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Opinion

The herbarium of the future

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The ~400 million specimens deposited across ~3000 herbaria are essential for: (i) understanding where plants have lived in the past, (ii) forecasting where they may live in the future, and (iii) delineating their conservation status. An open access 'global metaherbarium' is emerging as these specimens are digitized, mobilized, and interlinked online. This virtual biodiversity resource is attracting new users who are accelerating traditional applications of herbaria and generating basic and applied scientific innovations, including e-monographs and floras produced by diverse, interdisciplinary, and inclusive teams; robust machine-learning algorithms for species identification and phenotyping; collection and synthesis of ecological and genomic trait data at large spatiotemporal and phylogenetic scales; and exhibitions and installations that convey the beauty of plants and the value of herbaria in addressing broader societal issues.

Highlights

Plants are the foundation of our terrestrial biota but an estimated 40% of plant species risk extinction.

Herbaria, which have long been an essential tool for species discovery and identification, also harbor unparalleled genetic, genomic, and ecological trait data that remain largely untapped.

The herbarium of the future, the 'global metaherbarium', will be a common, global, digitally interlinked and open-access resource that will stimulate large-scale and novel science to directly address our current biodiversity crisis.

Recognizing and mitigating the colonial legacy of herbaria, supporting interdisciplinary scholars, enhancing digitization efforts internationally, and strategically expanding existing plant collections will greatly foster and sustain the global metaherbarium.

A revolution in herbarium use

The use of herbaria for basic and applied science is undergoing a revolution along two fronts that traverse a wide swath of scholarly domains. First, the online mobilization of vast amounts of specimen data, combined with novel tools and large interdisciplinary collaborations, are propelling biodiversity discovery and exploration at unprecedented scopes and scales. Second, scholarly domains ranging from ecology to computer science to art, that are well outside of those traditionally aligned with herbarium science (taxonomy, systematics, evolution) are facilitating novel applications and discoveries and infusing herbaria with a renewed sense of purpose. Overall, this revolution is vastly increasing the relevance of herbaria and stimulating science that will pave the way for the next half century and beyond. The emerging 'herbarium of the future' (or the 'global metaherbarium') will be the central element guiding the exploration, illumination, and prediction of plant biodiversity change in the Anthropocene [1,2].

The global metaherbarium

Herbaria are an essential source of biodiversity discovery (Figure 1) [1,3–5]. Longstanding applications of herbaria include species descriptions, identification, classification, and geographic range estimation [3,6,7]. Such data are used to create local and regional floristic inventories and are synthesized into comprehensive taxonomic monographs. However, classical approaches for summarizing plant biodiversity data are too slow to keep pace with rapidly mobilizing biodiversity data and ongoing species loss. Most existing monographs are long out of date and rife with inaccuracies, often even at the time of their initial publication. For example, an estimated one-quarter of new species described from herbaria involve specimens that are more than 50 years old [8,9] and at least 70 000 new species remain to be described from herbaria. At the same time, >50% of specimens from the tropics, where biodiversity is greatest, may be misidentified in herbaria [10]. Without accurate species identification, it is impossible to assess their current distributions or conservation status [e.g., International Union for Conservation of Nature (IUCN) Red List].

The herbarium of the future is a common, digitally interlinked, global open-access resource, a 'global metaherbarium', that is enabling three major synergistic directions in plant science:

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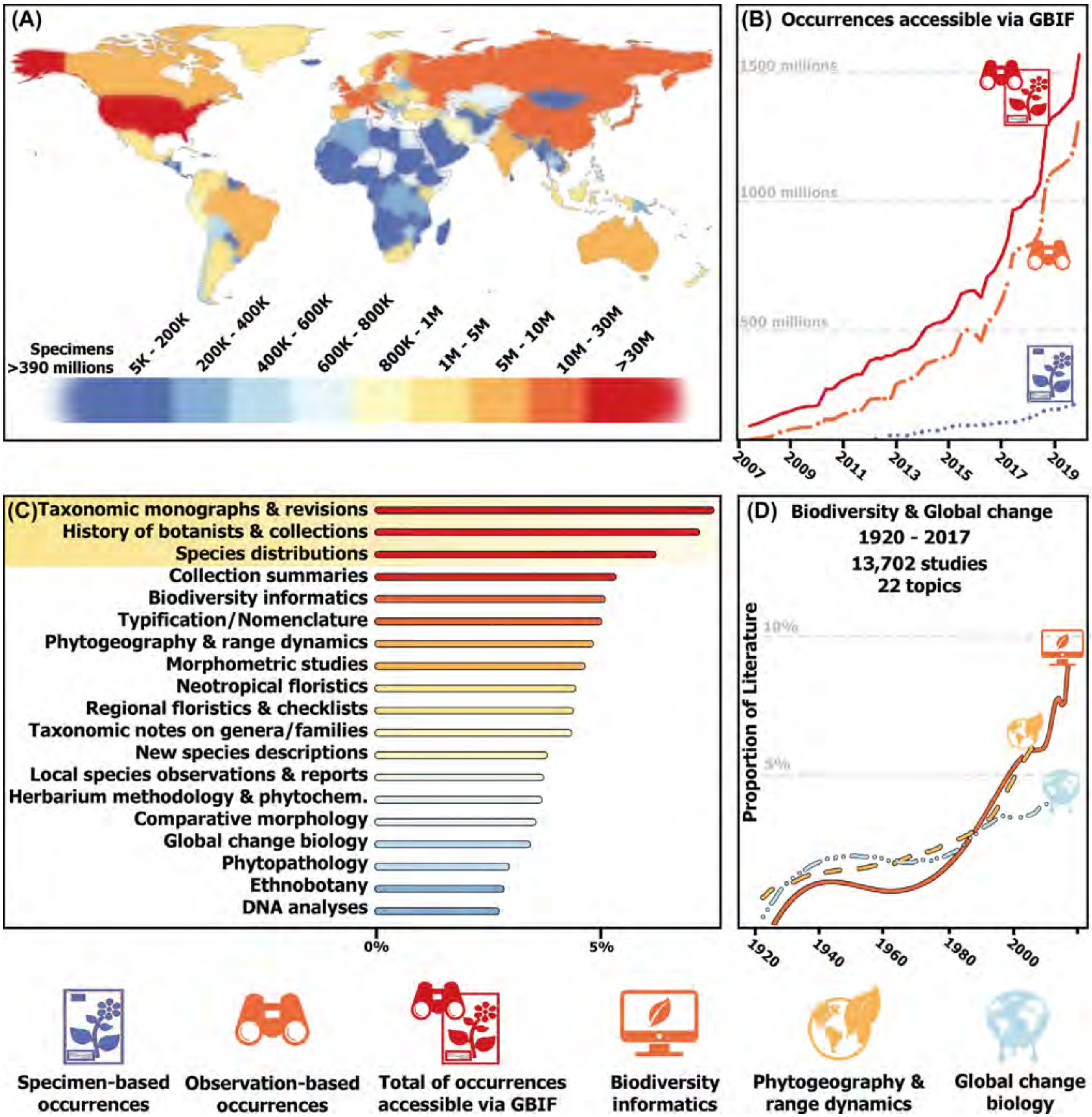

Figure 1. The global distribution and use of herbaria. (A) The global distribution of country-wide herbarium specimens. (B) The contrasting growth of digitized specimen versus observational data mobilized online by the Global Biodiversity Information Facility (GBIF). (C) Literature summary of traditional uses of herbarium specimens (shaded in yellow) versus the (D) expanding nontraditional uses of collections. Icon legend for (B) and (D) shown at bottom. (A), (B), and (D) redrawn from [3]; (C) redrawn from [32].

(i) innovations in traditional applications of herbaria to speed discovery, (ii) a dramatic expansion and diversification of the community of researchers taking advantage of these priceless resources, and (iii) development of strategic initiatives to stimulate new science and broad participation. Synergies among these directions will facilitate research of astonishing scale and novelty and directly contribute to solving our current biodiversity crisis.

Innovating traditional applications of herbaria to speed discovery

Plant discovery in the age of digitization

One of the greatest recent innovations in biodiversity science has been the digitization and online mobilization of specimens, which is facilitating the rapid exploration, synthesis, and dissemination of accurate biodiversity data at unprecedented scales [11]. A key early synthesis demonstrating the promise of these aggregated digitized herbaria was the massive floristic inventory of the Amazon [12], which sharply reduced the estimated number of species in this hyperdiverse region. This effort was facilitated largely by REFLORA (https://reflora.jbrj.gov.br/reflora/) [13], an open-access virtual herbarium developed and supported by more than 400 Brazilian botanists and biodiversity specialists. This monumental effort led to the first complete and revised flora, including images and metadata, for this megadiverse country [14]. REFLORA (https://reflora.jbrj.gov.br/reflora/), representing more than 51 000 species, together with SpeciesLink (https://specieslink.net/search), have become the key online resources for accessing herbarium specimens from Brazil. They include mobilized specimens from 40 major Brazilian herbaria plus all major European and American herbaria.

The more recent publication of the first comprehensive and expert-verified inventory of New Guinea [15] further exemplifies the power of this innovative approach. New Guinea includes massive climatic gradients, from lowland rainforest to alpine meadows, and has long been recognized as a center of plant biodiversity. Despite the low sampling intensity (fewer than 25 collections per 1000 km^2) the new flora of New Guinea identified ~13 000 species, nearly 70% of them endemic, and revealed that New Guinea harbors the world's richest island flora. This online and open-access resource has also illuminated the under-sampled regions of the island where thousands of species await discovery. Although >3000 species have been described since 1970, species discovery in New Guinea has not yet plateaued. Strategic synthesis of physical specimens with digitized data in the metaherbarium will continue to motivate the vigorous exploration of such biodiversity frontiers.

A revolution in monographic and floristic investigations

Like successful research programs in high-energy physics and astronomy, floristic and monographic investigations increasingly are embracing collaborative approaches involving large teams of researchers [15–17]. These are simultaneously increasing the scope of projects and greatly reducing the time for the resulting deliverables to reach key audiences and stakeholders, which is necessary to combat the rapid degradation of ecosystems and loss of biodiversity that characterizes the Anthropocene. The aforementioned floristic assessment of New Guinea involved more than 50 coauthors with diverse expertise and backgrounds. Other recent comprehensive floristic summaries of species diversity across the tropics further support this collaborative model of biodiversity synthesis and identified tropical Asia as the most biodiverse area for its size, the least well-known biota, and the area in greatest peril [18].

The most compelling example of modernizing and expediting monography via large collaborative teams is that of Muñoz-Rodríguez *et al.* [17]. This group of 15 coauthors published a monograph on the genus *Ipomoea*, which includes the domesticated sweet potato, *Ipomoea batatas*. The *Ipomoea* team included not only taxonomists but also evolutionary biologists, genomicists, and ecologists. Beyond the usual species descriptions, keys, and maps, the team described 63 new species and expanded the monographic concept to include comprehensive phylogenies and sophisticated analyses that localized the histories of *Ipomoea* species diversification [17]. They demonstrated that storage roots like sweet potatoes arose in this clade multiple times prior to human domestication, suggesting that this likely was a key trait predisposing it to human cultivation. Assembling large complementary teams to synthesize biodiversity knowledge to produce floras and monographs represents a new path for describing diversity comprehensively and efficiently and to create more and better resources for characterizing plant diversity across multiple scales.

Herbariomics

High-throughput genomic sampling of herbarium specimens combined with next-generation DNA sequencing and bioinformatics are facilitating the production of high-resolution phylogenies of entire clades, transforming the scope of monographs and floras and expanding the analysis of ecological communities of co-occurring taxa [5,16,17,19–22]. In these and other studies [23,24], herbaria have been crucial for expanding taxon or population sampling, adding rare and even extinct species [25], and offsetting prohibitive travel expenses, minimizing ones carbon footprint, and reducing the extensive time necessary to visit remote field locations. All these efforts are facilitated by enhanced DNA extraction methods, large plate formatting involving robotic liquid handlers, and sequencing techniques that better process degraded DNA like that found in herbaria [24,26,27]. Sophisticated open-access bioinformatic software pipelines are being developed and shared widely, enabling rapid and efficient large-scale phylogenomic inference [28]. The metaherbarium soon will become the central resource for such investigations spanning populations, communities, and whole continents. Indeed, in many ways, the herbarium has become the new frontier of 'fieldwork' with these many technical advancements. Actual field research can then be better targeted at particularly relevant taxa, localities, or other emergent questions.

Machine learning for automated species identification

Species identity is the foundation for describing and conserving biodiversity. Despite its importance, however, clade expertise is dwindling as systematic knowledge diminishes. Tools such as crowdsourcing and machine learning hold tremendous promise for bridging this impasse and have sparked renewed interest in taxonomic research [29]. Rapid advances in mobile app-driven resources like iNaturalist have demonstrated the possibility of automated species identification. Such apps have been essential for motivating new research projects and were an essential part of field courses taught under strict coronavirus disease (COVID) protocols [30]. Of course, these resources are in their infancy and remain unavailable or of little use for most species and regions around the world, especially in the tropics, where diversity is greatest. Nevertheless, the power and utility of these tools to identify species continue to be developed and refined. This is an intellectual frontier for biodiversity and computer scientists and for the large online amateur naturalist community. The promise of such synergistic efforts was demonstrated recently by the PlantCLEF2022 challenge targeted at automating the identification of nearly 100 000 plant species [31].

Breathing new life into herbaria: expanding users and novel applications

New users in related or disparate domains (ecology, genetics, anthropology, computer science, chemistry, and art; Figure 2) are taking advantage of herbaria in new, promising, and often unexpected ways (Box 1).

Herbaria as warehouses of large-scale ecological data

Ecologists are increasingly viewing herbaria as untapped resources from which to collect trait data at large spatial, temporal, and phylogenetic scales [4,32,33]. These approaches are simultaneously being enhanced by automating large-scale phenotyping using crowdsourcing and machine learning [11,34–37].

Perhaps the most well-characterized application in this realm to date, and one that continues to grow exponentially in terms of spatial, temporal, and taxon sampling, involves using herbaria to

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Figure 2. Herbaria are resources for addressing broader societal issues related to both the beauty and the imperiled nature of biodiversity. Visual artists are engaging with plant biologists in exciting new ways to convey biodiversity loss to a broader audience [80–82]. (A) Depicted here is a recent exhibit titled 'In search of Thoreau's flowers–an exploration of change & loss,' which opened in Cambridge, MA, USA at the Harvard Museum of Natural History in June 2022 and was co-curated by ecologist Emily Meineke, visual artists Leah Sobsey, Robin Vuchnich, and Marsha Gordon, and the author [80,81]. This multifaceted exhibit features a large digital wall (B) depicting the personal herbarium of the naturalist and transcendentalist Henry David Thoreau (C). The walls also feature large-format mosaics of plant diversity with an associated nature soundscape (D) and data summarized directly from research findings on plant loss associated with climatic change in this region (E). The mixed media provide a rich and immersive context for visualizing and understanding the science behind plant response to climatic change in New England [41,86,87]. The open-access nature of these digitized specimens, long ago mobilized online, have additionally allowed Leah Sobsey to create beautiful large-format cyanotype prints of herbarium specimens on gilded glass facsimiles of Thoreau's collections and journals (F). The combined effect invites visitors to emotionally experience the profound loss of biodiversity caused by human-induced climatic change and urges us to reflect on the beauty of the natural world, calling attention to our collective need to protect and restore it.

investigate phenological sensitivity to climatic change in the temperate zone [38] and, increasingly, in the tropics [39,40]. Large-scale spatiotemporal sampling has identified as much phenological variation within species as between them [41] and shown that sympatric species on average do not exhibit phenological displacement [42]. There also is far greater phenological variation in the tropics, the understanding of which has been obscured by temperate-centric biases [39,40].

Other exciting and emerging applications increasingly gaining traction include the utility of herbaria to investigate changing patterns of insect herbivory in response to warming and other climatic changes [43,44]. Traits measurable on herbarium specimens also are revealing other shifts in plant–animal symbioses, such as mutualistic interactions between plant nectaries or domatia and arthropods that provide the plant with protection from herbivores [45,46], phenological mismatches between plants and their primary pollinators [47], and other short-term phenotypic responses by plants that may alter their relationships with key pollinators (see Figure IA in Box 1). Essential plant functional traits also can be detected from specimens using hyperspectral imaging [48,49] (see Figure IB in Box 1). Finally, there is a growing interest in the characterization of small molecules involving plant metabolites that are important in plant medicines and which can be gleaned from herbarium and archeological collections that can be centuries old [50,51].

Herbaria as tools for conservation

Because the biodiversity crisis demands data syntheses and better conservation planning, large teams are working collaboratively to harmonize occurrence data from herbarium specimens with global-change data to understand the patterns, processes, and dynamics of past, present, and future biodiversity [52]. Specific results have included: elucidating deep-time factors that shape biodiversity using models of species diversity across vast spatiotemporal scales [53]; pinpointing eco-evolutionary drivers of diversification in biodiversity hotspots [54]; evaluating the effectiveness and coverage of protected areas in imperiled biomes [33,55] and expanding urban areas [56]; illuminating human-assisted species invasions and subsequent biotic homogenization [57] (see Figure IC in Box 1); circumscribing the genetic signatures of species and population declines [58]; and broadly characterizing the 'winners and losers' on our changing planet [2]. Characterizing the distribution, origins, and maintenance of diversity is crucial for: (i) delineating biogeographic regions to preserve maximal diversity, (ii) targeting key clades that represent long-lived lineages or potential future engines of diversity, (iii) identifying rapidly mutating lineages that can survive anthropogenic change, and (iv) compiling more accurate IUCN Red Lists [2,59,60].

Herbaria for understanding humans and plants

Evolutionary biologists increasingly are collaborating with anthropologists and archeologists to sequence and interpret complete genomes of plant specimens and subfossils in herbaria to illuminate the origins of domesticated species essential for feeding, sheltering, and physically, mentally, and spiritually healing humans [5,26,61–63]. Such explorations, once unimaginable, touch on myriad topics central to humanity, including: tracking the genetic history of domestication through time, illuminating patterns of human migration, characterizing anthropogenic change

Box 1. New directions and novel uses of herbaria.

Promising and novel applications of herbarium data for eco-evolutionary research include demonstrating that:

- UV-protecting pigments have increased on average in recent decades and that pigmentation specifically increased most dramatically in flowers with anthers that were directly exposed to ambient UV radiation (vs. those with anthers that were shielded and concealed) (Figure IA).
- A variety of functional traits for macroecological investigations can be obtained from herbarium samples and estimates from herbarium specimens of key functional traits [leaf mass per area (LMA), water-related traits, carbon fractions, and pigments] compare favorably with estimates of the same traits from fresh tissues (Figure IB).
- Biotic homogenization has been driven primarily by the human-assisted transport of non-native species during only the last 500 years [57]. Herbarium data also help identify key sources and sinks and directional transport of non-native species spread across the planet (Figure IC).

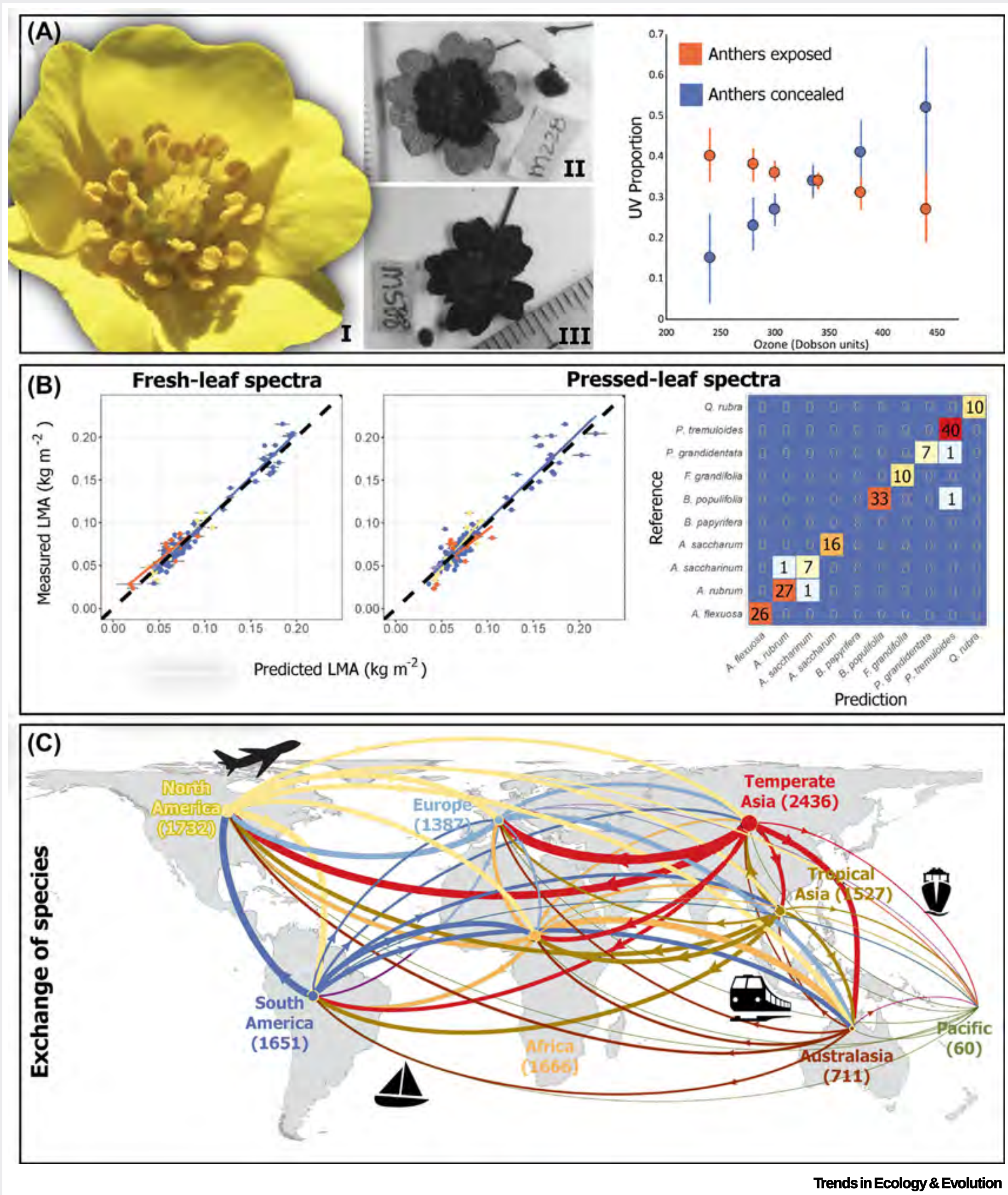
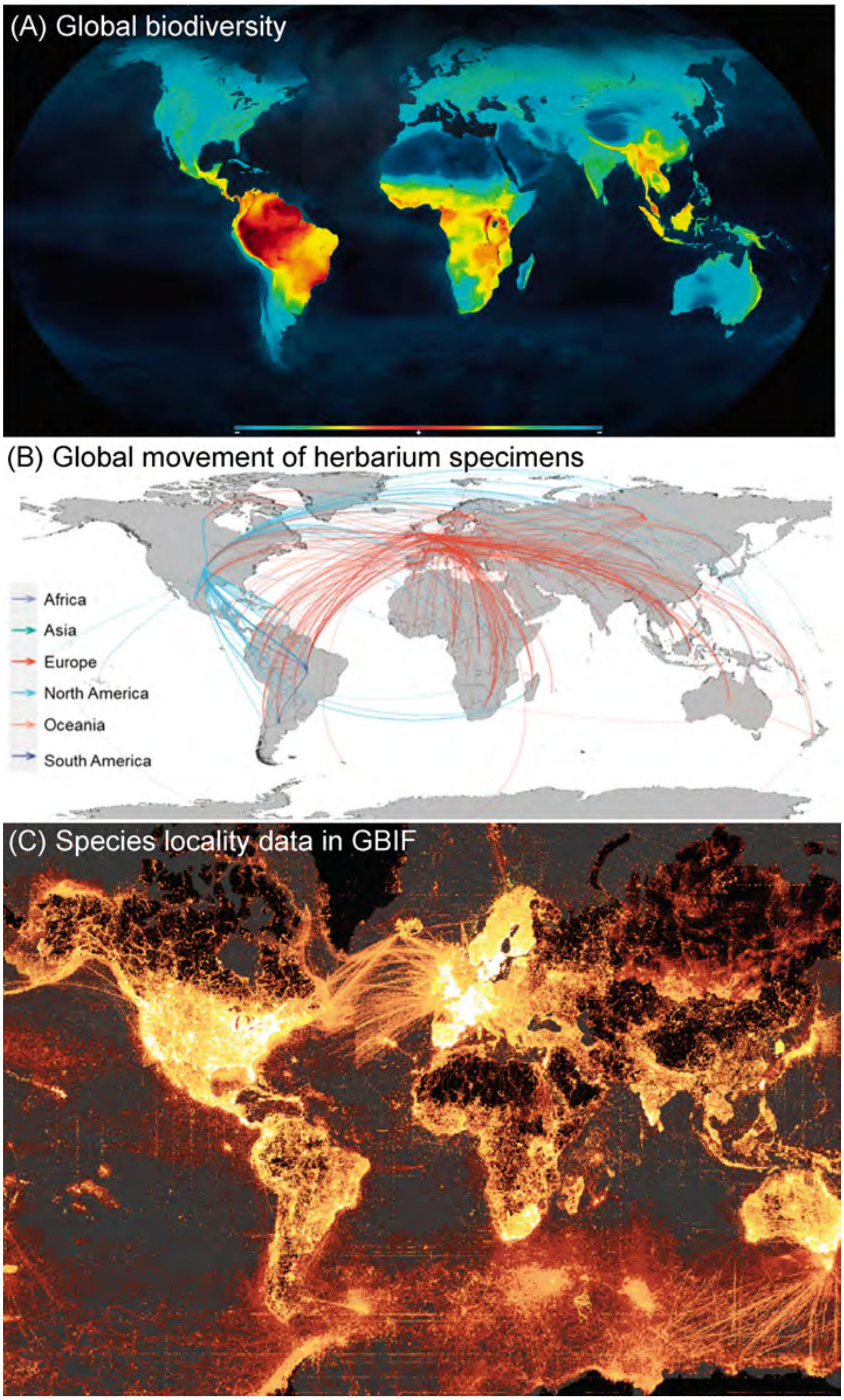


Figure I. Examples of novel findings from synthesis of herbarium specimens. (A) Reduced ozone is strongly correlated with increased UV-absorbing pigmentation in flowers with exposed anthers (red symbols in graph; shown in image of living flower on leftmost panel) relative to plants with concealed and protected anthers (blue symbols; flower image not shown); tremendous variation in UV protection is demonstrated in the alpine cinquefoil (*Potentilla crantzii*) when exposed to UV light (center panels: top, less UV pigmentation; bottom, greater UV pigmentation); UV proportion was measured from single petals as a function of UV absorption (i.e., nonpigmented UV-exposed) divided by area of the petals in mm^2. Redrawn from [85]. (B) Left. Relationship between estimates of leaf mass area (kg m^{-2}) for herbs (orange), shrubs (green), and trees (blue) from herbarium specimens and fresh material. Right. Confusion matrix showing identity of model prediction versus reference with near perfect alignment (numbers along the diagonal) of species identity for ten common North American trees in five genera (*Acer*, *Betula*, *Fagus*, *Populus*, and *Quercus*). Redrawn from [49]. (C) Major sources, sinks, and transport directions of non-native species derived from herbarium data. Numbers indicate non-native species by region; line thickness is proportional to the number of species exchanged and the arrow represents directionality; icons indicate putative anthropogenic dispersal vectors. Redrawn from [57].



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during the Quaternary, mapping the origin and spread of crop pathogens, exploring the genetic basis of species invasions and extinctions, resolving species boundaries, and incorporating extinct variation to investigate biodiversity change through time [20,26,58,64]. Beyond these applications of ancient DNA, herbaria also are central to understanding the fates of modern crops essential to humans. Recent efforts combining geographic ranges extracted from herbarium data with germplasm and seed-bank data indicate that the small number of species that separate us from starvation are facing dramatically shifting areas where they may grow. Generally, these taxa also are poorly represented in seed and germ-plasm banks required to safeguard us against their devastating and unexpected loss [65]. Moreover, similar large data syntheses and metanalyses are unavailable for the >30 000 medicinal plant (and fungal) species that form an important component of the modern pharmacopeia [66].

Concluding remarks

The accelerating innovations in applications of herbaria to scientific questions far beyond their traditional use, together with the rapid and dramatic expansion and diversification of the community of researchers using herbaria and poised to take advantage of the global metaherbarium, suggest three strategic directions to stimulate the utility of herbaria as centers of discovery and address a suite of key questions (see Outstanding questions). These directions will help to ensure that herbaria remain nimble as the pace of online data mobilization and interconnectedness of their digital resources accelerate and as nature becomes further degraded.

First and foremost, herbaria must work to acknowledge and mitigate the colonial legacy of collecting that has restricted access to biodiversity. Herbaria need to confront their colonial legacy, embrace and nurture the vibrant and emerging generation of biodiversity scientists, and implement inclusive solutions that recognize and reduce the obstacle that the most diverse herbaria are not housed in the tropics where nature's biodiversity is greatest [67] (Figure 3). Instead, they reside largely in the USA, western Europe, and parts of Asia (Figure 1A). Sadly, many of these colonial legacies are still being created in the digital realm as online options to document biodiversity become mainstream [e.g., iNaturalist data fed into Global Biodiversity Information Facility (GBIF)] (Figure 3C). These biases also feedback on software-driven image recognition. Digitally mobilizing the data associated with accessions acquired in colonial times, as exemplified by REFLORA and SpeciesLink, represent potentially powerful tools for restoring relationships between Indigenous communities and the biota of their lands, provided this is done in a way that recognizes their interests and includes their voices. Additionally, any future collecting efforts should be inclusive and yield agency and leadership to key stakeholders, especially from Indigenous groups [68], and must conform to local, national, and international regulations. The recent high-profile publication distinguishing two species of fruit trees long recognized by the Iban and Dusun peoples as distinct, but considered a single species in Linnaean taxonomy, was confirmed by molecular investigation [69]. This study provides an example of

Outstanding questions

How and in what ways do herbarium digitization and online mobilization continue to increase the numbers, diversity, and interactions among scholars who visit herbaria?

What are key spatial, temporal, and taxonomic biases in collections and how can these gaps be filled with future collecting efforts informed by sophisticated bioinformatic modeling?

How do we develop hardware and software technologies to facilitate internal staffing and stewardship while supporting the outward-facing research and public missions of herbaria?

How do we reorganize herbarium leadership and governance to take advantage of and use new learning modalities that are less tied to traditional scholarly boundaries to foster promising new directions in research and outreach?

How do we engage with industry and stakeholders beyond traditional governmental funding partners to bring dignity and advancements to all partners working in the herbarium of the future?

Figure 3. The past and present colonial legacy of herbaria. (A) Global heat map of biodiversity as modeled from vertebrates showing the classical latitudinal species gradient, with highest diversity depicted with warmer colors in equatorial regions, including in northern South America, sub-Saharan Africa, and East Asia (redrawn from [83]). (B) Global map of historical herbarium collecting efforts demonstrating the movement of plant specimens from high biodiversity regions in the Global South to the more species-poor countries of greater wealth in the Global North; directionality is especially apparent from the Global South to North America (blue lines) and from the Global South to western Europe (red lines) (redrawn from [67]). (C) Global map of biodiversity as inferred from Global Biodiversity Information Facility (GBIF) occurrence localities, which are largely drawn from amateur observational records, especially birds, from resources like iNaturalist (redrawn from [84]). (B) and (C) illuminate the colonial legacy of biodiversity and highlight that these biodiversity data continue to be biased in the digital age.

how such crucial stakeholders with essential local knowledge can be involved in collaborative research agendas.

Second, herbaria must continue to use digitization to reduce barriers to their access [11,70,71] and build partnerships to fully embrace the global interconnected herbarium of the future. Numerous institutions must collaborate and work together *en masse* to completely digitize collections, establish the global metaherbarium to complete these linkages, and better mobilize their physical and digital resources and expertise [11,71,72]. These networks are still best represented by domestic efforts in the Global North, such as those motivated by the US National Science Foundation that require the assembly of large and impactful teams with diverse leadership and representation, including large, small, public, private, free-standing, and university-affiliated institutions [11,73]. The effort by Brazilian scientists to create REFLORA and SpeciesLink is another exceptionally strong example and many similar initiatives are completed or well underway across Europe and Asia, but these efforts frequently remain highly nationalistic. In the future, these efforts must internationalize, especially in partnership with Indigenous groups worldwide. A good example of such an international effort is the African Genome Project, which seeks to collaboratively sequence 100 000 species to safeguard biodiversity [74]. Furthermore, as herbaria are digitized, the data must be better cited and tracked. Digital object identifiers (DOIs) should be minted for all digital herbarium products to provide credit for individual, institutional, and collaborative efforts and to monitor institutional citations. Despite the utility of, and urgency for, digitization, we also need to recognize the continued relevance of physical specimens for, among other efforts, genetic and genomic investigations; the identification of traits and species that are not clearly digitized; future-focused digitization as technology evolves (e.g., human-eye resolution cameras); ecological trait harvesting (e.g., hyperspectral data); and, perhaps most importantly, for applications that await discovery.

Third, clearer guidelines are required for expanding herbarium collections, especially those that reflect the ‘extended specimen’ concept [75]. The temporal, spatial, taxonomic, and phylogenetic biases in herbarium collections are strong [76] and further characterization is needed along these lines to develop better statistical models to better handle and harmonize imprecise data [77]. For example, efforts to characterize collector bias (e.g., when a plant is harvested) versus collection bias (e.g., making curatorial decisions to strategically remove collections from herbaria) need to be better explored and modeled. Future collections should be guided by data-driven efforts that prioritize geographic regions and taxa that have received little attention (as in the floristic inventory of New Guinea [15]). Additionally, collecting in areas that have been richly collected in the past should remain a priority, especially when they represent opportunities for long-term ecological monitoring. Indeed, it should be explored whether herbaria might be included as key hubs for national organizations that monitor future biodiversity change, such as the Long-Term Ecological Research (LTER) network in the USA. Such data should be linked with community floristic inventories and near-Earth remote-sensing initiatives to discern biodiversity pattern and process from individuals to communities and continents. We also need to better preserve and curate the vast genetic heritage represented in herbaria. Supporting extensive DNA barcoding and cryogenic storage for total genomic DNA will be essential for herbarium leadership, but we should also explore more speculative directions to supply samples to seed banks or for tissue culture to re-establish populations of extinct species [78,79].

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Declaration of interests

The author declares no competing interest.

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