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Ex situ conservation of plant diversity in the world's botanic gardens

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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 held 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.

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]. Recognizing 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 1990s[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. 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 supports human livelihoods and well-being[9]. The strategy outlines 16 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, they 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-centred, 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 digitized 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-centred global system that can prevent species extinctions in perpetuity.

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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 are 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 3,269 botanical collections in 180 countries around the world (BGCI, 2012) (Fig. 1a). Of these 3,269 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 present only a minimum estimate of the diversity held in botanic gardens and associated seed banks, as our digitized data are 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 (The Plant List 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 have 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. Figure 1a,b shows that the most dominant worldwide bias in the distribution of botanic gardens, and availability of associated digitized 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 (gross domestic product) and

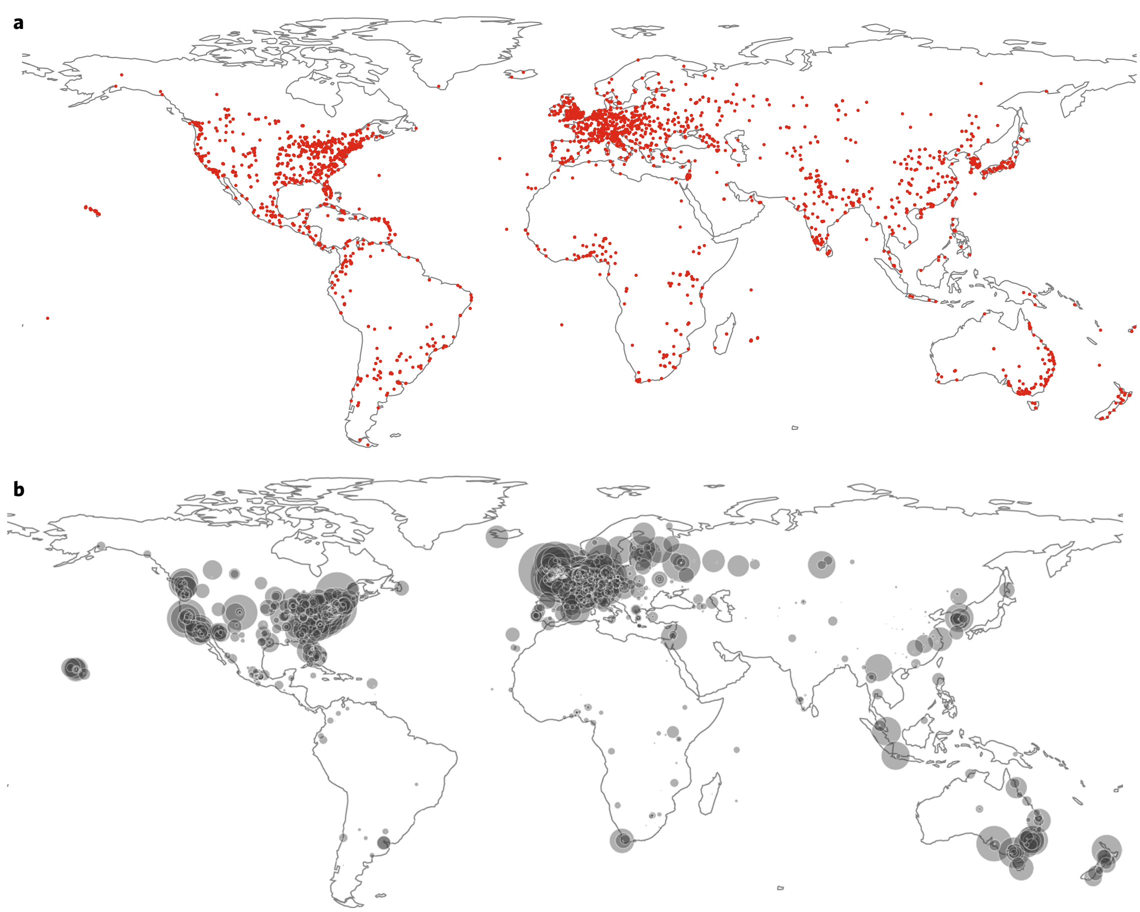

Fig. 1 | Global distribution of ex situ plant collections and the availability of data for the contents of these ex situ collections. a,b, Equirectangular projection maps demonstrating the location of all BGCI member institutions (**a**) and the relative species diversity present in each of the 1,116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

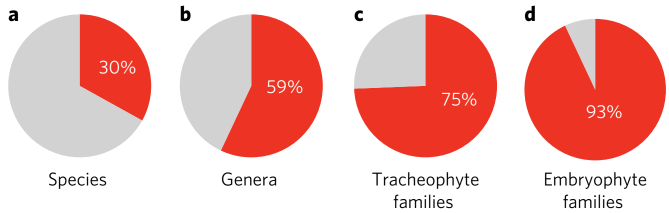

Fig. 2 | Percentage of plant diversity held ex situ at different taxonomic hierarchies. a–d, Botanic garden taxon coverage in terms of all accepted land plant species names (out of 350,699) (**a**), all land plant genera (out of 16,913) (**b**), all land plant families (out of 635) (**c**) and all vascular plant families (out of 458) (**d**).

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 within the botanic garden network, and visualized these data in Fig. 3b (Supplementary Table 2). We then refined the data set to species with at least five georeferenced 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 data set, 66,905 or 76% of species absent from the botanic garden network are tropical species. On the one hand, to harbour 60% of all the temperate species in our data set 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 and Anthocerotophyta—are

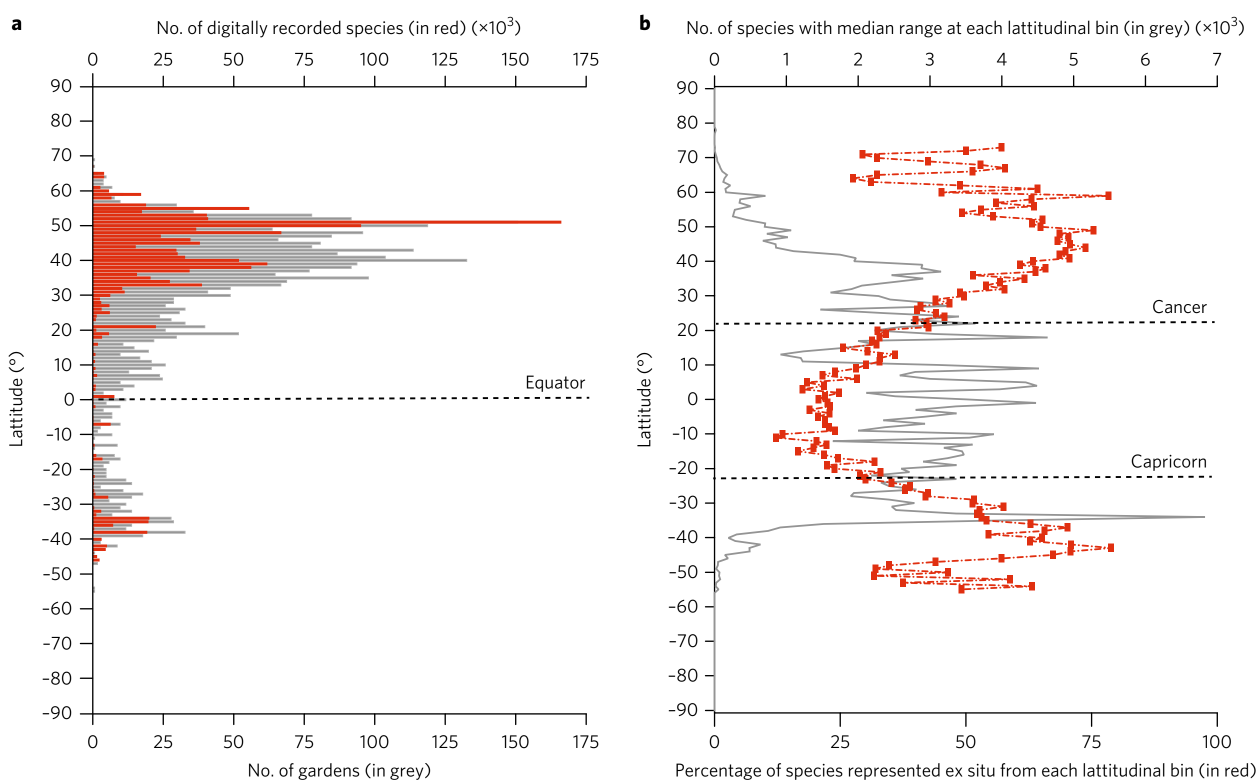

Fig. 3 | The distribution of ex situ collections and collection data relative to the natural distribution of plant diversity. a, Latitudinal distribution of ex situ plant collections and the availability of data for the contents of these ex situ collections with the number of gardens per latitudinal bin (grey, bottom *y* axis) and number of digitally recorded species per latitudinal bin (red, top *y* axis). **b**, 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 (grey, top *y* axis), and the percentage of species found in the botanic garden network per latitudinal degree (red, bottom *y* axis).

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 the 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, 12 are monotypic and 13 are monogeneric, with the majority being 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 4,000 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 represented by each genus. We then ranked all genera according to the amount of evolutionary distinctiveness 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, for example, the Grammitidoideae, a subfamily of the fern family Polypodiaceae, of tropical distribution, with 13 out of 16 (81%) genera missing, and the Helieae tribe, within Gentianaceae, which occupy highly restricted ranges in the New World, with 10 out of 12 (83%) 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 (Supplementary Table 6), and a list of all families ranked by their percentage of genera represented (Supplementary Table 7). Targeted acquisition strategies have the 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. The 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 that fall into the categories of 'Vulnerable', 'Endangered' and 'Critically Endangered', as per International Union for Conservation of Nature (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

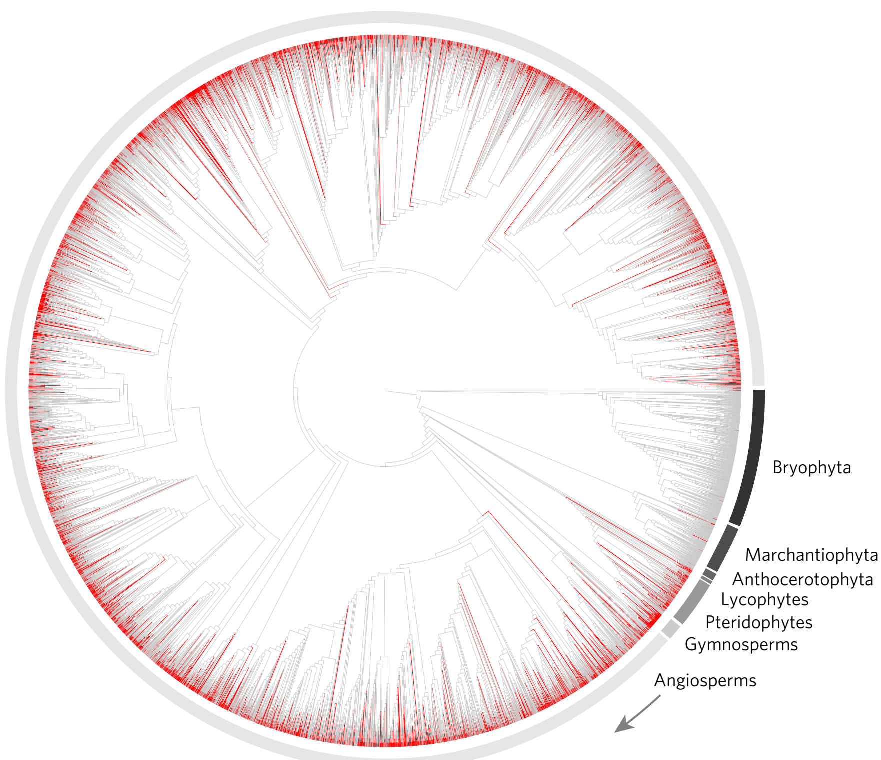

Fig. 4 | Phylogenetic gap analysis showing land plant genus-level phylogeny[16], where red edges indicate subtending edges and that tips are present in the botanic garden network.

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 probably 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 programmes, 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 data set, 80,990 species of angiosperms (26%) have been assessed for extinction risk, compared with 3,611 pteridophyte species (34.4%), 4,303 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, they 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

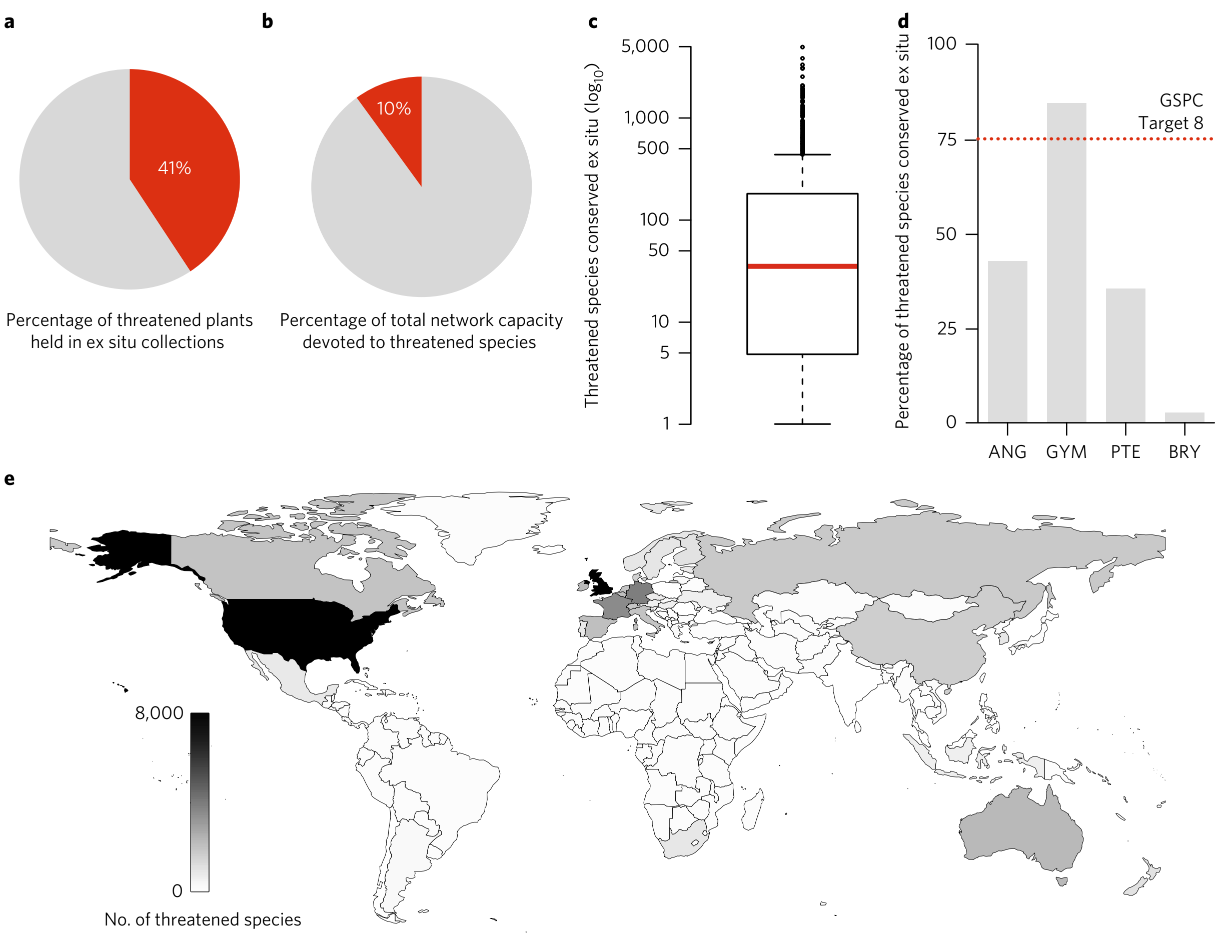

Fig. 5 | Threatened land plant species in botanic collections. a, The percentage of threatened plants held in ex situ collections (out of 34,442). **b**, The percentage of total accessions held ex situ that are threatened-species accessions. **c**, Absolute numbers of threatened species per garden. Data (mean ± s.e.m. (220 ± 14.3)) are presented as a box plot showing the upper (75%) and lower (25%) quartiles, with the horizontal line as the median and the whiskers as the maximum and minimum values observed. **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.

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 visualized 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 2,780 country-endemic, threatened species are present in the botanic garden network with 1,231 or 44% held in ex situ collections within their country of origin, and 56% or 1,549 species held only in ex situ collections outside their country of origin (Supplementary Table 8). While dispersed collections provide some security against extinction, if endemic species are held solely outside 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 a signal of this response within collections themselves. Here, we looked for evidence of that response using a data set 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 are 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 data set of globally assessed threatened species with at least five georeferenced 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 the 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

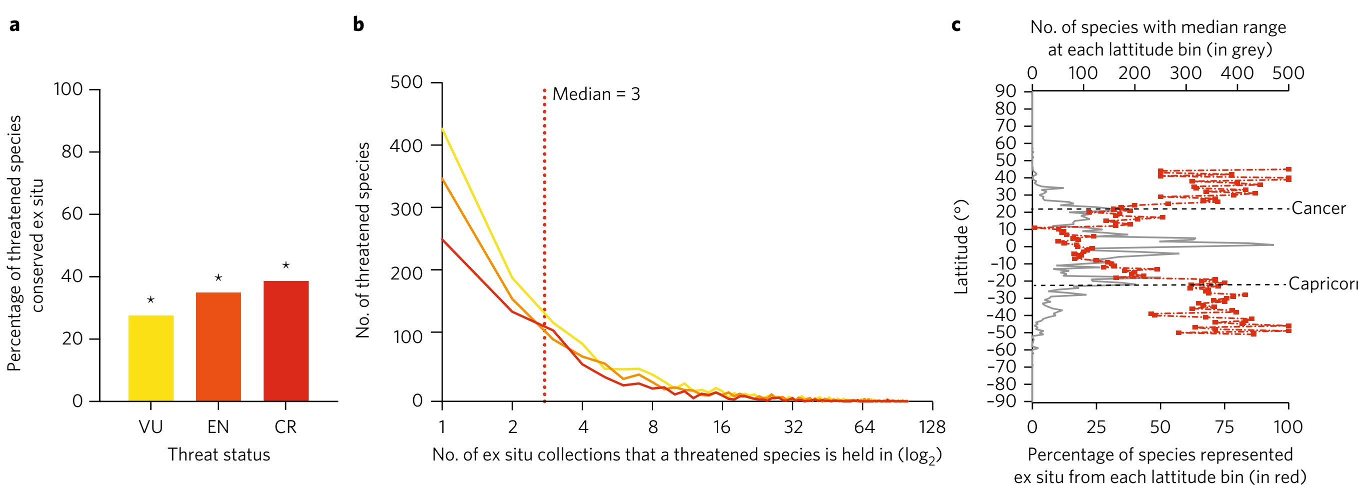

Fig. 6 | Presence and absence of IUCN Red List threatened plants in ex situ collections. a, The percentage of threatened species per threat status. *$P < 0.01$. **b**, The number of different ex situ collections that a threatened species is held in, with $\log_2$ scale yellow for Vulnerable (VU), orange for Endangered (EN), and red for Critically Endangered (CR). **c**, The native distribution of just threatened plant species ($n = 8619$) (as opposed to all species as shown in Fig. 3b) as recorded by the median latitude, with data binned per latitudinal degree (grey, top *y* axis), and the percentage of threatened species found in the botanic garden network per latitudinal degree (red, bottom *y* axis).

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. Thus, it is essential that the network continues 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 policymakers 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].

Methods

Data sources. We used the BGCI GardenSearch (www.bgci.org/garden_search.php) database (accessed 1 January 2016) 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 1 January 2016). For threatened plants we used a pre-release version of BGCI's ThreatSearch (https://www.bgci.org/threat_search.php) (accessed 1 January 2016). 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 Tree 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 used only 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 data sets, records were filtered to remove assessments of taxa that were not land plants, for example, fungal, algal and animal taxa. Undescribed taxa were ignored for these analyses, for example, *Asparagus* sp. nov. A. We discarded 'orphan' BGCI plant records that were not currently associated with any gardens in the network (for example, 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 standardization, and because we were interested in true biological species. We computationally normalized the taxonomy of records using the R package Taxonstand version 1.8 (ref. [25]), 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 The Plant List (TPL) v1.1 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 the 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 normalization to 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-normalized 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 data set 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 georeferenced location record. The downloaded data set equated to 8,246,424 unique geolocated 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 geolocated records, we then refined the data set to 171,472 species with at least 5 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 (minimum, maximum, median) entirely between 23.44° N and 66.5° N and between 23.44° S and 66.5° S. Tropical species were defined as having their latitudinal range (minimum, maximum, median) entirely within 23.44° N and 23.44° S. Using this refined data set, the percentage of species present in gardens from each latitudinal bin was averaged across all tropical latitudinal bins (between 23.43704° N and 23.43704° S) and compared with the average percentage across all temperate latitudinal bins (between 23.44° N and 66.5° N and between 23.44° S and 66.5° 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; that is, 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 10,133 genera known to be represented in botanic gardens, and which are also present in the tree. 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[28] of each taxon in the tree, and ranked all missing genera according to evolutionary distinctiveness. 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 cutoff at five consecutive absent tips or more. Due to the wholesale absence of genera from early diverging lineages (Bryophyta, Marchantiophyta and Anthocerotophyta) the search for absent genera-level clusters was focussed solely on Tracheophyte lineages (Pteridophytes, Gymnosperms and 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 1 January 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 the 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 2,780 IUCN globally threatened endemic species. Country-level endemicity was determined on the basis of the IUCN data associated with each IUCN Red List assessment record. Endemics in this sense were coded as plants that are documented to occur in only 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 (CR), Endangered (EN) and Vulnerable (VU) species held by botanical gardens differ 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 the R package rgbif version 0.9.7 to retrieve georeferenced occurrence data for IUCN threatened taxa, with at least one georeferenced location record. Geolocation data were retrieved for 8,619 out of the 11,055 IUCN threatened species. 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 8,619 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 geolocated records, we then refined the data set to 5,436 species with at least 5 georeferenced occurrences, and then refined this to 4,613 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 section. Using this refined data set, the percentage of threatened species present in gardens from each latitudinal bin was averaged across all tropical latitudinal bins (between 23.43704° N and 23.43704° S) and compared with the average percentage across all temperate latitudinal bins (between 23.44° N and 66.5° N and between 23.44° S and 66.5° 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 package fmsb v0.6.1. We formed 2×2 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 = FALSE.

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 P.S., Director-General of BGCI.

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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* (Progress Press, Malta, 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. *Ecol. Evol.* **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. *Trend. Plant Sci.* **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. *Trend. Plant Sci.* **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* **14**, 5–13 (2016).
11. Smith, P., Dickie, J., Linington, S., Probert, R. & Way, M. Making the case for plant diversity. *Seed Sci. Res.* **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? *Bot. Helv.* **117**, 15–28 (2007).
14. Golding, J. et al. Species-richness patterns of the living collections of the world's botanic gardens: a matter of socio-economics? *Ann. Bot.* **105**, 689–696 (2010).
15. Hillebrand, H. On the generality of the latitudinal diversity gradient. *Am. Nat.* **163**, 192–211 (2004).
16. Hinchliff, C. E. et al. Synthesis of phylogeny and taxonomy into a comprehensive tree of life. *Proc. 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* **13**, 612–627 (2010).
18. Kauserud, H., Mathiesen, C. & Ohlson, M. High diversity of fungi associated with living parts of boreal forest bryophytes. *Botany* **86**, 1326–1333 (2008).
19. Turetsky, M. R. The role of bryophytes in carbon and nitrogen cycling. *Bryologist* **106**, 395–409 (2003).
20. Westwood, J. H., Yoder, J. I., Timko, M. P. & dePamphilis, C. W. The evolution of parasitism in plants. *Trend. Plant Sci.* **15**, 227–235 (2010).
21. Possingham, H. P. et al. Limits to the use of threatened species lists. *Trend. Ecol. Evol.* **17**, 503–507 (2002).
22. Godefroid, S. et al. How successful are plant species reintroductions? *Biol. Conserv.* **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, Washington, DC, 2012).
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 (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. *Sov. Phys. Dokl.* **10**, 707–710 (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).

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Author contributions

S.B. and P.S. conceived the study, P.S. released the data, R.M. cleaned the data, S.B. designed the analyses, R.M. and S.B. performed the analyses, and S.B. and P.S. wrote the manuscript.

Competing interests

The authors declare no competing financial interests.

Additional information

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☐ Initial submission ☒ Revised version ☐ Final submission

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▸ Experimental design

1. Sample size

Describe how sample size was determined.	The samples sizes were essentially determined by available 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 species 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). At the point of access, and still currently, these data sources represent the largest sample sizes of data available to analyse the global state of ex-situ conservation by the world's botanic garden network. While in this scenario, more data is always welcome, these datasets are sufficient to reveal the fundamental patterns driving ex-situ plant conservation across the global botanic garden network, and to estimate baseline statistics with respect to conservation achievement.

2. Data exclusions

Describe any data exclusions.	Data sources were subject to extensive cleaning which led to data exclusion athe start of the process. We were interested in biological species only with accepted taxon names. However the data sources were derived from uploads from many institutions world wide, who use a variety of taxonomic systems and grow a range of horticultural varieties and cultivars, not just biological species. 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 also discarded records of horticultural taxa such as cultivars, as we were interested in true biological species. We computationally-normalised the taxonomy of records using the R package Taxonstand 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 using Damerau-Levenshtein distance 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. GBIF georeferenced location data was also cleaned 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 also refined location data to include only species with at least five georeferenced occurrences, whose latitudinal range is either temperate or tropical.

3. Replication

Describe whether the experimental findings were	Each analysis was repeated multiple times, to check internal consistency.

reliably reproduced.	Biogeographic analyses which used GBIF location data were repeated using a number of cut-offs (>5 georeferenced location, and >10 georeferenced location) to confirm that the findings held. We ultimately reported findings at the >5 georeferenced locations

4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.	Randomisation was not relevant in our analyses because all analyses depended on knowing the location of species within botanic gardens, and around the world. We did not perform any modeling estimates, that required random sampling.

5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.	Blinding was not relevant in our analyses because all analyses depended on our knowing and interpreting the location of species within botanic gardens, and around the world.

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
☐	☒	A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☒	☐	A statement indicating how many times each experiment was replicated
☐	☒	The statistical test(s) used and whether they are one- or two-sided (note: only common tests should be described solely by name; more complex techniques should be described in the Methods section)
☐	☒	A description of any assumptions or corrections, such as an adjustment for multiple comparisons
☐	☒	The test results (e.g. *P* values) given as exact values whenever possible and with confidence intervals noted
☐	☒	A clear description of statistics including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
☒	☐	Clearly defined error bars

See the web collection on statistics for biologists for further resources and guidance.

Software

Policy information about availability of computer code

7. Software

Describe the software used to analyze the data in this study.	Various analyses were implemented in the software package 'R', with individual packages and the version used cited in the methdology, and repeated here: 'Taxonstand' v1.8; 'stringdist' v0.9.4.4; 'rgbif' version 0.9.7; ‘chloroplethr' 3.6.1; 'fmsb' v0.6.1 . The software programme FigTree v1.4.3 was used to visualise and draw the phylogenetic tree. Prism V7.0c was used to draw all graphs. Illustrator 21.0.0 was used to assemble figures.

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). *Nature Methods* guidance for providing algorithms and software for publication provides further information on this topic.

Materials and reagents

Policy information about availability of materials

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.	No unique material were used.

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).	No antibodies were used.

10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.	No eukaryotic cell lines were used.
b. Describe the method of cell line authentication used.	No eukaryotic cell lines were used.
c. Report whether the cell lines were tested for mycoplasma contamination.	No eukaryotic cell lines were used.
d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by ICLAC, provide a scientific rationale for their use.	No commonly misidentified cell lines were used.

Animals and human research participants

Policy information about studies involving animals; when reporting animal research, follow the ARRIVE guidelines

11. Description of research animals

Provide details on animals and/or animal-derived materials used in the study.	No animals were used.

Policy information about studies involving human research participants

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.	No human research participants were used.