

1 **Digitization and the future of natural history collections**

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22

23 **Abstract**

24 Natural history collections (NHCs) are the foundation of historical baselines for assessing
25 anthropogenic impacts on biodiversity. Along these lines, the online mobilization of
26 specimens via digitization—the conversion of specimen data into accessible digital
27 content—has greatly expanded the use of NHC collections across a diversity of
28 disciplines. We broaden the current vision of digitization (Digitization 1.0)—whereby
29 specimens are digitized within NHCs—to include new approaches that rely on digitized
30 products rather than the physical specimen (Digitization 2.0). Digitization 2.0 builds upon
31 the data, workflows, and infrastructure produced by Digitization 1.0 to create digital-only
32 workflows that facilitate digitization, curation, and data linkages, thus returning value to
33 physical specimens by creating new layers of annotation, empowering a global
34 community, and developing automated approaches to advance biodiversity discovery and
35 conservation. These efforts will transform large-scale biodiversity assessments to address
36 fundamental questions including those pertaining to critical modern issues of global
37 change.

38 **I. The relevance and importance of digitization**

39 Anthropogenic impacts, including urbanization, globalization, and climate change, are
40 rapidly transforming our world. Despite our best efforts, however, quantifying the biotic
41 impacts of human activity has been challenging, as evidenced by the difficulty of
42 delimiting the onset of the Anthropocene (Lewis and Maslin 2015). Part of this
43 uncertainty stems from a lack of historical data that track biotic change over time.
44 However, natural history collections (NHCs), with their broad taxonomic, geographic,
45 and temporal scope, offer a key solution to this impasse. In the past twenty years, there
46 has been a dramatic increase in the use of NHCs for assessing a wide variety of scientific
47 questions (Suarez and Tsutsui 2004, Pyke and Ehrlich 2010, Park and Potter 2015,
48 Meineke et al. 2018, 2019). Indeed, they have emerged as one of the best resources for
49 establishing biological baselines to understand the impacts of, for example, the origins of
50 agriculture, the industrial revolution, the development of nuclear armaments, and more
51 generally the influence and acceleration of anthropogenic change on biodiversity (Moritz
52 et al. 2008, Johnson et al. 2011, Lister 2011, Funk 2018, Nelson and Ellis 2018).

53
54 Most large NHCs provide specimen data to researchers and the public by mobilizing
55 searchable collection databases online. We assert that these mobilized collections are
56 among the most important advances in museum curation in the past century, significantly
57 opening access to NHCs and greatly stimulating large-scale analyses that span novel
58 academic and societal enterprises. These resources are connecting diverse scholarly
59 domains, propelling a new generation of scientists forward, and removing financial,
60 sociological, institutional, and academic obstacles preventing access to these materials

61 (Drew et al. 2017, Sweeney et al. 2018). In short, digitizing a specimen–translating
62 metadata associated with a physical specimen object into flexible digital data formats–
63 increases the value of the physical specimen exponentially.

64

65 Here, we present an ambitious, two-pronged vision for digitization, which we term
66 Digitization 1.0 and Digitization 2.0. Digitization 1.0 represents the ongoing push to
67 create digital images and related content directly from physical voucher specimens;
68 Digitization 2.0, in contrast, relates exclusively to data gathering, tasks, or workflows
69 derived from digitized products of Digitization 1.0 rather than from the physical
70 specimens themselves (figure 1). In addition to the vast expansion and online aggregation
71 of these mobilized collections to create a truly global digital NHC, Digitization 2.0 offers
72 the promise of also shifting and growing the workforce and public who interface with
73 these objects to accelerate the progress of digitization.

74

75 **II. Digitization 1.0: The Past, Present, and Future**

76 Digitization of NHCs began with the overarching goal of documenting specimen
77 inventory and facilitating research by transcribing label information into centralized,
78 searchable databases as described recently by Nelson and Ellis (2018). These efforts have
79 given rise to Digitization 1.0, which has been widely embraced and continues to be
80 infused with innovation. Digital representations generated through Digitization 1.0
81 include specimen images and direct transcriptions of specimen metadata from
82 handwritten or printed collection catalogs or labels, including for example details on
83 coloration or measurements. As part of this effort, NHCs have generated millions of

84 digital representations of physical vouchers and have devised numerous technological
85 innovations to facilitate efficient data generation, including conveyor belt and robotic
86 imaging techniques for mass digitization of specimens (Tegelberg et al. 2014, Sweeney et
87 al. 2018). More recent next generation technologies, including photogrammetry, laser-
88 scanning, and computed tomography, create far richer digital representations of
89 specimens than can be visualized by eye or with standard microscopy (figure 2). Given
90 that large portions of most NHCs still remain unavailable in digital format, the
91 innovations and efforts within Digitization 1.0 will continue well into the future, likely
92 for decades. In the subsections below, we outline Digitization 1.0 through the lens of
93 digitization workflows, strategic prioritization, and solutions to impediments.

94

95 ***Digitization workflows and linking data***—The practice of digitization is broadly
96 consistent among projects and organismal groups, in so much as each specimen is
97 represented by textual metadata from labels or catalogs and typically digital two-
98 dimensional images, but increasingly also three-dimensional representations and audio or
99 video recordings where relevant. There exists great variation in specimen size, storage
100 conditions (e.g., fluid-preserved, microscope slides, dry storage), dimensionality (2D
101 versus 3D representation), and detail associated with specimens, not to mention widely
102 varying practices in specimen collection and curation across taxonomic domains and
103 institutions. This heterogeneity of collections and institutional policies and priorities thus
104 creates challenges to efficient mass imaging and gathering of metadata. However, at
105 minimum, digitization workflows should attempt to integrate all available specimen
106 metadata into digitization efforts and appropriately link these data to their associated

107 physical voucher specimens. Beyond traditional linkages, non-traditional metadata
108 associated with the specimen include biotic (e.g., mass) and abiotic data (e.g., climate),
109 media (e.g., video and audio recordings), community- and population-level metadata
110 (e.g., abundance), species observations in the field, and genetic samples (i.e., the
111 “extended specimen” *sensu* Webster 2017). Much of these digital data are served in part
112 or in their entirety via online collection databases (e.g., Arctos, Specify, Symbiota, EMu)
113 or in data aggregators (e.g., iDigBio, Global Biodiversity Information Facility–GBIF,
114 Botanical Information and Ecology Network–BIEN). Linking voucher specimens to these
115 new data layers generated post collection is important and has been facilitated by
116 associating URLs, data accession numbers, digital object identifiers (DOI), or ARKs with
117 specimen records in collection databases. In addition, trait data can be incorporated into
118 specimen records using extensions to the Darwin Core Archives (Yost et al. 2018). For
119 the next generation of collections, protocols are under development to expand the
120 digitization workflow to the collecting event itself (Heberling and Issac 2018).

121

122 ***Developing digitization priorities***—Given the limited resources available to many NHCs,
123 it is necessary to establish priorities for specimen digitization. Specimens at risk of
124 degradation, such as rare or fragile fossils, and those representing rare or threatened
125 species and habitats are candidates for high priority digitization. Further, efforts should
126 focus on specimens with rich associated metadata from the collection event. A growing
127 number of species are imperiled, and conservation biologists are increasingly reliant on
128 NHCs for baseline data to understand species ranges and climatic tolerances for assessing
129 future changes (Lister 2011). Distributing information for these rare or threatened taxa to

130 conservation biologists is increasingly critical to these species' management and survival
131 (MacDougall et al. 1998, Nualart et al. 2017). Finally, taxa representing a breadth of
132 evolutionary history or unique adaptations are important for research on phenotypic
133 evolution, community ecology, and biologically inspired design. We suggest that such
134 specimens have high priority for digitization.

135

136 Owing to the varying effort required by different digitization strategies (e.g., label data,
137 images, 3D reconstructions), data types that serve the largest diversity of use cases should
138 also be prioritized. For instance, key information including taxon name, collection
139 locality, and date can be captured relatively efficiently and can facilitate assessments of
140 species distributions through time. Rapidly expanding areas of research including
141 phenology (e.g., Primack et al. 2004, Willis et al. 2017), large-scale taxonomic
142 inventories (e.g., Cardoso et al. 2017), and morphometric investigations (e.g., Hedrick et
143 al. 2015), rely on such label data and data from post-digitization enhancement (Sweeney
144 et al. 2018). For example, in one of the first studies to demonstrate how historic
145 specimens can be used to quantify the biotic effects of climate change, Primack et al.
146 (2004) used flowering plant specimens collected between 1885 and 2003 in the greater
147 Boston (USA) area to demonstrate that plants were flowering up to eight days earlier in
148 recent years than in the early years of the 20th century. The utility of such diverse data
149 (e.g., geographic location, flowering date, anatomical measurements) is important to a
150 wide array of researchers and should be prioritized. Additionally, we feel it is best to only
151 apply more complex, holistic digitization methods on a key subset of data-rich specimens
152 as has been recently demonstrated in the openVertebrate (oVert) Thematic Collection

153 Network (Blackburn et al., NSF Abstract #1701714). Increasing the magnitude of the
154 collection of media files (e.g., photogrammetry of bird skins, nuts, etc.) for this subset of
155 data via new pipelines and technological advances will be critical to this effort.

156

157 ***Past impediments and future solutions***—Despite the success of Digitization 1.0, this
158 initiative has identified three issues that must be addressed to maximize efficiency of
159 information retention and distribution. First, museums are obligated to manage, store, and
160 steward additional digital data associated with their physical collections. However, the
161 act of digitization entails significant challenges since it requires sustainably curating both
162 the physical objects and rapidly emerging digital datasets. This issue will necessitate the
163 development of new tools, that centralized aggregators assume increasing responsibility,
164 and will require increased funding in the near future (see Digitization 2.0 below).

165

166 Second, there is concern that large aggregators aimed at connecting researchers with
167 NHCs (e.g., GBIF, iDigBio) (Edwards 2004) remove NHCs from the attribution chain.
168 NHCs are frequently funded on their research relevance, which is determined both from
169 within and outside institutions. When researchers view specimen images or harvest
170 metadata from aggregators, NHCs that contribute these data often receive little to no
171 credit (Rouhan et al., 2017). A mechanism for referencing these source collections needs
172 to be embedded in the publication process that requires that NHCs be acknowledged and
173 notified when publications incorporate their data. A viable solution to this problem is to
174 mint a digital object identifier (DOI) for a digitized specimen and establish a reporting
175 mechanism for collections to be alerted when their specimens have been cited.

176 Automating this attribution pipeline as part of the digitization workflow better ensures
177 that NHCs receive credit for stewarding both voucher specimens and also digitized data,
178 which is likely to stimulate NHCs to embrace open-access policies for their data.

179

180 Third, digitized data are inconsistently and redundantly spread across multiple databases
181 at different scales. NHCs often have their own databases, but some data are additionally
182 deposited in regional databases, taxon-specific databases, and national and international
183 data aggregators. This data dispersion causes information to be input/archived
184 redundantly such that each database has a variant of the post-digitization metadata,
185 leading aggregators to archive either inconsistent or duplicated copies of the same
186 primary data. This problem can be partially circumvented by more communication
187 among data aggregators, as well as between NHCs and aggregators. Algorithms linking
188 specimen numbers between aggregators could ensure that post-digitization enhancement
189 metadata are transferred to all aggregators mentioning particular specimens by unique
190 identifiers such as the specimen-based occurrenceID. This is done internally at iDigBio
191 through the iDigBio Record API, which retains current and previous iterations of a
192 specimen's data.

193

194 **III. Digitization 2.0: charting a road map for the future**

195 Unlike Digitization 1.0, which directly utilizes the physical specimen, Digitization 2.0
196 instead utilizes the digitized product from Digitization 1.0 for generating additional data
197 and metadata (figure 1). Digitization 2.0 is powered by the online aggregation of these
198 resources and enables digitization to assume new forms and engage vast new workforces.

199 As we outline below, Digitization 2.0 is already well underway and holds tremendous
200 promise. It includes semi- or fully automated data recording from digitized specimens,
201 which stimulates research and returns value to the physical specimen. Additionally,
202 Digitization 2.0 entails a shift in the workforce engaged in collections science and
203 stewardship. Finally, Digitization 2.0 leverages NHC resources to create trait databases,
204 either from aggregating and better indexing existing metadata or by allowing researchers
205 or citizen scientists to associate trait annotations with images served from NHC
206 databases.

207

208 ***Innovative tools for automating digitization: machine learning and neural networks—***

209 Given the massive number of specimen images in digital databases with minimal data, an
210 important first step is to better automate data transcription to augment these skeletal
211 records. The enormity of this task is quickly becoming impossibly large for collections
212 staff to manage without automation, especially considering that funding for NHCs has
213 been decreasing (Thiers 2018). In recent years, machine learning applications utilizing
214 convolutional neural networks have achieved stunning levels of performance in computer
215 vision tasks including image detection and classification (Sudholt and Fink 2016). Neural
216 networks have previously demonstrated promising results for handwriting recognition
217 systems, which could easily be applied to automated label transcription. These forms of
218 innovative technology, which have been applied to medical diagnoses, speech
219 recognition, and driverless cars, are now permeating NHCs (Schuettpelz et al. 2017) and
220 are likely to be enormously useful when trained on existing databases of handwriting
221 samples (Krishnan et al. 2016), as well as those from transcribed labels generated through

222 Digitization 1.0. These models can be further trained using existing semantic field
223 constraints to much more effectively parse specimen metadata into appropriate database
224 fields. Beyond capturing essential minimal data records in an automated manner, neural
225 networks have recently been implemented to accomplish far more sophisticated tasks
226 than text transcription (Wilf et al. 2016, Schuettpelz et al. 2017, Funk 2018). Wilf et al.
227 (2016), for example, used computer vision to classify fossil leaf images based on leaf
228 shape and venation with high accuracy. This proved not only to be an efficient protocol
229 for classifying images, but also discovered previously unidentified morphological
230 landmarks potentially useful for species identification and for understanding important
231 evolutionary and ecological innovations not previously documented. The community is
232 now ready for deeper exploration of minimal metadata capture using semi- to total
233 automation.

234

235 Further, the declining number of taxonomists in the global workforce severely impacts
236 our ability to address key questions concerning biodiversity in the face of global change
237 (Hopkins and Freckleton 2002). Combining taxonomists' expertise (past and present)
238 with student and public training and increased automation will facilitate enhanced
239 specimen curation, and greatly enable biodiversity discovery. Continued robust support
240 for taxonomic research and training is essential. However, given the enormity of the task
241 at hand, and the limited time for this effort, we believe that addressing many taxonomic
242 problems of identification, particularly for well-known groups of organisms, could be
243 greatly facilitated by automation, such as has been demonstrated through Kurator (Dou et
244 al. 2012). Reasonably successful early efforts are underway to machine-learn and

245 automatically identify large sub-collections of insects (e.g., butterflies) (Schermer and
246 Hogeweg 2018). Although simple taxonomic identification may seem rudimentary, it is
247 the foundation of all biological research, and in many groups remains problematic. For
248 example, it is estimated that more than 50% of tropical plant specimens in NHCs are
249 incorrectly identified (Goodwin et al. 2015). Together with the training of more expert
250 taxonomists and organismal biologists, the widespread use of neural networks to identify
251 specimens and target groups that need attention would enhance collection utility for
252 research, teaching, and management and further motivate the discovery and description
253 of new species.

254

255 ***Expansion of the digitization workforce***—Expanding digitization to involve a global
256 workforce is now possible and is a major advancement of Digitization 2.0 and is
257 motivated by the increasingly global accessibility of NHCs. These new workforces can
258 be developed to supplement existing NHC staff, especially to include enhanced
259 digitization from the millions of images in databases that have limited associated
260 metadata. One obvious group to engage in this effort are citizen scientists. NHCs
261 associated with museums typically have departments devoted to public outreach, which
262 can easily be tapped for aid, helping collections staff with the task of digitization while
263 simultaneously providing the public with ownership and agency. Using citizen science in
264 this manner has been fruitful in numerous contexts including the transcriptions of label
265 data, georeferencing, and physical specimen annotations (Hill et al. 2012, Ballard et al.
266 2017, Ellwood et al. 2015, 2017). For example, *CrowdCurio—Thoreau’s Field Notes*, an
267 online crowdsourcing platform has successfully facilitated climate change studies from

268 thousands of herbarium specimens utilizing thousands of non-expert crowdsourcers
269 (Willis et al. 2017). Quality control is always a concern in large-scale citizen science
270 projects (Willis et al. 2017, Zhou et al. 2018) and thus an easy-to-use graphical user
271 interface clearly demonstrating to the public how and what to digitize will be necessary
272 (e.g., Notes for Nature), as has been accomplished in several research-based projects
273 (Chang and Alfaro 2016, Cooney et al. 2017, Willis et al. 2017). Increasingly, such
274 citizen science efforts are being supplemented by machine-based learning as well (Unger
275 et al. 2016, Wilf et al. 2016, Schuettpelz et al. 2017). For instance, crowdsourced data can
276 potentially provide reliable and rapid data for training and testing machine learning
277 models, creating a positive feedback loop propelling digitization forward.

278

279 ***Layers of trait annotations***—Traits of organisms are fundamental for documenting
280 biodiversity but also for understanding how organisms evolve and respond to changing
281 environments. Building on investments in creating digital NHCs, there is now increasing
282 demand for creating and associating new layers of trait data to these collections. For
283 some taxa, these biological data are already captured in the digitized text of a specimen
284 record (e.g., Darwin Core fields: “organismRemarks”). In mammals and birds, it is
285 common to have measurements on the mass and length of both the whole specimen and
286 parts of the specimen (e.g., testes length, wing length). The aggregation of traits from
287 both the initial collecting event and new annotations will stimulate a wealth of questions
288 and generate a better understanding of global biodiversity through the development of
289 standardized trait vocabularies (Kissling et al. 2018). For example, recently developed
290 data-processing tools for the data aggregator VertNet standardized more than 1.5 million

291 measurements for vertebrates using digital data from collections (Guralnick et al. 2016).
292 Users can now search those specimen records by mass and length, as well as download
293 harmonized trait data associated with individual specimens. The latter allows for new
294 explorations of trait variation within and across species, including spatial and temporal
295 patterns in traits associated with specimens that have collecting dates and georeferenced
296 localities (Riemer et a. 2018). By expanding this framework to annotate traits to
297 specimens and utilizing online platforms for even 3D representations of specimens,
298 NHCs can facilitate the capture of not only simple traits, ranging from specimen length to
299 the presence of a flower, but also more complex traits requiring more sophisticated
300 representation (e.g., virtual automated dissection of the vertebrate nervous system).

301

302 **IV. Concluding thoughts**

303 Digitization facilitates the democratizing of collections-based research and is essential to
304 establishing and evaluating biological baselines to assess the impacts of climate change,
305 land use changes, species invasions, and the current mass extinction. It allows for the
306 mining of specimen data in much the same way that we explore organismal genomes.
307 The key to further developing Digitization 1.0 and establishing Digitization 2.0 lies in
308 building upon what the research, funding, and policy communities have learned in the
309 several decades since the initiation of this endeavor. Data-rich NHC specimens are useful
310 and provide unique perspectives on the diversity and distribution of a given taxon.
311 However, if a specimen is not searchable, it will likely not be found or studied despite its
312 potential use. We are already witnessing the fruits of the synergy between Digitization
313 1.0 and 2.0. This will no doubt expand dramatically in the coming decades to involve

314 new domains, new questions, and new audiences that are not yet realized (or even
315 imagined). Only with creativity and improved techniques, including automated and semi-
316 automated methods, a better distributed digitization workload making use of new
317 technologies and workforces, and conscientious attention to the attribution chain, will
318 researchers be best able to track ongoing biodiversity change from all existing data.
319 Moreover, even as new technologies and digitization techniques emerge, we will need to
320 always return to physical specimens, in ways that are unimaginable now, to generate
321 novel data to better understand our changing planet. Although we stress the importance of
322 improved methods and practices for digitization, the active collection and continued
323 curation of physical specimens by expert biologists remains the central pillar supporting
324 advancements in evolutionary biology and conservation represented so importantly by
325 NHCs.

326

327 **Box 1: *Estimating the size and scale of a global digitization effort***– Digitization 1.0 has
328 resulted in the mobilization of millions of specimen records and has created the
329 momentum for a massive, global digitization effort. To better establish target goals and
330 evaluate the success of this effort (e.g., estimating the proportion of specimen records that
331 have been digitized and mobilized online), obtaining accurate estimates of the number of
332 specimens housed in NHCs is necessary. Extrapolations from digitized content indicate
333 that roughly 2.5–3 billion specimens are housed in NHCs worldwide (O’Connell et al.
334 2004, Krishnan et al. 2016). However, more robust assessments of global specimen
335 numbers, including geographic and taxonomic distribution, are required to facilitate
336 thoughtful assessments of collection bias to better target digitization priorities (Meyer et

337 al. 2016). Making robust size estimates are particularly relevant as vended solutions are
338 utilized to achieve digitization milestones, including the mobilization of entire collections
339 like those at the Muséum National D'Histoire Naturelle (France), Naturalis
340 (Netherlands), and the Smithsonian Institution (US) (Rogers 2016, Le Bras et al. 2017).
341 Along these lines, a test case example to illustrate such an effort on a smaller scale comes
342 from the Harvard University Herbaria (HUH), which has been thought to contain 5.5
343 million specimens. Targeted subsampling of the HUH vascular plant collection facilitated
344 accurate estimates (with confidence intervals) of total specimen collection numbers and
345 their geographic distribution (figure 3A). Once the total number of specimens in NHCs
346 have been accurately quantified, it is necessary to establish the percentage of specimen
347 collection records that have been digitally mobilized.

348 Because imaging and serving metadata-rich collection information online requires
349 a large financial investment, as well as human labor, its impacts on research should be
350 documented and acknowledged. The most powerful outcomes of digitization would be
351 better characterized by relating these various forms of data usage to one another to
352 explore how digitization increases specimen usage. Along these lines, data relevant to
353 describing the scientific impact of physical specimens (pre-digitization), such as loans
354 and museum visits, remain largely confined to physical collection logbooks, thus limiting
355 assessment of the impact of Digitization 1.0 (figure 3B). Such efforts would allow us to
356 begin to understand the ways that digitization stimulates increased visitation and use of
357 the actual physical versus digital collection (figure 3C). As a community, we must be
358 better prepared to track and assess these questions.
359

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372 **References Cited**

373

- 374 Ballard HL, Robinson LD, Young AN, Pauly GB, Higgins LM, Johnson RF, Tweddle JC.
375 2017. Contributions to conservation outcomes by natural history museum-led
376 citizen science: Examining evidence and next steps. *Biological Conservation* 208:
377 87–97.
- 378 Cardoso D, Särkinen T, Alexander S, Amorim AM, Bittrich V, Celis M, Daly DC,
379 Fiaschi P, Funk VA, Giacomini LL, Goldenberg R. 2017. Amazon plant diversity
380 revealed by a taxonomically verified species list. *PNAS* 114: 10695–10700.
- 381 Chang J, Alfaro ME. 2016. Crowdsourced geometric morphometrics enable rapid large-
382 scale collection and analysis of phenotypic data. *Methods in Ecology and*
383 *Evolution* 7: 472–482.
- 384 Comoglio F, Fracchia L, Rinaldi M. 2013. Bayesian inference from count data using
385 discrete uniform priors. *PLoS One* 8: e74388.
- 386 Cooney CR, Bright JA, Capp EJ, Chira AM, Hughes EC, Moody CJ, Nouri LO, Varley
387 ZK, Thomas GH. 2017. Mega-evolutionary dynamics of the adaptive radiation of
388 birds. *Nature* 542: 344–347.
- 389 Dou L, Cao G, Morris PJ, Morris RA, Ludäscher B, Macklin JA, Hanken J. 2012.
390 Kurator: A Kepler package for data curation workflows. *Procedia Computer*
391 *Science* 9: 1614–1619.
- 392 Drew JA, Moreau CS, Stiassny MLJ. 2017. Digitization of museum collections holds the
393 potential to enhance researcher diversity. *Nature Ecology & Evolution* 1: 1789.

- 394 Edwards JL. 2004. Research and societal benefits of the global biodiversity information
395 facility. *Bioscience* 54: 485–486.
- 396 Ellwood ER, Dunckel BA, Flemons P, Guralnick R, Nelson G, Newman G, Newman S,
397 Paul D, Riccardi G, Rios N, Seltmann KC. 2015. Accelerating the digitization of
398 biodiversity research specimens through online public participation. *Bioscience* 4:
399 383–396.
- 400 Ellwood ER, Crimmins TM, Miller-Rushing AJ. 2017. Citizen science and conservation:
401 Recommendations for a rapidly moving field. *Biological Conservation* 208: 1–4.
- 402 Funk VA. 2018. Collections-based science in the 21st century. *Journal of Systematics
403 and Evolution* 56: 175–193.
- 404 Goodwin ZA, Harris DJ, Filer D, Wood JR, Scotland RW. 2015. Widespread mistaken
405 identity in tropical plant collections. *Current Biology* 25: 1066–1067.
- 406 Guralnick RP, Zermoglio PF, Wieczorek J, LaFrance R, Bloom D, Russell L. 2016. The
407 importance of digitized biocollections as a source of trait data and a new VertNet
408 resource. *Database* Volume 2016.
- 409 Heberling JM, Isaac BL. 2018. iNaturalist as a tool to expand the research value of
410 museum specimens. *Applications in Plant Sciences* 6: e1193.
- 411 Hedrick BP, Manning PL, Lynch ER, Cordero SA, Dodson P. 2015. The geometry of
412 taking flight: Limb morphometrics in Cretaceous theropods. *Journal of
413 Morphology* 276: 152–166.
- 414 Hill A, Guralnick R, Smith A, Sallans A, Gillespie R, Denslow M, Gross J, Murrell Z,
415 Conyers T, Oboyski P, Ball J. 2012. The notes from nature tool for unlocking
416 biodiversity records from museum records through citizen science. *ZooKeys* 209:
417 219.
- 418 Hopkins GW, Freckleton RP. 2002. Declines in the numbers of amateur and professional
419 taxonomists: Implications for conservation. *Animal Conservation* 5: 245–249.
- 420 Johnson KG, Brooks SJ, Fenberg PB, Glover AG, James KE, Lister AM, Michel E,
421 Spencer M, Todd JA, Valsami-Jones E, Young JR. 2011. Climate change and
422 biosphere response: Unlocking the collections vault. *Bioscience* 61: 148–153.
- 423 Kissling WD, Walls R, Bowser A, Jones MO, Kattge J, Agosti D, Amengual J, Basset A,
424 Van Bodegom PM, Cornelissen JH, Denny EG. 2018. Towards global data
425 products of essential biodiversity variables on species traits. *Nature Ecology &
426 Evolution* 2: 1531–1540.
- 427 Krishnan P, Dutta K, Jawahar CV. 2016. Deep feature embedding for accurate
428 recognition and retrieval of handwritten text. *Frontiers in Handwriting
429 Recognition (ICFHR)* 15th International Conference: 289–294.
- 430 Le Bras G, Pignal M, Jeanson ML, Muller S, Aupic C, Carré B, Flament G, Gaudeul M,
431 Gonçalves C, Invernón VR, Jabbour F. 2017. The French Muséum National
432 D’histoire Naturelle vascular plant herbarium collection dataset. *Scientific Data* 4:
433 170016.
- 434 Lewis SL, Maslin MA. 2015. Defining the Anthropocene. *Nature* 519: 171.
- 435 Lister AM. 2011. Natural history collections as sources of long-term datasets. *Trends in
436 Ecology & Evolution* 26: 153–154.
- 437 MacDougall AS, Loob JA, Claydenc SR, Goltzd JG, Hindse HR. 1998. Defining
438 conservation priorities for plant taxa in southeastern New Brunswick, Canada
439 using herbarium records. *Biological Conservation* 86: 325–338.

- 440 Meineke EK, Davis CC, Davies TJ. 2018. The unrealized potential of herbaria for global
441 change biology. *Ecological Monographs* 88: 505–525.
- 442 Meineke EK, Davies TJ, Daru BH, Davis CC. 2019. Biological collections for
443 understanding biodiversity in the Anthropocene. *Philosophical Transactions of
444 the Royal Society B: Biological Sciences* 374: 20170386.
- 445 Meyer C, Weigelt P, Kreft H. 2016. Multidimensional biases, gaps and uncertainties in
446 global plant occurrence information. *Ecology Letters* 19: 992–1006.
- 447 Moritz C, Patton JL, Conroy CJ, Parra JL, White GC, Beissinger SR. 2008. Impact of a
448 century of climate change on small-mammal communities in Yosemite National
449 Park, USA. *Science* 322: 261–264.
- 450 Nelson G, Ellis S. 2018. The history and impact of digitization and digital data
451 mobilization on biodiversity research. *Philosophical Transactions of the Royal
452 Society B*. 374: 20170391.
- 453 Nualart N, Ibáñez N, Soriano I, López-Pujol J. 2017. Assessing the relevance of
454 herbarium collections as tools for conservation biology. *The Botanical Review* 83:
455 303–325.
- 456 O'Connell AFJ, Gilbert AT, Hatfield JS. 2004. Contribution of natural history collection
457 data to biodiversity assessment in national parks. *Conservation Biology* 18: 1254–
458 1261.
- 459 Park DS, Potter D. 2015. Why close relatives make bad neighbours: phylogenetic
460 conservatism in niche preferences and dispersal disproves Darwin's naturalization
461 hypothesis in the thistle tribe. *Molecular Ecology* 24: 3181–3193.
- 462 Primack D, Imbres C, Primack RB, Miller-Rushing AJ, del Tredici P. 2004. Herbarium
463 specimens demonstrate earlier flowering times in response to warming in Boston.
464 *American Journal of Botany* 91: 1260–1264.
- 465 Pyke GH, Ehrlich PR. 2010. Biological collections and ecological/environmental
466 research: A review, some observations and a look to the future. *Biological
467 Reviews* 85: 247–266.
- 468 Riemer K, Guralnick RP, White EP. 2018. No general relationship between mass and
469 temperature in endothermic species. *eLife* 7: e27166.
- 470 Rogers N. 2016. Museum drawers go digital. *Science* 352: 762–765.
- 471 Rouhan G, Dorr LJ, Gautier L, Clerc P, Muller S, Gaudeul M. 2017. The time has come
472 for natural history collections to claim co-authorship of research articles.
473 *Taxon* 66: 101–1016.
- 474 Schermer M, Hogeweg L. 2018. Supporting citizen scientists with automatic species
475 identification using deep learning image recognition models. *Biodiversity
476 Information Science and Standards* 2: e25268.
- 477 Schuettelpelz E, Frandsen PB, Dikow RB, Brown A, Orli S, Peters M, Metallo A, Funk
478 VA, Dorr LJ. 2017. Applications of deep convolutional neural networks to
479 digitized natural history collections. *Biodiversity Data Journal* 5: e21139.
- 480 Suarez AV, Tsutsui ND. 2004. The value of museum collections for research collections.
481 *Bioscience* 54: 66–74.
- 482 Sudholt S, Fink GA. 2016. PHOCNet: A deep convolutional neural network for word
483 spotting in handwritten documents. *Frontiers in Handwriting Recognition
484 (ICFHR)* 15th International Conference: 277–282.

- 485 Sweeney PW, Starly B, Morris PJ, Xu Y, Jones A, Radhakrishnan S, Grassa CJ, Davis
486 CC. 2018. Large-scale digitization of herbarium specimens: Development and
487 usage of an automated, high-throughput conveyor system. *Taxon* 67: 165–178.
- 488 Tegelberg R, Mononen T, Saarenmaa H. 2014. High-performance digitization of natural
489 history collections: Automated imaging lines for herbarium and insect specimens.
490 *Taxon* 63: 1307–1313.
- 491 Thiers B. 2018. Using data from index herbarium to assess threats to the world's
492 herbaria. *Biodiversity Information Science and Standards* 2: e26440.
- 493 Unger J, Merhof D, Renner S. 2016. Computer vision applied to herbarium specimens of
494 German trees: Testing the future utility of the millions of herbarium specimen
495 images for automated identification. *BMC Evolutionary Biology* 16: 248.
- 496 Webster M. 2017. The extended specimen. In M. Webster [ed.], *The extended specimen:*
497 *Emerging frontiers in collections-based ornithological research*, 1–9. CRC Press,
498 Boca Raton, Florida, USA.
- 499 Wilf P., Zhang S, Chikkerur S, Little SA, Wing SL, Serre T. 2016. Computer vision
500 cracks the leaf code. *PNAS* 113: 3305–3310.
- 501 Willis CG, Law E, Williams AC, Franzone BF, Bernardos R, Bruno L, Hopkins C,
502 Schorn C, Weber E, Park DS, Davis CC. 2017. CrowdCurio: An online
503 crowdsourcing platform to facilitate climate change studies using herbarium
504 specimens. *New Phytologist* 215: 479–488.
- 505 Yost JM, Sweeney PW, Gilbert E, Nelson G, Guralnick R, Gallinat AS, Ellwood ER,
506 Rossington N, Willis CG, Blum SD, Walls RL. 2018. Digitization protocol for
507 scoring reproductive phenology from herbarium specimens of seed plants.
508 *Applications in Plant Sciences* 6: e1022.
- 509 Zhou N, Siegel ZD, Zarecor S, Lee N, Campbell DA, Andorf CM, Nettleton D,
510 Lawrence-Dill CJ, Ganapathysubramanian B, Kelly JW, Friedberg I. 2018.
511 Crowdsourcing image analysis for plant phenomics to generate ground truth data
512 for machine learning. *PLoS Computational Biology* 14: e1006337.

513

514 **Figures.**

515

516 **Figure 1.** Digitization 1.0 and 2.0. Digitization 1.0 is the creation and online mobilization
517 of digital content derived from physical specimens. This endeavor occurs locally within
518 institutions, most commonly Natural History Museums. Digitization 2.0, in contrast,
519 builds upon the digitized data, workflows, and infrastructure produced by Digitization 1.0
520 to facilitate enhanced digitization, curation, and data linkages to address increasingly
521 complex questions at a massive global scale not previously imagined. These efforts are
522 stimulating a new work force and connecting diverse scholarly domains, propelling a new
523 generation of scientists forward, and removing financial, sociological, institutional, and
524 academic obstacles restricting access to these materials. Some areas of inquiry that will
525 be greatly stimulated by both Digitization 1.0 and 2.0 are highlighted.

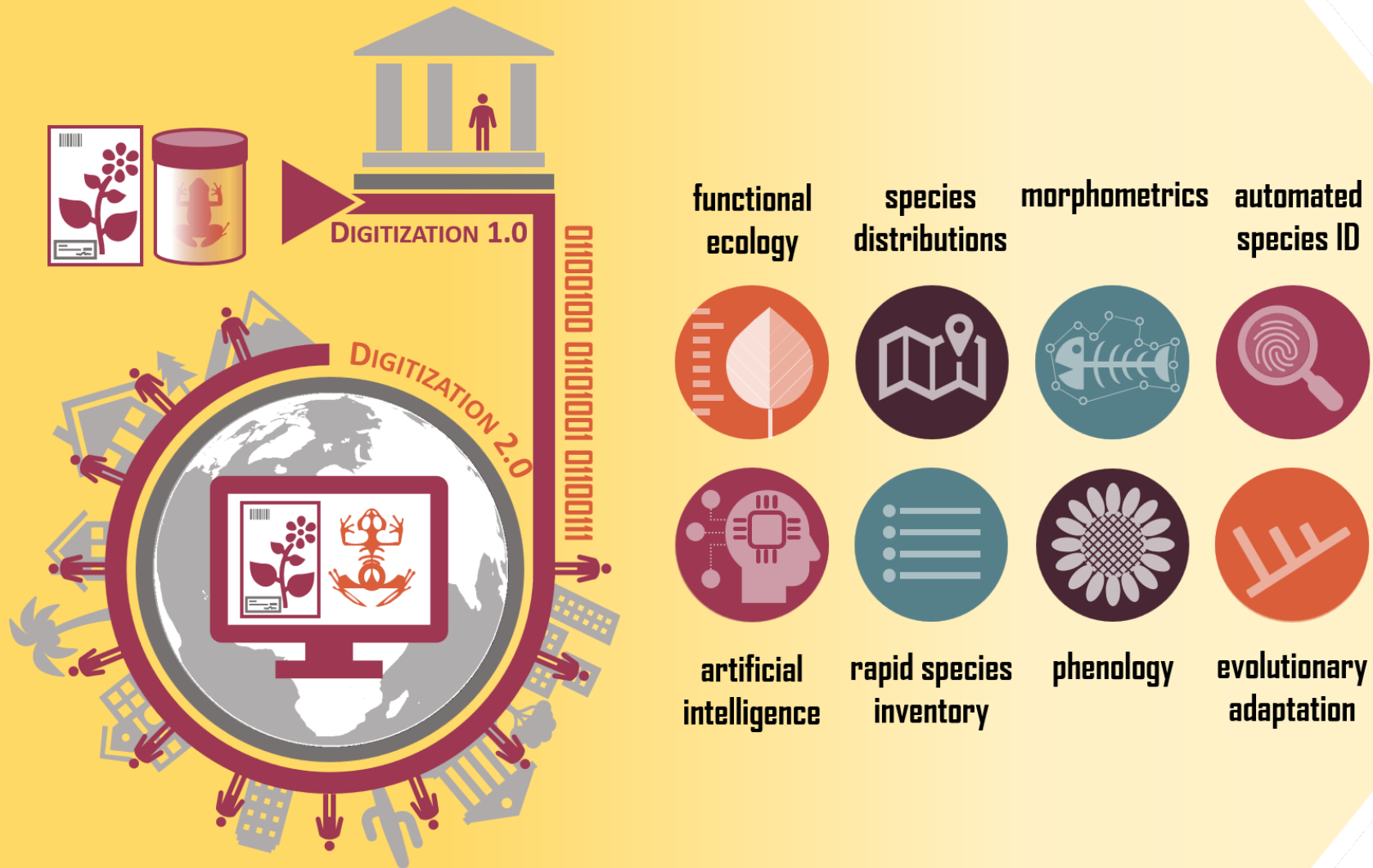
526

527 **Figure 2.** An end-to-end pipeline example to highlight the value and complementarity of
528 Digitization 1.0 and 2.0. The African pig-nosed frog (genus *Hemisus*) shown (A) was
529 collected during recent field research in Angola. In addition to metadata from the
530 collection event, a series of x-ray images (tomograms) were created using diffusible

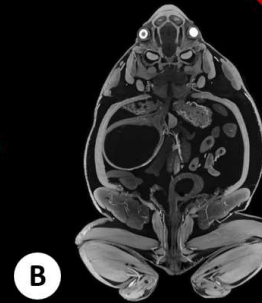
531 iodine-based contrast-enhanced computed tomography (diceCT) directly from the
532 voucher specimen. This product of Digitization 1.0 is shown in the black and white x-ray
533 image (B). From these digital x-ray images, a 3D volume was created from the digital
534 data generated during Digitization 1.0 from which students and scientists can digitally
535 dissect and manipulate regions of interest representing the frog's nervous (C), circulatory
536 (D), and muscular (E) systems (Digitization 2.0).

537

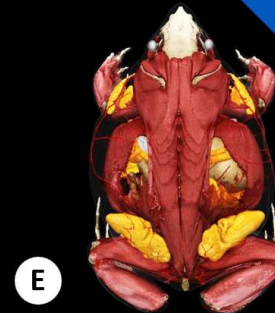
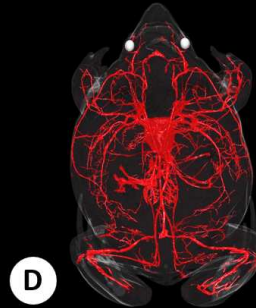
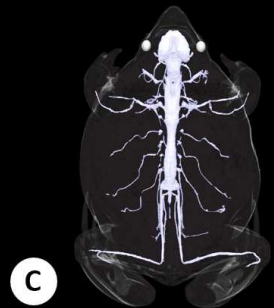
538 **Figure 3.** Estimating collection sizes and impact on research. (A) Size and geographical
539 distribution of the vascular plant collection at the Harvard University Herbaria (HUH).
540 To statistically estimate the size of this large collection, the total number of specimens in
541 randomly subsampled cubbies were counted. These data were then used to model a
542 probability distribution of the total number of specimens across the entire collection
543 (Comoglio et al. 2013). Three hundred fifty cubbies were sampled and counted,
544 establishing that the HUH has 3,701,695 vascular plants with a 95% confidence interval
545 spanning 3,644,497 to 3,759,803. A similar approach was applied to further assess
546 geographical distribution of the collection as well. (B) Loan use information for the
547 Harvard Museum of Comparative Zoology ichthyology collection. Digitization greatly
548 enhances the tracking of loan use history post 1980, until which point records are
549 confined to physical logbooks. (C) Cumulative number of HUH specimen loans post
550 1980. While the total number of physical specimen loans (red) have remained relatively
551 constant in recent years, the number of digital specimen images loaned has grown
552 substantially.



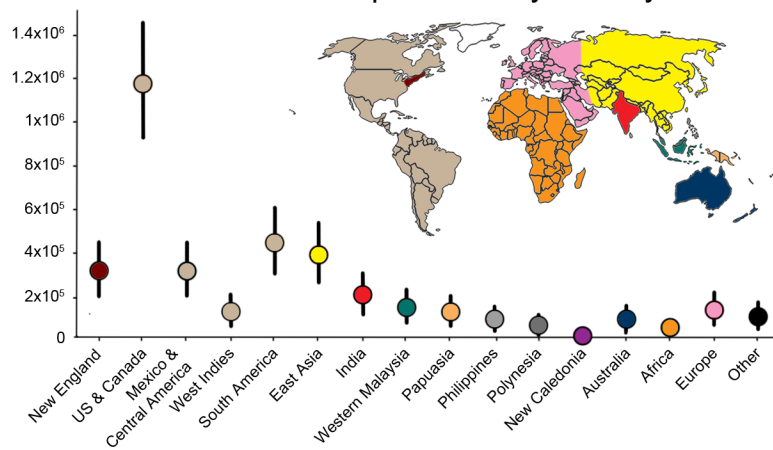
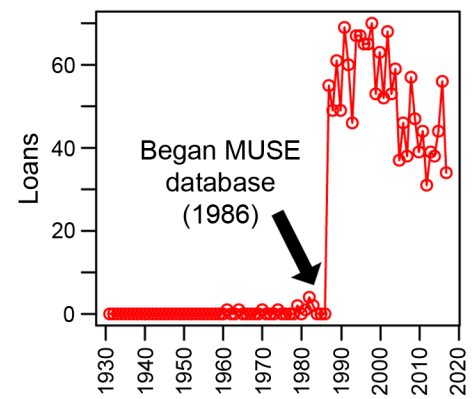
DIGITIZATION 1.0



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01111010 01100001
01110100 01101001
01101111 01101110
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DIGITIZATION 2.0

A Vascular Plant Specimens by Locality**B** MCZ Ichthyology Loans**C**