation. The garden aims to maintain a comprehensive multidisciplinary botanical garden, integrating scientific research, species conservation, public education and biological technologies, visitor services, general tourism, and the development of sustainable utilization of plant resources.

KBG covers an area of 44 ha, has 16 specialist plant collections, and contains over 7000 plant species and cultivars. The garden has received more than 40 national and provincial awards and 50 authorized patents. Some 100 plant cultivars have been bred and registered, and publications over the last decades have included about 60 monographs and 550 scientific papers (Fig. 1). The garden, which receives around 800,000 visitors per year, is an important center for species conservation (Fig. 2). The garden is an important center for species conservation (Fig. 2). Well-known gardens of KBG include the *Camellia* Garden (633 species and varieties), the *Rhododendron* Garden (about 200 species), the Medicinal Plant Garden (more than 1000 species), the Ornamental Foliage and Fruit Plants (more than 400 species), the Magnolia Family Garden (11 genera and about 110 species), the Rock Garden (more than 300 species), the Monocotyledon Garden (near 200 species), the Rose Family Garden (25 genera and more than 110 species), the Arboretum (about 1500 species), the *Begonia* Garden (about 500 species), the Plant Species with Extreme Small Populations Garden (27 species), the *Allium* Garden (about 30 species), the Greenhouses (about 4025 m<sup>2</sup> and 4430 species), the Gymnosperm Garden (more than 200 species), and more. There are more than 100 plant species which have fewer than five individuals growing in KBG. Having established these specialized gardens, the next step for KBG should be to evaluate their status from a conservation perspective. For example, research that evaluates the *Camellia* collection should identify what percent of the *ex situ* collection consists of Chinese plants, how many species are on the IUCN list, how many are on the national conservation list and more. Therefore, a conservation



**Fig. 1.** Representative research conducted at KBG: a) *Mucuna sempervirens* pollinated by squirrel (Chen et al., 2012); b) Auto self-pollination of *Hibiscus aridicola* (Zhang et al., 2011); c) Fetid odor of *Stemona tuberosa* attracts fly (Chen et al., 2017a); d) Inflorescence of *Amorphophallus konjac* mimics livor mortis to deceive pollinators (Chen et al., 2015b); e) Sexual reproduction of winter-flowering monoecious plant *Pachysandra axillaris* mediated by honeybee (Ge et al., 2017); f) Spore dispersal of fetid *Lysurus mokusin* by feces of mycophagous insects (Chen et al., 2014); g, h) Seed dispersal of *Stemona tuberosa* by hornet and ants (Chen et al., 2017b, 2018); i) Vulnerable *Byasa daemonius* consumes endangered *Aristolochia delavayi* (Chen et al., 2015a); j) New variety of *Camellia* "Spring Daze"; k, l) Pollination ecology of *ex situ* conservation *Acer yangbiense* and *Craigia yunnanensis* conducted by Jing Yang (unpublished data); m) Genomic *in situ* hybridization of *Camellia* conducted by Jing Yang. Photos taken by G Chen (a–i), ZF Chen (j), and J Yang (k–m).

strategy to capture the genetic variation of a wild population in a botanical garden must be developed to guide the *ex situ* conservation strategy in this garden.

Over the past few years, staff from KBG successfully introduced more than 58 pitcher plant species from areas with high elevation (Fig. 3). Because of the relatively high altitude of KBG, and the temperature difference between daytime and night, introduced pitcher plants from areas of high elevation grow much better at KBG than in their natural habitats. Over the next ten years, we plan to collect, conserve, and propagate more than 80% of the high-elevation nepenthes from around the world at KBG. Recently, to create new varieties of pitcher plants, Wang Xi has used horticultural techniques to conduct artificial pollination experiments in the botanical garden. We plan to collect, conserve, and propagate more than 80% of nepenthes in KBG from high altitude area in the world. His work on the *ex situ* conservation of these peculiar ornamentals had made a substantial contribution to the KBG.

The history of public education and citizen science at KBG started with the initial public announcement in the 1940s, although

KBG officially opened to the public in June 1996. Over the past twenty years, many environmental education and citizen science projects have been conducted at KBG (Fig. 3). For example, volunteers have investigated the diversity of ants (more than 42 species) and birds (more than 107 species), and studied interactions between animal and plant species at KBG. In addition, KBG staff hold an annual competition to honor excellence in the popularization of science, issue a themed calendar each year, and regularly lead capacity building and training courses in horticulture and landscape construction.

The Lijiang Alpine Botanical Garden and its associated Jade Dragon Field Station are a collaboration launched in 2001 between the Kunming Institute of Botany and the Royal Botanical Garden Edinburgh (Blackmore and Paterson, 2006). All the activities and developments within the Lijiang Alpine Botanical Garden and Jade Dragon Field Station are driven by the importance of plants and the role that they play in securing a future for humanity. The botanical garden is located in the Hengduan Mountains, which is a biodiversity hotspot in China. The aims of this botanical garden are



**Fig. 2.** Some representative plant species conserved in KBG: a) *Musella lasiocarpa*; b & c) *Buddleja delavayi* and its mutant; d) *Stemona mairei*; e) *Lilium sargentiae*; f) *Rhododendron delavayi*; g) *Holcoglossum rupestre*; h) *Camellia nitidissima*; i) *Manglietiastrum sinicum*; j) *Primula denticulate*; k) *Meconopsis racemose*; l) Plant Species with Extreme Small Populations garden in KBG. Photos taken by G Chen (a–d), CQ Liu (e), G Yao (f, h, j), ZL Dao (g), ZF Chen (k), and J Yang (i, l).



**Fig. 3.** Citizen science and public education: a) Greenhouse of KBG; b) Pitcher plant Garden; c) *Allium* Garden; d) Public education involved local primary school students; e & f) Local residents involved scientific research with staffs from KBG. Photos taken by ZF Chen (a, c, d, f), W Xi (b), G Chen (e).

research, public education, and conservation, in addition to harboring greenhouses that support integrated *in situ* and *ex situ* conservation in the area (Blackmore et al., 2011). The primary purpose of the Jade Dragon Field Station is the conservation of

threatened plants and habitats through capacity-building projects that aim to bring about sustainable land management.

Re-introduction programs and restoration are extremely important components of integrative conservation, especially for

plant species with small populations. Plant Species with Extremely Small Populations (PSESP), a conservation concept developed in China in 2005, are characterized by small remaining populations (lower than the minimum viable population), a restricted habitat, a high risk of extinction, and exposure to a high level of disturbance (Ma et al., 2013; Sun, 2013). A species with fewer than 5000 mature individuals in the wild and fewer than 500 in each isolated population qualifies for designation as a PSESP (Sun, 2016; Yang and Sun, 2017). The identification of a high level of disturbance and irreversible habitat destruction distinguishes PSESP from naturally rare species. To promote the conservation of PSESP, the Ministry of Science and Technology granted funding for a National Key Programme: Survey and Germplasm Conservation of PSESP in Southwest China (Yang and Sun, 2017). The program started in February 2017 and will last for 5 years, with funding of RMB 24.26 million. In the past 13 years, re-introduction programs and restoration of PSESP were conducted and achieved exciting successes in Yunnan province and KBG (Sun, 2016).

Scientific research at KBG focuses on different projects. The “Gold Dollar” tobacco cultivar was successfully introduced from the USA by KBG. This introduction and subsequent cultivar improvement substantially changed the cultivar structure of tobacco production and made a significant contribution to the tobacco industry in Yunnan province. Other examples include the investigation into and artificial cultivation of *Dioscorea* species; the introduction of olive trees and the study of their oil composition; the study of the life history, reproductive tactics, cultivation, and chemical composition of *Gastrodia elata*, *Cyanotis arachnoidea*, and *Paris* species, all of which have greatly promoted economic and social development in China. Research on the integrative conservation of *Camellia*, *Buddleja*, *Primula*, *Rhododendron*, *Cycas*, *Begonia*, *Magnolia*, orchids, *Stemona*, *Trigonobalanus*, as well as studies into the evolution of chromosomes in angiosperms, have established an important status of KBG in the field of conservation in China.

#### 4. Future challenges and responsibilities of botanical gardens in a changing world

Different human activities, such as *in situ/ex situ* conservation experiments and horticultural hybrid processes in botanical gardens, are bringing previously isolated populations and species into contact (Kramer and Havens, 2009; Blackmore et al., 2011). However, the artificial gene flow that this creates may lead to the decline or loss of plant species via outbreeding depression. Indeed, recent studies have indicated the negative effects of outbreeding depression on population persistence (Fenster and Galloway, 2000; Edmands, 2007). Therefore, care needs to be taken to ensure that inbreeding and outbreeding are avoided in those accessions grown in botanical gardens.

Botanical gardens aim to promote the awareness, study, and conservation of plant species diversity. However, few studies have investigated the species diversity of botanical gardens themselves. Pautasso and Parmentier (2007) suggested that the living collections of the world’s botanical gardens were not related to species-richness patterns observed in natural ecosystems. The authors call for an increase in funds to botanical gardens in species-rich regions and to scientists in underfunded countries. Additionally, botanical gardens should play key roles in the development of plant information data base to monitor variable environmental factors in gardens (Stevens, 2007; Paton, 2009). Accelerating global access to plant diversity information is necessary to managers from different botanical gardens (Lughadha et al., 2009).

Horticultural actions are important parts of *in situ* and/or *ex situ* plant conservation in botanical gardens, conservation horticulture

research is uniquely suited for staff in botanical gardens (Kay et al., 2011). In past decades, however, the positive contribution that botanical garden horticulture has on plant conservation has been neglected by many researchers (Blackmore et al., 2011). Therefore, we suggest that botanical garden horticulturists collaborate with other researchers in taxonomy, genetics, systematics, and environmental education.

In addition, conservation effect assessment and related studies are critical for conservation success in botanical gardens, and staff in these scientific centers should utilize their extensive field knowledge and experience to conduct these assessments. Otherwise, the aims of scientific conservation of threatened plant species may not be achieved.

Citizen science provides a special opportunity for botanical gardens, especially given the high visitor levels both on site and online (Donaldson, 2009). However, potential conflicts between scientific research, educational activities, and the motivation of people involved should be considered during citizen science program design (Jordan and Ehrenfeld, 2011; Chen et al., 2015a). Citizen science projects conducted in botanical gardens should adopt basic rules: data collected by public must be rectified by different experts; methods of data collection must be standardized; and volunteers must receive feedback about their contribution to botanical gardens.

Botanical gardens have great abilities to explore plant diversity and plant resource utilization. However, in mainstream plant science, research conducted in botanical gardens is often neglected. Scientists at botanical gardens do not frequently become leaders in the plant science community (Blackmore et al., 2011). Capacity building and training activities (plant collection and identification, species recording and assessments, horticulture and conservation techniques, public education and citizen science) need to be conducted to train potential botanists and horticulturists in botanical gardens.

Finally, since the earth is entering the Anthropocene, a ‘new conservation’ concept needs to be discussed, and new technologies may also present new opportunities for researchers at botanical gardens for the post-GSPC 2020 (Heywood, 2017). As a scientific botanical garden focusing on science and conservation, having a comprehensive collection policy for living collections is vital. This would consider, for example, plants of wild origin, representative populations, adequate sample sizes, explicit documentation of provenance and other collection details, and with collections being linked directly to botanical project design. To strengthen capacity and scientific research Chinese botanical gardens should i) construct specialized gardens and promote research related to those gardens, ii) improve and develop facilities for research that relies on molecular biology, and iii) construct digitized botanical gardens.

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#### Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.pld.2018.07.006>.

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