Title: The colonial legacy of herbaria

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Abstract

Herbarium collections shape our understanding of the world's flora and are crucial for addressing global
change and biodiversity conservation. The formation of such natural history collections, however, are not
free from sociopolitical issues of immediate relevance. Despite increasing efforts addressing issues of
representation and colonialism in natural history collections, herbaria have received comparatively less
attention. While it has been noted that the majority of plant specimens are housed in the global North, the
extent of this disparity has not been rigorously quantified to date. Here, by analyzing over 85 million
specimen records and surveying herbaria across the globe, we assess the colonial legacy of botanical
collections and how we may move towards a more inclusive future. We demonstrate that colonial
exploitation has contributed to an inverse relationship between where plant biodiversity exists in nature
and where it is housed in herbaria. Such disparities persist in herbaria across physical and digital realms
despite overt colonialism having ended over half a century ago, suggesting ongoing digitization and
decolonization efforts have yet to alleviate colonial-era discrepancies. We emphasize the need for
acknowledging the inconvenient history of herbarium collections and the implementation of a more
equitable, global paradigm for their collection, curation, and use.

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Main

The nearly 400 million specimens residing in the world's herbaria form the basis of the scientific understanding of our planet's flora and are a centerpiece of botanical research and discovery [1]. Since the 16th century, scientists including Linnaeus and Darwin have collected herbarium specimens principally to describe species and circumscribe taxonomic classifications. The past decade has seen a resurgence in herbarium collections research, which is driven in part by massive digitization efforts [2–4]. In particular, with advances in high-throughput methods and image analyses, herbarium specimens are increasingly being used in innovative ways [5,6] beyond their original intended purpose, including research pertaining to global change [7–9]. For example, herbarium specimens have been used to uncover the effects of climate change on plant phenology [10], ecophysiology [11], and herbivory [7]; as barometers for pollution [12] and eutrophication trends [13]; and to reconstruct the origin and spread of invasive species [14,15].

However, these collections are not free from the many sociopolitical issues that define our modern era. Despite increased efforts by natural history museums and other cultural institutions to address their legacy of colonialism and representation, such efforts have largely been focused on human- and animal-related collections and public exhibits [16,17]. In contrast, herbaria have received comparatively less attention, sidelined by their lower visibility; few herbaria offer public displays and plant awareness is generally lacking [18]. Nonetheless, botanists have contributed significantly to the colonial expansion of imperial powers through active participation in the overseas collection of plants and their scientific and economic development [19]. For instance, Hans Sloane (1660–1753), often credited as the inventor of chocolate milk, collected hundreds of plant specimens from overseas colonies via the slave trade, including those of cacao [20]. In Australia and other colonies, much of the early exploration of the continent by colonialists (during which many botanical specimens were collected) was done with the assistance of Indigenous peoples who acted as guides during expeditions – often under duress – or were forced to disclose their scientific knowledge of plants and place [21–23]. Though not specifically quantified, it has thus been noted that herbaria in the global north hold many of the voucher specimens and associated data from equatorial and southern hemisphere nations (i.e., the global south), owing to colonial-era explorations [24,25].

To address the past and present appropriation of plant diversity and to open a dialogue to help move us towards a more inclusive future, we must first understand the extent of disparity in herbarium collections across the globe – specifically, a more robust history of where they were collected and where they currently reside. Here, we, scientists and curators from herbaria across 40 countries from every continent, examine the colonial legacy of botanical collections by assessing the geopolitical distribution of herbarium collections and digitization efforts. Analyzing over 85 million plant specimen records from the

Global Biodiversity Information Facility (GBIF, April 23, 2021; https://doi.org/10.15468/dl.nt5wkx), the

largest repository of biodiversity data, and surveying herbarium staff an curators across the world, we

provide an in-depth view of the disparity present in herbarium collections and discuss the future of this

colonial legacy and how its effects can be mitigated (see Supplementary Information for discussions

about methods and assumptions).

The imprint of colonialism in online herbarium collections

Collection trends across the last four centuries strongly bear the imprint of colonialism, especially among

European institutions. These trends can be readily observed in the plant specimen records hosted on

GBIF, which represent a subset (~25%) of global herbarium collections (Fig. 1A). Large numbers of plant

specimens collected across the globe are currently housed in European countries, and to a lesser extent,

the United States. Indeed, the currently widely adopted taxonomy of life originated from European

scholars, most prominently Linnaeus and his acolytes, who were responsible for the relocation of massive

numbers of plant collections from across the globe into European institutions and their associated systems

of knowledge. This trend was further fueled by the desire by imperial powers to exploit the biological

resources of colonies abroad, a legacy of which persists to this day, for instance in the pursuit of

medicinal plants in tropical regions in search of profitable remedies for predominantly First World

ailments such as cancer or obesity [26].

The impact of this collecting legacy persists in the trends and patterns of more recent collecting activities.

Despite the era of overt colonialism drawing to an end after the Second World War, the historical trend of

specimen movement from Africa, Asia, and South America to Europe and North America has largely

remained constant (Fig. 1B, C), especially among countries that have historical connections [27]. In fact, the

proportion of specimens collected from other continents has increased in Europe and North America over

time. In particular, the United States emerged as the largest collector of overseas specimens after the

Second World War, acquiring massive collections from countries such as Brazil and Madagascar.

Notably, the proportion of specimens collected and housed in South America greatly increased during this

period, while collection activity in Africa remained largely driven by European and North American

countries, with the possible exception of South Africa. These trends are largely consistent when limiting

our sample to records with more complete information (e.g., geographic coordinates; Supplementary Fig.

1) or to collection activity in the 21st century (Supplementary Fig 2). However, we note that there are

other factors, such as the degree of economic development, regional policies, political stability, and

scientific interest that have likely influenced these patterns as well [28]. Also, though difficult to estimate, a

portion of the specimens that have been dislocated likely have duplicates deposited at local institutions,

especially among more recent collections that may yet remain undigitized and thus less discoverable.

Among the specimen data we examined from GBIF, only 2.8% were of the same species collected at the

exact same place and date and stored in different institutions.

Figure 1. The past movement of plant specimens across the globe based upon records from GBIF. The world map
depicts the top 10 percentile of intercontinental connections between countries where specimens have been collected
and where they are currently housed regardless of collection date (A). The widths of the arrows are proportionate to
the number of specimens dislocated and are colored by destination continent. Collections that remained in the
country of collection are not depicted. The lower panels illustrate the intercontinental flow of specimens before (B)
and after (C) the end of overt colonialism post World War II (late-1945). Arrows are colored by the continent of
origin. Numbers on the outer ring indicate specimen numbers collected from (lower half) or stored in (upper half)
each continent, and are in multiples of 100,000. Colors on the outer ring represent different continents.
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Figure 2. Disparity in the collection and housing of plant diversity. The top panel (A) maps the ratio of total number
of species with specimens housed in a country to the total number of species collected in that country (species
housed/collected). Ratios below one (blue) indicate areas where the number of species that have been collected from
that country is higher than the number of species housed in that country. Panel (B) shows the ratio of national versus
international collections held by each country, while (C) depicts the ratio of self-collected specimens in each country
versus those collected by other countries. Points sizes are log-scaled to the total number of specimens. Triangles
represent countries that have overtly colonized other countries in the past following reference [29].

Our analysis clearly demonstrates that colonial exploitation has contributed to a striking inverse

relationship between where plant biodiversity exists in nature versus where it is housed in herbaria. In

general, biodiversity is distributed along a latitudinal gradient, with most of the world's plant diversity

located in the tropics [30]. However, when we examine the number of species collected in a given country –

which reflects species richness – relative to the number of species with specimens housed in the same

country, striking disparities emerge (Fig. 2A). Specifically, most of the world's flora is stored in temperate regions in a reverse-latitudinal gradient. In particular, herbaria in the United States and several nations in western and central Europe house over twice the number of species that occur in these nations, demonstrating the international appropriation of large amounts of plant diversity (Fig. 2A). In contrast, much of Africa and Asia house fewer species than are collected there, because North American and European herbaria currently house much of the specimens and associated data from these regions owing, in no small degree, to their colonial past. Indeed, nations from these two areas simultaneously i) house a disproportionate number of internationally collected specimens (Fig. 2B), and ii) tend to have self-collected most of the specimens coming from their own countries (Fig. 2C). Further, over 80% of the specimens with digital images are held by European and North American institutions, the majority of which were collected from those two continents (Supplementary Fig. 3). We note that not all countries in these two continents have actively colonized others, but some have nonetheless amassed sizable international plant collections (e.g., Switzerland). Moreover, not all digitized specimen data online are available from GBIF – unique data can be found in smaller, regional repositories or institutional databases. Also, such online databases can harbor gaps and biases. Thus, the availability of digital data assembled for this study may be entirely reflective of the complete distribution of specimens collected and stored across the world [31,32]. Nonetheless, these results are based upon the single largest curated digital specimen dataset currently available and represent our best estimates. To address these inherent limitations of our assessment of digitized specimen content we examined the distribution of specimens within physical herbaria across the world.

A glimpse inside the cabinet

Increasing digitization of specimen data and their online mobilization have seemingly decentralized and democratized access to herbarium data greatly [33]. As demonstrated above, open access biodiversity data repositories such as GBIF and iDigBio allow researchers from around the world to query aggregated specimen metadata and images, alleviating some of the need for extensive and prohibitive travels to consult materials and requests for loans. Institutional databases, although containing fewer specimens than global databases, efficiently contribute to make available their own holdings, and encourage worldwide researchers to request free high-resolution images and better define loan requests. However, digitization requires significant investments in infrastructure (i.e., physical space, photographic devices, data storage) and personnel, which is often not financially feasible for smaller institutions and developing countries. Along these lines, it has been argued that digitization could exacerbate the exploitation of intellectual property and biological resources by developed nations in a form of neo-imperialism [34].

244 Further, only a small portion of specimen data are digitized and shared online at this point in time, and

245 there are many studies that require access to physical specimens.

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Figure 3. The percentage of internationally collected specimens in herbaria. Trends across physical specimens (A),
specimens with at least a portion of their metadata available online (B), and specimens with digital images shared
online (C) are illustrated as histograms where each bar represents a surveyed institution, and colors indicate different
continents. Boxplots to the right summarize this information among countries that have been colonized, versus those
that have colonized others following reference[29]. Countries that both experienced colonization and colonized others
are depicted under their most recent category.

According to *Index Herbariorum* [1], there are at least 3426 herbaria globally that together house

approximately 400 million specimens. Over 60% of these herbaria and 70% of specimens are located in

developed countries with colonial histories (Supplementary Fig. 4). To better understand the current state

of the world's collections and their digitization, we conducted a survey of major herbaria as listed by

Index Herbariorum and targeted representative regional herbaria. A total of 93 herbaria across 39

countries and 6 continents submitted at least partial responses to the survey that could be used. Similar to

the patterns observed using digitized data from GBIF, we found that herbaria in developed nations with

colonial histories in North America and Europe housed a higher proportion of internationally collected

specimens on average (Fig. 3A). This pattern generally held consistent across databased specimens with

collection date and location information (Fig. 3B) and specimens with digital images (Fig. 3C) shared

online. There were some exceptions; for instance, herbaria in Singapore hold a disproportionate volume

of international collections, possibly due to its small size, location, history as the main British colonial

outpost in the area, and past and present association with Malaysia.

Our surveys also revealed that the digitization of herbarium specimens remains in its infancy. We

estimated that overall, less than 30% of physical collections have at least collection location and date

information online, and less than 10% have available digital images (Fig. 4A). Nearly all surveyed

herbaria have ongoing digitization efforts with at least some specimen data provided online (Fig. 4B-C).

However, these data are not always widely accessible, and represent only the tip of the iceberg relative to

the physical collections and are thus woefully insufficient to address the reverse-latitudinal gradient of

diversity inside herbarium cabinets. Our results suggest that the patterns we observe from GBIF data are

likely representative of the larger reserves of specimen data yet to be digitized and mobilized online.

Indeed, most institutions gave equal priority to the digitization of national and international collections

(Fig. 4D) and submit their digitized specimen data to GBIF and/or regional databases that often share data

with GBIF (e.g., Consortium of California Herbaria, the Australasian Virtual Herbarium, eReColNat,

Virtual Herbaria - JACQ; Fig. 4E). Other aggregators such as JSTOR - Global Plants and iDigBio share

data with GBIF as well [35]. Our survey results also highlight the fact that we are still in the infancy of

digitizing herbaria, and thus retain the opportunity to reassess how ongoing and future digitization and

mobilization efforts can be organized to better address the colonial legacy of these collections.

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Figure 4. Trends in the digitization of herbarium specimens. The boxplot (A) summarizes the percentage of physical
collections in surveyed herbaria that have at least location and date information (metadata) or digital images
available online. Pie charts (B) and (C) show the percentage of herbaria that have at least some data and images of
their collections shared online, respectively. The digitization priority of herbaria in terms of where specimens were
collected is illustrated in pie chart (D), while pie chart (E) shows how the surveyed herbaria share and distribute
digital specimen data. Multiple answers were possible in panel (E).

Challenges and opportunities

Our study demonstrates a major disparity between where plant diversity naturally exists and where it is

artificially housed and catalogued. This renders much of the world reliant on botanical knowledge and

resources housed outside of their own borders. This disparity not only impacts capacity for conservation

and basic research, but commercial and government enterprises that seek to appropriate and monetize

biological resources and their derivatives as well. In addressing this disparity, recent discussions

regarding approaches to decolonize cultural institutions, natural history museums, and biogeographical

practices in general must be applied to herbaria as well.

First, as Das & Lowe (2018) note [36], it is important to acknowledge the colonial legacy of herbarium

collections and to present the history and circumstance of these collections alongside existing

interpretations about the specimens and their role in scientific research. They argue that such

acknowledgment is a critical step towards bridging the gap between natural history collections and

audiences in previously colonized nations and ensuring inclusiveness in the collection, curation, and use

of these collections. One way to openly share and communicate such narratives is via themed exhibitions

and tours, such as the black history tours of Hintze Hall at London's Natural History Museum or the First

Nations-led and informed "Unsettled" exhibition at the Australian Museum. These tours recognize and

emphasize the (unrecognized) contributions of Indigenous peoples to the culture, science, and natural

history on display. Though most herbaria traditionally do not offer public exhibitions and herbarium

specimens are rarely prominent in natural history museum displays (in part, due to their fragility),

increasing specimen digitization efforts have made it possible to curate digital exhibitions and virtual

tours without competing for space and attention with others considered more charismatic (e.g., large

mammals and dinosaurs). Awareness and acknowledgement can also be facilitated by including

positionality statements in grant proposals, research articles and other scientific communications that

involve herbarium collections. Positionality statements describe the position of a researcher in relation to

the social and political context of all phases of the research in question and are well-established in the

humanities but still rare in the natural sciences [37].

Second, we must continue to improve accessibility to the vast information held in herbaria worldwide, for

both scientists and the public. Though digitizing and sharing specimen data is hardly a new idea, our

survey suggests that the data currently available only represent a small portion of what resides inside

herbarium cabinets. Indeed, several of our survey participants noted that estimating the size and

distribution of their collections is difficult – only a small portion of herbarium specimens have been

databased by their respective institutions, and no formal inventories exist. Though massive digitization

efforts have been funded, particularly at institutions in developed countries, it is ironic that even these

institutions often lack the funding for adequate curation and processing of specimens. Our analysis of

available digital collection data also shows that higher-level data products (i.e., images) for many

previously colonized areas are lacking (Supplementary Fig. 3). Digitization efforts focused on increasing

representation from such areas could help bridge the reverse-latitudinal gradient of plant diversity

knowledge. Further, though much of the data that has been digitized from herbarium collections are

shared via open data repositories (e.g., GBIF, iDigBio, BIEN, SpeciesLink, AVH, eReColNat), a large

portion remain available only upon request (which can be denied), paywalled, or inaccessible outside of

specific groups. Targeted initiatives and funding opportunities that prioritize the curation, digitization,

and sharing of collections from developing countries can be one way to address these discrepancies.

There have been some promising efforts along these lines, such as the NSF supported GLOBAL

Bryophyte & Lichen Thematic Collections Network, and the Mellon Foundation's African Plants

Initiative [38]. We can also increase support for loan and exchange programs across herbaria, facilitating

access and repatriation of physical specimens as well. Such efforts must be mindful of the legacy of some

herbarium collections. For instance, specimen returns in accordance with permits or agreements are

traditionally referred to as "gifts", but it may be preferable to use a different term, such as "returns" [39].

Also, we must be mindful that specimens can contain biocultural information that is culturally

inappropriate for broader circulation, and can risk further exploitation of Indigenous cultural knowledge.

Thus, efforts to improve accessibility to botanical collections and share knowledge therein require careful

discourse with all parties.

Third, in in addition to recognizing the sovereignty of a nation's biological resources and that biodiversity

can be best studied where it occurs [40], capacity-building in previously colonized countries through the

sharing of tools and knowledge for contributing towards research is critical – if the science resulting from

collections is globally relevant, the means of contributing should be distributed as such [37,41]. In particular,

it is crucial to ensure that local contributions are sufficiently recognized and facilitate the development of

local research priorities and agendas during this process. Acknowledging the providing country personnel

in all aspects, from specimen labels to publication authorship to grant proposals is critical. Further, the

digital products of herbarium specimen data could be hosted and managed by researchers in the countries

where they were originally collected as a form of repatriation, who could be trained and supported as

necessary by institutions with greater capacity. Although the latter might not necessarily dispose of the

necessary funding to support the local partner, they could play a major role when a grant request is

addressed to an international agency, clearly stating their engagement in the transfer of technical and

scientific knowledge. International collectors should be mindful to leave duplicate specimens in the host

country – this practice has become increasingly adopted over recent decades, and at times enforced by

local governments, especially since the Convention on Biological Diversity was signed in 1992 and the

Nagoya Protocol on Access and Benefit Sharing was drafted in 2010 (https://www.cbd.int/abs/). Still,

many regions lack the facilities to store and curate collected specimens. In such cases, collectors could

gather and treat duplicate specimens as loans until the necessary local infrastructure is established. This

would in turn facilitate a more equitable, global view towards the collection, curation, and use of

herbarium specimens. To support such efforts, we strongly recommend that grant proposals involving the

collection/curation/digitization of specimens associated with developing countries include requests for

funding to support local colleagues and collaborators. Institutions and scientists need to seek ways to

expand opportunities for partners in providing countries to participate in research design and grant

application, in addition to activities directly pertaining to the collection and curation of specimens. In

turn, funding bodies must recognize the need to support local partners appropriately and guarantee access

to the knowledge and benefits arising from plant collections sampled abroad. Importantly, these and other

efforts to decolonize herbaria should be guided by the needs and wishes of previously colonized peoples.

One example of such a partnership can be found in a recent project to sequence and study the genome of

the tuatara, a cultural treasure of the Māori people [42]. The Indigenous peoples provided access to the

species and associated knowledge, and were involved in all decision-making regarding the use of the

genomic data generated by the study and any benefits that may accrue.

A profound set of challenges lie ahead if we are to address the still-persistent legacy of colonialism in our

plant collections. However, ongoing digitization efforts have offered us new avenues of deploying

knowledge and infrastructure and sharing the benefits arising from the utilization of herbarium

collections. Science is not exempt from sociopolitical realities and we should not avert our gaze from the

inconvenient origins of these otherwise precious resources. To this end, we have endeavored to provide a

glimpse into the extent of the colonial legacy that plagues our herbarium collections. Only by embracing

these realities can we progress towards a more inclusive global herbarium.

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Author contributions

D.S.P. conceived the initial idea with C.C.D. which was refined through discussions with X.F. D.S.P and X.F. analyzed specimen data and D.S.P. designed the survey with C.C.D. D.S.P. supervised the study and wrote the original draft with input from X.F. All other authors provided data from their respective herbaria. All authors contributed to further revising the manuscript.

Competing interests

The authors declare no competing interests.

Data availability

Data discussed in the paper are either publicly available through GBIF (https://www.gbif.org/), *Index Herbariorum* (http://sweetgum.nybg.org/science/ih/), or attached supplements.

References

1. Thiers, B. M. *The world's herbaria 2020: A summary report based on data from Index Herbariorum. Issue 5.0.* (2021).

2. Willis, C. G. *et al.* Old Plants, New Tricks: Phenological Research Using Herbarium Specimens. *Trends Ecol. Evol.* **32**, 531–546 (2017).

3. Heberling, J. M., Miller, J. T., Noesgaard, D., Weingart, S. B. & Schigel, D. Data integration enables global biodiversity synthesis. *Proc. Natl. Acad. Sci.* **118**, e2018093118 (2021).

4. Hedrick, B. *et al.* Digitization and the future of natural history collections. *Bioscience* **70**, 243–251 (2020).

5. Funk, V. A. 100 Uses for an Herbarium: well at least 72. *Am. Soc. Plant Taxon. Newsl.* (2003).

6.   Carine, M. A. *et al.* Examining the spectra of herbarium uses and users. *Bot. Lett.* **165**, 328–336
(2018).

7.   Meineke, E. K., Classen, A. T., Sanders, N. J. & Davies, T. J. Herbarium specimens reveal
increasing herbivory over the past century. *J. Ecol.* **107**, 105–117 (2019).

8.   Lang, P. L. M., Willems, F. M., Scheepens, J. F., Burbano, H. A. & Bossdorf, O. Using herbaria to
study global environmental change. *New Phytol.* **221**, 110–122 (2019).

9.   Lavoie, C. Biological collections in an ever changing world: Herbaria as tools for biogeographical
and environmental studies. *Perspect. Plant Ecol. Evol. Syst.* **15**, 68–76 (2013).

10.   Davis, C. C., Willis, C. G., Connolly, B., Kelly, C. & Ellison, A. M. Herbarium records are
reliable sources of phenological change driven by climate and provide novel insights into species'
phenological cueing mechanisms. *Am. J. Bot.* **102**, 1599–1609 (2015).

11.   Bonal, D. *et al.* Leaf functional response to increasing atmospheric CO2 concentrations over the
last century in two northern Amazonian tree species: a historical δ13C and δ18O approach using
herbarium samples. *Plant. Cell Environ.* **34**, 1332–1344 (2011).

12.   Rudin, S. M., Murray, D. W. & Whitfeld, T. J. S. Retrospective analysis of heavy metal
contamination in Rhode Island based on old and new herbarium specimens. *Appl. Plant Sci.* **5**,
1600108 (2017).

13.   Peñuelas, J. & Filella, I. Herbaria century record of increasing eutrophication in Spanish terrestrial
ecosystems. *Glob. Chang. Biol.* **7**, 427–433 (2001).

14.   Lees, D. C. *et al.* Tracking origins of invasive herbivores through herbaria and archival DNA: The
case of the horse-chestnut leaf miner. *Front. Ecol. Environ.* **9**, 322–328 (2011).

15.   Delisle, F., Lavoie, C., Jean, M. & Lachance, D. Reconstructing the spread of invasive plants:
taking into account biases associated with herbarium specimens. *J. Biogeogr.* **30**, 1033–1042
(2003).

16.   Vogel, G. Natural history museums face their own past. *Science (80-.).* **363**, 1371–1372 (2019).

17.   Wintle, C. Decolonizing the Smithsonian: museums as microcosms of political encounter. *Am.*
Hist. Rev. **121**, 1492–1520 (2016).

18.   Wandersee, J. H. & Schussler, E. E. Preventing plant blindness. *Am. Biol. Teach.* **61**, 82–86
(1999).

19.   Brockway, L. H. Science and colonial expansion: the role of the British Royal Botanic Gardens.
Am. Ethnol. **6**, 449–465 (1979).

20.   Imbler, S. In London, Natural History Museums confront their colonial histories. *Atlas Obscura*
https://www.atlasobscura.com/articles/decolonizing-natural-history-museum (2019).

21.   Shellam, T., Nugent, M., Konishi, S. & Cadzow, A. *Brokers and boundaries. Colonial exploration*

in indigenous territory. (ANU Press, 2016).

22.   Kennedy, D. *The Last Blank Spaces*. (Harvard University Press, 2013).

23.   Reynolds, H. *With the White People*. (Penguin, 1990).

24.   Peterson, A. T., Soberón, J. & Krishtalka, L. A global perspective on decadal challenges and
459   priorities in biodiversity informatics. *BMC Ecol.* **15**, 1–9 (2015).

460   25.   Bakker, F. T. *et al.* The Global Museum: natural history collections and the future of evolutionary
461   science and public education. *PeerJ* **8**, e8225 (2020).

462   26.   Voeks, R. A. *The ethnobotany of Eden: Rethinking the jungle medicine narrative*. (University of
463   Chicago Press, 2018).

464   27.   Webb, C. O., Slik, J. W. F. & Triono, T. Biodiversity inventory and informatics in Southeast Asia.
465   *Biodivers. Conserv.* **19**, 955–972 (2010).

466   28.   Hughes, A. C. *et al.* Sampling biases shape our view of the natural world. *Ecography (Cop.).*
467   (2021).

468   29.   Mayer, T. & Zignago, S. *Notes on CEPII's distances measures: The GeoDist database*.
469   https://papers.ssrn.com/sol3/papers.cfm?abstract_id=1994531 (2011) doi:10.2139/ssrn.1994531.

470   30.   Brown, J. H. Why are there so many species in the tropics? *J. Biogeogr.* **41**, 8–22 (2014).

471   31.   Paton, A. *et al.* Plant and fungal collections: Current status, future perspectives. *Plants, People,*
472   *Planet* **2**, 499–514 (2020).

473   32.   Daru, B. H. *et al.* Widespread sampling biases in herbaria revealed from large-scale digitization.
474   *New Phytol.* **217**, 939–955 (2018).

475   33.   Drew, J. A., Moreau, C. S. & Stiassny, M. L. J. Digitization of museum collections holds the
476   potential to enhance researcher diversity. *Nat. Ecol. Evol.* **1**, 1789–1790 (2017).

477   34.   Breckenridge, K. The politics of the parallel archive: digital imperialism and the future of record-
478   keeping in the age of digital reproduction. *J. South. Afr. Stud.* **40**, 499–519 (2014).

479   35.   Feng, X. *et al.* A Review of the Heterogeneous Landscape of Biodiversity Databases:
480   Opportunities and Challenges for a Synthesized Biodiversity Knowledge Base. *EcoEvoRxiv*
481   doi:10.32942/osf.io/9zt4a (2021) doi:10.32942/osf.io/9zt4a.

482   36.   Das, S. & Lowe, M. Nature read in black and white: Decolonial approaches to interpreting natural
483   history collections. *J. Nat. Sci. Collect.* **6**, 4–14 (2018).

484   37.   Eichhorn, M. P., Baker, K. & Griffiths, M. Steps towards decolonising biogeography. *Front.*
485   *Biogeogr.* **12**, 1–7 (2019).

486   38.   Smith, G. F. The African Plants Initiative: a big step for continental taxonomy. *Taxon* **53**, 1023–
487   1025 (2004).

488   39.   Rabeler, R. K. *et al.* Herbarium practices and ethics, III. *Syst. Bot.* **44**, 7–13 (2019).

489   40.   Tydecks, L., Jeschke, J. M., Wolf, M., Singer, G. & Tockner, K. Spatial and topical imbalances in
490   biodiversity research. *PLoS One* **13**, e0199327 (2018).
491   41.   Asase, A., Mzumara-Gawa, T. I., Owino, J. O., Peterson, A. T. & Saupe, E. Replacing "parachute
492   science" with "global science" in ecology and conservation biology. *Conserv. Sci. Pract.* e517
493   (2021).
494   42.   Gemmell, N. J. *et al.* The tuatara genome reveals ancient features of amniote evolution. *Nature*
495   **584**, 403–409 (2020).
496
497

 Supplementary Information

 Methods

 We downloaded plant specimen data (kingdom = Plantae; basis of record = preserved specimen) from

 GBIF on April 23, 2021 (https://doi.org/10.15468/dl.nt5wkx). We only kept specimen records with

 accepted scientific names, valid country code and publishing country names. With the remaining

 50,303,354 records, we compiled a country-by-country matrix that summarized the number of specimens

 collected from one country and housed in another. The country where a specimen was collected was

 based on the field "countryCode" and the country where a specimen was housed was based on the field

 "publishingCountry". We also grouped the country-by-country matrix into a continent-by-continent

 matrix. To examine the temporal trends of collection, we further examined the data after separating them

 into two subsets; before and after 1945, which marks the end of World War II and the era of overt

 colonialism. We finally verified our analyses on a subset of data that i) had coordinates; ii) had the

 "countryCode" field matching the location inferred from the coordinates; and iii) were determined to be

 without geospatial issues by GBIF.

 As records on GBIF represent a subset of the collections in herbaria across the world, we expanded our

 investigations to physical institutions. We sent out a survey in 2020 to major herbaria across the world as

 listed by *Index Herbariorum* (http://sweetgum.nybg.org/science/ih/) and select representative regional

 herbaria. Questions were focused on identifying the size of the collections, where they were collected, and

 the proportion digitized. A total of 93 herbaria across 39 countries and 6 continents submitted at least

 partial responses to the survey (Supplementary Data 1).

 We recognize that certain assumptions were made in these analyses. First, the Western scientific system is

 not the only way to understand and describe botanical knowledge, and though many of our discussions

 pertain to such as it is broadly adopted, we do not mean to devalue or reject other knowledge systems.

 Second, we use geopolitical constructs that are not free from the influence of colonialism. For instance,

 though we treat Australia as a single entity, it is home to over 500 Aboriginal nations. Finally, though we

 posit that the era of overt colonialism has ended, we realize that there was no single process of

 decolonization, and that the idea that colonization is over can be problematic as its legacy persists to this

 day, even in botanical collections. Along these lines, here we use the term colonization in a fairly general

 sense to describe a relationship between two countries, independently of their level of development,

 in which one has subjugated and governed the other over a period of time, contributing to the current

 state of its institutions following reference [29].

Supplementary Figure 1. The past movement of plant specimens across the globe based on GBIF records with
geographic coordinates. The world map depicts the top 10 percentile of intercontinental connections between
countries where specimens have been collected and where they are currently housed regardless of collection date
(A). The widths of the arrows are proportionate to the number of specimens dislocated and are colored by
destination continent. Collections that remained in the country of collection are not depicted. The lower panels
illustrate the intercontinental flow of specimens before (B) and after (C) the end of overt colonialism post World
War II (late-1945). Arrows are colored by the continent of origin. Numbers on the outer ring indicate specimen
numbers collected from (lower half) or stored in (upper half) each continent and are in multiples of 100,000. Colors
on the outer ring represent different continents.

Supplementary Figure 2. Global origins of specimens collected in the 21st century. The network illustrates the intercontinental flow of specimens. Arrows are colored by the continent of origin. Numbers on the outer ring indicate specimen numbers collected from (lower half) or stored in (upper half) each continent and are in multiples of 100,000. Colors on the outer ring represent different continents.

551
552 **Supplementary Figure 3.** Global origins of specimens with digital image data. The network illustrates the
553 intercontinental flow of specimens with digital images available. Arrows are colored by the continent of origin.
554 Numbers on the outer ring indicate specimen numbers collected from (lower half) or stored in (upper half) each
555 continent and are in multiples of 100,000. Colors on the outer ring represent different continents.
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Supplementary Figure 4. The distribution of herbaria and herbarium specimens across colonized and colonizing nations. Top panels depict the percentage of global herbaria and herbarium specimens situated in these nations. Lower panels contrast the number of herbaria and herbarium specimens held in institutions in colonized and colonizing nations. Countries that both experienced colonization and colonized others are depicted under their most recent category.

Supplementary Data 1. Survey results

Q. Approximately how many specimens does your institution house?

n = 93
median = 1100000
mean = 1998093
standard deviation = 2066601

Q. What percentage of your collections originate from the country your institution is situated in?

n = 83
median = 66
mean = 57.71
standard deviation = 27.82

Q. Select the country that accounts for the largest number of foreign specimens in your collection

country	responses
Brazil	7
United States of America	6
China	5
Mexico	5
Canada	4
Ecuador	3
Malaysia	3
Other	3
France	2
Papua New Guinea	2
Russia	2
Slovakia	2
Sweden	2
Ukraine	2
Argentina	1
Australia	1
Austria	1
Bhutan	1
Cambodia	1
Colombia	1
Costa Rica	1
Croatia	1
Democratic Republic of the Congo	1
Germany	1
India	1
Indonesia	1
Kazakhstan	1
Libya	1
Madagascar	1
Mongolia	1
Namibia	1
New Zealand	1
Norway	1
Peru	1
Philippines	1
Romania	1
South Africa	1
Spain	1
Taiwan	1
Tanzania	1
Unknown	1
Venezuela	1

Q. Are any specimen metadata (e.g., collection location, date) and/or images from your collections available online?

n = 83

16.9%   83.1%

0   25   50   75   100

Q. Which of the following is the geographic priority for your institution's databasing and/or digitization efforts?

n = 68

27.9%	69.1%

0   25   50   75   100

Q. Where/how do you make specimen metadata and/or images available to the larger community?

n = 68

answer	responses
BIEN	2
GBIF	51
iDigBio	16
Institutional webpage	44
Other (please specify)	21
Regional databases/consortia	37

specified other	responses
Atlas of Living Australia	2
Australasian Virtual Herbarium	2
Canadensys	1
e-ReColNat	1
Europeana	1
JACQ	1
JSTOR	11
ResearchGate	1
Sistema Nacional de Datos Biol?gicos de Argentina	1
speciesLink	1
Sweden's Virtual Herbarium	1
Taxonomic consortia (Mycoportal)	1

Q. What proportion of your total collections have at least the following associated metadata available online? –taxon name, collection location, collection date

n = 82
median = 25
mean = 33.55
standard deviation = 33.04

Q. What percentage of these online metadata records are from specimens collected in foreign countries (i.e., not from the country where your institution is located)?

n = 68
median = 20
mean = 28.84
standard deviation = 28.22

Q. Are any specimen images from your collections available online?

n = 68

Q. What proportion of your total collections have digital images available online?

n = 81
median = 5
mean = 18.10
standard deviation = 23.38

Q. What percentage of these online images are of specimens collected in foreign countries (i.e., not from the country where your institution is located)?

n = 62
median = 20
mean = 35.10
standard deviation = 36.53