EX-SITU CONSERVATION OF PLANT DIVERSITY IN THE WORLD'S BOTANIC GARDENS

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ABSTRACT

Botanic gardens conserve plant diversity *ex-situ* and can prevent extinction through integrated conservation action. Here we quantify how that diversity is conserved in *ex-situ* collections across the world's botanic gardens. We reveal that botanic gardens manage at least 105,634 species, equating to 30% of all plant species diversity, and conserve over 41% of known threatened species. However, we also reveal that botanic gardens are disproportionately temperate, with 93% of species in the northern hemisphere. Consequently, an estimated 76% of species absent from living collections are tropical in origin. Furthermore, phylogenetic bias ensures that over 50% of vascular genera, but barely 5% of non-vascular genera, are conserved *ex-situ*. While botanic gardens are discernibly responding to the threat of species extinction, just 10% of network capacity is devoted to threatened species. We conclude that botanic gardens play a fundamental role in plant conservation, but identify actions to enhance future conservation of biodiversity.

INTRODUCTION

Plants are essential for life, capturing solar energy, and creating the biomass that underpins the biosphere. Plants underpin ecological processes such as climate regulation, carbon dioxide absorption, soil fertility and the purification of water and air [1], and provide the food, medicines, building materials and fuel that sustain human life. Yet an estimated 20% of plant diversity is threatened with extinction [2]. The extinction threat is largely anthropogenic, including habitat degradation, invasive species, resource over-exploitation, and climate change [3]. It is estimated that 75% of the planet's land surface is experiencing human pressures such as expansion of built environments[4], with approximately 40% given to agriculture [5]. Even in wilderness areas, plant populations are vulnerable to invasive species, pests, diseases and a changing climate [6]. For plants with natural distributions within transformed environments, *ex-situ* conservation may be the only way they can survive in the short, medium and even long-term[7]. Crucially, threatened plant diversity may also hold the key to solving our major challenges in areas of food security, energy availability, water scarcity, climate change, and habitat degradation[8].

Botanic gardens are managed for many purposes, but offer the opportunity to conserve plant diversity *ex-situ*, and have a major role in preventing species extinctions through integrated conservation action [7]. Recognising the unique position of botanic gardens for plant conservation, the first *Botanic Gardens Conservation Strategy* was published in 1989, developing the role of botanic gardens in conservation throughout the 1990's [8]. Then, in 1998, Botanic Gardens Conservation International (BGCI), a consortium of 800 botanic gardens in >100 countries, launched an international consultation process to update the Strategy, taking into account the *Convention on Biological Diversity* (CBD). The consultation culminated in the adoption of the *Global Strategy for Plant Conservation* (GSPC), which seeks to halt the loss of plant diversity and to secure a sustainable future where human activities support plant diversity, and where the diversity of plants support human livelihoods and well-being [9]. The strategy outlines sixteen targets encompassing knowledge, conservation, sustainable use, awareness and capacity building activities. Botanic gardens contribute to meeting all targets, but as the main institutions for *ex-situ* plant conservation, are key to achieving GSPC Target 8, which calls for "*at least 75% of threatened plant species in ex-situ collections, preferably in the country of origin, and at least 20% available for recovery and restoration programmes by 2020.*"

BGCI recently published its vision for a botanic garden-centered, cost-effective, rational global system for the conservation and management of all plant diversity [10]. Two assertions lie at the core of the central role of botanic gardens in the conservation and management of plant diversity. First, that there is no technical reason why plant species should become extinct, given the array of *ex-situ* and *in-situ* conservation techniques such as seed banking, cultivation, tissue culture, assisted migration, species recovery, and ecological restoration [11,12]. And second, that as a professional community, botanic gardens possess a unique skill set that encompasses finding, identifying, collecting, conserving and growing plant diversity across the taxonomic spectrum [10]. While it is difficult to prove a plant species *cannot* be conserved vegetatively or as seed, it is possible to evaluate the potential for *ex-situ* conservation by assessing the extent of the plant diversity, including threatened species, that botanic gardens are already conserving and managing *ex-situ*.

In this paper, we explore how plant diversity is currently conserved across the world's botanic gardens, and how well botanic gardens are performing with respect to plant conservation priorities. We define the extent of the global network, and examine biases in the distribution of botanic gardens and the availability of digitised collection data. We estimate the minimum holdings of the global network of botanic gardens with respect to plant diversity, determine the impact of the biogeographic distribution of botanic gardens for conservation goals, and identify significant biogeographic and phylogenetic gaps in *ex-situ* collections. Finally, we quantify the number of threatened species within *ex-situ* collections and assess whether the global network of botanic gardens is discernibly responding to the threat of species extinction. We conclude by discussing how to build on these findings to further engineer a botanic garden-centered global system that can prevent species extinctions in perpetuity.

RESULTS AND DISCUSSION

Quantifying the Extent And Content of Botanic Gardens

To evaluate the geographic extent of the botanic garden network, and the degree to which digital collection data is available, we applied the most widely accepted definition of a botanic garden, as an institution '*holding documented collections of living plants for the purposes of scientific research, conservation, display and education*' [9]. BGCI have accumulated data on botanical institutions and have assembled a digital directory of the world's botanic gardens within a database called '*GardenSearch'* (https://www.bgci.org/garden_search.php). Applying this definition to the '*GardenSearch*' database, we estimated that there are over 3269 botanical collections in 180 countries around the world (BGCI, 2012) (Fig. 1a). Of these 3269 institutions, BGCI has amassed collection data from 34% or 1,116 institutions, in the '*PlantSearch*' database (https://www.bgci.org/plant_search.php), the most comprehensive list of botanic garden accession names, containing 1,330,829 records of 481,696 taxon names. We analysed the *PlantSearch* database set against the most comprehensive list of plant taxa, '*The Plant List*', and applied rigorous cleaning to these 481,696 '*PlantSearch'* taxa, removing invalid taxon names, deceased accessions, and horticultural cultivars. We can only present a minimum estimate of the diversity held in botanic gardens and associated seed banks, as our digitised data is derived from one third of documented botanic gardens within the *GardenSearch* database (See Fig. 1b). But we show that, of the 350,699 accepted plant species (TPL 2013), 105,634 or 30% are held within the living collections of the global botanic garden network **(**Fig. 2a). These numbers equate to 59% of all plant genera (Fig. 2b), 75% of all embryophyte plant families (Fig. 2c) and 93% of tracheophyte plant families (Fig. 2d), indicating a remarkable degree of taxonomic coverage within *ex-situ* collections (Supplementary Table 1).

Biogeographic Distribution of *Ex-Situ* Collections and Data

The relative number of species records in each of the 1,116 BGCI member institutions, is depicted in Fig. 1B where the diameter of each bubble is scaled to the number of species recorded at an institution. It is evident that there are biases both in the distribution of botanic gardens (Fig. 1a), and the extent to which the data that has been uploaded to the '*PlantSearch*' database (Fig. 1b). The absence of digital data does not necessarily equate to species absence, but in evaluating global targets and defining species conservation priorities, absence of a species and absence of data can be an equivalent problem, and here they are treated in the same way. Fig. 1A and 1B show that the most dominant world-wide bias in the distribution of botanic gardens, and availability of associated digitised collection data, is a phenomenon termed positive latitudinal bias[13]. Several countries in the southern hemisphere, such as South Africa, Australia, and New Zealand, are major contributors of digital collection data. Still, 91% of recorded accessions, and 93% of recorded species are documented from *ex-situ* collections in the northern hemisphere (Fig. 3a). This bias is due to the primary determinants of the geographical distribution of botanic gardens and species richness in botanic gardens, including socioeconomic factors such as GDP and metropolitan population size[14]. But although explicable, it remains essential that biogeographic gaps in digital collection data are filled, to provide the robust cyber-infrastructure needed for coordinated *ex-situ* plant conservation.

A positive latitudinal gradient, where botanic garden species diversity increases in temperate latitudes, runs counter to natural latitudinal gradients, where tropical ecosystems harbour the bulk of plant species diversity[15]. The consequences of this skewed latitudinal distribution of botanic gardens (Fig. 3A) for plant conservation has not been quantified on a global scale. Here we made that assessment, asking how the latitudinal distribution of a species affects the likelihood of its representation within the botanic garden network. We retrieved species occurrence data for 236,904 accepted plant species, calculated the median of the latitudinal range for each species, cross-referenced these data with recorded presence or absence of within the botanic garden network, and visualized these data in Fig. 3B (Supplementary Table 2). We then refined the dataset to species with at least five geo-referenced occurrences, whose latitudinal range is either temperate *or* tropical. Analysis of these tropical and temperate splits, showed that a temperate species has a 60% probability of *ex-situ* cultivation in the botanic garden network, but just 25% for a tropical species. Indeed from this dataset, 66,905 or 76% of species absent from the botanic garden network, are tropical species. On the one hand, to harbor 60% of all the temperate species in our dataset, reveals the extraordinary capacity of the world's botanic gardens. But on the other hand, *ex-situ* conservation of tropical taxa in temperate climates is unfeasible on a scale that is meaningful for conservation, in part due to limited space and high energy costs of glasshouses. Given the shortage of data from tropical regions, the tropical-temperate disjunction may not be as severe as we imply here, but it is clearly vital that the temperate network, with its associated conservation skills and resources, is extended to tropical latitudes, where many of the world's conservation priorities lie.

Identifying and Targeting Under-Represented Lineages

We then refined our understanding of how phylogenetic diversity is captured. We mapped all 10,133 genera, known to be represented in botanic gardens by at least one species, on a genus-level phylogenetic tree comprising 14,126 genera or 83.5% of all accepted land plant genera[16]. These results, depicted in Fig. 4, reveal striking macroscopic biases in *ex-situ* conservation of the land plant phylogeny. Whereas angiosperms, gymnosperms, and ferns enjoy 62.8%, 96.6% and 54.0% generic coverage respectively, the non-vascular early-diverging land plant lineages - Bryophyta, Marchantiophyta, Anthocerotophyta - are almost completely undocumented with less than 5% generic coverage across the global botanic garden network. Our visualization of this disparity is stark, revealing a weakness in the delivery of *ex-situ* conservation goals for the plant kingdom as a whole. The lack of coverage for 'Bryophyte' taxa denies their importance, as they represent key stages in land plant evolution, occur in endangered habitats such as peatland [17], host diverse microbiota [18], and play a central role in nutrient cycling [19]. Given the vascular plant emphasis of botanic gardens, this finding is unsurprising, however the magnitude of deficit calls for action. Many living collections host incidental collections of 'Bryophytes', and an increase in 'Bryophyte' representation could be achieved by documenting existing taxa, as well as through specific acquisition strategies and horticultural innovation.

Of the 34 missing vascular plants families, twelve are monotypic and thirteen monogeneric, with the majority restricted endemics, tropical trees, or parasites (Supplementary Table 3), indicating how species paucity, endemism, and life history can limit *ex-situ* conservation. The cultivation of certain plants can pose a challenge, and this may be especially true for the estimated 4000 species of parasitic angiosperms [20] However, below the rank of family, phylogenetic mapping provides a framework to target acquisitions to fill collection gaps. We exemplify this idea using two approaches. First, for all missing genera, we calculated the amount of evolutionary distinctiveness (ED; Isaac et al 2007) represented by each genus. We then ranked all genera according to the amount of ED that would be captured, if each genus was accessioned into *ex-situ* collections (Supplementary Table 4). Here, it is notable that many of the most important genera are also from early diverging land plant lineages, emphasizing the importance of conserving these taxa. In a second approach, we computationally searched for clusters of closely related but absent genera, below the taxonomic rank of family, to identify phylogenetic islands of evolutionary history, not captured within *ex-situ* collections. We list the top ten clusters in terms of numbers of absent genera e.g. the Grammitioideae, a subfamily of the fern family Polypodiaceae, of tropical distribution, with thirteen out of sixteen (81%) genera missing, and the Helieae tribe, within Gentianaceae, which occupy highly restricted ranges in the New World, with ten out of twelve (83%) of genera missing (Supplementary Table 5). Most absent clusters are tropical, emphasizing that latitudinal bias impacts on phylogenetic representation.

Through these gap analyses, we have generated resources that enable targeted acquisition, including a list of genera missing from gardens (Supplemental Table 6), and a list of all families ranked by their percentage of genera represented (Supplemental Table 7). Targeted acquisition strategies have potential to enhance the value of *ex-situ* collections, not just for conservation, but for research and education more generally. For example, comparative genomics depend on ready access to living material to sequence phylogenetically pertinent taxa, and cultivation of key phylogenetic lineages can provide essential material to teach evolutionary transitions. However, phylogenetically targeted strategies are just one approach to enhance the value of living collections, and future studies should also explore under-representation of environmental niches, life histories, and medicinal, ethnobotanical or crop plants.

Evaluating Progress Towards GSPC Target 8

BGCI '*ThreatSearch*' database, is the most comprehensive list of threatened plants, incorporating global, regional and national threat assessments (https://www.bgci.org/threat_search.php). Here, '*Threatened*' is defined as species, which fall into the categories of '*Vulnerable'*, '*Endangered*', and '*Critically Endangered*', as per IUCN criteria, or their equivalent designations, in the case of non-IUCN methodologies. By cross-referencing two data sources, an early release version of the '*ThreatSearch*' database and BGCI '*PlantSearch'*, we assessed progress towards achieving GSPC Target 8, which calls for "*at least 75% of threatened plant species in ex-situ collections, preferably in the country of origin*", First, we asked how many threatened species are present in the global network of botanic gardens and show that, currently, the global network is over half way towards achieving GSPC Target 8, with about 13,218 threatened species held in at least one *ex-situ* collection, equating to 41.6% of all plant species assessed as threatened (Fig. 5A). As with the total diversity estimates, our figures are likely an underestimate of threatened plant diversity held in botanic gardens, as only a third of gardens are analysed here (Fig. 5B). Unsurprisingly, the extent to which *ex-situ* collections contribute to these overall numbers varies considerably, from as little as one threatened species, to over five thousand, with a median number of threatened species per garden of 38 (Fig. 5C). Nonetheless, these figures are impressive, as threatened species are often range-restricted, harder to find, and more difficult to cultivate and manage in *ex-situ* collections. Although over 41% of all threatened species are currently held in *ex-situ* collections, there is scope to improve these global efforts. Of the 1,330,829 records in '*PlantSearch'*, 134,771 or about 10% are threatened species, with 90% of *ex-situ* collections devoted to species not yet identified to be at risk of extinction. If the network can hold over 41% of threatened species, with just 10% of current network capacity, there is potential to hold a greater proportion of threatened species. Furthermore, if *ex-situ* collections of threatened species are to be of value for *in-situ* restoration programs, it is imperative that large populations are maintained *ex-situ* to provide the necessary intra-specific genetic diversity for viable populations and species recovery. Such a goal will require the network to devote more collection capacity to conservation priorities.

Evaluation of GSPC Target 8 is problematic as it calls only for *a percentage* of threatened plants to be represented in *ex-situ* collections, and yet the focus of the threat assessments varies considerably across the plant phylogeny. For example, of the 89,810 assessed species in our BGCI '*ThreatSearch*' dataset, 80,990 species of angiosperms (26%) have been assessed for extinction risk, compared with 3611 pteridophyte species (34.4%), 4303 bryophyte species (12.2%), and 986 gymnosperm species (89.3%). In the context of a variable number of assessments and hence threatened species across major lineages, conserving a percentage varies in its significance. But with respect to GSPC Target 8, only gymnosperms meet the target threshold, with 89% of threatened species held *ex-situ* (Fig. 5D). Gymnosperms are a successful *ex-situ* conservation story as: they are the least speciose of the major plant lineages rendering the percentage based GSPC Target 8 more feasible; they have an international conifer conservation programme; like most botanic gardens are broadly temperate, and; they have horticultural value as evergreen collections. In stark contrast, the bryophytes, which have the poorest overall assessment rate of 12.2%, are similarly impoverished with respect to *ex-situ* conservation, such that only 2.6% of threatened bryophytes are documented in the botanic garden network. Evidently, poor performance of *ex-situ* collections with respect to non-vascular plants will further undermine *ex-situ* conservation goals for these important but under-represented plant groups.

We then sought to evaluate progress towards the clause in GSPC Target 8, which asks that threatened plants should be held "*preferably in the country of origin"*. Here, we mapped the *ex-situ* location of all globally and regionally threatened plants within '*ThreatSearch'*. As visualised in Fig. 5E, a relatively small number of nations are holding an exceptional number of threatened species, consistent with the skewed distribution of botanic gardens. Furthermore, using a set of IUCN-assessed threatened endemic species we found that 2780 country-endemic, threatened species are present in the botanic garden network with 1231 or 44% are held in *ex-situ* collections within their country of origin, and 56% or 1549 species are only held in *ex-situ* collections outside of their country of origin (Supplementary Table 8). While dispersed collections provide some security against extinction, if endemic species are held solely outside of their natural range, it seems less likely that they will be available for species recovery, and again, large *ex-situ* populations are needed to provide genetic diversity for viable populations.

Measuring Response to Species Extinction Risk

Threatened species lists are established tools that provide a scaled assessment of extinction risk, which can guide conservation actions [21].While scale of threat is not sufficient to define priorities[21], if botanic gardens are actively responding to perceived extinction risk, one might find signal of this response within collections themselves. Here, we looked for evidence of that response using a dataset of IUCN-globally assessed species. Ideally this question would be answered by a time series analysis, however the present study is the first global assessment of *ex-situ* conservation for threatened plant species, and as such, there is no historic data against which to compare. Consequently, to address this question here, we first asked whether threatened species at a higher risk of extinction were more likely to be found in at least one *ex-situ* living collection. We found that 39% of critically endangered species were held in *ex-situ* collections compared with 35% of endangered species, and 27% of vulnerable species, indicating that a greater proportion of higher risk species are held within the botanic garden network (Fig. 6A). Here, the relative proportion of each red list category held by botanical gardens differs significantly from the proportions held on the red list ($X^2_2 = 76.67$, $N_{obs,} = 3454$, $p<0.01$) suggesting an active response to increasing threat status for threatened species, as a whole. We then assessed whether threatened species at a higher extinction risk were more likely to be accessioned multiple times across the botanic garden network. Here, we found that 11% of IUCN red-listed species, were documented in just one institution, with a median representation of three. But we found that there was no relationship between elevated extinction risk, and the number of institutions that hold any given threatened species ($X^2_{20} = 28.63$, $N_{obs,} =3454$, $p>0.05$) (Fig. 6B), a result that suggests no coordinated shared global response to the extinction risk posed to individual species.

A signal of a global response to extinction risk is confounded by the fact that only a small fraction of capacity, 10%, is currently devoted specifically to conservation. Furthermore, most IUCN globally assessed species are centred in the tropics (Fig. 6C), and as global collections are deficient in tropical species, a tropical-temperate disjunction could underestimate any response signal. We therefore explored whether threatened species were more likely to be included in the botanic garden network if they were temperate in origin, rather than tropical, see Fig. 6C. Here we used a dataset of globally assessed threatened species with at least five geo-referenced occurrences, which had a latitudinal range that is *either* temperate *or* tropical (Supplementary Table 9). We find that the probability of *ex-situ* conservation for a globally threatened temperate species is 77% (a 17% increase relative to temperate species as a whole), but probability of *ex-situ* conservation for a tropical species fell to 24% (a 1% drop relative to tropical species as a whole). These findings suggest a differential response to threatened plants in temperate versus tropical environments. We further found that the odds of conservation of temperate threatened species is 1.8 times that of a near-threatened temperate species ($p<0.01$), but the odds of conservation of threatened tropical species is 0.35 times that of a near-threatened tropical species ($p<0.001$). Together these analyses indicate that botanic gardens are discernibly responding to threatened temperate species, but less so for threatened tropical species.

CONCLUSIONS

The global network of botanic gardens conserves an astonishing array of plant diversity, holding 105,634 species, equating to 30% of species diversity, 59% of plant genera, 75% of land plant families, and 93% of all vascular plant families. These numbers are all the more remarkable as they represent a minimum estimate, based on data derived from just one third of botanic gardens worldwide. Such numbers emphasize that botanic gardens possess unique skills for conserving plant diversity across the taxonomic spectrum. Furthermore, botanic gardens are discernibly responding to the threat of species extinctions, housing at least 13,218 species at risk of extinction, equating to just over 41% of the world’s known threatened flora.

However, our analyses reveal substantial biogeographic gaps in the representation of collections, with 93% of species occurring in the northern hemisphere. So it is essential that the network continue to incorporate institutions and collection data, particularly from tropical regions, but also from under-represented countries. The network is poorly positioned to protect tropical species, and substantial capacity building is needed here, as outlined in previous publications[10-12]. For example, an accessible cyber-infrastructure will be vital to collectively manage *ex-situ* conservation of the world's plant diversity. Importantly, the current global cyber-infrastructure in the form of *PlantSearch* is limited to taxon-level data, however effective *ex-situ* conservation depends on high intra-specific diversity, and for this, individual accession-level data are needed.

Only 10% of collections are dedicated to threatened species, and, to limit species extinction, it is essential that our full capacity is directed towards our most threatened plant species. Multiple accessions of threatened species across the network will buffer against loss of threatened species, and provide genetic diversity for ecological restoration efforts. However, 11% of globally threatened species are currently held in just one institution. Moreover, over half of endemic threatened species are not held *ex-situ* within their country of origin, implying reduced availability for ecological or species restoration. Many threatened species have utility in agriculture, horticulture and forestry, with species reintroduction an important element of conservation work[22-24]. Botanic gardens must engage with these organizations and industries with responsibility for plant diversity in the natural landscape. Finally, it is important that coordinated international conservation of threatened species continues in the face of legislation that seeks to enforce the intellectual property rights of individual nations.

Without deep sustained public support, the plant conservation movement will struggle. Fortunately, public-facing botanic gardens are typically near urban areas [14], and according to data within the *GardenSearch* database, collectively host 500 million visitors annually. Consequently, botanic gardens can deliver the necessary education, citizen science, and information to facilitate plant conservation action across the broader society. Given the quality of the collections, and their critical importance for conservation, it is vital that we speak to the strengths of the network, and promote its unique skills and resources to policy makers and funders. Despite impressive efforts by the world's botanic gardens, substantial investment will be required to build a fully functioning, cost-effective, rational global system for the conservation of threatened plant diversity, that can prevent species extinctions in perpetuity[10].

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AUTHOR CONTRIBUTIONS

SFB and PS conceived the study, PS released the data, RM cleaned the data, SFB designed the analyses, RM and SFB performed the analyses, and SFB and PS wrote the manuscript.

FIGURE LEGENDS

Figure 1. Global distribution of *ex-situ* plant collections and the availability of data for the contents of these *ex-situ* collections. Equirectangular projection maps demonstrating (A) the location of all BGCI member institutions (B) the relative species diversity present in each of the 1,116 BGCI member institutions that share plant record data with BGCI. The diameter of each bubble is scaled to the number of species recorded at the institution (Data from BGCI '*GardenSearch*' and BGCI '*PlantSearch*')**.**

Figure 2. Botanic garden taxon coverage in terms of (A) all accepted land plant species names (out of 350,699) (B) all land plant genera (out of 16,913) (C) all land plant families (out of 635) (D) all vascular plant families (out of 458).

Figure 3. Latitudinal distribution of (A) *Ex-situ* plant collections and the availability of data for the contents of these *ex-situ* collections with the number of gardens per latitudinal bin (gray, bottom y-axis) and number of digitally recorded species per latitudinal bin (red, top y-axis) (B) the latitudinal distribution of plant species (n=236,904) as recorded by the median latitude of all georeferenced GBIF records per species, with data binned per latitudinal degree (gray, top y-axis), the percentage of species found in the botanic garden network per latitudinal degree (red, bottom y-axis).

Figure 4. Phylogenetic gap analysis showing land plant genus-level phylogeny[16], where red edges indicate that all subtending edges and tips are present in the botanic garden network.

Figure 5. Threatened land plant species in botanic collections. (A) the percentage of threatened plants held in *ex-situ* collections (out of 34,442) (B) the percentage of total accessions held *ex-situ* that are threatened species accessions (C) absolute numbers of threatened species per garden (D) the percentage of threatened species held by botanic collections by higher-level phylogenetic lineages (ANG: Angiosperms; GYM: Gymnosperms; PTE: Pteridophytes; BRY: Bryophytes). (E) Number of documented threatened species in *PlantSearch*, held *ex-situ*, per country.

Figure 6. Presence and absence of IUCN red-list threatened plants in *ex-situ* collections (A) the percentage of threatened species per threat status (B) the number of different *ex-situ* collections that a threatened species is held in, with Lg^2 scale. Yellow for Vulnerable (VU), orange for Endangered (EN), and red for Critically endangered (CR) (C) the native distribution of just threatened plant species (as opposed to all species as shown in Fig. 3B) as recorded by the median latitude of all georeferenced GBIF records per species (n=8619), with data binned per latitudinal degree (gray, top y-axis), the percentage of threatened species found in the botanic garden network per latitudinal degree (red, bottom y-axis).

METHODOLOGY

Data Sources: We used BGCI '*GardenSearch'* (www.bgci.org/garden_search.php) database (accessed 2016-01-01) for the location of botanic gardens. For the presence and absence of taxa from gardens we used BGCI '*PlantSearch'* (www.bgci.org/plant_search.php) (accessed 2016-01-01). For threatened plants we used a pre-release version of BGCI's ThreatSearch (https://www.bgci.org/threat_search.php) (accessed 2016-01-01). The pre-release set of threat assessments included the official IUCN red list version 2015-4 (www.iucnredlist.org) as well as the following additional regional and national lists: Chinese Higher Plants Red List, NatureServe, Mexico Red List, Mesoamerica Red List, Brazil Tree Red List, Ecuador Red List, Threatened Plants of the Philippines, Ethiopia Eritrea RL, Andes Red List, Cuba Red List, Guatemala Red List, Caucasus Red List, Central Asia Red List, Trinidad and Tobago Red List, Vietnam Red Data Book Part II: Plants, South African Plants SANBI, South Africa Trees, Sao Tome trees list, Trees of Uganda, Red List of Korean Endemic Vascular Plants, Namibian Tree List, Malaysian Flora Database, and the Bolivian Red Book. For some analyses such as response to extinction we only used a subset of BGCI's '*ThreatSearch'*, namely only the global assessments derived from the official IUCN red list version 2015-4.

Data Cleaning: For all datasets, records were filtered to remove assessments of taxa that were not land plants e.g fungal, algal, and animal taxa. Undescribed taxa were ignored for these analyses e.g. "*Asparagus sp. nov. A*". We discarded 'orphan' BGCI plant records that were not currently associated with any gardens in the network (e.g. historical records of dead plants that are no longer held in a garden). We interpret living collections to include accessions that are maintained as part of an active cultivation cycle, and so retained seed-banked accessions held within the botanic garden network. We discarded records of horticultural taxa such as cultivars, due to the difficulties of taxonomic standardisation, and because we were interested in true biological species. We computationally-normalised the taxonomy of records using the *R* package *Taxonstand* v1.8 [25] version 1.8, so that all taxa match an accepted or unresolved taxon listed by The Plant List v1.1. Raw input species names that could not be automatically matched to a species name listed at The Plant List v1.1 were manually resolved to the correct species name. By matching to TPLv1.1 in a minority of cases we were back-converting names into older ones for the sake of consistency. BGCI records were de-duplicated using the R package *stringdist* 0.9.4.4 using Damerau-Levenshtein distance [26,27], so that there was only one record for each unique taxon, as gardens around the world can apply different names to the same taxon. After normalisation to The Plant List (TPL) some taxa were demoted from species rank in the original assessment to subspecies rank. For consistency and comparability only species-level taxa were retained for analysis, subspecies taxa were discarded. After these data processing steps we were left with: 105,634 BGCI recorded species of TPL-normalised land plants and a pre-release version of BGCI '*ThreatSearch*' comprising 89,810 assessed species and 31,812 threatened species. The subset of global threat assessments comprised 20,367 IUCN global dataset species assessments of which 11,055 species were threatened.

Biogeographic Bias Analyses: Using the R package *rgbif* version 0.9.7 we retrieved georeferenced occurrence data for 236,904 embryophyte species with at least one geo-referenced location record. The downloaded dataset equated to 8,246,424 unique geo-located records, with a mean of 34.8 records per species. Of these 236,904 species, 89,180 species were recorded as present in gardens, and 147,724 species were recorded as absent from gardens. We applied standard cleaning techniques to filter-out corrupt data indicated by coordinates that did not match the country stated on the record, or that had coordinates in marine areas. We then took the median of the latitudes for all georeferenced occurrences for each species, to serve as a proxy for the centre of a species' latitudinal range. The median latitude of these 236,904 plant species was then binned per latitudinal degree and plotted against the percentage of these same species, from each latitudinal bin, that are found in the botanic garden network. To mitigate against the risk of errors in single geo-located records, we then refined the dataset to 171,472 species with at least five georeferenced occurrences, and then further refined this to the 148,682 species whose latitudinal range is *either* temperate *or* tropical, and does not span both tropical and temperate latitudes. Temperate species were defined as having their latitudinal range (min, max, median) entirely between 23.44^{0}N and 66.5^{0}N and between 23.44^{0}S and 66.5^{0}S. Tropical species were defined as having their latitudinal range (min, max, median) entirely within 23.44^{0}N and 23.44^{0}S. Using this refined dataset, the percentage of species present in gardens from each latitudinal bin were averaged across all tropical latitudinal bins (between 23.43704^{0}N and 23.43704^{0}S) and compared with the average percentage across all temperate latitudinal bins (between 23.44^{0}N and 66.5^{0}N and between 23.44^{0}S and 66.5^{0}S).

Phylogenetic Bias Analyses. To estimate the proportion of species, genera, embryophyte families and tracheophyte families held in *ex-situ* collections, we used denominators from the *R* package *Taxonstand* v1.8 i.e all species = 350,699; all genera = 16,913; all embryophyte families = 635; all vascular plant families =458. For phylogenetic mapping of presence and absence of genera, we used a genera-level phylogenetic tree comprising 14,126 genera or 83.5% of all accepted land plant genera [16], which provided maximal phylogenetic coverage at the generic level. We then plotted the 10133 genera known to be represented in botanic gardens, which were present in the tree by at least one species. We scored each genus tip on this tree as a binary trait according to whether the genus is documented as absent (0) or present (1) in a garden with the global network. To determine the significance of absence of genera in terms of evolutionary history, we utilized the branch length information from the tree [16] to report the Evolutionary Distinctiveness (ED)[28] of each taxon in the tree, and ranked all missing genera according to ED. To detect notable clusters of absence within the large genus tree we employed an R script (available on request) to find the most absent clades in the tree with a cut off at 5 consecutive absent tips or more. Due to the wholesale absence of genera from early diverging lineages (Bryophyta, Marchantiophyta, Anthocerotophyta) the search for absent genera-level clusters was focussed solely on Tracheophyte lineages (Pteridophytes, Gymnosperms, Angiosperms).

Threatened Species Representation: To estimate the total number of threatened species held in *ex-situ* collections, we used a pre-release version of BGCI '*ThreatSearch'* (accessed 01/01/2016) cleaned to comprise 89,810 assessed species and 31,812 threatened species. To estimate the extent of the network capacity devoted to cultivating threatened species, we calculated the number of individual accessions of the 13,218 threatened species held in botanic gardens and expressed this as a fraction of the 1,330,829 accession records held in BGCI '*PlantSearch*'. Total accession records were used as the denominator because including all taxa such as horticultural cultivars better represents the total capacity of the network, which could potentially be devoted to threatened species. We mapped the *ex-situ* location of all globally and regionally threatened plants within '*ThreatSearch'* using R package '*chloroplethr'* v3.6.1. The extent to which threatened plants are held in their country of origin was assessed using as set of 2780 IUCN globally threatened endemic species. Country-level endemicity was determined based on the IUCN data associated with each IUCN-RL assessment record. Endemics in this sense were coded as plants that are only documented to occur in one nation state according to the IUCN assessment. Presence or absence of these endemic species in *ex-situ* collections within their country of origin was then recorded and summed.

Overall Response to Extinction Risk: For all assessments of response to extinction we used the official IUCN red list version 2015-4 (www.iucnredlist.org). We tested whether the relative abundances of critically endangered (CN), endangered (EN) and vulnerable (VU) species held by botanical gardens differs significantly from the relative abundances in the IUCN red list. Here we employed an extrinsic chi-squared test on the raw counts of observed number of species for each threat category held in botanic gardens versus expected number estimated from the IUCN red list. We use the term redundancy to describe when a species is held in more than one garden, such that a species that is held in more gardens exhibits greater redundancy. To determine whether there was a significant difference between the three levels of threat status (VU, EN, CR), with respect to redundancy, we represented redundancy as categorical binning from 0 to 10 gardens, and then aggregated all species redundancies in 11 to 100 gardens into a single category (>10). An intrinsic chi-squared test was then employed to assess whether there was significant independence between the three categories.

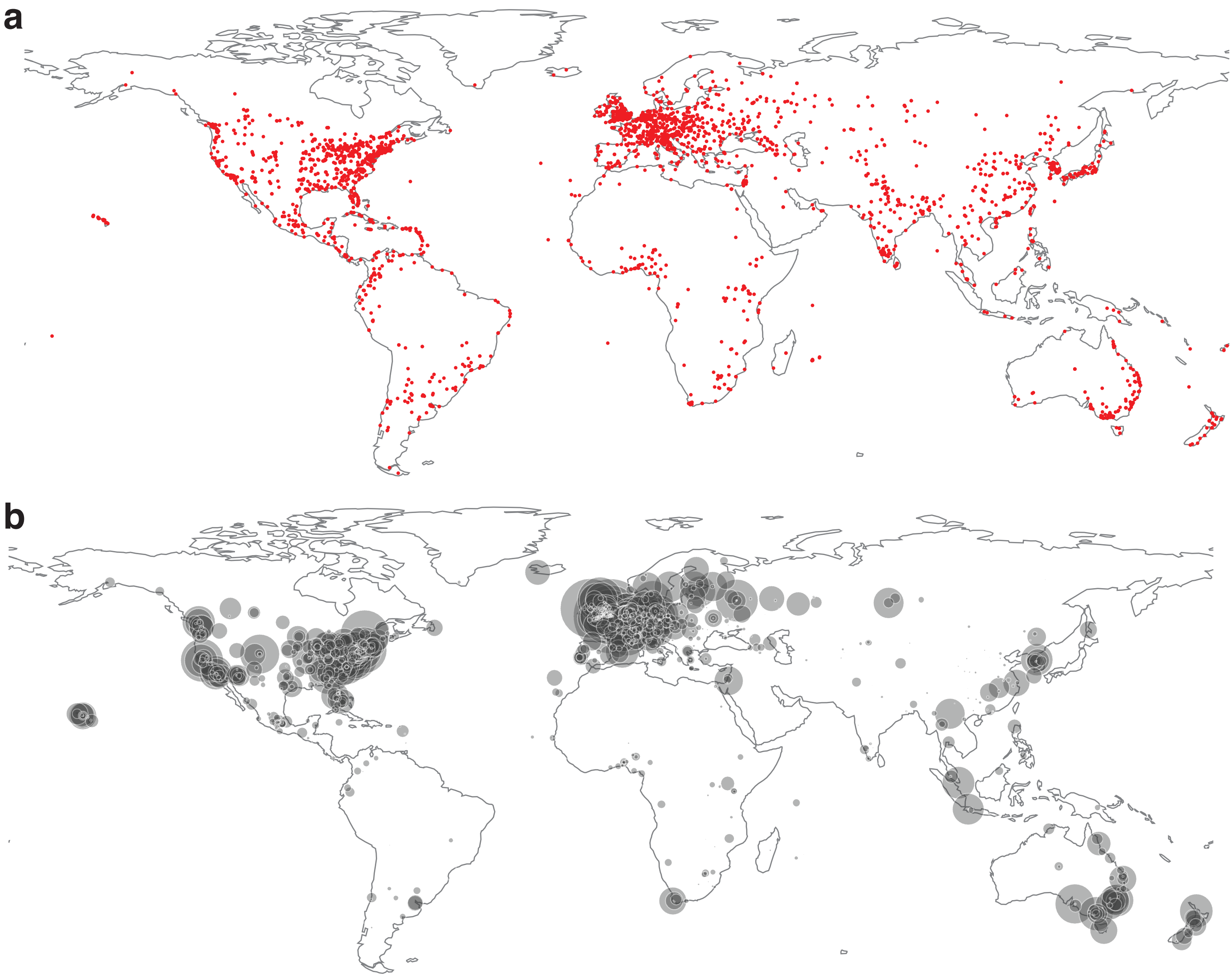
Differential Response to Tropical versus Temperate Threatened Species: To test the response of *ex-situ* conservation efforts to extinction risk in temperate versus tropical taxa, we used R package *rgbif* version 0.9.7 to retrieve georeferenced occurrence data IUCN threatened taxa, with at least one geo-referenced location record. Geolocation data was retrieved for 8619 out of the 11,055 IUCN threatened species. We then took the median of the latitudes for all geo-referenced occurrences for each species, to serve as a proxy for the centre of a species' latitudinal range. The median latitude of these 8619 species was then binned per latitudinal degree and plotted against the percentage of these same species, from each latitudinal bin, that are found in the botanic garden network. To mitigate against the risk of errors in single geo-located records, we then refined the dataset to 5436 species with at least five geo-referenced occurrences, and then refined this to 4613 species whose latitudinal range is *either* temperate *or* tropical, and does not span both tropical and temperate latitudes, following the methodology outlined in the '*biogeographic bias analyses'* methodology section. Using this refined dataset, the percentage of threatened species present in gardens from each latitudinal bin were averaged across all tropical latitudinal bins (between 23.43704^{0}N and 23.43704^{0}S) and compared with the average percentage across all temperate latitudinal bins (between 23.44^{0}N and 66.5^{0}N and between 23.44^{0}S and 66.5^{0}S). To test the differential response of *ex-situ* conservation efforts to temperate versus tropical taxa, we implemented tests of odds ratios using the R packages 'fmsb' v0.6.1. We formed 2x2 contingency tables with conservation status (threatened or near-threatened) on rows and *ex-situ* conservation (present or absent) in columns, and calculated odds ratios, log odds ratios and associated Wald confidence intervals and p-values in R, using the 'fmsb' function oddsratio with p.calc.by.independence = F.

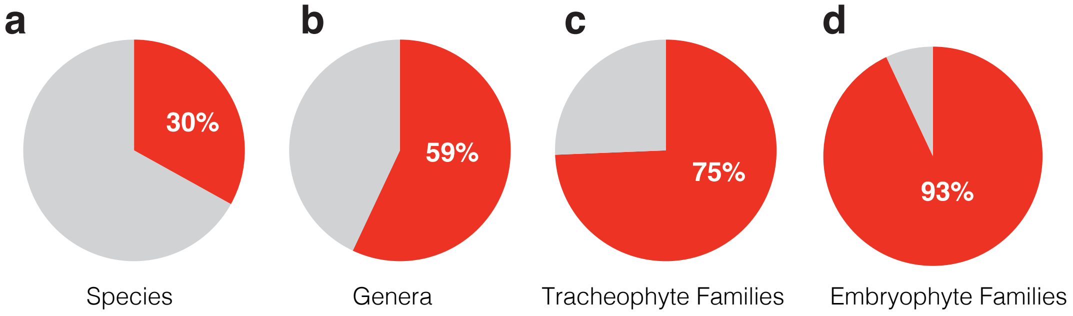
Data availability: The core data sources that support the findings of this study, namely '*ThreatSearch*, *PlantSearch*, and *GardenSearch*' were obtained from Botanic Garden Conservation International (BGCI) under a material transfer agreement. They are available from BGCI but restrictions apply to the availability of these data, and the relational use of these databases, which were used under license for the current study. Data are however available from BGCI upon reasonable request and with permission of Dr Paul Smith, Director-General of BGCI.

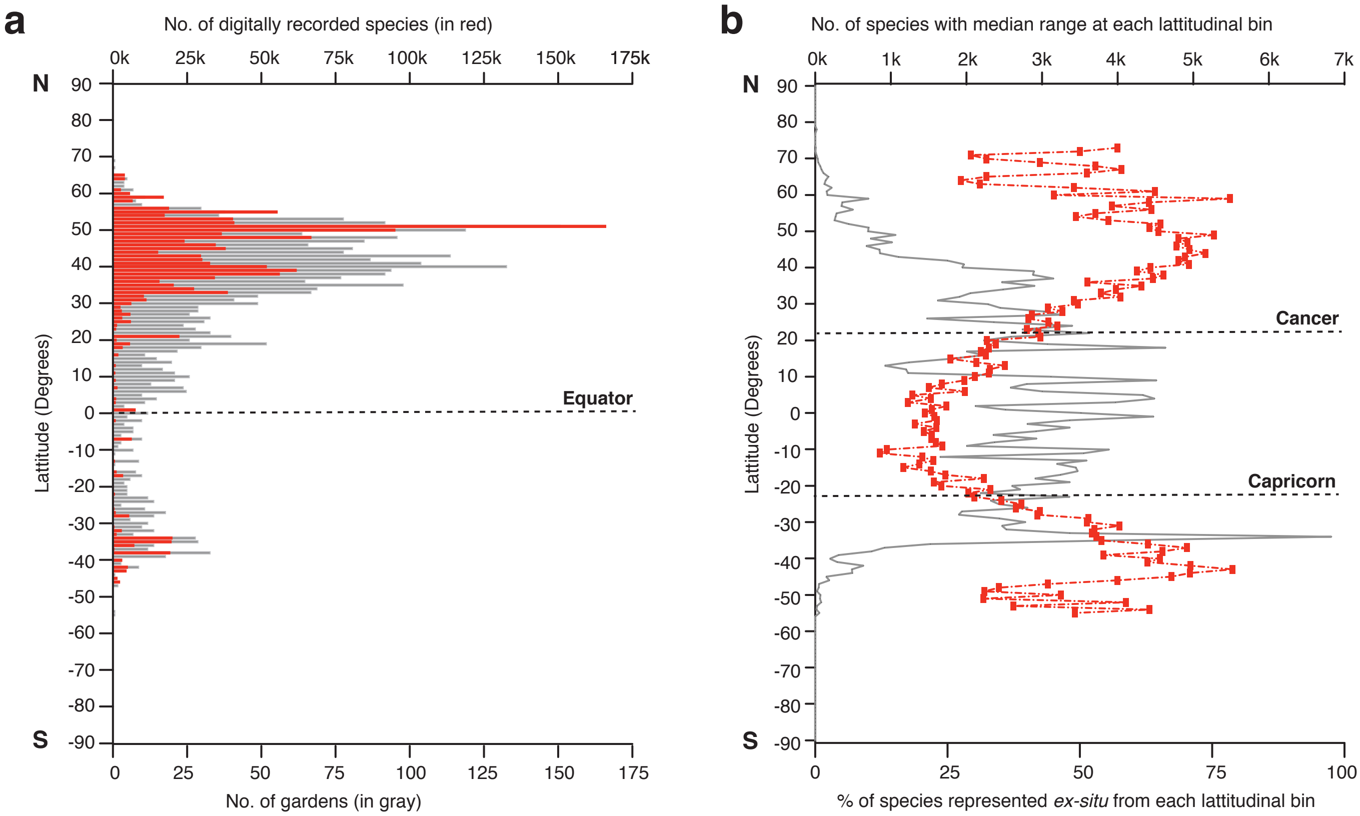
REFERENCES

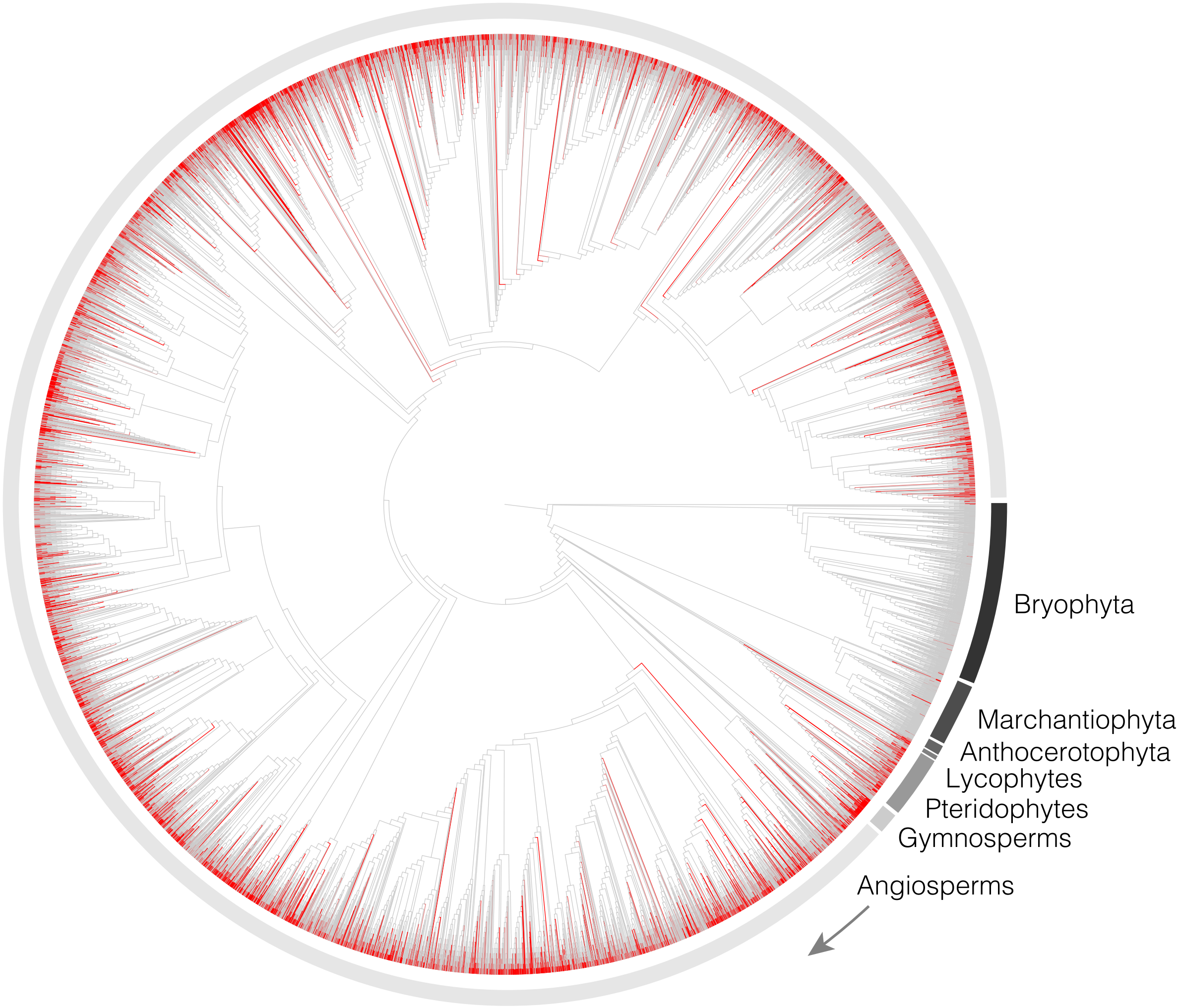
1. Sukhdev, P., Wittmer, H. & Schröter-Schlaack, C. The economics of ecosystems and biodiversity: mainstreaming the economics of nature: a synthesis of the approach, conclusions and recommendations of TEEB. (2010).
2. Brummitt, N. A. *et al.* Green Plants in the Red: A Baseline Global Assessment for the IUCN Sampled Red List Index for Plants. *PLoS ONE* **10,** e0135152 (2015).
3. Murphy, G. E. P. & Romanuk, T. N. A meta-analysis of declines in local species richness from human disturbances. *Ecology and Evolution* **4,** 91–103 (2014).
4. Venter, O. *et al.* Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nat Commun* **7,** 12558 (2016).
5. Hooke, R. L. B., Martín-Duque, J. F. & Pedraza, J. Land transformation by humans: A review. *GSA Today* **22,** 4–10 (2012).
6. Allen, J. A., Brown, C. S. & Stohlgren, T. J. Non-native plant invasions of United States National Parks. *Biol Invasions* **11,** 2195–2207 (2009).
7. Oldfield, S. F. Botanic gardens and the conservation of tree species. *Trends in Plant Science* **14,** 581–583 (2009).
8. Heywood, V. H. The role of botanic gardens as resource and introduction centres in the face of global change. *Biodivers Conserv* **20,** 221–239 (2010).
9. Wyse Jackson, P. & Kennedy, K. The Global Strategy for Plant Conservation: a challenge and opportunity for the international community. *Trends in Plant Science* **14,** 578–580 (2009).
10. Smith, P. Guest Essay: Building a global system for the conservation of all plant diversity: A vision for botanic gardens and Botanic Gardens Conservation International. *Sibbaldia: the Journal of Botanic Garden Horticulture* **0,** (2016).
11. Smith, P., Dickie, J., Linington, S., Probert, R. & Way, M. Making the case for plant diversity. *Seed Science Research* **21,** 1–4 (2011).

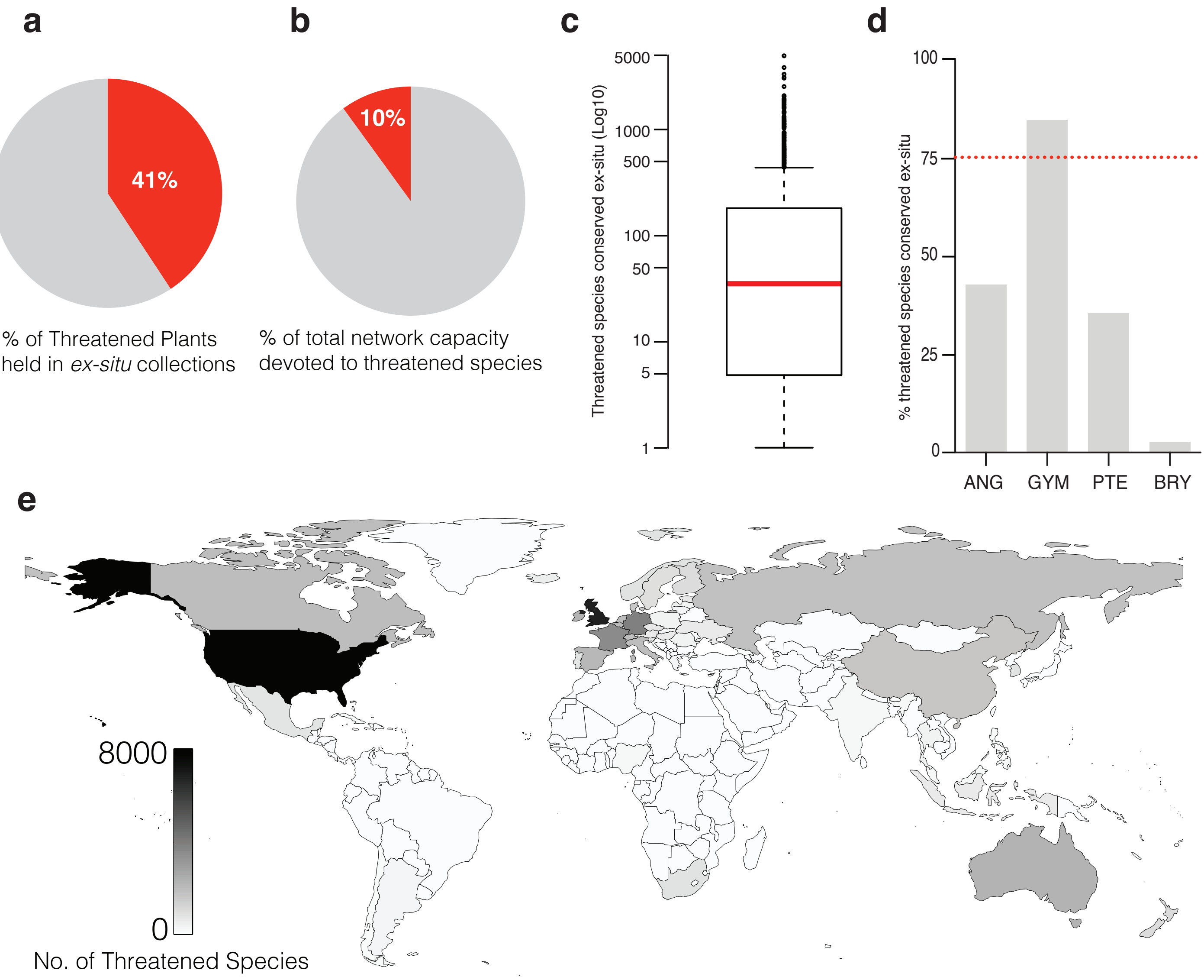
12. Raven, P. & Havens, K. Ex situ plant conservation and cryopreservation: Breakthroughs in tropical plant conservation. *Int J Plant Sci* **175,** 1–2 (2014).
13. Pautasso, M. & Parmentier, I. Are the living collections of the world's botanical gardens following species-richness patterns observed in natural ecosystems? *Botanica Helvetica* (2007). doi:10.1007/s00035-007-0786-y
14. Golding, J. *et al.* Species-richness patterns of the living collections of the world's botanic gardens: a matter of socio-economics? *Annals of Botany* **105,** 689–696 (2010).
15. Hillebrand, H. On the generality of the latitudinal diversity gradient. *The American Naturalist* **163,** 192–211 (2004).
16. Hinchliff, C. E. *et al.* Synthesis of phylogeny and taxonomy into a comprehensive tree of life. *P Natl Acad Sci Usa* **112,** 12764–12769 (2015).
17. Lindo, Z. & Gonzalez, A. The bryosphere: an integral and influential component of the Earth's biosphere. *Ecosystems* (2010).
18. Kauserud, H., Mathiesen, C. & Ohlson, M. High diversity of fungi associated with living parts of boreal forest bryophytes. *Bot.* **86,** 1326–1333 (2008).
19. Turetsky, M. R. The Role of Bryophytes in Carbon and Nitrogen Cycling. *The Bryologist* **106,** 395–409 (2003).
20. Westwood, J. H., Yoder, J. I., Timko, M. P. & dePamphilis, C. W. The evolution of parasitism in plants. *Trends in Plant Science* **15,** 227–235 (2010).
21. Possingham, H. P. *et al.* Limits to the use of threatened species lists. *Trends in Ecology & Evolution* **17,** 503–507 (2002).
22. Godefroid, S. *et al.* How successful are plant species reintroductions? *Biological Conservation* **144,** 672–682 (2011).
23. Guerrant, E. O. in *Plant Reintroduction in a Changing Climate: Promises and Perils* (eds. Maschinski, J., Haskins, K. E. & Raven, P. H.) 9–29 (Island Press/Center for Resource Economics, 2012). doi:10.5822/978-1-61091-183-2_2
24. Dalrymple, S. E., Stewart, G. B. & Pullin, A. S. *Are re-introductions an effective way of mitigating against plant extinctions? CEE review 07-008 (SR32)*. (Collaboration for Environmental Evidence, 2011).
25. Cayuela, L., Granzow-de la Cerda, Í., Albuquerque, F. S. & Golicher, D. J. taxonstand: An r package for species names standardisation in vegetation databases. *Methods Ecol Evol* **3,** 1078–1083 (2012).
26. Damerau, F. J. A technique for computer detection and correction of spelling errors. *Commun. ACM* **7,** 171–176 (1964).
27. Levenshtein, V. I. Binary codes capable of correcting deletions, insertions, and reversals. *Soviet physics doklady* (1966).
28. Isaac, N. J. B., Turvey, S. T., Collen, B., Waterman, C. & Baillie, J. E. M. Mammals on the EDGE: Conservation Priorities Based on Threat and Phylogeny. *PLoS ONE* **2,** (2007).

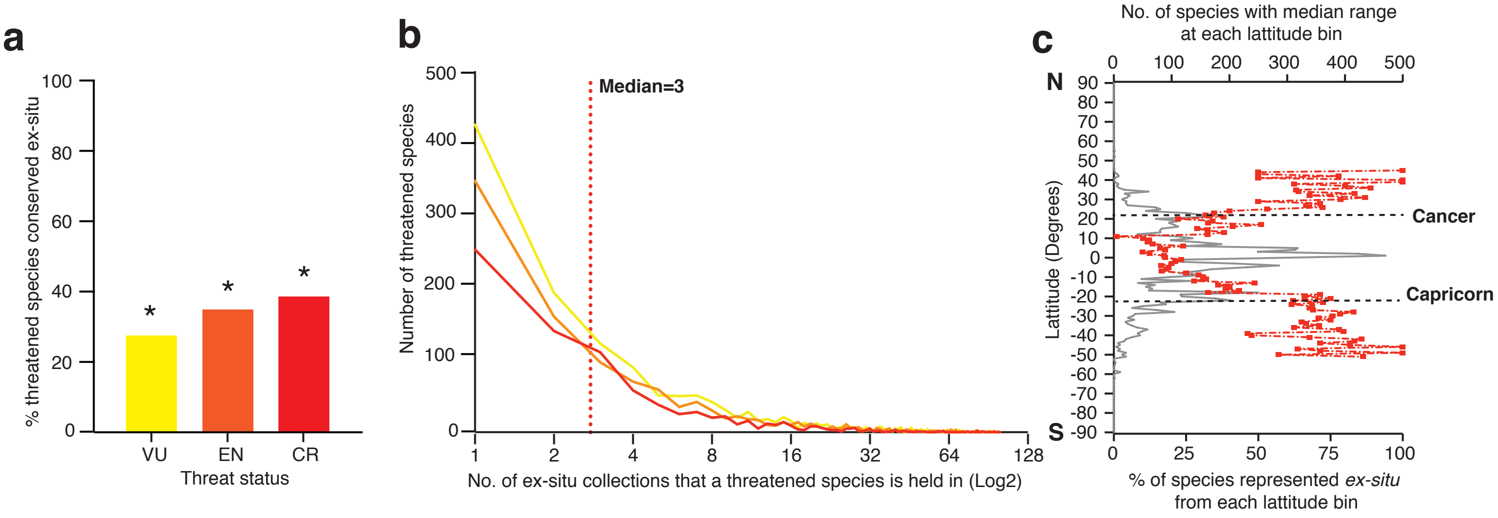

a
b


a
30%
Species
b
59%
Genera
c
75%
Tracheophyte Families
d
93%
Embryophyte Families


a
No. of digitally recorded species (in red)
0k
25k
50k
75k
100k
125k
150k
175k
N
S
90
80
70
60
50
40
30
20
10
0
-10
-20
-30
-40
-50
-60
-70
-80
-90
Lattitude (Degrees)
Equator
0
25
50
75
100
125
150
175
No. of gardens (in gray)
b
No. of species with median range at each lattitudinal bin
0k
1k
2k
3k
4k
5k
6k
7k
N
S
Lattitude (Degrees)
Cancer
Capricorn
0
25
50
75
100
% of species represented *ex-situ* from each lattitudinal bin


Bryophyta
Marchantiophyta
Anthocerotophyta
Lycophytes
Pteridophytes
Gymnosperms
Angiosperms


a
41%
% of Threatened Plants held in *ex-situ* collections
b
10%
% of total network capacity devoted to threatened species
c
Threatened species conserved ex-situ (Log10)
5000
1000
500
100
50
10
5
1
d
% threatened species conserved ex-situ
100
75
50
25
0
ANG
GYM
PTE
BRY
e
8000
0
No. of Threatened Species


a
% threatened species conserved ex-situ
100
80
60
40
20
0
*
*
*
VU
EN
CR
Threat status
b
Number of threatened species
500
400
300
200
100
0
Median=3
1
2
4
8
16
32
64
128
No. of ex-situ collections that a threatened species is held in (Log2)
c
No. of species with median range at each lattitude bin
0
100
200
300
400
500
N
S
Latitude (Degrees)
90
80
70
60
50
40
30
20
10
0
-10
-20
-30
-40
-50
-60
-70
-80
-90
Cancer
Capricorn
0
25
50
75
100
% of species represented *ex-situ* from each lattitude bin