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The Global Museum: natural history collections and the future of evolutionary biology and public education

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Natural history museums are unique spaces for interdisciplinary research and for educational innovation. Through extensive exhibits and public programming and by hosting rich communities of amateurs, students, and researchers at all stages of their careers, they provide a place-based window to focus on integration of science and discovery, as well as a locus for community engagement. At the same time, like a synthesis radio telescope, when joined together through emerging digital resources, the global community of museums (the 'Global Museum') is more than the sum of its parts, allowing insights and answers to diverse biological, environmental, and societal questions at the global scale, across eons of time, and spanning vast diversity across the Tree of Life. We argue that, whereas natural history collections and museums began with a focus on describing the diversity and peculiarities of species on Earth, they are now increasingly leveraged in new ways that significantly expand their impact and relevance. These new directions include the possibility to ask new, often interdisciplinary questions in basic and

applied science; inform biomimetic design; and even provide solutions to climate change, global health and food security challenges. As institutions, they are incubators for cutting-edge research in biology and simultaneously protect core infrastructure for present and future societal needs. In this perspective, we discuss challenges to the realization of the full potential of natural history collections and museums to serve society. After reviewing collections and types of museums, including local and global efforts, we discuss the value of specimens and the importance of observations. We then focus on mapping and modelling of museum data (including place-based approaches and discovery), and explore the main projects, platforms and databases enabling this. We also explore ways in which improved infrastructure will allow higher quality science and increased opportunities for interdisciplinary research and communication, as well as new uses of collections. Finally, we aim to improve relevant protocols for the long-term storage of specimens and tissues, ensuring proper connection with tomorrow's technologies and hence further increasing the relevance of natural history museums.

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The Global Museum: natural history collections and the future of evolutionary biology and public education

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Abstract

Natural history museums are unique spaces for interdisciplinary research and for educational innovation. Through extensive exhibits and public programming and by hosting rich communities of amateurs, students, and researchers at all stages of their careers, they provide a place-based window to focus on integration of science and discovery, as well as a locus for community engagement. At the same time, like a synthesis radio telescope, when joined together through emerging digital resources, the global community of museums (the 'Global Museum') is more than the sum of its parts, allowing insights and answers to diverse biological, environmental, and societal questions at the global scale, across eons of time, and spanning vast diversity across the Tree of Life. We argue that, whereas natural history collections and museums began with a focus on describing the diversity and peculiarities of species on Earth, they are now increasingly leveraged in new ways that significantly expand their impact and relevance. These new directions include the possibility to ask new, often interdisciplinary questions in basic and applied science; inform biomimetic design; and even provide solutions to climate change, global health and food security challenges. As institutions, they are incubators for cutting-edge research in biology and simultaneously protect core infrastructure for present and future societal needs. In this perspective, we discuss challenges to the realization of the full potential of natural history collections and museums to serve society. After reviewing collections

and types of museums, including local and global efforts, we discuss the value of specimens and the importance of observations. We then focus on mapping and modelling of museum data (including place-based approaches and discovery), and explore the main projects, platforms and databases enabling this. We also explore ways in which improved infrastructure will allow higher quality science and increased opportunities for interdisciplinary research and communication, as well as new uses of collections. Finally, we aim to improve relevant protocols for the long-term storage of specimens and tissues, ensuring proper connection with tomorrow's technologies and hence further increasing the relevance of natural history museums.

Keywords: collections, field education, Global Museum, innovation-incubator, natural history, place-based, specimens, transcriptomics, epigenomics.

Introduction

Natural history museums, which harbour extensive records of biological diversity, have always been meeting places for scientists, amateurs, and the public. By visiting a natural history museum and learning about nature, the lay citizen often tacitly endorses the information presented and considers it worthy of consideration and reflection. As such, museums are still considered trusted resources, at a time when many other institutions are bitterly mistrusted (*Foley, 2015*). Whereas this trustworthiness is true for most types of museum collections, natural history collections play a special role, in part because at the same time that they serve in public education, they are also actively used and curated by professional scientists to answer pressing problems in biology and beyond.

Museum biological collections are more than meets the eye. Each specimen harbours many kinds of data, such as information on locality and collection parameters, associated pathogens, biopolymers such as DNA and proteins, and metabolic compounds. This wealth of metadata across many specimens turns collections into powerful research tools, enabling scientists to test for historic environmental hypotheses and carry out diverse studies ranging from public health & safety (as cornerstones in studies of environmental health and epidemiology; *Suarez & Tsutsui*, 2004), biomimetic design –where naturally-occurring architectures and systems inspire technological innovation (*Jayaram & Full, 2016*; *Nirodi et al., 2018*), historical genomics (focussing on ancient alleles or past genotypes; *Bi et al. 2013; Besnard et al. 2014*), to global change (tracking shifts in phenotype across specimens through time; *Jones & Daehler, 2018*), something that a database of mere species observations cannot do. But natural history collections face challenges. They are in need of constant sustenance, funding, and curation.

Survey Methodology

This paper aims at reviewing and conceptualising how natural history museums have had and could have a continuing and increasing role in enabling discovery in evolutionary biology and beyond. We also discuss their central role in training the next generation of innovative thinkers. The paper is the result of a three-day workshop on 'The role of museums in modern evolutionary biology' organized by Chalmers University of Technology and the University of Gothenburg (Sweden), under the auspices of the Gothenburg Centre for Advanced Studies (GoCAS), and held during 7-9 June, 2017. Participants, most of whom were based at natural history museums (broadly defined to also include botanical gardens; see below) as researchers or directors, were chosen to represent diverse areas of museum-based science. They were often based in Europe, but also the United States, South Africa and South America (Peru). After several sessions of brainstorming about the current relevance of museums and roadblocks to expanding impact, we collectively drafted an outline and all authors participated in the writing and direction of the paper.

Collections & types of museums

We define natural history museums in a broad sense, as institutions containing diverse physical specimens, and sometime also including seed banks, substantial living, frozen, or dried tissue collections, and genomic data, among others. These collections include material from rapidly disappearing extant species, as well as extinct species, many of which are from the most inaccessible parts of the Earth. Collections may have innate, historic biases in taxonomic coverage and sampling design, which might need to be considered for their further development.

Whereas historically natural history museums, in particular those in Europe, have been linked to the colonialist enterprise, increasingly specimens are held in local museums and maintained by local scientists and students, and international specimen acquisition and study are conducted in strong partnership with these institutions. International agreements, such as the Nagoya protocol, rightly mandate such participation under the terms of Access and Benefit Sharing. Additionally, citizen science increasingly contributes to collections, which today are housed all over the world, and serve as gems of diverse global centres of cutting-edge research (see Fig. 1). Natural history museums may be located at universities, sometimes without exhibits, or may include public exhibits, such as typically occurs in national, state or regional entities. In many cases, regional collections, and their exhibits, reflect and strengthen visibility, appreciation, identity and awareness of local culture and fauna & flora, therefore playing an important and confirmative role for the visiting public. Collections that span long periods of time reflect the history of science as well as changes in norms and values in society: *what* was sampled, *how* and *why*. This emphasis is especially visible in open, regional, collections on display. Regionality therefore, can be considered a strength of collections and fulfills an important role in sustaining regional pride in biodiversity. On the other hand, for many scientists, usually on a global research mission, regional collections could appear to be insufficient as it needs 'global collections' (see below, *The Global Museum*), for instance, to capture the full extent of evolutionary and biogeographic diversity of particular clades. Still, given the increasingly connected network of regional museums, the local depth provided by such regionality would be impossible to recover – if only for practical reasons - in a single, global museum, were it composed solely of physical specimens.

139 The distributed nature of the world's museum collections increases long term data security.
140 Collections of natural objects will always require a specific physical location and this makes
141 them vulnerable to theft, fire and water damage. For instance, it was thanks to this distributed
142 nature that we still have duplicates of the tens of thousands of specimens of plants stored at the
143 Berlin Herbarium when it was almost completely destroyed during World War II. The Butantã
144 Museum in São Paulo had a world-renowned alcohol collection of 85,000 snakes and half a
145 million Arachnids. After it was drastically destroyed by a fire in 2010 (*Phillips, 2010*), it became
146 clear that there were virtually no duplicates for these two collections, either as specimens or
147 tissues, in other museums. Along with these concrete recent examples of natural heritage loss,
148 the infrastructure of many museums remains underfunded, exacerbating their vulnerability. A
149 grim example is the Brazil National Museum in Rio de Janeiro, where a fire destroyed an
150 estimated 90% of the collections in several divisions in September 2018 (*Phillips, 2018*).

151 Creating redundancies in collections, especially for extant species and genetic resource
152 collections, is key to ensuring the longevity of these samples and associated data. Initiatives such
153 as the Global Genome Biodiversity Network (GGBN; *Droege et al., 2016*) aim to collect,
154 catalogue, and "democratise" genomic resources across global collections, covering 50,626
155 species (as of 18 march 2019). Although this enterprise represents an important step in the
156 direction of a distributed collection, it will benefit from more coordination and financial support
157 for data security and achieving complementarity and redundancy among collections. These aims
158 are included in the mission of the pan-European Distributed System of Scientific Collections
159 (www.dissco.eu) initiative, which aims to extensively digitize and database diverse specimens
160 from across the museums of Europe. In comparison, in the US, a National Science Foundation-
161 funded major digitization initiative, named *Integrated Digitized Biocollections* (iDigBio), aims at

162 making data and images for millions of biological specimens available in electronic format "for
163 the research community, government agencies, students, educators, and the general public"
164 (*Page et al., 2015*). iDigBio serves as "the coordinating center for the national digitization
165 effort" fostering partnerships and innovations, and developing extensive content. iDigBio is
166 funded by grants from the NSF Advancing Digitization of Biodiversity Collections (ADBC)
167 program. In contrast, DiSSCo started by securing government buy-in, with content being part of
168 operational costs. Because it has become an established and recognized entity, governments can
169 fund the infrastructure because they need the services, thereby providing DiSSCo with
170 guaranteed political context. At the global level, the *Global Biodiversity Information Facility*
171 (GBIF) is "an international network and research infrastructure funded by the world's
172 governments and aimed at providing anyone, anywhere, open access to data about all types of
173 life on Earth." Being the main global database, a large proportion of its 1 billion records
174 comprises observations rather than specimens (see below).

175

176 **The value of specimens and the importance of observations**

177 All collections ultimately contain, or are dependent on, specimens. A specimen may consist of a
178 complete organism (collected by naturalists over the past few centuries) or parts of a single
179 individual organism. Increasingly, meta-data associated with the physical specimen - the
180 'extended specimen' (Webster, 2017) - add value and increase data richness through videos,
181 sound recordings, information on habitat, and photographs. For example, for birds, the extended
182 specimen may be comprised of records of the song, or recordings of behaviour of those
183 organisms, prepared in a way that preserves them for the future. Bioacoustic tools provide unique
184 collections that can include some of the last known evidence of extant species. Likewise, several

185 films exist (e.g. https://www.youtube.com/watch?v=nAzqGn-LHCw) portraying the behaviour
186 of now-extinct animal species, such as the Tasmanian tiger, the golden toad, and the Hawaiian
187 crow. Museums currently host increasingly diverse collections, which, in addition to DNA and
188 tissue banks, may be generated by core genomic facilities or imaging labs (isotopic, x-ray
189 computed tomography data [CT], scanning electron microscopy [SEM] images). Examples now
190 include rich stores of high-resolution CT data generated from museum specimens, which allow
191 investigators to look inside material in a largely non-destructive way. These require different
192 storage resources from those that traditionally constitute museum infrastructures, namely large
193 scale and secure long-term storage of image data. Integration of different data streams will allow
194 bridging among disciplines and the involvement of fields underrepresented in natural history
195 museums, such as engineering, biomedical sciences, and art. For instance, biomimetic design can
196 benefit strongly from inspiration from natural history collections (examples from robotics see
197 *Jayaram & Hull, 2016*), or solutions to global health or food security challenges can be based on
198 exploration of natural history specimen collections (see Table 3 *Specimens and pathogens*).

199 Specimens are at the heart of the discovery process and technological advances are increasing the
200 number and diversity of possible questions that can be addressed (e.g., *Schmitt et al. 2018*; see
201 below). For instance, bone fragment identification using collagen barcoding was difficult to
202 imagine before the rise of LC-MS technology, but *Welker et al. (2015)* used this to identify
203 Palaeolithic fragments of mammal bones in France. Genomic analyses of single bone fragments
204 can inform on the evolutionary and demographic history of our own species (e.g., *Slon et al.,*
205 *2018*). Future technologies may include more advanced chemical, biochemical, isotope or micro-
206 anatomical surveys, making maintenance of specimens even more critical because they connect

all data streams and facilitate data interoperability. At the same time, maintaining specimens is key to repeatability – a core requirement of science.

Museum specimens and data are stored and made accessible for future generations, enabling them having broad reference and context. Continued field collecting secures future access to time series of specimens, collected over decades or even hundreds of years. These long-term archives provide valuable and unique information (Graham *et al*. 2004) on changes in the species composition in our environments and habitats, due to factors such as climate change, human-mediated nitrogen deposition, or other anthropogenic activities (*Meineke et al*. 2019a; 2019b). An example is a large survey and collection of marine invertebrates from the Swedish west coast from the 1920´s and 30´s conducted by the Gothenburg Natural History museum (GNM), in which the exact sample locations could be deduced using modern methods, and consequently revisited during a new survey in the 2000´s, revealing a 60% loss of biodiversity (*Obst et al. 2017*). Specimens collected by researchers 200 years in the past can be compared with contemporary (and future) sampling-- as long as these collections and institutions persist. In fact, the specimen can be seen as the outcome of a combination of genotype and past environmental change or conditions (e.g., *Holmes et al., 2017*), and a well-curated collection captures the variation in phenotype as well as genotype (see *Bi et al*. 2013; *Rowe et al*. 2011; *Staats et al.* 2013; *Ruane and Christopher, 2017*). For instance, *Cridland et al. (2018)* comparing SNP patterns from historic museum and living specimens of bees, could not only infer 'rapid change' in genetic composition of honey bees in California, but also identify historic genotypes in candidate genes possibly involved in adaptation to new niches. As another, less-domesticated, example: reconstructing the shift to C4 photosynthesis in grasses could be conducted using DNA from a 100-year-old Malagasy herbarium specimen for which both its phylogenetic placement

and the assessment of its 'genetic make-up' with regards C4 photosynthesis could be assessed (*Besnard et al., 2014*).Therefore, specimen collections can provide a powerful reference for functional genomics studies, in a world where phenotyping different genotypes, retrievable from the specimen, becomes more important.

Increasingly, growth of museum collections is the result of their increased relevance for ecological studies, in addition to input from taxonomically-focused collecting activities, linked to specific inventories and research projects. Whereas museum staff and associated researchers and students still undertake expeditions to increase collections and make them available for future generations, many collections now come from large scale ecological studies (e.g. NEON in the US). Specimen collections enable answers to a large number of other scientific questions, some of which have not yet been posed. The earliest museums facilitated interactions among scholar-travellers, to share observational data from across the planet and to help build the core of what would become natural history and modern evolutionary biology. Increasingly, museums are leveraging new data from their specimens, and this integration of data types allows training in techniques that bridge among disciplines, as well as the generation of data sets that are of relevance to disparate traditional fields such as engineering, biomedical sciences, and art. Today natural history museums serve increasingly as a *nexus* for work that disregards disciplinary boundaries and addresses questions we did not know to ask before (see Fig 2). Because collections provide the opportunity to rigorously examine diverse aspects of taxonomic, morphological, genetic, and chemical variation across vast temporal and spatial scales, they can help diverse scientists bridge the gaps between traditionally distinct disciplines. Museum spaces ideally are filled with students who learn to think anti-disciplinarily and appreciate the

importance of the specimen. These spaces can therefore be considered 'Innovation Incubators' where a next generation of critical thinkers in biology and beyond will be trained.

A specimen constitutes a voucher, not only of the actual individual sampled at the time, but often also of its locality – including information about the soil and other biotic and abiotic conditions in which the specimen was collected (see below, the 'holistic specimen'). *Troudet et al. (2018)* describe how over the past decades the proportion of specimen-based occurrences in GBIF has decreased from 68 to 18%, in favour of observation-based occurrences, mostly from contributions by citizen science efforts such as iNaturalist and eBird (see Table 1). This will have affected repeatability and 'richness' of systematics and evolutionary studies and the authors urge that "when impossible to secure, voucher specimens can be replaced by observation-based occurrences", particularly when combined with 'ancillary' data such as recordings, pictures, DNA samples etc. In cases where ethical, conservational, or practical concerns exist, observation data instead of collected specimens provide additional (or occasionally substitute) contributions to our knowledge on where and when particular species occur. Recorded sightings, such as those from iNaturalist or e-Bird, include occurrences of diverse temporal range, and are pretty much the only observation-based data that are allowed in GBIF. In addition to such observations recorded in the field, however, collected specimens (when available) offer additional options for confirming or extending the original work using new analytical techniques. Similarly, sound recordings can be re-studied within the context of new evidence, leading to reciprocal illumination.

Place-based discovery: different specimen data sets connecting to a location

As *Miller (2007)* puts it, "Places are not simply a semantic convenience. It is a meaningful lens for viewing the world because it is orderly with respect to geographic space." As such, 'place-based' approaches in general focus on the characteristics and meaning of particular places as a fundamental starting point for a particular development or project. Especially in charity and community development work, place-based approaches aim at "giving power to the community in guiding systemic change" and therefore "being recognised as critical to responding effectively to certain community challenges" (www.qcoss.org.au/). In education, place-based approaches are thought to "identify, recover and increase the values of local cultural specificities" (*Monardo, 2018*).

Place-based learning and education is well developed (*Gruenewald and Smith, 2014*) and provides a context for local understanding and societal change. Natural history museums are well suited for hosting place-based activities, as well as making direct links between collections and associated data and societal activities and needs. The developing Island Digital Ecosystem Avatar (IDEA) project is one example (*Davies et al., 2016*), entailing "a systems ecology open science initiative to conduct the basic scientific research needed to build use-oriented simulations (avatars) of entire social-ecological systems." Many specimens will have been collected and stored, for instance for DNA barcode reference libraries, for making this possible.

For biological collections and their associated and ensuing process of discovery, the place-based approach is relevant. 'Place-based' here does not ignore external, or global, evidence or connections to other geographical localities, and indeed seeks to understand how local information and processes are interconnected with those at a larger scale. Best practices for biological collections include a geographical reference for each item, as is included in the

Darwin Core (see https://dwc.tdwg.org/). When collected together, sets of items are necessarily place-based. In addition to standardised metadata directly associated with biological items (*Kissling et al., 2018*), many other types of information are place-based and can be collected at the same location and super-imposed on point specimen data. Examples include information about geology, ground and atmospheric chemistry, and archaeology. These, and other data layers – such as from GBIF (species occurrences), NCBI (DNA and amino acid sequences), Open Tree of Life (phylogenetic trees), Map of Life (abundance data), TraitBase (traits), GloBI (biotic interactions), see Table 1 - can be associated or combined with geographical location through a geographical information system (HOLOS), integrating across diverse data types and enabling testing hypotheses concerning causal impacts - the 'holistic specimen'. In a sense, this approach is comparable to correlative species distribution modelling (SDM) approaches such as using Maximum Entropy (*MaxEnt;*, *Philips & Dudik, 2008*), focussing on mostly abiotic and edaphic correlates.

In addition, the place-based approach can provide a baseline for understanding changes over time (*Billick et al., 2013*; *National Research Council, 2014*). Of particular interest here is the context of historical environmental change to which current changes can be evaluated and compared. An understanding of historical processes provides a means for predicting, or forecasting, how biological systems may respond to change in the near future. For instance, *Willis et al. (2008)* studied how climate change may affect phenology in some angiosperm species in Concord, Massachusetts. *Slingsby et al. (2017)* studied the interaction between fire and climate change on species diversity in the South African Cape Floristic Region, allowing modelling of future vegetation response.

319 In general, the additional value of place-based approach for scientific discovery includes the
320 serendipity of collecting data over periods of change identified later, as well as the interaction of
321 researchers sharing an interest in the same geographical location or region (*Michener et al.,*
322 *2009*). Place-based initiatives associated with larger networks (see Table 1) can provide access
323 and understanding to a diversity of communities, which is both democratic and allows broad
324 participation in discovery. Examples of such initiatives include developing new natural history
325 museums (Darwin Initiative, www.darwininitiative.org.uk) and DNA barcoding of local
326 biodiversity (*van de Bank et al., 2008*; *Janzen & Hallwachs, 2016*). In addition to natural history
327 museums, the benefits of a place-based approach are also shared with field stations, botanical
328 gardens, and biological reserves (*National Research Council, 2014*).

329

330 **The Global Museum**

331 As indicated above, many museums serve regional communities, and collections in such
332 institutions usually reflect regional interests, fauna and flora, funding and research questions.
333 Given that science is an international endeavour, the question can be asked as to whether
334 evolutionary biology would be better served by enhanced ability to document and analyse
335 patterns across regions, such as with the use of GBIF. For instance, for taxonomy, having the
336 virtual, global, workbench of the Barcode Of Life Database BOLD (www.boldsystems.org;
337 *Ratnasingham & Hebert, 2007*) allowed taxonomists globally to harmonise species delineations
338 by collectively analyzing and interpreting DNA barcode patterns from global rather than regional
339 data sets. Historically however, collections have been mainly curiosity-driven, emphasizing
340 rarities (i.e. single individuals per species, a phenomenon which may actually be commonly-
341 occurring), a pattern that still exists for certain organism groups and regions (*Novotný & Basset,*

2000; *ter Steege et al., 2011*), and mostly the result of general collecting efforts. This *generalism* has resulted in an invaluable reference specimen base in today's museum collections, allowing comparison with living specimens, identifying relatives of medically- and economically-important species (for instance melon, *Sebastian et al., 2010*), or testing historic biological hypotheses (e.g. Délye et al. 2013). On the other hand, this patchy tradition of biological collecting has come at a cost to easily comparing organisms across large geographic regions or across temporal spans. For example, evolutionary biology would benefit from being able to analyze more common species represented in collections worldwide, because this would allow assessing phenotypic variation at much broader scales. In addition, assumptions about species ID based on morphology may be falsified by genetic data (*DeSalle et al.* 2005) - but also the reverse - revealing an unexpectedly high level of cryptic diversity in certain groups (e.g., *Hebert et al., 2004*). Such a mandate would require a concerted effort of museums globally to collect and archive specimens in a coordinated manner that would help document current biodiversity and variation of common species across the globe. Such an effort was originally planned to be conducted by NEON in the United States, but in some cases has fallen short of this goal (*Cook et al., 2016*). Other ventures include the above-mentioned BOLD (with iBOL extending its coverage) which holds 6.6M barcode records across 0.29M species, many of which are commonly-occurring. Future collections should continue to expand with specimens sampled widely across biodiversity, but in addition should amass commonly-occurring species, which can serve as environmental monitors, especially when sufficient metadata is also collected.

Museum communities are increasingly not confined by a single, local physical space but able to distribute their reach through innovations in technology. Databases and other online tools enable international access and an array of novel platforms facilitate participation of a broad swath of

the public in discovery and documentation, from undergraduate classes to young children participating in aspects of the scientific process. Examples of such activities include encouraging children to make observations of butterflies in drawers, thereby building their sense of biodiversity. Another example is citizen science projects in which volunteers help in interpreting and digitizing information on old collection labels, as has been done for the Paris Herbarium (http://lesherbonautes.mnhn.fr/) and for brachiopod fossils at the Swedish Museum of Natural History.

From a Global Museum perspective, we may ask whether phenomena such as global change have been effectively documented in collections in the past so that we can use that ensemble of past collections to forecast future conditions. For instance, collections can help scientists document how C4 photosynthesizing plants have spread during recent decades as a response to the global increase in atmospheric CO2 concentration (*Besnard et al., 2014*), or how species extinctions may be overrepresented in particular clades or areas (e.g., *Ricklefs, 2006*). Such work would be impossible without having the integrated, properly digitised and databased platform that a Global Museum provides.

Large international data sharing initiatives (e.g. LifeWatch ERIC, GBIF, Encyclopedia of Life, BOLD and iBOL, see Table 1) allow access to collections by scientists and the public living far from privileged historic western centres for inquiry. For instance, GBIF alone provides access to now over a billion records of specimens and observations from around the world. iDigBio, GBIF, and the Atlas of Living Australia (ALA) and its affiliated atlasses are the world's largest and best-developed biodiversity data aggregators and mobilizers. As outlined above, DiSSCo is a developing initiative of major significance that will unify natural science collections in Europe. With increasingly distributed access to large datasets and online portals to large-scale

388 computational resources, analysis of the "big data" of biodiversity records can also go global
389 (see *Antonelli et al. (2015)* for an example in global angiosperm biogeography and speciation).
390 Digitization of collections will be increasingly important in this respect; there are many valuable
391 but undigitized collections residing in museums.

392 Citizen science can contribute significantly to building collections, as for instance seen in many
393 entomological collections that grow these days by amateur entomologists donating their well
394 curated collections for posterity. *eBird* and *iNaturalist* are excellent examples of connecting
395 citizen with science in a highly-efficient manner (and then feeding into GBIF). The Gothenburg
396 Natural History Museum (GNM) malacological collections have benefitted tremendously by
397 citizen science efforts with devoted ('advanced') amateurs donating their often well-curated
398 private collections. Based on these collections, which can be considered 'environmental
399 archives', *Bolotov et al.* (2018) could infer from freshwater pearl mussel collections that
400 morphology has changed in time correlated to environmental alteration and climate change.
401 Based on historical and recent specimens from extensive geographical sampling, the authors
402 concluded that the latter may well have accelerated the population decline in pearl mussels over
403 the last 100 years. The study underlines the importance of preserving large collections (many
404 individuals) to enable meaningful statistical analysis of morphological measurements. Table 4
405 lists another example from the GNM concerning garden slugs sent in by the general public.

406

407 **Further increasing the relevance of museums through digitization and imaging**

408 To facilitate the coordination of collection and databasing efforts between museums – a necessity
409 to achieve the Global Museum – it is vital to increase awareness of what knowledge is available,

410 not only at regional museums but across museums globally. This is most easily achievable
411 through digitization of the collections. Moreover, such digitization also opens the collections for
412 a number of additional researchers interested in overall temporal or spatial patterns in
413 biodiversity. iDigBio provides a good example of how digitization can be successful and
414 provides outreach to a global user base. In its first 10 years, iDigBio has prioritized digitization
415 of specimens that can drive collaborative research and answer specific biological questions. This
416 specialization necessarily results in only a small fraction of available specimens being digitized.

417 A major question for the future is how the community should greatly expand the scope of
418 digitized specimens. Just as haphazardly collected historical specimens often prove useful for
419 research questions not envisioned during the collecting event, it is also likely that specimens
420 digitized without a specific research question in mind will prove useful for answering scientific
421 or societal questions, especially if digitized on a large scale. But digitizing 'blindly' must of
422 course be balanced with the pressure of meagre resources; enabling citizen scientists to assist
423 offers a good solution (*Rouhan et al., 2016;* see Table 4). Large amounts of metadata remain to
424 be digitized and would generate knowledge on biogeography (geographic data of specimens),
425 disease spread (genetic material from parasites), biological interactions (pollination data),
426 phenology, or shifts in species distributions (*Suarez & Tsutsui, 2004*; *James & al., 2018*). New
427 advances in image recognition through deep learning using neural networks are also likely to
428 enable easy identification of many species, such as already implemented in the iNaturalist
429 platform, and hence help digitization.

430 *Tracking specimen taxonomy.* For research on temporal patterns of global change, such as global
431 warming studies or analyses of movement of hybrid zones, museum records provide a unique
432 source of historical records. Because they are backed up by physical specimens, records can be

433 identified to individual species irrespective of how many taxonomic changes have occurred since
434 specimen collection, an endeavour that is often impossible if the records were purely
435 observational. However, an important caveat of this effort is that it is rarely obvious from online
436 databases on what taxonomical opinion each identification was based. Indeed, to capitalize on
437 the inherent strength of specimen-based records a citation to the taxonomic revision behind each
438 identification would be ideal, but is not always available.

439 *Combining specimen databases.* Another challenge related to digitization and to the value of the
440 physical specimens is that specimens may be one of the only clear, if frequently underutilized,
441 ways to identify duplicates between different databases. For example, this challenge is often
442 encountered among mammalian fossils where several databases, including New and Old World
443 Mammals (NOW) and PaleoDB, have been started independently. Together these databases
444 completely document diversity for some groups, and out of ~1586 accepted species of carnivores
445 and relatives (Carnivora, Hyanodonta and Oxyaenidae) in the fossil record, 1460 species are
446 included in at least one of them (*Faurby, Werdelin, Antonelli,* unpublished). However,
447 individually they are each highly incomplete (1121 species (6385 records) in NOW, 1040 species
448 (6756) in PaleoDB). Analyses attempting to summarize the complete fossil record therefore
449 needs to combine databases. For many uses, such as when estimating speciation or extinction
450 rates (*Silvestro & al., 2014*), it would be highly desirable to resolve redundancy between
451 databases, a challenging effort that could be made trivial if both databases contained the museum
452 specimen ids for the records.

453 *Big clades, large collections.* Digitization will be extremely challenging for the most diverse
454 taxonomic groups, such as typically large collections of insects, although there have been
455 attempts to automate digitization of such groups (*Hudson & al., 2015*). Knowing the limits in

geographical and temporal distribution and the size of the collection, especially for the most common groups, may suffice for further scientific analysis. Finer scale distributional data in such cases can easily be supplemented by citizen science initiatives (e.g iNaturalist), especially if associated with pictures or movies with smartphones that contain georeferenced and timestamped records that facilitate re-validation through inspection of the images by experts (see for instance iSpot; *Silvertown et al., 2015*).

Museums still harbour large amounts of undiscovered and undocumented information. The total number of specimens deposited in museum collections around the world may be as large as 1-2 billion (*Ariño, 2010*), and for herbaria an estimated 350 M specimens are known to be deposited in 3400 collections world-wide (*Soltis, 2007*). Moreover, statistical approaches to estimate the size of collections agreed in 2010 that less than 5% of the universe of natural history collections data is available in databases such as GBIF (*Ariño, 2010*), although this fraction has been decreasing, with the fast increase of observation data in GBIF (*Troudet et al.*, 2018). *Wilson (2003)* noted that the smaller the organism the more poorly known the group to which it belongs, exemplified by fungi, nematodes and microbes. For instance, a random selection of specimens collected in a tropical rain forest and deposited in jars at a natural history collection resulted in the description of almost 200 new species of ichneumonid parasitoid wasps to science (*Veijalainen et al., 2012*). *Bebber et al. (2010)* described a comparable case for angiosperm species, with an estimated 35,000 undescribed species already residing in herbarium collections. An abundance of undescribed species is only the tip of the iceberg on the amount of data undiscovered and undocumented in the world's museums.

In terms of species diversity, DNA barcoding reference libraries such as BOLD (*Ratnasingham & Hebert, 2007*) and UNITE (*Koljag & al., 2013*) provide a good framework against which the

479 extent of diversity deposited at natural history collections can be measured. However, molecular
480 approaches to identify hidden diversity remain debatable (e.g., *Brower, 2006*) but can be
481 overcome in large clades such as Lepidoptera (*Hebert et al., 2010*). In UNITE fungal species
482 hypotheses are generated and named, but also tagged with a citable digital object identifiers
483 (DOIs) so it can be unambiguously communicated, allowing harmonisation of species concepts
484 throughout communities. In comparison, BOLD allows barcode index numbers (BINs) to refer to
485 barcode clusters that have not been yet described taxonomically.

486 Programs like the UK Darwin Initiative to train observers and scientists in countries rich in
487 diversity but low in funding for conservation and science surveys can further support
488 democratization of not just specimens and data but also the knowledge for performing analyses
489 and conducting research. However, much more needs to be done in this area, especially in
490 capacity building, infrastructural development, and task distribution.

491 *Reference collections.* A major need for collections worldwide is to develop basic molecular data
492 associated with a given taxon. The key importance is the burgeoning use of metabarcoding in
493 ecological studies can be anchored to museum specimens, and thus linked to the associated
494 metadata. Many museums have embarked on such endeavors, for example in CSIRO, and efforts
495 of multiple museums ideally come together in clade-based DNA barcode projects in BOLD.

496 To enhance the broader relevance of natural history museums it is also important to message
497 effectively to industry and policy makers. In particular, the museum community should explore
498 ways to use specimens to find novel ways to bridge the traditional chasm between the sciences,
499 arts and humanities. Shared themes include place-based research and experiential learning, both
500 encouraged in instructional efforts in science, technology, engineering and mathematics (STEM
501 fields) and the arts. Both the arts and sciences depend on inspiration, creativity, and critical

assessment, and museum specimens serve well as sources for both inspiration and fascination. While scientific education and research offer rigorous methods for testing hypotheses and creating new knowledge, integration of experiential art and humanities work can into science fosters non-traditional ways of exploring and messaging about our world (Balengee 2010). Natural history museums should continue their efforts to train scientists and artists to develop novel solutions to emerging problems, especially as we face an increasingly uncertain environmental future.

Efforts by the Global Museum to assemble collections that will fulfil their key roles in the future require facilitating international agreement and participation. Such a massive effort cannot remain the province of a relatively few marginally resourced programs. Identifying the answers to the most pressing questions facing society and our environment require fertile spaces for cultivating innovation in the context of training in knowledge of biodiversity. This task is impossible without museum spaces and collection resources. We cannot afford to 'waste' the potential of natural specimens due to degradation, improper storage, or disposal, especially in the light of rapid biodiversity loss. They need space-efficient, climate-controlled and pest-free spaces. Innovations in these areas are likely needed to accommodate collections in the long term (hundreds to thousands of years) and to deal with preservation issues that may be exacerbated by global climate change (including increasing frequency of extreme weathers, hurricanes, flooding).

Public perception of natural history museums

We argue that natural history museums should be regarded as 'Innovation Incubators', places where 'anti-disciplinary' science is thriving by building bridges between otherwise or so far improbable disciplines, and scientists from various 'disciplines' meet, an *Academic Nexus of Integration*. Because natural history collections can facilitate examining diverse aspects of taxonomic, morphological, genetic, and chemical variation across vast temporal and spatial scales, they can help diverse scientists bridge the gaps between traditional disciplines. In places where this situation is not yet in place the way to get there would be to enable ready access to both collections and research facilities, an effort that has been highly successful, for example, under the European SYNTHESYS Access scheme for the last decade. The K-12 education project "Exploring California Biodiversity" at the University of California, Berkeley (http://gk12calbio.berkeley.edu; *Mitchell & Gillespie, 2007*), which takes grade school students and teachers into the field, provides an excellent example of natural history museum collections broadening access and opportunities for education. Efforts such as AIM-UP! combined the expertise of educators, curators, collection managers, database managers, and others in undergraduate education (*Cook et al., 2016*; *Lacey et al., 2017*).

In terms of public perception of natural history museums, it is important to safeguard their role in society and justify long-term funding by continuing outreach and engaging the general public by proper messaging, for instance by initiating citizen science projects. In some sectors of the US it is still clear that the public misunderstands the mission of museums and does not appreciate the need for continued responsible collecting. One recent example is the unwarranted overreaction against scientific collecting of a bird specimen from the Solomon Islands, information about which was placed on the web by well-meaning media directors at the American Museum of Natural History (*Johnson, 2018*). This sad event, which resulted in death threats and cyber-

harassment of the scientist involved, shows that many people see only the destructive, indeed amoral, aspects of collecting of individual specimens, and do not connect this act with the many beneficial services of museums to science and society. Additionally, the public in this case did not appreciate the relative insignificance of scientific collecting as an agent of species loss as compared with habitat loss and introduced or feral predators, such as house cats. In this case, the public seemed to place undue emphasis on the loss of life incurred by collection of a single bird, suggesting much more relevance of an emotional response rather than a scientific appraisal of the true impact of collecting data on species biology. Clearly, museum curators and scientists need to join forces in working proactively with the public to increase their awareness of, and appreciation for, the practice of rigorous biological sampling.

Collecting for the future: integrated analysis of museum specimens for evolutionary biology

Museums need room to grow in targeted ways that will allow us to address scientific issues critical to looming societal issues such as emerging pathogens and food security (*Morrison et al., 2017*; *Schindel & Cook, 2018*) (see Box 2). Specimen-based field work should aim to preserve extensive sets of natural history material at a particular time and place that would represent multiple individuals of each species, multiple species per collecting locale, and multiple diverse aspects of individual specimens. For example, collection of mammals and their associated ectoparasites and digestive tracts has led to detailed understanding of co-evolution of hosts and parasites (*Cook et al,. 2017*) and can fuel future studies of the role of the microbiome in such processes (*Roggenbuck et al., 2014, Greiman et al., 2018*). Such holistic collection events can better capture the complex interactions of biotic communities and, if repeated, over time could

provide key insights into changing conditions. Discussions should be held that address how we can best leverage collecting activities across the Global Museum and that planning should lead to a global effort to more rigorously inventory biodiversity.

Genomics is a key source of information and rapidly changing area in which the scope and potential of future applications are particularly promising. Nonetheless, there are several factors known to limit the utility of specimens for genomic analyses. For example, using 'methylated spirit' (methanol containing alcohol) instead of pure alcohol for field preservation of animal tissue can severely hamper retrieval of usable DNA later on (*Post & al., 1998*) (see Box 1). Heat treatment of plants, as typically applied in most historic herbarium collections, was found to lower genomic copy numbers but not cause significant miscoding lesions (*Bakker, 2015*; *Staats et al., 2011*). Conventional x-rays (as opposed to x-ray computed tomography with digital imaging) of mummies and bone or using pesticides on insect collections all negatively affect or destroy DNA (*Gotherstrom et al., 1995*). Use of formalin to preserve specimens limits extraction of usable DNA from both animal or plant tissues as it causes cross-links among DNA molecules, preventing PCR (*Ruane and Christopher, 2017*; *McGuire et al., 2018*).

For historic samples, significant progress in securing biopolymers has been made and museum and ancient genomics has attracted considerable interest, from researchers and industry (*Hofreiter & al., 2015*; *Lindqvist & Rajora, 2019*). Still, although some DNA sequencing technologies work well with degraded DNA, such as in herbarium DNA using Illumina sequencing (*Staats & al., 2013*; *Bakker et al., 2016*; *Hart et al., 2016*), single-molecule, '3rd generation', genome sequencing will never be applicable for most museum-preserved specimens given the fragmented nature of their DNA. In contrast, for cryo-specimens preserved in liquid nitrogen in tissue banks, 3rd generation sequencing may well be highly successful. But even here,

593 some of us have noted poor DNA retrieval from tissues collected with standard field-protocols
594 and ultimately preserved cryogenically (S. Edwards, pers. obs.). For birds, best practices for
595 genome sequencing may not include freezing in the short term, which can fragment DNA, but
596 rather unfrozen archiving of blood, which will preserve the longest DNA fragments. On the
597 other hand, whether or not EDTA or 95% EtOH was used for DNA sample storage can be
598 important too for successful long read sequencing (MI, pers. obs.).

599 'Re-sequencing', i.e. sequencing and mapping reads against a related reference genome
600 sequence, has been successful in museum plants, fungi and insects (*Bi et al., 2014*; *Staats et al.,*
601 *2013*). For organisms with relatively small genome sizes, such as birds the price for re-
602 sequencing a genome from a study skin has become so low that curators of bird collections may
603 consider to actually requiring complete genome sequencing for tissue from old museum samples.
604 In this case, all parties ideally would benefit, the user for having access to the specimen, the
605 museum for putting a halt to further specimen deterioration (as the genome sequence has been
606 generated), and the next user for have both specimen and genome sequence available. That said,
607 it is difficult to predict how DNA extraction techniques may evolve, and perhaps require
608 considerably lower tissue amounts to produce higher DNA yields, meaning that high-throughput
609 DNA extraction without an immediate use (DNA banking) is not an obvious choice for
610 museums.

611 Often scientists endeavour to see inside museum specimens. Previous approaches such as
612 dissection or histology are invasive techniques that necessarily result in the destruction of other
613 data. Although recent imaging techniques (diceCT; *Gignac et al., 2016*) enable largely non-
614 destructive work on these questions in non-model organisms preserved in alcohol, they do not
615 completely ameliorate data loss due to selectivity in field materials preserved. Specimen field

616 preparations may include freezing fresh tissue for DNA, preserving skeletons and skins but
617 removing most internal organs and muscles. The latter obviously limits the kinds and diversity of
618 research that can ultimately be performed on such specimens. For example, the vocal organ of
619 birds was often not collected in birds despite the perceived importance of bird song and other
620 vocalization. Some now broadly used imaging techniques (e.g. diceCT) have not been studied
621 for their effects on DNA/RNA amplification from formalin or alcohol-preserved specimens, and
622 it is unknown if they further inhibit downstream molecular work involving these specimens.

623 For most large multicellular organisms, it is challenging to collect large numbers of tissues.
624 However, more portions of an organism can be feasibly preserved before discarding tissues
625 when making new collections, particularly of common, easily accessed species. For example, at
626 the Museum of Comparative Zoology at Harvard University, a typical avian specimen is now
627 accompanied by 7-10 cryovials filled with DNA- and RNA-ready tissues from different organs,
628 as well as at least one tube of unfrozen but refrigerated blood for genome sequencing. Such
629 sampling will no doubt pose space challenges for long-term storage (which could be partially
630 solved through the use of space-efficient biobanks), but is essential for a deep understanding of
631 the effects of anthropogenic change on biodiversity (*Schmitt et al., 2018*). Integrating new
632 imaging techniques into museum work flows will increase documentation prior to destruction
633 (e.g. for genomic work). For instance, the Thermal Age Web Tool (http://thermal-age.eu/) was
634 developed to help collections managers and users to quantify the risks associated with
635 destructive analysis of specimens, based on calculated 'thermal ages' (*Smith et al., 2003*). The
636 Synthesis of Systematic Resources programme (see http://www.synthesys.info/joint-research-
637 activities/) provides further recommendations for non-destructive sampling of museum
638 specimens and decision analysis as to how to best sample specimens for genomic research.

639 Lower price points for acquisition of genome data and some imagining techniques makes
640 defining these best practices more urgent.

641

642 **Conclusions**

643 For hundreds of years, natural history museums around the world have provided the general
644 public and scientists with numerous opportunities to learn more about our natural world. Taken
645 together, this 'Global Museum' must be seen as one of the most valuable assets of modern
646 society and culture, providing the material to address challenges facing humanity today – such as
647 baseline information against which to test hypotheses of local and global environmental change –
648 and a critical regional cultural touchstone for the public. Natural history museums can function
649 as inter-disciplinary meeting places, or *innovation incubators*, where questions are addressed that
650 we did not consider asking before. The core of these institutions are the specimens. To maximise
651 their use, it is therefore imperative to carefully consider how to best sample, preserve, handle,
652 and store specimens in ways that not only meet today's demands but also new, unforeseen needs.
653 Viewing natural history museums as critical infrastructure for scientific inquiry and public
654 understanding may help raise their profile and awareness, facilitating continued support.

655 Despite their immense value, natural history museums are facing grand challenges. Taxonomic
656 expertise is decreasing for many organism groups or is not represented in the curation of some
657 collections. Funding often relies on public sources and may be adversely affected by political
658 and socio-economic changes, comprising the long-term continuity of a museum's activities. New
659 international regulations on the collection, export and use of specimens for non-commercial and
660 commercial purposes are now increasing administrative burdens and may prevent further

development of collections. Cross-institutional, international coordination of secure data standards has not yet been fully realised. We urge scientists, citizens, and policy-makers to give natural history museums the proper recognition they deserve as data archives, innovation hubs, and *Academic Nexūs of Integration*.

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682

683 **Figure legends**

684 Figure 1. The centrality of natural history collections to evolutionary biology and public
685 understanding. Users, contributors and stakeholders of natural history collections are indicated;
686 yellow arrows represent data flow, green arrows the flow of specimens.

687

688 Figure 2. Natural history museum specimens drive the cycle between inspiration and innovation,
689 which spans across exhibitions and collections.

690

691 Figure 3. Word cloud illustrating relative abundance of topics and themes covered in this study.

692

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Table 1 (on next page)

Main global and local aggregators of biodiversity data.

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Table 1. Main global and local aggregators of biodiversity data.

Acronym	Mission	Funding; scope	Type of data	Volume of records (M)
ADBC	Advancing Digitization of Biodiversity Collections	US		
ALA	Atlas of Living Australia. https://www.ala.org.au/	Australia	Observations, specimens	84.8
BOLD	Barcode of Life Database	Canada; global		6.8
DiSSCo	Distributed System of Scientific Collections; digitization and databasing of european specimen collections	Europe	Specimens	1500
eBird	Citizen science: the world largest biodiversity-related citizen science project, gathering information on bird sightings, archive it, and "freely share it to power new data-driven approaches to science, conservation and education." https://ebird.org/home	Global	Observations	100 'yearly'
EOL	Encyclopedia of Life; Global access to knowledge about life on Earth	Australia, Egypt, US; global	Species descriptions	<1,9
GBIF	Global Biodiversity Information Facility	Global	Observations, specimens	1300

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GGBN	Global Genome Biodiversity Network	Global	DNA, tissues, environmental samples	3.8
GloBI	Global Biotic Interactions; species interaction data by combining existing open datasets. https://www.globalbioticinteractions.org/	US; global	Species interaction data e.g., predator-prey, pollinator-plant, pathogen-host, parasite-host	>0.7
HOLOS	Berkeley Ecoinformatics Engine: accessing and visualizing integrated biological and environmental datasets to address questions of global change biology. https://holos.berkeley.edu/	US; global	Different kinds of biological and environmental datasets	n.a.
iBOL	International Barcode of Life; extending BOLD's coverage. iBOL's forthcoming BIOSCAN will activate a biomonitoring system for half the world's ecoregions, metabarcoding assemblages and studying species interactions from 2,500 sites. iBOL.org	Canada; global	DNA barcodes and metadata	see BOLD
IDEA	Island Digital Ecosystem Avatar; place-based systems ecology for building simulations of social-ecological systems	US; Moorea	Specimens, observations	?

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iDigBio	Integrated Digitized Biocollections; digitisation and databasing of US specimen collections	US	Specimens	117.5
iNaturalist	Citizen science: one of the world's most popular nature apps, sharing observations globally; https://www.inaturalist.org/	US; global	Observations	<1
LifeWatch	Biodiversity research, -management and -conservation priority setting	Europe	Research tools	n.a.
iSpot	Citizen science: experts helping citizen community to identify its wildlife observations. https://www.ispotnature.org/	UK; global	Species identifications	0.030
MoL	Map of Life; providing species range and dynamics information and species lists for any geographic area. https://mol.org/	Global	Occurrences, observations	8.8
NCBI	National Center for Biotechnology Information	Global	Nucleotide and amino acid sequences; genome annotations	0.37 species covered
NEON	National Ecological Observatory Network; continental-scale environmental data, infrastructure for research, educational tools to work with large data. https://www.neonscience.org/	US	Observations	?

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OToL	Open Tree of Life; construct a comprehensive, dynamic and digitally-available tree of life by synthesizing published phylogenetic trees along with taxonomic data. https://tree.opentreeoflife.org/	US; global	Phylogenetic trees and taxonomies	2.6 OTU's in taxonomy
Traitbase	Ecological species characteristics, individual level species information. https://traitbase.info/whatis	Spain; global	Specific characteristics e.g. body size, diet or fecundity	?

2

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Table 2 (on next page)

Specimens and best curation practices for the future.

Table 2. Specimens and best curation practices for the future.

Collecting. Recommendations for best preservation techniques for new specimens during field collection are as important as the final storage conditions for improving specimen long-term utility for genomics (*Matos-Maraví et al., 2019*). Documenting treatment practices is also key to facilitating future analyses enabled by as yet undiscovered technologies. The plethora of technological uses of museum specimens calls for a re-evaluation of how specimens are preserved. For centuries, plants have been pressed, animals mounted, marine specimens ethanol- or formalin-fixed and fungi dried. Although these standard preservation methods should still continue, if only because they constitute the bulk of biological collections thus far and have a proven track record of fostering discovery, whenever possible researchers should try to sample additional types of specimen parts, and organs and meta-data.

Storing. More studies need to be undertaken to improve relevant protocols for the long-term storage of specimens and tissues. Like digitization, banking of genetic resources by museums is an area of rapid innovation, particularly as next-generation sequencing methods have become more common. As museum tissue collections are accessed more frequently for genome projects, it has also become clear that the preservation standards and types of tissues preserved in museums are often inadequate for supporting the genomics enterprise. For example, a typical museum tissue sample from a bird, even if frozen in nitrogen hours after sacrifice in the field, yields DNA qualities and lengths unsuitable for 3rd generation long-read sequencing platforms such as PacBio and Oxford Nanopore. Such technologies rely on the use of long DNA fragments to start with, requiring specimen tissues be frozen immediately (within > 10-15 minutes) upon collection. Although it may be difficult to use liquid nitrogen in the field, one solution is to use so called Dry Shippers, which are dewars designed for safe transportation of tissues at the same

24 temperature as liquid nitrogen but without actually containing any free liquid nitrogen. Such
25 shippers are routinely allowed for transportation back to the lab by airlines and can often hold
26 cold temperatures for ~3 weeks. Innovations in cryogenics are likely to transform collecting of
27 genomic resources by museums in the future. Still, we can take comfort that even from dried,
28 centuries-old traditional specimens, valuable genetic information can readily be obtained by
29 hybrid-capture and other approaches (*Bi et al., 2013*; *Staats et al., 2013*).

30 At the same time, some genome sequencing strategies may alleviate the use of unwieldy
31 cryogenic methods altogether, at least for accessing DNA. What seems to be most important is
32 that DNA (and RNA) degradation is stopped as fast as possible after collection. For example, for
33 birds, one way to achieve long DNA fragments for next-generation sequencing is to use unfrozen
34 blood stored in Queen's lysis buffer, which has been used by ornithologists for decades and takes
35 advantage of birds' nucleated red blood cells. Blood stored in this way, with minimal shaking
36 that will cause shearing, is a reliable source of high molecular weight DNA and has been shown
37 to yield better genome assemblies than DNA retrieved from museum-grade frozen tissues (S.
38 Edwards, G. Bravo, pers. obs). An alternative could be to store collections in the field in DMSO,
39 although this appears to prevent RNA sequencing (Irestedt, unp. data). Such best-practices for
40 fieldwork and storage of genetic resources needs to be shared more widely and rapidly among
41 the museum community. A useful platform for identifying both repositories and tissues for a
42 wide range of taxa, often called biobanks, is provided by the Global Genomic Biodiversity
43 Network mentioned above (GGBN see http://www.ggbn.org/ggbn_portal/). Below we outline
44 various updates in storage of genetic resources for both animals and plants, highlighting issues
45 facing museum curators and collection managers looking at the future:

Transcriptomics and Epigenomics. The ever-increasing number of genome sequences becoming available can be efficiently explored in terms of gene function through transcriptomics - the sequencing of all transcribed mRNA expressed at a certain time, physiological or developmental state for a particular tissue. In this way, the 1Kite (http://www.1kite.org/) and 1kp (https://sites.google.com/a/ualberta.ca/onekp/) projects, assembling 1000 transcriptomes of insects and plants, respectively, have expedited progress in both comparative and functional genomics and a better understanding of gene function across these clades (see for instance *Gitzendanner & al., 2018*). We would expect future specimens to play an increasing role in this respect, but only if we make sure to store our specimens in such a way that RNA is preserved, for instance by rapid cryogenic storage of use of RNA-friendly buffers like RNA-later. Additionally, a diversity of epigenomics approaches, such as methylation, Chip-seq and ATAC-seq, are emerging and potentially of great use to the field of evolutionary biology (*Grayson et al., 2017*). Epigenomics is already commonly applied in evolutionary studies of adaptation and development, and has recently made headway in examining epigenetic maps of extinct human and plant populations (*Llamas et al., 2012*; *Gokhman et al., 2014*; *Smith et al., 2014*; *2015*). Best practices for preservation of biomaterials for epigenetics has not yet been discussed in the literature, and will be an important additional consideration for museum curators in the future.

Proteomics. Given future technological developments, it is likely that proteomes will be determined and used for further functional studies across the Tree of Life. Additionally, collagen from bone tissues have been demonstrated to give species-level amino acid variation from specimens several millions of years old using a ZooMS approach (*Welker et al., 2015*). *Portugal et al. (2010)* report on proteomics in museum egg specimens and conclude that current approaches to proteomics in such specimens may be limited in coverage of the proteome. In any

case, storing tissues in the best possible ways for proteomics, ideally, cryogenically in order to stop proteases from working, now ensures that such analyses can be conducted in the near future.

Secondary metabolites. Compounds such as alkaloids, glucosinolates, furanocoumarins, flavonoids or terpenes can be measured in museums tissues, especially from plants (*Berenbaum & Zan 1998*; *Colegate & al., 2014*; *Mithen et al., 2010*; *Raffauf & Von Reis Altschul, 1968*). Access to such metabolites enables testing historic biological hypotheses such as past responses to change in herbivores and climate; but also in case of invasive species and testing what secondary compounds may have driven invasive success in species such as *Vincetoxicum nigrum* (Asclepiadaceae) (*Liede-Schuman & al., 2016*).

Stable isotopes. Advancement of techniques for studying specimens include measuring of stable isotopes, allowing monitoring environmental/atmospheric changes over time, given a time series of museum specimens (reviewed in *Schmitt et al., 2018*). Because elements are not expected to degrade over time like biopolymers do, proper specimen storage conditions for isotope analysis is probably not critical. Limiting factors in such studies now is the availability of robust spatial sampling and time series of specimens for analysis. Properly tracking the vast quantities of data that are generated in these analyses directly to the specimens is also a challenge (*Pauli et al., 2017*).

Non-standard tissues. Classical botanical specimens comprise branches with leaves and fertile organs (flowers, fruits). For some vertebrates, such as birds and mammals, it is primarily the external morphology that is preserved in collections, whereas for amphibians, reptiles and fish, preservation in formalin and/or alcohol can yield DNA sequences with some effort (*Ruane et al., 2017*; *McGuire et al., 2018*). Many biobanks, particularly in US museums, now also include samples of frozen blood and tissue from vertebrates, typically heart, liver and muscle. However,

many other parts of organisms not conventionally stored in museums are becoming important in the effort to monitor global change. For instance, there is great interest among diverse scientists in investigating the microbiome of species - including the bacteria present in the digestive system, and what roles they may have to the species' adaptations to the local environments (*Roggenbuck et al., 2014*; *Alvisatos et al., 2015*; *Ingala et al., 2018*). Similarly, tree bark may provide important information on chemical defenses of plants and hold implications for medical applications (*Maldonado et al., 2016*). Transcriptome studies in vertebrates are becoming increasingly common as a means to study species' ability to adapt to changing environments and anthropogenic change (e.g., *Zhang et al., 2014*) and are widely used in phylogenomics of invertebrates and plants (*Wen et al., 2015*). Such studies encourage careful sampling and preservation of whole organisms or all organs separately when appropriate.

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Table 3 (on next page)

Specimens and Pathogens.

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Table 3. Specimens and Pathogens.

Museum collections have provided fundamental infrastructure for identifying and mitigating emerging pathogens and zoonotic diseases by public health agencies (*Dunnum et al., 2017*) such as the Centers for Disease Control (CDC). When a new pathogen emerged in 1993 in the southwestern United States, rapidly killing 7 people, authorities needed to know: had this pathogen accidently been released into the wild, or was it a newly evolved pathogen, or had the virus always been present and simply not previously identified? Without the availability of specimen archives, scientists would not have been able to efficiently determine the pathogen source and answer these fundamental questions. Large tissue archives from the Museum of Southwestern Biology and other museums (*Yates et al., 2002*) enabled virologists to quickly identify that this previously unknown zoonotic hantavirus pathogen was hosted by the locally common deer mouse (*Peromyscus maniculatus*). This virus is apparently transmitted to humans through inhalation of viral infected feces. Subsequent emergence of other human cases elsewhere in the Americas (e.g., Chile, Argentina, Panama), but with higher mortality, mobilized other specimen-based research efforts that identified other new strains of hantaviruses in many rodent species over the next 2 decades and on multiple continents. More recently, museum specimens of other groups of mammals were screened, leading to a radically reshaped understanding of hantavirus evolution, ecology and host occurrence (*Yanagihara et al., 2015*). Not only were more rodent host species for these viruses identified, but numerous species of shrews, moles, and bat species worldwide also harbor their own hantaviruses. These specimens originated from multiple continents and the new discoveries significantly expand the potential risk to humanity of these pathogens and increase the burden on public health systems worldwide.

Other examples of pathogen outbreaks have examined historical progression of diseases often decades or centuries after the outbreak (*Schmitt et al., 2018*). The impact of an invasive bacterial pathogen from poultry on native songbirds has been studied using avian tissue samples collected just prior to the outbreak in the eastern US, albeit without any foreknowledge of the impending epizootic (*Hess et al., 2007*; *Shultz et al., 2016*). The Norwegian fish fauna is well documented in the scientific collection of the Natural History Museum, University of Oslo and collection material was screened for monogenean ectoparasitic flatworms of the genus *Gyrodactylus* that were (unintendedly) collected along with the fish (*Zeyl et al.* 2012). This yielded 13 flatworm species that are new to science, and an additional seven parasite species new to Norway. Three *Gyrodactylus* species were also recorded from new fish hosts, and in particular *G. pterygialis* appeared to have a broad range of host species, helping fishery biologists tremendously in understanding and managing fish populations. From plants, *Yoshida et al. (2014; 2015)* used potato herbarium in order to determine the genotype of the *Phytophtera infestans* strain that caused the great Irish potato famine in the 19th century (and concluded it was a 'one-off' type, never seen again). Herbarium DNA was also crucial in discovering ancient alleles in the grass *Alopecurus myosuroides* that are relevant to herbicide resistance but pre-dating human influence (*Délye et al., 2013*). Studies using genomic data of a 5,310-year-old maize cob (*Ramos-Madrigal et al., 2016*) have shown that our understanding of the process of domestication and early selection pressures needs adjusting.

Table 4(on next page)

Citizen Science.

Citizen Science ‘Man-spread molluscs’ project: *send in the slugs from your garden to the museum for identification*.

Table 4. Citizen Science 'Man-spread molluscs' project: *send in the slugs from your garden to the museum for identification*.

Since 1986 the Gothenburg Natural History Museum (GNM) has offered a slug-identification service to the public. The project was initiated as the invasive Spanish slug (*Arion vulgaris* Moquin-Tandon) began to spread rapidly over the country, prompting the need to establish a way to follow the spread and the colonisation process. As the slug spreads passively, mainly by the trade with ornamental plants and also with garden soil, it easily establishes in residential areas, where it mass-propagates and causes severe damage to vegetables and plants. A proper determination of these species requires dissection, a service offered by GNM. The project was advertised on TV, radio, in the newspapers and on museum web pages and GNM even offered to send out a transportation box which could easily be returned by mail. The response from the public was immense, and up to today GNM has received > 6000 samples with slugs from all over the country. Together with the box, GNM sent out a questionnaire asking information about first year of occurrence, possible way of introduction etc. After determination of the specimens the senders got information of species identity, and in case *A. vulgaris* was concerned also advice for control measurements. Hence the project has been beneficial for both the gardeners and the museum. The colonisation process could be followed in detail and much information on the biology and behaviour of the species, as well as on the garden fauna of snails and slugs, was obtained. The latter included several other invasive species, from different parts of the country, and the development of this fauna over more than four decades could be monitored both geographically and chronologically. Furthermore, as at least one specimen from each species in the samples was preserved inEtOH, extensive material is available for DNA analysis, which has

proved highly useful as the taxonomy of the Spanish slugs is complicated, involving hybridisation with other native and introduced species (*von Proschwitz, 1997*).

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Figure 1(on next page)

The centrality of natural history collections to evolutionary biology and public understanding.

Users, contributors and stakeholders of natural history collections are indicated; yellow arrows represent data flow, green arrows the flow of specimens.

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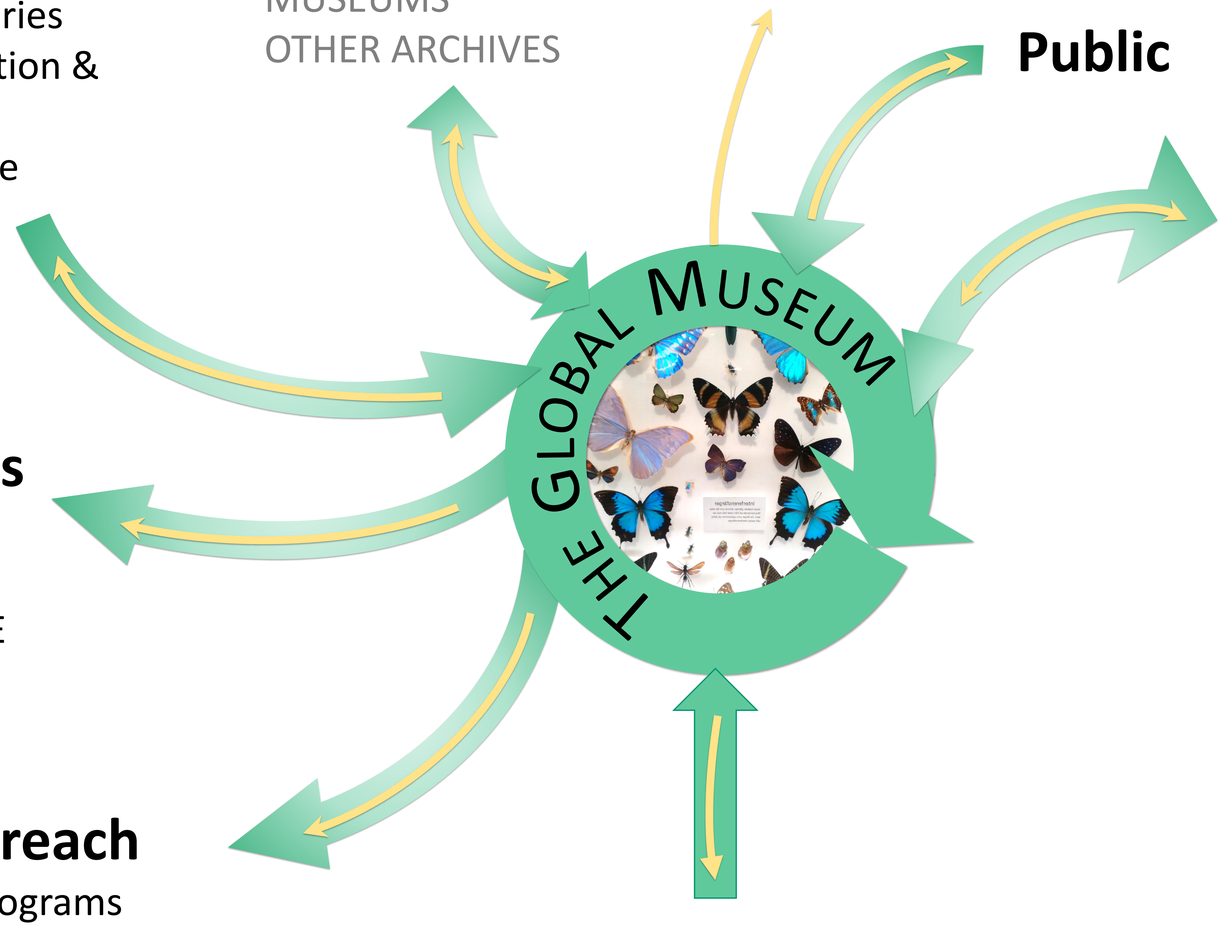
Sample providers

- Biodiversity Inventories
- Pathogen Identification & Monitoring
- Government Wildlife Agencies

UNIVERSITIES
MUSEUMS
OTHER ARCHIVES

WEBTOOLS
DATABASES

Public



Science

Conservation Biology

Population Status & Structure, Abundance, Bottlenecks, Invasives

Ecology

Distribution, Migration, Food Webs, Dispersal, Invasives, Stable Isotopes

Emerging Pathogen Detection

Identification, Monitoring
Host Switching, Range Expansion

Evolution

Response to Climate Change, Genome Evolution, Hybridization, Demography

Policy initiatives

- CITES
- CAFF
- NET-BIOME

Educational outreach

- Exhibits, Tours and Programs
- Curricula and Material for University Courses
- Web-accessible Biodiversity Data
- Internships (Field & Museum)

Teaching & Research

- Spatial and Temporal Perspectives
- Environmental Change
- Evolutionary Genomics
- Health and Economic Dimensions
- Systematics & Population Biology

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Figure 2(on next page)

Natural history museum specimens.

Natural history museum specimens drive the cycle between inspiration and innovation, which spans across exhibitions and collections.

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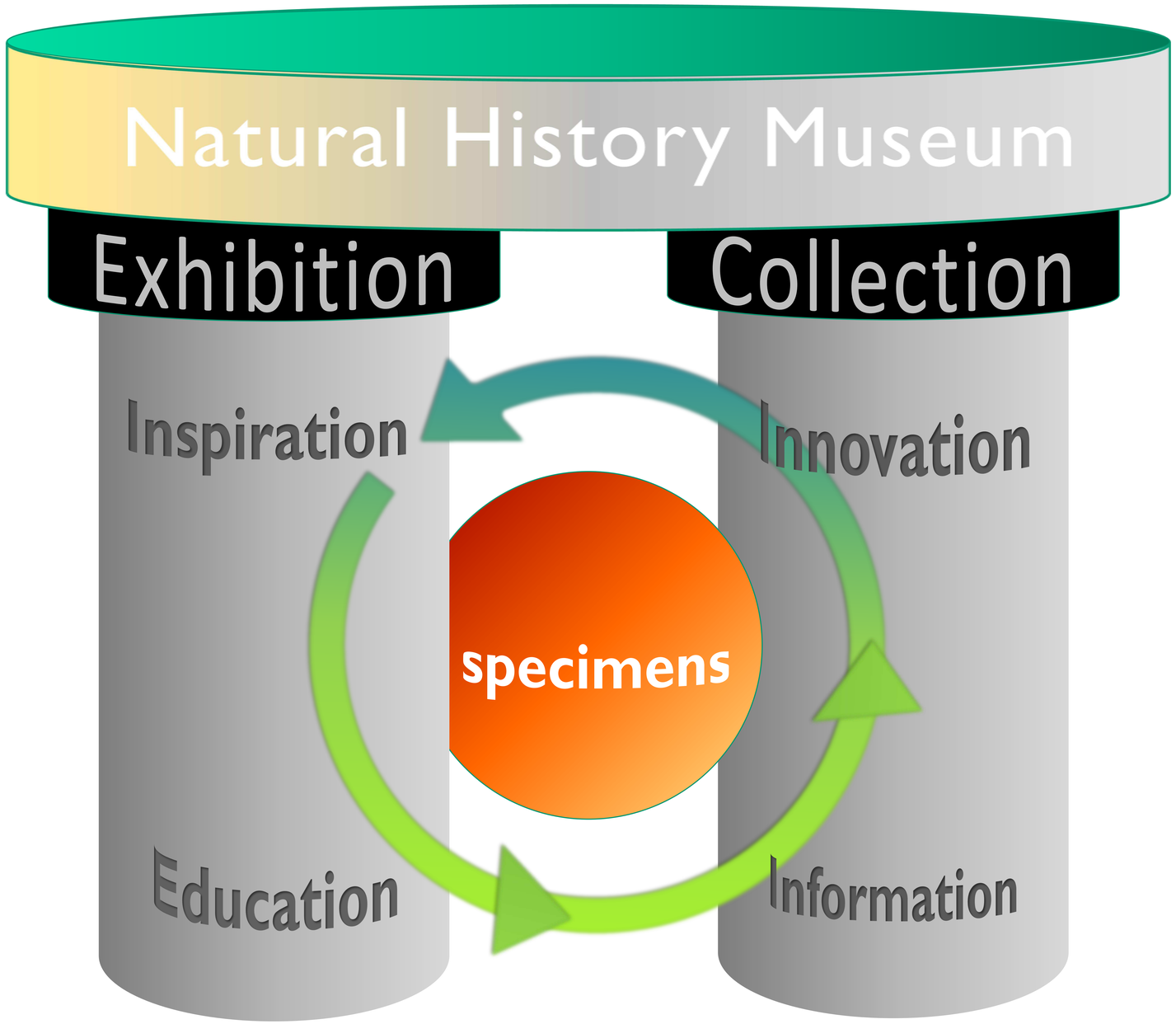

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Figure 3(on next page)

Relative abundance of topics and themes.

Word cloud illustrating relative abundance of topics and themes covered in this study.

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