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Review

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Botanic gardens are an untapped resource for studying the functional ecology of tropical plants

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Functional traits are increasingly used to understand the ecology of plants and to predict their responses to global changes. Unfortunately, trait data are unavailable for the majority of plant species. The lack of trait data is especially prevalent for hard-to-measure traits and for tropical plant species, potentially owing to the many inherent difficulties of working with species in remote, hyperdiverse rainforest systems. The living collections of botanic gardens provide convenient access to large numbers of tropical plant species and can potentially be used to quickly augment trait databases and advance our understanding of species' responses to climate change. In this review, we quantitatively assess the availability of trait data for tropical versus temperate species, the diversity of species available for sampling in several exemplar tropical botanic gardens and the validity of garden-based leaf and root trait measurements. Our analyses support the contention that the living collections of botanic gardens are a valuable scientific resource that can contribute significantly to research on plant functional ecology and conservation.

This article is part of the theme issue 'Biological collections for understanding biodiversity in the Anthropocene'.

1. Introduction

Functional traits are 'morpho-physio-phenological' characteristics that are measured at the individual-level, influence individual fitness and can be used to understand population, community and ecosystem-level processes [1]. Plant functional traits are increasingly being used to understand broad ecological and evolutionary patterns (e.g. [2–6]). Although certain functional traits are limited in their ability to predict demographic rates [7], they are potentially useful for predicting the distributions of species [4], ecosystems [8] and biomes [9], and for forecasting their responses to climate change [10,11]. Several extensive databases have collated and distributed data on plant traits (e.g. TRY [12] (www.try-db.org), BIEN ([13]; http://bien.nceas.ucsb.edu/bien/) and GIFT (http://gift.uni-goettingen.de/home)), which have facilitated the functional trait approach to plant ecology. While trait information is now available for thousands of plant species, a paucity of data still exists for some ecosystems and taxa. Namely, very few data are available for tropical species [12].

Tropical forests harbour a greater biodiversity than any other terrestrial ecosystem [14] and their estimated 40 000–53 000 tropical tree species [15] perform many invaluable ecosystem services. For example, tropical forests account for an estimated 70% of global forest carbon sequestration [16], offsetting anthropogenic emissions and thereby slowing climate change. Despite their importance, tropical forests are extremely susceptible to human disturbances, including deforestation

and climate change [17–19]. Indeed, a recent analysis predicted that species in the tropical continents of South America and Africa face a 23% and 12% risk of extinction, respectively, owing to climate change—significantly higher than the global average of 8% [20]. That said, very few studies have investigated how tropical plant species are actually responding to contemporary climate change [21]. Our ability to understand how tropical plant species will respond to climate change is hindered, in part, by the lack of relevant functional trait data and the logistical difficulties associated with measuring functional traits in tropical ecosystems.

The functional trait data that are available for underrepresented plant taxa, like tropical species, are generally easily measured functional traits, such as dry leaf mass per unit leaf area (LMA; or its inverse, specific leaf area [SLA]). Such functional traits are popular because they do not require specialized equipment and yet may be broadly indicative of some plant ecophysiological strategies [1,6,22]. However, these easy-to-measure traits are often poor proxies for species' physiological or environmental tolerances, with several studies showing that they are generally weak predictors of species' distributions, demographic rates and sensitivities to climate change [23]. By contrast, other 'hard' traits, such as maximum photosynthetic rate per leaf dry mass (A_{max}) and optimal temperature for photosynthesis (T_{opt}), are more direct measures of physiological parameters and hence should be better predictors of species' environmental tolerances. Unfortunately, measuring these functional traits requires specialized instruments and facilities; therefore, data on these traits are typically more difficult, time consuming and costly to collect. The logistical and physical difficulties inherent in collecting trait data, and especially hard-to-measure trait data, are exacerbated when working in remote and poorly accessible locations with limited infrastructure [24]. These practical constraints have likely contributed to the scarcity of trait data from tropical forests and their constituent plant species.

Botanic gardens and arboreta present a potential solution to the paucity of functional data for underrepresented plant taxa. The diverse living collections housed in botanic gardens represent roughly 30% of all plant species [25] and provide researchers with easy access to thousands of species from all over the world with diverse life and evolutionary histories. Botanic gardens also often have in-house laboratories and are associated with universities and other research institutions, thus allowing scientists to overcome many of the infrastructural difficulties associated with acquiring functional trait data for tropical forest species *in situ*.

In this review, we show that despite their potential value, botanic gardens remain grossly underused for studying the functional ecology of plants. We discuss the benefits and potential biases of botanic gardens for measuring functional traits and studying the ecology of tropical woody plant species. Finally, we combine publicly available trait data with data that we collected from woody plants in a North American tropical botanic garden (Fairchild Tropical Botanic Garden) to address the concerns about biases in functional trait measurements from botanic collections.

(a) Functional trait data are missing for most tropical species

To highlight differences in the amount of trait data that have been collected and made available for tropical versus

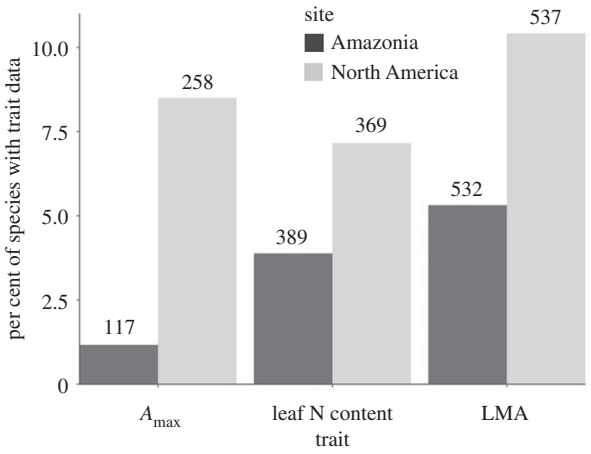

Figure 1. The per cent of woody Amazonian seed plants and woody North American species represented by one of three Leaf Economic Spectrum (LES) traits from TRY's public dataset; leaf mass area (LMA), leaf nitrogen content (N) and photosynthetic rate per dry mass (A_{max}).

temperate plant species, we compiled species lists of the named woody plants from lowland Amazonia (10 013 spp.) and North America (USA and Canada; 5157 spp.). Many species in these regions remain undescribed and, as such, these lists are far from complete. For example, our list of Amazonian woody plants included approximately 10 000 species, even though recent studies argue that there are at least 14 000–16 000 species of trees alone in this region. In addition, the regional species lists we compiled do not include all possible plant life forms [26]. For the North American species list, we only included trees, shrubs and palms; for the Amazonian species list, we included woody seed plants (trees, shrubs, lianas and palms). Given that unnamed species inherently do not have trait data available in any public trait databases and that woody species are generally better studied than other plant lifeforms, our estimates of how many species lack trait data (see below) are therefore likely to be highly conservative. This is especially true for the Amazon, where a much greater proportion of diversity remains unnamed [27,28].

When assessing the general availability of trait data for species in the Amazon and North America, we focused only on leaf traits. Leaf, stem and root traits all comprise important axes for defining plant functional types and all have been used in vegetation models to understand the responses of plants to climate change [29]. However, leaf traits are more commonly measured than stem and root traits, and thus should be available for the greatest number of species. Leaf traits also explain a large proportion of variance in the global spectrum of plant form and function that includes traits from other plant organs [5]. The leaf traits that we included in our tallies were LMA, leaf nitrogen content (N) and maximum photosynthetic rate per dry mass (A_{max}). These traits are widely measured and are all important components of global biogeochemical cycles [6].

Unsurprisingly, the easiest-to-measure trait, LMA, was available for the most species. At least one record of LMA (or SLA) was available for 10.4% (537) of the North American woody plant species, whereas LMA data were available for only 5.3% (532) of the Amazonian species (figure 1). Compared with LMA, fewer data exist for N, but species from North America are still proportionally better represented (7.2%; 369 spp.) than Amazonian species (3.9%; 389 spp.) (figure 1). A_{max} is available for only 8.5% (258 spp.) of the North American

species, and 1.2% (117) of the Amazonian species (figure 1). Interestingly, there are more Amazonian species with leaf N data than temperate species, but the breadth of trait coverage is clearly greater for North American species owing to the region's lower diversity. As indicated above, the true proportion of species represented by these traits would be considerably lower if unnamed species and non-woody species were included. For example, if we assume that there are, in fact, 16 000 Amazonian tree species, then only 3.3%, 2.4% and 0.7% of them have data available for their LMA, leaf N and A_{max}, respectively. North America and the Amazon are among the best-studied temperate and tropical systems, respectively, and thus the percentages would likely drop even further if we looked at other regions such as Africa or Asia.

We also investigated the functional trait data availability in TRY for species grown at the Fairchild Tropical Botanic Garden (FTBG, Coral Gables, FL, USA). Only 3.8% (97) of the 2549 species at FTBG possessed any LMA data, while fewer data were available for leaf N (3.1%; 79 sp.) and A_{max} (1.7%; 44 sp.). FTBG shared 230 species in common with the North American dataset and 142 species in common with the Amazon species list.

We observed an overall bias against tropical species in the proportions of functional trait data; we also found marked differences in availability depending on the type of functional trait measured—differences most probably attributable to the difficulty, equipment-needs and costs of measuring each trait. For example, LMA requires little specialized equipment to measure, but A_{max} requires expensive and specialized equipment often unavailable to researchers and incompatible with inclement field conditions.

Combined, the woody plant species of North America and the Amazon have a strong influence over the global carbon cycle and climate, but 10% or fewer of these species are represented by any trait data. Clearly, a great deal of work is required to increase the amount of data available for all plant species, but especially for tropical plant species. The lack of trait data (even easy-to-measure traits like LMA) for such a high proportion of tropical plant species mirrors general biogeographical biases that are present in many disciplines of ecology. Consequently, there is a limited breadth of data for global vegetation models or other models that are parametrized with functional traits to predict future ecosystem functions [11]. The low representation of traits from species grown at FTBG highlights the fact that botanic gardens are an untapped resource that can be used to rapidly increase the availability of trait data for these models, as well as for other areas of ecology and conservation research.

(b) Potential advantages and concerns of functional ecology research in botanic gardens

Several of the challenges associated with the acquisition of functional plant trait data *in situ* can be mitigated by working in botanic gardens. Botanic gardens are often designed with the intent of pubic engagement and thus are commonly located near urban centres [30]. Networks of well-maintained paths facilitate access to plants within the gardens and greatly enhance sampling efficiency, especially for studies that require substantial instrumentation.

Accurate taxonomic designations are often an issue for field-based studies in diverse ecosystems. For example, the flowers and fruits necessary to verify species-level identifications of tropical plants in the field are rarely found at the time of sampling [27]. Conversely, the living collections of botanic gardens are usually identified and permanently labelled. Indeed, plants from botanic gardens are already widely used in systematic and phylogenetic research [31] and are often used in the designation of formal species names.

Field studies of tropical forests typically only census trees, shrubs and lianas and thus other life forms are mostly unavailable for immediate trait sampling. Indeed, in most forest inventory plots, only freestanding woody stems ≥ 10 cm DBH are sampled (a notable exception are plots in the Forest Global Earth Observatory [ForestGEO] network, where all woody plants with DBH ≥ 1 cm are inventoried). In contrast, the living collections of botanic gardens often include herbs, succulents, epiphytes, grasses and other plant growth forms that can readily be sampled for traits or other information. Although field sites have the potential to include additional non-tree growth forms in their research programmes, doing so would require significant new investments of time, effort and money. Another way that botanic gardens diverge from field sites is in their meticulous curatorial records that can include provenance, phenology, fertilization and watering regimes, as well as ontogenetic information. These records can be used to help identify and partition sources of variation in functional data that may influence garden-based trait measurements. In field sites, such detailed individual-level information rarely exists.

(c) Concerns

Functional traits measured on plants growing in botanic gardens may not always represent the trait values of natural *in situ* populations. Indeed, *in situ* and *ex situ* differences in trait expression may arise owing to the effects of the genotype collected, the planting environment and plasticity of different genotypes in the garden environments [32,33]. In some instances, garden environments may be outside the realized biotic and abiotic niches of a given species, leading to trait values unrepresentative of data collected *in situ*. For example, planting in colder sites may cause decreases in LMA [34], and fertilization may cause roots to thicken (see §1e). While these concerns are valid for garden-based functional trait data, they can also apply to any field site. Field sites may include populations of species living at the edge of their climatic and edaphic niches, causing variability in plant performance and trait expression. Given the long-lived nature of trees and the absence of data on the niches of most species, researchers may fail to recognize if the individuals being sampled from plots represent sink populations. This is a problem, especially in the context of climate change, because some species may have established into forest plots under climates distinct from those of present-day [35,36].

Another potential concern with sampling from botanic gardens is that some species may only be represented by one or a few individuals. Because of small population sizes, gardens are clearly limited in their ability to capture phenotypic, genotypic or ontogenetic variation. A sample size of five individuals is typically recommended to estimate traits for individual species [22] and a minimum of three individuals is required to capture any measure of intraspecific variation. The issue of small sample size is not exclusive to botanic gardens. One defining feature of many tropical forests is high species diversity, including many rare species. As such,

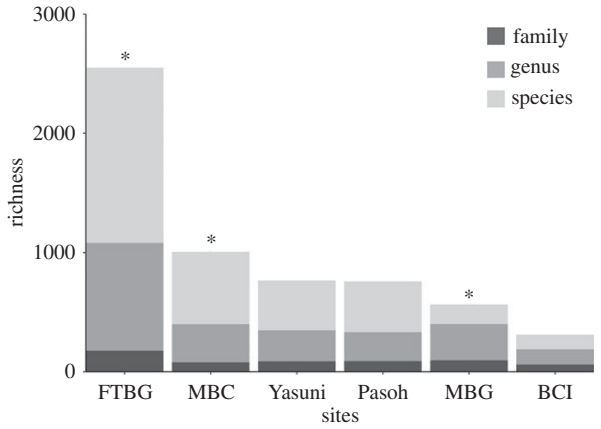

Figure 2. The family, genus and species richness for FTBG, MBC, Yasuni forestry plot, Pasoh forestry plot, MBG and Barro Colorado Island's forestry plot (BCI). Shaded bars are overlapping, not stacked, so that the height of each coloured bar indicates total richness. Sites are ranked from greatest to least species diversity; asterisks indicate gardens.

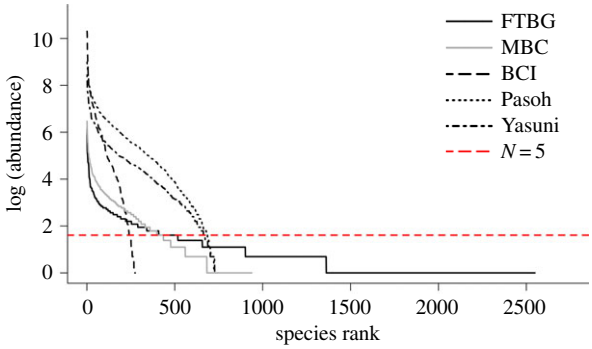

Figure 3. Species rank-abundances for FTBG, MBC, Barro Colorado Island forestry plot (BCI), Pasoh forestry plot and Yasuni forestry plot. Lines correspond to each site, and the horizontal dotted line indicates a sample size of five individuals. (Online version in colour.)

most tropical field plots include several species represented by few and rare individuals [26]. In the case of both gardens and field plots, scientists can augment their sample sizes for target species by working with multiple populations growing at different sites or in gardens.

(d) Botanic gardens offer access to a high diversity of species for trait sampling

To illustrate that gardens contain diverse collections, we compared the species counts of several tropical botanic gardens and tropical forest field sites for which comprehensive species lists were available. Our purpose was not to compare the true plant diversity of these sites *per se*, but rather to assess the number of tagged and identified species that can be readily sampled for functional traits in typical botanic gardens and tropical field plots. In other words, while each of these sites may contain species that are not included in the species lists owing to sampling criteria or protocols (for example, ForestGEO plots only sample woody stems with a diameter at breast height $\geq$1 cm), unlisted species are unavailable or effectively 'invisible' for rapid trait sampling.

Our datasets for these analyses included three tropical botanic gardens (FTBG, located in Coral Gables, FL, USA; Montgomery Botanical Center (MBC), located in Coral Gables, FL, USA; Medellin Botanical Garden (MBG), located in Medellin, Colombia) and three Smithsonian Forest Global Earth Observatory (ForestGEO) 50 ha tropical forest inventory field sites (Pasoh forestry plot, located in Pasoh Forest Reserve, Malaysia; Yasuni forest plot, located in Yasuni National Park, Ecuador and Barro Colorado Island (BCI) forest plot, located on BCI, Panama).

To compare taxonomic diversity among the gardens and field sites, we tallied the number of species, genera and families listed for each location. Names were standardized prior to counting (see §3 below) and only valid taxonomic names were included in counts of each taxonomic level. Based on these counts, FTBG contains the highest taxonomic richness among all sites at all taxonomic levels. Species richness was greatest for FTBG (2549 species), followed by MBC (1006), Yasuni (766), Pasoh (758), MBG (565) and BCI (311) (figure 2). Genus richness was highest for FTBG (1082), followed by MBG (401), MBC (399), Yasuni (348), Pasoh (333) and BCI (188) (figure 2). Family richness was also highest for FTBG (176) followed by MBG (96), Pasoh (90), Yasuni (88), MBC (80) and BCI (61) (figure 2). These simple counts confirm that large numbers of species, spanning a breadth of phylogenetic histories, are available for rapid sampling in botanic gardens.

To address the concern that gardens may retain few individual plants per species for sampling (see §1c), we analysed species rank-abundance data for two of the botanic gardens that had available abundance data (FTBG and MBC) and the three ForestGEO field inventory sites (BCI, Pasoh and Yasuni). The species rank-abundance curves indicate that sample sizes of at least five individuals per species are obtainable for more species in both of the botanic gardens than in BCI, but not in Yasuni or Pasoh (figure 3). If the minimum sample size is lowered to three individuals, FTBG offers access to more species (over 901) than any of the three field sites (Pasoh and Yasuni provide access to 704 and 701 species, respectively) (figure 3).

Our comparisons of species richness at botanic gardens and natural field sites demonstrate that botanic gardens, such as the FTBG and the MBC, can provide more tagged, mapped and taxonomically verified tropical plant species in their collections than do large field plots in some of the most diverse forests on Earth (figure 3). This is especially noteworthy considering that the FTBG and MBC are moderately sized gardens and their grounds include extensive areas (e.g. large ponds, roads and lawns) that are devoid of accessioned plants. Larger, more-diverse temperate and tropical gardens and arboreta (e.g. Xishuangbanna Tropical Botanical Garden, Rio de Janeiro Botanical Garden, Singapore Botanic Gardens, Kew Royal Botanic Gardens and Missouri Botanical Garden) can potentially provide access to even greater plant diversity and sample sizes than the gardens examined in our analyses. The high diversity of living collections in gardens is likely attributable to their explicit programmes promoting the exploration, documentation and conservation of plant diversity [31]. Through these programmes and collection efforts, botanic gardens collectively curate approximately one-third of all plant species and 40% of all threatened plant species [25]. Given the proclivity of botanic gardens for conservation, calls for improved collections of tropical species and the susceptibility of tropical plants to climate change and habitat loss, the diversity and importance of living collections in tropical botanic gardens are likely to increase in coming years [31,37].

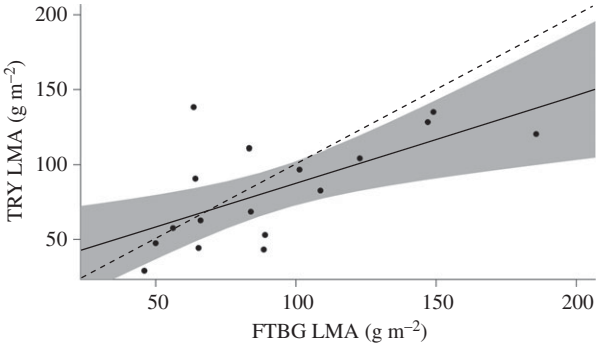

Figure 4. The relationship between species' mean LMA measured in FTBG and the global species' mean from the TRY database. The solid line indicates the relationship of the FTBG and TRY data, the shaded area is the 95% confidence internal of the linear model ($y = 0.59$ [± 0.18 s.e.] $\times x +$ 28.95[$\pm$ 17.68 s.e.]; $r^2 = 0.38$; $p < 0.001$; d.f. $= 15$), and the dashed line shows the 1 : 1 relationship.

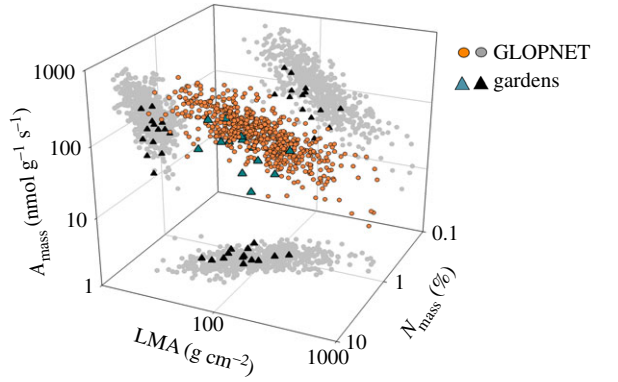

Figure 5. The three-dimensional relationship between LMA, N, A_{max} traits of the leaf economic spectrum. Orange dots and blue triangles represent the three-dimensionality of the data for GLOPNET and FTBG data, respectively. Grey dots and black triangles represent the two-dimensional relationships of the LES traits.

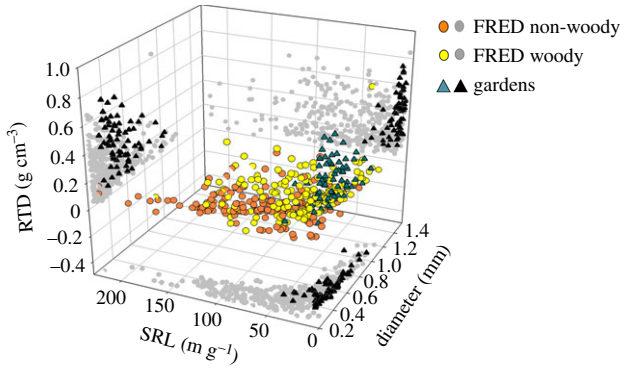

Figure 6. The three-way relationship between SRL, diameter and RTD root traits. Orange and yellow circles represent the non-woody and woody species from the FRED ([38] https://roots.ornl.gov/), respectively; green triangles indicate data from FTBG. Grey points and black triangles represent the two-dimensional relationships of the root traits.

Importantly, a growing number of gardens have recognized the importance of their collections for *ex situ* conservation and thus they are actively striving to augment the number of individuals per species and their representation of intraspecific genetic diversity [37].

(e) Botanic garden species can provide representative functional traits

Botanic gardens maintain diverse collections of species that can be sampled for functional traits; however, a valid concern is whether functional trait data measured from garden-grown individuals are representative of data collected at *in situ* field sites (see §1c). To address this issue, we selected a sample of woody plant species common to both FTBG and the TRY public trait database (often with measurements from multiple field sites). We then tested whether LMA measurements collected at FTBG are representative of the same species' mean LMA calculated from conspecific measurements from TRY. We found that our garden-based measures of LMA were significantly positively correlated with the mean LMA values measured *in situ* on wild conspecifics (Pearson's $r = 0.7$, d.f. $= 15$, $p < 0.01$) (figure 4). Next, we tested whether the trait values measured at FTBG are better or worse predictors of species' mean trait values than trait measurements collected at individual field sites. To do this, we calculated the correlation between the LMA values available in TRY from individual field sites with the mean LMA values of the corresponding species (mean values calculated excluding the individual site being tested). Based on this analysis, we found that our garden-based measures of LMA are, in fact, a better predictor of species' mean trait values than 80% of the plot-based studies (electronic supplementary material, figure S1).

In a second set of analyses using the same study species, we used a null-model bootstrapping procedure (see Material and methods) to test if the distributions of three leaf traits (LMA, N and A_{max}) measured on plants grown in FTBG are representative of the overall distributions of those trait values in the TRY databases. We found no significant difference between the trait distributions of these traits based on individuals sampled at FTBG and in TRY ($p = 0.39$; figure 5 and electronic supplementary material, figure S2).

Similarly, we collected data on root traits (specific root length (SRL), root diameter and root tissue density (RTD)) measured at the FTBG for 71 species to test if their distributions were representative of overall distributions of root trait data included in the global Fine-Root Ecology Database (FRED, [38]). The FTBG root trait data included a set of species distinct from those used in the analyses of leaf traits described above. Unlike leaf traits, the root traits measured at FTBG were significantly outside the distributions of these traits for woody species in FRED ([38] https://roots.ornl.gov/; $p = 0.02$; figure 6 and electronic supplementary material, figure S3). There are several potential reasons why the garden-based measures of root traits fell outside the field-based distributions of root traits even though leaf traits did not. The differences in root traits measured in gardens compared to those measured *in situ* may result from the management practices of gardens, such as mulching and fertilization, which can affect root morphology. Studies conducted in temperate forests indicate that trees growing in fertile patches tend to decrease SRL, increase diameter and increase RTD [39]. However, changes in belowground functional traits in response to environmental changes have been poorly studied, particularly in tropical systems. Furthermore, few tropical species are included in FRED or other available root trait databases [38]. Previous analyses of root traits have shown that tropical trees, like those we measured, tend to have thicker root systems and lower SRL than species from other biomes. This observation may reflect an acquisition strategy of species with longer lifespans and

higher mycorrhizal colonization in tropical than in temperate environments [40,41]. In support of this hypothesis, when the distributions of root trait values from the FTBG are compared with the distribution of root trait data from only woody species from tropical climates, we found no significant difference between root traits measured at the garden and those compiled in FRED (electronic supplementary material, figure S4, $p = 0.12$). However, this subset of the FRED database contained 57 species, and the lack of a significant difference we observed may be owing to the low statistical power of our test. Until more tropical root trait data become available to more rigorously test garden versus *in situ* trait representation, our results support the use of botanical gardens as favourable locations to acquire root trait information about species that are difficult to access in natural conditions, but also to study the responses of root traits to changing environmental conditions and their role as drivers of ecosystem processes [42].

2. Conclusion

The use of functional traits has the potential to facilitate studies investigating global patterns of biodiversity and the impacts of global changes on species and ecosystems. Unfortunately, functional trait data remain very sparse, with harder-to-measure traits and tropical species being especially underrepresented. Our analyses indicate that the high diversity and adequate abundances of tropical species within botanic gardens exceed those of many established field sites. Moreover, our findings indicate that the functional traits measured on garden plants are representative of the mean trait values measured on wild plants. These findings support our proposition that botanic gardens provide a powerful, but underused tool for rapidly augmenting functional trait databases.

Botanic gardens are known for having strong research programmes that include conservation, systematics and horticulture; and consequently they often possess multifaceted, multidisciplinary datasets about their collections. Functional ecology and climate change research are pragmatic additions to these existing programmes. Indeed, the utility of botanic gardens for research extends beyond plant biology. The dense diversity of plants and habitats that occur within botanic gardens can also support diverse animal communities. For example, within the FTBG, there exist many distinct habitats ranging from tropical rainforest, to dry forest, to desert. These habitats support a variety of different animal communities that can be used to study, for example, the connections between plant and animal species assemblages, the responses of animals to environmental change [43], as well as plant–animal interactions [44–46].

The proximity of most botanic gardens to urban centres overcomes many of the logistical barriers that plague fieldwork. Not only does this facilitate the use of gardens by scientists, it also promotes their use by the public. Botanic gardens provide a rare forum where scientists can connect with the public through both formal and informal interactions. In addition, botanic gardens often have established environmental education programmes that can greatly facilitate outreach activities (e.g. FTBG currently facilitates botanical research projects for over 125 000 elementary, middle and high-school students in Miami, FL, USA). In summary, research in botanic gardens can help to quickly advance research on the functional ecology of tropical species and tropical ecosystems.

3. Material and methods

(a) Functional trait data are missing for most tropical species

To contrast the availability of functional trait data between tropical and temperate species, we first gathered representative species lists for the Amazon and North America (USA and Canada). To represent tropical species, we selected a recently updated list of woody seed plant species occurring in the Amazon [47]; to represent temperate species, we used a species list for woody North American seed plants from the Biota of North America Program (BONAP; http://www.bonap.org/) excluding species from tropical territories. In addition to North America and the Amazon, we also assessed trait availability in a single exemplar botanic garden—the Fairchild Tropical Botanic Garden (FTBG). In contrast to the Amazonian and North American species lists, the FTBG species list includes herbaceous and woody taxa within Tracheophyta from throughout the global tropics and subtropics. Taxonomic names for trait comparisons and diversity analyses (following section §2b) from all the datasets used in this study were standardized by removing special characters and formats for accurate taxon counts and merging of datasets by species names. Species names were simplified to include only genus and specific epithet, excluding extensions such as subspecies and varieties. Taxa that were not identified to the genus level were excluded from diversity tallies. All names were further standardized using the Taxonomic Name Resolution Service (TNRS, http://tnrs.iplantcollaborative.org/) [48]. Family names were included with names submitted to the TNRS where available, and results from the Tropicos database (Missouri Botanic Gardens) were selected over others with a similar database-match score and taxonomic opinion.

To assess the availability of trait data for our FTBG, Amazonian and North American species lists, we focused on three widely measured leaf traits, LMA ($g\,m^{-2}$), leaf nitrogen content (N, %) and photosynthetic rate per dry mass (A_{max}, $nmol\,g^{-1}\,s^{-1}$). We obtained all of the publically available data for each of these three Leaf Economic Spectrum (LES) traits from the TRY database (www.try-db.org; accessed in January 2018) [12]. We then calculated the proportion and number of species from each checklist that have data available for each of the three leaf traits.

(b) Botanic gardens offer access to a high diversity of species for trait sampling

To compare the plant diversity contained in the living collections of tropical botanic gardens with that of field plots, we compiled lists of species occurring at FTBG, MBC and MBG, and three of the ForestGEO's most prominent and best-studied field sites (i.e. the forestry plots in Barro Colorado Island, Pasoh and Yasuni). The gardens we used to compare species diversity were chosen because they are representative botanical gardens for the Neotropics and provided us with access to detailed collection information. Similarly, the ForestGEO plots were chosen because of their large size and standardized measurement protocols that maximize estimates of species diversity by measuring small diameter trees and shrubs. The checklists from the three ForestGEO plots are open-access and available online (obtained from http://www.forestgeo.si.edu; accessed 23 February 2018).

For each garden and field site, we tallied the number of plant families, genera and species. Taxa identified to the genus level but not the species level were excluded from species richness counts, but were retained in genus and family richness counts. Species lists were cleaned and standardized as described above.

Species' abundance data were available for FTBG, MBC and the three ForestGEO plots. Species' abundances for BCI, Pasoh and Yasuni were taken from their 2005, 2003 and 2003 censuses, respectively. Species' abundances were ranked for each site and

used to determine the number of species at each site that met different minimum sample size criteria.

(c) Botanic garden species can provide representative functional traits

We collected leaf and root traits from tree and shrub species grown in FTBG to determine whether functional traits measured *ex situ* on individuals growing in the garden are representative of traits collected from plants growing in natural field conditions (i.e. *in situ*). Specifically, we collected data on the leaf traits of LMA, N and A_{max}. Since we were initially interested in the ability of LMA from species at FTBG to represent species' mean trait values calculated from data in TRY, our LMA data were limited to the woody species common to both FTBG and TRY. Our initial LMA dataset included 17 species (electronic supplementary material, Leaf Traits). The subsequent leaf trait measurements, N and A_{max}, were restricted to these same 17 species.

All traits were measured following standard protocols. LMA was calculated from at least three leaves per individual and up to three individuals were sampled per species. After fresh leaves were scanned, dried and weighed for LMA, they were ground and leaf tissue nutrients were measured using a CHN elemental analyser (Thermo Flash EA, 1112 series) to get total nitrogen content. Carbon assimilation rates were estimated for each species at approximately 400 ppm CO_2 as determined from A-CI curves using a LI-COR 6800 portable photosynthesis system. During the time of measurement, leaf chamber conditions were maintained at 28°C, 50% relative humidity and 1500 $\mu mol\ m^{-2}\ s^{-1}$ of photosynthetically active radiation. A_{max} was calculated by multiplying the assimilation rate by the inverse of LMA. Assimilation rates were measured for at least one leaf per individual and for up to three individuals per species. We present species' means for each trait. Our final dataset for LMA, N and A_{max} only included 13 species (electronic supplementary material, Leaf Traits) because of our inability to measure A_{max} on some species owing to Hurricane Irma.

Fine-root samples were collected for 71 woody plant species during the summer and autumn of 2017 (July–November) of 2017. Samples from each species were obtained from one to three relatively isolated, healthy adult trees from FTBG or at the nearby Kampong Botanical Garden (Miami, FL, USA). Root samples for each individual were obtained by tracing individual root branches within 2 m from the main stem, avoiding thick (more than 5 mm in diameter) roots. Root systems were carefully excavated and a small segment (approx. 10 cm long) that included three to four most-distal root orders was removed from the soil, placed in air-tight bags and stored at 4°C. In addition, a subsample was cleaned, tagged and preserved in a 45:5:50 water–acetic acid– formalin mixture as a reference sample. In the laboratory, all roots were gently washed with tap water and compared to the reference sample before further analysis. Five entire root systems (root system 5–10 cm long comprising the three most-distal root orders, *sensu* [49]) from each tree were weighed using an electronic analytical balance (Mettler Toledo—0.0001 g), scanned with a flat-top digital scanner (600 DPI resolution, 8-level grayscale, JPEG format; Epson Scanner Perfection V700 Photo), dried at 45°C for 48 h and reweighed. Image analysis of the entire root system scans was used for estimations of SRL ($m\ g^{-1}$) and RTD ($g\ cm^{-3}$) using WinRhizo software (2016 version, Instrument Regent, Quebec, Canada). In addition, small segments of the most-distal parts of the root system were reanalysed to estimate average diameter (mm) of the first root order. Our final dataset for SRL, RTD and root diameter is included in the electronic supplementary material, FTBG Traits.

The large quantity of data available for LMA in TRY allowed us to test whether species' LMA values from FTBG are representative of corresponding values for conspecifics in the TRY database [12]. This was not possible for additional leaf and root traits owing to the scarcity of data available for these traits in TRY for conspecifics. First, we calculated the Pearson's coefficient of correlation between LMA values for FTBG and the mean LMA value for all conspecifics in the TRY database [50–64] ([65] and M. Leishman, New South Wales Plant Traits Database; see https://www.try-db.org/de/DatasetDetails.php). We next calculated the coefficient of correlation between species' mean LMA within each individual dataset included in TRY and the corresponding species' mean LMA values from TRY while excluding that individual dataset. Finally, we compared the strength of correlation of FTBG versus TRY to the distribution of correlation coefficients for each dataset versus TRY.

We also tested whether the data collected from FTBG fell within the documented three-dimensional distributions for existing leaf or root trait databases. We compared FTBG's leaf trait data to the corresponding data from the Global plant trait network (GLOPNET) database [6], which was accessed through the TRY website (www.try-db.org) [12]. Root trait data measured at FTBG were compared to the global FRED [38]. We log-transformed LMA, N, A_{max} and SRL values, then scaled all LES and root trait variables to zero. We then calculated the mean Euclidean distance between the LES or root traits for FTBG species and all species in the existing GLOPNET or FRED databases. More specifically, we tested whether the observed mean Euclidean distance of LES or root traits collected at FTBG differed from null distributions created by repeated random sampling of species from published databases. The null distribution was created by removing a random subsample of the GLOPNET or FRED databases equal in size to the number of species in FTBG's leaf or root trait datasets. The mean Euclidean distance between this subsample and the remaining database trait values was then calculated. Five thousand random subsamples were used to create the null distribution of distances. We then compared the observed distances to the null distributions in order to test if the FTBG trait measurements are, or are not, significantly more different from the TRY/FRED measurements than expected at random.

The FRED database includes many non-woody species, potentially confounding our tests of overlap between the distributions of root trait data collected from the FTBG versus the FRED. To account for this, we repeated the above analyses while first including only woody species from FRED and again while including only woody species in FRED from climates similar to the FTBG species. To create this last subset of species, we estimated the climatic distributions of species in the FTBG and FRED datasets by retrieving all available georeferenced records for our target species from the Global Biodiversity Information Facility (GBIF) (www.gbif.org, GBIF accessed via the 'spocc' R package [66] on 23 February 2018). For all species with $\geq$25 georeferenced records, we estimated the mean annual temperatures (MATs) and annual precipitation (PPT) at each collection location for all occurrences by extracting the MAT (BIO1) and PPT (BIO12) values from the Worldclim v.1.4 database at a spatial resolution of 30 arc seconds [67]. To account for potentially erroneous georeferenced locations, we removed any occurrences lying outside the 2.5 and 97.5% quantiles of MAT and PPT for each species. We then selected the woody species from the FRED and FTBG with mean MAT $\geq$15°C and $\leq$30°C, and mean PPT $\geq$1000 and $\leq$3500 mm. All statistical analyses and name standardizations were performed in R unless otherwise noted [68].

Data accessibility. This article has no additional data.

Authors' contributions. Ca.B., Ch.B., B.F., K.J.F. and T.M.P. conceived of and helped design the project. All authors assisted in collection, analysis and interpretation of the data. T.M.P., O.V.-B., Ch.B. and K.J.F. wrote the manuscript. All authors provided critically important intellectual content and assisted in revising the paper.

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