Perspective

Mapping the history of botanical collectors: spatial patterns, diversity, and uniqueness through time

MALCOLM G. PENN1, STEVE CAFFERTY2 & MARK CARINE3

1Core Research Labs, Natural History Museum, London, UK
2(formerly) Plants Division, Life Sciences Department, Natural History Museum, UK
3Plants Division, Life Science Department, Natural History Museum, London, UK

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This study examines changing spatial patterns of botanical collections over a 400 year time frame, focussing on the collections at the Natural History Museum (BM) in comparison with global patterns. The Plant Collector Resource Database, which contains 68,000 collector records was used to generate 250,667 unique collector country date records.

We observe an exponential increase in the number of collectors over time. The activities of collectors were investigated in 50-year time-slices from 1650–2000. We specifically considered the geographic scope of collections (i.e., countries in which collections were made), the depth of collections (i.e., the number of collectors per country) and the uniqueness of collections (i.e., the proportion not duplicated in other herbaria). Uniqueness was highest for the earliest time-slice. Collector activity is shown to be strongly influenced by extrinsic factors such as the development of trade and empire, which allowed for collections to expand in scope and depth, and conflicts, which reduced collecting activity. A striking finding concerns the uniqueness of collections through time. The considerable unique element of the collections in herbaria highlighted by this study provides a strong motivation for digitization efforts to ensure that collections are accessible to address key questions in systematics, biogeography, and ecology.

Key words: collections, collector, geographical scope, Herbaria, spatial patterns, uniqueness

Introduction

There are nearly 3,000 herbaria worldwide that are collectively estimated to house more than 350 million botanical specimens (Thiers, 2016). The collections held by these herbaria constitute the primary source of evidence on global plant diversity. Herbaria are of fundamental importance for the discovery of plant species since it is in herbaria that most species are discovered (Bebber et al., 2012). The collections they contain are increasingly being used as a source of DNA to establish both baseline taxonomic patterns and investigate evolutionary, ecological, and biodiversity change (Lavoie, 2013). Herbaria and the collections they hold also play an important role in education and outreach (Cimi & Campbell, 2016; Snow, 2005).

The size of collections listed in Index Herbariorum (http://sweetgum.nybg.org/science/ih/) varies by orders of magnitude: from a few thousand to eight million specimens in the case of the Muséum National d’Histoire Naturelle, Paris (P) (Thiers, 2016). The geographic scope similarly shows considerable variation, ranging from the local to the global. Some collections were only recently established; others, such as P, established in 1635, span several collections. The scientific value of any one collection is perhaps impossible to quantify, since it will be largely question dependent: some questions may require recent material from a small geographic scale; others a much broader sample over a longer time-frame. Furthermore, the questions that herbaria may be used to address may change through time. Nevertheless, demonstrating the scientific value of herbaria and accelerating access to plant diversity information is becoming ever more necessary given the increasing threat to their long-term survival (Funk, 2014; Lughada & Miller, 2009).

Properties of a herbarium that might allow an assessment of its value relative to a particular question would include its geographic scope (hereafter its scope), the depth of sampling it provides – not only the total number of collections, but also the range of samples that make up a collection, an aspect we refer to here as depth.
The extent to which a collection provides a unique sample of plant diversity that is not duplicated elsewhere, its *uniqueness*, is also an important consideration.

This paper aims to assess these three properties of a collection focussing in particular on the herbarium of the Natural History Museum, London (BM). We make use of the Plant Collector Resource Database (PCRD) to consider how the scope, depth, and uniqueness of the BM herbarium has developed through time at a global scale and contrast the patterns observed with other herbarium collections globally. Our aim is to assess how the contemporary strengths and significance of a herbarium collection have been assembled and to consider the implications of this for the management, development, and use of such collections.

**Materials and methods**

The PCRD was developed, initially at BM, by David Sutton and more significantly by one of us (SC) over the last 20 years. It includes details of collectors who have deposited material at major herbaria with associated biographical data, together with additional information such as countries where they collected, plant groups collected, collaborators and also herbaria now holding their material. The PCRD was assembled through literature and internet searches with a focus on information available in the public domain. This has been supplemented by informal collaboration with a range of herbarium and research partners over this period. Over the last 10 years the BM has been a partner in the Global Plants Initiative, now known as Global Plants and hosted by JSTOR (https://plants.jstor.org) sponsored by the Andrew W. Mellon Foundation. As part of this initiative there has been an opportunity to increase proactive plant collector research, and the compilation of such data. The project has also benefited from increased formal collaboration with partners, many of whom have supplied large amounts of data or otherwise made their archive material and collections available for study. Notable amongst external contributions have been those from the South African National Biodiversity Institute (SANBI), The Muséum national d’Histoire naturelle Paris (P), The Herbarium of Université de Montpellier 2 (MPU), Institut de Botanique, The Conservatoire et Jardin botaniques de la Ville de Genève (G), The Real Jardín Botánico de Madrid (MA), and also the herbaria and libraries of the Australian National Herbarium, Centre for Australian National Biodiversity Research, Canberra, Australia (CANB), National Herbarium of Victoria, Royal Botanic Gardens Victoria, Melbourne, Australia (MEL), and the National Herbarium of New South Wales, Botanic Gardens and Centennial Parklands, Sydney, Australia (NSW). In addition to this, we have directly contacted many collectors and researchers, as well as conducting further extensive biographical research of archive material, both as an aid to identify collectors, and to supplement the main dataset with valuable life data. This has resulted in the PCRD used in this study, which we believe to be the most extensive and thorough review of botanical collectors’ data thus far.

The PCRD dataset used in this analysis comprises c. 68,000 individual collector records. Although we have resolved duplication wherever possible, we believe the dataset is likely to retain c. 5,000 duplicate collectors for which there are insufficient data to enable us to fully resolve them with confidence, for example because no initials or collection localities are provided in one or more of the possible duplicate records. Consequently the dataset as it currently exists probably represents c. 63,000 collectors. Of these, c. 41,000 have associated temporal data such as life dates, collecting or flourished dates, and these data span the time period from 1523–2013; a period of 490 years. Given that the number of potential duplicate records is relatively small and many duplicate records will have been discounted from the analysis on account of de-pauperate data, we do not believe they skew the research in any significant way, since they probably represent less than 0.5% of the records used for this research.

In order to analyse spatial patterns within collections over time we assigned a point date for all the records which held temporal data (41,000 of the 68,000 records held). Some records came with both complete biographical and collecting data, other records have only life dates, or a birth or death date, or simply collecting dates, and the most de-pauperate records just a flourished date. Consequently we needed to adopt different strategies for assigning a Point Date Data (PDD) for the different circumstances depending on what kind of data was held for any particular record. We aimed to be as accurate as possible, in assigning a PDD relating to the mid-point of any plant collector’s career, or at the least, a realistic and consistently applied PDD for a collecting period suitable to the aims of this analysis. This was done as follows:

- For records where we had full life dates, a simple mid-point was chosen as the point date, e.g., PDD = 1948 for (1920 to 1976).
- For records where only a birth date was known we took this and added 30 years to achieve a point date, e.g., PDD = 1550 for (1520).
- For records where only a death date was known, we took this and subtracted 30 to achieve a point date, e.g., PDD = 1690 for (1720).
- For records where only a flourished date was known, again a mid-point was used where these constituted a range, and where they comprised a specific date, this was used as the point date for the purposes of our research.
• For records where we had actual collecting dates and this was a range, a mid-point was taken, e.g., PDD = 1965 for (1960-1970).
• For records where we only had a specific collecting date this was taken as the point date for the purposes of our research.

Where collecting date data were known, these were always used to generate the point date required, even where other biographical data such as life dates were known.

In order to attach a collector event to a specific country or group of countries a set of country centroids was calculated using ArcGIS 10.3, using the Geometry tool – this calculates the mathematical centre of specific polygon. This works well for more regular-shaped country polygons, but not for countries where there are two or more different polygon areas (e.g., USA because of Alaska) or small island-based countries. In this instance a degree of human intervention was used to ensure the centroid was located within the country polygons.

Many collectors are neither country specific nor do their collections constitute a single collection event; many collectors have collected in multiple countries and/or on different occasions and there are often multiple collectors associated with a particular collection. Each collection event was assigned a specific geographic coordinate to take into account these multiple collection events and co-collectors etc., for example, Penn and Cafferty collected together in Belize 2004, and Cafferty also collected in Belize in 2001; these two collecting trips resulted in three specific collection events based on the country of Belize (e.g., Cafferty, 2001 and 2004; Penn, 2004).

The dataset was split into eight time slices, namely pre-1650; 1651–1700, 1701–1750; 1751–1800; 1801–1851; 1851–1900; 1901–1950; and post 1951. We discounted from the analysis any early collectors whose collections are no longer extant, or their whereabouts unknown. Seven collections were excluded as a result, including that of Lucca Ghini, whose collection was probably the earliest known. For both the entire dataset and for each time-slice, we assessed the total number of collectors, the total number for each country and the uniqueness – i.e., the proportion of collections not known to be duplicated in other herbaria. All maps were created using ArcGIS 10.3 (ESRI inc, http://www.esri.com).

We focussed on analysis of the data from BM which were then compared with global patterns in the dataset. We also contrasted patterns at BM with the following herbaria; P, The Smithsonian Institution, Washington DC, USA (US), and Natural History Museum, Vienna, Austria (W). For full listing of Herbaria mentioned in the text see Appendix 1 (see online supplemental material, which is available from the article’s Taylor & Francis Online page at http://dx.doi.org/10.1080/14772000.2017.1355854).

It should be noted the data held refer to collector activity and do not specifically relate to breadth of collections. However, we believe it is reasonable to make a connection between where and when collectors were active, and the geographic and temporal range of collections held within an organization where they are represented.

The 41,000 collectors with dates associated with them resulted in 250,667 collection events (a combination of date and country) represented at over 2,030 herbaria. As one might expect, the number of collector events, both globally and regionally (e.g., Caribbean) have exponentially increased over the period 1550–2000 (Appendix 2, see supplemental material online). At the same time the total numbers of collectors for the BM and global dataset have also increased exponentially during the full time period with notable increases from 1801 onwards (Fig. 1). Indeed, for the 12 focal herbaria examined, the number of collectors for 1801–1850, if compared with subsequent 50 year time-slices, increases by multiples of at least 3× for the subsequent periods for BM, K, P, and by significantly more for US, MO, and NY. For the 12 focal herbaria, the total number of collectors ranged from 9583 (BM) to 801 (FI) (Table 1).

Pre-1650

For the pre-1650 time-slice the earliest collections for which we have representative data show Europe as the epicentre for plant collectors with a few outlying regions (Fig. 2). Extant collections are known from 25 countries, eight of which are European and 17 non-European (Fig. 2). Within Europe, there were up to 10 collectors each for the UK, Spain, France, Switzerland, Germany, and Greece. A similar level of collecting activity is shown in near and Middle East countries such as Turkey, Syria, and Saudi Arabia. West Africa, Colombia in South America, and Jamaica, Cuba, and Mexico in Central America also show collector activity during this time-slice. Twenty six collectors are responsible for the pre-1650 collections documented and the material is distributed in 14 herbaria.

L is particularly rich in pre-1650 collections and holds the greatest geographic range for collections from this time-slice, with just over 52% of collected countries represented (Fig. 3). GH and the herbarium of the Universidad Nacional de Colombia (MEDEL) both have 24% of countries represented, mainly due to a single collector
(Francisco Hernandez). Overall, when the number of collectors is considered, BM has the most collectors represented (c. 18% of pre-1650 collectors followed by the University of Oxford herbarium (OXF) at 12% and L at 9%; Fig. 3). The collections at BM, P, G, and L are not duplicated elsewhere for this time-slice (Table 1).

1651–1700

For the 1651–1700 time-slice, we see a sizeable increase in the geographic scope of collections, as well as significant increases in the depth of collections from areas already collected. Fifty-four countries are represented in collections for the first time and collecting activity is evident on all the world’s continents with the exception of Antarctica. Several countries show a marked increase in the number of active collectors operating within their borders, specifically, the USA, UK, France, and South Africa. Interestingly, several countries for which collecting activity is newly recorded show a considerable amount of activity with numbers of active collectors of between 21 and 50 for India, Indonesia, and Japan (Fig. 2). One

Table 1. The total number of collectors, uniqueness number and percentage for the whole time period and for 50-year time-slices.

| Inst. | 1500–2000 | Pre-1650 | 1651-1700 | 1701-1750 | 1751-1800 | 1801-1850 | 1851-1900 | 1901-1950 | 1951-2000 |
|-------|-----------|---------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| BM    | 9588      | 1964    | 20.4      | 6         | 6         | 100       | 140       | 67        | 48        |
| K     | 7040      | 978     | 13.8      | 0         | 0         | 2         | 0         | 2         | 0         | 95        | 7         | 7         | 717       | 80        | 11        | 1557      | 251       | 16        | 1916      | 300       | 16        | 2751      | 340       | 12        |
| P     | 6874      | 982     | 14.2      | 2         | 2         | 100       | 15        | 2         | 13        | 19        | 9         | 6         | 1         | 639       | 67        | 10        | 1404      | 182       | 13        | 1734      | 201       | 12        | 2962      | 446       | 15        |
| MO    | 5664      | 857     | 15.1      | 0         | 0         | 0         | 0         | 0         | 2         | 0         | 0         | 38        | 1         | 3         | 218       | 2         | 1         | 505       | 16        | 3         | 1200      | 86        | 7         | 3700      | 753       | 20        |
| NY    | 4393      | 242     | 5.5       | 0         | 0         | 0         | 1         | 0         | 0         | 1         | 0         | 0         | 30        | 0         | 0         | 271       | 13        | 5         | 712       | 52        | 7         | 1476      | 121       | 8         | 1902      | 56        | 3         |
| US    | 3371      | 121     | 3.5       | 0         | 0         | 0         | 0         | 0         | 0         | 0         | 0         | 17        | 0         | 0         | 131       | 3         | 2         | 541       | 36        | 7         | 1121      | 48        | 4         | 1561      | 34        | 2         |
| GH    | 2394      | 118     | 4.9       | 1         | 0         | 0         | 0         | 0         | 2         | 0         | 0         | 9         | 0         | 0         | 163       | 4         | 2         | 461       | 25        | 5         | 984       | 49        | 5         | 774       | 40        | 5         |
| LE    | 1263      | 129     | 10.2      | 0         | 0         | 0         | 7         | 1         | 14        | 5         | 0         | 0         | 34        | 1         | 3         | 276       | 9         | 3         | 496       | 27        | 5         | 220       | 26        | 11        | 225       | 65        | 29        |
| G     | 2363      | 224     | 9.4       | 1         | 1         | 100       | 6         | 0         | 0         | 5         | 0         | 0         | 72        | 11        | 15        | 367       | 26        | 7         | 609       | 27        | 4         | 504       | 17        | 3         | 799       | 142       | 18        |
| L     | 1619      | 37      | 2.2       | 1         | 1         | 100       | 7         | 0         | 0         | 6         | 0         | 0         | 27        | 0         | 0         | 278       | 1         | 0         | 617       | 6         | 1         | 458       | 11        | 2         | 225       | 18        | 8         |
| W     | 1482      | 50      | 3.3       | 0         | 0         | 0         | 2         | 0         | 0         | 1         | 0         | 0         | 44        | 1         | 2         | 372       | 15        | 4         | 605       | 18        | 3         | 335       | 6         | 2         | 123       | 10        | 8         |
| FI    | 801       | 78      | 9.7       | 1         | 0         | 0         | 4         | 0         | 0         | 2         | 0         | 0         | 38        | 0         | 0         | 330       | 3         | 1         | 314       | 36        | 11        | 71        | 48        | 67        | 41        | 34        | 83        |

Fig. 1. No of collectors over the full time period for BM and global data trends (cumulative).
Fig. 2. Maps of pre-1650, 1651–1700 time-slices for BM and Global collectors’ activity.

Fig. 3. The percentage of known countries collected and percentage of collectors pre-1650.
hundred and eighty-four collectors are represented in collections from the 1651–1700 time-slice. BM again has the greatest number of collectors in our sample, representing c. 76% of known collectors (Fig. 4); 48% of collectors at BM are unique (Table 1).

1701–1750

This time-slice 1701–1750 is characterized by an overall reduction in collecting activity in Europe, although Austria and Denmark are represented for the first time. The early 18th century also shows new plant collecting activity for North Africa (Tunisia), and increased activity for South Africa and Madagascar (Fig. 5), the latter almost certainly reflecting the establishment of French trading posts on the island. There was only limited collecting activity in North and South America in the early 17th century with a similar number of collectors recorded for Mexico as for the previous time-slice (1–10); collector activity continues to gain pace in what is now the USA.

For this time-slice, OXF and the Herbarium Universität Basel (BAS) both have just over 19% of countries represented. Uppsala University (UPS), the BM, P, University of Bern herbarium (BERN), the University of Copenhagen herbarium (C), Universität Erlangen-Nurnberg Herbarium (ER), Christian-Albrechts Universität herbarium (KIEL), G and the FI, all have between 5 and 14% of collected countries represented.

The number of collectors increases to 226 for this time-slice and the number of newly collected countries also increases, although by only 19, in contrast to the increase of 54 for the preceding 50 years. The number of collectors operating in the USA, European countries, and Russia show the largest increases in activity, with Sweden (first collected 1651–1700 time-slice), showing a particularly large increase in plant collecting activity (from 1–10 in 1651–1700 to 21–50). Others areas of the world show a decline in collector activity compared with the previous time-slice, notably India, but overall, global collector activity remains relatively stable, with the Middle East showing the greatest increase in terms of geographic spread (Fig. 5).

BM and OXF are the two herbaria with the largest number of collectors represented for the 1701–1750 time-slice, with figures of c. 49% and c. 26% respectively, in both cases somewhat less than for the preceding 50 years (Fig. 4). The uniqueness of the BM collections is constant at 49% (48% in the preceding 50 years). In a similar vein, the number of newly collected countries that are only represented at BM decreases (only five of the 19 newly collected countries are unique to BM). The number of collectors at P increases as does their uniqueness (15%), but generally there is still limited collector activity across the globe with the exception of Europe where collector activity has increased quite significantly in comparison with the previous time-slice (Fig. 5).

1751–1801

For the BM the 1751–1800 time-slice shows a large increase in both geographic scope and in the numbers of...
active collectors operating in various areas (Fig. 5). The number of active collectors in the UK increases from just over 20 to c. 80, a four-fold increase and there is a significant spike in the number of collections over the whole of Europe. This time-slice is characterized by the increased breadth of collections from West and East Africa and from Madagascar. The geographic scope of collections increases for the Caribbean and the depth of collecting increases for South Africa, India, and Australia (Fig. 5). On a global scale however, the numbers of collectors active in any particular country still remains low and generally less than 10 for the BM. The uniqueness of the BM collections falls to 23%, whilst the total number of collectors rises to 231 for this time-slice.

The complete global dataset for the 1751–1800 time-slice shows large increases both in terms of geographic scope and depth. Central America, Southern Africa, the Middle East, Central and South-East Asia, and the South Pacific show the greatest increase in the geographic scope of collections. During this time-slice the first collections from Antarctica are made. North and South America, the Caribbean, Europe (especially France, Spain, Italy, and Germany), Madagascar, and the Mascarenes, China, India, Indonesia, Australia and New Zealand all show large increases in the number of collectors. Uniqueness of collectors is generally low at most of the 12 herbaria with the exception of G, which rises to 15% during this time-slice (Table 1).

1801–1850
For the 1801–1850 time-slice most countries in the world are represented within BM collections. Africa (with the exception of South Africa and Madagascar), and the Middle East generally show an increase in scope (the number of countries represented) rather than depth (the number of collectors per country). For Europe, North and South America, India, South-East Asia, China, Russia, and Australia, the converse is true and it is the increase in numbers of active collectors from those areas that is most marked with over 1,103 active collectors represented at the BM for this period. The uniqueness of the BM collections falls to 17% but the depth of collections increases markedly with the largest increases in terms of collectors for this time-slice outside of Europe, in China, and to a lesser extent South-East Asia.

By the 1801–1850 time-slice the majority of countries of the world had seen some plant collecting activity. However, this time-slice shows large increases in collector
activity in many parts of the world in terms of the number of collectors operating in any particular region or country. North, Central and South America show a marked increase in activity whilst the Caribbean remains relatively stable. The UK and Central Europe also show a large increase in activity, as do East Africa and the Middle East, albeit to a lesser extent than the Americas or Europe. Significant increases are also evident in Asia, notably in India, Myanmar, Vietnam, the Philippines, and Malaysia. Australia shows a steep increase in activity and the Pacific also shows increased activity. A few European countries, notably Spain and Iceland show small decreases in collector activity during this time (Fig. 6). There is a marked step up in the number of collectors at all the major herbaria and a rise in uniqueness at K (11%) and P (10%) during this time-slice.

1851–1900
The scope and depth of the BM collections continues to expand during the 1851–1900 time-slice with an increasing focus on North America, Europe, South-East Asia, and Australia (Fig. 6). The number of collectors increases markedly across Europe, notably in the UK (896 collectors), France, and Italy. The overall number of collectors increases to over 2,388 at the BM whilst uniqueness falls marginally to 16%.

The global data for this time-slice unsurprisingly reveal a further increase in the number of active collectors. The most noticeable increases occur in North and Central America, including the Caribbean, Africa as a whole, and Europe, especially Central Europe and Scandinavia. The Middle East, Central Asia, China, and Japan also show noticeably increased activity. For the first time outside of Europe however, some areas show a decrease in collecting activity, notably Peru in South America, whilst its neighbour Paraguay shows increased activity. South-East Asia and Australia display stable levels of collecting activity throughout the century. The number of collectors increases at the focal herbaria, and markedly so at K, P, NY. An increase in collector uniqueness is also observed at these herbaria (Table 1).

1901–1950
For the time-slice 1901–1950 the most marked change at BM is the reduction of collection activity within Europe (Fig. 7) where the number of collectors decreases for France, Ireland, and Italy. At the same time, there are increasing numbers of collectors from the Middle-East
and Australia. The same is also true for much of Asia. From a regional perspective, East Africa shows the greatest increase in active collectors. The Americas also show an increase in collecting during this time, particularly in Canada, Argentina, Central America, and the Caribbean region. The number of BM collectors peaks during this time-slice at 2,860 of which 19% are unique.

The most noticeable global pattern in the 1901–1950 time-slice is that collecting in Europe remains stable with numbers of active collectors showing no increase at all in most countries throughout the 1901–1950 and post-1951 time-slices, contrary to linear increases from previous time-slices. The most noticeable increase in activity is in Central America and the Caribbean in the first half of the century, along with East, West and Southern Africa, with smaller increases seen in Northern and South America and North and Central Africa. Asia and the Pacific region show moderate linear increases in keeping with the general pattern since the early 19th century, although within Asia, South-East Asia and Australia there is a considerable increase in collecting activity (Fig. 7). There is a marked increase in number of collectors during this time-slice at all the herbaria except LE, G, L, W, and FI; collector uniqueness remains consistent at K and P, and rises at FI and LE (Table 1).

1951–2000
The 1951–2000 time-slice shows a continued decline in collecting in Europe for BM, particularly in Eastern Europe. Other areas also show declines for this time-slice, notably Russia, China, India, and South-East Asia. East, West and South-West Africa show small declines whilst South Africa remains relatively stable. The number of collectors also decreases for Myanmar and India, but Nepal shows an increase. The most marked increases in activity for the second half of the 20th century are in the Andean countries of South America and Central America (Fig. 7). The uniqueness of the BM collections rises during this time-slice to 24% whilst the total number of collectors falls to 2,766 (Table 1).

Globally the latter half of the 20th century shows large-scale expansion of collecting in the Americas as a whole, a trend started in the late 18th century. The greatest expansion is in Central and Southern America, particularly the Andean countries, and also the Caribbean. East and West tropical Africa also show significantly increased activity along with the South Pacific, whilst all other areas show either small increases or stability in collecting. The number of collectors during this time-slice reaches a peak...
of 16,829, with very significant collector activity at P, MO, NY, and US. Collector uniqueness rise dramatically at MO (20%), LE (29%), and FI (83%).

A global map of collections from 1500 to the present day reveals that the most collected country is the USA. Second only to the USA is Mexico and Brazil with other South American countries, especially the Andean countries, and the Caribbean also heavily collected. For Africa, the countries showing the greatest collector activity are South Africa and Madagascar, with significant though lesser activity in East, and then West Africa. For Europe, as might be expected, collector activity has been heavily focussed on Western Europe. China shows the greatest activity for Asia with smaller but significant activity spread right across the region in places such as India, South-East Asia, and Papua New Guinea. Australia also shows high levels of collector activity on the same level as China, South Africa, and the Andean South American countries (Fig. 8). Apart from the Pacific Islands, the lowest levels of collector activity over time are seen in Central Africa, the Middle East, and Eastern Europe.

Discussion
This paper utilized the PCRD to investigate the development of herbarium collections through time focussing particularly on BM, but placing that collection in a broader context. Three aspects in particular were considered, namely geographic scope, number of collectors and uniqueness. Whilst the dataset will inevitably underestimate the number of collectors in herbaria worldwide and is not a direct measure of the number of herbarium specimens, it nevertheless provides a way to investigate how a large and historic herbarium has developed through time and to place that in a global context by comparing specific trends across the globe.

The analysis we present spans a period of more than 400 years; a period that has seen profound changes in our knowledge of the planet, the way in which plants were collected, classified, and housed, and the manner in which knowledge was disseminated. The role of both external and internal factors in shaping the development of collections is clearly evident.

Based on the data we have, the BM contains more pre-1650 collectors than any other herbarium and for the 1650–1750 time-slice, the BM and OXF have the largest number of collectors (Fig. 4), reflecting the remarkable endeavours of individuals in assembling collections: Sir Hans Sloane for BM, whose collection of 265 bound herbarium volumes, more than 100,000 sheets, and including plants collected by over 250 individuals formed the basis of the BM herbarium (Dandy, 1958); in Oxford, the
efforts of successive Professors of Botany, who were similarly adept at developing networks of collectors to expand the scope and depth of their herbaria (Clokie, 1964).

Subsequent expansion in the number of collectors and the geographic extent of collecting activity both at BM and globally (Figs 5, 6) mirrors the development of international trade and empire which opened up the world to European botanists. This is clearly evident in the time-slice 1750–1800 where collecting in Australia, West Africa, and the Caribbean appear to be a particular strength at the BM and collections globally. The growth in Australian collections at BM reflects the activities of Sir Joseph Banks and Daniel Solander on the Endeavour voyage (1768–1771), the first large-scale botanical exploration of the Australian continent by European botanists. Banks also supported continued exploration of the continent which led to further material from collectors such as Allan Cunningham and James Bowie, also being incorporated into the Bankian herbarium. The development of BM collections more generally during this time-slice reflects the central role of Banks in botany both within the UK and more broadly. Banks’s herbarium was expanded through the efforts of scientific explorations, dedicated plant collectors (e.g. Francis Masson; Saltmarsh, A. C., 2003) and gifts from his extensive network of correspondents. Following his death, the Banksian herbarium was bequeathed to Robert Brown, Banks’s former secretary and Keeper of Botany at the BM; it was subsequently incorporated into BM in 1827, building on the earlier collections of Sloane to form the basis of the herbarium which exists today (Carter, 1988; Murray, 1904).

By the latter half of the 19th century, BM had strong representation for most areas/regions, particularly East and West Africa, North and South America, Russia and China, in addition to Europe (Fig. 6). From looking at the BM data in a wider context it is evident that this time-slice represents a particularly rich time for BM with clear growth and global geographic coverage as well as the large number of active collectors. An early 20th century increase in collecting in Africa observed at BM (Fig. 7) correlates with British colonial expansion and associated efforts to document the flora of the region (Brockway, 1979); the slight decrease in activity observed in Europe during the same time-slice is probably explained by the impact of the two World Wars. A similar impact of the world wars was documented for botanical activity in Britain during this time-slice. These contrasting results probably reflect three factors: (i) the focus of British botanists on the British rather than the broader European flora, (ii) the lower priority afforded to British botany at BM during this time-slice and the consequent increase in importance of other herbaria, and (iii) increasing plant collections globally, which may hide the recent decline in collecting from some European countries (Molnár et al., 2012; Renner & Rockinger, 2016).

The most striking finding of this study concerns the uniqueness of collections, a finding that corroborates that of Chauvel et al. (2006) who used herbarium specimens to document the historical spread of Ambrosia artemisiifolia in France. Chauvel et al. (2006) found that the 10 largest herbaria they examined contributed 73% of specimens; the remaining 27% of specimens were highly distributed but were important in refining the reconstruction of the colonization history of A. artemisiifolia. In this study, 9.5% of collectors are found at the BM and 20% of these collectors are unique and not duplicated elsewhere. The time-slices to 1750 show particularly high levels of uniqueness (48–100%; Table 1). In some cases, these early collections are nomenclaturally significant (Jarvis, 2007), and they are of particular cultural and historical significance, providing insights into the discovery and documentation of the natural world. With the development of new analytical approaches, these pre-anthropocene collections also have potential to be mobilized to address key societal questions such as those relating to the scale and pace of responses to change (Callinger, Queenborough, & Curtis, 2013; Davis, Willis, Connolly, Kelly, & Ellison, 2015) and plant domestication (Ames & Spooner, 2008).

Whilst the percentage uniqueness of BM collections for post-1750 time-slices is lower compared with earlier time-slices (16–24% versus 48–100%), the total number of unique collectors shows an increase through time to the present day. This trend is not just BM specific; high levels of uniqueness are also observed for post-1950 collections in several other herbaria (Table 1). The high level of uniqueness amongst recent collections is at odds with the expectation that uniqueness would decrease towards the latter half of the 20th century as a result of the exchange of duplicate material and the efforts of collectors to distribute their collections widely.

The uniqueness of collections through time that we document here provides a strong motivation for continued efforts to mobilize herbarium collections through digitization. Whilst data quality is clearly an important consideration in herbarium digitization (Goodwin et al., 2015), there can be little doubt that, even with this important caveat, digitization is essential if the potential of herbaria for enhancing our understanding of key questions in systematics, biogeography, and environmental studies are to
be realized. The availability of type specimens online through the Global Plants Initiative (https://plants.jstor.org) has demonstrated the benefits of coordinated digitization efforts in dealing with plant nomenclature and typification. Herbarium digitization can also support the discovery of new species, of which perhaps half have already been collected and are awaiting discovery in the world’s herbaria (Bebber et al., 2010), by facilitating the examination of patterns of variation across the geographic range of taxa. Lavoie (2013) also concluded that the digitization of herbarium collections has been a major factor in their increasing use to investigate novel environmental research questions.

The overall average rate for collector uniqueness for the whole period of the study is 9.3%, whilst for individual institutions this ranges from a low of 2.2% for L, up to 20.4% for BM (Table 1). Although collector uniqueness on its own does not infer importance, it does infer potentially greater significance for collections at an institutional level. For an institution with high levels of collector uniqueness, if it can also be shown that there are known important collectors within those collections held, then that greatly increases the potential for unidentified type specimens or undiscovered new species to be present. Reinforcing this point, Bebber et al. (2010), showed that the way to identify these new species from within herbarium collections is to undertake a comprehensive study across the full taxonomic range for any group, and also the full geographic and temporal range of specimens and collectors found in herbariums.

Large herbaria such as BM, the focus of this paper, are worldwide in scope, rich in types, contain a significant proportion of unique collections, and cover a broad time period. Mobilizing large collections has been shown to be a cost-effective and time-efficient approach to tackle major challenges such as the monographing of large groups (Le Bras et al., 2017; Wood et al., 2015). Nevertheless, any individual collection may contain spatial and temporal biases that may limit its utility for the full range of potential questions those collections may be used to address. At a national level, Chauvel et al. (2006) demonstrated that sampling from both large herbaria and small collections that often include unique samples not duplicated in larger herbaria improved the reconstruction of a plant invasion in France. We similarly find that at a global level, biases such as the limited 19th century collections from China and Russia in BM may be ameliorated with a sample of collections held at other herbaria.

The distributed nature of the global resource of botanical specimens distributed across nearly 3000 herbaria ranging in size from a few thousands of specimens to several millions may be considered a strength insofar as the differing developmental trajectories of herbaria – reflecting the changing institutional priorities and political, economic, and scientific contexts within which they have developed through time – may help to offset the spatio-temporal biases evident in any one collection that could impede the effective use of herbarium data for addressing key scientific questions. At the same time, however, it is evident that the distributed nature of herbaria presents a significant challenge to effectively mobilizing collections, not least because, as we show here, they may each contain a significant proportion of unique collections.

Analysis of collector activity through time offers one approach to identifying historical and contemporary gaps and complementarity in collecting activity that can help to provide insight into the development of strategies to maximize the value of collections and their associated data for present and future uses.

As this study has shown, the number of botanical collectors has exponentially increased over the time period 1550–2000 (Fig. 8), with the major herbaria showing or reflecting different historical perspectives, and spatial patterns of collector activity. In summary and most importantly, the number of collectors increases dramatically for the major herbaria globally (BM, KEW, Paris, Smithsonian etc.) and this trend is continuing to the present day, mirrored by an ever-increasing geographic spread of collecting events.

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