



Review

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Museum specimens of terrestrial vertebrates are sensitive indicators of environmental change in the Anthropocene

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Natural history museums and the specimen collections they curate are vital scientific infrastructure, a fact as true today as it was when biologists began collecting and preserving specimens over 200 years ago. The importance of museum specimens in studies of taxonomy, systematics, ecology and evolutionary biology is evidenced by a rich and abundant literature, yet creative and novel uses of specimens are constantly broadening the impact of natural history collections on biodiversity science and global sustainability. Excellent examples of the critical importance of specimens come from their use in documenting the consequences of environmental change, which is particularly relevant considering the alarming rate at which we now modify our planet in the Anthropocene. In this review, we highlight the important role of bird, mammal and amphibian specimens in documenting the Anthropocene and provide examples that underscore the need for continued collection of museum specimens.

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

1. Introduction

Abundant evidence of human-driven environmental change supports the designation the Anthropocene as a new geological epoch [1]. Notable signatures of the Anthropocene include precipitous increases in global temperature and temperature anomalies (i.e. climate change) [2,3], contamination [4–6], emergence of infectious diseases [7], species' declines [8] and many others [1]. Prominent among indicators of environmental change are specimens curated in natural history museums [9–11]. Museum specimens are a particularly powerful resource for documenting change in the environment because they offer scientists snapshots of the Earth across spatial, temporal and taxonomic scales [12–16]. In this paper, we highlight the use of museum specimens of birds, mammals and amphibians as sensitive indicators of environmental change in the Anthropocene, reviewing exemplary studies that have employed museum specimens to document changes in emergent diseases, contamination, isotope/hormone ecology and climate. Central to our argument is the view that a well-curated museum specimen represents a multidimensional snapshot of the environment at a specific time and place in the past (figure 1, [17]). Ample evidence now exists to show that natural history museum specimens can be used for diverse applications of value to society, yet continued support of museums by funding agencies and dedication to specimen collection by museums are needed to build and maintain this critical scientific resource moving forward.

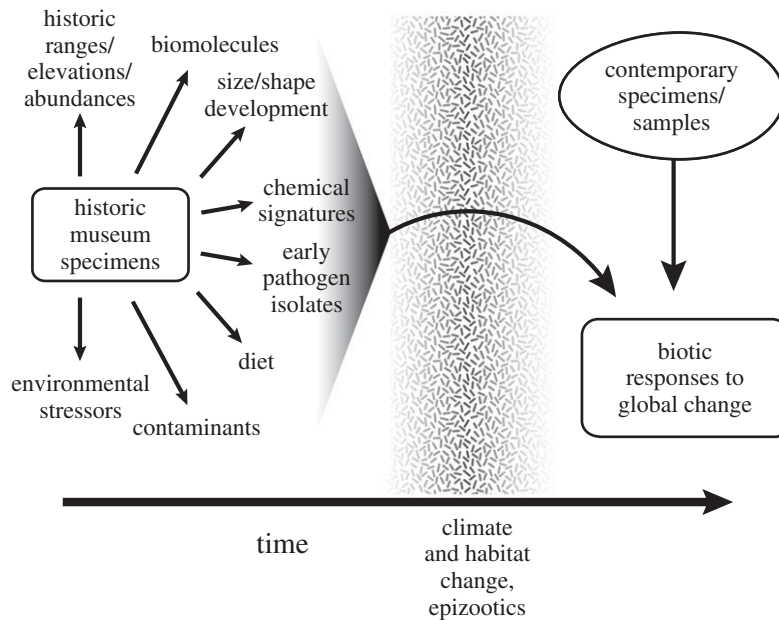


Figure 1. Vertebrate museum specimens as historical snapshots of the total environment. Diverse data types stemming from museum specimens (left of the figure) provide historical data that can be compared to data sampled from contemporary specimens or samples (right of the figure). Together these temporal datasets can shed light on how anthropogenic change (stippled bar at the centre of figure) drives diverse physiological, morphological, genetic and behavioural changes in vertebrate populations.

2. Museum specimens document the origin and spread of emergent infectious diseases

One characteristic of the Anthropocene is an acceleration in the emergence of infectious diseases [7]. Emergent diseases in natural populations are now increasing consistently [18] and will pose challenges for wildlife populations, humans and our domesticated or crop species in the near future [19–21]. Museum collections, including biorepositories of frozen vertebrate tissue, have played a central role in the discovery of previously unknown pathogens in the past 25 years [22–24]. That role is sure to increase in the future if we build the temporal, spatial and taxonomic breadth of these collections through continued fieldwork [25]. Through retrospective screening of museum samples, new insights in pathobiology include the rapid identification of key attributes of newly emergent pathogens, such as taxonomic identity, temporal dynamics and critical aspects related to spatial distribution [26,27]. In aggregate, museum collections often provide the detailed sampling of vertebrate hosts necessary to refine the potential spatial distribution of a pathogen and to confirm whether a pathogen is narrowly confined to a single host or instead ranges widely across multiple hosts [28,29]. These critical diagnostic features allow investigators to predict conditions associated with emergence [30], and also to design effective public health response efforts. More detailed assessments, using phylogeographic perspectives, for example, allow us to probe the dynamics of the historical association of both the pathogen and host. Importantly, because up to 75% of the emerging pathogens responsible for the most serious human disease outbreaks are zoonotic in origin [31], museum collections can play a critical role in public health [32], but only if this critical resource continues to be developed so it can serve as a temporal and spatial database of potential human diseases in animal hosts.

(a) Documenting fungal pathogens in declining amphibian populations

One of the best examples of the use of museum collections in documenting the spread of epizootics is the tracking the origin and spread of the chytrid fungus *Batrachochytrium dendrobatidis* (Bd), the cause of devastating declines in amphibian populations globally. Chytrid was first brought to the attention of the international community as a possible cause of global amphibian declines owing to chytridiomycosis in 1998 [33], over a decade after the first reports of amphibian declines in the mid-1980s [34]. Typically, amphibians and reptile specimens are stored in formalin and transferred to ethanol for long-term curation. These specimens are ideal for histology or dissection-based diagnostic tests; however, given the detrimental effects of formalin on the long-term quality of DNA [35], retrieving DNA sequences from formalin-fixed specimens has been a challenge. Recent advances in DNA extraction methods and next-generation sequencing have overcome significant obstacles to molecular analysis of amphibian specimens in museum collections [35–38]. Thus, museum collections proved critical in establishing Bd as the causative agent in amphibian declines and in tracing the routes by which this pathogen spread across the globe, both through morphological and genetic analyses of historical amphibian samples across diverse localities and habitats [26–28].

Soon after the discovery of the emergence of Bd, researchers turned to archived museum collections to better understand the origins, transmission and spread of the pathogen. These specimens yielded diverse types of useful data, such as multilocus genotypes of chytrid from skin swabs of diverse frog species and populations [39,40]; quantitative PCR measurement of pathogen levels [41]; and whole genome sequences of Bd isolates [42,43]. Bd has been retrieved from museum specimens collected in the late

nineteenth [26] and early twentieth centuries [44] and has been documented on multiple continents with the aid of museum collections [45,46]. The most recent surveys using whole genome sequencing, aided by museum collections, suggest substantial diversity of Bd in the Korean peninsula, suggesting that East Asia may have been the source of the ongoing epizootic and that international trade facilitated its spread [43].

A newly described chytrid fungus, *Batrachochytrium salamandrivorans* (Bsal), infecting primarily newts (salamanders in the family Salamandridae) has also emerged from Asia and is now threatening salamanders in western Europe and the New World [47,48]. The global scale of transport that characterizes the Anthropocene makes it likely that this pathogen will continue to spread to areas where native salamanders exist and have never been exposed to this pathogen before. To date, this newly emergent chytrid has been identified in museum specimens and natural populations from Asia [48,49], but has not been detected elsewhere, confirming that we are faced with an invasive emergent pathogen. As with frogs in the Bd invasion, salamander specimens in natural history collections will be a baseline for diagnoses of pathogen presence and absence for this newly emerging pathogen.

(b) Characterizing the *Sin Nombre* hantavirus

Museum collections and museum-based fieldwork played a central role in identifying, tracking and mitigating the deadly *Sin Nombre* hantavirus (Hantaviridae: Order Bunyvirales). The *Sin Nombre* virus [50] emerged in the Four Corners region of the American Southwest in the spring of 1993, killing 27 people that year. Because the virus was previously unknown, this emergence challenged our public health system, with local clinics and healthcare providers unable to diagnose, treat or in some cases even admit suspected cases [22]. Speculation about the origin of this pulmonary illness ranged wildly [51] but the availability of frozen archives of tissues from wild rodents with known collection dates and localities at the Museum of Southwestern Biology (MSB) allowed investigators from the Centers for Disease Control and University of New Mexico Hospital to quickly identify the pathogen as a hantavirus with a wild reservoir traced to the common deer mouse (*Peromyscus maniculatus*). In addition to identifying *Sin Nombre* as a hantavirus and demonstrating its zoonotic source, historic specimens also showed that this virus had been circulating in deer mouse populations since at least the earliest collections archived a decade earlier [22].

Since the identification of *Sin Nombre* virus in the early 1990s, our knowledge of this group of pathogens has been radically reshaped thanks to progress stimulated by access to extensive frozen (now more than 138 000 rodents, each with multiple tissues at MSB) and ethanol-preserved samples in museums [52]. More than 25 additional hantaviruses have been described in the Western Hemisphere in the past 25 years [52–55], some of which lead to high mortality in humans [23,24]. Further research based on intensive field surveys has also detected hantaviruses in mammals other than rodents [52,56,57], including moles (Talpidae), shrews (Soricidae) and bats (Nycteridae, Vespertilionidae, Pteropodidae). The discovery of diverse new hosts radically changes the way we think about these potentially zoonotic viruses [58], especially because some host species are commensal with humans and pose a critical public health issue [59,60].

Additionally, comprehensive phylogenetic analyses have clarified the evolutionary relationships of hantaviruses [61,62], and a growing number of cases of co-circulation of multiple hantaviruses opens the possibility of rapid virus evolution owing to reassortment among their tri-partite genomes.

Importantly, in response to the emergence of chytrid and hantavirus, several museum collections facilitated productive collaborations among public health agencies, virologists, evolutionary biologists and conservation biologists that have reshaped interdisciplinary approaches to pathogen discovery [32,43,52,63]. Temporally deep and taxonomically diverse biorepositories of vertebrates and their tissues allow scientists to search for and discover novel pathogens, essentially providing basic infrastructure for rapid and efficient assessment, prevention and mitigation of emerging diseases. Moving forward, we need to recognize that biorepositories and associated databases are critical infrastructure in pathobiology research [63]. Biorepositories have the potential to reveal key aspects of the biology of newly emergent diseases and their hosts, including some that could reduce the impact of catastrophic events [64].

3. Tracking the spread of contaminants across time and space

Environmental contamination is one of the most pervasive anthropogenic impacts and has obvious implications for ecosystem and human health. Museum specimens are a powerful and increasingly used resource for documenting anthropogenic contamination in the environment [65–72]. Vertebrates accumulate contaminants in their integument, feathers and organs, through physical contact with the environment and also through bioaccumulation of pollutants in their diet [73]. Many of these contaminants remain as traces in host tissues, sometimes for decades or centuries [74]. Accordingly, the amount of contamination on museum specimens or in associated tissue samples provides a sensitive index of ongoing contamination and a timeline of historical trends in the presence and concentration of particular contaminants in the environment. Importantly, collection data of museum specimens are spatially and temporally explicit, allowing researchers to investigate contamination in a geographical and temporal context. Two recent studies [75,76] demonstrate how temporally well-sampled museum specimens of birds are sensitive indicators of anthropogenic emissions of black carbon and mercury.

(a) Trends in black carbon pollution measured from bird specimens

Black carbon, or soot, is an atmospheric pollutant that arises from the inefficient combustion of fossil fuels and has negative impacts on human health and climate change [77–81]. Birds accumulate black carbon on their feathers, rendering otherwise white feathers a sooty grey colour. For example, a bird's plumage can become soiled by black carbon through physical contact with substrates where black carbon has precipitated from the air. The yearly replacement of a bird's plumage, or moulting, adds to the sensitivity of bird specimens as indicators of change because pollutant deposition on or within a feather provides an environmental snapshot from the specific year in which the specimen was collected

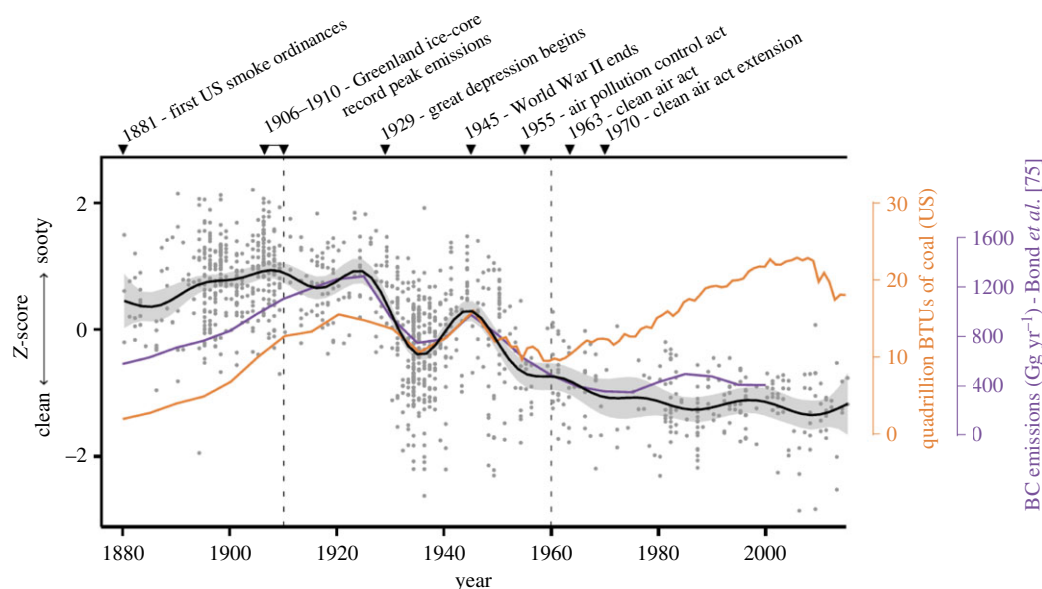


Figure 2. Black carbon soiling of museum specimens (black line) closely tracks previous estimates of black carbon emissions (purple line) [78] between 1880 and 2015. Estimates of black carbon decouple from coal consumption in the United States following progressive clean air legislation. Figure used with permission from DuBay & Fuldner [75]. BC, black carbon; BTUs, British thermal units. (Online version in colour.)

[75]. Although ornithologists have long been aware of the existence of sooty bird specimens in natural history museums, only recently have these specimens been examined in detail. DuBay & Fuldner [75] used scanning electron microscopy to confirm that the feathers of sooty specimens from the US Manufacturing Belt (Wisconsin, Illinois, Michigan, Indiana, Ohio and Pennsylvania) are covered in black carbon particulates, while melanin pigments in feathers are similar. This demonstrated that the variation in plumage of birds was a result of black carbon soiling rather than adaptive increases in melanin pigmentation such as in cases of industrial melanism. Using a time series of 1347 bird specimens collected between 1880 and 2015, the authors quantified the reflectance of breast and belly feathers as a relative measure of the amount of black carbon deposition on each specimen. They discovered that the amount of black carbon deposited on feathers decreased through time, closely tracking the implementation of environmental policies over that time period (figure 2). In addition, DuBay & Fuldner [75] showed that models of black carbon from the late 1880s [78] likely underestimate black carbon levels, underscoring the utility of museum specimens as inventories of environmental contaminants.

(b) Museum specimens track organic mercury contamination

Mercury is a significant environmental pollutant and an anthropogenic increase of mercury in the environment is a well-established trend that results directly from human discharge of mercury into the Earth's ecosystems [5,6]. Although IHg (inorganic mercury) is the predominant form of mercury pollution in the environment, it is converted into organic or methyl mercury (MeHg) by sulfate-reducing bacteria [82]. MeHg is an environmental toxin that bioaccumulates through food webs and builds up in animal tissues, including bird feathers [83,84]. Few studies have investigated whether anthropogenic increases in IHg have resulted in increased bioaccumulation of MeHg, much less the potential

effects of increased MeHg on avian communities or physiology [85]. Novel studies have used museum specimens to demonstrate increases in the amount of MeHg deposited in tissues of fish [65], birds [67–71,86] and bats [87]. One recent study used museum specimens to document MeHg contamination in black-footed albatross (*Phoebastria nigripes*), a seabird formerly designated as vulnerable and now near-threatened [88]. Vo *et al.* [76] measured both IHg and MeHg in the feathers of *P. nigripes* specimens collected in the Pacific Ocean across a 120-year period and documented a statistically significant increase in MeHg. Crucially, unlike most previous studies, the authors were able to distinguish between curator-mediated IHg and environmentally accumulated MeHg through creative use of control populations and by using a gas chromatography inductively coupled plasma mass spectrometry (GC-ICP-MS) approach, which can chemically distinguish between IHg and MeHg. Furthermore, Vo *et al.* [76] showed that a significant number of specimens collected after 1990 had MeHg concentrations above thresholds considered by the EPA to be adverse, highlighting the severity of mercury contamination in the Pacific Ocean. Museum specimens of birds and other vertebrates will undoubtedly have a prominent role in further documenting mercury and other contaminants across the planet's ecosystems, a critical first step in mitigating our impact on the environment.

4. Museum specimens record historical changes in diet, migration routes, environmental stress and morphology

In addition to providing detailed records of environmental pollutants, museum specimens can be used as sensitive indicators of changes in organisms' diet, changing migratory routes and stress as a result of changing environments [72]. These insights stem from the fact that stable isotopes [89,90] and hormones [91,92] remain relatively inert in museum specimens and can be detected reliably over periods of decades or centuries. Stable isotopes have been used to trace evolving diets of fish

[93], mammals [94–96] and birds [89,97–99], with ratios of isotopic nitrogen and carbon, in particular, providing insight into shifts in dietary regime over the past several decades. Isotopes can also be used to create ‘isoscaples’, maps of isotope isoclines across the landscape, allowing researchers to connect breeding and wintering ranges of migratory species [100], among other inferences such as elevational migration [101]. For example, Hobson *et al.* [100] used museum specimens to identify a migratory divide between western and eastern populations of rusty blackbird (*Euphagus carolinus*). Levels of corticosterone, an indicator of stress in natural populations, are increasingly being used to assess the activity of the hypothalamic–pituitary–adrenal axis, a measure of organisms’ response to environmental pollutants and other stressors [98]. In addition, multiple studies have documented consistent trends in morphological traits such as body size and wing-pointedness, often in response to anthropogenic change [102] and increasing habitat patchiness [103], although the precise drivers are still debated [104]. Although detection of such trends is not without biases in terms of location or temporal period sampled, museum specimens are providing unprecedented windows into organisms’ responses to environmental change, without which we would know far less about the impact of anthropogenic change on natural populations.

5. Measuring the effects of climate change on ecological communities using museum specimens

Understanding the current and future impact of climate change on Earth’s ecosystems is a fundamental challenge for humanity [105–107]. One critical goal is predicting how organisms and ecosystems will shift across landscapes in response to climate change. In general, climate change is linked to significant range shifts [108–110], extinctions [111] and potentially community reorganization [112]; however, the predictive power of models is often hampered by uncertainties in climate change trajectories [113] as well as limited knowledge of the distributions of species prior to the Anthropocene. Museum collections span the onset of rapid climate change, and thus have the potential to increase the resolution of climate change studies with precise records of where and when organisms occurred in the past as well as demographic information such as age distributions [114]. Furthermore, museum specimens and associated tissue samples provide opportunities to study both morphological and genetic responses to climate and habitat change [115].

(a) Museum specimens of small mammals reveal climate-associated range shifts

One of the best examples of the potential of museum collections to document climate change is the Grinnell Resurvey Project. From 1904 to 1940, Joseph Grinnell and colleagues from the Museum of Vertebrate Zoology (MVZ) at the University of California, Berkeley, collected and thoroughly surveyed the terrestrial ecosystems of California and the western United States to document vertebrate diversity in time and space. Their legacy of specimens, meticulous field notes and photographs are a veritable ‘gold mine for investigations of species’ responses to climate change, changes in human land use and other stressors’ [116]. Grinnell and colleagues

knew that their efforts would establish a baseline for future studies, although it would be nearly a century before the power of their work would be fully realized. In the early 2000s, the Grinnell Resurvey Project (GRP) was started by MVZ researchers and collaborators who set out to follow in Grinnell’s footsteps by collecting and resurveying sites that had been visited in the early twentieth century. As of today, the GRP has produced many publications and resources that illustrate the importance of scientific specimens in documenting climate change [109,117–120].

One influential study resulting from the GRP investigated distributional changes of small-mammals across a 3000 m elevational gradient in California’s Sierra Nevada Mountains. Moritz *et al.* [109] minimized the confounding effects of land-use change on small-mammal distributions over time by repeating Grinnell’s surveys and collecting efforts across Yosemite National Park, a protected and pristine landscape established in 1890. Furthermore, standardized field protocols and detailed field notes from historical and contemporary surveys allowed the researchers to robustly estimate species’ absences through occupancy models. On average, the ranges of 14 species shifted 500 m upwards across the Yosemite transect over nearly a century. The shift in species’ ranges was consistent with a 3°C increase in temperature recorded between historical and contemporary surveys, with high-elevation species exhibiting range contractions and low-elevation species exhibiting range expansions. Overall, the observed pattern of upslope range increases and associated range contractions does not bode well for high-elevation species whose distributions may become highly fragmented or potentially ‘pushed’ off of mountain tops [121,122].

The genetic consequences of such historic range contractions have been revealed in spectacular detail owing to methodological and technological innovations over the past 20 years in extracting and sequencing highly degraded DNA from historical specimens [123]. A salient example of the use of specimens and novel next-generation sequencing in documenting the impacts of climate change is a study of alpine chipmunks (*Tamias alpinus*) [117], a species that has experienced significant range contractions since the surveys of Grinnell and colleagues in the early 1900s [109]. Using a novel exon capture protocol and robust bioinformatic pipelines, Bi *et al.* [117] investigated the impact of range contractions on the genetic diversity and population structure of *T. alpinus*. Following extensive data filtering and DNA damage corrections of single nucleotide polymorphisms from 10 583 exons, the authors [117] found no change in genetic diversity between historic samples collected by Grinnell and colleagues and modern samples collected by the GRP; however, they uncovered newly arisen population subdivision as a result of range retractions, a pattern also found in other alpine species [124]. Such studies illustrate how museum specimens and their associated tissue samples are invaluable resources for documenting climate change and its impacts on biodiversity.

6. Discussion

(a) Maximizing the utility of vertebrate specimens for the Anthropocene

We have reviewed exemplary studies that use museum specimens to document anthropogenic change and conclude by

discussing the importance of continued collecting of specimens, as well as best practices for museum scientists moving forward. Although it is widely accepted that existing specimens curated in natural history museums document the past, continued dedication to collecting new specimens is often criticized and overlooked as an invaluable investment in the future [125]. We argue that continued collection of new specimens is a necessity without which future scientists will be severely limited in their abilities to document and predict the impact of climate change and other rapidly intensifying anthropogenic pressures on biodiversity and the environment [15,126]. It is imperative that biodiversity scientists continue to direct their efforts to collect specimens across time, space and taxonomic diversity with sufficient sample sizes, metadata and breadth so as to ensure maximum impact across multiple disciplines [13,14].

A concerted effort to maximize the potential of museum collections to document the changing planet will depend critically on greater collaboration between field ecologists, government permitting agencies, citizen and museum scientists. Different questions and goals for documenting the Anthropocene will require different breadths and intensities of sampling and different modes of preservation. For example, the National Ecological Observatory Network (NEON) gives unprecedented opportunities to provide snapshots of continent-wide ecosystems via the collection of animal populations [127,128], and there is ongoing discussion about what to collect and how best to preserve it [25,129]. Collection of vertebrate populations has always been challenging in terms of the labour, cost and museum space required to document diversity adequately. These challenges are exacerbated because we do not know what types of specimens and samples will allow us to monitor future change in multiple dimensions, and because infrastructural constraints place limits on the breadth of samples that can be collected from any given specimen. To the extent that it can be accommodated by the museum community, the ‘total specimen’ [130]—one that maximizes the preservation and availability of the phenotypic and genotypic variation in lineages across space and time—is our best option for providing an ongoing record of biodiversity on a rapidly changing planet.

It is already clear that in order to maximize specimen value for tracking environmental change, extensive re-collecting of high quality, data-rich specimens will be necessary, such as envisioned by the Global Genome Initiative [131]. Best practices for museums moving forward include preserving high-quality tissue samples, associated parasites and multi-part specimens [130]. First, we encourage museums to preserve tissue samples capable of yielding high-molecular-weight DNA for whole-genome sequencing. Similarly, we recommend that RNA-quality tissues of multiple organs be preserved for transcriptomic and epigenomics studies [132]. Parasites associated with host specimens should also be preserved to foster integration across diverse sets of questions, such as whether hosts and parasites respond concordantly to anthropogenic change [25]. We also advocate preserving diverse voucher specimens per individual, such as skeletons and skins from the same individual, spread-wings and other non-traditional vouchers [133] or fluid-preserved specimens commonplace in herpetological collections; such specimens have tremendous potential to be analysed with modern scanning technologies [134,135]. Ongoing salvage will continue to be a mainstay for vertebrate collections, but ultimately active,

research-grade collections will prove the most valuable. Finally, we stress that online access to original specimen data linked to research data subsequently derived from each specimen (e.g. gene sequences, CT scans, photographs, sound recordings, etc.) provides a powerful nexus for integrating diverse investigations [74,136–138]. The responsibility for reporting the detailed provenance of and metadata associated with specimens used in scientific research falls equally on researchers, museum curators, authors, reviewers and most critically on the editors of journals that publish the research. The reporting of many types of data archiving, such as DNA sequences and phylogenetic trees, is now standard across many journals in the biological sciences, but the reporting of original specimen information from such data, or links to them, is haphazard and inconsistent at best.

(b) The role of the public and the evolving perception of museums

Paramount in the effort to document changing biodiversity through time is the involvement of the general public, which often grossly misunderstands the intent behind vertebrate collections and their value to society [139]. It is often challenging for the public to separate the negative consequences for individual animals incurred by collecting from the often imperceptible impact at the population level. Not only the general public but also often scientists and wildlife managers themselves oppose continued collecting, often owing to misconceptions about the perceived negative impact of museum collecting on vertebrate populations [140,141]. Involvement of the public through citizen science in ongoing specimen-based documentation of biodiversity, for example, through ‘BioBlitzes’, and in decision making as to what to collect, will be essential [142]. Specimens and associated data can readily be incorporated into educational enterprises and provide powerful opportunities for student-led, inquiry-driven lessons about diverse aspects of our natural world, including climate change and the Anthropocene [136,143,144].

The public and non-museum research communities often have the mistaken perception that museum specimens are collected for a narrow range of uses in the fields of taxonomy, systematics and biogeography, or perhaps that specimens collected for such these fields will have little use outside them. By highlighting the utility of both historical and modern museum specimens in documenting change in the environment, we showcase uses of museum collections in research and teaching that may be less well known outside the museum community. The examples presented here illustrate how museum specimens are a powerful, albeit underutilized resource for documenting the Anthropocene—the emergence and spread of zoonotic diseases, environmental contamination, environmental stressors and climate change—among other assaults to our planet and its inhabitants. The continued collection of museum specimens will ensure detailed documentation of the Anthropocene and its myriad effects [145,146]. With the long time-scales they represent, museum specimens will play an even more important role in future studies of environmental change as preservation methods improve, novel technologies are developed, and creative thinking is applied to unlock their as yet unrealized potential.

Data accessibility. This article has no additional data.

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