

RESEARCH ARTICLE

Documenting the flora of a diversity hotspot: Richard Thomas Lowe (1802–1874) and his botanical exploration of Madeira island

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Abstract Oceanic island floras often exhibit remarkable concentrations of endemic diversity, provide spectacular examples of rapid evolutionary radiations and harbour floras under significant threat due to anthropogenic pressures. They have attracted the interest of biologists for centuries, but their floras continue to yield new taxa and, at a global scale, the extent of their plant diversity remains imperfectly known. Both natural characteristics and historical factors have shaped the development of knowledge of island floras. In this paper, we investigate the approach of Richard Thomas Lowe (1802–1874), to documenting the flora of Madeira island in the North Atlantic. Lowe collected abundantly in Madeira between 1826 and 1873, resulting in several works on Madeira's flora, published from the 1830s. At a time when taxonomic research on island floras was often based on limited collections made during brief expeditions, Lowe's research on the flora, spanning almost half a century, was exceptional. In this study, 2579 herbarium specimens collected by Lowe were georeferenced and used to investigate temporal, spatial and taxonomic patterns in Lowe's collecting activities. We also examine the distribution of specimens by Lowe to other botanists. Some biases are evident in Lowe's collecting efforts, with steep slopes under-sampled and coastal sites over-sampled. These reflect constraints imposed by topography and transport links. These limitations aside, Lowe's work on the Madeiran flora was conducted in a systematic manner, resulting in a comprehensive study of the entire flora. His approach was distinctly modern: he gathered and studied all available information in herbaria and in the published and unpublished writings from earlier visitors; his initial fieldwork was conducted widely to gain knowledge of all habitats and their floras; later fieldwork focussed on less-explored and most promising areas; duplicates were sent to other botanists, facilitating taxonomic exchanges on critical taxa; and his later fieldwork focussed on plant groups where taxonomic problems had been detected. As a result of Lowe's sustained and systematic approach, he is the single most prolific contributor to the study of Madeira's endemic flora. His approach is a model to documenting island floras still relevant today. Areas poorly sampled by Lowe were areas that were difficult to access, which also protected them from anthropic destructive activities and allowed them to serve as refuges for endemic flora. Those areas deserve particular attention in efforts to complete the survey of Madeira's plant diversity, using technological advancements such as drones to prospect areas that are otherwise still largely inaccessible.

Keywords georeferencing historical data; historical herbaria; history of botany; island flora; Macaronesia

Supporting Information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

The volcanic oceanic archipelago of Madeira in the North Atlantic (Fig. 1) has a flora typical of oceanic islands more generally: a remarkable concentration of endemic diversity (172 species in 801 km²; see Appendix 1), examples of rapid evolutionary radiations (Whittaker & Fernández-Palacios, 2006) and significant threats to the survival of the flora from anthropogenic pressures with 50% of endemics considered threatened (Jardim & al., 2006). Moreover, many endemic taxa were certainly extinct before the first naturalists arrived to the island and thus can't be accounted for (Menezes de Sequeira & al., 2013).

Madeira is also an island where new taxa continue to be discovered and described. Joppa & al. (2011) suggested that island

floras are well documented and, in the case of Madeira, the exploration and description of its flora by natural historians has a history spanning more than 350 years (Menezes de Sequeira & al., 2010). Nevertheless, seven endemic taxa—*Echium portosan-tense* J.A.Carvalho & al., *Holcus pintodasilvae* M.Seq. & Castrov., *Musschia isambertoi* M.Seq. & al., *Pericallis menezesii* R.Jardim & al., *Sonchus parathalassius* J.G.Costa ex R.Jardim & M.Seq., *Teucrium francoi* M.Seq. & al. and *Viola sequeirae* Capelo & al.—all rare, have been described as new to the Madeira archipelago in the last 20 years (4% of the endemic flora), an observation consistent with the findings from a survey of biologists working on oceanic islands that knowledge of the taxonomy, distribution and threat status of plants on oceanic islands remains insufficient (Caujapé-Castells & al., 2010).

The development of knowledge of the taxonomic diversity of island floras has been shaped both by their natural characteristics and by historical factors (Romeiras & al., 2020). Remote islands may be difficult to access and thus, historically, infrequently visited by botanists; topographically complex islands may be difficult to explore and both of these characteristics have constrained the development of knowledge of the diversity of island floras.

Globally, more than half of all botanical type specimens were collected by less than two per cent of the collectors (Bebber & al., 2010), and the disproportionate contribution of a small number of botanists to the description of island floras is also clearly evident from the episodic patterns of discovery of their endemic floras through time. In the case of Madeira, two major periods of description of the endemic flora are evident (see Jardim & Menezes de Sequeira, 2008). The first dates from the late 1700s when 20 endemic taxa (12% of the endemic flora) were described in works by William Aiton (14) and Linnaeus filius (6) based on collections made by Banks and Solander in 1768 and by Francis Masson during 1776–1779. The second dates from the mid-1800s when 81 taxa were described, 47% of the endemic flora. This second period of discovery and description was largely through the efforts of the English naturalist and clergyman Richard Thomas Lowe (1802–1874) (Fig. 2). His work represents the largest single contribution to the description of the endemic flora of Madeira.

Lowe lived in Madeira from 1826 to 1852, regularly returning afterwards. In 1833, he became English chaplain,

a post he held until 1847, when he was formally dismissed for supporting the Oxford Movement within the Anglican Church, a movement developed from 1833 in favour of reinstating older Roman Catholic traditions. This caused a temporary schism in Madeira's Anglican Church and Lowe remained on the island at the head of an alternative Church, the “Becco Chapel” (Nash, 1990).

As a naturalist, Lowe explored the islands of the Madeiran archipelago and actively contributed to the knowledge of its flora, land molluscs and fish fauna, collecting abundantly on Madeira island between 1826 and 1873. Lowe is best known as the author of Madeira's first comprehensive Flora (*A manual flora of Madeira*), published between 1857 and 1872, although it remained incomplete due to the unexpected death of its author in a shipwreck.

At a time when the Floras of oceanic islands were often written based on limited collections made during relatively brief excursions (e.g., *Flora Azorica* [Seubert, 1844], *Histoire naturelle des Iles Canaries* [Webb & Berthelot, 1836–1850], *Flora der Cap Verdischen Inseln* [Schmidt, 1852]), the decades of collecting that underpin Lowe's research on the Madeiran flora is a notable exception. In this paper, we utilise Lowe's extensive surviving botanical specimens to investigate how his herbarium was assembled over the course of almost 50 years. Through georeferencing of Lowe's specimens, we examine spatial, temporal and taxonomic patterns in his collecting activities and consider how Lowe used his collection to document Madeira's plants, their ecology and distribution.

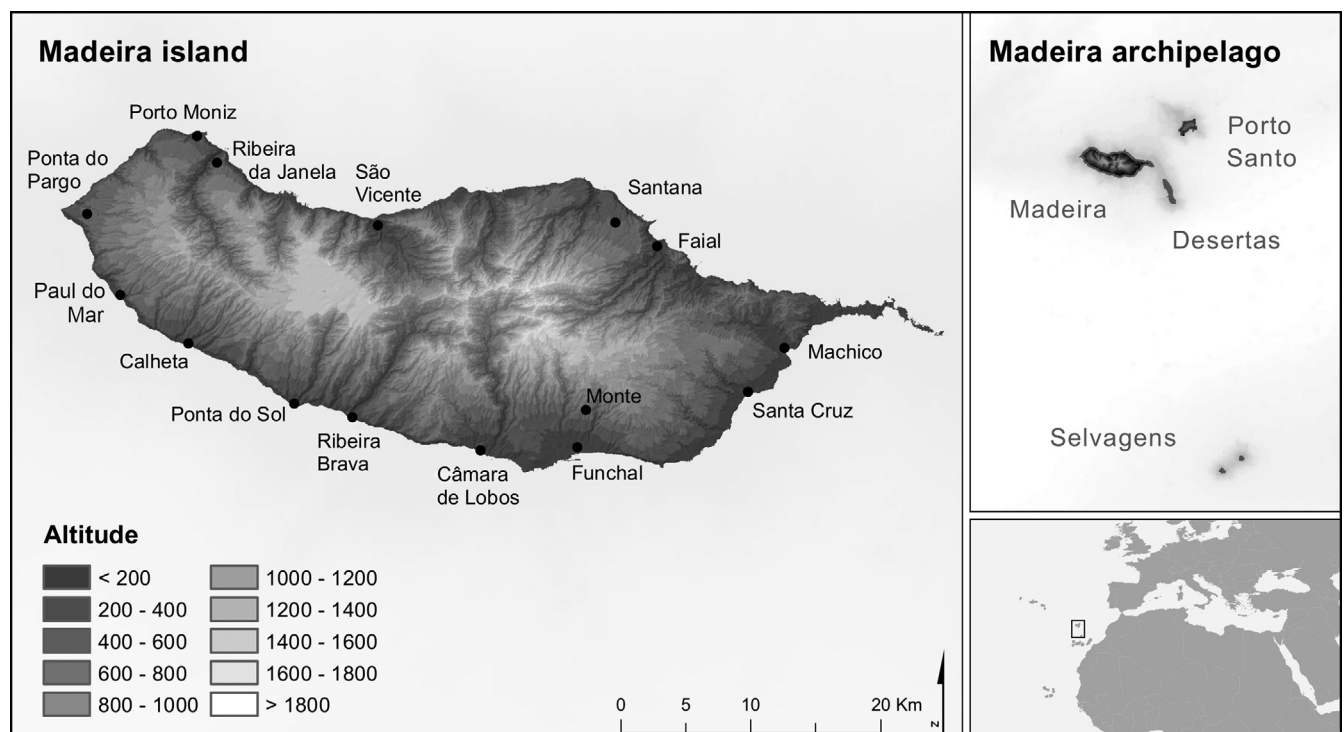


Fig. 1. Location of Madeira island and archipelago.

■ MATERIALS AND METHODS

Study area. — The Madeira archipelago includes the islands of Madeira, Porto Santo and the Desertas Islands, as well as the Selvagens Islands, often described as a distinct archipelago since these are located 280 kilometres south of Madeira. The archipelago is located in the Atlantic Ocean, between latitudes 33°07' and 30°01'N and longitudes 15°51' and 17°20'W. Madeira is a volcanic island, located at latitude 32°45'N and longitude 17°W, whose last volcanic activity dates from six to seven thousand years ago (Geldmacher & al., 2000; Fernández-Palacios & al., 2017). The island is made up of a central mountain ridge, 1862 m in height at the highest peak, aligned from east to west. It is profoundly affected by fluvial erosion, and separates the island's north from its south. It has a dramatic landscape, with deep valleys and ravines; most of the island has slopes steeper than 30%. The coastline is mostly formed of tall cliffs, occasionally with flat rocky wave-cut platforms below.

As in most volcanic islands, soils in Madeira are derived from basaltic rocks and pyroclastic materials, and are generally fertile (Pinto Ricardo & Madeira, 2002). With regard to its



Fig. 2. Richard Thomas Lowe. The National Archives Kew, ref. J121/2416. Source and © The National Archives Kew.

climate, the difference between the north and south faces of the island is of particular relevance, the south face hotter and drier. This adds to the well-known variation of precipitation and temperature along altitudinal gradients in islands, resulting in a wide range of climatic types in a small area. As a result, the coastal areas have a Mediterranean climate—hot and dry, with a distinct summer drought—and the remaining part of the island has a temperate climate—with a significant temperature variation throughout the year, but without a dry summer season (Mesquita & al., 2004).

Herbarium specimen sampling. — Lowe collected botanical specimens in Madeira spanning the period from 1826 to 1873. The plant specimens he collected were used to reconstruct his field collecting efforts during this period. Most of his specimens are held in the herbaria at The Natural History Museum Herbarium, London (BM) and at the Royal Botanic Gardens, Kew (K), and for this paper, data from a database of specimens at BM and K assembled by Marian Stafford (formerly at The Natural History Museum, London) for the *Flora of Madeira* project (Press & Short, 1994), was used. The total number of specimens in the database is close to 6500, but our study was restricted to 2473 specimens that were (i) collected by Lowe on the island of Madeira and (ii) included information on the place and date of collection. This data can be partly retrieved at <https://doi.org/10.5519/qd.kwnefguk>.

Additional searches of other herbaria for Lowe's specimens that could add further localities were conducted through herbarium visits and by consulting online databases. Other collections were observed at BR, CGE, E, FI, G, GH, JE, LE, LISU, M, MO, NY, P, S and US. A total of 217 additional specimens collected by Lowe in Madeira were found through these searches, of which 106 included information on the place and date of collection.

In total, 2579 plant specimens were included in this study, corresponding to 800 vascular plant taxa. Taxonomy and nomenclature follow Press & Short (1994).

Lowe's correspondence. — Information from Lowe's published material and from his letters, in particular those sent to William Jackson Hooker (1785–1865), John Stevens Henslow (1796–1861), Robert Brown (1773–1858) and Philip Barker Webb (1793–1854), was used to interpret Lowe's collections in Madeira (for more information on these personalities, see Appendix 2). A complete list of these letters is presented in Mesquita & al. (2021).

Georeferencing protocols. — For each specimen, the collecting locality described on Lowe's herbarium label was georeferenced.

Coeval maps were used of Funchal (Carvalho, 1805 [Fig. 3B]) and of Madeira island (Almeida, 1817 [Fig. 3A]; Wyld, 1844; Vidal, 1861, 1873; Stanford, 1901) as sources of information on nineteenth-century roads and paths, as well as toponyms in English and Portuguese that are no longer used. Nineteenth-century maps were georeferenced and all roads and paths in them drawn in vector files for reference. We worked on the assumption that most herbarium specimens

were collected near roads (Daru & al., 2018), more so in mountainous areas, where roads are often sided by cliffs.

Present-day georeferenced military maps (IGeoE, 2003), associated to georeferenced vector files for island limits, streams and *levadas* (small channels built for conducting water from wet and rainy areas at higher altitudes to the dry and sunny areas near the coast) were also used. Auxiliary geographic information was made available in a common coordinate system (EPSG:2942 Porto Santo / UTM zone 28N). All operations involving geographic information were carried out using ArcGIS v.10.7.1 (ESRI Inc., <http://www.esri.com>).

Information on properties available for rent located in and around Funchal—the *quintas*—as well as property belonging to English merchants living in Madeira was also valuable since several specimens came from their gardens (Hancock, 2009; Matos, 2016). Research in Google Earth Pro (2018), gazetteers and postal code databases was often crucial to uncover less well-known localities.

Once correspondence with a Portuguese name currently used as a toponym was established for a locality given in each examined label, its location was mapped, obtaining a geographic coordinate for each specimen. Positional uncertainty of the georeferenced locations was also addressed. In Lowe's labels, references to a riverbank, without any further detail to what part of the river, or to the vicinity of a village are common and indicate a wide geographical area. The use of altitudes to specify a position on a road or mountain is common and decreases the inaccuracy of descriptions, but some imprecision remains. The positional uncertainty of locations was classified using a 4-class ordinal scale, using the following criteria: (i) *Very high* when a precise location is given, e.g., “Lowe's garden”; “in front of the Curral church”. (ii) *High* when a location within a narrow geographic area is provided, e.g., “beach near Calheta”; “First ravine East of Santana”; “Fajã da Ovelha”; “near the Icehouse”. (iii) *Medium* when a vague location is given, referring to a medium-sized or broad area but with additional detail, e.g., “Paul do Mar”; “Monte road,

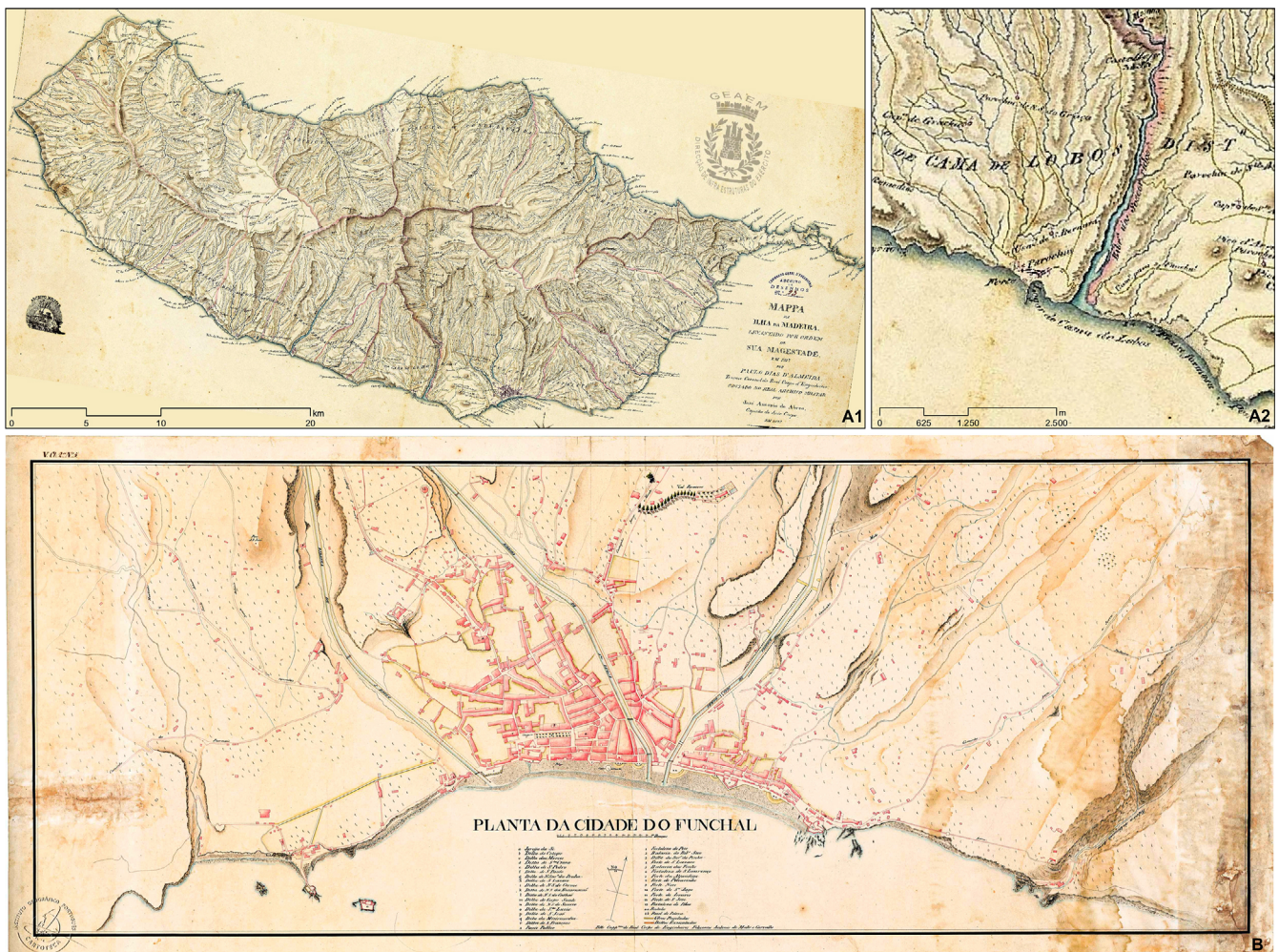


Fig. 3. Two of the historic maps used. **A**, Early 19th century map of Madeira (Almeida, 1817), island (A1) and detail (A2). Source and © Instituto Geográfico do Exército, GEAEM/DIE. **B**, Early 19th century map of Funchal, the largest village in Madeira (Carvalho, 1805). Source and © Direção-Geral do Território – <https://www.dgterritorio.gov.pt>.

1500 ft”; “nearly at the top of the Voltas”, “Curral das Freiras”. (iv) *Low* when a vague location is given, encompassing a broad geographic area, e.g., “Santana”; “Sea cliffs between São Vicente and Seixal”; “Ribeira do Faial”. Resulting data will be the subject of further analysis, therefore not presented here.

Locations were analysed over a relief map of Madeira, using tools for visualising temporal data. Apparent errors were detected by visual inspection of locations while testing for spatial and temporal consistency as well as for obvious outliers. Four types of inconsistent data were double-checked: (i) specimens collected in distant places on the same day; (ii) single specimens collected in remote locations; (iii) specimens dating from the first day of each month (which may correspond to the absence of a collection day in the original label); and (iv) species with awkward numbering—Lowe used a sequential numbering system for species (not specimens), so unusually high numbering for species in the first years suggests a mistake in collection date.

Temporal, spatial and taxonomic patterns of collecting. — The final set of georeferenced and dated collecting data was used to establish (i) the geographical localities explored by month and year and (ii) the taxonomic groups collected in each year. (iii) We also considered the impact of topography on sampling effort. Specifically, collection localities were plotted on top of a slope map; additionally, a histogram of slopes estimated in collection localities was overlain on a histogram of slopes for the island. To estimate slope at collection localities, focal statistics were tested (average value), using a window of 50 and 100 m, for coping with positional uncertainty of locations. However, since the general trends were the same as

observed in point estimations (except for the expected decrease in extreme values) we report only the latter here.

■ RESULTS AND DISCUSSION

Georeferenced specimens. — Out of the 2579 Madeiran specimens we initially considered, a total of 2288 plant specimens (89%) were georeferenced (Fig. 4). Two hundred and sixty-one specimens of the initial set (ca. 9%) were not considered for analysis due to the absence of geographical information (other than “Madeira”). Additionally, about 11% (291) of all specimens that we tentatively georeferenced were discarded for having too vague or ambiguous descriptions of localities (e.g., “sea cliffs”, “rocks by the waterfall”). In some cases of ambiguity, for instance, when a single toponym designates two different places, information from other specimens collected on the same day was used to clarify which one was right (e.g. “Lamaceiros”).

Of the 2288 georeferenced specimens, 48% were classified as having high or very high precision (totalling 1093 specimens), 33% (768 specimens) with medium precision and only 19% (427 specimens) with low precision (Fig. 5).

The specimens were collected from 1350 different locations, and around 800 different taxa are represented among the specimens sampled. Locations, in some cases, correspond to more than one specimen, not only due to duplicates (included in the same or distinct herbaria) but also because often several plants were collected at the same location and many localities were visited more than once.

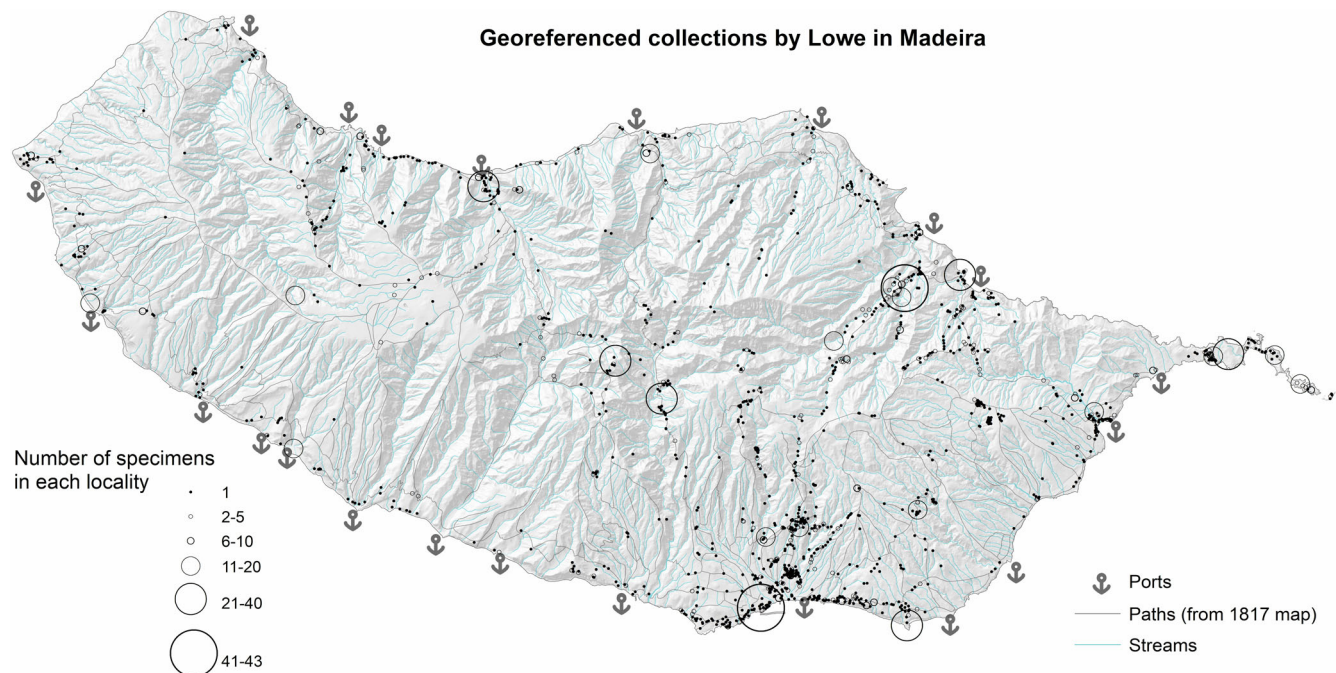


Fig. 4. Georeferenced collection locations of R.T. Lowe on a map of Madeira.

As with other studies that aim to produce spatially explicit information from sources that are naturally qualitative and not prepared for such intent (e.g., Guo & al., 2008; Lavoie, 2013; Heberling & Isaac, 2017), a robust set of both geographical and alphanumeric auxiliary information was necessary to retrieve an approximate location from a textual description without explicit geographical coordinates on a specimen's label. When interpreting the resulting dataset, potential biases due to recording, transcription and georeferencing errors must be taken into consideration, as well as potential biases resulting from missing specimens that may result in gaps in temporal and spatial information.

These caveats notwithstanding, the resulting database encompasses a wealth of information for analysing Lowe's botanical work. It will be made public as part of the "Lowe's Plants Project", to be launched on the 220th anniversary of Lowe's birthday, in 2022. Until then, the data will be made available by the authors upon request. A general inspection of the complete set of georeferenced collections shows that Lowe visited the whole island, although some areas were more densely surveyed than others (Fig. 4). For example, coastal areas were much more explored than inland areas; the west part of the island was barely visited, while the zone between Funchal, Monte and Faial was thoroughly surveyed. Comparing the collecting localities with the vegetation model by Capelo & al. (2004), it is clear that Lowe visited and collected in all vegetation zones occurring on the island (Fig. 6). The collection of specimens within species described by Lowe shows a similar pattern of collecting widely across ecological zones. His work in exploring the island's phytodiversity was thorough and directed at all vegetation types, from the microforests in the driest areas on the south-facing slopes to the

high-altitude vegetation complexes. Whilst not all vegetation types were necessarily present, since Madeira's landscape went through significant changes as a result of 400 years of human activity, patches or mosaics of natural vegetation could probably still be found (see Carine & Menezes de Sequeira [2020] on Joseph Hooker's description of the human impact in Madeira). Lowe was well aware of the altitudinal vegetation zonation in Madeira, which he describes in the first pages of his *Flora* (Lowe, 1857: iii–vii), and, in his correspondence, he often describes his efforts to explore the whole island (e.g., Lowe, 1829e). Therefore, the broad ecological amplitude of Lowe's collections must be interpreted as the result of an attempt to collect in diverse ecosystems.

It is also clear, however, that Lowe's collecting endeavours were strongly restrained, even driven, by the difficulty of access. The location of collections on a slope map and a histogram of slopes in collection localities superimposed to that of the whole island (Fig. 7) suggest that different survey densities are probably attributable to difficulties in reaching areas: the most unsurveyed or poorly surveyed areas have slopes steeper than 30%; in some locations, steeper than 100%, with no roads or paths represented on the 1817 map. Even today, some of these areas, such as the easternmost part of the north slope and the slopes over Ribeira da Janela (see map presented in Fig. 1), also in the north part of the island, are not accessible by car and are poorly covered by trails. Many of the Madeiran plants missed by Lowe and described later are rare taxa that thrive only in remote and inaccessible places Lowe wasn't able to explore, e.g., *Geranium maderense* Yeo (published in 1969), found wild only in vertical sea cliffs; *Sedum brissemeretii* Raym.-Hamet (published in 1925), which grows in shady rocky slopes up to 500 m; or *Orchis scopulorum* Summerh.

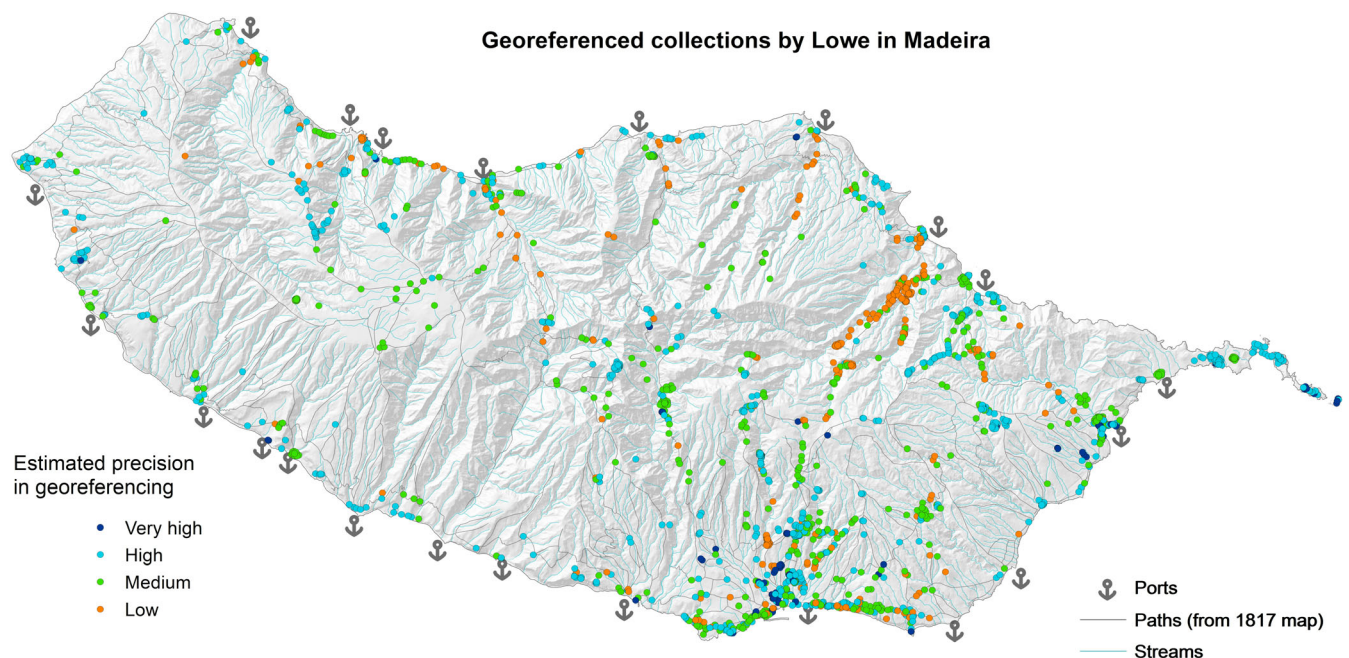


Fig. 5. Estimates of positional accuracy for the georeferenced locations.

(published in 1961), from slopes at high altitudes. These biotopes were inaccessible not only to botanists, but also to agents of destruction—lumbermen exploring native forests for timber and firewood and, to a lesser extent, sheep and goats grazing freely. The system of canals established to direct water from the mountains to crop lands at low altitudes, sided by narrow paths for maintenance, developed mostly in the late nineteenth and twentieth centuries, made these biotopes easier to reach.

When Lowe explored Madeira, most of the roads on the island were so steep that they could not support the transit of vehicles, and the rivers were often crossed through a series of stepping-stones that were impossible to use after winter rains. People travelled on foot, horseback and on ponies, or in hammocks and palanquins carried by local men, as can be seen in many of the records produced by visitors (Fig. 8A) (Loureiro, 1910; Smith, 2003). Travelling by sea was the only alternative in Lowe's time, although often impossible during winter (Simões & al., 1983). In the early twentieth century, the islanders relied on a transport system consisting of small boats connecting coastal villages that had a port or mooring structures (Fig. 8B,C) (Loureiro, 1910). The clustering of Lowe's collections in coastal areas, sometimes in locations hard to reach by land, and collections on the same day in distant places, strongly suggest that Lowe often used this mode of transport during his botanical collecting activities. For instance, in April 1860, Lowe collected in Paul do Mar and Ponta do Pargo on the same day, which would be hard to accomplish using exiting paths.

Temporal and taxonomic patterns. — The analysis of maps of specimen collection locations per year reveals the

pattern of Lowe's collections on the island of Madeira. Figure 9 summarises Lowe's collecting by year, for years 1827, 1837, 1850, 1851, 1855 and 1860 (see suppl. Appendix S1, "Maps_year.mp4" for the complete set of maps produced).

From the earliest dates in Lowe's specimens, we can conclude that he arrived in Madeira in the first half of 1826. During this year, he collected sporadically in the area around Funchal, and on two occasions during brief two-day excursions to the southwest part of the island in September and December.

The irregular collection pattern was repeated in the following years, with excursions of two to three days to Pico Ruivo and the north of the island (in March 1827 and again in August 1829), from Machico to Porto da Cruz (in May 1827), across the island through Encumeada to São Vicente (in late July 1827), and from Funchal to São Roque and Faial (in April, June and November 1828).

The practice of revisiting a set of places several times a year, and over several years, is recurrent in Lowe's approach to studying the island's flora and land fauna as explained by Lowe (1829d): "The North side the Island is almost (entomologically in particular) a terra incognita. I am even yet constantly getting new plants in this neighbourhood searched as it has been by others as well as myself over and over again." Moreover, specimens of interest and eventually new species were sometimes detected in an immature state and had to be revisited so that a complete plant could be observed and collected. For example, *Musschia wollastonii* was first observed in June 1847 but only confirmed as a new species as late as the end of August 1855, when part of a flowering panicle was provided by an unknown collector (Lowe, 1856).

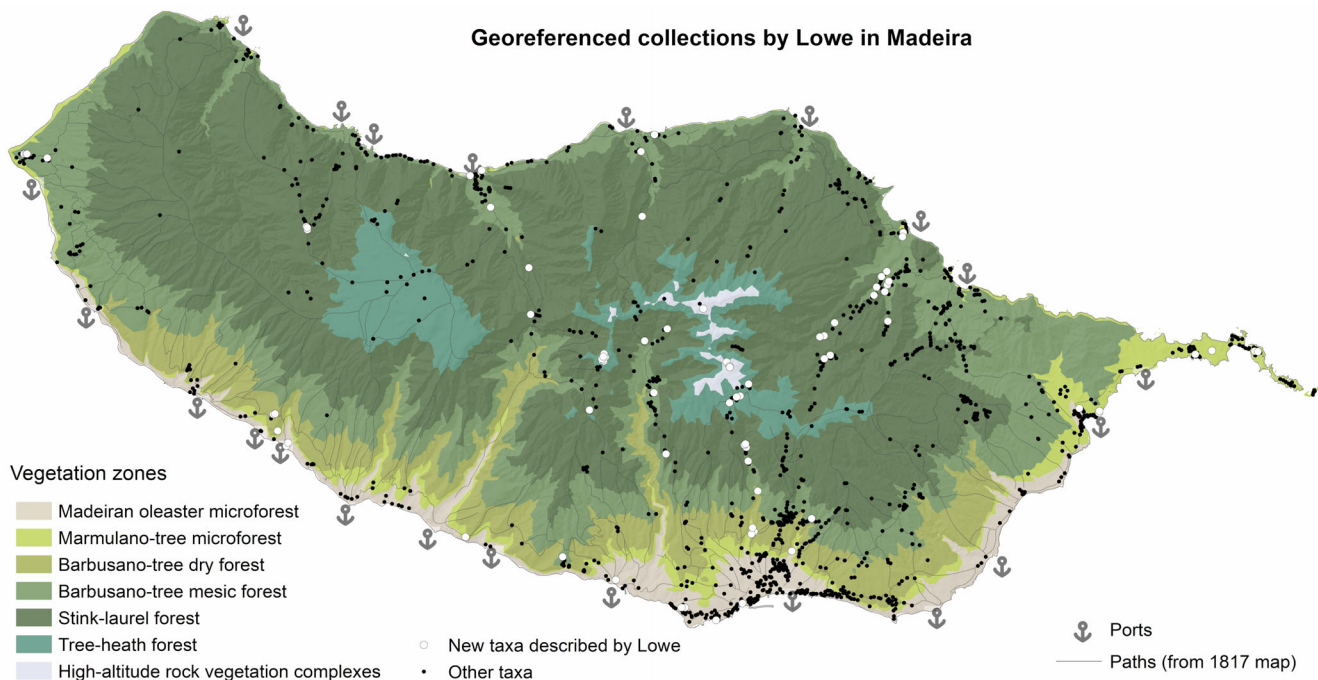


Fig. 6. Georeferenced locations on top of a vegetation zones map.

Lowe described his excursions for exploring the island flora and fauna to his correspondents (e.g., Lowe, 1827c) and discussed the specimens collected and sent to England (e.g. Lowe, 1827b, 1828c). Some of the specimens mentioned in these letters can be traced in the database, but some are missing—demonstrating that the current collection is only part of the specimens collected and sent by Lowe. Absences may be attributed to several causes, e.g., loss during the voyage from Madeira to England; specimen destruction (potentially long after collection, e.g., by bomb damage to the herbarium at the Natural History Museum during World War II); errors in transcribing label information to the database; or simply by omission from the database, regardless of the specimen being present in the herbarium.

Occasionally, Lowe spent long periods of time away from his home in Funchal. In 1829, he spent all of September and October in Santana, a small village in the north of Madeira (Lowe, 1829c), and from there, he explored the north face of the island, where “I have made the complete tour [...], and added greatly to my stores” (Lowe, 1829b). In 1832, Lowe went to Monte for the summer since this small village, at an altitude of around 600 m above the sea, is much cooler than Funchal, which is often too hot. He ended up staying until December (Lowe, 1832a,b). During this period, Lowe made several brief excursions to neighbouring areas, as well as to the north part of the island, feeling he was “well placed again this year for continuing my botanizing” (Lowe, 1832b). Extended expeditions were not common while Lowe lived in

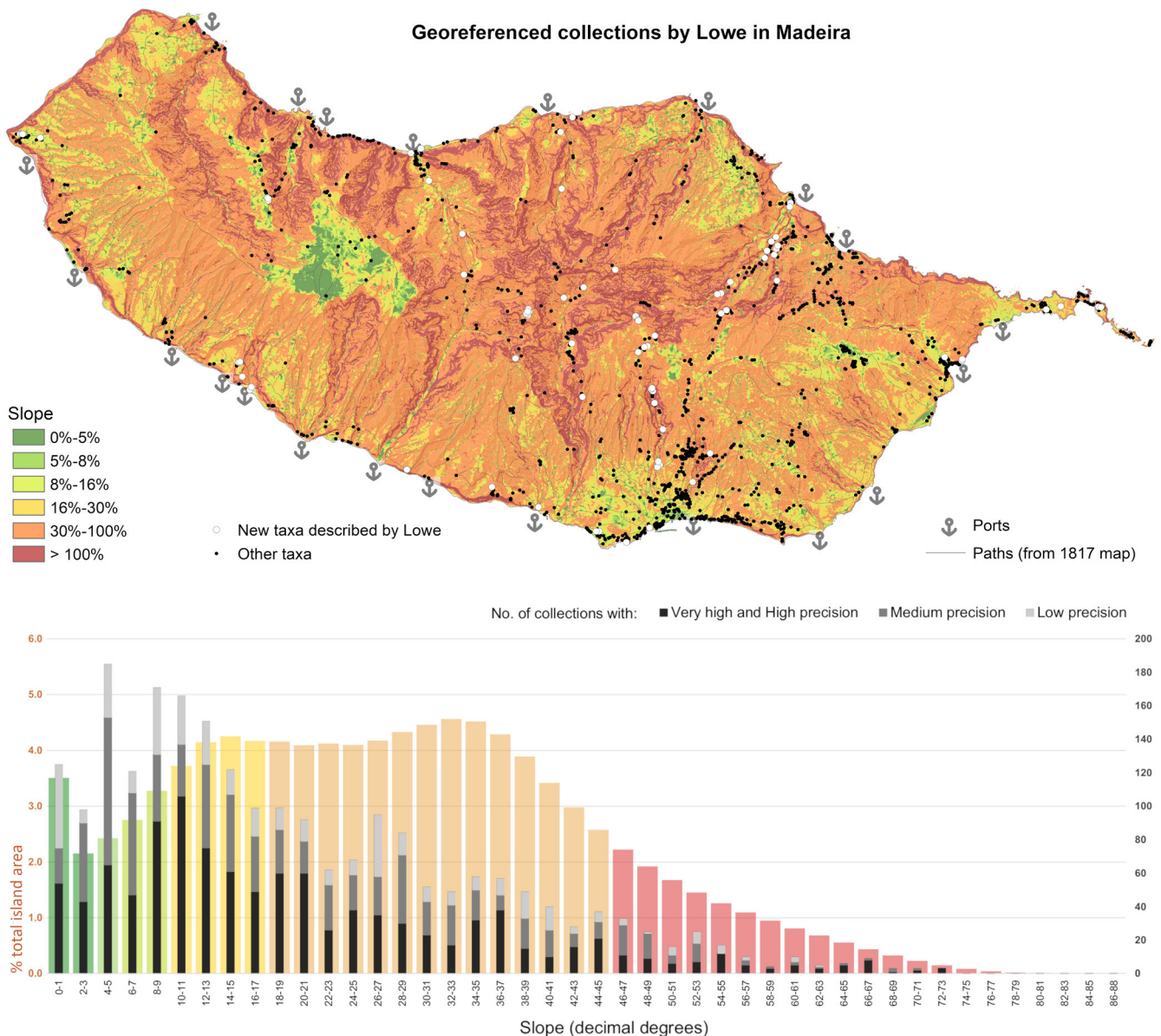


Fig. 7. Georeferenced locations on top of a slopes map (in %) and histogram of slopes (in decimal degrees) in collection localities and on the whole island of Madeira.

Madeira, when his botanizing expeditions usually took only one or two days. An excursion between August 8th and 13th, 1831 to the central part of the island—to Serra de Água, Pico dos Bodes, Pico Grande and Pico do Furão—is the only exception that can be reported.

Lowe was ordained a minister in the Church of England in September 1830 (Peile, 1910). He informally became the local chaplain in Madeira in 1832, and was officially nominated on the 31st of December, 1833 (Newell, 1931). The slowing down of his collecting activity from 1833 to 1845 conceivably reflects an increase in clerical duties. The year 1837 was an exception, undoubtedly because of the presence of the German botanist Johann Lippold (1790–1852) in Madeira (Wilhelm, 1996), recommended to Lowe by his friend William Hooker, to whom Lowe wrote: “Next month and the following I shall get him off into the mountains. [...] If Lippold is to do anything effectual here he should not go away before July” (Lowe, 1837). He probably followed this advice, since Lowe’s specimens included several collections in the mountains and

on the north slope from July and August when the high-altitude flora is well developed.

From 1846 to 1851, Lowe focussed his efforts on surveying specific areas that were either unknown to him until then or poorly explored previously: the west part of the north face of the island, around Ribeira da Janela, in June 1846; Pico Grande and Ribeiro Frio in June and August 1847; Curral das Freiras and the central north coast in 1848; Ribeira da Metade and Ribeiro Frio in 1849; the slopes surrounding Ribeira do Seixal, from the sea to its head in Paul da Serra, in July 1850; the southwest coast in May 1851 and Curral das Freiras again in August 1851.

Lowe moved permanently to England in 1852 (Lowe, 1852), but in the subsequent years he often returned to Madeira—in 1855, and then every year from 1858 to 1874 (Administração do Concelho do Funchal, 1859–1868/1871–1873, 1864–1876), although never reaching the island in the last journey.

The first year Lowe returned to Madeira, 1855, was his most prolific year, resulting in almost 600 collected specimens:

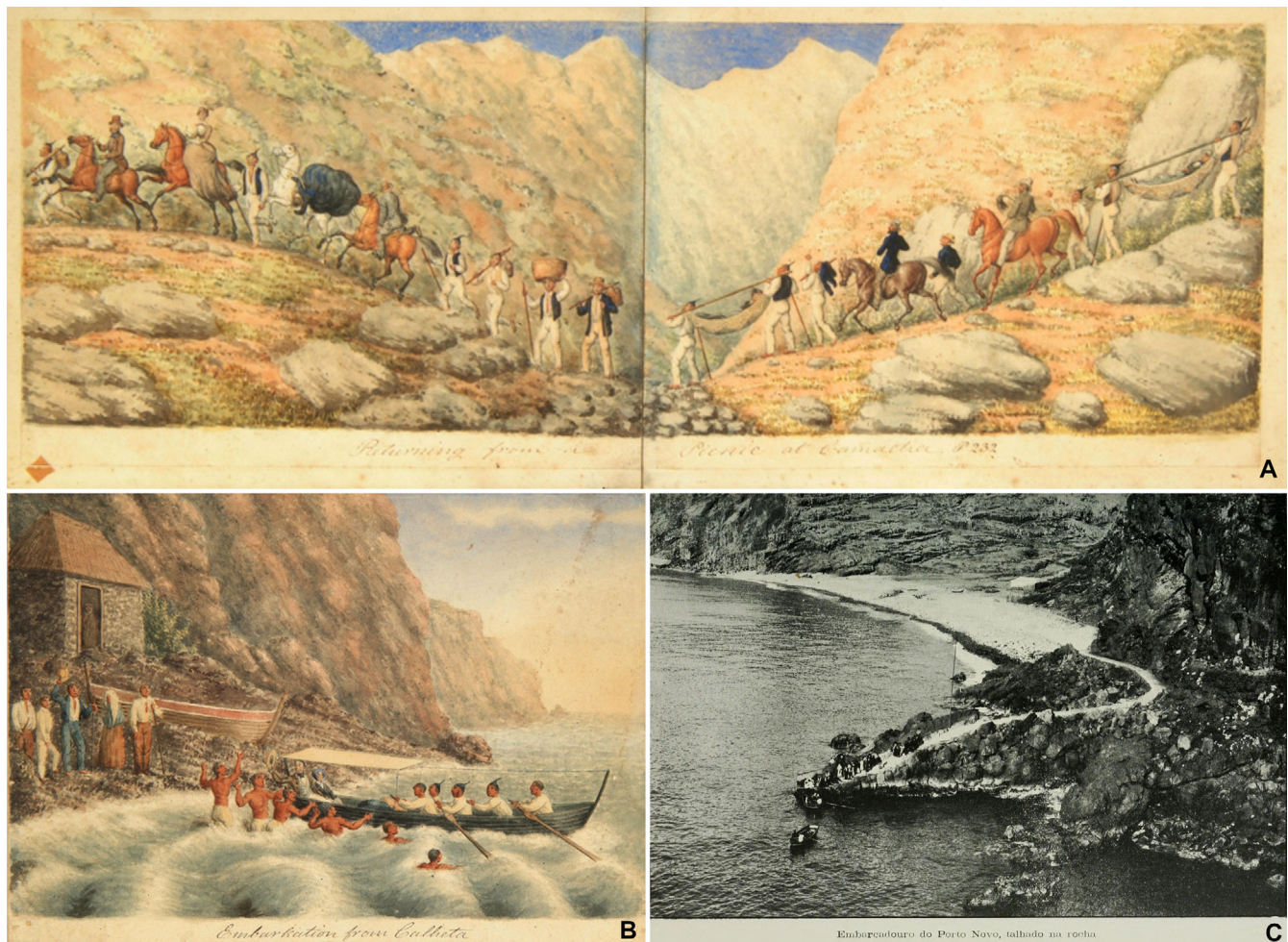


Fig. 8. Travelling in nineteenth century Madeira. **A**, “Returning from a Picnic at Camacha”. Watercoloured drawing by Isabella Hurst de França, from the Diary of her visit to Portugal and Madeira in 1853 and 1854. Source and © Casa-Museu Frederico de Freitas (Inv. CMFF 181;5), Funchal. **B**, “Embarkation from Calheta”. Watercoloured drawing by Isabella Hurst de França, from the Diary of her visit to Portugal and Madeira in 1853 and 1854. © Casa-Museu Frederico de Freitas (Inv. CMFF 178;5), Funchal. **C**, Pier at Porto Novo. Source: Loureiro (1910: 149).

186 specimens in Madeira, 316 in Porto Santo and 69 in the Desertas Islands (shown in Fig. 1). From the collection dates on his specimens, we can assume Lowe arrived in Madeira in March and for some time only collected plants around Funchal. In mid-April, he left for Porto Santo, located about 40 km northeast of Madeira, where he spent about a month; and in late May and early June, he explored the Desertas, a group of three islands (Deserta Grande, Ilhéu Chão, Bugio), located about 19 km southeast of Madeira. During these surveys, Lowe was accompanied by his friend, entomologist Thomas Vernon Wollaston (1822–1878) (Lowe, 1856), who probably also accompanied Lowe on some of his excursions in Madeira, since Wollaston collected material on the island during 1855 (Wollaston, 1871). Back in Madeira, Lowe probably stayed in Santo da Serra during June, from where he explored the surrounding areas, and then took long excursions to the

northwest during July and to the central north coastal areas during August. He returned to England in September.

Lowe dedicated most of his time abroad to the Canary Islands from 1857 to 1861, with brief excursions to the Moroccan coast and Cape Verde from 1864 to 1866. When in Madeira, he would usually stay in Porto da Cruz, a small village on the north coast—as indicated by the location “Porto da Cruz, at the door of our house”, on a specimen collected in 22 April 1860 (BM000056314).

From 1860, Lowe focussed his efforts not only on specific geographical areas but also on specific plants within the families he was working on for his *Flora*. Fabaceae is the plant family best represented in Lowe’s collections from 1860, the year he started an intense exchange of correspondence focusing on details of species of legumes (e.g., Babington, 1860; Bennett, 1861; Carruthers, 1861). These discussions lasted

Plant collections by Lowe in Madeira

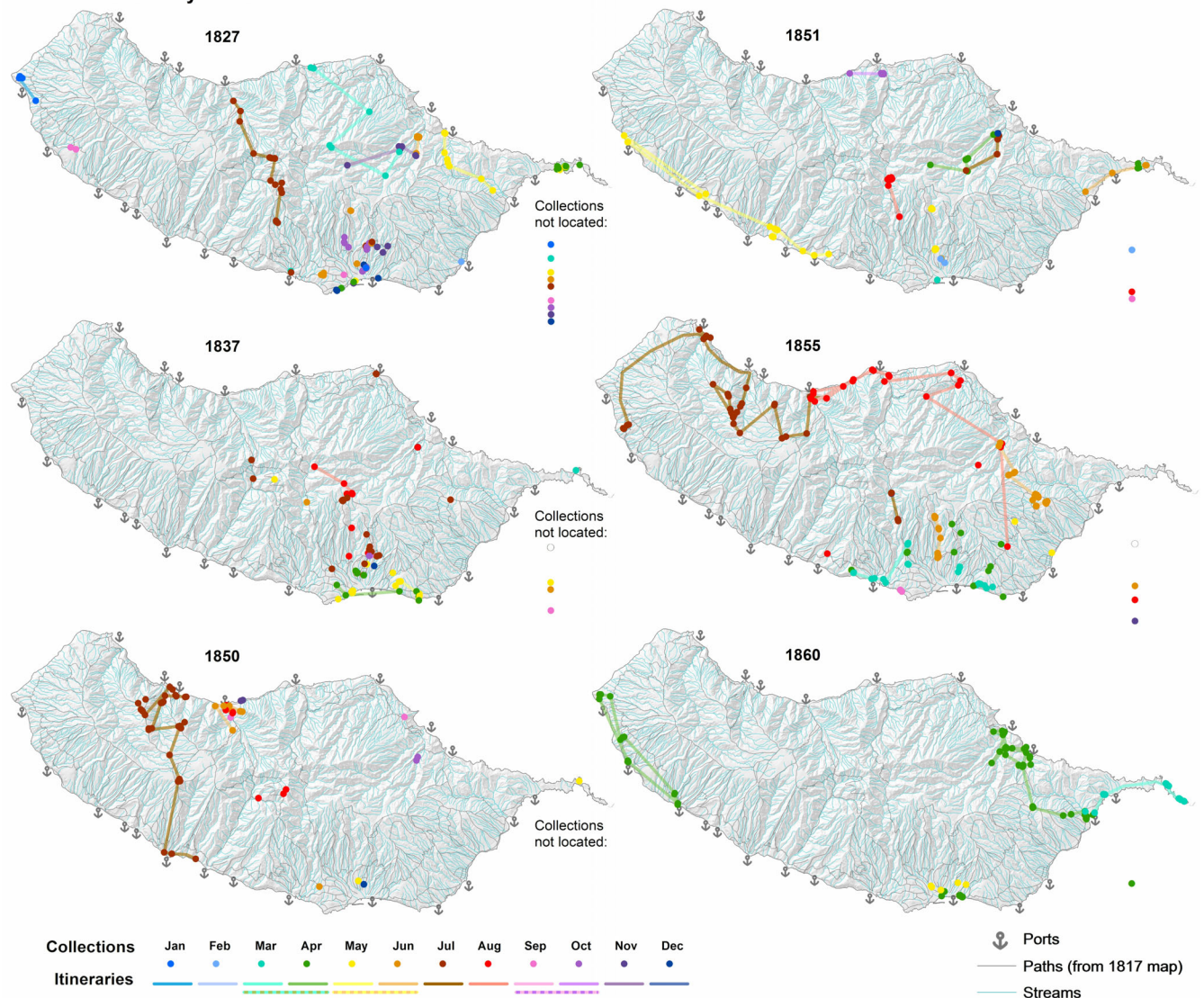


Fig. 9. Maps of plant collections by Lowe in Madeira island for the years 1827, 1837, 1850, 1851, 1855, and 1860.

until early 1862, when the second part of *A manual flora*, which includes this family, was published (Lowe, 1862: 113–232).

This pattern was repeated the following years and is most evident for the larger families (see Fig. 10): Apiaceae plants were sought in the 1863 campaign. During this year, Lowe discussed these plants at length with his correspondents from September to November (e.g., Carruthers, 1863; Newbould, 1863), and by December, the third part of *A manual flora*, that includes Apiaceae, was finished and delivered (Lowe, 1863b: 341–376). The same applies to Asteraceae, which form almost half of the plant collections from 1867, discussed at length in letters exchanged with William Carruthers (1830–1922) from the British Museum (e.g., Carruthers, 1867; Lowe, 1867) and published in the fourth and fifth parts of *A manual flora*, finished in February and December of 1868, respectively (1868b: 411–522; Lowe, 1868a: 523–567; dates as established in Williams, 2017).

After 1868, Lowe spent three to four months in Madeira every year, arriving in January or March and leaving before the beginning of summer. He continued to collect, although irregularly, with a peek for Fabaceae in 1870 and Solanaceae in 1871. He never went back to the mountains or the northwest part of the island, limiting his collections to areas around Funchal, Porto da Cruz and the coastline between these villages. On April 11, 1874, Lowe embarked on the SS Liberia in Liverpool, once again on his way to Madeira. However, the ship never reached its destiny and is believed to have sunk in a storm off the Isles of Scilly (Anonymous, 1874).

Lowe’s herbarium specimens. — Lowe’s own herbarium collections were critical tools for his research on the Madeiran flora as is evident from the fact that the majority of the specimens he collected remained in his possession until his death. According to Nash (1990), Lowe sent notes and specimens

at least twice a month to his friend William Jackson Hooker, Professor of Botany at Glasgow University and later Director of the Royal Botanic Gardens at Kew. Indeed, in Lowe’s correspondence to William Hooker, there are several references to “packages of plants” that were sent, although with much longer intervals, e.g., in July 1827, January 1828, August 1829, etc. (Lowe, 1827b, 1828a, 1829a).

A careful reading of the labels on specimens in K, where Hooker’s herbarium was integrated (FitzGerald, 2009), and of Lowe’s correspondence suggests a different story. Some of the specimens collected by Lowe are mounted on sheets of paper stamped “Herbarium Hookerianum 1867”, confirming that Hooker received plants from Lowe (image K1 in Fig. 11). Nevertheless, most of the specimens bear a label with the inscription “Herbarium of Rev. R. T. Lowe. Received April 1875” (image K2 in Fig. 11), meaning they arrived at Kew after Lowe’s death, presumably thanks to Thomas Vernon Wollaston, executor of Lowe’s will. In it, Lowe specified that “my collections of plants shall be distributed between the Royal Herbarium at Kew and that of the British Museum [now the herbarium of The Natural History Museum, London (BM)]” (Lowe, 1863a).

Specimens at BM show a similar pattern. Some of Lowe’s specimens collected in his early years in Madeira were sent directly to Robert Brown as Keeper of the Banksian Botanical Collection, later to become the Botanical Department at the British Museum, and can now be seen in BM (Lowe, 1827a, 1830a). They are distinguishable from specimens received after Lowe’s death (image BM1 in Fig. 11) due to the absence of the label with the inscription “HERB. R. T. LOWE, 28 May 1875” (image BM2 in Fig. 11). However, these early specimens represent but a small part of Lowe’s collections in BM.

In addition, there are several references to plant specimens sent to John Stevens Henslow and Augustin de Candolle

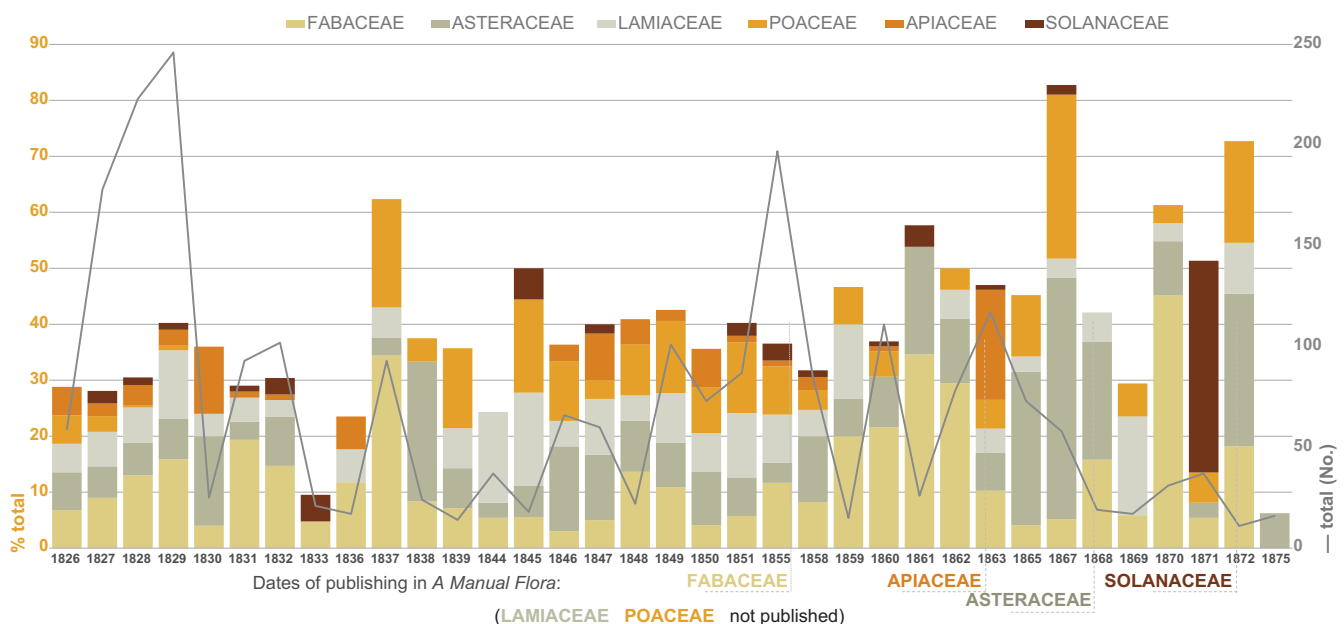


Fig. 10. Number of specimens collected by Lowe within the largest families, per year.

(1778–1841) in Lowe’s surviving correspondence. Lowe went to Madeira as a travelling bachelor to the University of Cambridge, sending botanical and zoological specimens for the Cambridge Philosophical Society to Henslow, Professor of Botany, at least between 1827 and 1831 (Lowe, 1827c, 1832c). These Cambridge collections may include Lowe’s first collections from Madeira. They are now part of the Cambridge University Herbarium (CGE). The early specimens at CGE again reveal two distinct patterns: some specimens were inserted as part of Henslow’s collection, marked “Mus. Henslow” (Museum of Henslow) near the top-left corner, in Henslow’s typical style (Pearn, 2009) (image CGE1 in Fig. 11); others were mounted on unmarked sheets, with an additional label printed “Madeira. R. T. Lowe.” (image CGE2 in Fig. 11).

Analysis of the labels in other herbaria confirms that most of the specimens collected by Lowe were received at K or BM after Lowe’s death and subsequently sent to other herbaria.

Specimens sent to other botanists allowed Lowe to benefit from their expert opinions or from comparative material received in return. Material sent to Augustin de Candolle is mentioned by Lowe in a letter to William Hooker: “I have just received a very gratifying letter from de Candolle and I am about sending him my new sp[ecie]s & the Compositae” (Lowe, 1831). Lowe also writes of specimens sent to de Candolle in his *Manual flora*, e.g., in the description of *Andryala cheiranthifolia* var. *sparsiflora* subvar. *coronopifolia*: “for

which, indeed, till recently mistaking it, I sent it as a mere var. of *A. cheiranthifolia* or *varia* in 1832 to the late Chev. De Candolle” (Lowe, 1868b); or of *Gnaphalium calycinum*: “of which I sent spec[imens], to the late Prof. De Candolle and to HB. and HK., which are still extant” (Lowe, 1868a). Lowe’s specimens in the Candolle Herbarium, now at G, can easily be recognised by the labels in his handwriting, on which someone else wrote “M. Low 1832” (G1 in Fig. 11), or “Flora maderensis / leg. R. T. Lowe” (G2 in Fig. 11).

Specimens sent by Lowe to his correspondents were often the subject of taxonomic discussions, using Lowe’s numbering system of species or putative species as reference, as detailed in Mesquita & al. (2021).

Lowe sent plants to other fellow botanists, although on a less regular basis, probably as part of a practice of specimen exchange in supporting each other’s work. For instance, Webb sent specimens from the Canary Islands (Lowe, 1862, 1868b). This exchange provided both naturalists with the necessary material to compare similar species from the Madeira and Canary archipelagos, both part of Macaronesia and, thus, with great biogeographical similarities, sharing many species. It was accompanied by detailed discussions about specific taxa, e.g.: “I send you a small packet of 2 or 3 plants and shells particularly the *Genista* you mention” (Lowe, 1830b).

A comparison of the identities, and dates and places of collection of specimens databased indicates the existence



Fig. 11. Examples of labels in Lowe’s specimens. **K1**, *Carlina salicifolia* (31 Jul 1827, K000418486); **K2**, *Musschia wollastonii* (2 Aug 1853, K000814252); **CGE1**, *Bupleurum salicifolium* (21 Sep 1827); **CGE2**, *Tolpis macrorrhiza* (Jul–Aug 1828); **BM1**, *Bystrpogon punctatus* (6 Jun 1828, BM000083289b); **BM2**, *Saxifraga maderensis* (30 Jul 1827, BM000056061); **G1**, *Crepis andryaloides* (25 May 1830, G00492034); **G2**, *Berberis maderensis* (13 Sep 1838, G00022642). Source and © K1 and K2: Board of Trustees of the Royal Botanic Gardens, Kew. Image used under a CC-BY Licence; CGE1 and CGE2: Cambridge University Herbarium; BM1 and BM2: The Trustees of the Natural History Museum, London. Image used under a CC-BY Licence; G1 and G2: Catalogue des herbiers de Genève (CHG), Conservatoire & Jardin botaniques de la Ville de Genève, <http://www.ville-gene.ch/musinfo/bd/cjb/chg>.

of many duplicates—about one-quarter to one-third of all specimens. There are several specimens, nevertheless, in E, P and US, which do not seem to be duplicates of those in BM and K.

Whilst Lowe's work on the Madeiran flora was largely based on his own collections, with the majority of new taxa based on original material collected by him or by his associates in Madeira, he nevertheless also utilised collections made by earlier collectors of specimens from the island. After his first collecting efforts in the island, when back in England in 1827 and 1828, Lowe examined the plants from Madeira in the Banksian collections at the British Museum, namely those collected by Banks and Solander in September 1786 on James Cook's *Endeavour* voyage; and by Francis Masson, the first official collector of plants for the Royal Gardens at Kew, who collected in Madeira from 1776 to 1779 (Lowe, 1828b,d). He also studied Solander's manuscripts, where he found information on many of the taxa previously collected but never published (Lowe, 1828b).

■ CONCLUSIONS

Lowe's personal herbarium was extensive and forms the bulk of the nineteenth-century collections from Madeira in BM and K. It was undoubtedly an essential asset for Lowe while writing *A manual flora* and supporting his frequent taxonomic discussions by letter, with other botanists (Mesquita & al., 2021).

The labels on Lowe's herbarium specimens include information with a varying degree of detail; in most cases, enough to provide useful data concerning the time and place of his field activities as a botanist.

Diachronic analysis of Lowe's collecting activities reveals the patterns and evolution of the geographic scope of Lowe's expeditions, as well as the depth of his collecting activity. Whilst some biases are evident, for example the under-sampling of plants on steep slopes, Lowe's work on the Madeiran flora was conducted in a systematic manner, resulting in a comprehensive study of the entire flora, something that was not common practice until the nineteenth century and that had never been done previously in Madeira.

When most accounts of oceanic island floras were based on material collected during brief exploratory journeys, often by others, Lowe made repeated and continuous observations—both in time and in space—of the organisms he studied in their natural habitat. His approach to the study of the flora of Madeira followed a coherent methodology: he gathered and studied all available information in herbaria and in the published and unpublished writings from earlier visitors; his initial fieldwork was conducted throughout the whole area in order to get to know all the habitats present and their flora; later fieldwork focussed on the less-explored and most promising areas; duplicates were sent to other botanists, followed by taxonomic discussions and including renowned experts on specific taxonomic groups, creating a collaborative work;

and finally, fieldwork was refocussed on plant groups where taxonomic problems were detected. His approach follows the same model that would be used today to address a poorly known area.

As a result of Lowe's sustained and systematic approach to documenting the flora of Madeira, he is the single most prolific contributor to the study of the island's endemic flora, having described about 13% of all currently accepted native taxa, including more than one-third of its endemic taxa (42%). Additionally, 5% to 10% of the remaining endemic taxa were described by others, but based on Lowe's collections. Most endemic taxa discovered after Lowe's work—more than 20% of the currently accepted endemic flora—came from Lowe's sampling gaps, which proves the importance of these areas. They were under-surveyed by Lowe due to access limitations, which also protected them from destructive anthropic activities, allowing them to serve as refuges for the endemic flora. Today, Lowe's sampling gaps still deserve attention. Contemporary efforts to complete the survey of Madeira's plant diversity should focus on those steep slopes, today made accessible by technological advancements, such as the use of drones to prospect otherwise inaccessible areas.

■ AUTHOR CONTRIBUTIONS

All authors conceived and designed the study. SM analysed the data. SM, MC and MMS wrote the first draft of the manuscript. All authors revised and approved the manuscript. — SM, <https://orcid.org/0000-0001-7522-3493>; MC, <https://orcid.org/0000-0002-1817-0281>; CCB, <https://orcid.org/0000-0003-1876-3818>; MMS, <https://orcid.org/0000-0001-9728-465X>

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Appendix 2. Short biographic notes about the personalities mentioned in the text.

- Babington, Charles Cardale (1808–1895). British botanist and archaeologist. Professor of botany at the University of Cambridge 1861–1895. One of the founders of the Entomological Society 1833. Chairman of the council of the Cambrian Archaeological Association.
- Bennett, John Joseph (1801–1876). British botanist. Assistant in the Department of Botany at the British Museum 1827–1859, later Keeper of Botany 1859–1871. Secretary of the Linnean Society 1838–1852.
- Brown, Robert (1773–1858). Scottish botanist and palaeobotanist. Sir Joseph Banks’s librarian 1810–1820. Keeper of the Banksian Botanical Collection 1827, later Keeper of the Botanical Department at the British Museum 1837–1858. President of the Linnean Society 1849–1853.
- Carruthers, William (1830–1922). Scottish botanist. Assistant in the Botanical Department at the Natural History Museum 1859, later Keeper 1871–1895. President of the Linnean Society 1886–1890.
- De Candolle, Augustin Pyramus (1778–1841). Swiss botanist. Worked in Paris from 1798. Professor of botany at the University of Montpellier 1807–1816, then at Geneva. Proposed one of the first natural systems of botanical classification.
- Henslow, John Stevens (1796–1861). British botanist, geologist and clergyman. Professor of botany at Cambridge University 1825–1861. Founder of the Cambridge University Botanic Garden 1831.
- Hooker, William Jackson (1785–1865). British botanist. Regius Professor of Botany at Glasgow University 1820. Editor and illustrator of Curtis’s *Bot. Mag.* from 1827. Director of the Royal Botanic Gardens, Kew 1841–1865.
- Lippold, Johann (fl. 1824–1837). German botanist who visited Madeira in 1836–1837 to collect plants and other objects of natural history.
- Masson, Francis (1741–1805). Gardener at the Royal Botanic Gardens, Kew, and the first official collector of plants for the garden. Collected in South Africa 1772–1774, 1786–1795, Macaronesia 1776–1778, West Indies 1779–1781, Iberian Peninsula 1783–1785, North America 1798.
- Newbould, William Williamson (1819–1886). British botanist and clergyman. Made several excursions in Great Britain with Babington. Assisted many colleagues in their botanical work, but didn’t publish in his own name.
- Webb, Phillip Barker (1793–1854). British botanist and traveller. Collected plants in the Canary Islands 1828–1830 and in Mediterranean Europe. Published an account of the natural history of the Canary Islands, with Sabin Berthelot 1836–1850.
- Wollaston, Thomas Vernon (1822–1878). English entomologist and malacologist. Visited Madeira 1847–1848, 1855. Visited the Canary Islands with Lowe and John Gray 1858; with Lowe 1859. Went to Cape Verde Islands with Lowe and Gray 1866.