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BAUHINIA

Die Zeitschrift BAUHINIA publiziert wissenschaftliche Arbeiten auf dem Gebiet der pflanzlichen Systematik, Vegetationskunde und Ökologie. Sowohl beschreibende Studien als auch experimentelle Arbeiten über Gemeinschaften, Populationen, Individuen und Artikel über Interaktionen von Pflanzen mit anderen Organismengruppen werden veröffentlicht. Artikel mit einem Bezug zur erweiterten Regio Basiliensis sind besonders willkommen. Die BAUHINIA veröffentlicht darüber hinaus botanische Arbeiten allgemeinverständlicher Art sowie Rezensionen von Büchern und anderen Medien.

The journal BAUHINIA publishes scientific papers in the field of plant systematics, vegetation science and ecology. Descriptive studies as well as experimental work on communities, populations, individual(s) and articles on interactions of plants with other organismal groups are published. Articles related to the extended Regio Basiliensis are particularly welcome. BAUHINIA also publishes botanical works of a generally understandable nature as well as reviews / recension of books and other media.

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The manual labor of herbarizing plants has changed little since its inception 450 years ago, but the research using herbaria is broadening (see this issue of BAUHINIA). Depicted is Aurélie Grall, curator at the Herbaria Basel, preserving a fragment of the Type specimen of the fern *Diacalpe aspidioides* var. *membranulosa* Christ (Dryopteridaceae). Fritz and Paul Sarasin collected this plant on the Lompobattang volcano of Sulawesi (Indonesia) on October 14th, 1895. The 2nd-degree cousins from Basel privately funded their pioneering collecting expeditions in South East Asia, a life that spurs debates on the role of colonialism in natural history to today. Later, Fritz became director of the Basel museum of natural history, and Paul fulfilled a prominent role in early Swiss nature conservation efforts. Little was known about the botanical heritage of the Sarasins, but digitising their recently rediscovered specimens is now revealing their botanical and historic significance. See Grall et al., pp 119–120 in this issue.

Photo Beat Ernst, Basel, 2023

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Proceedings Bauhin2022

International Conference in Honour of Caspar Bauhin (1560–1624)
Thursday 15 & Friday 16 September 2022
University of Basel, Switzerland

400 Years of Botanical Collections – Implications for Present-Day Research

Inspiring and showcasing herbarium-based scientific research, in the broadest sense, celebrating 400 years since Bauhin's pioneering Flora of Basel

EDITORIAL

A second Renaissance of herbarium-based research, almost five centuries after their invention

Jurriaan M. de Vos and Jürg Stöcklin

The present issue of Bauhinia presents the Proceedings of the Bauhin2022 conference, that the authors organized at the University of Basel, Switzerland, from 15-16 September 2022 in honor of Caspar Bauhin (1560–1624), celebrating his pioneering Flora of Basel 400 years after its publication (Bauhin 1622). This meeting, with ca. 100 participants from 14 countries, with 25 invited and contributed talks, 31 posters, and a discussion workshop fueled our thinking on the increasingly pivotal role of herbaria in current day research.

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Herbaria as scientific instruments arose in the 16^{th} century in the context of the Renaissance in Italy, at the confluence of a renewed interest in classic botanical-medical texts, a rise in humanist thinking, an increasingly empirical rather than scholastic approach to plant species knowledge, and an influx of unknown exotic plants from colonial activities that also spurred an excitement to observe European plants in their native habitats (Reeds 1991; Ogilvie 2006). Besides the availability of paper, creating herbaria from living plants involved only desiccation while applying pressure as a preservation technique, and was thus in principle at everyone's disposal. An early term for herbarium was „hortus siccus" (dry garden), emphasizing that they enabled scientific inquiry at all times of the year and everywhere. Assembling herbaria, which also spurred botanical expeditions to distant areas (Walter et al. 2022), is generally ascribed to Luca Ghini (1490–1556), who advised many influential students that went on to collect the plants for the earliest surviving herbaria (Baldini et al. 2022). The ability to study, exchange and compare plants year-round culminated in revolutionary scientific progress with lasting impacts over centuries (Arber 1912). One particularly profound example is the „Pinax Theatrum Botanicum" (Bauhin 1623), the first approximately global catalogue of plants, which already included >90 % of the species of Linnaeus' „Species Plantarum"(Linnaeus 1753). Bauhin based the „Pinax" on his immense herbarium that he had assembled using a network of contacts from all over Europe since the 1570s. The precursor of the „Pinax", the „Phytopinax", even states in the title that plant descriptions were derived from herbarium specimens („Phytopinax seu enumeratio plantarum ab herbariis nostro seculo descriptarum…" Bauhin 1596), reinforcing the centrality of herbarium specimens in the early development of botany as a scientific discipline.

From early herbaria to the present day

Since their invention, herbaria have never left scientific botany, even though not all botanical disciplines require a comparative approach. Currently, ca. 3500 herbaria hold almost 400 million plant specimens worldwide (Thiers 2023), of which about 0.004% were collected prior to 1600 (Baldini et al. 2022). Their enduring value is widely acknowledged (e.g. Besnard et al. 2018; Marsico et al. 2020, Burbano & Gutaker 2023), yet they remain under threat by closing facilities or moving collections off-site, away from the scientists that consult them (Miller et al. 2020), mainly for economic reasons. The monetary cost of maintaining herbaria are large: a simple back-of-the-envelope calculation for the Herbaria Basel (BAS/BASBG/RENZ; 700 000 specimens), Switzerland, gives a conservative, minimal estimate of the equivalent of 0,18 EUR or 0.19 USD per specimen per year (summing the yearly housing plus curatorial costs), on top of which come all other costs including processing new specimens, digitalization, and research. To ensure this support, herbaria need strong advocates and justification from their value for current research, not least because the highest-impact research may be conducted by researchers with a different primary affiliation than the collecting holding institution. Therefore, the significant, recurrent institutional investments that herbaria require should be broadly carried (Miller et al. 2020). Intriguingly, many herbaria are increasingly recognized as formally protected cultural goods (e.g., Swiss Inventory of Cultural Goods of National Importance), broadening the palette of arguments for the preservation of herbaria as accessible, pertinent research infrastructures.

Concerns for the future of herbaria are broadly shared, but we recognize a change in the wind. In our time of human induced climate change and radically altered land use, herbaria also represent long time-series that provide direct evidence of how the world changes. This enables addressing questions in ecology, physiology, and evolution using herbaria (e.g. Meineke et al. 2018; Albani Rocchetti et al. 2021), much expanding their original taxonomic, systematic, and biogeographic scope. Scientific revolutions frequently are preceded by technological innovation (for instance, how the polymerase chain reaction fueled genetic discoveries) and the future of herbaria is no different. To be mentioned first is the innovation of the digital specimen (Hedrick et al. 2020), allowing to consult and query specimens in ways and magnitudes unthinkable just a few years ago. Here, the trend is towards increased digital connectivity in the form of a „global metaherbarium" (Davis 2023) and artificial intelligence applications extracting a multitude of information layers from specimens (Hussein et al. 2022). We note, however, considerable challenges in maintaining links between specimens and the (digital) data derived from them, that are necessary to preserve reproducibility (Manzano & Julier 2021). Secondly, it is now possible to obtain DNA sequences from even the oldest herbarium specimens for large portions of their highly degraded ancient genomes (Kistler et al. 2020) and target-enrichment methods (e.g. Johnson et al. 2019) unlock herbarium specimens for broad-scale phylogenomic research. Though much potential remains to be realized, progress for the broadening of specimen utility on both fronts is reassuringly rapid.

A second renaissance of herbarium-based research

As historic specimens become increasingly relevant, their remarkably challenging interpretation requires intensified collaboration between historians (of science) and natural scientists (e.g., Walter et al. 2022; Van Andel et al. 2022). Likewise, millions of natural history objects were collected or acquired during expeditions in the Global South that benefitted from collaborations with colonial powers, when not outright forcibly removed from foreign lands, leaving collection holding institutions today with the obligation to morally justify their inventory (Park et al. 2023). Discussions on how to identify and settle putative moral debts require multidisciplinary perspectives, but such debates are not yet very frequent.

Overall, researchers from very diverse scientific fields, administrators from collection-holding institutions, and funding agencies are all increasingly aware of the power of the existing 400 million herbarium specimens worldwide, yielding a novel potential for collection-holding institutions as sources of research. We believe that the combination of new technological possibilities, a renewed interest in the past from both ecological and historical perspectives, and the societal challenges posed by the worldwide biodiversity crisis are so profound that they may amount to a second renaissance of herbarium-based research (Burbano and Gutaker, 2023), almost five centuries after their invention. Capitalizing on these developments requires also strategically expanding collections for the future. Here, both promoting of local collecting, for instance in the context of citizen science, and a global, collaborative perspective on collecting priorities are needed. Given the multitude of current uses of specimens – many of which were unlikely to be envisioned by their collectors – it would be arrogant to assume that we foresee all future uses of herbarium specimens. What we can confidently hold, however, is that herbaria have proven their worth and potential repeatedly for over almost half a millennium. We see no reason to think that collections will ever become irrelevant.

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Caspar Bauhin's life (1560–1624) – Academic career, achievements as a botanist and his herbarium

Jürg Stöcklin and Jurriaan M. de Vos

Caspar Bauhin was born 1560 in Basel as a refugee child from a distinguished Protestant family which escaped persecution of the Huguenots in France. He studied Medicine and Botany at the University in Basel, in Italy and France and became the first professor for medical Anatomy and Botany in Basel. He is the founder of one of the first Botanical Gardens north of the Alps, and the first to offer regularly botanical excursions and courses in systematics and taxonomy for medical students. In his many publications, C. Bauhin aimed to give a systematic overview of all c. 5600 plant species known at the time, based on meticulous comparison and descriptions by himself, renaming them by distinguishing clearly between genus and species and by adding the synonyms of other authors. Thereby Caspar Bauhin was paving the way for botany as an independent scientific discipline and for Linnaeus, who heavily relied on him for the further development of botanical systematics and nomenclature more than a century later. His herbarium, which today is kept at the University of Basel, served him as working tool and included more than 4000 species, which he collected himself or through exchange with a wide net of correspondents. Not the least of Bauhin's achievements is the publication in 1622 of one of the first comprehensive local floras, which until today is used as a reference for floristic changes in the surroundings of Basel.

Keywords
Carl von Linné, Classification, Herbals, Medieval botany, Renaissance botany, University of Basel

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Caspar Bauhin was born on January 15, 1560 in Basel, where he died on December 5, 1624 at the age of 64. He originated from a distinguished Protestant family from Picardy (France), whose members held high offices in Paris. His father Johannes Bauhin (1511–1582) fled the political persecution of the Huguenots and arrived in Basel in 1543/1544, where he practiced as a wound surgeon and became a naturalized citizen. As a medical doctor, Caspar Bauhin's father showed great interest in medicinal plants and maintained a small, private botanical garden (Fuchs-Eckert 1977, Reeds 1991).

Caspar Bauhin was the seventh and youngest child and the second son of the Bauhin couple. His brother Johannes Bauhin (1541–1613), who was almost 20 years older, was also interested in botany and studied in Universities of northern Italy and in Montpelier, paving the way for his brother Caspar in later years. Johannes Bauhin became a city doctor in Lyon and then in Montbéliard (France). He made a name for himself, among other things, as the author of a botanical encyclopaedia (Historia plantarum universalis), which remained incomplete at his death, was then completed by his son-in-law Johann Heinrich Cherler (1570–1609), but published in 1650 in Yverdon (Switzerland), only (Fuchs-Eckert 1979, 1981, 1982).

Education and academic career

In 1575, Caspar Bauhin enrolled at the Faculty of Medicine at the University of Basel. He studied medicine under Felix Platter (1536–1614) and Theodor Zwinger (1533–1588). In 1577, Cas-

Fig. 1. Portrait of Caspar Bauhin from the rectorate year 1598. Rectorate register of the University of Basel, vol. 2, f. 71r.

par Bauhin went to Padua (to Jacobus Antonius Cortusius), to Bologna (to Ulisse Aldrovandi), Montpellier and Paris (among others to Jean Robin) to study Medicine and Botany. The contacts during this „Grand Tour" at Universities became the backbone of his network of correspondences, which later in his life fed his botanical studies. In 1580, Caspar Bauhin returned to Basel, and visited Tübingen the same year. In February 1581, he publicly dissected a corpse during five days, passed his doctoral examination in April and then held his disputation. As he demonstrated exceptional didactical skills in a botanical course, Caspar Bauhin was commissioned to offer botanical excursions for students in Medicine. In April 1582 he was elected as a professor for Greek language, and from now on devoted himself intensively to medical practice, anatomical research and botanical studies. On September 10, 1589, at the age of 29, Caspar Bauhin was appointed the first professor for Medical Anatomy and Botany at the University of Basel, a chair established at his request, and after he had declined to accept the professorship for Theoretical Medicine after the death of Theodor Zwinger. A Theatrum anatomicum for courses in dissecting and a botanical garden (Hortus medicus) were set up for his teaching activities. Botanical excursion became a regular and important part of his activity, in which he not only made the students familiar with spontaneously growing plants, but confronted his students with the confusing diversity of plant names and the mistakes in contemporary herbals. The field excursions also fed his interest as a researcher. In his publications, unlike other herbalists, he emphasized description, nomenclature, and classification of plants rather than their medicinal properties (Reeds 1991). As early as 1586 he wrote in a letter to one of his friends that he was working on a „compendium of synonyms" and an arrangement of plants into classes. The task became the preoccupation for the rest of his life. Caspar Bauhin held the chair for Anatomy and Botany until 1614. When Felix Platter died in the same year, Bauhin became his successor as a professor for Practical Medicine and became also City Physician, but he remained preoccupied with plants until his death in 1624.

In the course of his life, Caspar Bauhin worked his way up both materially and socially and gained an international reputation as a scientist (Fig. 1). He was married three times. From his first marriage (1581–1594) to Barbara Vogelmann, daughter of a high official from Mömpelgard (today Montbéliard, France), whom he had met during a visit to his older brother living there, only one daughter remained alive longer. His second short marriage (1596–1597) to Maria Brüggler from Bern (Switzerland) remained childless. With his third wife Magdalena Burckhardt, who survived him, he had a son and two daughters. Caspar Bauhin's personality was characterized by diligence, meticulous work mentality and ambition (Burckhardt 1917). On the other hand, he lacked (according to Burckhardt 1917) the amiability and humanistic „joie de vivre" of his older colleagues Felix Platter and Theodor Zwinger.

Caspar Bauhin's merits as a physician

Caspar Bauhin must have had enormous creative power. He published around 30 scientific treatises, about half with medical or botanical content. With the establishment of a Theatrum anatomicum and his public autopsies, he made medical anatomy in Basel a centre of attraction for foreign students (698 awarded doctorates in Medicine). His achievements in medicine were based on the improvement and systematisation of anatomical terminology, especially in his book „Theatrum Anatomicum" published 1605. This comprehensive and handy textbook of anatomy was based on his lectures and anatomical-pathological demonstrations. In this book Bauhin comprehensively arranged the anatomical knowledge of the time and illustrated it with many figures. Of practical importance was also his pharmaceutics, in which he described the usual remedies of the time in details with regards to their composition, preparation and prescription method, drawing on his profound, practical knowledge.

Caspar Bauhin's merits as a botanist

Compared to his merits as a physician, Caspar Bauhin acquired far greater historical fame as a botanist. It is thanks to him that the University of Basel founded one of the first Botanical Garden north of the Alps, offered regularly botanical excursions in the surrounding of Basel for the practical knowledge of plants in nature, and botanical lectures on systematics and taxonomy within the Faculty of Medicine at the University of Basel. In 1622, Caspar Bauhin published one of the first comprehensive local floras in the world (Bauhin 1622), which until today remains a reference for judging floristic and vegetational changes and losses in the surroundings of Basel (Fig. 2–4; Meier-Küpfer 1985). Bauhin maintained a Europe-an wide network of contacts with the leading botanists of his time, and left the presumably largest botanical correspondence of that time (thousands of unpublished letters) as his legacy. In his botanical publications, Caspar Bauhin aimed to give a complete overview of all plants known at the time and to arrange them systematically, based on meticulous morphological inspection of specimens by himself. In doing so, he critically examined each entry and aspired to provide the corresponding herbarium specimen to other botanists' plant names in order to clarify their taxonomic affiliation. In this way, he achieved that his herbarium finally contained about two thirds of the plant species known in the early 17th century AD, many of them with the specimens collected by contacts from Caspar Bauhin's network. This herbarium formed his actual working and research tool and served as the basis for the development of his classification.

During his lifetime, Caspar Bauhin published original botanical books by himself, and edited, revised and commented on three important herbals (Matthioli 1598, Tabernaemonta-

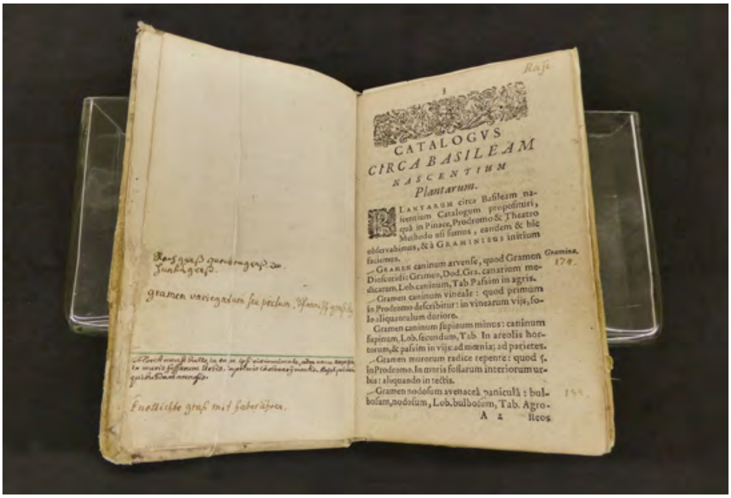

Fig. 2. Open first page of Caspar Bauhin's Flora of Basel, the „Catalogus plantarum circa Basileum sponte nascentium" from the year 1622 (Library of the Botanical Institute, University of Basel).

Fig. 3. *Thymelaea passerina* from the Herbarium of Caspar Bauhin *(Lithospermum Linariae folio germanicum)*. Bauhin collected this plant around Basel, where it does not occur any more. Today the species is on the Red List of Switzerland and is considered as endangered (Herbarium of the University of Basel, BAS-B11-076).

Fig. 4. *Androsace lactea* from the Herbarium of Caspar Bauhin *(Sedum alpinum gramineo folio, lacteo flore)*, who collected this plant «ob Monte Wasserfallen», a mountain near Basel, which he visited on botanical excursions (Herbarium of the University of Basel, BAS-B13-018).

nus 1613, Bauhin (ed) 1601). His final intention was to publish a comprehensive, richly illustrated encyclopaedia of all known plants, Theatrum Botanicum, by critically revising the confusion between the identity of plants and their given names by classical and contemporary authors. In the „Pinax Theatri Botanici“ (Bauhin 1623), intended as an index to the „Theatrum Botanicum“, Bauhin listed some 5600 plants (only 300 less than Linnaeus' in „Species Plantarum“ in 1753), divided in 12 „liber" (books), each with six sections. He referred to all important earlier authors that mentioned them and gave the plants a new, succinct diagnostic name on the basis of his own observations, an effort which then was enormously useful for botanical science, and still is today. His nomenclature was a ground-breaking advance because he was the first to establish the clear distinction between genus and species and grouped them together. His short species names could still contain several words, but they were structured hierarchically (Selosse 2005). Only the first volume of the intended 12 of the „Theatrum Botanicum“ appeared posthumously in 1658, after being edited by his son Johann Caspar. The Pinax had two forerunners. The „Phytopinax“ (Bauhin 1596) contained the first 8 books of the „Pinax“, but in a much shorter form. It famously contains the first scientific description of the potato. Bauhin described it as *Solanum tuberosum* (amended to *Solanum tuberosum esculentum* in the Pinax), a name that was adopted by Linnaeus and is still used today. In the „Prodromus“ (Bauhin 1620) about 600 plants are described and 138 are pictured accurately for the purpose of diagnostic recognition, many for the first time.

Bauhin's publications were „extremely important" (Jarvis 2007) to Carl von Linné (Linnaeus 1707–1778), the founder of modern plant nomenclature. When Linnaeus compiled „Species Plantarum“ (Linnaeus 1753), the earliest work of nomenclatural relevance (Turland et al. 2018), Bauhinian names were still widely in use, and more than one thousand are cited in it. Linnaeus interpreted these based on the herbarium of Bauhin's student Joachim Burser (1583–1639), which was arranged and labeled according to the „Pinax“, assembled in collaboration with Bauhin, and available to Linnaeus in Uppsala. More than 300 Burser specimens are formally designated Type specimens for Linnean names (Jarvis 2007), as are a large number of illustrations in Bauhin's works, including *Cardamine resedifolia* L., *Fagonia cretica* L. and *Peucedanum alsaticum* L. from the „Prodromus“ and *Cyperus esculentus* L. and *Phalaris utriculata* L. from the „Theatrum Botanicum“. Thus, through his botanical publications and via his influence on Burser's herbarium, Bauhin greatly influenced Linnaeus, who heavily relied on him for the further development of plant systematics and nomenclature.

Caspar Bauhin's herbarium

In the second half of the 16th century, herbaria became an essential working tool for the developing scientific botany. According to Caspar Bauhin's own information (Praefatio of the „Pinax" 1623), his herbarium finally contained more than 4000 plant species, of which about half survives to today. We discern four phases in the history of Bauhin's herbarium: assembly (1577–1624), family possession (1624–1772), major revisions (1772–1908), current day (1908–present). The first phase started when Bauhin collected his first plants, probably during his trips to Montpellier and Italy in the 1570s. After returning to Basel, Bauhin amassed his great herbarium through collecting and through exchange of specimens, seeds, and propagules with 65 correspondents (Reeds (1991) and Benkert (2020) detail these processes). Other herbaria of his time, such as that of his teacher in Basel, Felix Platter (1536–1614), were usually bound into books, but Bauhin kept the pressed plants loose in folded sheets of paper. Each specimen was labeled with the name according to his „Pinax" (1623), selected synonyms, and frequently also their origin, often together with printed illustration of plants mainly from the herbals of Tabernaemontanus and Clusius (Reeds 1991). This loose form of the herbarium facilitated the comparison and systematic ordering of the plants but became only later widely adopted (cf. Linnaeus 1751, section 11).

The second phase entails the period that his herbarium was inherited within the Bauhin family (1624–1772), a period of slow disintegration. Via his only son Johann Caspar I (1606–1685) and probably Friedrich Bauhin (1656–1696), it ended up in the possession of the merchant Johann Caspar II (1690–1753; Andreae 1763). The latter had been unwilling to let botanists study the herbarium, because he considered selling it to „an Englishmen" for a hefty sum (perhaps to Hans Sloan; letter of Emanuel König to Albrecht von Haller, 29 December 1735). Nevertheless, his son Emanuel Bauhin (1715–1746), a student of Haller's friend Professor Emanuel König (1698–1752), was persuaded to let König send multiple parcels of Bauhin's herbarium to Albrecht von Haller (1708–1777), Switzerland's most influential botanist, who was a practicing physician in Bern at the time (letters of König to Haller from December 1735 to 1736 that had thus far been overlooked). This allowed Haller to study the herbarium in great depth (Haller 1736, footnote in section 12) and to incorporate numerous fragments of specimens of Bauhin into his own herbarium (Zoller 1958), before returning the fascicles. Suggestions in the literature that Haller visited and plundered the Bauhin herbarium in Basel around 1728 appear to be erroneous: Haller's diaries do not indicate him studying the herbarium in Basel (Hintzsche 1968). In 1763, apothecary Johann Andreae observed that the herbarium „must have occasionally been brutally abused" (Andreae 1763). It was stored in the attic of the home of Sarah Socin (1697–1770), the widow of Johann Caspar II, and organized in fascicles exactly by sections in the „Pinax". Of the 72 expected fascicles, only 55 were found, plus „2 or 3" unmarked fascicles. Andreae blames poor storage conditions and its loose-leaf state for the herbariums condition; on the other hand, he had just visited Johannes Gesner's immense, beautifully bound herbarium in Zurich six weeks prior (Andreae 1763), possibly making Bauhin's herbarium unimpressive in comparison. Socin was unwilling to sell it to Andreae at the time.

The third phase of the herbarium, that of major rearrangements, started in April 1772 at the latest, when the herbarium became in the possession of Wernhard Lachenal (1736–1800), who became Professor of Botany and Anatomy at the University of Basel in 1777 (letter of Lachenal to Haller, 11 Apr 1772). Lachenal filed the Bauhin's specimens within his own, large herbarium. After Lachenal bequeathed his collections to the University of Basel, A.-P. de Candolle revised it in 1818 by adding contemporary names for many specimens, that still only carried Bauhinian labels (de Candolle 1904). Burckhardt (1917) claims that the Lachenal and Bauhin specimens were separated again during the tenure of Röper (1801–1885; Prof. of Botany 1827–1836). In the early twentieth century, shortly after arriving in Basel in 1902, Professor Alfred Fischer ordered as head of the „botanical committee" to thoroughly revise the herbaria of the University and „in particular to remove everything bad, decayed, and eaten by insects" (Binz, 1908). August Binz (1870–1963) was appointed and meticulously executed the task, retaining the 639 labels of the rejected specimens.

Today, the herbarium of Caspar Bauhin is kept as a separate collection at the University of Basel, Herbaria Basel (Index Herbariorum: BAS), in the systematic order that Binz imposed. It consists of 20 boxes with 1921 species folders, each containing one or more original, folded sheets of paper with unmounted plants, usually one label in Bauhin's hand, and often illustrations and other annotations (mostly by de Candolle and/or Binz; total folded sheets: 2357). In addition, some 650 herbarium labels without plants exist. The number of vouchers and labels outside BAS is not known. The herbarium is imaged; a current project (2023–2024) improves metadata capturing and will make the specimens of this invaluable herbarium collection available online.

Original botanical publications by Caspar Bauhin

Bauhin C (1596) **Phytopinax** seu Enumeratio Plantarum ab Herbariis nostro seculo descriptarum cum earum differentiis, cum plurimarum hactenus ab iisdem non descriptarum succinctae descriptiones et denominationes accessere: additis aliquot hactenus non sculptarum Plantarum vivis Iconibus. Basilea, per Sebastianum Henricpetri. 669 pp.

Full text: https://www.biodiversitylibrary.org/item/30648

The „Phytopinax" is a plant directory of 2460 known and 164 new plants in „liber" (books) of six sections each, corresponding to the first eight of the „Pinax". The genera are briefly characterised. The polynomial names of the individual species are practically without exception of Caspar Bauhin himself. For the already known species, the synonyms of the authors, who described the species for the first time, are listed. Caspar Bauhin presents here for the first time his innovations in botanical systematics and nomenclature.

Bauhin C (1620) **Prodromus Theatri Botanici,** in quo plantae sura sexcentae ab ipso primum descriptae cum plurimis figuris proponuntur. Francofurti a. Main, Typis Pauli Jacobi, impensi Johann. Treudelii. 160 pp. 10.3931/e-rara-25436. Full text: https://www.biodiversitylibrary.org/item/14431

In the „Prodromus", Bauhin describes 618 species, 138 of which are illustrated. Among them are many species from America, which Bauhin received by exchange from European colleagues. The classification and nomenclature correspond to that of the „Pinax". This work probably comes close to what Bauhin intended to do in the planned „Theatrum Botanicum". The descriptions of new plants are methodical, very precise, mirror his skilful observations and are often complemented with illustrations.

Bauhin C (1622) **Catalogus Plantarum** circa Basileam sponte nascentium cum earundem Synonymiis et locis, in quibus reperiuntur: in usum Scholae Medicae, quae Basileae est. Basilea, Typus J.J. Genathii. 111 pp. 10.3931/e-rara-28834. Full text: https://www.biodiversitylibrary.org/item/30649

The „Catalogus" is an index of the plants growing naturally in the vicinity of Basel (radius of a German mile, approx. 7500 m, plus the nearby Wasserfallen region in the Swiss Jura Mountains). Bauhin's Basel Flora contains c 800 species. The „Catalogus" is a pocket flora intended for excursions, in this form one of the first local floras worldwide.

Bauhin C (1623) **Pinax Theatri Botanici** sive Index in Theophrasti, Dioscoridis, Plinii et Botanicorum, qui a Seculo scripserum Opera: Plantarum circiter sex millium ab ipsis exhibitarum nomina cum earundum Synonymiis et differentiis methodice secundum earum et genera et species proponens. Opus XL. annorum hactenus non editum, summopere epetitum ad auctores intelligendos plurimum faciens. Basilea, Sumptibus et typis Ludovic. Regis. 522 pp. 10.3931/e-rara-26291. Full text: https://www.biodiversitylibrary.org/item/14431

The «Pinax» is a plant directory of all 5640 plant species known at that time, a more systematic and complete version of the Phytopinax, clearly structured in 12 „liber" (books) of 6 sections each, and more useful thanks to a detailed index. The individual species are accompanied by a complete list of synonyms, overcoming the Babylonian confusion of the time when naming plant species. The Pinax is Caspar Bauhin's most important work and had a great influence on Linné's „Species Plantarum" (1753).

Bauhin C (1658) **Theatri botanici** sive Historiae Plantarum ex Veterum et Recentiorum placitis propriaque observatione concinatae. Liber Primus. Johann Caspar Bauhin Basilea, Ioannem König 340 pp. 10.3931/e-rara-73659. Full text: https://www.biodiversitylibrary.org/item/ 30654

This is the first volume of the „Theatrum Botanicum", on which Caspar Bauhin worked throughout his life, and for which „Phytopinax", „Prodromus" and „Pinax" were only intended as preliminary contributions. Systematics and nomenclature correspond to the first liber of Bauhin's system, as in the „Pinax", mostly treating grasses and other monocots. The description of each species is extensive, and contains detailed information on distribution and (medicinal) use. Caspar Bauhin's son, Johann Caspar Bauhin (1606–1685), published this work. What happened to the other planned volumes, of which at least the second volume was already ready for printing, remains currently unknown.

Sixteenth century herbals edited and revised by Caspar Bauhin

Matthioli PA (1598) **Opera quae extant omnia:** Hoc est, Commentari in VI. libros Pedacij Dioscoridis Anazarbei de Medica materia … nunc a Caspara Bauhin aucti. Nicolaus Bassaeus Frankfurt am Main. https://www.e-rara.ch/zut/doi/10.3931/e-rara-4171. Full text: https://www.digitale-sammlungen.de/de/view/bsb10209643?page=7

Since the first edition in 1544, the commentary of Matthioli on Dioscorides circulated in many editions and translations. Caspar Bauhin checked the text for mistakes, compared earlier editions, added comments on confusions with earlier authors, listed more synonyms, described more than 300 new plants, and added illustrations.

Tabernaemontanus J Th (1613) Neuw vollkommentlich Kreuterbuch/ Mit schönen und künstlichen Figuren aller Gewächs der Bäumen/ Stauden und Kräutern … mit sonderem Fleiss gemehret durch Casparum Bauhinum. Nicolai Bassaeus, Johann Dreutels, Nicolaus Hoffman, Frankfurt am Mayn. Full text: https://www.digitale-sammlungen.de/de/view/bsb11057665?page=7

This book was for a wider public. Caspar Bauhin corrected errors, added references to other herbals, more details for identification, and added new plants and illustrations. The edition by Caspar Bauhin of Tabernaemontanus became very popular and was reprinted several times.

Bauhin C (editor) (1601) **Animadversiones in Historiam generalem plantarum Lugduni editam.** Item Catalogas plantarum circiter quadrigentarum eo in opera bis terue positarum. Frankfurt. Excudebat Melchor Hartmann, Impensis Nicolai Bassaei, Bibliopolae. Full text: https://www.digitale-sammlungen.de/de/view/bsb10954094?page=,1.

Herbal prepared by students of Guillaume Rondelet (Montpellier, France), anonymously published 1586/1587 with many mistakes and illustrations taken from earlier herbals. Caspar Bauhin made corrections, added comments and pointed to illustration faults.

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From Brunfels to Bauhin – The first 100 years of „botany" in the German-speaking area

Tilmann Walter

This article examines how Caspar Bauhin (1560–1624) became famous as a scientific author and University teacher in Basel focusing on the evolution of scientific practices such as botanizing and herbarizing in the German-speaking world. In the early 16th century German-speaking publishers were the first to sell well-illustrated books that would be of great help to readers in identifying plants. After 1550, Swiss and German physicians such as Felix Platter, Leonhard Rauwolf, Kaspar Ratzenberger and Johann and his brother Caspar Bauhin began collecting plants for their herbaria, some of which are among the oldest still preserved today. The Rauwolf herbarium, with its most „scientific" design, shows how plant identification was done in practice. Rauwolf also was the first to leave behind a comprehensive report of his fieldwork in Syria, Lebanon and Iraq, written in German. In Basel, Caspar Bauhin was to become a particularly influential academic teacher in the German-speaking world and beyond when he took over the newly established chair for Botany and Anatomy in 1589. He trained a total of nearly 800 students during his University career. Moreover, Bauhin's extensive correspondence comprises over 2500 letters and provides insights into the lively discussions among the fellow botanists with whom Bauhin corresponded.

Keywords
Academic teaching of botany, Caspar Bauhin, Herbaria, History of botany

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In the 16th century, at the beginning of the modern era, the science later called „botany" emerged from the subfield of pharmacy within the academic training of physicians. The present paper[1] focuses on scientific practices of botanizing and herbarizing, providing the context to understand the important role of Caspar Bauhin for the academic training of „botany" in the German speaking realm. The first medical chairs for herbal medicine and anatomy were established in northern Italy as part of medical studies, and the earliest *horti medici* or botanical gardens were likewise constructed around 1545 at the Universities of Pisa, Padua, and Bologna (Egmond 2021, 2022). For the German-speaking students, medical education in Montpellier in France also played an important role. When Caspar Bauhin (1560–1623) became prominent as a scientific author and University teacher in Basel around 1600, a new centre for training botany emerged in the German-speaking area itself.

Pre-Bauhinian botanical works – Text studies and empirical observations

Because of their essential publications in this field of knowledge, the Germans Otto Brunfels (1488–1534), Euricius Cordus (1486–1535), Hieronymus Bock (1498–1554), and Leonhard Fuchs (1501–1566) were referred to as the „fathers of botany". Among them, Otto Brunfels and the Strasbourg publisher Johann Schott (1477–1548) were the first to publish a distinguished three-volume edition of „Herbarum vivae eicones" (Strasbourg 1530–1536) or ‚lifelike images of plants' (Fig. 1). For systematic botanical identification it was particularly valuable,

[1] The present paper is a shortened translation of the article: Walter T (2023) Pflanzen, Gärten und Herbare: Ärzte als die frühesten Botaniker im deutschen Sprachraum. In: Tacke A, Lauterbach I, Wenzel M (eds) «Gartenlust» und «Gartenzier». Aspekte deutscher Gartenkunst der Frühen Neuzeit. Michael Imhof Verlag, Petersberg. pp 21–38.

Fig. 1. Otto Brunfels: Herbarum vivae eicones (1530). Staatsbibliothek Bamberg, 70 B 1#1, urn:nbn:de:bvb:12-bsb11412431-0.

Fig. 2. Portrait of Leonhard Fuchs from: De historia stirpium commentarii insignes (1542). Staatsbibliothek Bamberg, 1 A 20, urn:nbn:de:bvb:12-bsb11394427-0.

because until then there was nothing comparable on the book market in terms of the quality of the illustrations. The woodcuts by Hans Weiditz (†1536) found at the very beginning of the articles on the respective plants had initially been financed by the publisher at great expense. As a philologically proven medical expert, Brunfels added to them compilations from ancient and medieval writings as well as from works of more recent humanist authors, such as the Italians Niccolò Leoniceno (1428–1524) and Giovanni Manardo (1462–1536).

Euricius Cordus, who was professor of medicine in Marburg, described in his „Botanologicon" (Cologne 1534) a learned conversation on botanical issues with friends in an idealized or fictional form, which included his brother-in-law, the pharmacist Johannes Ralla (1509–1560). Interspersed among the lively discussions of the names and effects of various medicinal plants there is a brief description of the methodology of botanical field research: the scholars used the book editions of the relevant ancient and modern authors as textual guides to help them identify the observed plant species on site during their excursions. In order to learn more about the possible healing effects, they interviewed local people, preferably old women (Egmond 2018; Marsh 2022). As a result of such field studies Hieronymus Bock, a Protestant pastor of the Hornbach parish and a medical layman, in his „New Kreütter Bůch" (Strasbourg 1539) or ‚New herbal book' listed nearly 250 medicinal plants or *simplicia* to be found in Germany, giving their species, identifying characteristics, names, and internal and external pharmaceutical effects.

Generally, in this era the medical literature of antiquity was given the highest rank in Renaissance medicine (Nutton 2022). In addition to Hippocrates and Galen, the most prominent ancient medical authors, Theophrastus, Dioscorides and Pliny the Elder were considered valuable with regard to herbal remedies. The botanical knowledge of the ancient writers referred to the Mediterranean region, and in the Early Modern Period many herbal medicines that were used north of the Alps were imported from this region via Venice. Against this background, Leonhard Fuchs (Fig. 2), who taught from 1535 as a professor of medicine at the University of Tübingen, like Cordus and Bock emphasized the importance of a detailed knowledge of local medicinal herbs. Therefore, he also botanized together with his medical students in his garden and in the surrounding area (Seybold 2001). In the eyes of early modern specialists like Brunfels and Fuchs, the study of useful plants ultimately aimed at the praise of God. Leonhard Fuchs added to this notion in his dedicatory letter to Elector Joachim of Brandenburg (1505–1571) for his „De historia stirpium commentarii insignes" (Basel 1542; Fig. 3) or ‚Commentary and illustrations on botany', by stating that the observation of native plants in fields, forests, and mountains could also bring pleasure and enjoyment to humans. Fuchs' Latin explanations of individual plant species were no longer limited to compendia from other authors, as was the case with Brunfels. Like Bock, he added information on the various names, species, forms, habitats, times of flowering and seeding, as well as the „temperament" of the plant species according to the humoral medicinal concept of his age.

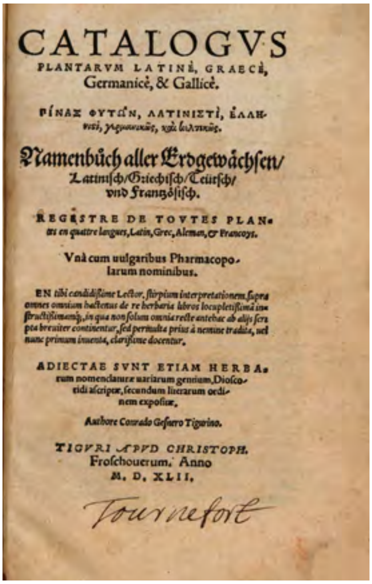
Botanical fieldwork was also given great weight at the medical faculties of northern Italy (Egmond 2018; Zemanek 1998). The students, who were to study the Mediterranean flora there with their own eyes, gained first-hand knowledge not available to the German pioneers Brunfels, Bock, and Fuchs in their interpretation of ancient texts. Euricius Cordus had been fortunate to study with Leoniceno and Manardo in Ferrara, and among the first Germans to devote themelves to study the *res herbaria* or botanical issues in Italy, following his example, was his son Valerius Cordus (1515–1544). The younger Cordus had first learned pharmaceutical practice from his uncle, the aforementioned pharmacist Johannes Ralla. Initially a student of Philipp Melanchthon (1497–1560) at the University of Wittenberg where he also lectured about remedies, Valerius Cordus went to Italy in 1543, visiting Florence, Pisa and Lucca, but died soon after in Rome at a young age. His „Dispensatorium" was posthumously printed in Nuremberg in 1546 as the first official pharmacopoeia and had a fundamental influence on the development of pharmacy in the following decades.

Medical professionals, who were particularly active in field research, such as Melchior Wieland (and Leonhard Rauwolf, whom we will hear about later), followed the ancient authors' information about healing plants as far as the Levant. The Prussian Melchior Wieland (c. 1520–1589), who came to live and work in Italy, can be called an early professional botanist, because he was employed as a prefect of the botanical garden in Padua from 1561 on (Trevisan 1995). Previously, Wieland also had traveled to Egypt, Palestine, and the Levant on behalf of the University of Padua and the Republic of Venice in search of herbal drugs and marketable medicines (Herrmann 2015). However, all scientific notes he had made during this journey (from which Wieland had hoped to be able to present a comprehensive work on natural history like that of Dioscorides or Pliny) were lost on the way (Fantuzzi 1774: 222). As Conrad Gessner reported about him, Wieland had also traveled to Germany, Italy, Greece, and Asia Minor for research purposes, which is why the Zurich naturalist held him in exceptionally high esteem for the knowledge Wieland had acquired while traveling in Europe and around the Mediterranean Sea (Wieland and Gessner 1557).

The Zurich physician Conrad Gessner (1516–1565; Fig. 4), who by his numerous publications was known as a connoisseur of ancient literature and an encyclopedist of the animal world, is also to be counted among the German-speaking botanists *avant la lettre* (Leu 2016; Leu and Opitz 2019; Nyffeler 2016). In 1541, he completed his medical studies in Basel, and later worked in Zurich, first as a lecturer, and from 1546 as *Professor physicae* at the *Collegium Carolinum*, Zurich's college for the education of its clergy, and from 1554 onward also as town physician. In the meantime, Gessner achieved great fame by publishing numerous philologi-

Fig. 3. Illustration „Acanthus / Teütsch bernklaw" in: Leonhard Fuchs: De historia stirpium commentaii insignes (1542). Staatsbibliothek Bamberg, 1 A 20, urn:nbn:de:bvb:12-bsb11394427-0.

Fig. 4. Tobias Stimmer (1439–1584): Conrad Gessner, portrait of the scholar at the age of forty-eight (1564), oil and tempera on canvas, Museum zu Allerheiligen Schaffhausen.



CATALOGVS
PLANTARVM LATINÈ, GRAECÈ,
Germanicè, & Gallicè.

ΠΙΝΑΞ ΦΥΤΩΝ, ΛΑΤΙΝΙΣΤΙ, ἙΛΛΗ-
ΝΙΣΤΙ, γερμανικῶς, καὶ γαλλικῶς.

Namenbůch aller Erdgewächsen/
Latinisch/Griechisch/Teütsch/
vnd Frantzösisch.

REGESTRE DE TOVTES PLAN-
tes en quattre langues, Latin, Grec, Aleman, & Francoys.

Vnà cum uulgaribus Pharmacopo-
larum nominibus.

EN tibi candidissime Lector, stirpium interpretationem supra omnes omnium hactenus de re herbaria libros locupletissimã instructissimamq́, in qua non solum omnia recte antehac ab aliis scripta breuiter continentur, sed permulta prius à nemine tradita, uel nunc primum inuenta, clarissime docentur.

ADIECTAE SVNT ETIAM HERBA-
rum nomenclaturæ uariarum gentium, Dioscoridi ascriptæ, secundum literarum ordinem expositæ.

Authore Conrado Gesnero Tigurino.

TIGVRI APVD CHRISTOPH.
Froschouerum. Anno
M. D. XLII.

Tournefort

Fig. 5. Conrad Gessner: Catalogus plantarum (1542). Bayerische Staatsbibliothek München, 4 Phyt. 105, urn:nbn:de:bvb:12-bsb10166776-8.

cal and natural history works. As a trained physician, he never lost sight of the pharmaceutical value of plants. One example of this is that the young Gessner compiled a handy „Historia plantarum" (Basel 1541) from the classics, whose alphabetically-arranged articles with an attached index provided readers with information on the plants' healing properties. Only one year later he presented a „Catalogus plantarum" (Zurich 1542; Fig. 5), which juxtaposed the Latin, Greek, German and French names of plants commonly used in pharmacies forming a multilingual dictionary. The edition of a „Lexicon rei herbariae trilingue" based on ancient and contemporary authors by the Hebraist David Kyber (1515–1553) was supplemented by Gessner in print (Strasbourg 1553) with advice and tables on how to collect plants with the greatest benefit according to the months they flower and bear fruits and seeds.

Conrad Gessner himself made regular botanical trips to the Alps. In „De raris et admirandis herbis" (Zurich 1555), a treatise on the genus *Lunaria* as well as luminescent plants and natural objects in general, taken from the literature, a personal report by Gessner on an exploration in the Pilatus region, which he had undertaken in the Alps accompanied by a wound surgeon, an apothecary and an artist, was added in print. The Zurich physician also made a name for himself among botanists with an edition of the Dioscorides commentary and unpublished botanical writings from the estate of the early deceased Valerius Cordus (Strasbourg 1561). The volume also contained the earliest printed illustration of a garden tulip with the first report by Gessner himself about the specimen in bloom, which he had visited in April 1559 in the Herwart family garden in Augsburg (Zäh 2022).

Another very influential figure in empirical botanical studies in the German-speaking area was the Dutch-born Carolus Clusius (1526–1609) from Arras. Under the influence of Melanchthon, he began to study medicine in Wittenberg and continued in Montpellier from 1551 to 1554. In the coming decades, Clusius made a name for himself throughout Europe with his own treatises on the flora of Spain and Austria and as a translator of works on herbal remedies of India and America (Clusius 1576, 1583; D'Orta 1567; Monardes 1574). His international correspondence of about 1500 letters[2] focused largely upon the exchange of knowledge about plants and also plants themselves which were sent by post (Egmond 2010; Egmond et al. 2007). Like Melchior Wieland, Clusius was employed for a time as a botanist in order to establish the imperial court garden in Vienna in 1574. Already at an advanced age, in 1593 Clusius finally became professor of Botany in Leiden and prefect of the botanical garden, positions in which he remained until the end of his life.

[2] https://digitalcollections.universiteitleiden.nl/clusiuscorrespondence; https://clusiuscorrespondence.huygens.knaw.nl/edition/ (visited 15. 8. 2023).

Meanwhile, the German book market was flooded by authors, compilers and printers with a plethora of more or less original herbals: Publishers like Christian Egenolff and Nicolaus Bassaeus in Frankfurt a. Main sold editions of numerous works by Eucharius Rösslin (1470–1526), Jacobus Theodorus Tabernaemontanus (c. 1522–1590), Adam Lonitzer (1528–1586) and others with pictorial material printed first by Brunfels and Fuchs. The practical value of illustrated herbals was emphasized already by Leonhard Fuchs in 1542: the illustrations were especially helpful for botanically-interested people to identify a plant as the full lifespan of the plant could be demonstrated (Fuchs 1542: βr–v). As a humanist, Fuchs believed that the knowledge of plants originated from antiquity: like all medicine, for him it came with the Greeks from Moses, the Chaldeans and the Egyptians. In the meantime, however, it had become so „plebeian" that it was only available among apothecaries or old women from among the common people. For the Tübingen professor of Medicine, the restoration of this knowledge by rereading the ancient texts was the task of book scholars like himself. In addition, sound knowledge about plants, as it could be acquired in the fields or on mountains and other remote areas, also belonged among the educated and not only among the common people.

From the perspective of the history of science, illustrations, which were created on the initiative of authors and publishers, also played an important role (e.g., Fig. 3). Images helped clarify the nomenclatural confusion. Without them, the essential question of whether the various words named in the texts referred to identical plants in nature could hardly have been settled with certainty. In fact, the illustrated herbals from Germany originated as much from the business acumen of printers as from the skills of draftsmen and woodcutters (Kusukawa 2012). As textual guides, multilingual plant catalogs printed in smaller book formats, such as those edited by Conrad Gessner (Fig. 5), were far more suitable for practical use in the field, as they were handier than unwieldy and expensive classic editions or illustrated herbals with their usually large formats. Likewise, a significant role in the production of all these books was played by the professional knowledge of pharmacists, as „botany" remained closely associated with medicine and pharmacology until the end of the 16th century. By elaborating on how apothecaries knew to distinguish genuine from adulterated medicinal plants, Euricius Cordus (1534: 53) also took a clear stand against the common attitude among humanists, who were often unwilling to question or add something new to what was found in ancient writings. As far as the empirical knowledge in the field of botany was concerned, local „Kräutler" or herbalists who were familiar with the conditions on site were indispensable as guides in the field for botanically-interested scholars – a fact that was emphasized by prominent field researchers of the time, such as Carolus Clusius and Leonhard Rauwolf.

Early herbaria and botanical field trips

Around the mid-16th century, a certain extension of botanical methods became widespread: the herbarium as a *hortus siccus* offered the possibility of studying plants in detail in a dried state even outside their vegetative periods (Baldini et al. 2022; Fleischer 2017; Thijsse 2016). Its inventor is considered to be Luca Ghini (1490–1556), professor of Medicine in Bologna, who started a collection of dried plants in the 1530s and in 1544 was commissioned to establish the very first botanical garden in Pisa. The oldest preserved specimens come from among his students, such as the herbarium owned by Gherardo Cibo (1512–1600), created by Francesco Petrollini, or the En Tibi herbarium (Stefanaki et al. 2019). The earliest herbaria preserved in the German-speaking world were in the possession of Felix Platter (1536–1614), Leonhard Rauwolf (1535?–1596), Kaspar Ratzenberger (1533–1603) and Caspar Bauhin (1560–1624), all candidates of medicine in Montpellier.

Platter started collecting dried plants about 1552, Ratzenberger about 1556, Rauwolf about 1560 and Caspar Bauhin about 1577. Felix Platter studied with Guillaume Rondelet (1507–1566) in Montpellier from 1552 and also made closer acquaintance with Carolus Clusius there. Here he lived in the house of the apothecary Laurent Catelan, whom he aided in his pharmacy to acquire knowledge of remedies (Platter 1976). Platter had begun his academic training in his hometown Basel, where he returned in 1557 and earned his medical doctorate. After years as a general practitioner, he was appointed city physician and professor of Medicine there in 1571. As part of his collecting activities, which served both scientific and representative purposes (Walter 2013), he supplemented the pages of his herbarium with artistic works and printed illustrations, including 79 originals of drawings by Hans Weiditz, which he had once made for the herbal of Otto Brunfels.

Leonhard Rauwolf from Augsburg matriculated at the University of Tübingen in 1554 and then went on to the University of Wittenberg in 1556. After 1560, he was to study in Montpellier. A few weeks after Rauwolf, Kaspar Ratzenberger also enrolled there. Ratzenberger had also studied in Wittenberg from 1548 and had moved to Jena in 1558. Before going to Montpellier in 1560, he had herbarized in Italy, Switzerland, and southern Germany. In 1561, he received his doctorate in Orange and went to Naumburg, where he became town physician. Unlike Rauwolf, both Platter and Ratzenberger did not publish on botanical matters.

The layout and production of Leonhard Rauwolf's prominent herbarium, now preserved in Leiden, appears particularly „scientific" by today's botanical standards. It was begun in 1560 in France, as was noted on the title pages of the first two volumes (Stefanaki et al. 2021). After having completed his studies in 1562 with a doctorate from the University of Valence, Rauwolf traveled through Italy, where he collected the plants for the third volume of his herbarium. On his way back home, Rauwolf visited Leonhard Fuchs in Tübingen in the fall of 1563 to show his dried plants to his former teacher. At that time, Fuchs added identifications to 162 specimens or tried to correct already noted plant names.

As the close examination of the handwritten entries in Rauwolf's herbarium has recently shown (Stefanaki et al. 2021), most of the plants in the first two volumes were identified by his fellow student Johann Bauhin (1541–1613) from Basel, the elder brother of Caspar Bauhin, whereas only a few entries in Rauwolf's hand can be found there. Therefore, it can be concluded that Rauwolf was still a beginner in the botanical field when he began his studies in Montpellier and that he had a more experienced fellow student help him with the entries. Together with Johann Bauhin, who had previously studied with Leonhard Fuchs in Tübingen as well, Rauwolf went on excursions in Languedoc and Provence. Having returned to his hometown of Basel, Johann Bauhin also embarked on a subsequent study trip to Italy. Rauwolf accompanied Bauhin on his return journey from Italy, and the two arrived together in Zurich, as Conrad Gessner noted in his *Liber amicorum* (Durling 1965). A lively correspondence developed between Bauhin and Gessner on botanical questions, which decades later also appeared in print (Bauhin 1591). In 1565, Bauhin lent his herbarium (which is lost today) to the Zurich scholar, from which the latter had drawings made of numerous plants (Gessner 1577: 121v).

Leonhard Rauwolf had become more confident in his botanical judgment, so that the third volume of his herbarium with plants from Italy only has entries by Rauwolf himself and subsequent corrections by Leonhard Fuchs (Stefanaki et al. 2021). After returning to Augsburg, Rauwolf reorganized his herbarium in 1564, adding missing entries and creating an index in which he also marked some plants whose previous identification seemed questionable to him. Financed by the Augsburg trading house Manlich, Rauwolf undertook an expedition to Syria, Lebanon, and Iraq from 1573 to 1576, during which he collected 200 plants, which can be found in the fourth volume of the herbarium (Ghorbani et al. 2018). Recent analyses of the fourth herbarium volume have shown that Rauwolf's botanical work met the highest methodological standards even by modern criteria: he identified the foreign plants by morphological comparisons with related species known to him in Europe, documented the local names for them, and brought everything in the herbarium together with their presumed names in antiquity.

Rauwolf's extensive travelogue from this trip, written in German and first printed in 1582 (Fig. 6), also deserves very special attention here, as it described in great detail his expedition to an unexplored area (from a European point of view), undertaken out of scientific interest in the natural world (Rauwolf 1582). The book chronicles how he observed and collected these and many other specimens during visits to ornamental and kitchen

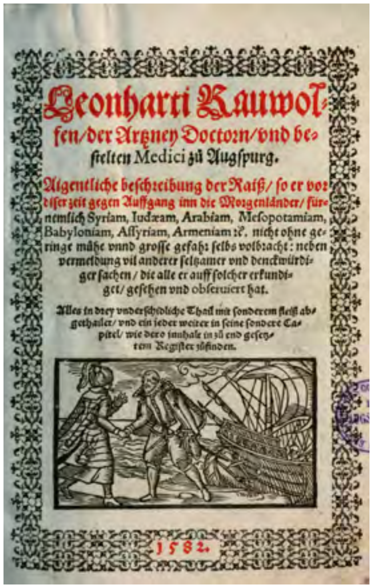

Leonharti Rauwolfen/der Artzney Doctorn/vnd bestelten Medici zu Augspurg.
Aigentliche beschreibung der Raiß/ so er vor diser zeit gegen Auffgang inn die Morgenländer/ fürnemlich Syriam, Iudæam, Arabiam, Mesopotamiam, Babyloniam, Assyriam, Armeniam &c. nicht ohne geringe mühe vnnd grosse gefahr selbs volbracht: neben vermeldung vil anderer seltzamer vnd denckwürdiger sachen/ die alle er auff solcher erkundiget/ gesehen vnd obseruiert hat.
Alles in drey vnderschidliche Thail mit sonderem fleiß abgethailet/ vnd ein jeder weiter in seine sondere Capitel/ wie dero innhalt in zu end gesetztem Register zufinden.
1582.

Fig. 6. Leonhard Rauwolf: Aigentliche beschreibung der Raiß […] inn die Morgenländer (1582). Staats- und Stadtbibliothek Augsburg, 4 Gs 1872, urn:nbn:de:bvb:12-bsb11212041-5.

gardens, markets for vegetables and fruits, and on his field trips guided by locals (Walter 2009; Walter et al. 2021). This scientific genre would later reach its literary heights with Alexander von Humboldt (1769–1859) and Charles Darwin (1809–1882).

Caspar Bauhin and the institutionalization of botanical education in the German-speaking area

The preceding sections reveal a slow development from a close association of medicine and botany to the study of plant diversity independent of their medicinal value. This development is epitomized by the works of Caspar Bauhin in Basel, where botanical education became prominently institutionalized in the late 16th century. His legacy allows well-founded insights into the history of botany. Bauhin had a very extensive letter network and left behind over 2500 preserved letters, the largest botanical correspondence of his time[3], larger even than the Clusius correspondence. There were personal overlaps with the correspondences of his contemporaries Carolus Clusius and Joachim Camerarius (1534–1598), a Nuremberg doctor interested in botany who left behind a large collection of letters, due to their common field of interest.

After having studied in Basel and visiting Padua, Bologna, Montpellier, and Tübingen, in 1589, Caspar Bauhin assumed the newly established position of full professor of Anatomy and Botany at the University of Basel, where he was to become a particularly influential academic teacher within the German-speaking world (Benkert 2020; Fuchs-Eckert 1979, 1981, 1982; Stöcklin and de Vos 2023). Between 1581 and 1624, when Bauhin taught at the University, first as a lecturer, then as a professor, a total of 795 medical students were enrolled and 698 of them were awarded doctorates; no larger medical faculty existed in the German-speaking world (Burckhardt 1917). Caspar Bauhin and his colleague Felix Platter were both sons of immigrants in the city of Basel. Access to prominent and well-paid University posts was not a matter of course for these families. Concentrating on medical practice and teaching, the pride in their own achievements that corresponded to a meritocratic upward mobility mentality is easily recognizable in their publications.

Bauhin also saw to the establishment of a botanical garden in Basel in 1589, the oldest north of the Alps. For teaching purposes, especially during the winter months, he used his herbarium, which eventually contained more than 4000 plants, of which about 2330 specimens survived. Even as a lecturer, he was concerned about good teaching: for example, in 1586, he wrote to his student Sigismund Schnitzer (c.1560/1565–1622) that he had hesitated to use the works of Andrea Cesalpino (1519–1603) for teaching botany, because he found them difficult to understand himself due to its complicated Latin style[4]. Bauhin's own publications, on the other hand, were highly appreciated by readers like Schnitzer because they were so valuable not only to students but also to practicing physicians[5].

[3] https://www.e-manuscripta.ch (visited 15. 8. 2023).

[4] Letter from Caspar Bauhin to Sigismund Schnitzer, 11. 12. 1586 (Hornung 1626: 334).

[5] Letter from Sigismund Schnitzer to Jakob Zwinger, 27. 10. 1598 (UB Basel, Frey-Gryn Mscr I 12, Nr. 331).

In his early career, Caspar Bauhin only published works on anatomy, but soon he was to provide botanically-interested readers with his „Phytopinax" (Basel 1596), a list of the nomenclature used by 44 botanical authors for 163 plants, giving the genus, synonyms, and a list of species, each of which includes exact page numbers in the works cited (which makes it very valuable for today's scholars as well; Fig. 7). As a handbook it could be easily carried into the field to identify plants; the idea for it (and the Greek-language title) had apparently been borrowed by Bauhin from Gessner's plant catalog of 1542. For the systematics of the plant world, Bauhin's order of species according to (presumed) genera was to have a lasting effect on later botanists. Carl von Linné (1707–1778) in particular made frequent use of Bauhin's designations in the development of his classification system (Offerhaus et al. 2023; Selosse 2005).

In 1598, the Basel professor published an illustrated edition of Pietro Andrea Mattioli's (1501–78) works and in 1601 corrections and additions to Jacques Daléchamps' (1533–1588) „Historia plantarum universalis" (Lyon 1586/1587), according to the information given in his own „Phytopinax". In these years, Bauhin was very productive as an author and editor: in 1609 he had eight different publications in preparation or in print at the same time. He could not afford more, he wrote to the medical professor and botanist Ludwig Jungermann (1572–1653) in Giessen, because of his University official business and domestic obligations[6]. While teaching botany, Bauhin never lost sight of pharmaceutics, as evidenced by the publication „De compositione medicamentorum" (Offenbach 1610) based on his lectures. In 1622 Bauhin published a „Catalogus" (Basel 1622) of the flora around Basel for his medical students.

For many years, Bauhin endeavored to expand the beginnings laid out in his „Phytopinax" into a comprehensive botanical compendium. But, as in the case of Leonhard Fuchs and Conrad Gessner, a planned survey of all known plants from his pen remained unprinted during his lifetime. Like these two authors before him, the Basel professor included a stock of pictures with independent plant illustrations, taken as far as possible from nature[7]. As preliminary works, he published during his lifetime a „Prodromos theatri botanici" (Frankfurt a. Main 1620) and a „Pinax theatri botanici" (Basel 1623). But the first volume of Bauhin's „Theatrum botanicum sive historia plantarum" (Basel 1658), which was printed posthumously, was to remain the singular published text of the entire work.

Having been a professor of medicine for many years, Bauhin was contacted by many of his colleagues and seen as a beacon for innovative science. Looking at the sheer number of letters, it is not very credible to see in him an „egocentric, introverted" character (Fuchs-Eckert 1982: 144), since he was well accessible as a „public" person and as a mentor for his former students. Yet, Bauhin also knew how to gain benefits from his correspondence (Benkert 2020: 129–133),

221

LIBER QVARTVS.

SECTIO PRIMA.

TANACETVM: PARTHENIVM. CHRYſanthemum: Buphthalmum: Chamamelum: Cotula.

TANACETVM, eiuſq; ſpecies.

TANACETVM fortè à Tannaco, quo nomine Parthenion appellatum fuiſſe reſtatur Plinius: Parthenion microphyllon fortè Hippocr. Hermolao. Dioſcoridis [illegible] lib. 3. cap.128. quibuſdam videtur, nobis non item.

I.

Tanacetum inodorum montanum.

Tanacetum non odorum, perperam Sideritis Italorum Lobel.obſer. pag.432.& icon. pag.750. & hoc aliquid ſimilitudinis habet cum Sideritide tertia Matthioli icon. 8. pag.671. quoad folia: at ſi ramos & capitula perpendas conueniet cum Ruta canina.

II.

Tanacetum inodorum flore Bellidis maioris.

Tanacetum inodorum primum Cluſ. hiſt. Pann. pag. 550.lib.3.cap.33.

III.

Tanacetum vulgare.

Tanacetum, ſecunda Matricariæ ſpecies & Partheniū Brunf.fol. pag.251. tom. 1. rhapſ.46. iconem repetit.tom.2.pag.88. Rhapſ.21.ſine deſcript.& in 4.pa.98.

Tanacetum millefolij folijs Lobel.icon. pag.749. & obſer.pag.432. Tanacetum.

Flore eſt communiter luteo: rariùs reperitur albo, quare Tabern.icon.pag.10.duas habet icones.

Ee 3 *IV.* Tana-

Fig. 7. Page 221 from the Phytopinax (1596) of Caspar Bauhin: Bayerische Staatsbibliothek München, 4 Phyt. 23, urn:nbn:de:bvb:12-bsb00022752-7.

[6] Letter from Caspar Bauhin to Ludwig Jungermann, 24. 8. 1609 (Wein 1937: 159).

[7] UB Basel, K IV 3, A–D: https://swisscollections.ch/Record/991170502487205501 (visited 15. 8. 2023).

such as when he sent a list of plants to Ludwig Jungermann, which the latter had mentioned in his „Catalogus" of the flora around Nuremberg (Altdorf 1615). Bauhin asked his colleague in a rather direct or brusque manner to send him the plants on the list in a specific state – dried, with root and flower – or his herbarium[8]. And like Conrad Gessner before him, Bauhin held out the prospect of his contributor being mentioned in his works and receiving his books as gifts.

Bauhin's numerous students in particular sought to maintain contact with their noted academic teacher. Among these, Leonhard Dold (1565–1611), who had received his doctorate in Basel in 1594 and who was also well acquainted with Joachim Camerarius in his hometown of Nuremberg, was particularly versed in botany. After the death of Camerarius in 1598, Bauhin turned to Dold when he needed a contact person in the Franconian trading metropolis for the exchange of seeds and plants, botanical information and illustrations[9]. As plants for Bauhin's herbarium were concerned, Joachim Burser (1583–1639) from Kamenz became a particularly important contact. Burser had earned his doctorate in Basel in 1614 and had corresponded with Bauhin since 1615 as the town physician of St. Annaberg. After 1625, he was to teach at the Danish Knight's Academy Sorø as professor of Medicine and Physics. Burser's personal herbarium was destroyed by fire in Uppsala in 1702; what remained was used by Linné in writing his „Systema Naturae" (Fuchs-Eckert 1982: 138). Another herbarium from the circle of Bauhin's students, which has been preserved and is now kept in Basel, was begun by Jakob Hagenbach (1595–1649), a Basel native, who later taught at the University of Basel as a professor of Logic and Ethics (Stöcklin and de Vos 2022). Further prominent Bauhin students in medical circles were, for example, the Frankfurt physician Johann Hartmann Beyer (1563–1625) and Johann Rudolf Saltzmann (1574–1656), later professor of Medicine and, from 1619, also director of the botanical garden in Strasbourg. The correspondence with Saltzmann clearly proves that Caspar Bauhin permitted students from outside to visit his herbarium[10].

Since they already have been researched in their entirety, letters from the Bamberg court physician Sigismund Schnitzer to Caspar Bauhin can give the best insight into the high scientific level of plant observation and description at the turn of the 16th and 17th centuries (Häberlein and Walter 2022). After becoming physician at the bishop's court in the Franconian city of Bamberg in 1589, he reported to his teacher Bauhin on rare plants, for example in the court garden of the Bamberg bishops. Even decades later, detailed botanical information about the Bamberg gardens continued to arrive in Basel. The Bamberg doctor also thought about cataloging the flora of Franconia, although this apparently never happened[11]. Meanwhile, Schnitzer had paid great attention to the individual peculiarities or special environmental conditions under which plants grew. In the Bamberg court garden, for example, never-before-seen cultivars of tulips and hyacinths could be admired, and a *[Dianthus] caryophyllus* had

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[8] „Fac rogo ut cum flore habeam": letter from Caspar Bauhin to Ludwig Jungermann, 24. 8. 1609 (Wein 1937: 159).

[9] Letters from Caspar Bauhin to Leonhard Dold, 1599–1611 (UB Erlangen, Trew, C. Bauhin Nr. 15–47).

[10] Letter from Johann Rudolph Saltzmann to Caspar Bauhin, 29. 5. 1621 (UB Basel, G2 I 2, fol. 408); letter from David Schobinger to Caspar Bauhin, 4. 12. 1613 (UB Basel, G2 I 2, fol. 367).

[11] Letter from Sigismund Schnitzer to Caspar Bauhin, 28. 5. 1601 (UB Basel, Frey-Gryn Mscr II 1, S. 311).

developed quite differently from the parent plant[12]. Regarding such natural phenomena, the Bamberg court physician asked himself, as Carl von Linné did later, whether the special colors and shapes of the blossoms of such „monsters" were a whim or a miracle of nature[13].

Conclusion

After 1530, publications with high-quality illustrations provided a novel basis for pharmaceutical or botanical practice, since no text, no matter how sophisticated, could replace visual comparison. These prints from the German-speaking area were to become direct models for the illustrated Mattioli editions in Italy or the herbal book productions of Dutch publishers. Conversely, the educational paths of the German-speaking physicians who became known as „botanists" in the 16th century often point to international influences, first in northern Italy, Montpellier, and Tübingen, and later especially in Basel and Leiden. From the 1540s onward, medicinal gardens and herbaria provided methodological opportunities to study plants outside their distribution areas and growing seasons. The practice of botanical field research has been documented by many personal statements since the beginning of the 16th century, but it was first documented in print by Leonhard Rauwolf in 1582 in the form of a comprehensive 487-page German scientific travelogue. By the end of the 16th century, through research and trade journeys, scientific exchanges and commercial trade, the plants growing regionally in Europe were recorded and those outside Europe were increasingly known.

In 1596, Caspar Bauhin collected the plant names with their synonyms and provided usable literature references in his plant catalog „Phytopinax", which he increasingly expanded until the end of his life. With his attempts at classification, however, Bauhin laid valuable foundations for botanical systematics. Of greatest importance was the systematic training of an entire generation of capable botanists by Caspar Bauhin, with the University of Basel being the undisputed leader as a location in the German-speaking world around 1600. The botanical discussions on plants and transfer of knowledge about morphology and variability of plants in gardens and in the field proved the attentiveness of his students as demonstrated here by the example of Sigismund Schnitzer. Observations on high variability as well as morphological dynamics, for example in the context of breeding, were to become the basis of scientifically-pursued observation of nature in the coming centuries, up to the foundation of modern evolutionary theory in Charles Darwin. Just as importantly, the scientific networks established by Basel students achieved an unexpected continuity, with sons even later standing in for their fathers once the latter had passed away. Further research into these large scientific correspondences promises to provide in-depth insights into the history of botanical practice and education.

[12] Letter from Sigismund Schnitzer to Andreas Libavius, 11. 8. 1611 (Hornung 1626: 84).

[13] Letter from Sigismund Schnitzer to Caspar Bauhin, 24. 8. 1611 (UB Basel, Frey-Gryn Mscr II 1, S. 312).

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Impossible to press? – Succulents in Renaissance herbaria

Urs Eggli[1], Reto Nyffeler[2] and Felix Merklinger[1]

Several Renaissance herbaria, including the herbarium by Caspar Bauhin, contain preserved specimens of different succulent plants, such as cacti, stonecrops, palm lilies or aloes. In view of the difficulties experienced even today when preparing succulents for the herbarium, the efforts of the Renaissance botanists to meet this challenge is remarkable. The view that succulents by definition are unsuitable for pressing for the herbarium, as for instance expressed by Richard Bradley in his 1716 book, prevails to these days. We first provide a condensed overview of standard preparation techniques for succulents advocated in the literature of the past forty years. Then, a selection of specimens of succulents in early herbaria, from several plant families, is discussed and the preparation methods used at that time, and possible solutions of the difficulties involved, are outlined.

„So, do not be afraid of the spines. With a bit of patience, anyone can produce good-quality herbarium specimens of cacti" (De Groot 2011: 989)

Keywords
Cacti, Exotics, Herbarium techniques, Succulents

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Today, if botanists are asked about their experience in preparing succulents in the conventional manner for the herbarium by pressing and drying, most will likely confess that they never preserved succulent plants in this way – too difficult or outright impossible, time consuming, and with little-pleasing results is the general attitude in the field. Indeed, succulent plant species are under-represented in most herbaria, at least as conventional pressed sheet specimens. The English gardener-naturalist Richard Bradley (1688–1732) even employed this purported impossibility to define succulents in his famous book „The history of succulent plants, containing the Aloes, Ficoids …, Torch Thistles, Melon Thistles, and such other as are not capable of an Hortus-siccus" (Fig. 1) (Bradley 1716; see Eggli and Nyffeler 2009 for a discussion of the definitions of the term succulence).

Notwithstanding the alleged impossibility to press and dry succulents, there are thousands of specimens of succulent plants conserved in the herbaria of the world – alone the small specialized herbarium at the Sukkulenten-Sammlung Zürich (ZSS) counts some 8000 sheet specimens amongst its 29300 accessions of preserved plants (data from December 2021).

In this paper, we first summarize different methodologies advocated over time for preparing succulents for the herbarium. Then we showcase four different lineages of succulents *(Aloe, Opuntia, Yucca, Sedum)* for which we surveyed a selection of Renaissance herbaria to establish when the first specimens of these taxa were pressed, and how Renaissance botanists tackled the difficulties involved in pressing and drying these plants for the herbarium.

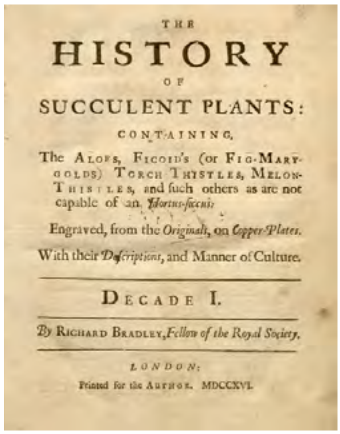
THE
HISTORY
OF
SUCCULENT PLANTS:
CONTAINING,
The ALOES, FICOID'S (or FIG-MARYGOLDS) TORCH THISTLES, MELON-THISTLES, and such others as are not capable of an *Hortus-siccus*;
Engraved, from the *Originals*, on *Copper-Plates*.
With their *Descriptions*, and Manner of Culture.
DECADE I.
By RICHARD BRADLEY, *Fellow of the Royal Society*.
LONDON:
Printed for the AUTHOR. MDCCXVI.

Fig. 1. Title page of Bradley (1716). (Biodiversity Heritage Library / Missouri Botanical Garden; http://www.biodiversitylibrary.org/item/14649#page/1/mode/1up)

Fig. 2. Herbarium press placed on a gas stove to benefit from passive convectional heating.
Photograph F. F. Merklinger

Table 1. List (ascending by date of making) of the herbaria cited in the text, with details on the dates of making, holding institutions, specimens cited, and digital accessibility

Herbarium	*Period*	*Holding Institution*	*Specimens cited in the text*	*Digital access*
Mendoza herbarium	1539–1554	Real Biblioteca del Monasterio de San Lorenzo de El Escorial, Spain	*Aloe*	none
Francesco Petrollini (Vols. 1–4 , formerly known as „Cibo", and „Rome Herbarium")	c. 1550–1553	Biblioteca Angelica, Rome	*Aloe*	none
Erbario A	c. 1550–1553?	Biblioteca Angelica, Rome	*Opuntia*	none
Ulisse Aldrovandi	c. 1551–1586	Herbarium BOLO, Orto Botanico & Herbario, Università di Bologna	*Aloe, Opuntia*	http://137.204.21.141/aldrovandi/Explore
Felix Platter	c. 1552–1614	Burgerbibliothek Bern	*Sedum, Hylotelephium*	http://www.burgerbib.ch/de/bestaende/privat-archive/platter-herbarium
Caspar Ratzenberger	1556–1592	Naturkundemuseum Ottoneum, Kassel	*Aloe*	none
Leonhard Rauwolf (Vols. 1–3)	1560–1563	Herbarium L, Naturalis Biodiversity Center, Leiden	*Opuntia*	none
Hieronymus Harder	1576–1594	„Herbarium Vivum", Bayerische Staats-biblitothek München	*Sedum, Hylotelephium*	München: https://bildsuche.digitale-sammlungen.de/index.html?c=viewer&bandnummer=bsb00011834&pimage=00001&v=150&nav=&l=de
Caspar Bauhin	(1577?–) 1579–1624	University of Basel, Basel	*Opuntia, Sedum, Yucca*	none

Fig. 3. Flowering *Aloe vera* in the herbarium of Ulisse Aldrovandi (volume 3, fol. 21). (http://137.204.21.141/aldrovandi/Explore, Università degli Studi di Bologna, Sistema Museale di Ateneo, permission granted for educational use).

Fig. 4. Contemporaneous specimen of a flowering *Aloe* in the herbarium of the Sukkulenten-Sammlung Zürich (ZSS 312: *Aloe* sp. aff. *officinalis,* Collenette 5481: Saudi Arabia, Jabal Radhwa, 1950 m, prepared from cultivated material ZSS 85 3914 /0, 9. June 1989).

Standard preparation techniques for succulents

Clearly, drying the voluminous leaves, stems and/or roots of succulent plants with their extensive water-storage tissue needs careful preparation techniques – over the past forty years a number of publications have described specific approaches and methods, and herbarium management manuals (e.g., Bridson and Forman 1998, Victor et al. 2004) usually have at least a short section on handling succulents. Two main problems in preparing conventional dry pressed specimens have to be addressed: **a** The plant tissue should be killed quickly to enable rapid desiccation – succulent plants have evolved numerous adaptations to cope with water stress, and to conserve stored water over prolonged periods of time, and can survive for months in herbarium presses. **b** Drying of the killed pressed material should be quick and thorough to prevent microbial decay, which can start within 48 hours especially in warm and humid climates.

Fig. 5. Sterile *Aloe vera* in the herbarium of Caspar Ratzenberger, with added lumps of dried *Aloe* exudate (Volume 3, fol. 401). (Courtesy Naturkundemuseum Kassel)

Baker et al. (1985) and De Groot (2011) provided short summaries of the techniques advocated in the literature for rapidly killing the plant tissue, focusing on stem succulents: After

Fig. 6. *Opuntia ficus-indica* with immature fruits from the herbarium of Ulisse Aldrovandi (volume 5, fol. 201). (http://137.204.21.141/aldrovandi/Explore, Università degli Studi di Bologna, Sistema Museale di Ateneo, permission granted for educational use)

Fig. 7. *Opuntia ficus-indica* with a separated flower from the Herbarium Rauwolf, Vol. 1. (Courtesy Naturalis Biodiversity Centre)

slicing specimens vertically and horizontally, and possible removal of the bulk of the succulent tissue, the material can be immersed into an ethanol bath for 24–48 hours, or frozen, thawed and then blotted, boiled and then blotted, or ordinary salt or borax can be liberally applied to the cut surfaces which is then blotted before conventional pressing. A further approach to kill plant tissues rapidly is the use of a microwave oven [first briefly mentioned by Fuller and Barbe (1981), then described in more detail by Leuenberger (1982)]. For stem succulent Euphorbias, Leach (1995) advocates first boiling the material, pressing it, and to „paint" it with petrol to control decay, while for the stem succulent Asclepiads and leaf-succulent Aloes, he suggests to first immerse the material in a petrol bath. Burgoyne and Smith (1999) suggest a combination of freezing the freshly collected material with subsequent thawing using the „defrost mode" of a microwave oven. Reyes-Agüero et al. (2008) advocate to spray the cut surfaces of *Opuntia* cladodes with 70 % formaldehyde and leaving them to dry exposed to direct sun for two to three hours prior to conventional pressing.

For pressing and drying of the specimens, conventional herbarium presses are universally suggested, with ample use of blotters and cardboard or plywood layers; Eggli and Leuenberger (1996) and De Groot (2011) in addition suggest interspersing sheets of perforated or corrugated aluminium sheets. Presses can then be placed in the sun or another warm and dry place (including on gas stoves, Fig. 2, only recommended with great care), with frequent change of humid blotters and cardboards. De Groot (2011) advocates using „a conventional herbarium specimen dryer" without further details, while Reyes-Agüero et al. (2008) use a „forced-air furnace at 85–90°C". Eggli and Leuenberger (1996) described an easily portable method that provides forced warm air circulation using a small hair dryer and a semi-air-tight bag. With this latter method, specimens can be dried within 24 hours in dry climates, without any pretreatments apart from cutting the plants into manageable parts and removing the bulk of succulent tissue, and without need to change blotters or papers. For processing larger numbers of specimens, a comparative setup using room or industrial electric heaters is a good option.

Apart from conventional pressed specimens, succulents can also be successfully preserved as spirit specimens or „carpological" specimens, such as voluminous dried plant bodies or part of bodies. Most herbaria prefer conventional sheet specimens, however, because of volume considerations and ease of handling and preservation.

Succulents in Renaissance Herbaria

Renaissance botanists had none of these commodities, as just described, available. Nonetheless, they were not afraid of handling native juicy stonecrops, or exotic leaf succulents and spiny cacti, as witnessed by the specimens in the surviving early herbaria (see Baldini et al. 2022 for a list of extant 16th century herbaria). We carried out a non-exhaustive search for succulents present in these precious collections as far as available in digital form, or on the base of published inventories. Here, we discuss a few selected examples to highlight how Renaissance botanists met the challenge of making informative herbarium specimens that allow us today to reconstruct early gain of succulent plant knowledge (see table 1 for list of Herbaria).

Aloe vera (Asphodelaceae; syn. Aloaceae; a cultivar not known from the wild; the closely related *A. officinalis* is native to Saudi Arabia and the Yemen): Specimens of flowering *Aloe* are present in the herbaria of Ulisse Aldrovandi (Fig. 3), Francesco Petrollini (formerly known as „Herbario Cibo" or „Rome Herbarium", cf. Stefanaki et al. 2019, Baldini et al. 2022) and in the so called Mendoza herbarium, and a sterile specimen is present in the herbarium of Caspar Ratzenberger (Fig. 5) (Urs Eggli et al., pers. comm.). *Aloe vera* was used medicinally since at least the Greco-Roman period and is described and illustrated in very numerous medieval manuscripts as well as Renaissance books. It was cultivated in Europe at least since the 1530s, likely having been introduced from the Arabian Peninsula or the Near East (Grace et al. 2015). The flowering specimens in the herbaria of Aldrovandi and Petrollini were preserved in the period between 1551 and 1553, and that in the Mendoza herbarium at some unknown time between 1539 and 1554. Surprisingly, it took at least some 10 years before illustrations of flowering *Aloe* were published independently but almost simultaneously by Marini (1562) and Mattioli (1562). The specimen in the Mendoza herbarium is broken and fragmentary, but the specimens of Aldrovandi and Petrollini give a good idea of the plants then cultivated. Their quality compares favourably with modern herbarium specimens (Fig. 4), testifying the ability of their makers to deal with the juicy mucilaginous leaves. The available illustrations of the specimens do not permit a judgement whether complete leaves were pressed, or whether the lower face and the water-storage tissue was cut away before pressing.

The specimen in the Ratzenberger herbarium (Fig. 5) is notable for two reasons: Firstly, an entire young plant (judged by the size), including stem and roots was pressed and mounted. Secondly, Ratzenberger added two samples of dried *Aloe* exudate (the form in which *Aloe* was traded for medical applications), together with a long note excerpted from Garcia de Orta (1567) or a later edition of that work.

Fig. 8. *Opuntia ficus-indica* from the Herbarium Bauhin, BAS B05-015. This specimen is notable since part of the vascular system has been prepared and mounted separately. (University of Basel, Herbaria Basel (BAS), CC BY 4.0)

Fig. 9. *Yucca gloriosa* cf. with flowers from the herbarium of Caspar Bauhin (BAS-B02-111), ex cult. London (without date) & Paris (1614). (University of Basel, Herbaria Basel (BAS), CC BY 4.0)

Fig. 10. *Sedum album* from the herbarium of Caspar Bauhin (BAS-B08-047), collected from roofs in Basel, without date. (University of Basel, Herbaria Basel (BAS), CC BY 4.0)

Fig. 11. *Sedum album* on a page from the „Herbarium Vivum" of Hieronymus Harder with several specimens of Crassulaceae: *Sedum album* top row middle and right, *S. acre* bottom left and *Hylotelephium telephium* (bottom right) plus *Saxifraga paniculata* cf. (top row left). (Bayerische Staatsbibliothek, Cod. Icon 3, fol. 11v (scan 45), https://www.digitale-sammlungen.de/de/view/bsb00011834; Creative Commons BY-NC-SA 4.0)

Opuntia ficus-indica (Cactaceae; since ancient times widely cultivated as crop in Mexico, and now an invasive neophyte elsewhere): The prickly pear cactus was observed growing in Rome as early as 1549 by Johannes Kentmann (Eggli et al. 2018), and Ulisse Aldrovandi observed it, also in Rome, in 1550 and 1553 near Pisa (Soldano 2000, Soldano and Borgi 2007, Stefanaki et al. 2021). North of the Alps, Conrad Gessner was likely the first who cultivated this species; he received his material in 1558 from Italy (Eggli 2019). Material in the herbarium of Aldrovandi (Vol. 5, p. 200.1 and 200.2, sterile specimens; p. 201, specimen with 4 immature fruits; Fig. 6), is dated to 1553 by Soldano and Borgi (2007: 8) and Stefanaki et al. (2021: 454). A sterile specimen is also present in the „Erbario A" (Stefanaki et al. 2021: 455), and a specimen with a flower, prepared in southern France between 1560 and 1562, is conserved in the herbarium of Leonhard Rauwolf (Stefanaki et al. 2021; Fig. 7). A further sterile specimen is present in the Bauhin herbarium, is without provenance details, and was prepared at some unknown time between 1577 and 1624. This specimen is notable because part of the vasculature was pressed separately (Fig. 8).

The specimen in the Ulisse Aldrovandi herbarium appears to be the oldest extant specimen of *Opuntia ficus-indica.* Aldrovandi described the difficulties of preparing *Opuntia* for the herbarium in a letter in 1553 to Pietro Andrea Mattioli (Soldano 2002: 62–63), which roughly translates as follows: „… these leaves are more juicy than those of the terrestrial *Aloe.* I cut the leaf in half … and cut out the juice, but the quantity of humidity was such that I could not preserve its natural colour, despite I worked with great care and changed the paper in which they were placed every day for 7 or 8 times". Whether these remarks apply to the very specimens present in his herbarium (Fig. 6) is unclear, but they are a vivid description of the necessary pretreatment of the stem segments and the difficulties to dry the material quickly without artificial heat.

Yucca species (Agavaceae / Asparagaceae: Agavoideae): A very well prepared specimen of a *Yucca* species (determined as *Y. gloriosa* by an unknown hand; *Y. gloriosa* is widespread in the E USA) is present in the Bauhin herbarium. According to the labels, it is a composite specimen, partly from the garden of „D. Cargillus", London (James Cargill (c. 1565–1616), a student of Caspar Bauhin in Basel), and the longer leaf supplied 1614 by „D. Burserus" (likely Joachim Burser, who was a student of Caspar Bauhin in Basel) from Paris („Lutetia") (Fig. 9). We know from Ewald (1995, citing Thacker 1979) that *Yucca gloriosa* was first introduced to England in 1593. Gerard (1596) mentions that he cultivated material in his garden, and later (Gerard 1597) gave a more detailed account including a woodcut of a sterile plant. The first illustrations of a flowering *Yucca* cf. *gloriosa* were published by L'Obel (1605), Aldini (1625) and Parkinson (1629: 435). No other specimens of *Yucca* have been located in Renaissance herbaria (A. Stefanaki, pers. comm. November 2022), and the specimen in the Bauhin herbarium is thus the earliest extant *Yucca* specimen.

Sedum album (Crassulaceae; widespread throughout Europe): Species of the genera *Crassula, Hylotelephium, Sedum, Sempervivum* and *Umbilicus* (all Crassulaceae) are native to Europe, and accordingly, specimens of these appear frequently in Renaissance herbaria. By way of example, and to show the particular difficulties of pressing herbs with relatively small succulent leaves, we refer to the various approaches favored by different botanists with the help of specimens of *Sedum album:* The specimen from the Bauhin herbarium (Fig. 10) shows the common condition that the succulent leaves in their majority fall off in the pressing and drying process. One way of overcoming the problem is to add an illustration cut from a printed book, as Bauhin commonly did (Fig. 10). Another and rather innovative solution was implemented by Hieronymus Harder, who added the missing leaves of *Sedum album* in

Fig. 12. *Hylotelephium telephium* from the herbarium of Felix Platter (Vol. 6, page 373). (Burgerbibliothek Bern, https://www.burgerbib.ch/de/bestaende/privatarchive/einzelstuecke/platter-herbarium; Public Domain Mark 1.0)

the form of colour drawings (Fig. 11, upper right). The same herbarium page also has a specimen of *Hylotelephium telephium* with similarly added leaves and tuberous roots, but the stem and inflorescence now missing (Fig. 11, lower right), as well as a depauperate specimen devoid of leaves of *Sedum* cf. *acre* (Fig. 11, lower left). On the other hand, the herbarium of Felix Platter includes some very diligently prepared specimens with part or all of the leaves present (Fig. 12) – one wonders how Felix Platter achieved this quality with the equipment available at his time: Producing such quality of specimens is only possible by killing the tissues rapidly before abscission layers form. But whether Felix Platter killed his plants by using hot water, or perhaps placed the tightened herbarium press on a well-heated tiled stove, remains unknown.

Conclusions

Specimens of the exotic succulents *Aloe vera* and *Opuntia ficus-indica* appeared almost concurrently in the 1550s in several of the 16th century herbaria. In contrast, the first specimen of *Yucca gloriosa* cf. is some 50 years younger, in parallel to its supposed later introduction into cultivation. The early specimens of these exotic succulents together with those of the native European *Sedum album* show the ability of Renaissance botanists to successfully deal with plants difficult to press for the herbarium. At the same time, these renaissance specimens provide an interesting possibility to learn more about the introduction of hitherto unknown succulents into European horticulture.

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Jurriaan de Vos kindly provided a list of specimens of succulent plants in the Bauhin herbarium Basel. Anastasia Stefanaki (University of Utrecht) kindly checked for specimens of *Opuntia* and *Yucca* in numerous Renaissance herbaria. We further gladly acknowledge the help of Adriano Soldano with details of the correspondence between Aldrovandi and Mattioli on *Opuntia*.

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Plant exchange networks in the 19th century – 200 years of citizen science

Christof Nikolaus Schröder

Plant exchange networks in the 19th century have been investigated in a large-scale study, firstly by identifying as many plant exchange organizations (PEOs) as possible and secondly by searching for exchange partners in a 19th century private herbarium from Southwest Germany, and by analysing exchange activities related to the rare central European endemic *Saxifraga rosacea* subsp. *sponhemica* (C.C.Gmel) D.A.Webb. In this paper a first overview on selected results is given: 101 PEOs – founded from 1819 to 1947 – with a total of 3000 to 5000 members have been found; they distributed 15 to 20 million specimens; 111 collectors have been identified in the exemplary private herbarium, from which specimens have been found in 27 herbaria; *S. rosacea* subsp. *sponhemica* has been collected by 242 individuals, 233 exchange partners received duplicates distributed by 12 PEOs.

Keywords
Database, Herbaria, Networks, Plant exchange, *Saxifraga sponhemica*, 19th Century

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Herbarium specimens are not only documents of biodiversity, but also historical sources, collected by various people, from a day labourer to a judge at a High Court. They are made to be preserved for a long time, in contrast to daily correspondences, which are archived only if the sender or recipient was an important historical person, e.g., Linnaeus. Therefore, herbaria reveal social networks hardly visible in correspondences.

During decades of work in herbaria we became aware of stamps, printed labels, hand written annotations and cryptic abbreviations (Schröder 2019) indicating that a specimen has passed through several hands until it arrived at the institutional herbarium where it is hosted today. Exchange of herbarium specimens between individuals is well investigated (Groom et al. 2014), but increasingly we gained the impression, that there existed a well-organized plant exchange network driven by clubs, societies etc. as well. We could find few studies only, dealing with a very limited number of organizations (Foster 1979; Robin 2004, 2006; Bange 2012; Groom et al. 2014), but we identified several organizations, regularly mentioned on labels but not listed in the current literature. We therefore established a study focusing on exchange activities managed by organizations dedicated to the exchange of dried plants (herbarium specimens).

As a first step we intended to discover where and how many organizations dedicated to the exchange of plants sensu latissimo (incl. Cryptogams, Algae, etc.) were established during the years 1819 to 1947. Then we looked for two appropriate examples, one concerning an individual person, actively collecting and exchanging specimens, and one concerning a plant species intensively collected and exchanged during the period of time we are focusing on (19th century). Here we present a first brief overview on selected results. A monograph with all results in detail is planned for late 2023.

Fig. 1. Stamps of the Association (Société) Pyrénéenne pour l'échange des plantes (CHE015821) and the Watson Botanical Exchange Club (BIRM 025119).

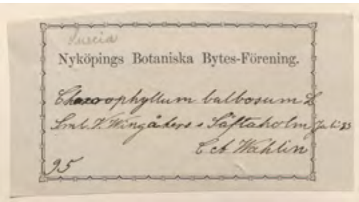

Fig. 2. Printed label of the Nyköpings Botaniska Bytes-Förening (CHE005000).

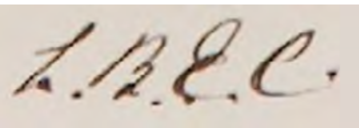

Fig. 3. Hand written abbreviation „L.B.E.C." on a specimen exchanged by the London Botanical Exchange Club (BIRM 009596).

Material and methods

Definition of „plant exchange organization" (PEO)

Several types of organizations have been established in the past to facilitate exchange of herbarium specimens. One type was a kind of stock corporation, issuing shares to finance expeditions. Shareholders received a pre-defined number of specimens for each share after fortunate return of the collectors (e.g., „Unio Itineraria", Wörz 2016). A different type was the classical botanical society, holding meetings, organizing excursions, publishing a journal, and exchanging more or less small numbers of specimens on the sideline, usually at meetings. However, there have been a lot of organizations primarily or more often exclusively dedicated to plant exchange. In our project we define a real plant exchange organization (PEO) by three properties:

- exchanges solely of plants for plants (i.e., not plant for butterfly etc.)
- „pro mutua commutatione" = mutual exchange
- no commercial or financial interest (i.e., not for money)

Principally, there are two corpora of sources which have to be examined when searching for PEOs: herbaria and literature.

Herbaria: Most PEOs marked specimens when preparing them for exchange, either with stamps (Fig. 1), printed labels (Fig. 2), or sometimes with hand written abbreviations (Fig. 3), but there are cases without any indication of the PEO, like Opiz' Anstalt in Prague. Not all databases store information about PEOs involved in the exchange of a specific specimen, but there are a few very helpful exceptions like Herbaria@home (Botanical Society of Britain & Ireland, herbariaunited.org), where clubs and societies are recorded as „collectors", „com" and „ex herb". The database of the Muséum national d'histoire naturelle at Paris allows search for collections, unfortunately not in the search form, but in an URL like „https://science.mnhn.fr/all/list?originalCollection=societe". Others store information on the provenance of a specimen in non-searchable fields like „annotations" (e.g., jacq.org).

We found the first records of PEOs by chance during our daily herbarium work when we noticed several stamps on the labels. For this study we used all available methods to systematically search digital repositories for relevant strings like „exchange club", „Tauschverein", „échange" etc.

Literature: Within the last two decades large amounts of literature have been digitized and made available. The most important repository for bioscience is The Biodiversity Heritage Library (biodiversitylibrary.org). Several national or state libraries run similar projects, without restriction to bioscience, like the Bayerische Staatsbibliothek of Munich (bsb-muenchen.de), the Bibliothèque nationale de France (gallica.bnf.fr) or the Norwegian Nasjonalbiblioteket (nb.no). They provide not only digitized books, but newspapers, magazines and journals as well. We carried out full text searches in these repositories as well as in GoogleBooks (books.google.com).

In a second step we made two approaches to analyse and depict exchange activities: Firstly, we used an average size private herbarium of the 19th century and secondly, we analysed a rare Central European species, just described at the beginning of the 19th century.

The Bochkoltz-Herbarium: missing for 140 years and re-discovered

Wilhelm Christoph Bochkoltz (1810–1877) belonged to a bourgeois family in Trier (Southwest Germany). He studied Chemical Engineering in Metz and Paris. As a Civil engineer he was director of steel works, retired 1858, and after that – he was unmarried –, dedicated himself to nothing else but botany. Bochkoltz was one of the most important collectors of *Saxifraga rosacea* subsp. *sponhemica* (see below). His private herbarium was missing for 140 years, and we re-discovered it by accident in the herbarium of Heidelberg University (HEID) in late 2016. It comprised ca. 10 000 specimens, about half of them collected by himself, the other half acquired by exchange. He contributed to several series of exsiccata. In 2017 to 2018 a sample of 723 Bochkoltz specimens in HEID has been checked for collectors, revisors, exchange partners etc. in the so called „Old Herbarium" (pre-World War II-collections): all Cryptogams and Gymnosperms, two cabinets in the Angiosperm collection completely, and some further families due to our personal scientific interest, e.g., Saxifragaceae. Additionally, digital repositories have been searched for Bochkoltz-specimens.

Saxifraga rosacea subsp. *sponhemica* (C.C.Gmel.) D.A.Webb — a rare Central-European endemic

In the year of 1787 Carl Christian Gmelin (1762–1837) discovered an undescribed Saxifrage (Fig. 4) in Southwest Germany (Schröder 2023). In 1806, he published this novelty under the name *Saxifraga sponhemica* (Gmelin 1806: 224). Most modern floras accept the name *Saxifraga rosacea* subsp. *sponhemica* (C.C.Gmel.) D.A.Webb (Schröder 2023). This cespitose *Saxifrage* is a rare Central-European endemic with a very limited distribution and a disjunct areal (Decanter et al. 2020). As a glacial relict it grows on scree slopes facing from Northwest to Northeast, ideally above streams or small rivers. It does not tolerate full sun, but it is threatened by too much shadow as well. Some populations are currently endangered by shrubs, trees, and especially blackberries, benefitting strongly from atmospheric nitrogen impact.

Fig. 4. *Saxifraga rosacea* subsp. *sponhemica* in the valley of river Nahe (South-West Germany), CNS 2020/102, 2020-05-27.

Plant hunters from all Europe began to search for new localities of this desirable rarity and collected a large number of specimens, which were intensively exchanged by individuals as well as exchange clubs. Nowadays, specimens are found in many herbaria. As *S. rosacea* subsp. *sponhemica* was published shortly before the first plant exchange club was founded, and thanks to its rarity, it seems to be a good taxon to study exchange activities: the expected number of specimens is limited and it was immediately a focus of exchange clubs.

It has been collected, published, or stored under several names, like *S. affinis* D.Don, *S. aggregata* Lej., *S. c(a)espitosa* L. et subspp., *S. condensata* C.C.Gmel., *S. confusa* Lej., *S. decipiens* Ehrh. et subspp., *S. drucei* E.S.Marshall, *S. gmelinii* Host, *S. hartii* D.A.Webb, *S. hibernica* Haw., *S. hirta* Sm., *S. hypnoides* L. et subspp., *S. incurvifoli*a D.Don, *S. multifida* Rosbach, *S. palmata* Sm., *S. rosacea* Moench, S. *sponhemica* C.C.Gmel., *S. sternbergii* Willd. All these names have to be checked searching for specimens and references of *S. rosacea* subsp. *sponhemica.*

Within the years 2019 to 2022, 44 herbaria have been checked for specimens of *S. rosacea* subsp. *sponhemica*, 13 of them on site (B, BNL, HAL, HEID, JE, M, MSTR, NHV, SAAR, STU, W, WU & Herb. C.N.Schröder; acronyms according to Thiers 2022), the others digitally (naturalis.nl, jacq.org, gbif.org, mnhn.fr, recolnat.org, etc.) using the species search with the search string *„sponhemica"*. Fortunately, only one species with this epithet has been published. Beyond that we searched for specimens cited in publications and references, using the digital libraries listed above.

Technical Notes

The backbone of the project are two relational databases (MySQL) with PHP-scripts as frontend, one for *Saxifraga rosacea* subsp. *sponhemica* and one for the herbarium Bochkoltz. The first is composed of three main modules: specimens, persons & institutions, and bibliography. The Bochkoltz database has a highly normalized design to store collecting events and specimens coming from these events. A module for Bochkoltz-localities has been implemented but not yet filled with data. For collectors a relation to the persons module of the *Saxifraga rosacea* subsp. *sponhemica* database is implemented but not yet completely assigned for all datasets. The databases are hosted by a commercial service provider.

Two WikiProjects proposed a new Wikidata property „CNS-flora ID" (P10219). This was accepted by the community and implemented in December 2021. Subsequently we created Wikidata elements for all individuals and organizations in the database if not yet existing.

Results and Discussion

Plant Exchange Organisations (PEOs)

To our surprise we could identify no less than 101 PEOs (Fig. 5, Table 1 and 2), represented by digital specimens, exchange catalogues or cited in literature.

The first one was founded in the year 1819 (the letter of invitation was sent in 1818) by Philipp Maximilian Opiz (1787–1858) in Prague, the „Pflanzen-Saamen- und Insekten-Tausch-Anstalt" (Opiz 1818) with 36 founding members from Central Europe. In the last year of activity, this organization had 856 members worldwide (Opiz 1858). It was likely the largest organization, the smallest one we found was the Société d'échanges à Vierzon with eleven members and 233 numbers in the catalogue 1904 (Anonymous 1905: 17). Taking into account that some collectors were members in more than one PEO, we estimate the total number of collectors organized in PEOs with between 3000 and 5000. The largest PEOs distributed in total nearly two million specimens each, the smaller a few thousands only (Table 1).

With the Société d'Échange des Micromycètes in 1947, the last PEO was established, and around 2015 the last surviving organization, the Société pour l'Échange des Plantes Vasculaires de l'Europe et du Bassin Méditerranéen, established 1911 as Société Française pour l'échange des plantes vasculaires at Versailles, terminated with their dissolution two centuries of intensive plant exchange.

PEOs distributed a total of about 15 to 20 million specimens. Their members accumulated personal herbaria containing between some thousands and up to three million (Herbarium Roland Napoléon Bonaparte; cf. Anonymous 2022) specimens, exceeding all institutional herbaria of their time. Only a few members were professional academic botanists, most members had completely different professions: pharmacists, catholic priests, protestant pastors, teachers, entrepreneurs, judges, civil servants, day labourers, etc. – citizens of all kinds.

Table 1. Examples for the number of specimens exchanged by PEOs.

PEO	duration of activity	total of specimens exchanged
Wiener Botanischer Tauschverein	1845–1914	1'800'000
Pflanzen-, Samen- und Insekten-Tausch-Anstalt (Prague)	1819–1857	1'700'000
Den botaniske Forening i København	1848–1905	750'000
Botanischer Verein von Elsass-Lothringen	1880–1887	150'000
Malmö botaniska förening	1868–1871	3'000

Table 2. 101 plant exchange organizations, with year of founding, and place, if not part of the name.

1819	Pflanzen-Tausch-Anstalt in Prag (CZ)
1825	Apotheker-Verein in Norddeutschland, Botanische Tauschanstalt, Herford (DE); Süddeutsche Pflanzen-Tauschanstalt, Tübingen (DE)
1830	Botaniska Bytes-Sällskapet, Uppsala (SE)
1832	Botanischer Tauschverein, Erfurt (DE)
1836	Botanical Society of London (GB); Botanical Society of Scotland, Edinburgh (GB)
1840	Botaniske Forening i København (DK)
1842	Comptoir d'échanges botaniques, Strasbourg (FR)
1843	Stuttgarter botanische Tauschanstalt, Stuttgart (DE)
1844	Den botaniske Forening i København (DK); Skandinavisk-botaniske Bytteforening, Danske Afdeling, København (DK); Società di cambio di piante secche, Pisa (IT)
1845	Botanischer Tauschverein in Arnstadt (DE); Botanischer Tauschverein in Wien (AT); Botaniska Sällskapet i Götheborg (SE); Leipziger botanischer Tauschverein (DE)
1852	Upsala Botaniska Bytesförening (SE); Wiener Tausch-Herbarium (AT)
1854	Foreign Exchange Club, London (GB)
1856	Tausch-Verkehr mit mikroskopischen Präparaten, Gießen (DE)
1857	Botanical Exchange Club of the Thirsk Natural History Society (GB); Kryptogamen-Tauschverein, Gießen (DE)
1858	Botanischer Tauschverein [L. Fuckel], Nassau an der Lahn (DE); Botanischer Tauschverein ‹Trilobiten›, Praha (CZ); Lunds Botaniska Förening (SE)
1859	Botaniska Bytesföreningen i Strängnäs (SE); Stockholms Lycei Botaniska Bytesförenig (SE)
1862	Schlesischer Botanischer Tauschverein, Wroclaw (PL)
1863	Norrköpings botaniska bytesförening (SE); Société d'échanges Vogéso-rhénane, Mulhouse (FR)
1865	Jönköpings botaniska förening (SE); Kristianstads botaniska förening (SE)
1867	Botaniska föreningen i Carlskrona (SE); Kalmar botaniska förening (SE); Sällskapet Linnæas botaniska bytesförening, Karlstad (SE)
1868	Berliner Botanischer Tauschverein (DE); Botaniska Bytesföreningen ‹Rosa›, Visby (SE); Malmö botaniska förening (SE)
1869	Falun Botaniska Bytesförening (SE); Helsingfors botaniska bytesförening, Helsinki (FI)
1870	Schweizerischer Botanischer Tauschverein, Zürich (CH); Société Helvétique pour l'échange des plantes, Neuchâtel (CH); Tauschverein für Deutschlands Pflanzen, Königsberg (PU)
1872	Christiania botaniske Bytteforening, Oslo (NO); Nyköpings Botaniska Bytes-Förening (SE); Sociedad Botánica Barcelonesa (ES)
1873	Association rubologique, Lille (FR); Société dauphinoise pour l'Échange des plantes, Grenoble (FR)
1875	Société d'échange pour l'avancement des sciences naturelles, Cannes (FR)
1876	Növény-csereegylet Budapesten (HU)
1878	Deutscher Botanischer Tauschverein, Annen in Westfalen (DE); Société botanique rochelaise pour l'échange des plantes françaises, La Rochelle (FR)
1879	Comptoir parisien d'échange de plantes, Paris (FR); Internationaler botanischer Tauschverein, Berlin (DE); Nya Elementarskolans Botaniska Bytesförening, Stockholm (SE); Rheinischer Tauschverein, Wiesbaden-Biebrich (DE)
1880	Botanischer Verein von Elsass-Lothringen, Wasselonne (FR)

1882	International Botanical Exchange Club ‹Linnæa›, Lund (SE)
1883	Botanischer Tauschverein für Baden, Freiburg im Breisgau (DE); Botanischer Tauschverein in Sondershausen (DE); Europäischer Botanischer Tauschverein, München (DE)
1884	Botaniska Bytesförbundet Falun (SE); Malmö Botaniska Bytesförening (SE); Watson Botanical Exchange Club, York (GB)
1887	Linköpings Botaniska Bytesförening (SE); Thüringischer Botanischer Tauschverein, Schulpforte (DE); Västerviks botaniska bytesförening (SE)
1888	Botanical Exchange Club, Washington, D.C. (US); Bytesföreningen Flora, Uppsala (SE)
1890	Association Pyrénéenne pour l'échange des plantes, Foix (FR); Società Italiana per scambio di piante, Palermo (IT)
1891	Société pour l'Étude de la Flore Franco-helvétique, Paris (FR)
1892	Bryologischer Tauschverein, Annen in Westfalen (DE)
1893	Botaniska Bytesföreningen VIOLA, Kalmar (SE); Exchange Club of the Botanical Seminar of the University of Nebraska, Lincoln (US); Sandberg's Botanical Exchange Bureau, Minneapolis (US); Société du Sud-Est pour l'échange des plantes, Crémieu (FR)
1894	Stockholms Botaniska Bytes-Förening ‹Floras Vänner› (SE)
1895	Norsk botanisk Bytteforening, Sandefjord (NO)
1896	The Moss Exchange Club, Saintfield (GB)
1897	Botanische Tauschanstalt am Jurjew'schen Botanischen Garten, Tartu (EE); Glumaceen-Tauschverein, Annen in Westfalen (DE); Wiener Kryptogamen-Tauschanstalt (AT)
1898	Prager Botanische Tauschanstalt (CZ)
1899	Tauschvermittlung für Herbarpflanzen, Berlin (DE)
1901	Société cénomane d'exsiccata, Le Mans (FR)
1903	Nürnberger Botanischer Tauschverein (DE)
1904	Österviks botaniska bytesförening (SE); Société d'échanges à Vierzon (FR)
1905	Canadian Botanical Exchange Bureau, St. Thomas (CA); Stettiner Vermittlungsanstalt für Herbarpflanzen, Szczecin (PL)
1906	Botanisk bytesförening vid Göteborgs latinläroverk (SE)
1907	Internationale Botanische Tauschanstalt zu Weimar (DE)
1911	Société Française pour l'échange des plantes vasculaires, Versailles (FR)
1913	Upsala Nya Botaniska Bytesförening (SE)
1914	American Botanical Exchange Bureau, Houston (US)
1920	Botanisk Bytteforening i København (DK)
1937	Société d'échanges Pteridophyta exsiccata, Paris (FR)
1947	Société d'Échange des Micromycètes, (FR); Société d'Échange des Muscinées, Saint-Étienne (FR)

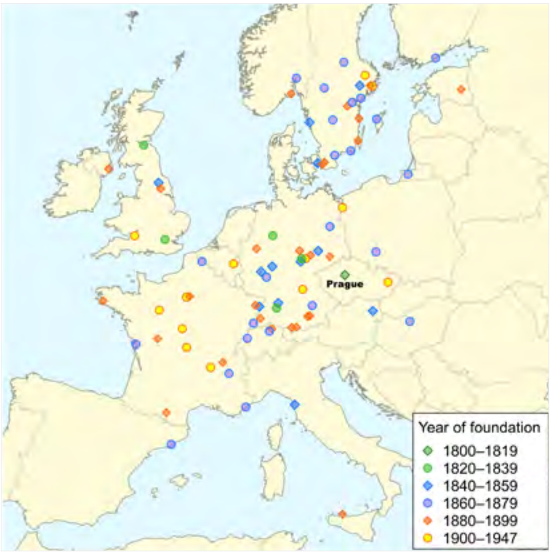

Fig. 5. PEOs by year of foundation. Not on the Map:
Botanical Exchange Club, Washington, D.C. (US, 1888);
Exchange Club of the Botanical Seminar of the University of Nebraska, Lincoln (US, 1893);
Sandberg's Botanical Exchange Bureau, Minneapolis (US, 1893);
Canadian Botanical Exchange Bureau, St. Thomas (CN, 1905);
American Botanical Exchange Bureau, Houston (US, 1914).

Fig. 6. Domiciles of collectors in herb. W. C. Bochkoltz and herbaria with specimens leg. Bochkoltz; not on the map: Herbarium US. PEOs only existing within the lifetime of Bochkoltz.

Wilhelm Christoph Bochkoltz

As a member of the Wiener Botanischer Tauschverein (WBT) Bochkoltz sent more than 1500 specimens to be distributed by the WBT. We identified, besides those in HEID, 79 Bochkoltz specimens in 27 herbaria: AMD, B, BM, FR, GJO, GOET, HBG, IBF, K, KONL, L, LD, LI, NAM, NHV, P, POZ, STR, STU, SZE, TLMF, US, W, WAG, WHB, Z (Fig. 6). We estimate, that he received an equivalent number of specimens from the WBT, which represent about one third of the specimens in his herbarium not collected by himself. Our sample revealed 111 collectors in his herbarium (Fig. 6), e.g., the young student Adolf Engler (1844–1930, author of „Die natürlichen Pflanzenfamilien" together with Karl Anton Eugen Prantl, 1887–1999 and „Das Pflanzenreich" 1900–1937), Carl Baenitz (1837–1913, editor of Herbarium Europaeum), and Anton Joseph Kerner (1831–1898, editor of Flora exsiccata Austro-Hungarica). His most important personal contact was Rupert Huter (1834–1919) who exchanged and sold large quantities of specimens from Tyrol, Dalmatia etc. (Fink et al. 2017), collected by himself and received from others. Bochkoltz had hundreds of specimens from Huter in his herbarium.

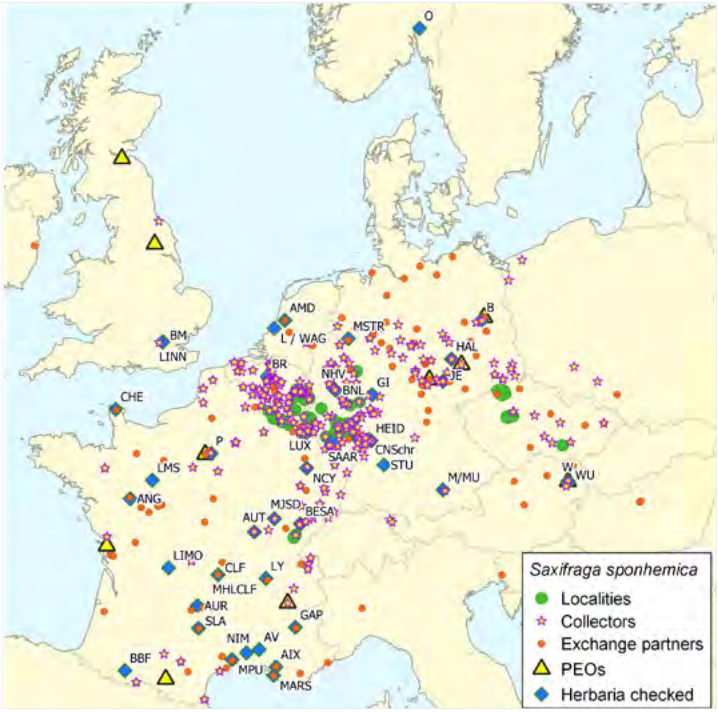

Fig. 7. *Saxifraga rosacea* subsp. *sponhemica* and exchange activities.
Shape files for this and maps in Fig. 5 and 6: Natural Earth. Free vector and raster map data@naturalearthdata.com. All maps: CNS using QGIS 3.4.

Saxifraga rosacea subsp. *sponhemica*

Specimens: We found 917 specimens (all Figs. as of 2022-11-30) of the *S. rosacea/sponhemica*-aggregate, 427 digitally and 490 on site. We determined that 649 (70.8.%) of them belong to *S. rosacea* subsp. *sponhemica*, 177 (19.3.%) of these originally had been determined as different taxa, mainly *S. c(a)espitosa* or *S. decipiens.* Conversely, 104 (11.3 %) specimens originally collected as *S. rosacea* subsp. *sponhemica* have been proven to belong to other taxa of cespitose Saxifrages. These specimens were collected for the most part at sites outside the distribution of *S. rosacea* subsp. *sponhemica.* We consider this is a consequence of the desire to find a new locality of this rarity, to increase the value of the own herbarium, and of the specimens sent to a PEO.

We could show that collecting and exchange activity started and increased about four decades later than publication activity (398 references published between 1806 and 2020 are recorded in the database). That is not surprising as the description of the new species had to be publicized before collectors could recognize it in the wild. Therefore, the peak of collecting was reached in the middle of the 19th century, declined at the turn of the 20th century, and completely collapsed during World War II, with one exception: Belgian botanists stayed very busy collecting *S. rosacea* subsp. *sponhemica* until the 1970s!

Within our dataset we identified 12 PEOs who exchanged specimens of *S. rosacea* subsp. *sponhemica,* four each in France and Germany – which is not surprising as most of the localities are situated in Germany, France, Belgium and Luxemburg (Fig. 7) –, and two each in Austria and Great Britain.

Collectors: Most collectors of *Saxifraga rosacea* subsp. *sponhemica* (242 individuals have been identified) lived near the initially discovered populations, but some enthusiasts travelled long distances to collect this rarity (Fig. 7). Exchange partners (233 individuals) who received specimens from PEOs or individuals usually lived more or less far away from the localities. Some recipients and collectors lived near institutional herbaria, and some of them may have bequeathed their collection to such a herbarium.

Conclusion

With thousands of active members, the 101 PEOs were a significant social and cultural phenomenon. With their tireless curiosity and relentless passion these early „citizen scientists" founded and accumulated the basis of institutional herbaria and digital repositories of the biodiversity data age, a treasure of inestimable value for research on future topics like biodiversity loss and climate change.

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Credits: Fig.1, CHE015821 & Fig. 2: RECOLNAT (ANR-11-INBS- 0004) – picturae – 2016, CC BY 4.0; Fig. 1, BIRM 025119 & Fig. 3: University of Birmingham Herbarium, Winterbourne House and Garden, with kind permission; Figs 4–7: CNS.

URL for further data (most pages currently in German only), specimens, references, biographies, stamps etc.: https://cns-flora.de/plantexchange/

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The collection of letters addressed to D.F.L. von Schlechtendal in the University herbarium in Halle (Saale), Germany (HAL)

Natalia Tkach and Martin Röser

D.F.L. von Schlechtendal (1794–1866) was one of the most important botanists of the 19th century. From 1833 to 1866 he was professor of botany at the University Halle-Wittenberg, where his collection of some 70 000 plant specimens is kept. Schlechtendal described more than 1600 new taxa, including 78 genera, mostly from the New World. Schlechtendal's dense network of scientific contacts is documented by his correspondence, comprising some 5600 letters he received from about 500 persons, including many famous contemporary botanists, natural scientists, travelers and plant collectors. The letters mostly refer to publications and scientific questions concerning the journals ‚Linnaea' and ‚Botanische Zeitung' edited by Schlechtendal. In particular, the letters of scientists dealing with African, Central and South American, and Australian plants are an important source of taxonomic information. The letters are mostly written in the old German Kurrent script, the ink is fading and the paper is disintegrating. We therefore have started to transliterate all letters (54 % completed), index and digitize them and make them available online. Here we explain their importance, highlighting letters dealing with the plants from Humboldt's and Bonpland's travels and from the correspondence with R.A. Philippi (Chile, 1808–1904) and H. Christ (Switzerland, 1833–1933).

Keywords
Botany, Herbarium Halle, Letters, Linnaea, *Pinus halepensis, Pinus maritima,* Scientific publishing

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The University Halle-Wittenberg emerged in 1817 under Prussian rule from the union of the University ‚Leucorea' founded in Wittenberg (Electorate of Saxony) in 1502 and the Friedrichs University founded in Halle (Electorate of Brandenburg) in 1694. The University herbarium in Halle (Index Herbariorum acronym: HAL) was also founded during this period. Director of the herbarium from 1833 was Diederich Franz Leonhard von Schlechtendal (1794–1866), who worked as professor of botany and director of the botanical garden until his death and was one of the most important botanists of the 19th century (Fig. 1). In the course of his scientific activity, Schlechtendal described and named for the first time about 1600 new plant taxa (genera, species, etc.), most of them from Central and South America (Heklau 1998, Heuchert et al. 2017).

Before his appointment as professor in Halle, he had served as first curator of the Royal Herbarium in Berlin (1819–1833) since his University education. Numerous sources show how he worked intensively throughout his life to increase the plant collections of the University Halle-Wittenberg. Above all, Schlechtendal acted through communication with renowned collectors and scientists on all continents, whom he asked for plant material, mostly in connection with scientific publications in the very important journals ‚Linnaea' (from 1826) and ‚Botanische Zeitung' (from 1843), which he edited and published, and in which very many descriptions of new plant species and genera were published. Schlechtendal showed great skill in this, so that

Fig. 1. Diederich Franz Leonhard von Schlechtendal. Photography from around 1866. Schlechtendal has his hand on a volume of the journal ‚Linnaea' he published and edited, which is written in capital letters on the spine. Original photograph is kept in the herbarium of the University Halle-Wittenberg.

in this way extremely important plant collections from Central and South America, Australia and Africa came to Halle.

Herbarium Halle under Schlechtendal's Directorship

Halle also owes Schlechtendal duplicates of numerous plant specimens from Berlin, his former place of work. This transfer of herbarium specimens from Berlin to Halle was actually born out of necessity. Schlechtendal was used to having a rich and well-organized herbarium for his scientific work in Berlin, which was not the case in Halle, especially because the important private plant collection of his predecessor in Halle, Kurt Polykarp Joachim Sprengel (1766–1833), could not be purchased for the University herbarium. The catalog of the University herbarium of 1825 contained only 4300 species. Shortly after taking office, Schlechtendal complained in a letter to the management of the University that the existing collection was „so astonishingly meager and deficient" and „does not remotely meet the requirements that one is entitled to make of such a collection in the present time" (Werner 1955: 775). Among other things, he suggested to ask the ‚Königliche Pflanzensammlung' in Berlin for duplicates, whereupon in the following years more than 1600 plant specimens arrived, among them many from the Willdenow herbarium. Carl Ludwig Willdenow (1765–1812) was director of the Royal Botanical Garden in Berlin from 1801 and one of the formative botanical research personalities of his time. In addition, Schlechtendal was also bequeathed an extremely extensive private herbarium by his father, Diederich Friedrich Karl von Schlechtendal (1767–1842), which also contained many specimens from the Willdenow collection, including in particular specimens from Alexander von Humboldt's and Aimé Bonpland's American voyage (1799–1804) (cf. Tkach et al. 2016, 2019).

Schlechtendal's private herbarium, which was sold to the University Halle-Wittenberg after his death by his widow in 1867, comprised about 70 000 specimens in the ordered part alone. Also sold to the University was Schlechtendal's extensive library of botanical works, which had been described by Heinrich Gustav Reichenbach (1824–1889) as the best private botanical library in Germany (Reichenbach's letter of 28 September 1861 in the Schlechtendal correspondence collection in HAL).

The herbarium of Schlechtendal formed the basis of the present herbarium of the University Halle-Wittenberg. It is very rich in type specimens, including not only those of the species newly described by Schlechtendal himself, but also those of many other botanical authors, including G. Bentham, P.E. Boissier, R. Brown, A.P. de Candolle, A. von Chamisso, C.F. Ecklon, A. Gray, A.H.R. Grisebach, C.F.F. Hochstetter, J.D. Hooker, K.S. Kunth, G. Kunze, J.J.H. Labillardière, C.F. von Ledebour, C.F. Lessing, C.F.P. von Martius, E.H.F. Meyer, F. Miquel, F.J.H. Mueller, C.G.D. Nees von Esenbeck, P.S. von Pallas, E.F. Poeppig, C. & J. Presl, H.G.L.

Reichenbach, A. Richard, C. Schkuhr, C.P.J. Sprengel, E.G. Steudel, C.L. Willdenow, C.L.P. Zeyher.

Funded by the ‚Global Plant Initiative' of the Andrew W. Mellon Foundation in the USA, type specimens and their associated data could be indexed and digitized to a large extent within the framework of a long-term project from 2008–2017. Currently, more than 15 250 type specimens have been identified and processed, which are available as part of the databases ‚JACQ Virtual Herbaria' and ‚JSTOR Global Plants' as high-resolution images with the detailed associated data on the Internet (JACQ Virtual Herbaria 2023, JSTOR Global Plants 2023).

Schlechtendal's Correspondence

The collection of Schlechtendal's correspondence with about 500 contemporaneous botanists comprises about 5600 letters. The list of senders reads like the ‚who is who' of the 19th century: P.E. Boissier, A.L.P.P. de Candolle, A. von Chamisso, J.F. Drège, A. Gray, J.C. von Hoffmannsegg, R.F. Hohenacker, W.J. Hooker, A. von Humboldt, G. Kunze, C.F.P. von Martius, F. Miquel, R.A. Philippi, E.F. Poeppig and many others are represented (Schubert 1964, Tkach et al. 2014).

Many botanists sent specimens of new plant taxa to Schlechtendal as gift for review and publication in the journals ‚Linnaea' or ‚Botanische Zeitung'. The specimens were usually accompanied by letters to Schlechtendal. There are letters with references to and discussions about many type specimens now held in HAL (Heuchert et al. 2017). In addition, the letters contain information on itineraries of collectors and buyers of plant collections, on the exchange of plant material and discussions on botany, publication activities, the management of botanical gardens, fundraising and academic matters. The importance of correspondence can be explained by the following three examples.

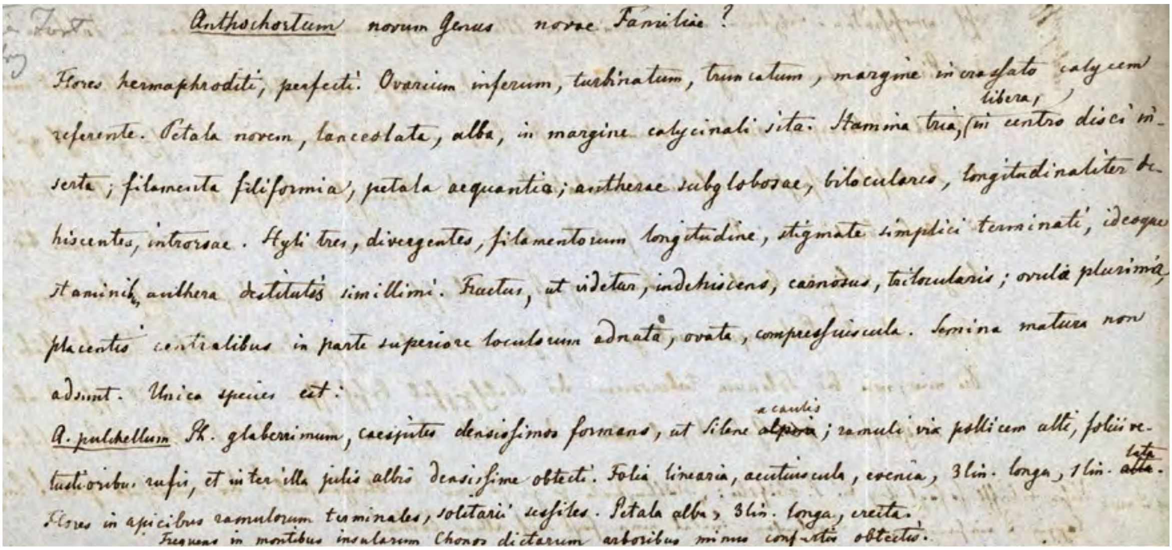
Synonymy of the new plant species from Humboldt's and Bonpland's voyage to America

It has long been known, and has often caused wonder (McVaugh 1955, Hiepko 2006), why there are so many plant names based on the above-mentioned collections of Humboldt and Bonpland published almost simultaneously by Joseph August Schultes and Johann Jacob Römer in Germany on the one hand and by Karl Sigismund Kunth in France on the other.

The background to this is the parallel processing of collections from the voyage to America, which Humboldt and Bonpland had sent in part to Willdenow in Berlin, but for the most part to the Muséum National d'Histoire Naturelle in Paris. After several unsuccessful attempts (with Bonpland and Willdenow), the latter were thoroughly examined and scientifically processed by Kunth on Humboldt's behalf starting in 1813.

The diagnoses of the plants of Humboldt and Bonpland published by Schultes and Römer had been written by Willdenow in Berlin and noted on the herbarium specimens. These were copied and provided to Schultes by D.F.K. von Schlechtendal (pat.). Schlechtendal (pat.) was a lawyer by profession and an enthusiastic naturalist with botanical preferences who had a close friendship with Willdenow (see above) and was in charge of Willdenow's herbarium after his death, as can be seen from a letter from Schultes to Schlechtendal (fil.) (6 June 1821, Landshut in Bavaria). Schlechtendal (fil.) was still chief curator of the Royal Herbarium in Berlin at that time.

The letter shows that the diagnoses for Humboldt's and Bonpland's plants were not written by Schultes and Römer themselves, but came from Willdenow and were sent to them by Schlechtendal (pat.). Furthermore, Schultes asked Schlechtendal (fil.) for additional information on Humboldt's and Bonpland's specimens in Willdenow's herbarium in Berlin and at the same time repeats the disapproval of Kunth voiced by many colleagues, in which certainly also the Prussian/German-French hostility resonates in the background.



Anthochortum novum Genus novae Familiae?
Flores hermaphroditi, perfecti. Ovarium inferum, turbinatum, truncatum, margine incrassato calycem referente. Petala novem, lanceolata, alba, in margine calycinali sita. Stamina tria, libera, in centro disci inserta; filamenta filiformia, petala aequantia; antherae subglobosae, biloculares, longitudinaliter dehiscentes, introrsae. Styli tres, divergentes, filamentorum longitudine, stigmate simplici terminati, ideoque staminibus anthera destitutis simillimi. Fructus, ut videtur, indehiscens, carnosus, trilocularis; ovula plurima, placentis centralibus in parte superiore loculorum adnata, ovata, compressiuscula. Semina matura non adsunt. Unica species est:
A. pulchellum Ph. glaberrimum, caespites densissimos formans, ut Silene acaulis; ramuli vix pollicem alti, foliis veluti oribus rufis, et inter illa pilis albis densissime obtecti. Folia linearia, acutiuscula, evenia, 3 lin. longa, 1 lin. lata. Flores in apicibus ramulorum terminales, solitarii sessiles. Petala alba, 3 lin. longa, erecta.
Frequens in montibus insularum Chonos dictarum arboribus minus confertis obtectis.

Fig. 2. Cut-off lower part of a letter sheet belonging to a letter from R.A. Philippi to Schlechtendal, dated 13 August 1857. The text is written in particularly careful, clear handwriting and was obviously intended to be passed directly to the typesetter. Schlechtendal's letter collection in the herbarium of the University Halle-Wittenberg.
The text reads: „*Anthochortum novum* Genus novae Familiae? Flores hermaphroditi, perfecti. Ovarium inferum, turbinatum, truncatum, margine incrassato calycem referente. Petala novem, lanceolata, alba, in margine calycinali sita. Stamina tria, libera, in centro disci inserta; filamen-ta filiformia, petala aequantia; antherae subglobosae, biloculares, longitudinaliter dehiscentes, introrsae. Styli tres, divergentes, filamentorum longitudine, stigmata simplici terminati, ideoque staminibus anthera destitutis simillimi. Fructus, ut videtur, indehiscens, carnosus, trilocularis; ovula plurima, placentis centralibus in parte superiore loculorum adnata, ovata, compressiuscula. Semina matura non adsunt. Unica species est: A. pulchellum *Ph. glaberrimum*, caespites densissimos formans, ut *Silene acaulis;* ramuli vix pollicem alti, foliis veluti oribus rufis, et inter illa pilis albis densissime obtecti. Folia linearia, acutiuscula, evenia, 3 lin. longa, 1 lin. lata. Flores in apicibus ramulorum terminales, solitarii sessiles. Petala alba, 3 lin. longa, erecta. Frequens in montibus insularum Chonos dictarum arboribus minus confertis obtectis."

Letters of R.A. Philippi and the fate of *Anthochortum pulchellum* Phil. in mscr.

The letter collection comprises about 14 letters and letter fragments of Rudolf Amandus Philippi (1808–1904), German emigrant to Chile, who carried out extensive natural history work and served as director of the Chilean National Museum, whose collections he considerably expanded (Reiche 1904, Zirnstein 2001). Philippi described numerous plant genera and species, including quite a few in publications printed by Schlechtendal in ‚Botanische Zeitung' and ‚Linnaea'. In the collection of letters there is, for example, the essay on the new genus of the Solanaceae, *Latua* Phil., published in ‚Botanische Zeitung' (vol. 16, issue 33, 13 August 1858), in which also the extreme poisonous effect of this plant on humans was described (Philippi 1858). On the letter there are additions and deletions in Schlechtendal's handwriting, so that it is recognizable that this letter served the typesetter directly as a template.

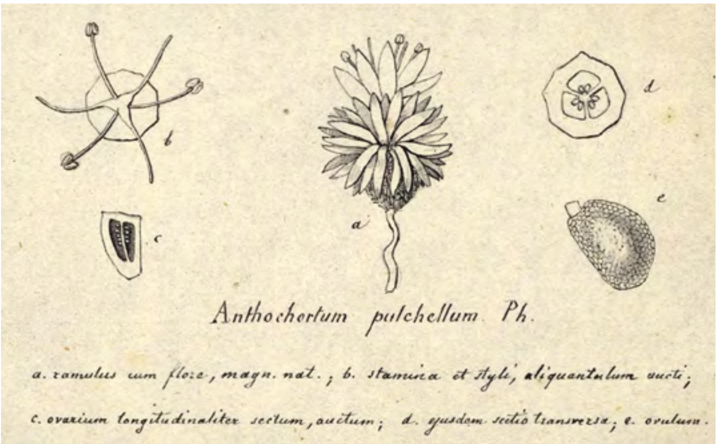


Fig. 3. Original ink drawing by R.A. Philippi with still faintly recognizable preliminary drawing executed in pencil. The detailed drawing shows features of the genus *„Anthochortum"* Philippi intended to describe. The plant belongs to the genus *Donatia* J.R.Forst. & G. Forst described already in 1775 by father and son Forster and represents *D. fascicularis* J.R.Forst. & G.Forst., which was noticed by Schlechtendal, so that Philippi's planned publication was omitted. Schlechtendal's letter collection in the herbarium of the University Halle-Wittenberg.
The text reads: *"Anthochortum pulchellum* Ph.; **a.** ramulus cum flore, magn. nat.; **b.** stamina et styli, aliquantulum aucti; **c.** ovarium longitudinaliter sectum, auctum; **d.** ejusdem sectio transversa; **e.** ovulum."

Of other letters, only cut-out parts have survived, which were apparently intended directly for the typesetter by Schlechtendal. For example, two fragments of one of Philippi's letters from 13 August 1857 have survived, namely the upper and lower parts of the sheet, the middle is missing. On the lower part of the back of the letter there is a 7-line Latin diagnosis of a supposedly new genus or possibly even new family written by Philippi in particularly legible handwriting (Fig. 2). It begins with *„Antho-*

chortum novum Genus novae Familiae?" This is followed by a 3-line species description of „*A. pulchellum* Ph." and the locality. There is also a beautiful ink drawing by Philippi of the plant, on which the preliminary pencil drawing can still be faintly recognized (Fig. 3).

This drawing as well as the diagnosis were never printed, because firstly in a letter written four weeks later on 14 September 1857, Philippi informed Schlechtendal that Grisebach (professor of botany in Göttingen, Germany) had written to him that the name *Anthochortum* had already been given to a Restionaceae by Nees. Philippi asked Schlechtendal to change the name *Anthochortum* to *Chartanthus*. Also the latter name was not published, because secondly Schlechtendal seemed to have noticed that the plant Philippi's was the already 1775 described genus *Donatia* J.R.Forst. & G.Forst. (Forster and Forster 1775). Schlechtendal noted this genus name written in pencil in the upper left corner of the leaf section with Philippi's handwritten diagnosis of *Anthochortum*. Schlechtendal, in contrast to Philippi, apparently knew the work „Characteres generum plantarum quas in itinere ad insulas maris australis collegerunt…" by father and son Forster, which contained an exactly correct diagnosis (p. 5) and correct illustration (Tab. V) of their new genus *Donatia* with the single species *D. fascicularis* included (Forster and Forster 1775), thus even conspecific with the plant Philippi's.

However, one cannot blame Philippi for this error with his supposedly new genus „*Anthochortum*", because in his letters to Schlechtendal he repeatedly complained about the lack of necessary scientific literature and the extremely slow procurement by the national library of Chile. In the present example, he absolutely correctly recognized that it was a special plant that did not belong to any of the families known to him, and he made a diagnosis that was as extensive as it was accurate, as well as an exact and detailed drawing, which emphatically underlines his outstanding talent as a natural scientist.

Correspondence of the Basel jurist and naturalist Hermann Christ on the publication process and nomenclatural confusion in *Pinus*

The four letters from Basel lawyer and naturalist Hermann Christ-Socin (1833–1933) provide a clear insight into the nature of the publication process of scientific papers and highlight nomenclatural challenges that remain to today. August H.R. Grisebach, a German botanist at the University Göttingen, commented in a short publication in the journal ‚Flora' (Grisebach 1863) on a survey of the European Pinaceae published by Christ (1863a). Grisebach praised Christ's treatment in principle, but disagreed with Christ's classification/evaluation of *Pinus maritima* Lamb. because Christ considered the species conspecific with *P. halepensis* Mill., while Grisebach himself considered it conspecific with *P. brutia* Tenore. With the first letter from Christ to Schlechtendal (9 September 1863), Christ sent along a manuscript, in which he replied to Grisebach's criticism.

Already a few days later (12 September 1863), Christ had found out in the meantime that Schlechtendal was not the editor of the journal ‚Flora oder allgemeine botanische Zeitung...', in which Grisebach had published his article but of the ‚Botanische Zeitung', another journal with a similar title. Schlechtendal evidently sent the manuscript to the editors of the ‚Flora' in Regensburg according to Christ's request, as ‚Flora' published it in the issue 24 of volume 46 on 2 October 1863 (Christ 1863b).

A third letter (15 January 1864) accompanies a manuscript on *Pinus sylvestris* and related species in the Lower Engadin (Southwest Switzerland). Apparently Schlechtendal rejected this manuscript of Christ, probably because he himself was working on a publication on *Pinus* that appeared in Linnaea 33, issues 3–4 (December 1864) and issue 6 (June 1865) (Schlechtendal 1864a,b, 1865). Christ's manuscript finally appeared in March 1864 in ‚Flora' (Christ 1864) as a continuation of his earlier publication „Beiträge zur Kenntnis südeuropäischer *Pinus*-Arten" (Christ 1863b). Schlechtendal's earlier publication in „Linnaea XXIX 1857", to which Christ refers (Christ 1864: p. 147), included observations on German and Swiss *Pinus* species (Schlechtendal 1857).

A final letter was sent from Christ to Schlechtendal (7 June 1865) to request publication of another paper „on the forms in which the European *Pinus* species occur", underlining how prolific Christ was. This publication was accepted by Schlechtendal and printed in three issues of the ‚Botanische Zeitung' (Christ 1865). In *P. halepensis* Mill., Christ distinguishes three forms on the basis of characteristics of the strobilus, including one which he calls „*maritima* Lamb." (Christ 1865: p. 223).

Interestingly, the debate about the correct name of the *Pinus* species discussed by Christ and Grisebach is by no means closed, as the application of the names *P. halepensis and P. brutia* is indeed unclear due to questions of their nomenclatural types. Therefore, a proposal has recently been made to conserve the name *P. halepensis* Mill. with a conserved type to avoid the name *P. halepensis* having to replace *P. brutia* Ten. and the name *P. maritima* Mill. having to replace *P. halepensis* (Ferrer-Gallego and Farjon 2019). However, the proposed type specimen from the Algarve in Portugal is perhaps not the most fortunate choice for a species that bears as epithet the name of a city at the opposite end of the Mediterranean, Aleppo in Syria *(‚P. halepensis').*

As can be seen from the long list of Christ's publications (Senn 1934), the works mentioned in the letters to Schlechtendal belong to his early botanical works. The journals ‚Linnaea' and ‚Botanische Zeitschrift', published and edited by Schlechtendal, corresponded quite well to the character of Christ's publications and seemed to be a suitable publication organ. Apparently, Christ did not resent Schlechtendal's rejection of a manuscript, which can be assumed on the basis of the letters. It is possible that he would also have placed his further works in these journals, but after Schlechtendal's death in 1866, no publication by Christ appeared in either of the two journals.

It is also interesting to note the short time span of only 3.5 weeks from the submission of a manuscript to its appearance in ‚Flora', although the manuscript was erroneously sent first to Schlechtendal in Halle instead of to the editorial office in Regensburg (letters 1 and 2). The time span for publication in ‚Botanische Zeitung' was 4 weeks (letter 4). Today's authors can only dream of such a rapid pace of publication.

Edition of Schlechtendal's Correspondence

The approximately 5600 surviving letters from his contemporaries to Schlechtendal are mostly written in the old and long-unused German Kurrent script. Moreover, some of the authors had quite illegible handwriting, which makes the recording of the letters very difficult and time-consuming. The translation work is mainly done by mostly elderly volunteers of the ‚Sütterlinstube Halle' and Mrs. Elfriede Wagner (1926–2023), a former teacher in the Vogtland (Saxony, Germany), who specialise in reading old manuscripts, an activity that can be described with the modern term of ‚citizen science'.

So far, about 54 % of the letters have been transliterated, i.e. transferred into a legible modern handwriting. Some of them have already been transferred into word processing software. Letters from several authors have been processed as topics of scientific term papers by biology students. We intend to publish the letters of Schlechtendal's correspondents with plant-scientific explanations and other comments important for understanding, i.e. in edited and annotated form. The letters of Kurt Sprengel, Schlechtendal's predecessor as director of the Botanical Garden in Halle, and Wilhelm Sonder in Hamburg, have already been edited and published (Machoy et al. 2021, Tkach et al. 2022).

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Herbarium DNA degradation – Falling to pieces non-randomly

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Post-mortem damage in herbarium DNA, mostly from 18th and 19th century collections, and with specimens usually heat-treated for conservation, consists mainly of genome fragmentation (single- and double-stranded breaks) rather than miscoding lesions. With typical herbarium DNA fragment sizes encountered (20–200 bp) this easily leads to insert sizes in library construction being smaller than Illumina read lengths applied (i.e. 100–250 bp).

Using a previously-published series of 56 genome-skimmed herbarium DNA extracts representing 10 angiosperm families, overlapping read pairs were found to occur in roughly 80 % of all read pairs obtained. After merging such overlapping pairs, the resulting fragments and their length-distributions are considered to reflect actual DNA fragmentation. Similar to occurrence in ancient DNA, we found over-representation of purines at fragment-ends in herbarium material. Distributions of fragment lengths fit gamma rather than exponential distributions, without apparent correlation with specimen age. The observed gamma distributions would indicate higher-order degradation kinetics, implying multiple processes acting during degradation. Possibly, the genome skimming data used here, in which repetitive sequences or compartments are over-represented, has biased genomic fragment-length distributions and half-lives as compared to the non-repetitive fraction of plant genomes, but no data was available to test this hypothesis. Overall, our results imply that we cannot confirm whether a plant archival DNA half-live exists and what its rate would be.

Keywords
DNA degradation, Genomic fragmentation, Herbarium DNA, Plant aDNA

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Herbarium collections constitute an enormous repository of botanical (meta)data, centred around the specimens and often including a range of different kinds of evidence such as biosequences and genomes, chemical and isotope data, data on associated microbes, pathogens and, obviously, collection locality as well as data relevant to taxonomy. Herbarium collections can be considered important ‚instruments' for testing historical hypotheses (Bakker et al. 2020), such as species' response at the genetic level to global change (Lang et al. 2020), or reconstructing the domestication/evolutionary history of crops (e.g., Sebastian et al. 2010; Gutaker et al. 2019), or for making taxonomic decisions (e.g., Bebber et al. 2010; James et al. 2018), providing the specimens are well-accessible and post-mortem genomic damage (see below) can be overcome. There are an estimated 397 million herbarium specimens deposited in 3500 herbaria world-wide (Thiers 2022). Collectively, these represent a huge past collection effort, sometimes under severely sub-optimal conditions, and in many cases the actual localities may no longer exist.

Herbarium collections enable a time-series perspective in plant species' past ecology, phenotypes, pathogens, and demography (Bieker and Martin 2018). We refer to Bakker (2017, 2018) for an overview of studies including on organelle genomes from extinct species, historical pathogens, and shift to C4 photosynthesis in grasses, and see Lang et al. (2020) for a great example in herbarium-based study of global change biology.

With regards to taxonomy, Bebber et al. (2010) estimated that around 70 000 new species are already in herbarium collections, „waiting to be described", which further indicates the relevance of herbarium genomics, as it is expected to expedite archival DNA barcoding (see Xu et al. 2015). In fact, we are currently at the dawn of a herbarium genomics era (Buerki and Baker 2015, Bieker and Martin 2018, Olofsson et al. 2016), and chances are high that a large body of plant archival genomic data is generated in the years to come. In museomics, plants take a special position as their cell walls probably offer increased protection against oxidative DNA damage (see Bakker 2018). Their nuclear genomes are usually much larger in size than those from animal or fungal genomes (Gregory et al. 2007) and contain many repeats, which can hamper genome sequence assembly. Plant genomics is therefore inherently challenging, be it from archival or fresh DNA, although plastomes have both a small size (around 160 kb) and exhibit extensive structural conservation across land plants (Wicke and Schneeweiss 2015), enabling straightforward (re)sequencing with genome skimming (Straub et al. 2012; Bakker et al. 2016). Nevertheless, getting full nuclear genomic sequences from herbarium DNA is still rare to date, although the approach by Hart et al. (2016) and Brewer et al. (2019), targeting 353 nuclear genes in DNA from a range of herbarium specimens, provides a highly promising alternative.

For a summary of published studies on extraction of herbarium DNA (e.g., Särkinen et al. 2012, Gutaker et al. 2017, Xu et al. 2015) and the occurrence of possible post-mortem damage (Staats et al. 2011, 2013) we refer to Bakker (2017, 2018). Post-mortem damage in herbarium DNA consists mainly of genome fragmentation (single- and double-stranded breaks) caused during specimen fixation by heating, and herbarium specimen age since fixation does not appear to play a role (Staats et al. 2011, based on comparison of living trees and their historic herbarium vouchers; Staats et al. 2013). Herbarium specimens are often dried with heat, which can typically be 60–70°C, causing living cells in the specimen to rupture quickly, releasing nucleases and other cellular enzymes (Gill and Tuteja 2010), as well as reactive oxygen species (ROS). Such physiological conditions resemble necrosis, and this cellular stress typically causes DNA to degrade randomly into smaller fragments, running as a smear on agarose gels (Reape et al. 2008; McCabe et al. 1997). Indeed, herbarium DNA is typically highly-degraded into low molecular weight fragments (Doyle and Dickson 1987; Pyle and Adams 1989; Harris 1993) and this genomic fractionation causes the number of PCR amplifiable template molecules to be reduced (Staats et al. 2011). Heating is known to cause de-purination and subsequent hydrolysis of the DNA sugar-phosphate backbone (Lindahl and Andersson 1972). This process is therefore expected to result in an excess of AG purines just before fragment break-points. In addition, de-amination of C to U, which is read as T by the polymerases during sequencing, results in C→T transitions. Excess of AG purines has been observed to occur just before the ends of fragments in studies on ancient DNA (aDNA) (Briggs et al. 2007), suggesting they are the cause of breaks. The same study showed the occurrence of over-representation of CT at fragment ends, which can probably be attributed to oxidation of ‚loose' single strands at fragment endings. These typical aDNA patterns have also been observed in historic (heated) herbarium DNA (Weiss et al. 2016), suggesting that aDNA and (heated) herbarium DNA share the same sequence damage-characteristics. Therefore, the conclusion is probably fair that historic herbarium DNA from heated specimens looks rather similar to (non-heated) ancient DNA.

To what extent the C→T/G→A transitions at the ends of the reads drives post-mortem transitions in herbarium DNA sequences the authors do not mention, but possibly the post-mortem transitions reported by Staats et al. (2013) correspond to these.

Herbarium DNA fragmentation can occur sometimes to the extent that the efficiency of paired-end sequencing using Illumina HiSeq (and hence subsequent sequence assembly) is affected. When template insert sizes are shorter than twice the Illumina read lengths applied, the actual sequencing reads will ‚meet in the middle' of the insert and start to overlap (Fig. 1). However, when template insert sizes are smaller than the Illumina read length applied, this will result in the presence of adapter sequence at the end of the read (Turner 2014). In both scenarios of read-overlap, the two reads can be merged into a single, longer read. In a previous study we used a series of 93 herbarium DNA samples (some of which 146 years old), representing 10 angiosperm families (Bakker et al. 2016). Overlapping read pairs were found to occur in roughly 80 % of all read pairs obtained. After merging such overlapping pairs the resulting fragments and their distribution can be considered to reflect (the ongoing process of) genome fragmentation up to the moment of DNA extraction. Merging reads enables assessing the distribution of genomic fragment lengths

Fig. 1. Herbarium DNA fragments (orange) may be longer **a** or shorter (**b** and **c**) than Illumina read lengths, in which case reads are overlapping and could be merged. From Bakker (2018), with permission from Springer.

(fragment length distribution or FLD) in a herbarium DNA extract, as was carried out in Weiss et al. (2016). Here the authors inferred FLDs for a series of non-heated herbarium specimens of up to 300 years old, by merging overlapping reads as outlined above. By assuming a log-normal FLD the authors claimed they were able to deduce decay rates for their genomic extracts, based on the slope of „the exponential part" of the FLD. Weiss et al. (2016) conclude that the herbarium decay rate is „six times the rate of bone DNA decay".

Here, we infer the pattern of fragmentation and the FLD in degraded herbarium DNA, as measured from genome skimming data. With our data we confirm that the duration of being in the herbarium affects the average fragment lengths but that the FLDs appear not correlated with specimen age. We explore to what extent the data can be explained by de-purination and de-amination known to occur upon heating (and applied to the majority of specimens in herbarium collections today). We elucidate whether typical plant genomic fragment-length distributions can tell us whether genome degradation is a first- or higher-order kinetic process, i.e. whether a single or more processes are involved in fragmentation. A better understanding of such processes could help in assessing whether **1** a general herbarium DNA decay rate actually exists, and **2** what drives fragmentation in repetitive genomic compartments in plants.

Material and Methods

Herbarium genome fragment-merging

In order to explore the distribution of short-sized fragments in herbarium DNA and the extent to which read-overlap was occurring among them we re-analysed a subset of 56 Illumina genome skimming historic herbarium samples from Bakker et al. (2016) which included species of *Lactuca, Karelinia* and *Nicolasia* (Asteraceae), *Polyscias* (Araliaceae), *Pelargonium* (Geraniaceae), *Aethionema* and *Tarenaya* (Brassicaceae), *Anthochortus*, *Dovea* and *Hypodiscus* (Restionaceae), *Anaxagorea*, *Desmopsis* and *Monanthotaxis* (Annonaceae), *Hymenostegia* and *Duparquetia* (Fabaceae), *Begonia* (Begoniaceae), *Paphiopedilum* (Orchidaceae), and *Rinorea* (Violaceae). Most of these specimens were expected to have been fixated after collection, by heat treatment. This could be in ovens at around and perhaps up to 70°C in (local) herbarium facilities, or in situ using hot air from hair driers or camping cookers (Jan Wieringa, pers. comm). In addition, other techniques have been used for field drying, including kerosene stoves, 100-watt lightbulbs, and air-drying on a moving vehicle (Staats et al. 2011). Some of our historic specimens, especially from the wet-tropics, may have been subjected to ‚Schweinfurt' treatment (i.e. the temporary fixation with methylated spirits or 30 % formaldehyde) to prevent specimens from moulding, whilst underway to local herbarium facilities. As discussed in Bakker et al. (2016), clear documentation for the fixing method actually applied to each herbarium specimen is usually lacking, and therefore no specific hypotheses regarding preservation method effects can be tested. Wet-tropical specimens gave lower N50 values (N50 is similar to a mean or median of assembled contig lengths, but with greater weight given to the longer contigs) and concomitantly higher number of contigs in plastome assemblies (Bakker et al. 2016).

We used BBMerge from the BBTools package (http://jgi.doe.gov/data-and-tools/bbtools) in order to check whether overlap exists between read-pairs (Fig. 1) and in case it was, reads were subsequently merged. When insert size is shorter than the read length (in this case 100 bp) reads will have adapter sequence at the tail end, which was removed by using BBMerge after merger (Brian Bushnell, pers. comm.). When insert size is the length of two read lengths, i.e. 200bp, reads cannot be merged anymore because there is no overlap. Using the default mode in BBMerge, the proportion of overlapping reads, as well as the average fragment length and its standard deviation were recorded. The FLD that resulted from merging the overlapping reads was plotted for each accession and in order to make the FLDs comparable we compared relative frequencies of read pairs. Fragment lengths were between 26 and 184 bp, which reflects the minimum and maximum fragment length given the adapters used.

In order to investigate a time-series of specimens, and hence whether older specimens yield higher fragmentation, we compared length distributions for two series of accessions from the Bakker et al. (2016) data, one for species of *Aethionema* (Brassicaceae), used and further described in Mohammadin et al. (2017) for phylogenetic analysis, and for *Lactuca* (Asteraceae), used and further described for the same purpose in Wei et al. (2017). The *Aethionema* series included both silica gel-dried and historic herbarium specimens of 23, 33, 40, 44, twice 50, 66 and 146 years old. The *Lactuca* series included silica gel-dried and historic herbarium specimens of 7, 36, 42, 43, twice 49, 54 and 64 years old. By comparing these congenerics it can be assumed that genome size, GC contents, specimen tissue characteristics, and specimen fixation histories (in most cases) are comparable too. Differences in FLD should therefore be due to specimen age, different specimen fixation (if applicable), herbarium collection locality or perhaps even stochasticity. Reads were merged using BBMerge as described above and fragment lengths between 26 and 184 bp plotted and their relative frequencies compared.

We used MapDamage 2.0 (Jónsson et al. 2013) in order to investigate over-representation of purines (A and G) at fragment endings, by mapping reads against a set of assembled contigs, enabling assessment of nucleotide positions around fragment-ends, summarised across all reads.

Fitting models to distributions of genomic fragment-lengths

If breakpoints in DNA fragments are randomly-distributed, one would in principle expect an exponential distribution of resulting fragments (simulation data, not shown). In order to investigate what model fits our observed genomic FLDs best we fitted an exponential distribution and a gamma distribution (Bolker 2008) to each of the 56 data sets. We estimated the rate parameter of the exponential, and the shape and scale parameters of the gamma distribution. It should be noted that the exponential function is a special case of the gamma distribution (i.e. when the shape parameter is 1). The AIC criterion (Bolker 2008) was used to select for each of the 56 datasets which distribution fitted best. The fitting procedure and model selection was performed in R version 4.2.1 (R Core Team 2022) using the fitdistr function of the R-package MASS (Venables and Ripley 2002).

Results

Herbarium DNA reads

Across the 56 samples, the average fragment length appeared to be negatively correlated with specimen age ($R^2 = 0.29$), which confirmed earlier studies indicating that older herbarium DNA extracts contain smaller fragments (Fig. 2a). We found the standard deviation of the average fragment lengths to increase with longer fragments (Fig. 2b; polynomial regression, $R^2 = 0.94$), i.e. short fragments were less length-variable and occurred in ‚peaks' within a fragment length distribution. In contrast, longer fragments occurred across broader size ranges. Apparently, genomic fragments ‚end up' in increasingly small, uniform, sizes, but in the same time, the smaller sizes are correlated with higher specimen age as seen above. The percentage of read pairs that can be merged appeared to be fairly independent of specimen age (Fig. 2c). The actual numbers of reads was lower in older specimens, but these yield lower amounts of reads in the first place (Bakker et al. 2016), therefore also lower amounts of read pairs that can be merged.

Fitting models to distributions of genomic fragment lengths

Fragment length distributions (FLDs) for a subset of all 56 accessions, representing the two time-series *(Aethionema* and *Lactuca),* are given in Fig. 3. (In addition, FLDs for another subset of 36 of the 56 accessions, are given in Suppelementary Fig. 1, with specimen age indicated by colour-coding.) There does not appear to be a correlation between FLD and specimen age. As outlined above, we fitted both exponential and gamma distributions to the 56 FLDs contained in our data. All distributions appeared to fit well to a gamma distribution: either there are many short fragments

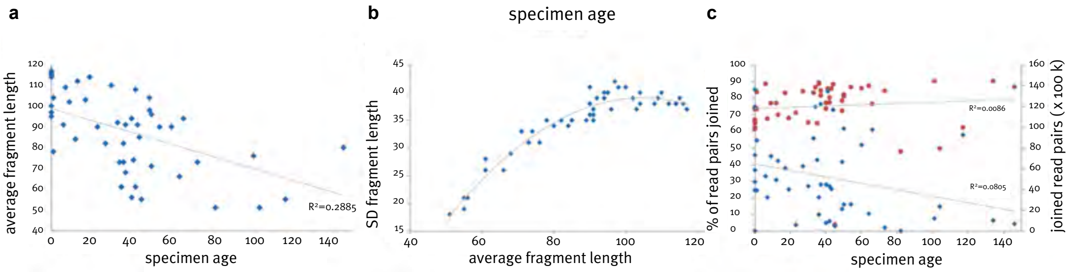

Fig. 2 a-c: Overlapping Illumina HiSeq reads from herbarium DNA extracts; the average fragment length after merging reads **a** plotted against specimen age; the SD of average fragment length **b** plotted against average fragment length; and **c** the percentage of total reads that could be merged (red dots) and the actual number of merged read pairs (blue diamonds). From Bakker (2018), with permission from Springer.

and few longer ones, or there is a gradual increase in longer fragments (Fig. 3 and Suppelementary Fig. 1; and see Suppelementary Appendix 1 for histograms of the 56 datasets with the fitted exponential and gamma distributions plotted). The values for rate, shape and scale parameters showed an average value of 0.0122, 8.1267 and 13.1067 resp., with associated standard deviation values of 0.0046, 6.0394 and 4.2897 (see also Suppelementary Appendix 2 for histograms of all values for these parameters in the 56 analysed datasets). For all 56 datasets, the gamma distribution had the minimum AIC value and Δ-AIC was on average 5 313 812 in a range of (11 267 to 15 712 447) as is shown in Suppelementary Appendix 3. The high standard deviations reflect the range of fragment-length distributions among the accessions included, and indicates that fragmentation dynamics differs across all accessions. It should be noted that some of the datasets are bimodal and that although the gamma distribution fits best, when choosing between exponential and gamma only, the gamma distribution is a bad choice for these datasets (see X002Paustr, X27mult, X21abro in Suppelementary Appendix 1). In our taxonomic sampling 14 accessions (i.e. from Annonaceae, Araliaceae, Fabaceae, Begoniaceae, Orchidaceae and Violaceae) had been collected in the wet-tropics. As outlined above and based on previous studies (Bakker et al. 2016), wet-tropical origin appeared to be the main factor correlating with plastome-assembly success, possibly due to difference in underlying genomic fragmentation patterns. These 14 accessions however did not seem to differ in rate, shape and scale parameters for their FLDs (indicated in green in Suppelementary Appendix 3).

Purine over-representation at fragment endings

Weiss et al. (2016) found over-representation in A and G (purines) towards fragment ends, a pattern that reflects what is encountered in ancient DNA (Briggs et al. 2007). Depurination, or loss of A and G bases, is known to be a first step towards double-stranded breaks (Lindahl and Andersson, 1972). Therefore, it is expected for purines to be overrepresented towards fragment ends and some of the samples analysed here with Map Damage 2.0 indeed did show this pattern (Suppelementary Fig. 2), but predominantly in herbarium (not fresh) accessions.

Discussion

Herbarium genomics has seen great opportunities and development over the past decade, mainly driven by the ever-increasing availability of NGS technology. Especially when concerned with organelle genomes and other repetitive genomic compartments, approaches such as genome skimming appear effective in extracting DNA sequence data from large series of archival specimens (Straub et al. 2012; Bakker 2017). As a general feature of herbarium DNA, genomic fragment size can be small (25–300bp). Overlapping read pairs are the result of template insert size being smaller than twice the read length applied (or even smaller than the read length itself). Using a genomic skimming series of 56 herbarium DNA samples, representing 10 angiosperm families, overlapping read pairs were found to occur in roughly 80 % of all read pairs obtained for most samples. Fragmentation is therefore confirmed to occur across families, and insert sizes can be as small as <100 bp that still represent a majority of fragments. As outlined above, the distribution of herbarium DNA fragment-lengths could in principle inform us about biases or trends that may exist in the actual process (or processes) by which herbarium genomes break down.

Intuitively one would expect older specimens to be more fragmented than younger ones, given that more post-mortem time has been available. On the other hand, the experimental herbarium results by Staats et al. (2011), comparing fresh and century-old DNA from the same individuals of trees, indicated that this does not need to be the case (see above, and Fig. 3). We compared genomic fragment-length distributions (FLDs) for two series of herbarium samples (included in our set of 56 accessions), each from the same genera *(Lactuca* and *Aethionema)* and each also including non-historic (i.e. silica gel-dried) samples for comparison. For the *Lactuca* series, the oldest sample was indeed the most highly fragmented (Fig. 3a). For the *Aethionema* series however, the older specimens did not appear to have highest proportion of small fragments, but specimens around 50 years did (Fig. 3b). For both series, we saw that the silicagel-dried samples showed a gradual increase in occurrence of longer fragment lengths that would probably have extended beyond 200 bp, had current Illumina read lengths of 150bp or more been used.

Following our FLD model-fitting analysis we found the best-fitting models to be gamma distributions, as indicated by the AIC criterion used. As indicated above, the high standard deviations for the shape and scale parameters for the gamma distribution probably reflect the range of FLDs among the accessions included, and indicates that fragmentation dynamics apparently differs

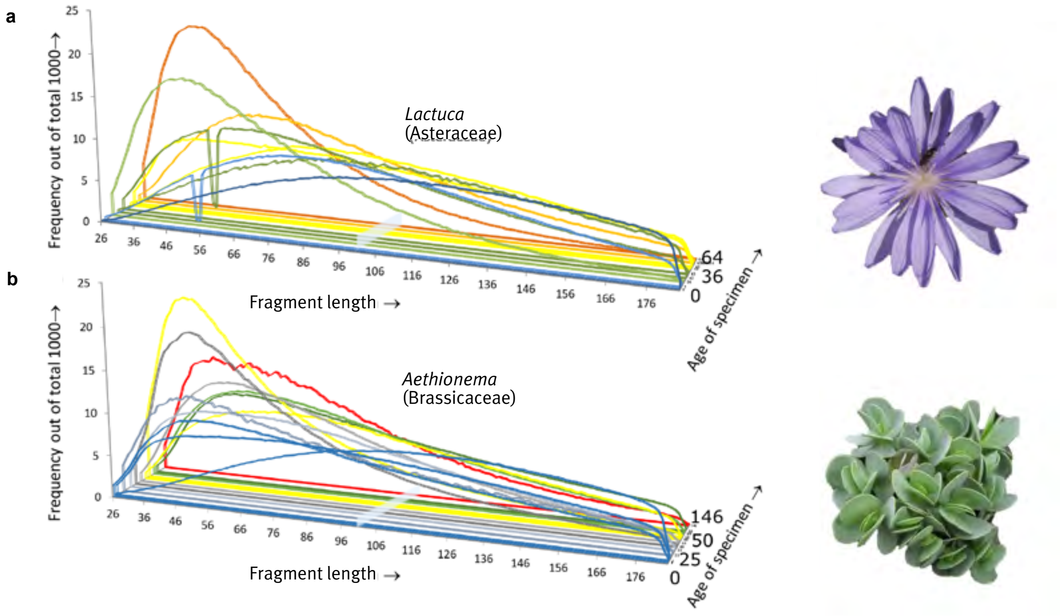

Fig. 3. Distributions of fragment lengths (in bp) from fresh and herbarium specimens of different ages of *Lactuca* a and *Aethionema* b, with distributions sorted by (increased) specimen age. The transparent bar indicates the read length used (100 bp). Fragments were produced after merging 100 bp Illumina reads, with reads up to 25 bp discarded, and reads with length <100 trimmed with regard to adapter sequences (see text). The distribution resembles a gamma function, with either a maximum of lengths around 30bp, or a wide length-range. From Bakker (2018), with permission from Springer.

across all accessions. Weiss et al. (2016) and Allentoft et al. (2012) suggested lognormal distributions of fragment lengths fit best in historic *Arabidopsis,* and bone DNA, respectively, and based this partly on the observed linear relation after loglog transformation. Yao et al. (2016) found the same for DNA degradation in human serum, urine, and saliva DNA. These distributions would be consistent with a first-order kinetics at which DNA degrades, i.e., DNA has a half-life and the rate of degradation is constant (Allentoft et al. 2012). However, Weiss et al. (2016; in their Fig. 2) appear to consider the „exponential decline" to start after the median of their genomic FLD. The first part of the distribution would then not be taken into account. Only considering the second half (> median) of the distribution leads indeed to an exponential distribution, as the authors emphasize, especially after log transforming the y-axis (Weiss et al. 2016). In contrast, we chose to include the entire fragment-length distribution and find that gamma distributions fit the distributions significantly better than exponential distributions. As the exponential is a special case of the gamma distribution this indicates a higher order kinetics underlying fragmentation in these data sets.

Looking directly into the herbarium break-points, by summarising nucleotide composition at fragment endings (Supplementary Fig. 2) indicates that there is over-representation of purines (A and G) in case of (heat-treated) herbarium DNA. This would imply that the distribution of purines in the herbarium genome would drive the FLDs observed, and hence that purines are gamma distributed in the genome (which would probably be unrealistic). However, our data was generated using genome skimming, which means that repetitive compartments and sequences are probably overrepresented in all samples. To what extent such regions are non-representative of general genome composition and complexity is difficult to say. Possibly the repeats themselves may contain purine biases but no published studies indicating this exist to date. If the herbarium DNA degradation investigated here indeed fits a gamma rather than a lognormal or exponential distribution, this would indicate either a non-constant rate of degradation, or decay consistent with a higher-order kinetics, differing from the usually-observed first-order genomic degradation kinetics. In the latter, break-points are randomly distributed in DNA sequences and therefore would be expected to yield exponential FLDs. Our data as used in this study is genome skimming data, derived from genomic repetitive regions. Possibly, degradation of repetitive genomic compartments occurs at higher-order kinetics, i.e., a different half-life is present compared with non-repetitive DNA. However, this would need to be tested with (ancient) genomic samples that are deep-sequenced rather than genome-skimmed.

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Improving procedures for obtaining Sanger sequences from old herbarium specimens

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Because DNA degrades over time, extracting DNA of sufficient quality for sequencing is presumed to be more difficult from older than younger herbarium specimens. Although massive parallel sequencing techniques have clear advantages when it comes to sequencing ancient DNA, Sanger sequencing is still in frequent use, prompting us to test and improve its application on herbarium specimens. During molecular phylogenetic investigations of the subfamily Lamioideae (Lamiaceae) and subgroups, we extracted DNA from 651 herbarium specimens collected between 1826 and 2006 using regular mini-prep methods. The aim was to obtain DNA of sufficient quality for Sanger sequencing of various plastid and nuclear genetic markers. Here, we report successful Sanger sequencing of the commonly used plastid marker, rps16, as a conservative measure of DNA quality, and logistic regression to investigate the relationship between age of the material and DNA quality. Our result indicates that the upper age limit for obtaining DNA suitable for Sanger sequencing from herbarium specimens using regular mini-prep DNA extraction methods has not been reached. After simple modifications to the regular DNA mini-prep and PCR procedures, at least one genetic marker was successfully sequenced for about 90 % of the specimens tested, the oldest being 168 years old. Jointly, despite the technique's drawbacks, these results demonstrate a high success rate of Sanger sequencing of herbarium specimens.

Keywords
DNA extraction, Herbarium specimens, Lamiaceae, Mini-prep, PCR, Replicates, Sanger sequencing

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Fresh, silica dried, or frozen plant tissue is ideal for obtaining DNA sequences. However, such material is often not available due to a variety of reasons, such as rarity, geographical restriction or remoteness of the taxon of interest, or even extinction. Most taxa are available, however, as preserved specimens in at least one of the World's many natural history collections. Archived scientific collections provide verifiable and unique records of the existence of an organism at a given time and place. Moreover, herbaria, fungaria, and seed-, culture-, in vitro-, tissue-, and DNA collections, often contain expert-curated specimens collected throughout the world, some of which are several 100 years old.

Herbarium specimens are relatively easily accessed due to international specimen exchange agreements and represent a great resource for biological research (e.g., Andrew et al. 2018; Bebber et al. 2010, Kohn et al. 2005) – not only for morphological investigations but also for molecular research (Bieker and Martin, 2018), provided DNA of sufficient quality for successful DNA sequencing can be obtained (hereafter referred to as ‚quality-DNA'). Botanical collections have been used in a vast number of molecular studies since the mid-80s to address questions related to phylogenetic relationships, nomenclatural identity, origin of populations, function and evolution of genes (e.g., Ames and Spooner 2008, Andreasen et al. 2009, De Castro and Menale 2004, Jankowiak et al. 2005, Lambertini et al. 2008, Rogers and

Bendich 1985), and more recently for the studies of ancient plant genomes (Bieker and Martin 2018, Kistler et al. 2020).

Because DNA degrades and becomes recalcitrant over time, obtaining ‚quality-DNA' is expected to be more difficult from older than younger plant material (Pääbo 1989). Substantial degradation of DNA is reported in investigations of old biological collections with DNA fragments usually ranging in size from 50–500 bp (Soltis and Soltis 1993). Post-mortem degradation of DNA is an inherent trait and unending process of biological materials, challenging the usability of archived biological specimens in studies on DNA (e.g., Allentoft et al. 2012). The application of PCR on such materials often requires significant modification to standard protocols (Fulton and Stiller 2012). Recently developed PCR-free high-throughput sequencing (HTS) approaches mitigates some of the challenges with recalcitrant DNA. Such HTS approaches are, however, still not available nor affordable in many labs, and in the field of phylogenetic systematics, Sanger sequencing remains a much-used technology.

For our molecular investigations of the subfamily Lamioideae and subgroups (e.g., Bendiksby et al. 2011a, b, c, 2014; Scheen et al. 2010), we extracted and PCR amplified DNA from more than 650 herbarium specimens collected between 1826 and 2006. We used regular mini-prep DNA extraction kits and standard PCR reactions (referred to hereafter as ‚the regular procedure'; Box 1) prior to Sanger sequencing several plastid and two nuclear DNA regions. Several specimens, some of which were of high importance for understanding the phylogenetic relationships, did not amplify. We therefore put effort into testing several minor modifications to the ‚regular procedure' to obtain quality-DNA from these important accessions.

The aim of this short communication is **1** to showcase how valuable herbaria are as a data source for molecular biosystematics research and **2** to present the modified procedures that made us able to obtain DNA suitable for Sanger sequencing from specimens that were previously discarded as useless for molecular studies. We show the relationship between the age of the plant material and sequencing success, using successful rps16 sequencing as a conservative measure of DNA quality. We use logistic regression to illustrate the relationship between age and DNA quality in the material.

Material and methods

We compiled information about sequencing success and age of the 651 herbarium specimens that were used in our biosystematics studies of the subfamily Lamioideae and subgroups (Bendiksby et al. 2011a, b, c, 2014; Salmaki et al. 2013, 2015; Scheen et al. 2010). For these studies, we targeted six plastid (*trn*L intron, *trn*L-*trn*F spacer, *rps*16 intron, *mat*K, *trn*S-*trn*G spacer, *psb*A-*trn*H spacer) and two nuclear (NRPA2, 5S-NTS) DNA regions for all or subsets of the specimens.

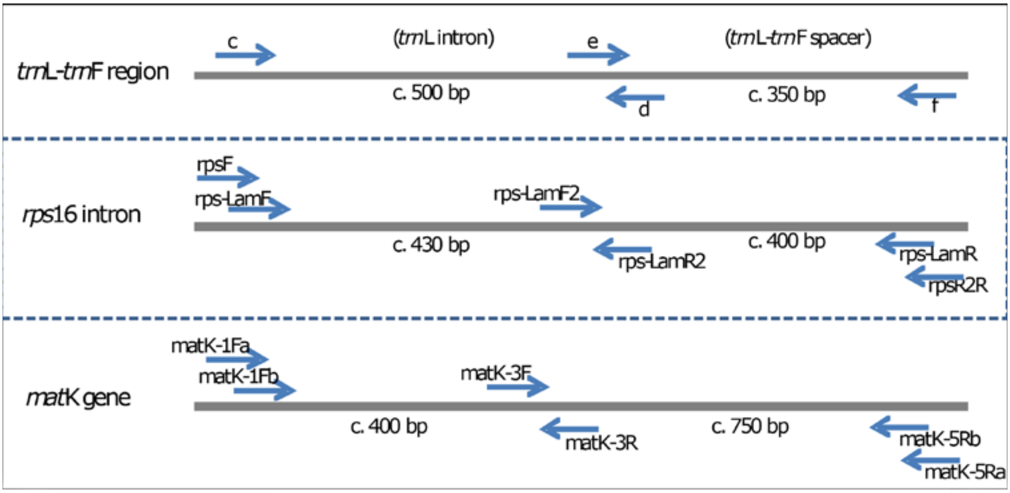

Fig. 1. Primer locations for the plastid regions amplified as one or two fragments (schematic), indicating approximate fragment lengths in base pairs (bp). The primers c, d, e, and f were published by Taberlet et al. (1991), rpsF and rpsR2R by Oxelman et al. (1997), and the remaining illustrated primers by Bendiksby et al. (2011 b). Regions amplified as single fragments: *psb*A-*trn*H (c. 330 bp) using the primers psbAF and trnHR (Sang et al. 1997), *trn*S-*trn*G (c. 530 bp) using the primers trnS^{GSU} and trnG (Hamilton 1999), NRPA2 (c. 700-830 bp) using primers published by Bendiksby et al. (2011 a), and 5S-NTS (c. 400 bp) using the forward primer 5S-30 (5' GGATCCCATCAGAACTCCG 3'; Bendiksby 2002) and a non-degenerate version of PII from Cox et al. (1992) as the reverse primer (5' TGCGATCATACCAGCACTAA 3').

We had amplified the *trn*L intron, *trn*L-*trn*F spacer, *mat*K, and *rps*16 intron mostly as a single fragment, but in some cases as two shorter fragments (see Fig. 1 for relative positions of the primers, approximate lengths of the fragments, and references to all primers used). We had amplified the remaining regions as single fragments. Most DNA was extracted, amplified, and sequenced using the ‚regular procedure' (Box 1). For DNA extracts that would not amplify using the ‚regular procedure', a nested PCR approach or a ‚replicate PCR procedure' was used (Box 2). In a few cases, DNA was extracted anew using a ‚replicate DNA extraction procedure' (Box 2). To validate the identity of the obtained sequence, we checked it against nucleotide sequences in GenBank through BLAST searches, and against our own unpublished sequences.

For the *rps*16 intron, which is >800 bp long and one of the longer plastic loci, amplification attempts had been made for 611 accessions of varying age (Fig. 2). As this material is sufficient to perform a formal statistical analysis of the relationship between sequencing success and the age of material, we selected *rps*16 as a conservative measure of DNA quality in this short communication. We used binary sequencing success q of the plastid *rps*16 intron as the response variable in a logistic regression (generalised linear models with logit link function and binomial errors; Venables and Ripley [2002]). The age t of the material (i.e. year

Box 1

The regular procedure

DNA extraction: We crushed 10 to 30 mg of leaf tissue in a 2 mL plastic tube with two tungsten carbide beads for 2 × 1 minute at 30 Hz on a mixer mill (MM301, Retsch GmbH and Co., Haan, Germany). We extracted total DNA from the crushed samples using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) or the E.Z.N.A™ SP Plant DNA Mini Kit (Omega Bio-tek, Inc., Norcross, GA, USA) according to the manufacturers' manual.

PCR amplification: We amplified DNA in 25 µL reactions using the AmpliTaq DNA polymerase buffer II kit (Applied Biosystems, Foster City, California, USA) and 0.2 mM of each dNTP, 0.04% bovine serum albumin (BSA), 0.01 mM tetramethylammonium chloride (TMACl), 0.4 µM of each primer, and 2 µL unquantified genomic DNA. Amplifications were performed in a GeneAmp PCR System 9700 (Applied Biosystems). We performed all PCR amplifications under the following cycling conditions (annealing temperature adjusted according to primer length and GC-content): 95°C for 10', 31 cycles of 95°C for 30", 55-60°C for 30", 72°C for 1', followed by 72°C for 10' and a final hold at 10°C. AmpliTaqGold® DNA Polymerase (Applied Biosystems) was used for amplifying DNA obtained from old herbarium specimens or DNA extracts of reduced quality, whereas AmpliTaq® DNA Polymerase (Applied Biosystems) was used for all high-quality DNA extracts.

PCR purification and sequencing: PCR products were purified using 2 µL 10 times diluted ExoSAP-IT (USB Corporation, Cleveland, Ohio, USA) to 8 µL PCR product, incubated at 37°C for 45 minutes followed by 15 minutes at 80°C. Prepared amplicons for sequencing contained: 9 µL 0-30x diluted purified PCR product (depending on product strength) and 1 µL of 10 µM primer (the same primers as used in the PCR). Cycle sequencing was performed by the ABI laboratory, Department of Biology, University of Oslo. The ABI BigDye Terminator sequencing buffer and v3.1 Cycle Sequencing kit (Applied Biosystems) was used for the cycle sequencing reaction, and sequences were processed on an ABI 3730 DNA analyser (Applied Biosystems).

Box 2

The replicate DNA extraction procedure: We extracted DNA as described in Box 1, but in 2–4 replicate tubes that each included smaller amounts (< 10 mg) of leaf tissue. We performed the DNA elution twice in the same tube using the first eluate in the second elution step. Finally, we pooled DNA extracts from replicate tubes prior to use.

Nested PCR: In this procedure, a second set of amplification cycles are performed using a pair of ‚nested' primers sited within the DNA sequence defined by the original primers (Barbara and Garson, 1993). We performed the pre-nested PCR (i.e. the first set of amplification cycles) as described in the regular procedure (Box 1), but with only 25 amplification cycles. As template for the nested PCR (i.e. the second set of amplification cycles), we used a dsH2o-diluted (100×) product from the pre-nested PCR, and otherwise identical conditions as described in the regular procedure (Box 1). Optimizations to improve sequence quality included: **1** adjusting the number of amplification cycles in the two separate runs; **2** testing various dilutions (10×–1000×) of the PCR product used as template for the second run.

The replicate PCR procedure: We added template DNA to multiple identical PCR reactions (8–16 tubes) and performed the PCR amplification using the same PCR mix and cycling conditions as described in Box 1, but with 34 cycles. For purification of the PCR products, we added five times the PCR volume of PBI-buffer from the QIAquick PCR Purification Kit (Qiagen, Hilden, Germany) to each replicated PCR product before applying all to the same QIAquick DNA-binding column (Qiagen). For the remaining of the procedure, the columns were treated as described in the manufacturer's manual.

of sequencing minus collection year) was used as predictor in this model. The significance of the logistic model was evaluated by comparison with a null model by which only the intercept was modeled, by use of an *F*-test. Modeling results were visualized graphically by showing back-transformed predicted values for sequencing success as a function of age. A 95 % confidence interval for sequencing success as function of age was obtained by inserting $\beta_0 \pm 1.96SE$ and $\beta_1 \pm 1.96SE$ into the expression for back-transformed predicted values for sequencing success *q*, as given by the model:

$$q(t) = \frac{e^{\beta_1 t + \beta_0}}{1 + e^{\beta_1 t + \beta_0}}$$

All calculations were carried out using R version 2.11.1 (R Development Core Team, 2010).

Results and Discussion

A range of mini-prep kits for accomplishing the tissue-to-sequence process, without having to deal with toxic reagents, has become available at a continuously reduced price. However, because of degradation of DNA over time, it is presumed that more comprehensive and laborious techniques, which often include toxic reagents (e.g., Cota-Sanchez et al. 2006), are required to obtain quality DNA from the older material (Fulton and Stiller 2012).

We obtained plastid and nuclear DNA sequences from herbarium specimens up to 168 and 163 years old, respectively (Supplementary Table 1) using regular procedures for DNA extraction and PCR amplification (Box 1). In fact, most specimens collected between 1826 and 1927 did amplify (see Supplementary Table 1), and at least one genetic marker was successfully sequenced for about 90 % of all 651 extracted herbarium specimens.

Of the 611 specimens subjected to *rps*16 sequencing, sequences were obtained for 438 (71.7 %). Although the frequency of specimens in each age class was unevenly distributed, with highest frequency of recently collected material (Fig. 2), a significant relationship between sequencing success and age was found by logistic regression (logit $q = -0.01113 \cdot t + 1.3939$, $p = 2.7 \cdot 10{-}5$, $n = 611$). The model explained 2.43 % of the total deviance. The graph of back-transformed predictions from the model (Fig. 3) shows that the expected sequencing success decreases from c. 80 % for recently collected material to c. 60 % at an age of 100 years. Beyond 100 years, the model indicates a slightly accelerating decrease, but the amount of available old material is insufficient to tell if this is a real trend. Although the model indicates a nearly linear relationship between sequencing success and age, a larger number of old specimens is needed to infer the shape of the relationship, for example if it is close to linear, as indicated (Fig. 3), or logarithmic (i.e., that a constant fraction of successful sequencing trials remains after each doubling of the age of the material).

Both the statistical analysis of results for the rps16 intron and inspection of data for the other markers (Supplementary Table 1) indicate that the upper age limit for herbarium material, from which DNA can be successfully sequenced using regular methods, has not been reached. This is exemplified by the three samples next to the oldest, all of which produced sequences for the DNA regions we attempted to amplify (Supplementary Table 1). Thus, although the negative relationship between age of the material and DNA quality is beyond doubt, other factors are also likely to affect the quality of the DNA. This is evident from the difference in DNA quality and amplification success between equally old accessions of the same species (Supplementary Table 1): the two accessions of *Eriophyton rhomboideum* from 1879 and the two accessions of *Lamium macrodon* from 1902). Already in 1985, Rogers and Bendich wrote „…the extent of DNA degradation for the herbarium specimens appeared to be related to the condition of the leaf rather than the year in which it was dried". Taylor and Swann concluded in 1994 that „...in general, old, air-dried material that has neither been treated with chemical preservatives nor with high heat has the best chance of yielding useful DNA". Our results corroborate their conclusion; our attempts to extract DNA from chemically treated or poisoned specimens never yielded amplicons. It seems that massive parallel sequencing techniques have had more success with such materials (Weiss et al. 2016, Gutaker et al. 2017). More research is needed, however, before we have a full understanding of the conditions other than age and toxic chemicals that affect DNA quality. Such knowledge is important to guide us how to best preserve our valuable collections for the future.

The nested PCR procedure proved successful for obtaining amplicons from degraded DNA. However, optimization was often required to obtain acceptable sequences (Box 2). Moreover, nested PCR is highly prone to contamination, and some of the sequences we obtained were contaminated by modern DNA sources. DNA degradation leads to more fragmented DNA and fewer copies of the entire target sequence for the PCR to work on (Soltis and Soltis, 1993). This, in turn, increases the likelihood of amplifying contaminants. The reason for this is that amplification of damaged or modified DNA is less efficient than amplification of intact template, and that intact DNA always will be amplified preferentially (Pääbo 1989). Although contamination is usually easy to detect by stronger than expected PCR bands as well as the ‚wrong' sequence, it is preferable for obvious reasons to avoid amplification of contaminants altogether. Use of taxon-specific primers and amplification of shorter fragments reduces the risk of contamination.

The ‚replicate PCR procedure' (Box 2) enabled acquisition of DNA sequence data from DNA templates previously discarded as unsuitable for PCR-based methods. Often, only a barely visible band was obtained in one or more of the 8–16 PCR reactions, and in most cases, pooling of near invisible PCR bands resulted

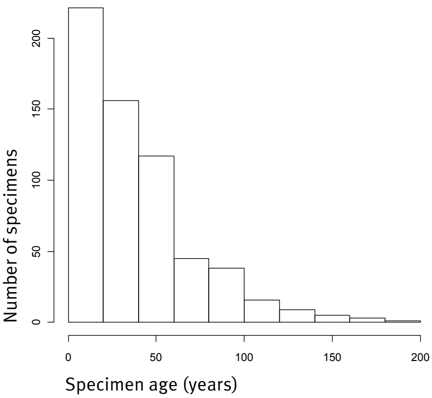

Fig. 2. Histogram of number of specimens subjected to *rps*16 sequencing as a function of the age of the material.

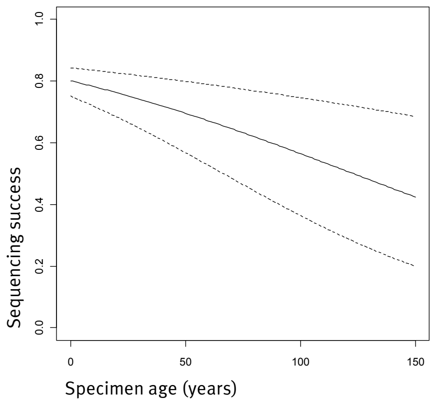

Fig. 3. Predicted relationship between sequencing success (y-axis) and age of material (x-axis), as given by the logistic regression model logit (Sequencing success)= -0.01113·Age + 1.3939 ($p = 2.7 \cdot 10^{-5}$, $n = 611$). Broken lines indicate the 95 % confidence interval for sequencing success.

in excellent sequences. That bands occur in only few of the replicated reactions, suggests that PCR is a somewhat random process that by chance manages to pick up rare fragments. The larger the number of reactions in the replicate procedure, the more likely this is to happen. We have so far never experienced contamination using this method. Increasing the relative volume of template DNA in the PCR reaction never resulted in amplification, possibly due to inhibitory substances extracted along with the old DNA, as previously demonstrated by e.g., Savolainen et al. (1995).

Performing replicate DNA extractions (using smaller volumes of tissue in each tube; Box 2) from the same voucher, with subsequent pooling of the extracts, seems to further increase the chances to obtain good sequences from old herbarium material. In order to minimize destruction of valuable old herbarium specimens, we recommend that this procedure is applied from the beginning in certain cases, instead of extracting larger amount of material in single tubes.

Although neither of the ‚replicate procedures' described in Box 2 would be cost or time efficient for many samples, they may prove useful for complementing datasets with the few difficult-to-amplify templates. Moreover, time and costs can be saved by escaping the need to establish alternative methods that may require additional equipment or chemicals, which is indeed the case still for many labs in the world.

The data used herein were generated as part of a molecular systematic project of the subfamily Lamioideae (Bendiksby et al. 2011a, b, c, 2014; Salmaki et al. 2013, 2015; Scheen et al. 2010) and were not produced specifically for testing the maximum age of herbarium material that can be sequenced using regular procedures. Thus, the upper limit for fragment length and specimen age is likely to be higher than what is reported herein.

We have reasons to believe that our own studies (e.g., Scheen et al. 2010) are not the only ones in which taxa have had to be omitted due to unsuccessful amplification of DNA extracted from archived specimens. Accordingly, we believe that our modifications to the regular procedure, which significantly increased our ability to obtain DNA sequences from most of the DNA extracts omitted by Scheen et al. (2010) and additional old herbarium specimens (e.g., Bendiksby et al. 2011a, b, c, 2014; Salmaki et al. 2013, 2015), may be of interest to other molecular systematists still using PCR-based methodologies.

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Author contributions statement

Mika Bendiksby designed the study concept and drafted the article. Liseth Thorbek and Mika Bendiksby did the molecular work. Rune Halvorsen did the statistical analyses. Rune Halvorsen and Mika Bendiksby interpreted the results and finalized the manuscript. Charlotte Bjorå was involved in early discussions, commented on and improved the manuscript. All authors approve of the published version.

Conflict of interest statement

The submitted work was not carried out in the presence of any personal, professional, or financial relationships that could potentially be construed as a conflict of interest.

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An integrated approach to studying tropical plant diversity – Taxonomic monographs, herbarium specimens and the sweet potato *(Ipomoea batatas)*

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Recent decades have witnessed a massive increase in data accumulation, but our knowledge of the world's biodiversity is still fragmentary: data accumulation has not been matched by a parallel taxonomic effort, and many groups of organisms have never been comprehensively studied. In the current context of climate change and biodiversity loss, we need to accelerate taxonomy and species discovery. This, however, requires a good taxonomic and phylogenetic framework, which is lacking for most groups of tropical plants.

This contribution discusses the role of botanical monographs in accelerating taxonomy. We argue that the increasingly easier access to data in the world's herbaria and the availability of DNA sequence data place botanists in an unparalleled position to produce taxonomic monographs, the forefront of taxonomic research.

We illustrate the discussion with the results of a monographic study of the genus *Ipomoea* (Convolvulaceae). We integrated herbarium-based morphological studies with techniques of phylogenetic and genomic analysis of thousands of specimens to develop more robust species delimitation hypotheses and a comprehensive phylogenetic framework. Monographs such as ours have implications for other disciplines beyond taxonomy. We specifically show how it enabled important discoveries related to the origin of sweet potato, a worldwide staple crop.

Keywords
Crop wild relatives, Natural history collections, Plant diversity, Species discovery, Taxonomy

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Charles Darwin travelled across the world on board the Beagle from 1831 to 1836. Observations during that trip and back home in England inspired what would later become a seminal work in biology. However, The „Origin of Species" was not Darwin's first relevant contribution to science. Darwin's most important work until then and, in fact, the work that established his reputation as a zoologist was a monograph of barnacles. His interest in barnacles began with the collection of a specimen off the coast of Chile in 1835 during the voyage of the Beagle; it then took him eight years of intense work (1846–1854) to complete his monograph (Darwin 1851, 1854). Darwin's monograph includes a detailed account of the world's barnacles known at the time, both living and fossil, descriptions of new species, first-time observations on barnacle biology and the confirmation that cirripeds are not molluscs but crustaceans (Richmond 2007).

At the start of his work on barnacles, Darwin realised barnacle taxonomy was in much need of study[1]. Undaunted, his initial confusion was soon replaced by excitement for the task[2]. Finally, towards the end of his work, he felt exhausted[3]. Luckily, Darwin finished his monograph, and the rest is history. The work made Darwin's reputation among his contemporaries and in 1853 the Royal Society presented him with a Royal Medal „For his work entitled Geological observations on coral reefs, volcanic islands, and on South America, and his work, Fos-

[1] „Literally not one species is properly defined: not one naturalist has ever taken the trouble to open the shell of any species to describe it scientifically, & yet all the genera have ½ a dozen synonyms. […] The subject is heart breaking." (Darwin 1849a).

[2] „How I shall enjoy getting back to Down with renovated health, if such is to be my good fortune, & resuming the beloved Barnacles." (Darwin 1849b).

[3] „I am at work on the second vol. of the Cirripedia, of which creatures I am wonderfully tired: I hate a barnacle as no man ever did before, not even a Sailor in a slow-sailing ship." (Letter to W.D. Fox 1852).

sil Cirripedia of Great Britain, Section Lepadidae, Monograph of the Cirripedia" (Hooker 1853, Jackson 2014). The address delivered by the then President of the Royal Society, William Parsons, 3rd Earl of Rosse, speaks about the merit and contribution of Darwin's monograph to science[4]. Since its publication, Darwin's monograph has accumulated thousands of citations (cf. Google Scholar), and, 170 years on, it is still relevant to researchers working on Cirripedia (e.g., Buckeridge et al. 2018, Simon-Blecher et al. 2021). More importantly, Darwin learnt new methods and arguments through his monographic work and built a global view of biology that was of utmost importance to his later works.

The past and present of botanical monographs

A taxonomic monograph is a compendium of all existing systematic knowledge about a group of organisms, ideally a clade (i.e., a monophyletic group; Box 1), and its importance and uses far exceed taxonomy, as we show later in this paper. In botany, the first so-called „taxonomic monograph" was Robert Morison's Plantarum Umbelliferarum Distributio Nova, published in Oxford in 1672 (two-hundred years before Darwin's monograph of *Cirripedia).* Morison was followed by others in the 17th and 18th centuries, and monographs were most common in the 19th century and the first half of the 20th century, during the so-called Golden Age of Botany. Alongside some of the most ambitious global botanical works, such as de Candolle's Prodromus (de Candolle and de Candolle 1824) or Engler's Das Pflanzenreich (Engler 1900), this period witnessed the publication of many botanical monographs, such as those on *Geranium* Tourn. ex L. (Andrews 1805), *Paeonia* L. (Anderson 1818), *Dianthus* L. (Williams 1893), *Mimulus* L. (Grant 1924), and *Heuchera* L. (Rosendahl et al. 1936), to name just a few.

Box 1. Content of a monograph
A taxonomic monograph is the systematic study of a group of organisms (normally an order, family, or genus) at a global scale and combining morphological, ecological and, at the present time, molecular data. Comprehensive Monographs include a range of information for every species, including:

> Nomenclature and types
> Descriptions
> Distribution, habitat, ecology
> Conservation status
> Uses
> Reference specimens
> Photographs, maps, illustrations
> Identification keys
> Cytology, micromorphology
> DNA and phylogenies

Since around the 1950s, taxonomic monographs have focused on small to medium-sized genera (e.g., Harris and Wortley 2018, Boza Espinoza and Kessler 2022) or genera geographically restricted to one country (Martins and Almeda 2017; Cardona-Cruz et al. 2021). Large, mega-diverse genera are rarely monographed as a whole; instead, work normally focusses on specific subgenera or sections within them (e.g., Bohs 2001, Luceño et al. 2021).

A monograph of *Ipomoea*

In 2013 we set out to monograph *Ipomoea* L., a megadiverse genus in the Convolvulaceae Juss. family with c. 800 species and a pantropical distribution. Within just seven years, we published sixteen papers on the genus, one of them a monograph of all 425 species in the American continent (Wood et al. 2020). To date, we have described 70 species new to science; identified and re-organised synonyms in the genus to a 69% synonymy rate (i.e., 7 out of every 10 names published in relation to *Ipomoea* are synonyms); designated almost 300 lectotypes; and published over 400 species

[4] „In your Monograph of the Pedunculated Cirripeds, you have treated generally of the structure, economy and zoological relations of these animals, and given a systematic arrangement and description of the different species. In the accomplishment of your task, you have not only made use of previously existing materials with sound and enlightened criticism, but, by the discovery of new facts and the promulgation of original views, contributed most materially to advance the department of knowledge to which your researches more immediately belong, and rendered valuable service to physiological science in general." (Earl of Rosse 1854, pp 355–356)

descriptions, distribution maps, phylogenies, and identification keys (Muñoz-Rodríguez et al. 2019, Wood et al. 2020). We also investigated the relationship between *Ipomoea* and other formerly recognised genera in the tribe Ipomoeeae *(Argyreia* Lour., *Rivea* Choisy, etc.), showing that they were all nested in *Ipomoea* and proposing the recognition of an expanded, monophyletic *Ipomoea* (Muñoz-Rodríguez et al. 2019, 2023). We have provided extensive detail on the taxonomic results of our monographic work (description of new species, synonymy rates, extensive lectotypification, etc.) in different publications (Wood et al. 2015, 2017, 2020, Wood and Scotland 2017a; b; Muñoz-Rodríguez et al. 2019, 2023).

Importantly, this monographic work not only overhauled the generic and species-level taxonomy of *Ipomoea* but provided insight on a range of topics, including trans-oceanic contact theory (Muñoz-Rodríguez et al. 2018), evolutionary radiations and biogeography (Muñoz-Rodríguez et al. 2019; Carruthers et al. 2020), the extent of specimen mis-identification in natural history collections (Goodwin et al. 2015, 2020), and the origin and evolution of a crop species – the sweet potato (Muñoz-Rodríguez et al. 2018). This reflects the value of overhauling the taxonomy of a group in a phylogenetically informed way, which in turn acts as a springboard for insight into a range of topics.

In the rest of this paper, we discuss how a taxonomic monograph of *Ipomoea* enabled the study of the origin and evolution of the sweet potato, including the identification of its closest wild relatives and the living species that are most likely direct descendants of its progenitors.

Sweet potato knowledge

Sweet potato, *Ipomoea batatas* (L.) Lam., is the most well-known and economically important member of the genus *Ipomoea.* Cultivated in all tropical and subtropical regions of the world for its edible storage roots, it is among the ten most consumed crops worldwide (Food and Agriculture Organization of the United Nations, 2022). Orange-fleshed sweet potato varieties are rich in β-carotene, a vitamin A precursor, and their consumption helps to alleviate vitamin A deficiencies which affect millions of children worldwide (Kurabachew 2015).

In 2013, at the start of our project, many aspects of sweet potato evolution remained poorly understood. It was not known, for example, whether the sweet potato had a single origin or multiple origins, as there were papers supporting both conflicting views (Muñoz-Rodríguez et al. 2018). In addition, it was not known whether *Ipomoea batatas,* a hexaploid species, originated by direct autopolyploidization from a wild ancestor – or which ancestor species it was – or whether it was the result of hybridisation between different species. Studies aiming to clarify the relationship between the sweet potato and its wild relatives were numerous, but knowledge about the species closely related to the crop species was generally inadequate. Among other prob-

Fig. 1, A–D. Sweet potato wild relatives are morphologically very similar.
A *Ipomoea batatas*
B *Ipomoea grandifolia*
C *Ipomoea ramosissima* and
D *Ipomoea triloba*
Photographs: J.R.I. Wood / R. Scotland

lems, evolutionary studies were often based on wrongly identified specimens (e.g., Jones 1967, Muñoz-Rodríguez et al. 2019). A consequence of the lack of a sound taxonomic framework was that different authors had proposed almost all species in the sweet potato group as possible progenitors of the crop, mostly with little evidence.

In summary, at the beginning of our study, species boundaries in the sweet potato group were ill-defined; misidentified specimens were common in herbaria and the literature; and the phylogenetic relationship between wild relative species and the crop was uncertain.

Sweet potato studies in the context of a taxonomic monograph

The basis for our work on sweet potato was the study of *Ipomoea* herbarium specimens. During this project, we studied thousands of herbarium collections; our specimen database currently includes c. 14 000 collections (c. 22 600 specimens) from around 100 herbaria and virtual herbaria worldwide, and many other specimens have been studied but not databased. As of May 2023, 1750 collections in our database correspond to the sweet potato group, i.e., species closely related to sweet potato (see below). At the time of writing, we have also sequenced over 2500 herbarium specimens representing c. 460 *Ipomoea* species, ~60 % of species in the genus, using either Sanger or high-throughput sequencing. Although it was not our original goal, this comprehensive taxon and data sampling allowed us to study sweet potato and its relatives in depth.

First, we aimed at species delimitation. Our methodology (Scotland and Wood 2012, Muñoz-Rodríguez et al. 2019) combined herbarium-based (i.e., morphological) analyses with phylogenetic analysis of DNA sequence data, with constant cross referencing between the two. The integration of DNA sequence data in the taxonomic process allowed us to detect misidentified specimens and, secondly, to generate more robust species delimitation hypotheses with both morphological and DNA support.

Ipomoea batatas has been traditionally classified in *Ipomoea* section or series Batatas alongside a variable number of wild species (Choisy 1845, Grisebach 1864, House 1908, van Ooststroom 1953, Austin 1978, 1988). Hereinafter we refer to this group of species as the Batatas group (or Clade A3 sensu Muñoz-Rodríguez et al. 2019). The wild species in the group are of interest for sweet potato improvement and food security. However, species differentiation in the Batatas group based on morphology is difficult and often relies on subtle differences in sepal size and shape (Fig. 1, A–D, Austin 1978, Wood et al. 2020). Other morphological characters are not reliable given the variability within species and frequent character overlap. For that reason, species identification in the Batatas group is challenging and specimen misidentification is frequent. A consequence of this is that phylogenetic analyses that do not include an *Ipomoea* taxonomist or do not challenge prior identifications of the specimens sequenced almost always include misidentified specimens. It is therefore essential for such works to include voucher specimens, the identification of which can subsequently by verified.

As explained above, we generated comprehensive DNA sequence data for *Ipomoea*. Our aim was to incorporate as many species as possible, and several specimens per species when possible. Specifically, for the Batatas group, we first sequenced multiple specimens of every species using Sanger sequencing to obtain DNA barcodes *(nrITS, matK, rpl32-trnL)*. In other clades of the *Ipomoea* phylogeny, DNA barcodes enable a quick, reliable differentiation between species. In the Batatas group, however, DNA barcodes do not provide enough resolution to differentiate species; except for a small number of species, most species within Batatas form a largely unresolved polytomy in DNA barcode phylogenies (Muñoz-Rodríguez et al. 2018). We thus incorporated high-throughput sequence data in our sweet potato studies. We specifically used HybSeq to obtain whole chloroplast genomes and 386 putative single copy nuclear coding regions from multiple specimens of every species. This allowed us to obtain phylogenetic trees with strongly supported nodes and, for the first time, to define clear boundaries between species and to better understand their evolutionary relationships (Muñoz-Rodríguez et al. 2018).

Thus, as currently recognised and supported by our results, the Batatas group includes *Ipomoea batatas* and 15 wild relatives: *I. aequatoriensis* T. Wells and P. Muñoz, *I. australis* (O'Donell) J.R.I. Wood and P. Muñoz, *I. cordatotriloba* Dennst., *I. cynanchifolia* Meisn., *I. grandifolia* (Dammer) O'Donell, *I. lactifera* J.R.I. Wood & Scotland, *I. lacunosa* L., *I. leucantha* Jacq.,, *I. littoralis* Blume, *I. ramosissima* (Poir.) Choisy, *I. splendor-sylvae* House, *I. tenuissima* Choisy, *I. tiliacea* (Willd.) Choisy, *I. trifida* (Kunth) G. Don and *I. triloba* L.. We confirmed that most species are monophyletic, with only the two putative hybrid species, *I. leucantha* and *I. grandifolia* needing further study, and clarified the relationship between them and with sweet potato itself. Importantly, three of these species were described as new to science by us: *Ipomoea australis, I. lactifera,* and *I. aequatoriensis.* The discovery of *Ipomoea aequatoriensis* turned out to be especially important, since we were able to show that this species is the sweet potato's closest relative and, most likely, a direct descendant of sweet potato's progenitor species (Muñoz-Rodríguez et al. 2022).

Subsequently, having comprehensive *Ipomoea* phylogenies also allowed us to show that storage roots are commonplace in *Ipomoea,* and that the storage root of *Ipomoea batatas* is not the result of domestication but a trait that predisposed the species for cultivation. We were also able to show that the origin of sweet potato predates humans, and that at least part of the diversity existing within the crop also predates human involvement (Muñoz-Rodríguez et al. 2019).

In summary, in the context of a taxonomic monograph, we produced extensive data that allowed us to study sweet potato's origin in detail. We identified all sweet potato wild relatives, including its closest relatives. Our work is just one example of how the results of a taxonomic monograph have implications that go beyond taxonomy to dramatically improve our understanding of the natural world.

The future of botanical monographs

Good taxonomy provides a solid foundation for the conservation of the world's biodiversity. In the current context of climate change and biodiversity crisis, we need to accelerate the speed at which biodiversity is studied and new species are described, and to provide a robust taxonomic backbone to integrate existing knowledge. A monograph may simply assemble all existing knowledge of a group of organisms in the same publication, but more often monographs comprise new research that comprehensively revises the existing taxonomy and systematics of a group with new data building on previous research efforts. Although underutilised, they stand at the forefront of taxonomic research and thus have the potential to be key resources for biodiversity studies.

Modern-day taxonomists willing to start a monograph must deal with three main challenges. First, they face centuries of accumulated, sometimes obscure literature, which frequently contains as much error as useful information. Second, the number of specimens in the world's herbaria has increased exponentially in recent decades (Bebber et al. 2010), making it logistically complicated to study a representative number of specimens of any one group. Third, the current publishing environment and rewards system in science do not encourage researchers to produce taxonomic monographs. Instead, researchers prioritise smaller, often DNA-focused approaches that can be published faster in higher-impact journals, although the results may be relatively trivial. These problems are further exacerbated in the case of the very big genera (Frodin 2004), where the sheer amount of information available inhibits attempts to monograph them (Scotland and Wood 2012).

Although the number of botanical monographs decreased in the second half of the 20th century, they have received renewed support in recent years and there seems to be revived interest in them (Gorneau et al. 2022). Furthermore, we argue that the integration of herbarium-based research, readily-available techniques of molecular data analysis and big data places present-day botanists in an unparalleled position to study the world's plants. First, the number of herbaria worldwide has doubled in recent decades and the number of collections they preserve has grown exponentially (Bebber et al. 2010, Goodwin et al. 2015). This presents a challenge but also an opportunity to monographers, who now have more information than ever before to refine and enhance their morphological studies and avoid potential errors (Bakker et al. 2020). Secondly, as the price of molecular sequence data generation steadily decreases, molecular data, even if only DNA barcodes, are now accessible to most researchers. Thirdly, high-resolution specimen images, especially images of type specimens, are increasingly available via virtual herbaria, JSTOR or other online repositories. Fourthly, we now have almost unrestricted access to historical publications via the Biodiversity Heritage Library, JSTOR, or herbaria Digital Libraries (e.g., Royal Botanic Garden in Madrid). In the case of more recent publications, those not published in open access journals can be easily accessed through platforms such as ResearchGate, or simply by e-mailing the authors.

In summary, the number and diversity of specimens in herbaria worldwide, the increasing affordability of sequence data generation, and the immediate online access to voucher specimens, species information and researchers worldwide, make taxonomic monographs more feasible and faster to produce than ever before, and should lead to a renaissance of botanical monographs. Whether the taxonomic community has the motivation, the funding and the workforce required remains an open question, but, as we have shown with the sweet potato, the results of these much-needed studies have implications far beyond taxonomy.

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A large phylo-floristic study on the present and future assembly of the Wisconsin flora – An area unique in North America

Kenneth M. Cameron

With 1.4 million specimens the Wisconsin State Herbarium (WIS) is one of the largest in the Americas and Wisconsin offers botanists a unique opportunity to study species representing a confluence of global biomes. The state harbors >2640 species of vascular plants which have been sequenced for the two-gene plant DNA barcode to reconstruct a community phylogeny. At the same time >300 000 georeferenced specimens were used with bioclimatic and soil data to produce species distribution models for the flora, then subsequently aggregated to determine current and future patterns of species richness and phylogenetic diversity. Among the many surprising results uncovered are predictions that whereas species richness will increase as c. 850 taxa move into the state, c. 242 species will become extirpated by 2070. These most vulnerable species will not be affected at random. Furthermore, models suggest that Wisconsin's projected climate will be unsuitable for most species to be able to retain their present distributions; only 65 s% will be able to retain more than half of their current distributions. However, the state's well known unglaciated Driftless Area may be able to serve as an Anthropocene refugium better than anywhere else in the region and should be targeted for increased land conservation.

Keywords
Climate, Community, Discovery, Niche, Phylogeny, Spatial, Taxonomy

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The 2019 United Nation's Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES 2019) Global Assessment Report states that „around 1 million animal and plant species are now threatened with extinction, many within decades, more than ever before in human history [and] … the average abundance of native species in most major land-based habitats has fallen by at least 20 %, mostly since 1900." With these sobering statistics in mind a team of researchers within the Department of Botany at the University of Wisconsin-Madison, including this author, initiated a multi-year project funded by the US National Science Foundation entitled „Roles of functional, phylogenetic, and genetic diversity in structuring and sustaining plant communities through environmental change". Our subject was the flora of the state of Wisconsin located in the Upper Midwest Great Lakes Region of North America. Why Wisconsin? One reason is access to the large repository of herbarium specimens within the Wisconsin State Herbarium (WIS), a collection of c. 1.4 million specimens housed at the University of Wisconsin-Madison and among the ca. 12 largest herbaria in the Western Hemisphere (Thiers 2022). For decades regional specimens collected since the mid-19th century (WIS was only established in 1854) have been actively used to document changes in the flora of the state.

Unfortunately, Wisconsin's unique landscape has been greatly altered by human activity. Today it is home to 11 federally recognized Native American tribes, more than any other state east of the Mississippi River, but their ancestors who first came to the state >10 000 years ago had minimal impact on the biota compared to the transformation that occurred during colonization in the 19th century. This was especially pronounced during the waves of massive immigration from Europe that occurred between the years 1850–1900 when the state's human population increased from a mere 305 000 to a staggering 2 060 000. The current population is c. 5.9 million centered in a few rapidly expanding urban areas (e.g., the cities of Milwaukee and Madison) but also is scattered widely across the state where logging and agriculture continue to impact biodiversity across ecosystems. Human population growth, industrialization, farming, and other factors have led also to noticeable changes in local climate. In fact, Wisconsin recently was considered to be tied for first place among the 48 contiguous states of the USA for having experienced the largest annual average temperature increase (+0.67F/+0.37C per decade) since the first Earth Day was held on the campus of UW-Madison in 1970 (data from February 21, 2013 at https://www.climatecentral.org/news/winters-are-warming-all-across-the-us-15590).

Another reason to target Wisconsin is that although it is small in area, the state offers botanists an unparalleled opportunity to study terrestrial species representing a unique confluence of global biomes: boreal conifer forests, eastern deciduous forest, savannas, mixed hardwood forests, and grasslands, as well as various Great Lakes freshwater communities distributed across both a historically glaciated and unglaciated landscape. In total it is estimated that the state harbors at least 2640 species of vascular plants, of which 1873 are native and 767 are introduced; there are at least 158 families and 779 genera represented (Wetter et al. 2001).

The primary purpose of the study was to use Wisconsin as a model system in order to contrast patterns of vascular plant species richness with phylogenetic diversity by employing a comprehensive spatial phylogenic (i.e., phylofloristic) approach. Much of this study, including more details of methodology and results than summarized below, was published by Spalink et al. (2018) with related papers published subsequently by Beck et al. (2022), Givnish et al. (2020), and others.

Methods

An ambitious specimen digitization effort by students and curators at WIS in recent years has resulted in >490 000 in-state records being databased of which >75 % have been precisely georeferenced (see https://www.herbarium.wisc.edu). Furthermore, in order to provide phylogenetic information to ecologists and others interested in studying changes in floristic composition through time (past, present, and future), we sequenced the two-gene universal plant DNA barcode (plastid rbcL+matK) and reconstructed a complete community phylogeny for the Wisconsin flora with genomic DNA extracted almost exclusively from historical herbarium specimens. To our knowledge no other state in the USA has achieved this level of data completeness. At the same time >300 000 georeferenced specimens collected in the state were used together with bioclimatic and soil data to produce species distribution models for the entire native flora, which were subsequently aggregated in order to determine patterns of potential species richness and phylogenetic diversity across the state.

Result and discussion

Curiously, the pattern of species richness we revealed closely resembles the plant hardiness zone maps that are published and updated regularly by the US Department of Agriculture. These show a gradient from the SE corner of the state (updated recently to hardiness zone 5b) toward the NW (currently hardiness zone 3b). Likewise potential species richness is greatest in the southeastern and central regions of Wisconsin as shown in Fig 1. Some of these areas are precisely those that were rapidly cleared for agriculture in just one generation's time during the mid-1800s. Relatively few herbarium specimens exist from some of these human-altered areas, but we can hypothesize based on our models that they once supported high levels of vascular plant diversity, now lost forever.

In contrast, our estimation of phylogenetic diversity (a metric that not only considers numbers of species / richness, but also lineages or branches of the tree of life) shows a strikingly different pattern. Wisconsin is most phylogenetically diverse in the northern half of the state. The southern areas are species rich, but most of that diversity is attributable to many species from just a few families such as Asteraceae, Cyperaceae, and Poaceae. Thus, Southern Wisconsin is species rich, but phylogenetically poor. Even without sophisticated models or access to advanced computing, plant ecologists such as J. Curtis (1959) were able to document that the flora of the northern tier of the state is qualitatively different from the southern tier. For example, he documented Wisconsin's well known „tension zone" – an imaginary diagonal line that divides the vegetation of the state between the northeast and the southwest – a pattern that closely resembles our map of statewide phylogenetic diversity (see Spalink et al. 2018).

Of course, we not only wish to look back in time or to document patterns of species richness and phylogenetic diversity today, but also to use our data to inform conservation biologists interested in what effects climate change may have on this region of North America in the next century. In order to predict future phylo-floristic change, a much larger supermatrix of c. 2300 Eastern North American vascular plants (i.e., not only those documented from Wisconsin) also was analyzed under models that account for 50 years of predicted climate change.

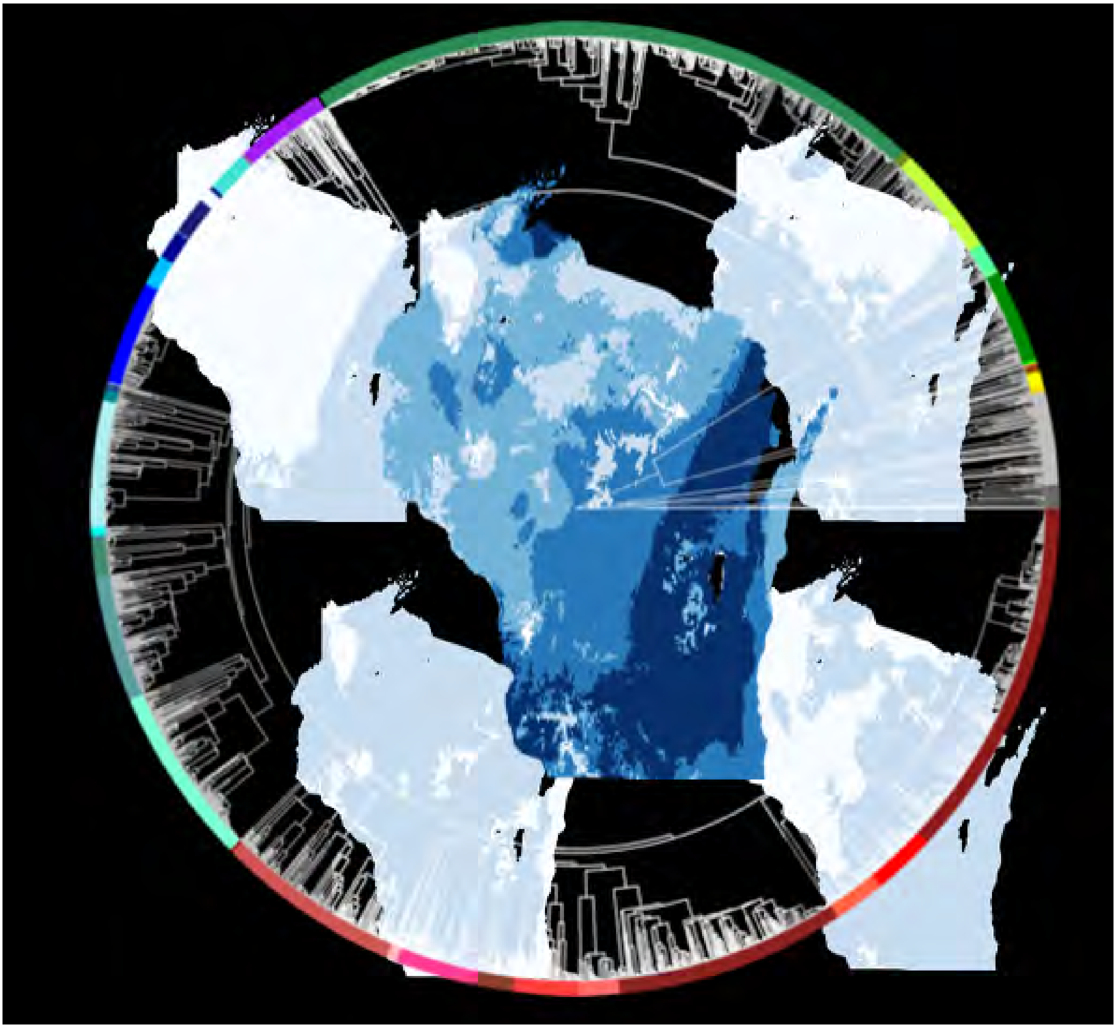

Fig. 1. Phylo-floristic summary figure. More than 300'000 specimen occurrence records were employed to generate individual species distribution models such as the four inset maps (where the shade of blue scales with habitat suitability) for every native vascular plant species found in Wisconsin and then to aggregate them in order to document potential species richness across the entire state (central map, where darker blue indicates higher potential species richness). In addition, a time-calibrated community phylogeny of the state's entire vascular flora (circle tree, where colors indicate plant orders) was used with distribution maps to identify areas with high phylogenetic diversity (not shown). See Spalink et al. (2018) for further information regarding this phylo-floristic approach.

This approach was necessary because each year we document new occurrence records for species that were originally non-indigenous, but are now migrating into Wisconsin, especially from the south, as the climate becomes more mild. Among the many surprising results we uncovered are predictions that whereas overall species richness will actually increase as c. 850 southern taxa move northward into the state, some 242 species may become extirpated by 2070. Unfortunately, these most vulnerable species will not be lost at random from our flora, but instead represent 15 % of monocots, 28 % of ferns / lycopods, and 30 % of orchids, for example. In fact, we can predict exactly which species may be most at risk by using Schoener's D statistic that measures the overlap in species' ranges comparing their present to future predicted distributions in Wisconsin. Sadly, our models suggest that Wisconsin's projected climate will be unsuitable for most species to be able to retain their present distributions; only 65 % will be able to retain more than half of their current distributions in the state. If these future predictions hold true, then attempting to restore past or maintain present floristic communities may need to be reconsidered. Already there is documented evidence that many vascular plants have shifted their center of distribution significantly to the northwest from comparisons of vegetation plots conducted in the 1950s then again in the 2000s (Ash et al. 2017). Of course it is important to consider also that these models and predictions based on climate do not take into account the role of various biotic factors on vegetation, such as overgrazing by herbivores including white tailed deer, death by pathogens, competition with or harm by invasive species including insects such as emerald ash borer, or effects of acid rain and nitrogen deposition on the soil mycobiome. Without human assistance (e.g., assisted migration) the fate of many threatened species may be even more grim than our models of future distribution suggest.

Conclusion

The same UN report cited earlier (IPBES 2019) also tells us that „it is not too late to make a difference, but only if we start now at every level from local to global. Through ‚transformative change', nature can still be conserved, restored and used sustainably." One bit of optimism revealed by our study is that our model of future phylogenetic diversity indicates that although Wisconsin's „Driftless Area" is not a hotspot of species richness or phylogenetic diversity today, this region located in the SW corner of the state will become one of the few areas that is likely to maintain a relatively high percentage of phylogenetic diversity, even while it is lost elsewhere. This is an intriguing prediction because the Driftless Area is so named on account of the fact that it has never been glaciated, even while surrounded on all sides by ice sheet lobes at one time or another. It is a rugged landscape of forested hills, mesic valleys, spring fed trout streams, limestone caverns, and sandstone ridges. There is growing evidence that it once served as a Pleistocene glacial refugium for organisms including mollusks, small mammals, amphibians, and herbaceous vascular plants during the Last Glacial Maximum (see Li et al. 2013 for a review). What was once a refugial sink, later became a source as these plants and animals migrated northward behind with the retreating ice sheets. Could it someday become an important refugial sink again? This time for biodiversity under threat from a warming planet? If so, then land stewards are encouraged to focus their conservation efforts in this most unique region of the Upper Midwest and Western Great Lakes of North America.

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The impact of climate change on plant distribution and niche dynamics over the past 250 years in Switzerland

Jessica Wang[1], Markus Fischer[1,2], Stefan Eggenberg[3], Katja Rembold[1]

Herbarium specimens provide an irreplaceable source of historical plant distribution data, enabling analysis of changes in plant distribution spanning centuries. Most studies on plant distribution shifts focus on recent decades and rare species, especially along elevational gradients. We examined about 2000 historical herbarium specimens from the Botanical Garden of the University of Bern, representing 30 plant species from five Swiss lowland habitats (six species per habitat) dating back to 1768 and covering all Swiss cantons. All historical data were transcribed, georeferenced and then combined with current data resulting in about 170 000 plant records over 250 years. Combined with climatic data from the same period, we found that all habitats increased their potential distribution area with a significant gain in the semi-arid grasslands (+8.15 %, p-value = 0.031). On species level, 75 % of the selected species expanded their distribution, while 25 % of the species retracted. Despite these shifts, 90–99.6 % niche stability was observed between historical and current climatic niches across all species. Shifts in co-occurring species were specific to the species, not to the habitat. The consistent overlap in historical and current climatic niches suggest that distribution expansion is due to the growth of areas with suitable climates, pointing to climate change as a driving factor for plant distribution changes over the past 250 years.

Keywords
Climatic niches, Climate warming, Drivers of plant distribution, Herbarium, Niche analyses, Historical data

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Climate change has been shown to elicit an array of ecological responses, such as rapid shifts in plant distribution. Most of these distribution shifts are currently observed to be moving in poleward and upslope directions to cooler latitudes and elevations (Chen et al. 2011, Lenoir et al. 2008). However, it is unclear whether the effects of climate change on the observed distributional shifts translate into changes in the climatic niches as well (Di Marco et al. 2021).

A species' climatic niche reflects the set of temperature and precipitation conditions where the species can occur. Assessing the climatic niches of species may therefore determine how it responds to changes in climate over time (Bonetti and Wiens 2014). The unifying niche analyses framework developed by Broennimann et al. (2011) and Guisan et al. (2014) has since gained widespread popularity for invasion risk assessments. The same framework has explicitly been proposed to be well-suited for a more general assessment of the effects of climate change.

In Switzerland, the average annual temperature has increased by 2 K (2°C) since 1864 and is thus, rising two to three times faster than the global average (MeteoSwiss 2022). Yet, there has been no study to date employing the niche analysis framework to discern the climatic effects on plant species in Switzerland. Previous studies have predominantly focused on the impacts of climate change on climate-sensitive plants along elevational gradients (Vitasse et al. 2021, Stöckli et al. 2012). However, in lowland areas, differences in temperature can exceed hundreds of kilometers along the latitudinal gradient and could potentially modify spe-

Perennial ruderals | Trockenwarme Mauerflur

Annual ruderals | Einjährige Ruderalflur

Semi-arid grasslands | Halbtrockenrasen

Moist grasslands | Nährstoffreiche Feuchtwiese

Tall herb fringes | Hochstaudenflur

Fig. 1. Pictures of the investigated habitat types. Habitat names are given in English and German (as originally published in Delarze et al. 2015).

cies distribution to a greater extent than in highland areas (Jump et al. 2009). Furthermore, most of the previous studies of climate change on plants were either single snapshots in time before 1950 or as continuous historical data starting from 1970 (Wipf et al. 2013, Stöckli et al. 2012, Vitasse et al. 2021)

In this context, herbaria are underutilized treasure troves of historically and floristically diverse samples, whose use is only now beginning to be resurrected (Lang et al. 2018). Recent studies have emphasized their scientific value in addressing a diverse range of global change-related topics (Meineke et al. 2018). The Herbarium of the Botanical Garden of the University of Bern in Switzerland (Herbarium Bernense, Index Herbariorum: BERN) harbors an estimated 500 000 herbarium specimens dating back to the 18th century. Since most of the collection is not yet inventoried, it represents an untapped key resource for research on historical species ranges and niches.

We collected historical and modern distribution data from 30 plant species, representing five Swiss habitats. In combination with climate data, we were able to employ the niche analysis framework to discern the climatic effects on species distribution. Specifically, the following questions were addressed: **1** Have the selected habitats and plant species shifted their distribution during the last 250+ years? **2** Did potential changes in the plants' distribution area happen within the bounds of their historic climatic niche space or are distribution changes due to adaptations through new climatic niches? **3** Have co-occurring plant species from the same habitat type shifted their climatic niches in a similar fashion or were the observed shifts species-specific?

Methods

Selection of habitat types and species

We selected five representative habitat types after Delarze et al. (2015) that are mostly from the lowlands of Switzerland: **1** perennial ruderals; **2** annual ruderals; **3** semi-arid grasslands; **4** moist grasslands; and **5** tall herb fringes (Fig. 1). For each habitat, six character plant species were chosen, yielding 30 herbaceous angiosperms from 20 different plant families (Table 1).

Environmental data

The cutoff between „historical" and „current" observation data was defined as the year 1950, since this is commonly regarded as the beginning of the Anthropocene and is characterized by the rise of abrupt ecological shifts in both terrestrial and aquatic ecosystems (Ludwig and Steffen 2017).

All herbarium records obtained from herbarium specimens in the Herbarium Bernense were carefully examined and excluded if the collection date or location was missing. Label data information were transcribed and location information were manually georeferenced based on historical maps of Switzerland dating back to the year 1844 (swisstopo 2022). For herbarium specimens dating back further than 1844, we used the maps of the Aargauisches Geografisches Informationssystem AGIS (2021). The resulting dataset of herbarium specimens consisted of 1800 occurrence records across 30 plant species with 25–114 records per species. In addition, the National Data and Information Center on the Swiss Flora (Info Flora) provided an additional 2899 historical occurrence records. The total historical dataset based on herbarium specimens and Info Flora data consisted of 4699 data points covering the period 1768–1950. Current plant data for the years 1951 until mid-2022 were provided by the Info Flora database (Info Flora 2022) and included 166 634 data points, yielding 171 302 in total (Table 1).

The climatic data consisted of monthly mean values for precipitation and temperature, covering the period 1763–2020, provided by the Institute for Geography at the University of Bern. This long-term, high-resolution, and continuous spatial dataset covers Switzerland using spatial grids at 2.2 × 2.2 km resolution (Noëmi Imfeld and Stefan Brönnimann 2022, unpublished data).

Statistical analyses

All statistical analyses were performed using R software version 3.5.1 (R Core Team 2020). To account for seasonality effects pertinent to the main analyses with MaxEnt and environmental principal component analyses (PCA-env), the data on precipitation and temperature were delineated into 19 bioclimatic variables following Fick and Hijmans (2017). This included annual trends, seasonality, and extreme environmental factors. To avoid multicollinearity between climatic variables, any pair of variables above a Pearson correlation coefficient of $|r| > 0.8$ was considered highly correlated (Graham 2003) and was excluded. As a result, seven bioclimatic variables proved suitable and were retained for further analyses (Supplementary Fig. S1).

Species distribution modeling

For all 30 species, we modelled distributions and created maps showing the historical species distribution, the current distribution, and their difference. The distribution areas were modeled with MaxEnt using the default settings within the package dismo (Hijmans et al. 2021). By applying the Maximum Entropy principle, MaxEnt calculates a probabilistic estimate of species distribution that is the most spread out while still subject to environmental constraints. Its output is a prediction of habitat suitability represented by a probability of occurrence scale ranging from 0 (low) to 1 (high) (Elith et al. 2011). Moreover, the areas of distribution gained or lost over the last 250+ years are expressed as positive or negative percentages based on the difference in the number of pixels of each prediction map. Each pixel represents a spatial resolution of 1.580 × 2.290 km. The thresholds that were used for deciding whether a grid cell counts as absence or presence of the species was 1, which is a strict classification for a grid cell to be significantly accounted as a presence (Liu et al. 2005).

Table 1. All species and the total sample size across the historical and current datasets. The species' respective habitat types are denoted as: **PR** = perennial ruderals, **AR** = annual ruderals, **SG** = semi-arid grasslands, **MG** = moist grasslands, **TF** = tall herb fringes.

Species	Sample size
Adenostyles alliariae | **TF**	6'251
Ajuga genevensis | **SG**	2'895
Ballota nigra | **PR**	1'243
Campanula patula | **SG**	3'015
Campanula rapunculus | **SG**	2'651
Centranthus ruber | **PR**	1'699
Chelidonium majus | **PR**	6'501
Crepis paludosa | **MG**	17'438
Crepis vesicaria subsp. *taraxacifolia* | **AR**	33
Cymbalaria muralis | **PR**	3'766
Descurainia sophia | **AR**	1'120
Galium uliginosum | **MG**	7'853
Geranium molle | **SG**	3'269
Geranium rotundifolium | **AR**	2'551
Helictotrichon pubescens | **SG**	16'841
Lactuca serriola | **AR**	6'614
Lamium album | **PR**	1'487
Lilium martagon | **TF**	8'919
Malva moschata | **SG**	3'290
Myosotis scorpioides | **MG**	10'848
Parietaria judaica | **PR**	834
Polygonatum verticillatum | **TF**	9'339
Ranunculus platanifolius | **TF**	2'073
Reseda lutea | **AR**	4'720
Rosa pendulina | **TF**	8'294
Sanguisorba officinalis | **MG**	14'009
Saxifraga rotundifolia | **TF**	5'290
Silene flos-cuculi | **MG**	13'066
Sisymbrium officinale | **AR**	2'335
Stachys palustris | **MG**	3'058
Total	**171'302**
Mean sample size per species	**5'710**

Following Phillips et al. (2008), each species' historical and current plant occurrence data was split into 75 % for model training and 25 % for model testing, with 500 iterations. Validation of the models was carried out with the threshold-independent-value of the area under the receiver operating characteristic curve (AUC) (Fielding and Bell 1997). These values are derived from the receiver operating character (ROC) plot and provide a measure of overall model accuracy. Models with AUC <0.7 are considered to perform poorly (Phillips et al. 2008; Fielding and Bell 1997), and are unreliable for predicting species distributions. Lastly, to examine whether the plant distribution across habitats were significant, we performed a nonparametric one-sample sign test.

Niche dynamics modeling

The niche dynamics of all species were analyzed using the environmental principal component analysis (PCA-env), as initially proposed by Warren et al. (2008) and further modified by Broennimann et al. (2011). The environmental space of the PCA-env was defined by the seven previously identified bioclimatic variables across the whole study region. As a preliminary step before analysis, the kernel density function was applied. This allowed for the correction of potential sampling biases by determining the smoothed density of occurrences by their prevalence in the environmental space generated from the PCA-env (Broennimann et al. 2011). Next, the species' historical and current niches were tested for niche overlap. This was analyzed using Schoeners' D index, obtained using the R package ecospat (Di Cola et al. 2017) and ranging from 0 to 1 (no niche overlap and complete niche overlap, respectively). Because Schoeners' D addresses niche overlap but not the directionality of changes in niches, Schoener's D was further defined according to niche stability (0 = low stability, 1 = high stability), niche expansion, and the environmental conditions available to the current niche but unoccupied (niche unfilling) between historical and current niches.

Results

Impact of climatic changes on plant species distribution

Over two centuries, all five habitats expanded in distribution area, but only the semi-arid grassland did so significantly (Table 2). The moist grasslands had the highest median increase in distribution area (+18.75 %), while it was close to negligible for the tall herb fringes (+1.05 %). Interestingly, the semi-arid grasslands stand out as the only habitat type with a uniform increase across all associated species. The annual ruderals, on the other hand, show a high variability across the associated species (Table 2). Overall, the distribution area increased for 22 out of 30 plant species (75 %) and decreased for the remaining eight (see Fig. 2 and Supplentary Figs. S2–S5). The species with the highest loss of distribution area was *Descurainia sophia*

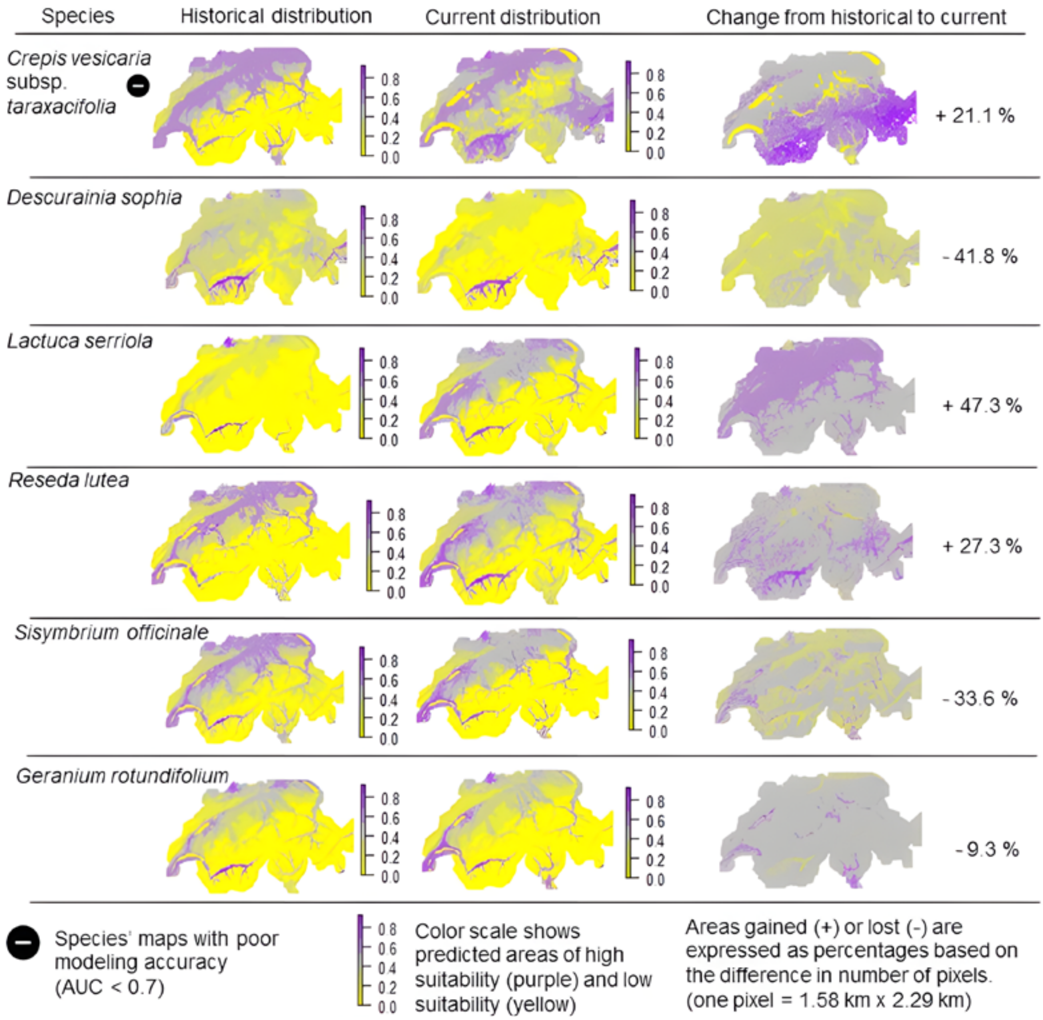

Fig. 2. Summary of the prediction maps for the six plant species of the annual ruderals (historical and current distribution plus the difference map showing the change from historical to current distribution).

(-41.8 %), while *Lactuca serriola* had the highest gain (+47.3 %). Both species occur in the habitat of annual ruderals, so the changes in distribution are species-specific, not habitat-specific.

Models with an AUC <0.7 are considered to perform poorly (Phillips et al. 2008; Fielding and Bell 1997), and are unreliable for predicting species distributions. This applied to the model evaluation of six species variable AUC values ranging between 0.50 and 0.69 (mean 0.63, SD 0.0735) *(Crepis paludosa, Crepis vesicaria* subsp. *taraxacifolia, Helictotrichon pubescens, Lilium martagon, Myosotis scorpioides,* and *Sanguisorba officinalis).* This indicates that the models for these six species are unreliable for predicting the past and current distribution. The models of the other 24 species performed well, with AUC values ranging from 0.70–0.83 (mean 0.77, SD 0.0493, Supplementary Table S1).

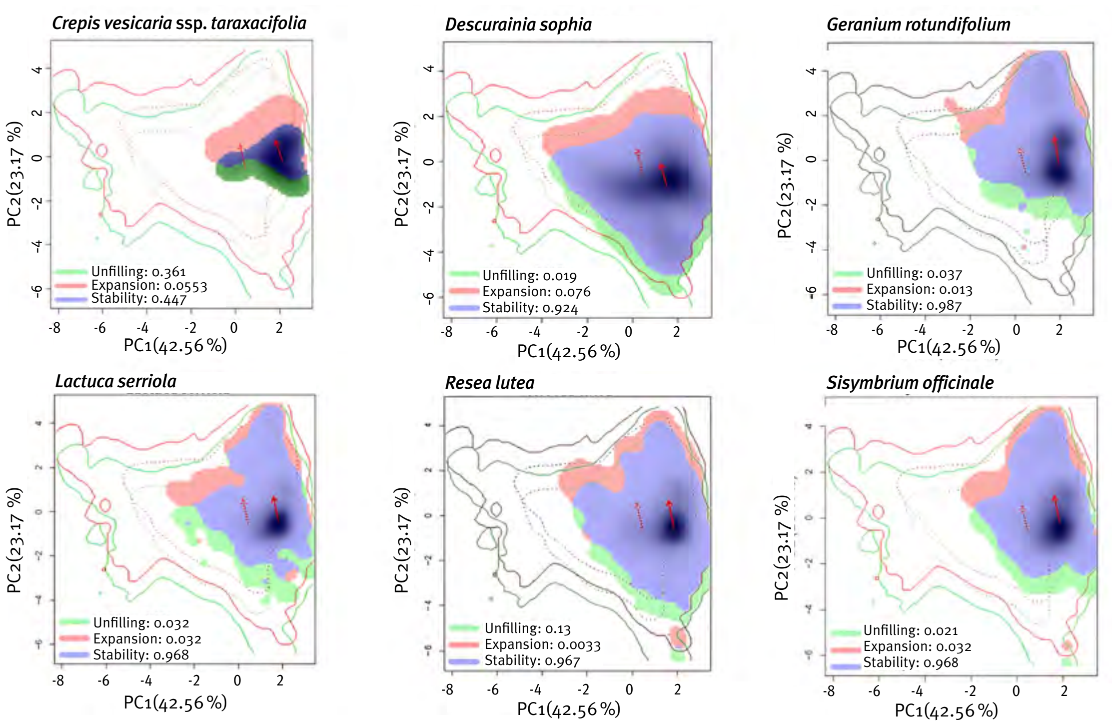

Fig. 3. Niche dynamics plot for the six plant species of the habitat annual ruderals. Solid range lines (red = current, green= historical) represent 100 % of the available environmental space, and dashed lines represent 50 % of that space. Blue shading represents the shared niche space (= niche stability) between the historical and current niches. Red shading indicates the expansion of the current niche and green shading shows the unfilling (contraction) of the historical niche when compared to the current niche. The calculated values for niche stability, niche unfilling (contraction), and niche expansion are also indicated.

Table 2. Median change of the distribution for each habitat expressed in percentages. Indicated is the median and the corresponding min. and max. values of change across all 30 species within the five habitat types (six species per habitat). Significance level: (*) when p ≤ 0.05, (**) when p ≤ 0.01, (***) when p ≤ 0.001.

	Habitat type	Perennial ruderals	Annual ruderals	Semi-arid grasslands	Moist grasslands	Tall herb fringes
Plant distribution	Median change %	7.85	5.9	8.15	18.75	1.05
	Minimum change %	13.6	-41.8	8.15	-33.3	-11.8
	Maximum change %	15.6	47.3	25.3	30.5	12.9
	p-value	0.687	1.00	**0.031 (*)**	0.219	1.00
Plant niche	Climatic niche stability %	97.8	96.2	96.4	92.9	96.7
	p-value	**0.0198 (*)**	**0.0396 (*)**	**0.0198 (*)**	**0.0198(*)**	**0.0198(*)**

The climatic niche analyses revealed that the distributional shifts on species level took place within the according climatic niches. For each species, the current climatic niche was significantly equivalent with their historical niches (Supplementary Table S2) and maintained niche stability of 90–99.6 %. The colonization of species into new regions where they had not been growing before 1950 indicates that they are able to inhabit those because they are now climatically suitable. The results of the niche dynamics analysis corroborate this explanation, as the species' niches remained highly stable within their available climatic niche space despite having moved to new regions in Switzerland.

Impact of climatic changes on plant species niches

After examining the changes in plant species distribution on geographical maps, each species' niche was analyzed to investigate whether observed geographical changes translate to changes within its climatic niche. The first two principal component (PC) axes accounted for 65.7 % of the total climatic variance (PC1 = 42.6 %, PC2 = 23.2 %; Supplementary Fig. S6). PC1 was mainly explained by mean annual temperature, mean annual precipitation, and temperature seasonality. In contrast, PC2 was principally weighted by the mean diurnal range and temperature annual range. The PCA-env revealed that all species niches remained stable, despite previously demonstrated evidence that all species occurrences have shifted (Fig. 3, Supplementary Figs. S7–S10; Supplementary Table S2).

Both, niche expansion and niche contraction, are characteristics that indicate a change of niche space positioning between the historical and current realized available climatic niche. Although every species revealed some degree of climatic niche contraction and expansion, these values were generally very low, with contraction varying from 0.012–0.094 (mean 0.032, SD 0.017) and expansion ranging from 0.003–0.122 (mean 0.039, SD 0.0209). The exception to this general pattern of stability is *Crepis vesicaria* subsp. *taraxacifolia* (stability = 0.42), which also showed the most extensive niche expansion and contraction (0.58 and 0.39, respectively; Fig. 3, Supplementary Figs. S7–S10). In contrast, *Parietaria judaica* exhibited the most stable niche (0.996), with the lowest value for niche expansion and relatively modest niche contraction (0.003 and 0.049, respectively).

To address whether the habitat types differ from each other, the overall mean stability was calculated across the species of each habitat. The climatic niche stability among the habitats remains significantly stable and relatively invariable with values ranging between 92.9 % and 97.8 % (Table 2).

The results of the niche overlap analyses and niche stability calculations highlight that the studied climatic niches of the 30 species have generally remained stable over the last 250+ years within Switzerland. Therefore, the increased distribution areas are not due to adaptations to new climatic niches, but to an increase of the area with the according climatic conditions.

Discussion

Distribution shifts without associated climatic niche shifts

The climatic niche analyses revealed that the distributional shifts on species level took place within the according climatic niches of each species with a niche stability of 90–99.6 %. Although not explicitly tested for, our results suggest that newly colonized regions shown in our distribution maps correspond to the warmer temperatures within these areas today. In the past, these areas were climatically unsuitable for the according species, but due to the warmer climate they now provide a suitable climatic niche. Most of the 30 plant species benefit from warmer temperatures, as demonstrated by their increased distribution area. *Lactuca serriola* expanded its distribution most of all, gaining almost an additional 50 % compared to the historical distribution. This is in line with the study from D'Andrea et al. (2009), who found that climate warming has increased the number of suitable and inhabited sites for *Lactuca serriola* across Europe. Thus, the increased distribution area shown here for 22 species, is likely the result of spreading to areas that were getting warmer and, thereby, became more suitable today than in the past.

Eight species showed a reduced current distribution area compared to their historical distribution while the distribution area of their habitats increased. One of those species is *Stachys palustris,* which was shown to perform poorly in pollination competition experiments (Chittka and Schürkens 2001) and both *Chelidonium majus* and *Geranium rotundifolium,* showed a pronounced decrease in plant height when grown with other ruderal plants (Steingräber and Brandes 2019). As it was shown for all eight species that they are likely to be outcompeted by other species (e.g., Fazlioglu et al. (2016) for *Cymbalaria muralis* and Mark and Brown (1992) for *Sisymbrium officinale),* it is more likely that biotic factors such as competition were the drivers for their distribution decline.

Crepis vesicaria subsp. *taraxacifolia,* showed the lowest niche stability and the highest degree of niche contraction and expansion. With only 33 records, this species had by far the lowest sample size (mean sample size = 5,710 per species, Table 1). A larger sample size is required to better understand the niche dynamics of this species.

Distribution shifts vary among habitats

Across the five habitats, changes in distribution area exhibited high variability. While the overall distributional shift for the tall herb fringe was close to negligible, the semi-arid and moist grassland habitats gained the most. Both grasslands have an agricultural importance in Switzerland, and the area of land being converted and used as grasslands has increased over the last decades (FOEN 2010). Our modelled distribution maps for both grassland habitats substantiate previous findings on land-use change in Switzerland (Schmidt et al. 2018, FOEN 2010). Treatments such as fertilization and weeding have intensified over the last two centuries. It has been established that the addition of nitrogen and pesticides impacts plant functional traits, which in turn explain niche optima of these species (Guo et al. 2022). The overall highest gain in distribution for both grassland habitats is also reflected in the comparatively lower climatic niche stability. This indicates that the increased distribution area of the semiarid and moist grassland habitats was more driven by land-use change and intensification than by climate change. The observed distribution shifts revealed species-specific responses to environmental change. Except for the semi-arid grasslands, where all six species extended their distribution, each of the other habitats contained up to three species that decreased in distribution area. A possible reason for these species-specific responses could be biotic factors such as different dispersal abilities, population growth dynamics and competition (e.g., Chen et al. 2011). Urban et al. (2012) showed high interspecies variance in dispersal abilities, with the best dispersers being able to reach suitable new habitats when the climate changes, while outcompeted slower dispersers experienced local extinctions. Thus, while climate and land-use change are drivers of plant distributions, the species-specific responses lead back to biotic factors.

Importance of unlocking information from herbarium specimens

We georeferenced 1800 previously inaccessible historical herbarium specimens, resulting in a total dataset of 4699 historic data points and 166 634 current data points. Despite our efforts, a bias towards current distribution data persisted. It is commonly recognized that biodiversity data from historical inventories are often biased (Hortal et al. 2008) and that those biases in occurrence information remain a central problem in ecology and conservation (Meyer et al. 2016). The comparison between historical and current distribution data often serves as a basis for conservation decisions, but Grand et al. (2007) showed that biased data required more area to protect fewer species. The increasing georeference and digitization of herbaria worldwide facilitates a growing understanding of the potential of this rich data source. This enhances our understanding of climate change effects and guides sustainable conservation decisions. We strongly encourage researchers to turn to the vast historical plant collections to study environmental change.

Conclusion

All five habitats and 75 % of the investigated species showed an increase of their distribution area during the past 250+ years while maintaining their climatic niches. The high degree of niche stability and niche overlap between the historical and current climatic niches exemplified that the increase in distribution areas are not due to adaptations to new climatic niches, but to an increase of areas with suitable climatic conditions. This strongly indicates that climate change drove the shown shifts in plant distribution area, while other influencing factors such as land-use change and intensification had an additional impact, especially on the grassland habitats.

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A 150-year-old herbarium exemplifies change of a regional flora

Michèle Büttner[1], Urs Weibel[1], Michael Jutzi[2], Ariel Bergamini[3], Rolf Holderegger[3,4]

The loss of biodiversity in terms of plant species in a certain region can be shown by a comparison of historical herbarium records with the present-day occurrence of species. This holds especially true for time periods before 1900, when only few floristic data are otherwise available. Such a comparison can also show whether the distribution area or the abundance of plant species have changed, which habitat types were especially affected by extinction or whether species with specific environmental requirements showed higher extinction rates than ubiquists. Corresponding results can guide conservation authorities in defining appropriate management actions.

During the years 1820–1847 the pharmacist Johann Conrad Laffon (1801–1882; Fig. 1) collected a herbarium and published a species list for the Swiss Canton of Schaffhausen with the aim to completely compile the flora of the canton (Laffon 1847). By using this rather complete historical herbarium (kept at herbarium SCH) and the published species list we investigated **1** which and how many plant species do no longer occur in the Canton of Schaffhausen today, **2** what the driving forces of potential species decline have been, and **3** which implications can be drawn for nature conservation management.

First, we compiled a list of all plant species in the herbarium and the published species list of Laffon and compared it with species occurrence in 2000–2020 by using a list of all vascular plants of the Canton of Schaffhausen provided by the national data and information centre on the Swiss flora, the Info Flora (Büttner et al. 2022). In order not to miss plant species currently occurring in the Canton of Schaffhausen, this list was checked for completeness by experts for the flora of the canton. We then determined the percentage of extinction of plant species in the Canton of Schaffhausen during the last 153 years (i.e. 1847–2000). In order to identify possible driving forces of species decline, we examined differences in extinction among habitat types and in the environmental requirements of extinct and extant plant species by using ecological indicators values (continentality K, light L, moisture F, soil reaction R, nutrients N and temperature T) and additionally analysed Grime's plant strategies (competition, stress and ruderality), all according to Landolt et al. (2010).

We found that 154 of the 987 species in Laffon's herbarium and species list do no longer occur in the Canton of Schaffhausen, which refers to 15.6 % extinct species in 153

Keywords
Habitat change, Herbarium specimens, Species extinction

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Fig. 1. Johann Conrad Laffon (1801–1882), collector of the first complete herbarium of the Canton of Schaffhausen, Switzerland

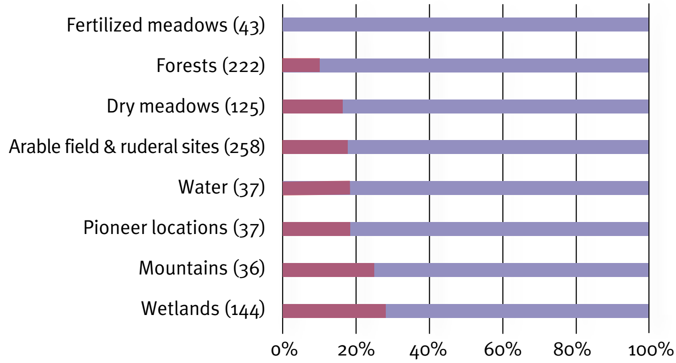

Fig. 2. Percentage of extinct (red) and extant (blue) vascular plant species per habitat type in Johann Conrad Laffon's herbarium and published species list for the Canton of Schaffhausen (Laffon 1847; total number of species at Laffon's time in brackets; figure modified from Büttner et al. 2022).

Fig. 3. Specimen of *Conringia orientalis* collected by J. C. Laffon between 1820–1847. This typical weed from agricultural and ruderal habitats is nowadays extinct in the Canton of Schaffhausen.

years or to an extinction rate of one species per year. Habitat types were differently affected by extinction (Chi^2-test: $p \leq 0.001$). Wetlands, mountain, pioneer and ruderal species as well as agricultural weeds were particularly affected by extinction, while extinction was lower in forests (Figs. 2–4). Even though the Canton of Schaffhausen still harbours a fair number of dry meadows, the decline in species from dry meadows was also considerable with 16.8 %. Concerning ecological requirements, light-demanding species showed highest extinction (t-test: $p \leq 0.001$), while for plant strategies, the less competitive and more stress-tolerant species disappeared more often (t-test: $p \leq 0.001$). Hence, species of habitats affected by extreme environmental conditions disappeared at higher rates.

In summary the extinction of plant species in the Canton of Schaffhausen was exceptionally strong in habitats affected by drainage, intensified agriculture, and river management, and habitats under extreme conditions. Our results inform conservation management about particularly endangered habitat types and stress the importance of restoring extreme habitat conditions.

As part of the Swiss digitization initiative SwissCollNet, the Museum zu Allerheiligen will digitize and geo-reference the Laffon herbarium and make it available online.

Fig. 4. Specimen of *Bupleurum longifolium*, collected by J. C. Laffon. It is still occurring in the Canton of Schaffhausen.

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The genomic uses of a 200 year-old herbarium – Pitfalls and potentials

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Major herbaria, such as the one hosted by the botanical garden of Geneva (G) have played a central role in the development of plant systematics over the last 200 years. Today, advances in high throughput sequencing technologies (HTS) together with the development of targeted capture, where DNA extracts are enriched for preselected loci using hybridization probes prior to sequencing, have considerably improved the use of herbaria as a source of genetic data, opening new avenues in the study of plant biodiversity.

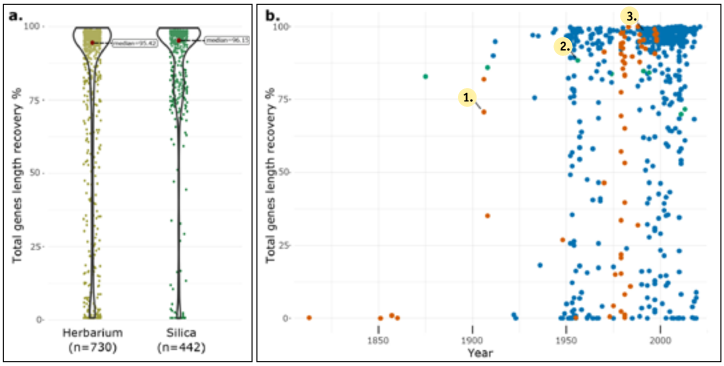

Fig. 1 a. Total genes length recovery for samples extracted from herbarium sheet and silica dry leaves. **Fig. 1 b.** Total genes length recovery versus time of collection for samples extracted from herbarium sheets only. Blue points correspond to *Sapotaceae* samples, orange to *Silene* samples and green to *Arecaceae* ones. Numbers correspond to example herbarium sheets: **1.** *Silene lagunensis* (Fig. 2), **2.** *Hyphaene* sp. (Fig. 3) and **3.** *Capurodendron nanophyllum* (Fig. 4).

Since 2016, research conducted at Conservatory and Botanical Garden of Geneva using HTS approaches on herbarium specimens were mainly focused on three taxonomical groups. First, the genus *Silene* in the Caryophylaceae family was investigated with the aim of defining the relationship and species boundaries in the section Italicae. Specimens were mainly from the Mediterranean region, with a total of 133 samples, with 56 % of herbarium origin (oldest 1813, mean 1970, SD 37.4 years). The kit used targeted 256 regions for a total of 650'000 bp. Secondly, the Sapotaceae family was investigated with the aim of refining generic and species circumscriptions in the family. Specimens were collected from tropical regions, mostly from Madagascar. They are the results of years of collections that evidence the

Keywords
Hyphaene, *Sapotaceae*, *Silene*, Targeted capture

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Fig. 2. *Silene lagunensis*, collected in 1906 in the Canary Islands (recovery 70.7 %; labelled as 1 in Fig. 1b).

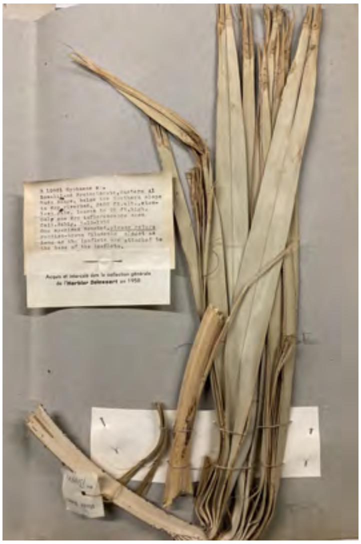

Fig. 3. *Hyphaene* sp. collected in 1956 in Somalia, a region difficult to explore today but key to understand the diversification of this genus (recovery 88.4 %; labelled as 2 in Fig. 1b).

Fig. 4. *Capurodendron nanophyllum*, the species with the smallest leaves in the Sapotaceae. Described in 2018 as already critically endangered due to deforestation (recovery 99.4 %; labelled as 3 in Fig. 1b)

dramatic loss of biodiversity due to deforestation. From the 995 samples, 70 % were extracted from herbarium sheets (oldest 1911, mean 1993, SD 21.4). The kit used was specially design for Sapotaceae (Christe et al. 2021) and targeted 792 regions for a total of > 870 000 bp. Lastly, the genus *Hyphaene* in the Arecaceae family was investigated in order to define its position within the sub-family Coryphoideae and to address species delimitation issues within the genus. Only nine herbarium specimens out of 124 samples were used (oldest 1875, mean 1959, SD 50.5) but they represent valuable samples. The kit used targeted 916 regions for a total of > 1 500 000 bp (Loiseau et al. 2019).

Results deriving from these studies helped us gaining experience with the use of herbarium specimens for HTS, and their chance of success in terms of maximum age and sequence recovery. We found that the total maximum base pairs (bp) recovery for herbarium specimens was on average very good and highly similar compared to silica gel preserved samples (median 95.42 and 96.15 bp, respectively; Fig. 1). The oldest sample with a good recovery rate, i.e. the percentage of the maximum genes length recovery for each taxonomical group, (83 %) is almost 150 years old. Unfortunately, we could not achieve such rates for older samples. Globally, the recovery rate is correlated with the collection year (Spearman's $\rho = 0.37$, $p = 4.66e^{-25}$), meaning that the older the sample is the less chance we have to obtain a good recovery rate.

We conclude, based on our experience with three taxonomic groups spanning different climates and collection times, that fragmented DNA does no more represent an absolute limit in using herbarium material. We are now ready to genetically explore the herbarium at a higher scale than before, with some prospective applications such as the discovery of undescribed diversity, or the monitoring of regional flora. However, the relatively high quantity of DNA that is needed for HTS, the destructive nature of the sampling, and the reduced chance of success with specimens older than 50 years, request a wise selection of the samples to be sequenced. Despite these pitfalls, we foresee that the use of herbaria as a source of genetic data will play a central role for the completion of the plant tree of life and the accurate quantification of plant diversity at all taxonomical levels.

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Bridging herbaria cultural heritage and digital art – Immaterial herbaria

Rhinaixa V. Duque-Thüs[1], Helmut Dalitz[2], Philipp M. Schlüter[3] and María Beatriz Eggli-Yánez[4]

Migratory movement changes the way in which people perceive and feel their nations. Art allows us to enquire about the way members of diasporas are stimulated and confronted with a plethora of feelings as loss and grief, empathy, hope and joy when they see familiar plants collected from their countries of origin among herbarium samples. In the case of the Venezuelan diaspora, nostalgia for a recent past and memories of the homeland configure the imagined Venezuelan nation now that people living abroad („diasporic subjects" in the sense of Martinez Parra 2020). Some Venezuelans take plants from their gardens with them when they leave their country. Many of these people take orchids with them, that remind them of their origin and which they nurture in their new countries.

Cattleya mossiae C. Parker ex Hook (Orchidaceae), the national flower of Venezuela is a particularly valued species and often seen in the homes of Venezuelans in their new countries of residence. This plant is widely cultivated in Venezuela, and this is the main reason why, for many Venezuelans, orchids in general are a symbol of resiliency. An epiphytic lifestyle, with roots not in soil, is reminiscent to the life situation of human migrants, who have had to „move" their cultural roots, and settle in a new region, where it is often difficult to make new roots, forcing them to rely on their resilience also in a cultural context. In a changing environment even some terrestrial orchids in Europe, like *Himantoglossum hircinum* (L.) Sprengel, are showing more resilience than previously expected and under a warming climate, they start to expand into new territories (van der Meer et al. 2016).

This inspired María Beatriz Eggli-Yánez, the Swiss-Venezuelan visual artist, to merge the botanical background information about various species of orchids with her vision for their artistic representation. She combined photographic details of *Himantoglossum hircinum* (L.) Spreng and *H. adriaticum* H. Baumann in her artwork together with other structures of the plants, which for laymen, represent characteristic features of orchids (e.g., flowers).

Herbarium specimens are established aids in documenting e.g., climate and environmental changes or in population studies. As the information on the sheets is digitized and enters the public realm, an increased awareness for the importance of herbarium specimens is generated and spread, not only among scientists but also to artists (Brueggemeier 2017). The aim of this project is to show the development of „immaterial herbaria", based on the idea of Eggli-Yánez, of creating several art works su-

Keywords
Cultural heritage, Digital art, Herbarium digitisation

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Fig. 1. Digitally superposed images of specimens of *Himantoglossum hircinum* (L.) Spreng and *H. adriaticum* H. Baumann (Orchidaceae)

perposing digitised images of different species of Orchidaceae. This recreates the sensation of looking at superposed old family slides, where individuals look slightly different, although they belong to the same family.

Herbarium specimens were selected from HOH historical collections. Part of the images were generated with the help of IRIS Book 5, a lightweight portable scanner and with a Nikon DF camera and subsequently superposed (Fig. 1). The specimens were taxonomically updated, catalogued, and included in the database. The result of this work creates a bridge between the public and science through art, exemplified by the artistically constructed image of resilience and migration in species of Orchidaceae. The artist sees the way orchids use their roots as holdfasts as a trait that corresponds to the feelings of many migrants, who settle in new countries and cultures, carrying their own roots for holding themselves to a substrate where they will be able to thrive and bloom again. This artistic project leverages the metaphor of „being uprooted" which applies to immigrants or members of Diasporas as well as to orchids. Both travel either with the migrating human communities or expand their distributional range by themselves following changes in the climatic framework of previously uninhabitable areas. The narrative of being uprooted reformulates a subjective diaspora members' experience of belonging to both the nation they currently live in and the country of origin, in a constant dialogue between feelings of belonging and uprootedness.

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Towards digitizing the botanical legacy of Fritz and Paul Sarasin in Basel and Zurich

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The botanical heritage of multitalented naturalists Paul Benedict (1856–1929) and Karl Friedrich (Fritz) (1859–1942) Sarasin of Basel is poorly known. The second-degree cousins from Basel inherited great wealth, which funded their expeditions to the tropics in India, Sri Lanka, Sulawesi, and New Caledonia. Both were doctors in zoology with interdisciplinary interests from geography and anthropology to botany. They mixed race theories with traditional descriptions of biodiversity, blurring boundaries between anthropology and natural sciences. With the help of the local colonial governments where they travelled, they avidly collected many thousands of natural history objects and human artefacts, now kept in institutions across Europe.

After having led a considerable part of their career and personal life as a team and a couple, they pursued different interests after they returned from their last Sri Lankan trip in 1907. Paul ended his tropical explorations and switched his focus to nature conservation and cofounded the Swiss league for nature preservation (today's Pro Natura) in 1909 (Fig. 1). Fritz kept exploring remote areas and from 1911, he travelled with the Swiss zoologist Jean Roux in New Caledonia and the Loyalty Islands, resulting in extensive collections and a series of books.

Here, we provide a first glimpse into the volume and impact of the two cousins' botanical heritage, prompted by the rediscovery of 18 boxes containing some 3000 herbarium specimens labeled „Sarasin" in the backlog of the Herbaria Basel (BAS; Table 1), that are currently being curated and digitized.

Keywords
Botanical heritage, Curation, Ferns, Herbaria, Plant collectors, Sulawesi

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Table 1. The c. 3000 rediscovered Sarasin specimens at BAS

Collector	*Provenance*	*Description*
Fritz & Paul	Sri Lanka & India (not dated)	Flowering plants, c. 300 unmounted. Sri Lankan collections partially determined by M. Gürke and K. Schumann (B)
Fritz & Paul	Sulawesi: 1893–1896, 1902–1903	Ferns, c. 700 unmounted. Mostly determined by H. Christ, some by R.E. Holttum, B.S. Parris, and Cheng-Wei Chen
Fritz & Paul	Sulawesi: 1893–1896	Flowering plants, c. 400 pocket-sized, mounted, but several plants missing, annotated on sheet. Sporadic recent determinations by A.K. Poulsen
Fritz	New Caledonia: 1911–1912	Flowering plants, c. 750 unmounted. Partially determined by H. Schinz and A. Guillaumin
Fritz	New Caledonia: 1911–1912	Fungi & Lichen, c. 300 bags. Partially determined
Fritz	New Caledonia: 1911–1912	Mosses & Ferns, c. 75 unmounted. Partially determined by R. Bonaparte
Paul	Switzerland: 1918–1926	Flowering plants, c. 560 unmounted. Determined by P. Sarasin

Fig. 1. Paul Sarasin photographed at the Val Cuozza in 1897. As the president of the Swiss Natural Research Society, Paul organised the protection of the area, which officially became the first Swiss National Park in 1914.

Fig. 2. BAS Sarasin Herbarium collection S1030 from Takale Radjo (Sulawesi) described by H. Christ in 1895 as *Nephrolepis dicksonioides* Christ and then chosen as Lectotype by Chen C.W. et al. in 2022.

The literature paints an incomplete and distorted picture of the Sarasins' botanical collections. Almost sixty species of plants commemorate their name Sarasin (incl. 47 basionyms, IPNI, July 2022) and an unknown but large number of Sarasin specimens are Types or cited in important taxonomic treatments. Most fern species named after the Sarasin cousins stem from pteridologist Hermann Christ (Basel, 1833–1933) who based several works on the Ferns of Sulawesi (1894–1904) on the BAS Sarasin collections (Fig. 2). Those Sulawesi Ferns were also partially consulted by Holttum in 1957 before he published some accounts of Flora Malesiana (Morton, 1968).

Mysteriously, however, van Steenis-Kruseman and van Steenis' (1950) Malaysian collectors and collections guide, now cited over 200 times, states that the Basel Herbarium is „of little importance" since Christ's fern collection had been incorporated to Herb. Bonaparte before being transferred to Paris, failing to mention that the Sarasin material that Christ studied was not entirely incorporated in Herb. Christ. In fact, the BAS specimens were most likely the first set.

Overall, cross-referencing curator's knowledge, patchy available online collections, scattered literature, and herbarium backlogs (including the 3000 BAS specimens) jointly suggests that between 3500 and 4500 Sarasin plant specimens may exist. Most are today in Basel, Paris, Kew and Zurich, but an unknown number of specimens have also survived the bombing in Berlin during WWII and others are sporadically found in other institutions (BISH, L, FI).

The rediscovery of the Sarasin specimens in BAS, of which the Sulawesi ferns are probably the most valuable due to their relevance for Christ's impactful taxonomic work, prompted a collaborative project at the Herbaria Basel (BAS/BASBG) and the United Herbaria Zurich of the University and ETH Zurich (Z/ZT), that started July 2022. Inter-institutional collaboration includes using explicit and identical synonymy lists and transferring specimen metadata from duplicates across institutions, facilitated by the use of the same herbarium collection management software. So far, reassessing the Sulawesi ferns at BAS revealed that ca. 10 % of the specimens are nomenclatural Types, underscoring the importance of making them digitally available.

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Stable isotopes from herbarium specimens reveal physiological responses of plants to global change

Ansgar Kahmen, Daniel B. Nelson, Jurriaan M. de Vos, and David Basler

Investigating the impacts of global environmental change on plants remains a challenge. Experiments that scale from leaf to ecosystem have provided important insights into the ways plants and ecosystems respond to changing environmental drivers. Yet, experiments are often short-lived and can not realistically simulate long-term environmental changes. Monitoring programs and historical observations are thus valuable alternatives for studying the impact of environmental change on plants. These are, however, unfortunately rare and often poorly suited to identify the mechanistic and physiological basis by which changes in the environment impact plant life. Analyses of biological collections and in particular herbarium materials could be a valuable complementary approach that allows assessing functional responses of plants to global environmental change.

Specifically the analysis of stable carbon and oxygen isotopes of archived plant material offers the exciting opportunity to reconstruct long-term physiological responses of plants to environmental change (Dawson et al. 2002). The carbon isotope composition of plant materials is a reliable proxy for leaf-level intrinsic water use efficiency (iWUE), which describes the ratio of net photosynthesis over stomatal conductance and thus combines two key plant physiological processes. The oxygen isotope composition of plant materials provides time-integrated information on leaf stomatal conductance. In combination, carbon and oxygen isotope measurements thus allow integrated values for net photosynthesis and stomatal conductance to be explicitly determined (Scheidegger et al. 2000).

The analysis and interpretation of the carbon isotope composition of plant materials is already well established in dendrochronology. Their analysis in tree ring archives have shown that iWUE in trees has generally increased since 1900 by 40 % and that these increases are mostly the result of increases in net photosynthesis in response to increasing atmospheric CO_2 (Mathias & Thomas 2021). In temperate ecosystems, the majority of plants are, however, herbaceous. These plants do not preserve annual growth rings that persist for decades, so isotope-based assessments of their physiological responses to global environmental change are much more difficult. Herbarium specimens fill this shortcoming and can provide valuable study material helping us to understand how global environmental change has been impacting non-woody plant species (Fig.1).

Keywords
Botanical collections, Ecophysiology, Elevated CO_2, Intrinsic water use efficiency, Time series

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Fig. 1. Collecting for the herbarium of the Basel Botanical Society (BASBG), a primary source of specimens for this study. Scheltenpass, BE, Switzerland, 22 June 2022. Photo Aurélie Grall

We analyzed the carbon isotope values ($\delta^{13}C$) of over 3000 Swiss specimens from the Herbaria Basel (BAS/BASBG), representing 89 species and the years 1900–2020. Our analysis shows (Fig. 2) that harbaceous plants improved their iWUE over the past century. The increase in iWUE was, however, smaller than that of trees reported previously. Moreover, responses differed significantly among forbs, legumes, grasses and sedges. Future analysis of the oxygen isotope composition of these samples will help to identify if changes in the intrinsic water use efficiency in herbaceous plants are the result of higher net photosynthesis or the result of reduced stomatal conductance. Already, our study demonstrates that all plants, not just trees, respond sensitively to global environmental changes with possible implications for ecosystem carbon and water relations. Our study also shows that stable isotope analysis of herbarium materials is a powerful tool to address the effects of global environmental change on the physiology of a large range of plant species, and that important differences in these responses among plant functional groups exist.

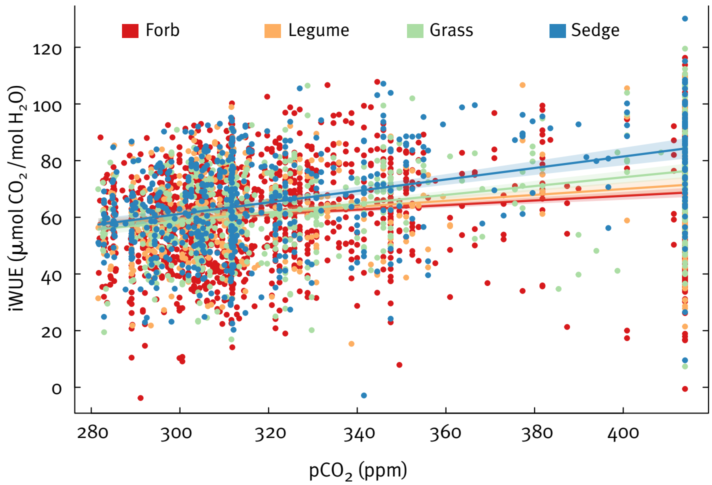

Fig. 2. Changes in intrinsic water use efficiency (iWUE), which is the ratio of photosynthesis over stomatal conductance in response to increasing atmospheric CO_2 concentrations revealed by the stable carbon isotope analysis of over 3000 herbarium specimen from 89 temperate herbaceous plant species collected in Switzerland between 1900 and 2020.

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Using herbarium specimens to test for effects of climate change on the time of flowering

Thea Kull, Kätlin Langerpaur, Tiiu Kull

Climate change has been a serious problem for many decades already. According to the Intergovernmental Panel on Climate Change (IPCC) human activities are estimated to have caused approximately 1.0 K rise in global mean temperature since the pre-industrial times and the process has intensified in the last decades (Masson-Delmotte et al. 2021). In the Baltic Sea region, the warming has been even more rapid than globally. Mean annual air temperature during the period 1951–2015 in Estonia has increased by 2.0–2.5 K (Jaagus et al. 2017). Considerable changes have taken place in the month of March where the mean temperature has risen 3–5 K (Jaagus 2006). Climate change has an influence on both individual organisms as well as on ecosystems. Especially sensitive to temperature change is flowering – other studies have found one degree of temperature rise can prompt flowering 2–10 days earlier. Temperature change in different seasons has various impacts on phenological events. In recent times herbarium material has become more relevant in studying ecological consequences of climate change. Digitalized historical herbarium provides useful material in addition to observational data. This study is the first to use Estonian herbarium material to test the usefulness of herbarium material for studying phenological changes due to climate change.

We hypothesized that during the last 120 years flowering time has shifted to earlier dates and that there is a difference in the rate of change in mainland and coastal areas.

The Ranunculaceae was selected as the study group because it is a species-rich family with a wide distribution over the whole of Estonia. The family contains both species flowering in spring and in summer. This allows to compare the impact of climate change on flowering in different seasons. Flowering herbarium specimens (Fig. 1), in total 3083, with correctly filled labels from the largest four Estonian herbaria (TAA, TAM, TALL, and TU), were included in the study, representing material that was collected from all over Estonia between 1901–2020 (Fig. 2). 22 species of Ranunculaceae were studied out of which half were spring and the other half summer flowering. Temperature data used in the study was acquired from the Estonian Environmental Board.

Linear regression and analysis of variance with programming language R were used for statistical analysis.

Results indicated that on average the flowering time has advanced 16 days (Fig. 3) since 1900. Similar trends in Estonia

Keywords
Estonia, Global warming, Phenology, Ranunculaceae

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Fig. 1. Herbarium specimen of *Ranunculus fallax* (Herbarium of Estonian University of Life Sciences, TAA).

Fig. 2. Location of herbarium specimen of Ranunculaceae in Estonia used to test for changes in flowering time between 1901–2020.

have been found before through direct phenological observations. In the course of the last 45 years the change has intensified (Fig. 4). The strongest correlation was found between the flowering time of spring flowering species and spring temperature. Within single species, the impact of climate change on phenology was not significant.

The strongest changes in the time of flowering for spring flowering species were found in central and south-eastern Estonia, where the time of flowering in 120 years has shifted earlier 21 and 13 days, respectively. Changes in flowering time in areas close to the sea in northern and western Estonia were statistically insignificant (P > 0.05).

To conclude, Estonian herbarium material is suitable for studying climate change effects on phenology and results based on herbarium material are comparable with results from other observations.

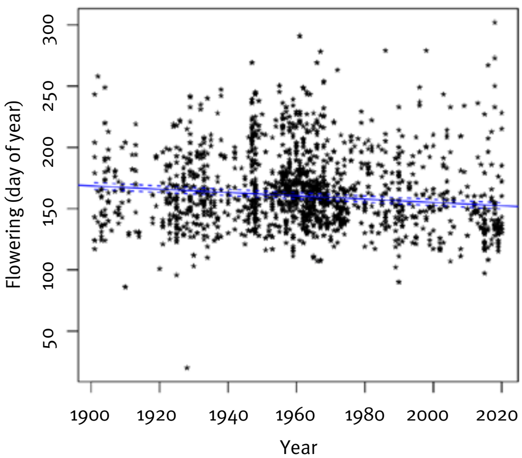

Fig. 3. Change of flowering time between 1901–2020 as shown by herbarium specimen of 22 species of Ranunculaceae. Linear trend -0.13 day/year (P < 0.001).

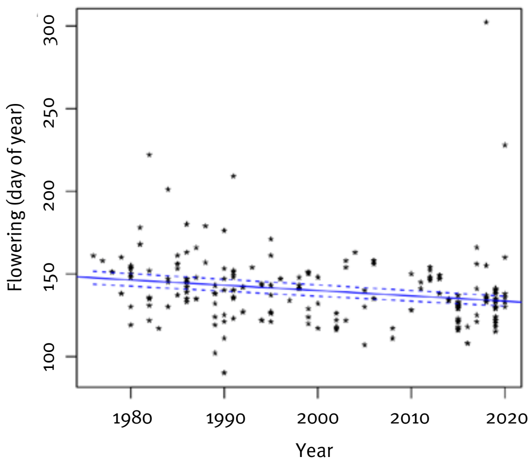

Fig. 4. Change of flowering time between 1976–2020 as shown by herbarium specimen of 22 species of Ranunculaceae. Linear trend -0.32 day/year (P < 0.001).

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Finding biotic anomalies described in specimen label text is a challenge that artificial intelligence can address

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Biodiversity specimen collectors are on the front lines of observing biotic anomalies, some of which herald early stages of significant changes (e.g., the arrival of a new disease; Pearson and Mast 2019). Online data sharing has opened new possibilities for the discovery of anomaly descriptions on collectors' labels, but it remains a challenge to find these needles in the haystack of many millions of specimen records available at aggregators like iDigBio and Global Biodiversity Information Facility. In a recent community survey, over 200 collectors identified 170 unique words and phrases (e.g., atypical) that they would use to describe six types of anomaly (Pearson and Mast 2019). Left unanswered was the relative efficiency with which anomaly descriptions can be found using the simple presence of these words. Here, we address that question with a focus on one type of anomaly (phenological; related to the timing of life history events) and ask a second question: can we further improve the efficiency of anomaly description discovery by engaging artificial intelligence (AI)?

We focused on six words that we expect to be used in most descriptions of phenological anomalies: early, earlier, earliest, late, later, and latest. We examined every use of those words in 50 metadata fields (those in Fig. 2 of Pearson and Mast 2019) in the 125 million records aggregated by iDigBio as of early 2022. Every text string in which a focal word occurred was independently classified by two technicians as either an anomaly description, not an anomaly description, ambiguous, or uninterpretable (e.g., in a non-English language). An example of an anomaly description is „aberrantly late flowering individual"; that of a non-anomaly is „Herbarium of the late East India Company"; and that of an ambiguity is „extremely early individual" (which could reference phenology or a portion of a life history stage). When the two technicians disagreed on a classification, Mast made a final decision.

Our six focal words appeared in 516 129 text strings in 43 of the metadata fields. Only six fields (dynamicProperties, occurrenceRemarks, eventRemarks, habitat, locationRemarks, and locality) had >10 records describing an anomaly. We reduced our focus to the 194 377 text strings that were deemed interpretable in these six high-value fields, then distilled it down further to the 110 922 unique text strings among them. We discovered that only 3 % of these unique text strings described an anomaly or potentially did so (i.e., were ambiguous).

Keywords
Anomaly detection, Artificial intelligence, Biodiversity specimens, Global change, Phenology

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To explore whether artificial intelligence could introduce new efficiencies to the discovery of these relatively rare anomaly descriptions, we split the data into training (63.7 %), validation (11.3 %), and test (25%) sets. We encoded the data using two alternative approaches: (1) term frequency multiplied by inverse document frequency (TF-IDF) of n-grams 1 to 5 words in length and (2) the pre-trained language model Bidirectional Encoder Representations from Transformers (BERT). We processed the TF-IDF encoding using, in turn, the XGBoost machine learning (ML) model and a deep learning (DL) model of a feedforward neural network with one hidden layer of 256 neurons, dropout, and ReLU activation function. We processed the BERT-encoding using DL alone.

Performance of all three approaches produced accuracies greater than 97 % (97.2 % for TF-IDF + ML; 97.7 % for TF-IDF + DL; and 98.6 % for BERT + DL). However, the false negative rate for the methods, where a text string classified as describing an anomaly or as ambiguous is deemed a non-anomaly by the approach, was relatively high (48.6 %, 38.0 %, and 25.1 %, respectively).

The simple presence of words likely to be used to describe phenological anomalies has a low rate of return of text describing anomalies (3 %). In contrast, our early results classifying text strings containing six other anomaly terms (aberrant, abnormal, atypical, odd, unusual, and weird) produce a much higher rate of return (> 50 %), but the type of anomaly being described is less consistent. We demonstrate that artificial intelligence approaches introduce valuable efficiencies to discovery. In the most effective approach, AI finds many (75 %) of the needles (i.e., anomaly descriptions) in the haystack. This work moves us closer to being able to flag and deliver high-value anomaly descriptions to interested stakeholders as the data is shared at aggregators, a potential next step.

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SNP genotyping and environmental niche modelling using herbarium specimens of the northern dragonhead, *Dracocephalum ruyschiana* (Lamiaceae)

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Maintenance of genetic diversity is a central aim of species conservation, given its positive effect on species survival and adaptation in a changing environment. Data from different time points is key for understanding how populations behave under various conditions. In this regard, herbarium specimens are an invaluable source of information from the past. Still, utilizing archived biological material for studying trends of genetic diversity offers challenges such as DNA degradation and the lack of standardized, cost- and time efficient methods.

We have studied change in genetic structure and diversity through time in the northern dragonhead *(Dracocephalum ruyschiana,* Lamiaceae; Fig. 1; Nygaard et al. 2022), a plant species that has experienced a drastic population decline and habitat loss in Europe. A microfluidic array consisting of 96 SNP markers selected from modern Norwegian populations (Kleven et al. 2019) was applied on 130 herbarium specimens. The selected specimens were collected from year 1820 to 2008, mainly from Norway but also from Sweden, Russia, Belarus, Ukraine, Switzerland, and France. The obtained genotype data were compared with data from 355 modern Norwegian samples generated using the same SNP array (Kyrkjeeide et al. 2022) to assess genetic structure and diversity across space and through time. Finally, we used 4092 records of georeferenced herbarium specimens and species observations to model the species' environmental niche and potential distribution in Norway. We included three environmental variables: mean summer temperature, mean annual precipitation, and precipitation seasonality (coefficient of variance of monthly precipitation). The final spatial prediction of Northern dragonhead resulted from averaging across seven different distribution models, all with five replicated runs (Nygaard et al. 2022).

The SNP array successfully genotyped all included herbarium specimens. The call rate varied from 96–100 % and 95–100 % for historical and modern samples, respectively, indicating that the proportion of successfully genotyped loci was little affected by the age of the specimens. The genotyping success may, however, be dependent on inherent biology among species, and preservation techniques and conditions.

Within Norway we were able to compare genetic diversity and structure between historical and modern samples of norther dragonhead, thereby adding a temporal monitoring aspect. Our results displayed similar genetic structure and diversity

Keywords
Biodiversity conservation, Genetic diversity, Microfluidic SNP array, Retrospective monitoring, Spatiotemporal stasis

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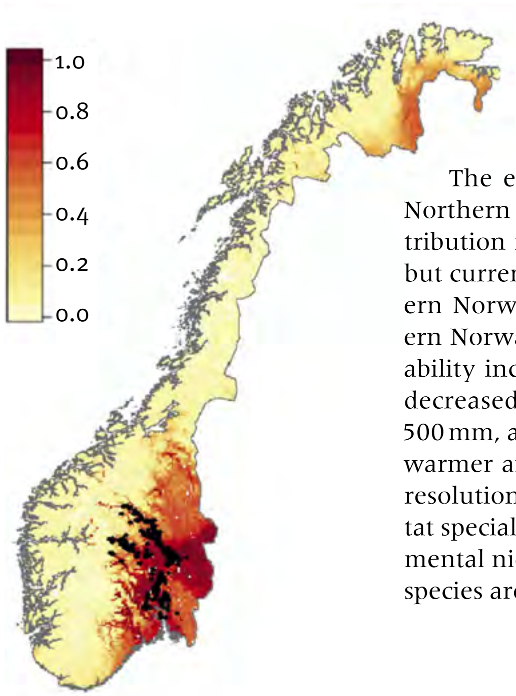
Fig. 1. Northern dragonhead, *Dracocephalum ruyschiana*.

across space in Norway and limited genetic changes through time. Across Europe, the Norwegian population separated as a distinct genetic cluster. Given the genetic divergence between regional populations within Norway, and more so from populations outside of Norway, continued protection of Northern dragonhead remains relevant. The captured genetic diversity across Europe was, however, significantly and negatively correlated with distance from Norway. This negative correlation is likely due to ascertainment bias of the SNP array, which should be solvable with appropriate design adjustments. As such, this standardized, modern monitoring method also seems promising for retrospective monitoring using herbarium specimens.



The environmental niche modelling results suggest that Northern dragonhead has not fully achieved its potential distribution in Norway. Our results revealed potentially suitable but currently unoccupied niche space in central and northeastern Norway, as well as the inner parts of the fjords in western Norway (Fig. 2). According to our results, the climate suitability increased with mean summer temperature > 10°C and decreased when mean annual precipitation increased over 500 mm, anchoring the distribution of Northern dragonhead to warmer and drier regions. Despite limitations in climatic data resolution and considering that northern dragonhead is a habitat specialist, geographical representations of modeled environmental niches can still provide valuable information on where species are not likely to thrive.

Fig. 2. Spatial prediction of Northern dragonhead across Norway based on 4092 occurrence records, displayed as black points. Darker red color represents higher modeled niche suitability, and yellow color represents lower suitability.

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What does the „true" Boerhaave herbarium tell us about the practice of collecting plant specimens in the botanical garden Leiden?

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The Dutch physician Herman Boerhaave (1668–1738) was famous for his clinical teaching, but his botanical research was also renowned. Boerhaave (Fig. 1) inspired his pupils to set up botanical gardens and devise their own classification systems. His research resulted in the publication of two editions of the garden catalogue of the Leiden Hortus Botanicus, of which the latter (Boerhaave 1720), was deemed important enough to be used extensively as reference by Linnaeus (Linnaeus 1737). Devising a classification system was a major enterprise and must have required a substantial herbarium. Two herbaria were attributed to Boerhaave, but it appears unlikely – even though they have not yet been researched – that they were actually composed by him. From the collection of Naturalis Biodiversity Center, Leiden, we selected 100 specimens that were listed as collected by Boerhaave and verified 88 specimens as having been collected by Boerhaave. However, this small number raises the following questions: What happened to the rest of the herbarium that Boerhaave created? And how can we recognise a Boerhaave specimen?

We verified specimens as Boerhaave's by comparing the handwriting on the adjoining labels with that of his handwritten seed registers (Leiden University Library: special collections BPL 3654). We identified specimens using floristic literature, comparing them to specimens on the Naturalis BioPortal (https://bioportal.naturalis.nl) and physically examining them. We studied the descriptions on the labels and their relation to the seed registers and garden catalogues, the decorations and the manner of mounting. In doing so we got a clear picture of how seeds were obtained, registered, cultivated and classified and how the specimens were mounted and decorated.

We considered a specimen to be Boerhaave's when it contained a label in his handwriting or when it was mentioned on the sheet that it came from his collection or herbarium (Fig. 2). Our study showed that almost half of the plant species originated in the Mediterranean, Lamiaceae being the dominant family. Some specimens were exclusively described by Boerhaave, but successive garden curators and others also provided descriptions. Around 1900 the labels were glued to the sheets, which showed that they were originally stored alongside the sheets, not attached to them. This could explain why so few Boerhaave specimens are known as such: over time labels presumably vanished from the collection and as a result, specimens were appropriated by successive curators.

Keywords
18th Century, Botany, Gardening

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Fig. 1. Portrait of Herman Boerhaave, painted by Cornelis Troost (Rijksmuseum Amsterdam, CCO 0.1)

Fig. 2: Specimen of *Teucrium spinosum* L. with a label in Boerhaave's handwriting: „*Chamaedrys; spinosa; quaerenda.* 557/21" referring to no.557 in the seed register of 1721 (see Fig. 3). „Quaerenda", „it needs to be checked", means that he wanted to verify the identification.

Fig. 3: A page from the seed register of 1721, where seeds are described from a „*Chamaedrys spinosa*", sent to Boerhaave by Michelangelo Tilli (1655–1740). Boerhaave registered the seeds under no. 557 and later added a reference to an entry number in an ultimately never published edition of the garden catalogue.

The seed registers gave an insight into the „commercium botanicum". The many correspondents listed show that Boerhaave was part of a vast network of botanists from all over Europe. He recorded the incoming seeds under the description supplied by his correspondents. On occasion he described the mature plant, or he added the number the species was assigned in the second catalogue (Boerhaave 1720) and even continued assigning numbers after publication (Fig. 3). In the 1718 register seeds sent to Boerhaave by Sebastien Vaillant (1669–1722) were described as coming from „a tomentose and broadleaved Lavender". The similarity between an equally tomentose and broadleaved specimen of *Lavandula latifolia* L. collected by Boerhaave and one collected by George Clifford (1685–1760) suggests that Boerhaave provided Clifford with this particular species (Offerhaus et al. 2023).

The majority of the descriptions on the labels were linked to entries in the catalogue, where information was found on methods of propagation (e.g., by taking cuttings), wintering (e.g., in a hibernacle) or on the life cycle of a species. Only five species were listed as medicinal.

The decorative vases and ribbons applied to the specimens were produced by Leiden craftsmen. Their use, the variety of plant species and the precise and symmetric way of mounting links Boerhaave's specimens to contemporary herbaria, particularly two anonymous collections. Similarities between these herbaria (the Zierikzee herbarium and the D'Oignies herbarium) and the existence of corresponding descriptions in auction catalogues after the death of Boerhaave and his head-gardener Jakob Ligtvoet (1684–1752) suggest that these herbaria were part of one collection originating in the Leiden botanic garden during the first half of the 18^{th} century (Offerhaus et al. 2023).

Gardeners were invisible technicians: knowledge generated by their activities was transferred to the curator of the garden, the professor of botany, who in turn was responsible for describing the plant species. Gardeners weeded, watered, digged, planted, fertilised and propagated. Did they also collect specimens, dry them to perfection and decorate them? We think it highly likely that – given the vast undertaking of cultivating plant species and collecting, drying and describing thousands of specimens – the involvement of gardeners was far greater than surviving sources suggest.

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Looking back to move forward – Impact of historical moss specimens on modern systematics

Michelle J. Price

Natural history collections reflect our desire to understand the living world. Each collection is unique based on how it was composed, who composed it, where the specimens originated from, and how it has been enriched. Natural history institutions preserve, curate and enhance their collections on an ongoing basis and they serve as a powerful scientific resource. Collections provide a window into past, present and future biodiversity via the information contained on and in specimens. They play a crucial role in the documentation, description and understanding of species themselves, with the specimens held in global collections forming the foundation for all taxonomic endeavours.

Historical specimens add an important time dimension to the description, circumscription and understanding of species. They show how species were interpreted and how concepts may have evolved over time. Historical collections often contain a disproportionally large number of types which form essential reference points in the taxonomic process. An example of the importance of historical specimens is the moss collection of Johannes Hedwig (8 Dec. 1730–18 Feb. 1799), who was a medical doctor by training and bryologist by passion. Known as the „Father of Bryology," Hedwig revolutionised the way mosses were interpreted by using his 50× linear magnification microscope to observe and document their macro- and microscopic features. He was among the first to fully appreciate their diversity and his opus Species muscorum frondosorum – SMF (Hedwig, 1801, Fig. 1) set out one of the foremost systematic frameworks for mosses. Due to this his work was designated as the starting point of moss nomenclature (excepting the Sphagnaceae) in 1910. SMF contains 372 descriptions of mosses, including 3 *Sphagnum* species and 75 moss species that were new to science. As a result of the designation of this later starting point, the 294 names in SMF from earlier authors were ascribed to Hedwig. The Hedwig herbarium, held in the Conservatory and Botanical Garden of Geneva (G), became a rich source of nomenclatural types for early moss names (Fig. 2).

The cataloguing of the Hedwig type material and collation of typifications of the Hedwig moss names revealed that many of the names in current use, even for common and widespread species, were lacking any formal type designation (Price 2005). Typification of the Hedwig material requires the consultation

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Diversity, Early bryology, Hedwig herbarium, Microscopy

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Fig. 1. An illustration from Hedwig's Species muscorum frondosorum of 1801 (Tab. X of Encalypta crispata Hedw. and E. streptocarpa Hedw.). He taught himself to draw to facilitate his work and his hand coloured plates are a testament to his observations and understanding of moss morphology.

Fig. 2. Hedwig's herbarium contains a set of standardised herbarium sheets (16 × 21 cm) that hold pressed specimens and a handwritten label. Here is the original specimen of Hedwig's *Mnium palustre* Hedw. (*Aulacomnium palustre* [Hedw.]Schwägr.).

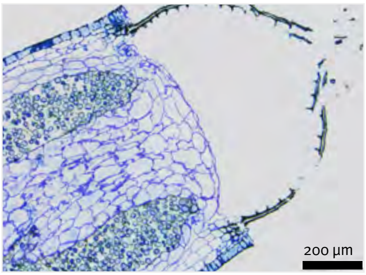

Fig. 3. An image of a longitudinal section of a peristome of *Dicranum scoparium* Hedw. taken by Mathilde Ruche as part of her PhD research into peristome architecture.

of the sources cited in the protologues, disentangling the concepts of early authors and careful examination of the plants on the sheets of original material to confirm their taxonomic identity. In some cases, issues need to be resolved as part of the typification process (e.g., the presence of material added to the original specimens at a later date, two or more species present on a sheet or two sheets present for one name that contain two different species). This careful procedure ensures that the plant or plants from amongst the original material that may serve as the nomenclatural type is/are identified, and that the name is correctly applied.

A series of collaborative articles typifying Hedwig names have been published since 2010, with the most recent on *Polytrichum commune* Hedw. (Kariyawasam et al. 2021). Efforts are currently focused on *Dicranum* Hedw., as work on the original material in G revealed that all was not as it should be for the ubiquitous *D. scoparium* Hedw., the type species of the genus itself. Different taxa are present on the two original herbarium sheets under *D. scoparium* and the protologue contains a mixture of features from two distinct taxa. This discovery led to a more intensive focus on the genus with the aim of establishing solid taxonomic and nomenclatural foundations for it. Research activities explore species circumscriptions and relationships as well as the potential of peristome traits for use in taxon discernment. Histological (Fig. 3) and Scanning Electron Microscopy studies of peristomes across *Dicranum* have revealed novel results. Newly generated data from the sporophyte will contribute to the circumscription of the genus and Hedwig's *Dicranum* species. In addition to the typification of the names, including the troublesome *D. scoparium,* full species descriptions and illustrations will be produced. The careful examination of the over 200 year old material in the Hedwig collection will ensure a better taxonomic understanding of *Dicranum,* with modern microscopy and imaging techniques complementing the traditional approaches.

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Using herbarium specimens, botanical gardens, historical data, and citizen science to study climate change

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Over the past two decades, researchers and others involved in plant science have developed innovative and powerful methods to investigate the effects of climate change on plants. First, botanical garden staff are using their diverse collections to understand plant responses to climate change, test possible conservation actions, and engage the public in climate change science (Primack et al. 2021). These approaches are evident at two international networks of botanical gardens (Fig. 1). One network, focusing on the phenology of over 1000 species of woody plants, has demonstrated that leafing out phenology is strongly connected to spring temperatures, phylogeny, whether plants are deciduous or evergreen, and plant anatomy, whereas leaf senescence in autumn responds to a wider range of environmental triggers and local factors. Another network focused on perennial wildflowers has demonstrated that plant phenology is affected by plant functional traits, particularly plant height and leaf size, as well as local site factors.

Second, scientists are using historical databases of plant phenology and abundance combined with modern observations to determine how climate change has already affected plants. In many cases, these data sets demonstrate that plants are flowering and leafing out earlier over time and in warmer years. This is illustrated most distinctly by comparing data collected in the 1850s by the famous environmental philosopher Henry David Thoreau with modern observations. In this study, plants that have flowering times that are less responsive to spring temperature variation and plants that generally grow in colder climates have tended to decline and go locally extinct to a greater extent than other plant species. These striking results have been confirmed by studies elsewhere. As more historical data sets become available online, scientists are using powerful analytical tools to understand how climate change responses of plants vary around the world, improving forecasts of future global changes. These botanical data sets are also demonstrating that groups of species that interact with one another have different phenological responses to climate change, setting up the possibility of phenological mismatches. Such possibilities of phenological mismatches are being actively investigated among birds, plants, and insects, and between trees and wildflowers, using field observations and experiments.

Third, millions of herbarium specimens and photographs of plants are being digitized, allowing researchers to study flow-

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Flowering times, Leafing times, Mismatches, Phenology

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Fig. 1. Botanical gardens are great places to do climate change research, such as the Arnold Arboretum of Harvard University.

Fig. 2. Herbarium specimens can be used to investigate the effects of climate on flowering, leafing out, and fruiting times.

Fig. 3. Using citizen science in climate research is an exciting opportunity for both science and public education, illustrated by this example from the Royal Botanical Garden Edinburgh.

ering, fruiting, and leafing out times at unprecedented geographic, temporal, and taxonomic scales (Fig. 3). These studies convincingly demonstrate that herbarium specimens are a powerful tool to determine quantitatively that plants flower and leaf out earlier now than in the past and earlier in response to a warming world (Lee et al. 2022). One recent example illustrates that phenological mismatches between trees and wildflowers are more likely to occur in eastern North America than in East Asia and Europe. Also, the correlations between temperature and phenology are substantially stronger in eastern North America than in East Asia and Europe, a novel result that requires further inquiries.

Fourth, community and citizen science programs, such as iNaturalist, iSpot, and the National Phenology Network (USA), have greatly expanded, increasing the data available to researchers and engaging the public in climate change research Fig 3). Researchers are now challenged to develop methods to combine these diverse data sources in ways that take advantage of the special characteristics of each. For example, a study from Denmark found that flowering dates from herbarium specimens and photographs submitted to iNaturalist could be readily combined in phenological studies because they both represent peak flowering dates, whereas observations from a citizen science network captured first flowering dates, which is a different metric (Iwanycki et al. 2022).The insights gained from such plant ecology research at botanical gardens, herbaria, and citizen science programs will greatly advance our understanding of the effects of past climate change, and anticipate the impacts of future climate change, on plants and ecosystems around the world. Such research with plants also has the potential to educate the public about climate change happening in their own communities and motivate them to become advocates for addressing the crisis of climate change.

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Ampelographic (grapevine) collection in the 230-year-old Herbarium Wolnyanum (Sremski Karlovci, Serbia)

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Vitis, Vojvodina, Wine

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The herbarium collections in Southeast Europe were mostly founded in the 19th century or later. However, the oldest collection in Serbia dates back to the 18th century. It was founded in the Habsburg Monarchy as a school herbarium in the first Serbian gymnasium in Sremski Karlovci, where it is still kept today. The founder was Andreas Wolny (1759–1827), first professor of geology, mineralogy, botany and zoology (and various other subjects), and soon after professor and director of the gymnasium. He worked and lived in Sremski Karlovci in the period from 1793 to 1816. Wolny was a respected botanist and mineralogist at this time and had been a member of the Regensburg Botanical Society since 1801, and a member of the Society of Mineralogists in Jena since 1805. He was an esteemed teacher, known for his systematic approach. He collected plants in the surroundings of Sremski Karlovci and the mountain Fruška Gora and described them with data that proved their practical value. The herbarium served as a handbook for various subjects, with a focus on plant systematics, pharmacy and agriculture. In modern times, this collection is valued as an important museum treasure that has little or no floristic value, as the place and date are not indicated on most labels. The inventory part of the collection comprises nearly 7000 herbarium sheets. The exsiccates are organised into subcollections: Algae, Fungi, Lichens, Bryophyta, Pteridophyta, Monocotyledons and Dicotyledons. Also subdivided as subcollections are material collected by: Andreas Wolny, Josip Pančić (1814–1888), and material obtained by exchange or sent by foreign botanists (Josephine Kablick (1787–1863), Jacob Juratska (1821–1878) and Rat (2023).

Since the end of the 19th century, the collection has been closed and no new plant material has been added. Due to its historical and cultural significance and especially its importance as a natural document, it has been legally protected as a cultural monument by the Republic of Serbia since 1950. In 2017, modern research began on this forgotten and neglected collection, now recognized as Herbarium Wolnyanum (Rat 2023). The first goal was to re-inventory the herbarium sheets, review the material and prepare it for further study. As the process of revision began, many interesting discoveries were made. Among them was the discovery of an ampelographic collection of grape varieties grown on Fruška Gora Mountain at the beginning of the 19th century, before the phylloxera plague in Europe. The

Fig. 1. Herbarium sheet of grapevine cultivar ‚Mala Zelena Smederevka', Herbarium Wolnyanum (Sremski Karlovci, Serbia), collected by „Issan Popovics, im Doboschevaz" (= Ivan Popovic, Doboševac, Sremski Karlovci, Serbia)

oldest known ampelographic herbarium collection in the world is kept in Spain (Gago et al. 2019). It was established in 1803–1804, almost 20 years before the *Vitis* collection in Sremski Karlovci. All other known *Vitis* collections in the region date back to the beginning of the 20th century, a time when phylloxera was already present in Europe and contributed significantly to the disappearance of old autochthonous varieties (Ollat et al. 2016). Given these circumstances, the importance of these two collections is exceptional.

The first results of the revision of the Herbarium Wolnyanum have shown that 122 herbarium sheets of different *Vitis* varieties are kept in the collection. Of these, 75 have so far been preserved with pressed material. Each of these sheets contains at least one leaf, a pressed grape and one or more herbarium labels (Fig.1). The list of grape varieties includes old, autochthonous grape varieties that have been cultivated in the region for centuries, many of which are no longer known today. The specimens are divided into the „white grape" group and the „red grape" group. Based on the information on the labels, 55 *Vitis* varieties are preserved on sheets, some of which come from several different vineyards. All the material was collected in the surroundings of Sremski Karlovci, in the Fruška Gora mountains. However, the subsequent changes in the names of the settlements (due to geopolitical changes) as well as the labels written in several old languages (Old Serbian, Old German as well as Spanish, Hungarian, Latin and French) require a detailed analysis of the material to confirm the locations and other details listed on the labels.

The first scientific result provided the list of grape varieties, while further research, including molecular analysis of aDNA, will contribute significantly to the identification, confirmation, and knowledge of the development of viticulture in Serbia, but also in the Balkan Peninsula and the Pannonian Plain.

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Looking into 16th-century botanical history to understand the complex taxonomy of *Tulipa sylvestris* in Europe

Aastasia Stefanaki[1,2], Tilmann Walter[3], Tinde van Andel[1,2,4]

Tulipa sylvestris is a small yellow tulip that was introduced to northern Europe in the 16th century. Unlike the tulips that came from the Ottoman empire and gave birth to modern cultivars, *T. sylvestris* came from the Mediterranean and became a garden escapee that successfully naturalized across Europe. Its taxonomy is complex due to morphological diversity, polyploidy and naturalization of cultivated plants. Two subspecies are provisionally accepted in Europe: subsp. *australis*, a diploid native in the Mediterranean (up to Central Asia) that grows on mountainous rocky grasslands, on poor soils; and subsp. *sylvestris* a tetraploid that is naturalized across Europe and grows in rich soils at low altitudes, mainly at field margins, vineyards and gardens. Sometimes these two subspecies are regarded as distinct species, but their taxonomic delimitation is unclear.

In an article recently published in Scientific Reports (Stefanaki et al. 2022), we looked into the introduction history of *T. sylvestris* attempting to elucidate this species' complex taxonomy. By reviewing original 16th-century botanical literature, specimens, illustrations, mail correspondence and archives we identified the areas in the Mediterranean where this tulip came from, when and who spread it across Europe.

The first seeds of *T. sylvestris* that crossed the Alps came to Zurich. The Swiss naturalist Conrad Gessner is known as the first who scientifically described a (red) tulip in 1561, but his interest in this exotic flower was triggered years before, when he saw a watercolor illustration of *T. sylvestris* in a manuscript known as the Codex Kentmanus. This image was drawn after a tulip grown in the botanical garden of Padua in northern Italy, originating from material that most likely came from Bologna. Gessner requested seeds of this tulip from the prefecture of the Padua garden, Melchior Wieland, and received them between 1554 and 1559. He kept a copy of Kentmann's illustration (Fig. 1), drew the seeds he received from Padua on the sheet, but probably did not further distribute this material in his network, because he died a few years later, in 1565.

Around that same year, the Flemish botanist Matthias De Lobel dug out bulbs of *T. sylvestris* from the Cevennes mountains, north of Montpellier in southern France, and sent them to Antwerp. He was acknowledged by his contemporaries as the first to bring this tulip to northern Europe. De Lobel's tulips eventually reached the garden of the Flemish nobleman Charles de Saint Omer near Bruges and survive today

Keywords
Conrad Gessner, Matthias De Lobel, Tulip history, *Tulipa australis*, Wild tulip

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Fig. 1. Gessner's personal copy of the oldest surviving illustration of *Tulipa sylvestris* originally contained in the manuscript Codex Kentmanus from 1549.
Image credit: University of Tartu, Mscr 55, f. 3v.

Fig. 2. *Tulipa sylvestris* from Montpellier depicted in a watercolor contained in the Libri Picturati collection.
Image credit: Jagiellonian Library Krakow, A30.056v.

in a watercolor illustration contained in the famous Libri Picturati collection (Fig. 2). This illustration served as a model for the woodcut that accompanied the first scientific description of *T. sylvestris* published by the Flemish botanist Rembert Dodoens in 1568.

In the 1570s, another important Flemish botanist, Carolus Clusius, based at that time in Vienna, received bulbs of *T. sylvestris* from Montpellier, Bologna and the Apennines from several influential men of his network, including the Italian naturalist Ulisse Aldrovandi and Clusius' patron Jean de Brancion, a rich man from Mechelen.

The tulips that came from Montpellier, Bologna, and the Apennines further circulated among 16th-century European naturalists, started escaping their gardens and spread in the wild. The first written evidence of *T. sylvestris* turning wild comes from a letter of Clusius from 1577. With this letter, Clusius sent bulbs of the „Tulipas Bononieses" and „Mompelianas" to his friend Camerarius in Nurnberg, instructing him to plant them apart from other tulips and restrict them with tiles or bricks, because they have the tendency to spread and conquer the whole garden.

Linking these historical findings with the taxonomy of *T. sylvestris* gives interesting insights. Among the three places of origin of the first bulbs that reached northern Europe (Bologna, Montpellier, Apennines), subsp. *sylvestris*, i.e. the subspecies that is naturalized across Europe as commonly believed, grows only in Bologna. The plants growing in the Cevennes and the Apennines belong to subsp. *australis*. It is thus evident that the currently accepted subspecific classification of *T. sylvestris* is not supported by the introduction history of the species, because both subspecies were introduced to northern Europe.

Our research group is currently working on genomic repeat profiling of *T. sylvestris* to further elucidate this species' complex taxonomic status.

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What did 16th-century tomatoes look like?

Tinde van Andel[1,2] and Anastasia Stefanaki[2,1]

Soon after the Spanish conquest of the Americas, the first tomatoes were presented as curiosities to the European elite and drew the attention of 16th-century Italian naturalists. Despite their scientific interest in this New World crop, most Renaissance botanists did not specify where these „golden apples" or „pomi d'oro" came from. It is likely that tomatoes were brought to Europe after the Spanish sieged the Aztec city of Tenochtitlan (now Mexico City) in 1521 and after they conquered the Peruvian Inca emperors in 1531. Tomatoes and other New World domesticates must have been brought to the Spanish court, and were probably planted in the royal gardens in Madrid, after which they were likely shipped from Sevilla to Italy, but no written evidence have been found so far for these events. The debate on the first European tomatoes and their origin is often hindered by erroneous dating, botanical misidentifications and inaccessible historical sources. So, who saw the first 16th-century tomatoes that entered Europe? What did they look like? Who made the first botanical description, collection and/or illustration? And where did these tomatoes come from?

Recent digitization efforts greatly facilitate research on historic botanical sources. Van Andel et al. (2022) provide an overview of the ten remaining 16th-century tomato specimens, early descriptions and 13 illustrations. Several of these specimens, descriptions, garden inventories and illustrations had never been digitized and/or published before. The historical findings are compared to recent molecular research on the ancient chloroplast and nuclear DNA of the tomato specimen in the „En Tibi book herbarium" (Vos et al. 2022), dated around 1558 and produced in Bologna by the Italian botanist Francesco Petrollini, and by some claimed to be the oldest tomato specimen.

Our survey showed that the earliest tomatoes in Europe came in a much wider variety of colors, shapes and sizes than previously thought, with both white and yellow, simple and fasciated flowers, round and segmented fruits in various colors. Pietro Andrea Matthioli gave the first description of a tomato in 1544, and the oldest specimens were collected by Ulisse Aldrovandi (Fig. 1) in c. 1551 and Francesco Petrollini (Fig. 2), possibly from plants grown in the Pisa botanical garden by their teacher Luca Ghini. The „En Tibi" specimen thus is not the oldest extant tomato. Due to the close network of Renaissance

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Early book herbaria, Renaissance, Tomato

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Fig. 1. Tomato specimen by Aldrovandi, Bologna, c. 1551.

Fig. 2. Specimen by Petrollini in the „En Tibi" herbarium, c. 1558.

Fig. 3. Specimen by Caspar Bauhin (1577–1624), Basel.

botanists, tomato seeds rapidly spread to northwest Europe, and also were planted in Caspar Bauhin's garden in Basel. The oldest tomato illustrations were made in the early 1550s in Germany (by Leonhard Fuchs and Georg Oellinger) and Switzerland (by Conrad Gessner), but the Flemish Rembert Dodoens published the first image in 1553. The names of early tomatoes in contemporary manuscripts varied a lot but some suggest a Mexican and others a Peruvian origin.

DNA analysis of the 464-year-old „En Tibi" specimen recovered only 1.2 % of its genome, but still showed that it was a fully domesticated tomato. It clustered neatly with the domesticated tomatoes in a comparison with genome assemblies of 114 accessions of wild species and traditional cultivars from Latin America that were retrieved from an earlier published 360-tomato resequencing project. The „En Tibi tomato" was genetically close to three Mexican landraces and two Peruvian specimens that probably also had a Mesoamerican origin.

Molecular research on the other 16th-century tomato specimens may reveal other patterns of genetic similarity, past selection processes, and geographic origin. Clues on the „historic" taste and pest resistance of the 16th-century tomatoes should be sought in those landraces in Central and South America that are genetically close to them. With decreasing crop diversity and the social, economic and ecological challenges faced by small farmers of indigenous descent to preserve their traditional agricultural practices, tracing the „sisters" of the „En Tibi" tomato back to Mexican or Peruvian smallholders' gardens will be difficult. The landraces that were genetically close to the „En Tibi" tomato were collected between 36 and 52 years ago: they may have already disappeared from indigenous gardens and survive only as seeds in germplasm institutes. The indigenous farmers growing traditional tomato varieties should be supported to conserve these heirloom varieties *in-situ*.

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Network analysis of the herbarium collection of the Moravian Church from the 18th century

Sarah T. Wagner[1], Richard Ehrlacher[1], Lena Frenzke[1], Frank Müller[1], Christoph Neinhuis[1], Thomas Ruhland[2]

The Herbarium Dresdense (DR), Germany, houses about 500 000 specimens of worldwide origin. One of the oldest collections is the *Herbarium Barbiense* of the Moravian Church from the mid to the late 18th century. On their mission to spread Christianity, the Moravians settled on many continents and took the advantage of exploring culture and nature of their new home countries. Being excellent observers and documentarists, they left a barely explored corpus of objects and texts of tremendous importance for natural sciences and humanities. Since 1754 the educational centre of the community was located in Barby, Saxony-Anhalt, Germany. To support the scientific training and to gather objects send home by the missionaries, a cabinet of natural curiosities was established in 1756. The collections of minerals, fossils, conchylia and plants were unique and soon attracted other European academics (Augustin 2005).

The Moravian Church teachers Friedrich Adam Scholler (1718–1785) and Johann Jakob Bossart (1721–1789) initiated the botanical education at the community's academy in Barby. Their various manuscripts and documents proof that both were excellent botanists who incorporated the latest contemporary concepts into their work. Bossart's catalog of the cabinet's botanical contents („Index Plantarum siccarum Systematicus eo ordine, quo sunt in Fasciculis dispositae") testifies that an herbarium collection of about 3200 specimens was gathered in Barby until the end of the 18th century (Fig. 1). This collection fell into oblivion during the 20th century, but was recently rediscovered in Dresden (Ehrlacher et al. 2023). In a current project the 1260 remaining herbarium samples from the cabinet of natural curiosities in Barby are being analysed. Within the collection specimens are found from the proximity of Barby, but also from India, Greenland, Labrador, Russia, North Carolina and Tahiti. Locality information is only given for about a quarter of the specimens, and collectors names apart from a few exceptions are not mentioned (Ehrlacher et al. 2023). In order to enrich the specimens with additional metadata and contextualize the collection, the specimens are examined with respect to e.g., mounting techniques, original paper characteristics, such as size and watermarks as well as handwritings. Matchings between individual specimens allow conclusions to be drawn about secondary information, such as localities, collectors, or collection dates. This shows that beyond the plant material itself important additional information can be derived

Keywords
Barby, Johann Jakob Bossart, Herrnhuter Brüdergemeine, Plant specimen, Friedrich Adam Scholler

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Fig. 1. Specimen of the Herbarium Barbiense: *Anemone pulsatilla* L., today synonym to *Pulsatilla vulgaris* Mill., collected *„Im Busche bei Friderikenberg"*, a locality in Saxony-Anhalt, close to Barby (now housed in Herbarium DR, inventary number 024129; https://dr.jacq.org/DR024129).

from historical herbarium specimens. To link the specimen's metadata with further sources, TEI (Text Encoding Initiative) tools are being tested. Wikidata keys are applied as identifiers to link plant names, persons and localities with other sources, such as personal correspondence and botanical manuscripts. All specimens are digitized and available online in the herbarium database www.jacq.org and at www.gbif.org.

The Moravian's scientific heritage proves that they were strongly integrated into the scientific network of the 18th century. Letters in the collections of the Linnean Society prove that Friedrich Adam Scholler was in close contact with leading scientists, e.g., Carl von Linné, discussing questions of plant taxonomy, exchanging specimens and presenting own field work, such as his most important book, „Flora Barbiensis", published in 1775 (Scholler 1775). The book lists 1007 species in the vicinity of Barby, a very thorough record of the known plants, along with characteristics, localities and uses. Matching the information on the herbarium specimens with the Flora Barbiensis and the information in a 40-page handwritten field trip diary allows verification of taxa listed and provides insights into the botanical practice in the mid-18th century (Ehrlacher et al. 2023).

The ongoing study aims to further contextualize and enrich the specimens of the *Herbarium Barbiense* with metadata, break up the anonymity of collectors and participants and to investigate the contribution of Moravian Church botanists to the 18th century scientific network and the development of modern natural sciences. Further anonymous herbarium collections and sources with a Moravian Church context will be analysed and integrated into the network analysis. The processing of data that is also relevant for other research areas (e.g., humanities, digital humanities, linguistics, history of garden monuments, cartography, data science, horticulture) will enable their interdisciplinary use and linkage.

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Flora of the Canary Islands – revised checklist to a classic arena of botany

Anna Walentowitz[1], Walter Welss[2], Carl Beierkuhnlein[1]

The Canary Islands are a popular location for botanical collections that resulted in a series of seminal works, including the description and documentation of many endemic plant species (Fig. 1, 2, 3) in herbaria. Viera y Clavijo, Christ, Webb, Berthelot, Sventenius, Pitard, Kunkel, or Bramwell, to name but a few, majorly contributed to the knowledge about the flora of the Canary Islands. Alexander von Humboldt's botanical description of Tenerife during his stay in 1799 also motivated Charles Darwin to explore the island. Unfortunately, Darwin was not allowed to set foot on land during his voyage with the Beagle due to quarantine restrictions. In recent years, a number of data bases containing detailed information about the plants of the Canary Islands emerged. This botanical legacy evokes the expectation that detailed information about the flora of the archipelago is available, with high agreement about taxa and status between different sources. To test this expectation, we elaborated an extensive floral checklist for the Canary Islands, documented which taxa are accepted in global taxonomic reference systems, and additionally checked their coverage in databases that are a common sources in biogeographical and ecological research.

To do so, we compiled information on the occurrence of species and infraspecies (subspecies and varieties) on the seven major Canary Islands (namely El Hierro, La Palma, La Gomera, Tenerife, Gran Canaria, Fuerteventura, and Lanzarote) from published floras and plant species lists and complemented these with scientific literature. As a taxonomic backbone of the resulting list, we used Kew's Plants of the World Online (POWO 2021). Coverage of all listed taxa in World Flora Online (WFO) and The Catalogue of Life was also documented. As supplementary information, we checked for the data coverage, deficiencies, and related fundamental restrictions of all taxa in the databases GBIF (Global Biodiversity Information Facility) and TRY (Plant Trait Database), which are commonly used in ecological and biogeographic research.

For the Canary Islands, we deduced 2812 taxa in total (1781 native, 1031 non-native), of which 2416 (1452 native, 964 non-native) are species and 396 are infraspecific taxa (329 native, 67 non-native). The underlying checklist is available in the Supplementary Materials of Beierkuhnlein et al. (2021) and openly accessible. The number of taxa, species and infraspecies differed between islands (Fig. 4) and was highest for Tenerife that has a pronounced topography and diverse

Keywords
Biodiversity, GBIF, Island biogeography, Macaronesia, TRY

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Fig. 1. *Echium webbii* Coincy. Species of the genus *Echium* in the Canary Islands are an example for adaptive radiation.
Photo Carl Beierkuhnlein

Fig. 2. *Echium bethencourtii* A. Santos
Photo Carl Beierkuhnlein

Fig. 3. *Echium thyrsiflorum* Masson ex Link, also known under its synonym *Echium gentianoides* Webb ex Coincy. Photo Carl Beierkuhnlein

climatic conditions. Surprisingly, we found a considerable proportion of taxa that have been recorded in scientific papers but are missing from current floras and data bases. Furthermore, we identified taxa with deviating status (e.g., surely native, probably non-native) between taxonomic databases. And still, new species are being detected and described. Data coverage of the Canary Island flora in different databases is far from being complete.

Despite the fact that the Canary Islands are a popular natural laboratory of botanical, evolutionary and biogeographical research, the documentation of the flora of the Canary Islands is work in progress. Updating such an important data source is a prerequisite for macroecological and biogeographical studies. Our new checklist reflects the current state of knowledge and can function as a basis for further amendments.

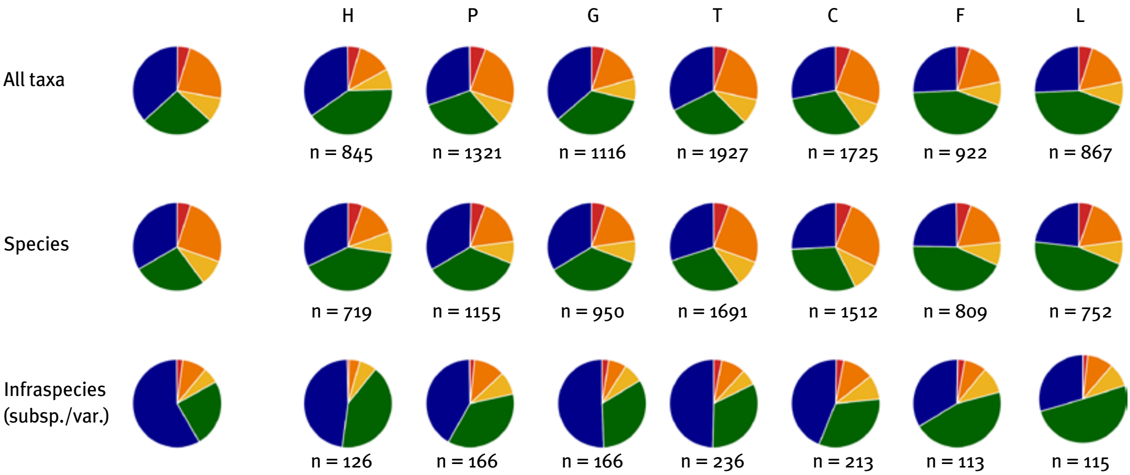

Fig. 4. Categories of native and non-native taxa in the Canary Islands and for the individual islands El Hierro (H), La Palma (P), La Gomera (G), Tenerife (T), Gran Canaria (C), Fuerteventura (F) and Lanzarote (L) based on the here presented checklist. Proportions are given at the level of all taxa, and separately for species and infraspecific taxa (subspecies and varieties). Absolute numbers of taxa are given below the pie charts. Generally, the proportion of accepted native infraspecific units (subspecies, varieties) is higher compared with the accepted species.

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A plant's path to publication – Caspar Bauhin (1560–1624) and Johann Theodor de Bry (1561–1623)

Karen Reeds[1] and Davina Benkert[2]

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Florilegium, Herbarium, Renaissance botanical illustration, University of Basel

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The Basel botanist Caspar Bauhin is justly famed for bringing order to late Renaissance botany. Through his *Phytopinax* (Basel, 1596), *Prodromos Theatri Botanici* (Frankfurt, 1620), and, above all, *Pinax Theatri Botanici* (Basel, 1623), Bauhin prepared the way for his *Theatrum Botanicum.* He envisioned this as a comprehensive, systematic, illustrated account of all six thousand-plus plants known to him. His contemporaries had high regard for these works (Reeds 1991; Benkert 2020); a century later, Linnaeus found them indispensable. Today, they remain our key to pre-Linnaean botanical literature.

Sadly, of *Theatrum's* twelve planned sections, only Liber I was published. Those 700 pages on grasses, edited by Bauhin's son, Johann Caspar Bauhin (1606–1685), finally appeared in 1658, long after Bauhin's death. To illustrate *Theatrum,* Bauhin had to choose: copperplate engravings? Or woodcuts? Two sets of virtually unstudied material in the Universitätsbibliothek Basel (UBB K I 6a, b; K IV 3, B,C. Sackmann 1991) reveal why Bauhin's past experience with floral engravings made him follow the Renaissance herbal tradition of woodcut illustrations instead.

Around 1613–1614, Johann Theodor de Bry (1561–1623) – the successful publisher of Bauhin's anatomical works – had enlisted Bauhin's expertise for a deluxe album of engravings of ornamental flowers: *Florilegium novum* (Oppenheim, 1612, 1614, 1618). Through Bauhin's herbarium specimens and a handful of watercolors and engraver's proofs (Bauhin Herbarium: BAS B15-078B; UBB K IV 3, B,C) depicting *Stramonia Aegyptiaca (Datura stramonium* L.), we can follow that plant's path to publication (Fig. 1 a-i) and to appreciate Bauhin's rejection of engravings for *Theatrum.*

Bauhin's herbarium specimens of *Datura sive Stramonia Aegyptiaca* had come from Giovanni Pona of Verona and Prospero Alpino of Padua in 1614 (Fig. 1a). The two flamboyant *Stramonia* watercolors, by an unidentified artist, are labeled in Bauhin's hand (Fig. 1b, c). The copperplate proofs of the *Stramonia* flowers (Fig. 1d, e, f) – possibly engraved by de Bry himself – together with the artist's watercolor of the completely unrelated hyacinth (Fig. 1d) show how de Bry squeezed the images of *Stramonia Aegyptiaca* (Fig. 1e) and *Hyacinthus ramosus (Hyacinthus racemosus* L.) (Fig. 1d) into a single *Florilegium* plate (Fig. 1h). These engraved images reached their biggest audience through *Florilegium renovatum et auctum* (Frankfurt, 1641; plates 115, 116),

Fig. 1a. Two specimens of *Datura/Stramonia*

Fig. 1b. Watercolor, *Stramonia Aegyptiaca… flore gemino.*

Fig. 1d. Watercolor, *Hyacinthus Ramosus.*

Fig. 1c. Watercolor, *Stramonia Aegyptiaca… flore… purpurascente.*

Fig. 1a–i. A plant's path to publication.
Sources:
Fig. 1a. Bauhin Herbarium, University of Basel: BAS B15-078B.
Fig. 1b–c. UBB K IV 3: B [5] 3r, B [1] 1r.
Fig. 1d. UBB K IV 3: C [3] 2r.
Fig. 1e–f. UBB K IV 3: B [7] 4r, [3] 2r: https://www.e-manuscripta.ch/bau/content/structure/773810.
Fig. 1g–i. De Bry/Merian, *Florilegium renovatum et auctum* (1641), plates 116, 115: https://www.digitale-sammlungen.de/en/details/bsb11057823

published by de Bry's son-in-law and heir, Matthaeus Merian (Fig. 1g, h, i). Because the printing technology for engravings could not accommodate copperplates and typeset text on the same page, only brief labels identified the plants.

But, for Bauhin, combining two unrelated plants in one picture and omitting all commentary was unacceptable. Serious readers needed his images and text side-by-side – possible only with woodcuts and traditional typesetting. Two extraordinary volumes, *De Graminibus,* demonstrate the difficulties of assembling the *Theatrum's* illustrations (Sackmann 1991; UBB K I 6a; 6b). The two Bauhin's painstakingly prepared the unique cut-and-paste draft by first interleaving a copy of *Pinax* with blank sheets, then, onto those, gluing hundreds of manuscript labels, annotations, and clippings of new or recycled woodcuts of plants (Fig. 2). It was Bauhin's – and botany's – misfortune that all that effort came to naught.

Fig. 1e. Engraver's proof, *Stramonia Aegyptiaca… flore gemino.*

Fig. 1f. Engraver's proof, *Stramonia Aegyptiaca… flore… purpurascente.*

Fig. 1g. Title page. De Bry/Merian, *Florilegium renovatum et auctum* (1641).

Fig. 1h. Two images combined onto a single plate: *Stramonia Aegyptiaca flore gemino…* and *Hyacinthus ramosus…* (plate 116).

Fig. 1i. Oversize engraving, *[Stramonia Aegyp]tiaca f[lore extrinsecus… purpura]scente…* (plate 115).

Fig. 2. Bauhin's *Theatrum Botanicum* as a work-in-progress: interleaved page with attached manuscript labels and woodcuts of the potato, *Solanum tuberosum esculentum*, and other *Solanums*, facing *Pinax*, p. 167. UBB K I 6a, *De Graminibus.* Photo by KM Reeds

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