Introduction

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Biological collections for understanding biodiversity in the Anthropocene

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Global change has become a central focus of modern biology. Yet, our knowledge of how anthropogenic drivers affect biodiversity and natural resources is limited by a lack of biological data spanning the Anthropocene. We propose that the hundreds of millions of plant, fungal and animal specimens deposited in natural history museums have the potential to transform the field of global change biology. We suggest that museum specimens are underused, particularly in ecological studies, given their capacity to reveal patterns that are not observable from other data sources. Increasingly, museum specimens are becoming mobilized online, providing unparalleled access to physiological, ecological and evolutionary data spanning decades and sometimes centuries. Here, we describe the diversity of collections data archived in museums and provide an overview of the diverse uses and applications of these data as discussed in the accompanying collection of papers within this theme issue. As these unparalleled resources are under threat owing to budget cuts and other institutional pressures, we aim to shed light on the unique discoveries that are possible in museums and, thus, the singular value of natural history collections in a period of rapid change.

This article is part of the theme issue 'Biological collections for understanding biodiversity in the Anthropocene'.

1. Introduction

The Anthropocene is a new geological epoch proposed to recognize the significant impact humans have had on Earth's biogeochemical cycles, biodiversity and ecosystems [1]. Because geological epochs are defined by demonstrable changes in Earth's stratigraphy—captured in glaciers, rock, or sediment resulting from myriad factors including meteor strikes, alterations in global cooling or warming, sea-level change and volcanism—whether the Anthropocene is a genuine epoch and, if so, when it began, remain debated. This is largely attributable to the fact that the Anthropocene has not been defined by conventional geological impacts, but rather by human influences. This has made timing the starting point of the Anthropocene, following the Holocene epoch, challenging and controversial. The most plausible stratigraphic signatures of the Anthropocene include megafaunal extinctions, evidence for widespread agriculture, ash particles from burning, radionucleotide fallout and persistent industrial chemicals, including plastics and other decay-resistant chemicals. Here, clear 'golden spikes', which are global, near simultaneous signatures in strata that demarcate this epoch are debated. A prevailing, but by no means universally adopted, view favours either 1610 or 1964. The former coincides with the widespread arrival of Europeans to the Americas, which triggered precipitous human population declines in the New World leading to the uptake of CO_2 by the re-greening of the Americas; the latter involves 'The Great Acceleration' marked by increased human
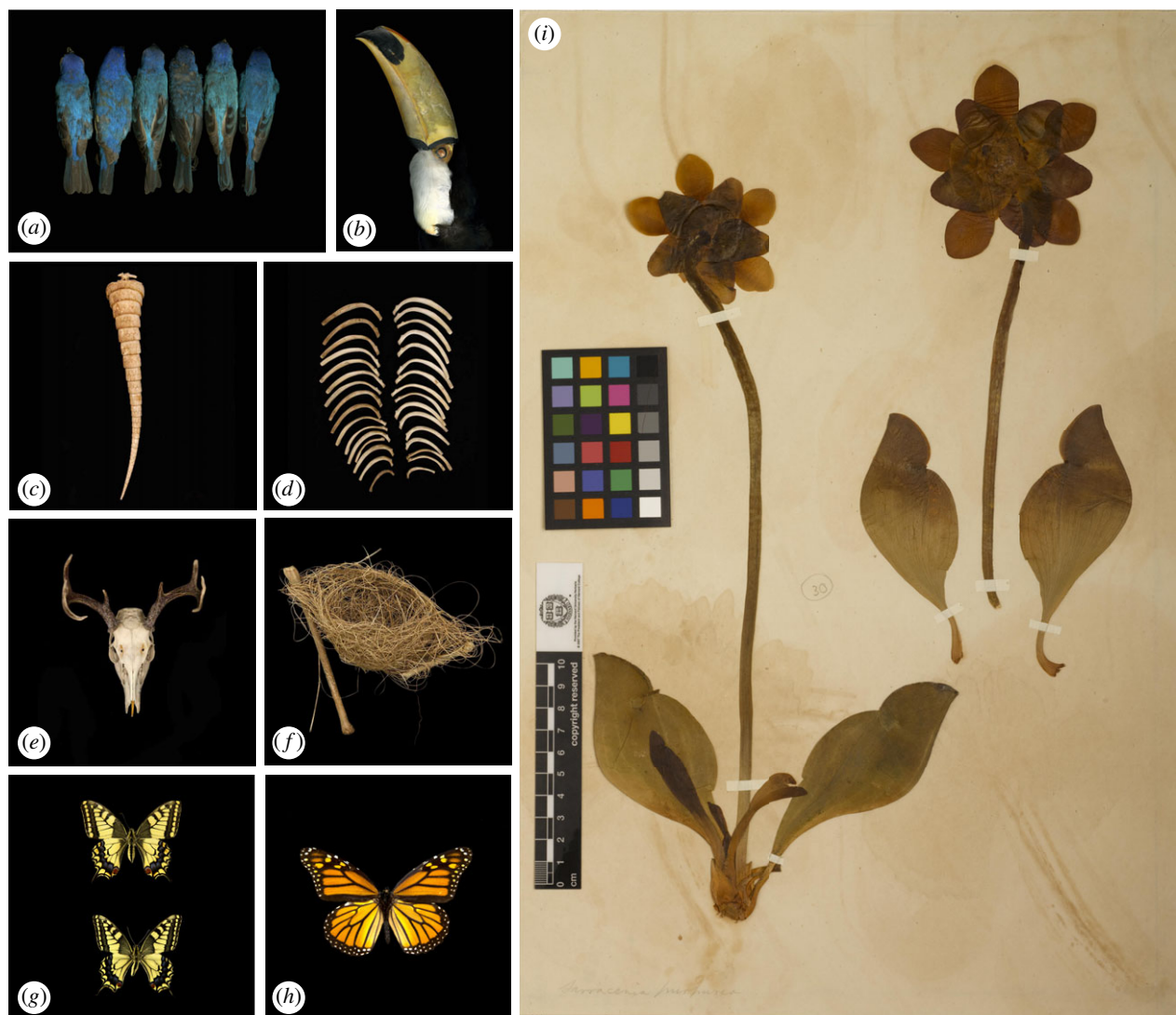
Figure 1. The diversity of taxa represented in biological collections, (*a*) indigo buntings (*Passerina cyanea*) from the North Carolina Museum of Natural Sciences, (*b*) the common toucan (*Ramphastos toco*) from the North Carolina Museum of Natural Sciences, (*c*) bones of Dasypodidae from collections at the Everglades National Park, (*d–e*) bones and a skull, respectively, of the white-tailed deer (*Odocoileus virginianus*) from collections at the Grand Canyon National Park, (*f*) an unidentified nest from collections at the Everglades National Park, (*g*) the common yellow swallowtail (*Papilio machaon*) from the North Carolina State University Insect Museum, (*h*) the monarch butterfly (*Danaus plexippus*) from the North Carolina State University Insect Museum, and (*i*) the purple pitcher plant (*Sarracenia purpurea*) from Thoreau's collections at the Harvard University Herbaria (this species has declined in abundance since the 1800s according to data from Willis *et al.* [12], potentially in response to global change). All images except that of the purple pitcher plant are by Leah Sobsey, who is an Assistant Professor of Photography in the School of Art at University of North Carolina at Greensboro.

populations and the fallout from nuclear bomb testing recorded by atmospheric ^{14}C in tree rings and ice cores.

Regardless of our attempts to precisely bookend the Anthropocene, the signatures of human activity are clear and, though variable through time, have been variously distributed across thousands of years. Despite our best efforts, however, quantifying the effects of humans on the biosphere has been challenging. Part of this results from the dearth of evidence to track the effects of this human-driven change. Over the history of global change biology, field observations and experiments have been the standard methods by which researchers have investigated biological shifts in response to the five dominant drivers of global change: habitat conversion, climate change, invasive species, human exploitation and pollution [2]. Despite the incredible utility of field studies thus far in global change biology (e.g. [3]), the data they produce are limited across space, time and clades. These limitations arise because collecting vast amounts of field data spanning these scales is either impossible—one cannot travel back in time to

collect field data, for example—or impractical. Given the limitations of these more traditional data sources, biological collections are increasingly recognized as among the best resources for reconstructing the human impacts of global change during the past century [4–7]. These include documenting changes in plant and animal morphology [8], species decline [9] and shifts in the timing of life-history events, such as flowering [10,11].

Natural history collections house vast amounts of data representing diverse taxa in centralized locations (e.g. see figure 1). Physical specimens hold data that are of great interest in global change biology, such as nutrients [13], heavy metals [14] and signatures of pollinator interactions [15–17], herbivore interactions [6,18–20], disease [21,22] and physiological processes [23]. In recent years, researchers have increasingly begun to harness digital collections. Major digitization initiatives are now making museum specimens more accessible as images and label data are mobilized online. For example, the 5.4 million vascular plant specimens,

which compose 90% of the physical collection stored in the Muséum national d'histoire naturelle in Paris, are now digitized and searchable online (https://science.mnhn.fr/institution/mnhn/collection/p/item/search/form) and the NSF funded Integrated Digitized Biocollections (iDigBio: https://www.idigbio.org/portal/) has compiled 114 million occurrence records representing an estimated 300 to 400 million specimens. These digital collections span three centuries and represent floras and faunas globally. Digital natural history collections provide unprecedented opportunities for collaboration across disciplines and among institutions, including those in the tropics, which have historically had limited access to specimens held in museums throughout North America and Europe. This is perhaps best exemplified by the Reflora project of Brazil, which has sought to repatriate its collections from institutions outside of their country via digitization [24]. Thus, digitization has the potential to diversify hypothesis testing by promoting cultural diversity in science [25] and by providing unique, vast datasets at reduced costs to researchers regardless of location [5].

The importance of natural history collections has received growing attention in the literature over the past 15 years [4,5,26–28], but we assert that a new creativity around the scientific use of collections is emerging. It is in this spirit that we were motivated to assemble this theme issue 'Biological collections for understanding biodiversity in the Anthropocene', a compilation of studies demonstrating the singular role of natural history collections for describing and predicting biological responses to recent global change. By collating these cutting-edge studies in a single issue, we draw attention to the role of collections in fundamental and applied science. To introduce this theme issue, we describe the unique data in museum specimens for global change research and areas of global change biology where these data have been applied, with an emphasis on studies employing novel methods and those that show promise for conservation.

2. Data types from museum specimens for global change research

Natural history collections have transitioned from the curio cabinets of Victorian collectors into the largest repositories of biological data, housing an estimated 2–4 billion specimens worldwide [29]. Historically, a primary function of collections has been as a record of biological diversity and as references for taxonomists. In addition, collections frequently hold a large volume of unsorted material and today the majority of newly described species are discovered within existing collections [30].

Increasingly, collections now also serve as repositories for ecological data and are widely used to characterize species' phenology and distributions. Phenology is the study of periodic plant and animal life cycle stages, especially how these are influenced by climate [31]. Long-term monitoring is one method for deriving phenology data over time; however, these datasets are limited in that they cover a small proportion of species, typically within single ecosystems [32]. The use of museum collections as records of phenology can help overcome these limitations because museum records can span several decades and even centuries in some cases, capturing phenological variation over years and across climatic space (notably temperature and precipitation, e.g. [33]). Similarly,

specimen images and label data contain information on species locations and how geographical ranges have shifted through time (see e.g. [34] for a review). These data are now already well integrated in global change research, providing insights into shifting distributions [35,36] and community composition [37,38]. Specimens can also capture information on morphology, such as leaf shape (e.g. leaf blade length and width), which may be particularly powerful when data extraction is automated and conducted across large numbers of specimens [39]. Changes in morphology might be indicative of shifting selection pressures and thus natural history collections can become records of evolutionary change [40].

New technologies have been developed for rapidly extracting species occurrence, phenology and morphology from digital collections, allowing for unprecedented 'big data' on these responses to global change. For example, convolutional neural networks are currently being investigated for rapidly tracking phenology (buds, flowers and fruits) and signs of insect damage and disease on plants. While the progress in rapid digitization has been astonishing—for example, through whole drawer, robotic imaging of entomological collections [41] and resolution of digital data (see the remarkable images from the Museum of Natural History of Berlin [zoosphere.net])—some data are impossible to extract without access to physical specimens. Stomatal densities that provide information on gas exchange efficiencies [42] might be difficult to quantify from digitized herbarium specimens, for example. Measurement of certain morphological traits might also require physical manipulation of specimens; the phenotypic change in beak length in the soapberry bug (*Jadera haematoloma*) in response to the increasing availability of non-native plant species was measured using a stereo microscope and dial callipers [43]. Here, it is unlikely that such data could have been extracted from digital images alone. Other types of data will most likely always require physical material. Stable isotope analyses of animal and plant tissue can provide data on species' ecologies and life histories that are difficult to collect in the field [8]. Specimens in natural history collections can also capture incidental information, for example, on species ecological associates, such as plants and their insect herbivores [6,44] or pathogens [21] that would be difficult, but perhaps not impossible in all cases, to extract from digitized specimens.

Over the past two to three decades, perhaps the most rapid technological advances have come from the development of molecular techniques that allow the extraction and sequencing of DNA from preserved specimens. The DNA from specimens allows rapid identification of material that may otherwise lack key distinguishing traits, such as flowers or fruits. This genetic approach to species identification has been facilitated by efforts to generate a barcode of life database (http://www.boldsystems.org/) of standardized genetic markers (DNA barcodes) for all of life [45]. Population markers and genetic fingerprinting can provide a record of population bottlenecks, hybridization events, introgression, range contraction and range expansion [46]. In one recent example, Garcia-Elfring *et al.* [47] compared historical and recent collections to map the northward range expansion of the white-footed mouse (*Peromyscus leucopus*) and revealed novel hybridization with the native deer mouse (*Peromyscus maniculatus*) as the two species come into more frequent contact. In another recent example, modern and historic herbarium samples were used to assess mutational changes

following the recent introduction of thale cress (*Arabidopsis thaliana*) to the New World [48]. Using whole genome sequencing, it was possible to date the timing of introduction to the early seventeenth century and to identify several new mutations in modern populations that are tied to important phenotypic variance and potentially adaptive in their invaded habitats. As molecular techniques improve further, exciting new avenues of research continue to emerge. DNA from pathogens, including viruses and fungi, can now be detected from the organs or skins of preserved specimens using highly sensitive genomic tools (e.g. see [8,49]). Transcriptomics could provide novel insight into gene functioning by measuring gene expression [8]; although RNA required for all transcriptomic method is inherently unstable and thus difficult to obtain from collection vouchers, cryogenically preserved specimens and living collections might provide suitable material.

3. Diverse applications of collections data in global change research

The diversity of data that can be extracted from biological collections is matched by the diversity of applications in which it can be used. In this theme issue, this variety of uses is evident in the examples provided, highlighted in part by the cross section of taxa, from birds to fungi, that feature in the following papers. We can classify these uses into four broad applications: gap-filling, historical reconstructions, records of change through time and conservation.

In their article for this theme issue, Perez *et al.* [50] describe how living collections may fill a key gap in plant trait data. While a greater emphasis has been placed on preserved collections in museums and herbaria, living collections provide a wealth of information on species that may be difficult to collect in natural populations. Perez *et al.* [50] illustrate how botanic gardens can be a source of valuable trait data for tropical plants—species for which even basic ecological and morphological data are frequently lacking owing to the financial and logistical difficulties in working in remote, hyper-diverse locations in the tropics. Plant traits underlie plant ecological function [51] and allow us to make predictions on their future fates [52]. While some traits, such as leaf mass area, are more reliably measured from living collections than others, such as root traits, Perez *et al.* [50] demonstrate that trait measurements derived from specimens growing in botanic gardens are as accurate as estimates published in widely used trait databases. Specimens can similarly capture trait shifts through time. In an empirical example of tracking functionally significant traits on butterfly specimens, MacLean *et al.* [53] measure wing melanism—a trait that controls butterfly body temperature—in montane butterflies from North America across 60 years using museum specimens.

When measured on historical collections, the link between traits and function can provide the opportunity to reconstruct past environments. In this issue, Soul *et al.* [54] combine data from living specimens and fossils to refine our reconstructions of paleoclimate in the Late Cretaceous–Palaeogene. Leveraging the human power of citizen scientists through the Zooniverse web portal to overcome bottlenecks in counting cells, the authors calibrate the stomatal index (representing the proportion of epidermal cells on leaves that are stomatal pores) on living *Ginkgo biloba* grown under varying pCO_2, to match stomatal counts with *Ginkgo wyomingensis* fossils. This study not only demonstrates how living and preserved collections can inform one another, but also provides one example of how citizen scientists can contribute to palaeontological research.

In addition to allowing historical reconstructions, collections also provide records of environmental and biological change through time. Schmitt *et al.* [55] in this issue review how vertebrate collections have revealed the emergence and spread of pathogens and pollutants and document the response of species to global change. Morphological and genetic analyses of historical amphibian samples trace the routes that chytrid fungus (*Batrachochytrium dendrobatidis*), a major diver of amphibian extinction, has spread across the globe. Atmospheric black carbon—soot—on plumage from birds in historical collections reveals the effectiveness of environmental policies aimed at reducing pollutant levels in the US. Resurveying sites of historical small mammal collections details range shifts upwards in elevation in response to climate warming, DNA analyses capture the signal of shifting population demographics and fragmentation and stable isotope analyses reveal shifts in diet through time, perhaps reflecting changes in migration patterns or phenologies [55]. Similarly, Andrew *et al.* [56] detail how recent efforts to digitize fungaria are revealing parallel shifts in the distribution and phenology of fungi, including Red List species. Fungi remain understudied, but are hyper-diverse and may use different environmental cues from green plants, responding more sensitively to changes in precipitation and thus provide an alternative biotic index of climate change impacts. Yet, distinct challenges remain, including the under-collection of fungal groups lacking conspicuous fruit bodies.

With increasing pressures imposed by global change, there is a critical need to identify taxa at risk and prioritize conservation efforts. In this issue, Kling *et al.* [57] demonstrate how herbaria have helped inform spatial conservation using digital records for the more than 5000 species that comprise the Californian native flora. Moving beyond species conservation, DNA from these same herbarium specimens has allowed the reconstruction of phylogenetic relationships, from which it is possible to derive metrics of phylogenetic diversity that capture components of anagenesis, cladogenesis and evolutionary time. Despite the large biases evident within herbarium data [58,59], Lughadha *et al.* [60] reveal that it is also possible to use herbarium records as a guide to infer species extinction risks, with extinction risk estimates showing high correlation with expert assessments performed for IUCN Red Listing. Herbarium data are perhaps most robust for quantifying extent of occurrence, area of occupancy and fragmentation of range, while estimates of population size and demography may be less reliable. Surprisingly, simple specimen counts may provide a reasonable first approximation of extinction risk and could help identify potentially vulnerable species without the need to wait for additional data collection and risk further population decline.

4. Natural history collections as unique records of changing species interactions

In addition to capturing the responses of individual species, museum collections can serve as records of how species

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interactions have shifted over time and with environmental change. As associated species respond differently to warming in space or time, species interactions are also likely to shift. Yet, species interactions are underrepresented in historical observations and are difficult to study in the context of experimental warming chambers. To highlight the unique role of museum collections in documenting how species respond to global change, we dedicate a section of this issue to the signatures of species interactions present in natural history collections.

Most research on species interactions with global change, including those using natural history collections data, has focused on plant–pollinator interactions, particularly with respect to pollinator decline or the potential for phenological mismatches between plants and their associated pollinators. In this issue, Bartomeus et al. [61] review the opportunities for museum specimens as occurrence records representing the most abundant and accessible data for documenting pollinator declines worldwide. While some studies demonstrate pollinator decline in response to various drivers of global change, including climate and land use change, estimates of bee, hoverfly and butterfly decline are limited geographically, with heavy biases toward Europe and the United States. Museum specimens could fill this major knowledge gap, but their contribution relies on widespread digitization, which is a challenge for insect specimens because they are three-dimensional and label data are difficult to capture. However, once digitized, they can serve as reliable sources of pollinator occurrence data despite biases, as shown by Bartomeus et al. [61] using data from Spain and New Zealand.

In a general review of the potential for insect collections in global change research, Kharouba et al. [62] highlight applications in addition to plant–pollinator interaction research, but discuss the challenges they present for studying changing phenology, distributions and morphology. Also in this issue, Meineke & Davies [63] demonstrate that despite these challenges, plant and insect collections show promise for addressing key hypotheses on changing plant–herbivore interactions in the context of rapid warming and urbanization. In a powerful example that encompasses both the process of species invasion and shifting biotic interactions, Beaulieu et al. [64] document increasing herbivore damage to leaves over time after the introduction of purple loosestrife Lythrum salicaria, an invasive plant that arrived in North America in the early nineteenth century.

While ecology has long focused on the interactions between macroscopic organisms, the importance of microbes and microbial diversity has attracted much recent attention [65–67]. How microbial diversity, evenness and abundance affect host fitness and interactions between macrobiota is still unresolved and presents an important area for research innovation. In this issue, Daru et al. [68] test methods for extracting historical microbial communities from leaves of herbarium specimens. Focusing on the endophytic microbiomes of two plant species from imperiled boreal biome—Andromeda polifolia and Ledum palustre subsp. groenlandicum (Ericaceae)—they find that cloning and next generation sequencing may allow us to reconstruct historical microbial communities and, potentially, to determine how these communities affect interactions between plants and their associated pollinators and herbivores.

5. Next generation collections research

To maximize the impact of natural history collections, it is necessary to innovate ways to collect data that span the full temporal, spatial and phylogenetic scales represented by museum specimens. Digitization is a first, if deceptively simple sounding, step for leveraging the potential of museum data. In addition to providing the opportunity to collect big data, digital collections serve an important role in research planning (e.g. choosing species for which there is appropriate coverage for hypothesis testing), for collecting preliminary data and for providing broader access to collections [25]. In this issue, Nelson & Ellis [69] detail the history of digitization, the research made possible by digitized collections and the biases in digital specimen data, including that few digitized records are available from Russia, India and the continent of Africa (though South Africa is an emerging leader in digitization).

Following digitization, the next challenge is to extract relevant data from a large number of digitized records. Two key ways this has been achieved are through citizen science and (increasingly) machine learning, both of which automate the data collection process, removing major barriers to analysing the large volume of museum data that is coming online. An important innovation along these lines has been to use computer vision to identify herbarium specimens to species [70]. In this issue, McAllister et al. [71] automate digital capture of grass spikelet morphology, allowing correlations between plant morphology and phylogeny and between morphology and climate. Such automated techniques for capturing phenotypes could revolutionize our understanding of how species are related to one another and how they have responded to environmental change by providing large amounts of data on key response traits across axes of time and space.

Park et al. [72] demonstrate the power of citizen science for similarly capturing phenotypes. They enlist hundreds of citizen scientists via the platform CrowdCurio [73] to count buds, flowers and fruits on over 10 000 herbarium specimens of 30 species. Consistent with previous studies, they show that plants across clades and latitudes flowered earlier in response to warmer temperatures and that fruiting was less sensitive to temperature than flowering. However, contrary to another recent study [74], their data indicated that plant species at lower latitudes were more phenologically sensitive to warming than those at higher latitudes. This study captures a larger number of species and a broader range of latitudes than most experimental or observational studies on plant phenology and includes a long time series, highlighting the unique contributions of museum data to documenting phenological response.

6. The future of natural history collections

In this issue, the contributed papers present novel research, reviews, opinions and perspectives that outline the potential of physical and digital natural history collections for global change biology research. These studies span taxonomic groups, including vascular plants, fungi, insects, birds, mammals and amphibians; and diverse responses, including shifts in species distributions, phenology and phenotype. With this issue, our primary aim was to provide a perspective on the many ways we can employ museum specimens to understand the past, present and future of biodiversity. Our hope was to stimulate a diverse readership to

envision novel uses of collections for fundamental and applied research.

A secondary goal was to address the gaps, limitations and biases prevalent in museum data and detail how such challenges may be overcome. Though natural history collections show great promise for informing global change biology, they also present barriers to wide application. Museum collections are extensive but are rarely the product of systematic and representative sampling and often present a variety of sampling biases not present in data from carefully designed field studies [58,59]. Thus, despite their uniqueness, data from collections present particular challenges. Well-established ecological methods and new analytical tools developed for such data, including machine learning, novel Bayesian statistical modelling approaches and methods for assigning appropriate climatic data to specimens [75], are amenable to address many of these challenges [6,62]. However, other challenges, such as the loss and damage of specimens, may be more difficult to overcome.

We hope this series of papers will contribute to the ongoing conversation about how natural history collections are managed as specimens become increasingly digital and are used for a greater diversity of purposes than in the past, when collections research was the domain of taxonomists and systematists. It is important to recognize that these fields remain central foci of collections research and, in fact, are made more critical as other fields now making use of natural history collection data require taxonomic identifications and an understanding of species' evolutionary histories. However, the broader use of collections also requires rethinking how specimens in natural history collections are stored and expanded. For example, there is an ongoing discussion about whether physical collections are redundant with their digital counterparts and, given limited space and staff in museums, how we should prioritize future collection efforts to maximize benefits considering their multiple uses. Through diverse representations of the importance of physical and digital museum collections in the Anthropocene, we hope to contribute perspectives that help chart a future for these singular resources in a time of rapid global change.

Editor biographies

Emily K. Meineke is a National Science Foundation Postdoctoral Fellow at the Harvard University Herbaria. She received her PhD in 2016 from North Carolina State University, where she was an EPA STAR Fellow studying how urban heat islands affect insect pest populations of urban trees. She currently investigates the effects of global climate change and human development on plant–insect interactions and is interested in pairing long-term museum data with other datasets to provide insights into the ecological effects of global change.

T. Jonathan Davies is an Associate Professor in the departments of Botany, Forest and Conservation Sciences at the University of British Columbia. His work addresses questions related to the distribution of biodiversity and the challenges posed to its conservation through recent changes to the environment. He is interested in how information on species' evolutionary histories—their phylogeny—can help us understand their present-day ecologies. He has recently been thinking about moss.

Barnabas H. Daru is an Assistant Professor of Biology at Texas A&M University-Corpus Christi. He did his postdoctoral fellowship at Harvard University, where he studied uses of herbarium specimens in ecology and evolutionary biology. His research interests focus on how the evolutionary history of species—their phylogenetic relationships—can inform our understanding of the origin and distribution of biodiversity and how this understanding can guide conservation decisions across local and regional scales. You can read more about his research at https://barnabasdaru.com/.

Charles C. Davis is Professor in the department of Organismic and Evolutionary Biology at Harvard University. He is also Director and Curator of the Harvard University Herbaria, the world's largest university herbarium. His work takes a distinctly phylogenetic approach to address a variety of questions ranging from classification to biogeography to molecular evolution. Increasingly, he is exploring ecologically-themed topics related to plants and global change and is especially excited about the use of digital herbarium records and applications in computer sciences to leverage these resources.

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