The destructive sampling conundrum and guidelines for effective and ethical sampling of herbaria

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Abstract

The use of herbaria for science and conservation is revolutionizing the discovery, exploration, and protection of biodiversity at unprecedented scopes and scales. The Global Metaherbarium—a digitally interlinked, open-access resource—is stimulating these efforts and helping to facilitate massive investigations that utilize aggregated digital derivatives of physical herbarium specimens. Simultaneously, the growing use of this virtual resource is expanding the use of physical collections by researchers from many scholarly domains who increasingly are sampling specimens for multiomic investigations (e.g., genomics, transcriptomics, metabolomics, proteomics, and microbiomics). These investigations are leading to new scientific insights and supporting the development of conservation actions, but they come with a substantial cost: the (partial) destruction of priceless and often irreplaceable specimens, which constitute a global heritage that should be permanently safeguarded for future reference. The absence of a comprehensive set of "best practices" for destructively sampling herbarium specimens leads to confusion and uncertainty from researchers and institutions alike and risks over-exploitation of precious collections when the research is executed. Here, we provide a set of best practices aimed at reducing these uncertainties and creating a framework for sustainably and ethically sampling herbarium specimens. Our recommendations are intended for two complementary but overlapping audiences—users and stewards—who together build, use, and protect herbarium collections.

Keywords: biodiversity, herbaria, genomics, metabolomics, multiomics, museum ethics, natural history collections

The world's herbaria house approximately 400 million specimens[1,2], including extinct species or populations, and represent the diversity required to understand the origin, past and future evolution, and ecology of plants and fungi. Herbaria are one of the most important places in which to study nature in the face of continued threats to biodiversity and its importance to humankind for food, medicine, spiritual comfort, and shelter [3]. They also are being used increasingly by educators and artists to draw attention to broader societal issues[3], and to develop plans for conservation, restoration, and sustainable use of natural resources.

Traditional uses of herbaria mainly have included species descriptions and associated floristic investigations and monographic treatments; determining species' geographical ranges; and historical perspectives on collectors and collections[3,4]. Since the 1920s, additional uses of collections have expanded tremendously, continue to grow and, in combination with 21st-century digitization and next-generation integrative multiomic approaches, are ushering in a new era of herbarium and biodiversity science [3,5]. In short, the 'Herbarium of the Future' is propelling basic and applied science in ways that were never imagined when these institutions and their collections were established centuries ago [3].

We applaud the ongoing renaissance of herbaria, but over many years in our professional roles we have become increasingly aware of what we could call the "destructive sampling conundrum:" how to foster innovative research while permitting destructive sampling of specimens meant to be protected permanently. However, best practices for destructively sampling herbarium specimens have not yet been explicitly developed or agreed. The lack of common guidelines and best practices results in inconsistent practices by stewards of these collections, especially when newcomers to the field want to destructively sample specimens but are uncertain how to do so effectively and responsibly. Conversely, the pool of herbarium users has expanded to include students, researchers, and other professionals from a wide range of disciplines, many of whom are not educated in collection stewardship and do not understand the range of costs of their requests. In this **Perspective**, we propose clear guidelines for the effective and ethical sampling of herbaria. A central premise of

these guidelines is that herbarium specimens are a limited and priceless resource that must be protected for current and future generations.

These guidelines imply best practices, and we outline below best practices for two groups of stakeholders: i) herbarium *users*, and ii) herbarium *stewards*. Herbarium stewards include a broad swath of backgrounds and expertise, including digitizers, curatorial assistants, collections managers, keepers, curators, and directors. We recognize that individuals may be both users and stewards, and although some of our specific guidelines may appear to treat them separately, recommendations for users and stewards intersect and inform one another. Whereas institutional priorities may vary, we hope that our recommended best practices will stimulate discussions that lead to establishing clear guidelines for destructively sampling herbaria. Finally, although our focus is on herbaria, many of our guidelines and best practices apply equally to any natural history collection.

Background and rationale

The online mobilization of digitized herbaria is sparking a renaissance in the use of natural history collections[6]. Inherent to digitizing and mobilizing herbarium collections is the creation of the 'Global Metaherbarium,' a 'common, digitally interlinked and open-access resource that will stimulate large-scale and novel science'[3]. The Global Metaherbarium is more than the sum of its parts: it is an ideal platform for connecting essential biodiversity data (often physically scattered) in a virtual, searchable framework, and represents far more information content than is available from physical specimens alone. 'Extended' specimen data may include not only digital derivatives of the physical specimen (i.e., a digital photograph and label transcription) but also its genomic sequence, field images, and inferred species distribution models (SDMs), literature citations, among other data types that can be linked to it[7,8]**.** Although the Global Metaherbarium is virtual, it makes specimens

and their extended data interconnected and discoverable, which in turn stimulates increased visitation of herbaria by diverse scholars who study and sample physical collections[6,9] (**Fig. 1**).

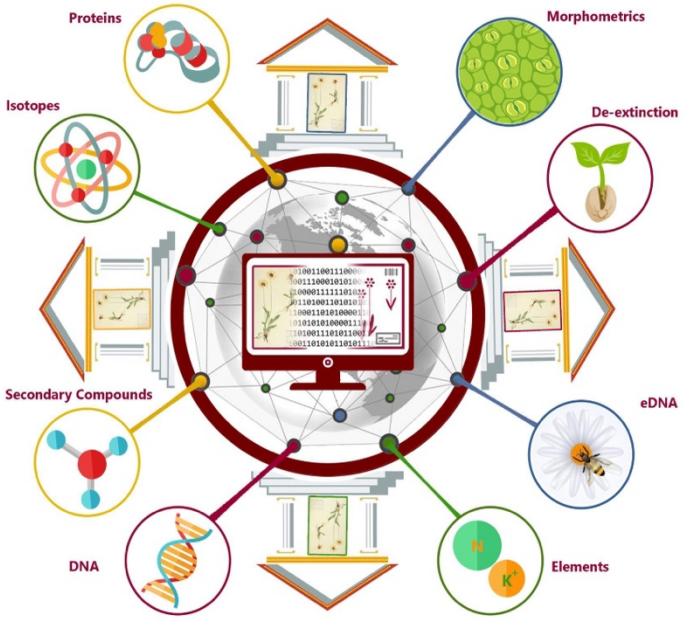

Figure 1. The Global Metaherbarium seamlessly accommodates the extended specimen and greatly facilitates searchability. Using this virtual framework, key extensions of the physical specimen, such as multiomic data, can be recorded easily and integrated for findability at a global scale, facilitating more effective destructive sampling. For example, if a duplicate at one herbarium were sampled for genomic sequencing, similarly sampling a duplicate from the same collection at another herbarium should be avoided or receive lower priority. Open access icons by macrovector/Freepik.

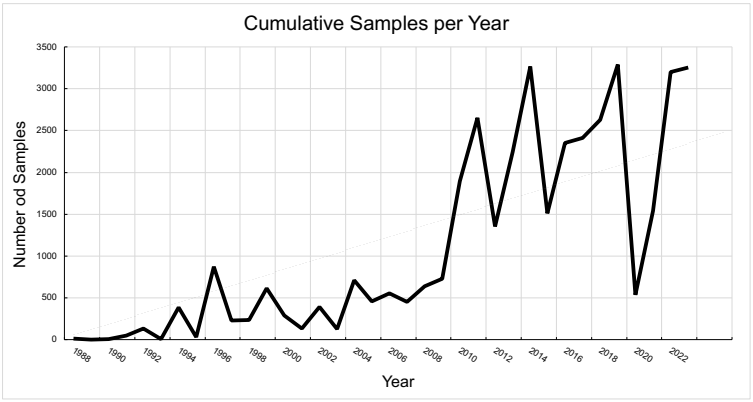

Figure 2. Annual cumulative growth in the number of destructively sampled specimens for DNA sequencing, from 1988–2023. Data tabulated from records from the Harvard University Herbaria (HUH), the Missouri Botanical Garden herbarium (MO), the New York Botanical Garden herbarium (NY), and the Royal Botanic Gardens herbarium (K).

Alongside these exciting advancements, we have witnessed a dramatic increase in the destructive sampling of herbarium specimens for scientific and scholarly pursuit (**Fig. 2**). Research topics that necessitate destructive sampling include: expanded DNA barcoding efforts; high resolution phylogenomics; tracking the genetic history of domestication; illuminating human migration; characterizing anthropogenic change during the Quaternary; mapping the origin and spread of crop pathogens; exploring the genetic basis of species invasions and extinctions; investigating microbial associations across time and space; resolving species boundaries; and incorporating historical variation to investigate biodiversity change through time[3,5,10-16]. Relatedly, we have observed growth in destructive sampling of herbaria for isotopic

assessments to characterize temporal changes in atmospheric CO2 and other pollutants[17], and to extract and characterize small metabolites of potential medicinal value[18-20].

Destructive sampling of herbarium collections is not new. It has occurred continually since the earliest herbaria were established in the 1500s and 1600s (e.g., boiling flowers to measure the living size of their floral organs; harvesting anthers and pollen grains for detailed microscopic investigation). Since the late 1980s, the discoverability of specimens facilitated by digitization combined with cutting-edge multiomic approaches have bolstered macroevolutionary investigations[21,22] and fueled explosive growth of molecular systematics[23]. However, destructively sampling specimens for multiomic investigations and other research has a serious cost: the (partial) destruction of the specimen. This cost will continue to grow as the Global Metaherbarium becomes fully realized, new questions arise, and novel tools are developed. The convenience and relative ease of sampling herbarium specimens, as opposed to generating new collections from fieldwork, also may have undesirable and unintended consequences. We must work collectively to ensure that collections are preserved and research using their finite resources can be pursued vigorously and fairly. Our proposed set of best practices are designed to facilitate and encourage research while minimizing the destructive cost to priceless collections.

Best practices for herbarium users

1. Always consult other available resources before destructively sampling herbarium specimens. There are a variety of tissue resources distinct from conventional pressed and dried herbarium specimens that can be destructively sampled and are especially useful for multiomic investigations. Such resources include DNA cryofacilities held at institutions (such as at K and NY; herbarium acronyms follow Thiers[1]) and extensive silica-dried leaf collections (such as at K and MO). These other resources should always be consulted *before* resorting to destructive sampling of conventional herbarium specimens. Silica-dried samples, albeit finite, are an excellent resource for initial exploration because they tend to produce higher quality DNA with greater yields than conventionally dried herbarium specimens[24,25]. This option also can be used to establish positive lab controls for

downstream investigations with more degraded tissues. Another viable option is to contact and ask researchers who have access to living plants or have destructively sampled herbaria previously for multiomic investigations to share tissue or aliquots. Finally, the Plant Search database allows searching for taxa held within a network of > 1000 living collections. Any use of shared resources normally should lead to a formal collaboration (including co-authorship).

2. Herbaria are not a substitute for fieldwork. Herbaria increasingly are viewed as the first target of genetic sampling[3,26]. However, continuing to build these collections increases their value and sustains their utility for future research[27]. Thus, whenever possible, herbaria should not be the first resort for sampling. Rather, new specimens collected during fieldwork—including generating new herbarium collections as vouchers for future generations—should be sampled first; herbarium specimens should be used only as needed to fill gaps or if sampling from herbaria is the only practical means to conduct a study (e.g., in situations of wars, political strife, funding restrictions).

This 'field-first' approach is how herbaria have been used historically for multiomic investigations, in part because of the inability to obtain reliable 'omic data from so-called 'antique samples.' Although next-generation approaches are removing some obstacles and further unlocking these collections, these advances should not lead to less field sampling or collecting whenever and wherever possible. Fieldwork inspires curiosity and question-oriented science and provides researchers and students with a first-hand understanding of the threats and ecological dependencies that species face. Targeted field work, even done on a small scale, also can help build collections and generate goodwill when making later requests for destructive sampling. In-country institutions should be the primary partners in fieldwork and joint participation from study planning through collection and publication are important aspects of Access and Benefit Sharing under the Convention on Biological Diversity.

3. Ensure that institutional permission to destructively sample specimens is granted. Herbaria typically require explicit permission to destructively sample their collections; users must

obtain appropriate permission from institutions and those who steward these collections. If users are uncertain how to do this, simply ask. Institutional guidelines vary among herbaria and, in some cases, among collections within an institution, and users should not assume that sampling protocols and permits are the same in every herbarium. Furthermore, permission to destructively sample usually are granted only on a specimen-by-specimen basis; permission to sample one specimen normally does not imply or grant permission to sample other materials. Destructive sampling of type specimens is strictly forbidden by some institutions, but others may consider such requests while subjecting them to additional evaluation and scrutiny, which may involve input from multiple stakeholders (e.g., curatorial boards at local institutions or colleagues and stakeholders spanning multiple institutions). Such scrutiny and evaluation can take months, so requests for permits should be made well in advance. In some cases, institutions also may have formal understandings with governmental agencies or other stakeholders that go beyond international treaties like the Nagoya Protocol that restrict particular kinds of multiomic sampling[28,29]. Many countries have developed legislation governing access to genetic resources, their use, and related benefit sharing. Collections will enter into written agreement with institutions or government agencies in the provider country and in some cases these agreements will prohibit external transfer to third parties without prior permission[30,31]. To prove that institutional permission to sample was granted, publishers and aggregators of genomic data (e.g., GenBank) normally require copies of permits before a paper can be published or sequences deposited, respectively. Proof of permissions also may be required by federal granting agencies.

4. Prioritize destructive sampling of more recent collections. Newer specimens generally yield higher quality and more abundant DNA[18,24,32]. Whenever possible, older specimens should not be used and historic vouchers should not be destroyed. In some cases, sequencing the type specimen of the species—which in many cases also is the oldest specimen—may be thought to be crucial[33,34]. However, some institutions may not allow destructive sampling of type specimens (see #3, above).

241 *5. Destructively sample only the amount of tissue required for the analysis*. A comprehensive
242 sampling plan for a project should be determined before initiating any destructive
243 sampling and the plan should be submitted along with an application for a permit or visit to
244 the herbarium. Because, many biodiversity investigations require only a single placeholder
245 taxon, e.g., a single species representing a much larger clade (genus) may suffice. In such
246 cases, rare or threatened species should be sampled only as a last resort, only after
247 protocols have been well established, and only for science deemed most impactful.
248
249 Data acquired through destructive sampling often improve the value of the physical (and
250 extended) specimen, but destructive sampling should be done skillfully and minimally (i.e.,
251 measure twice, cut once). In general, a good rule of thumb is to sample in such a way that it
252 is impossible to identify that the collection has been sampled, except of course for the
253 required addition of an annotation label indicating that the specimen was sampled (**Fig. 3**).
254 Ideally, the annotation would be both physical and digital to enhance local and more global
255 efforts to track sampling. We strongly advocate using QR codes to allow rapid access to
256 specimen metadata and annotation histories with readily available devices, such as phones
257 or tablets. Documenting and tracking this information with globally unique identifiers[35] is a
258 hallmark of good science and stewardship of these collections.
259

Any destructively sampling must maintain the future utility of a specimen. Thus, from any specimen, take only what is required for the planned research—i.e., do not take 'rainy day' surplus samples for potential or undefined future uses. Sampling should always be prioritized from collections with abundant materials (**Fig. 3**).

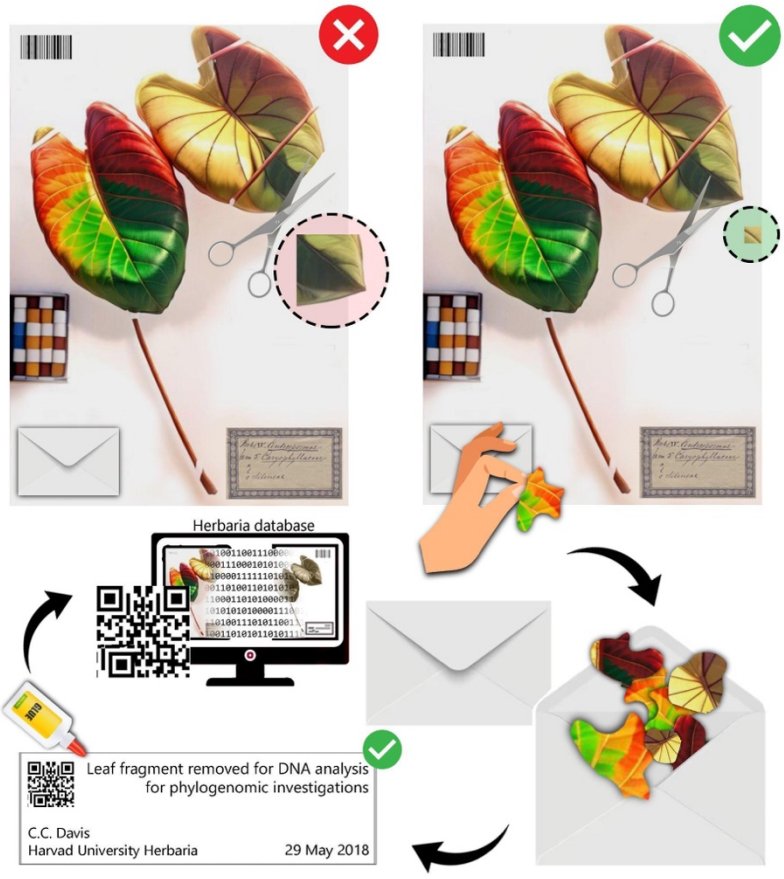

Figure 3. Recommended guidelines for destructive sampling of herbaria. Remove only very small tissue fragments and prioritize specimens with abundant material; start first with packeted fragments when they are available. Upon sampling, it is essential to immediately add an annotation label documenting the destructive sampling event. This can be accomplished with a conventional physical label as shown or with a digital QR barcode for more easily viewing the entire history of specimen metadata, including a detailed annotation timeline.

It is also imperative to ensure that crucial developmental stages or morphological features are not destroyed completely. For example, the upper and lower surfaces of leaves may have distinct morphological differences that are important for species identification. Thus, if only a single abaxial (lower) surface of a leaf is showing on an herbarium sheet, leaves in which the adaxial (upper) surface is exposed should be prioritized for sampling. This recommended approach also preserves, for example, key climate-change response traits such as stomatal size and density, which tend to be abundant on the lower leaf surface[17,36].

6. Apply effective and proven methods. It is important to apply state-of-the-art protocols and experimental designs whose success has been demonstrated. For example, in the last three decades, numerous DNA extraction techniques have been developed and evaluated,

including bulk cesium chloride extractions, cetyltrimethylammonium bromide (CTAB)-based extractions, silica columns, and magnetic beads[37-39]. A key to successful experimental design and implementation is to continually refine and perfect multiomic methodologies to require only miniscule amounts of tissue. For some requests for DNA extraction may be for ≥ 4 cm^2 of leaf tissue (D. White, pers. comm.) even though 1 cm^2 of leaf may be more than adequate and is a rule of thumb dimension. We advocate more sophisticated explorations of these parameters—see below.

Good models for such efforts comes from the burgeoning field of ancient DNA (aDNA)[40] and DNA-based forensics[11], where novel laboratory and bioinformatics techniques have sparked methodological sea changes in multiple fields of scholarship. New methods and best practices for extracting tissues that were thought to be intractable, including formalin-[41] or ethanol-preserved tissues, also have been developed[42]. As they become available and more widespread, these advanced methods also should be applied to destructively sampling herbarium specimens[43-45].

Research limitations resulting from taxon or sample specificity also should be explored and identified by researchers before beginning any larger destructive sampling initiative. In addition to age-related degradation of DNA, DNA extraction from conventionally prepared herbarium specimens from wet tropical environments may be poorer for multiomic investigation than species from drier tropical environments[24]. Similarly, there is substantial variation in DNA extraction success across clades (e.g., Cyperaceae and Sapindaceae have higher yields than Fabacaeae and Melastomataceae; [24]).

If multiomic extractions are to treated as loans to be returned (see Best Practice #3 for Herbarium Stewards), the information on extraction method and concentration and quality should also be provided and catalogued. Sequences should be accessed simultaneously into local institutional databases and in NCBI/Genbank or similar publicly accessible database so that others can use the data and avoid unnecessary sampling of the same or related specimens.

Finally, if proposed methodologies are based on data-free folklore or rules of thumb, or are new and unproven, it is important to provide proof-of-concept alongside institutional requests to sample herbaria. For example, 'rule-of-thumb' tissue sizes often overlook its thickness, density, or the reliability of extraction success within a particular taxon or from a particular habitat or biome. The amount of tissue yields can vary greatly by tissue density, age, taxon, habitat, or preservation mode[24], and more careful and systematic investigations of these factors considering specific protocols to be used should be done before destructively sampling specimens. In such cases, 'test' herbarium samples can be sampled destructively to demonstrate feasibility (e.g., harvesting spectral signature data for species identification and functional trait assessments[46]).

7. Confirm specimen determinations prior to sampling. Many herbarium users assume that previous determinations of the identity of specimens are always correct. However, specimens are often misidentified or are labeled with outdated names (e.g.,[47]). Confusing or nonsensical research results can occur simply because sampled specimens were mis-identified or mis-labeled[48]. Thus, users should verify the determinations of all specimens prior to sampling. For systematics and phylogenetic research, this issue can be addressed by deliberately factoring in some revisionary taxonomic work as part of the project. As intuitive as such a proposition sounds, it is more common than not for users to request destructive samples from an herbarium while declining to see and verify the physical vouchers.

For broader-scale phylogenetic or non-systematics projects, where researchers lack the experience necessary to identify requested specimens, collaboration with a taxonomist, systematist, or phylogeneticist should be the norm. Similarly, if expert identifications are already available for a group of specimens because of the recent work of a taxonomist who is alive and active, those determinations should be recognized for the genuine intellectual contributions they are and collaborations involving co-authorship should be seriously explored (see also Best Practice #9 for Herbarium Users, below).

352 *8. Annotate specimens after sampling.* Clear annotation, both physical and digital, and
353 associated record-keeping are essential for documenting destructive sampling of
354 herbarium specimens. An annotation should be made immediately upon sampling and
355 should minimally include: the name of the sampler or research team, contact information of
356 sampler, date of collection when the sample was taken, what kind of material was removed,
357 and the title and goal of the project (**Fig. 3**). This annotation should be digitized
358 simultaneously as part of the extended specimen both in local institutional databases and
359 in large data aggregators such as GBIF and iDigBio. If herbarium staffing is minimal, the
360 user should extend support to help complete this important step.
361
362 *9. Make data from destructive sampling publicly available immediately.* Any data derived
363 from destructive sampling should be made publicly available as soon as it is produced.
364 Larger federal funding agencies, such as the United States National Science Foundation,
365 have timeline requirements for data delivery and serve as good models. Similar examples
366 of such policies include the Darwin Tree of Life project and the Fern Tree of Life.
367
368 *10. Ensure credit to herbaria in publications and grants.* Natural history collections,
369 including herbaria, are under-funded and under-appreciated[49,50]. To remedy this, herbaria
370 should be formally recognized for supplying tissues for destructive sampling. Minimally,
371 herbarium vouchers utilized for multiomic initiatives should be prominently cited in
372 publications ensuing from these initiatives. Such recognition should be prominent and
373 extend beyond simple acknowledgement statements that conclude a scientific paper[26].
374 Specifically, more formal attributions of herbaria and natural history collections are
375 required, including possibly co-authorship of institutions that is tracked by citation
376 aggregators such as Google Scholar[51]. Minimally, authors should formally recognize the
377 herbaria that supply tissue in some format that is trackable and citable, such as working
378 with herbaria to ensure that clear records to track sampled specimens are available via
379 GBIF, which can provide a citable DOI for relevant datasets. Such metrics are essential for
380 justifying the use and importance of herbaria for stewardship and funding. FAIR standard
381 conventions should apply here[52].
382

Similarly, curators, support staff, and especially collectors of sampled herbarium specimens should be invited to participate in research as co-authors whenever possible. Contributions should be indicated through the Contributor Roles Taxonomy (CRediT) system, especially for larger, more substantial requests[26]. We have witnessed researchers systematically harvest in a single short visit hundreds of samples that encompass the entire career of collectors and researchers at those institutions. In most cases, these individuals were not consulted or extended an invitation to be involved in the research produced by the destructive sampling or the ensuing large grants and publications derived from them. These approaches are predatory and should be avoided at all costs. An appropriate alternative to such sampling is to canvas more broadly the community of herbarium staff who supported these collection and identification efforts and offer formal collaborations or co-authorship.

Finally, destructive sampling requests make enormous demands on staff and their institutions, whose budgets are already thin. Research grants that use herbarium specimens should explicitly include funds to herbaria to offset staff costs and the associated curation and stewardship of such collections, which in many cases have been ongoing for centuries. Indeed, funding for participating herbaria that have contributed sampling specimens for multiomics should be formally included in all budgets, just as is done for other field and lab expenses and fees. Specifically, we advocate that users explicitly include herbaria as funded subcontractors/subawardees in grants that are written in good faith and with careful consultation with partner herbaria. Moreover, the funding allocation of any request should scale with the age and rarity of material requested. Appropriate and fair cost models need to be established for such efforts. To this point, NY has created a sophisticated calculator for its curators that can be used to calculate all costs associated with accessioning new specimens into the herbarium. Such approaches can be used to estimate the long-term and substantial costs of stewarding any individual specimen.

Best practices for herbarium stewards

1. Evaluate individually each request for destructive sampling. Destructive sampling requests should be considered on a specimen-by-specimen basis, ideally with each sampled specimen recorded in a Material Transfer Agreement (MTA). This transparency ensures that no material is sampled without the explicit permission of the institution; stewards of collections can check to ensure institutional obligations have been met (e.g., Nagoya Protocol requirements, CITES, Memoranda of Understanding (MOUs), permits or other agreements with other countries or institutions, bioculturally sensitive materials, rare or threatened species restrictions)[53]; and users of those collections can be confident that they have documented permission to conduct their proposed project. Best practice dictates that institutions should always track transfers of their specimens and derivative samples and for countries and material falling under the scope of the Nagoya Protocol, which is a legal commitment for signatories[30].

2. Destructive sampling of bioculturally sensitive plants requires special considerations. Certain specimens, plant species or populations, and research topics necessitate an additional level of care and attention when it comes to destructive sampling. Many plants have spiritual and ceremonial importance and are essential to Indigenous groups who steward or govern nearly 40 million km^2 of land and inland waterways in 82 countries, including 25% of earth's terrestrial lands[54,55]. The colonial legacy of herbaria is well documented, and most herbarium collections are housed in the Global North[56]. This creates additional responsibilities for most stewards of herbaria to ensure these specimens are treated with care and are not used as a means of circumventing the sovereignty of nations and Indigenous people as pertains to their biodiversity and associated knowledge. Established guidelines for respectful, responsible, and ethical partnership with Indigenous communities in the context of field biology[57] should be extended to herbarium sampling. If an activity would be considered unethical in the context of newly collected specimens, it should not be done using herbarium specimens.

Multiomic sampling of extinct, rare, or bioculturally sensitive plants (whether alive or preserved in herbaria) should proceed only after careful user consideration and stewardship deliberations[20]. Users should be made aware that requests to sample such

materials make unique demands that potentially impinge on many groups and individuals. In these cases, provenance, acknowledgement, and collaboration are essential to advancing research with such collections[58], whose use also may be regulated by international treaties and domestic laws (e.g., CITES). Stewards must make users aware of these added requirements and sensitivities during planning and permitting discussions.

3. Treat destructive multiomic samples from collections as loans. The active loan and exchange of physical specimens among herbaria has been ongoing for more than a century. They have been an essential and effective means to more comprehensively study biodiversity and obviate extensive, unnecessary, and expensive travel. Multiomic derivatives resulting from destructive sampling should be considered a part of the physical collections and should be treated in a similar way as loans of physical specimens. Unused materials and aliquots of extracted DNA should be returned to the institutions who steward these collections, or at least repatriated to a related herbarium where duplicates of sampled specimens are held (see Best Practice #6 for Herbarium Users, above). We recommend that multiomic loans derived from specimens be returned within two years of sampling regardless of publication status and following established MTAs and Data Use Agreements (DUAs). Such loan returns can be accomplished using infrastructure within an institution (e.g., cryofacility) or by aggregated stock facilities that supply samples, such as the algal facility at Bigelow Labs (https://ncma.bigelow.org/).

Relatedly, just as digitization has created a revolution in the biodiversity sciences and has increasingly become a standard curatorial practice in herbaria[6,9], the community should embrace curating multiomic samples in botanical collections. For example, genomic and biochemical resources in herbaria are invaluable elements of the extended specimen and should be stewarded accordingly. Such stewardship will vary with institutional resources, e.g., providing extraction in on-site labs (at K, for example), cryogenic facilities for storing extracted DNA aliquots, or partnerships with existing facilities to safeguard these samples on behalf of the herbaria which house their associated voucher specimens. Uncountable aliquots of DNA from finite and irreplaceable specimens have been discarded or lost when researchers move, retire, or die, and because of the lack of a standardized process for

475 depositing extracted samples. Curating a collection of extracted DNA (or other related
476 multiomic sample) is costly and time-consuming, but will extend the research value of
477 herbarium specimens immeasurably into the future[30].
478
479 *4. Develop a succession plan for derivative (e.g., multiomic) collections from destructive*
480 *sampling.* Academics frequently move as their career trajectories develop, and eventually
481 retire or pass on. It is imperative that a clear succession plan be in place for multiomic
482 samples after their initial use has been completed. This can be clarified in an MTA.
483 Minimally, the sample should be searchable online and available to the community.
484 Succession plans are of particular importance for large research labs where faculty and
485 staff careers may span decades, during which time a very large number of potentially useful
486 samples may accumulate. In this case, users will assume a stewardship role and work with
487 herbarium leadership to ensure safe transfer of derivative collections.
488
489 *5. Protect against hoarding.* Any serious inquiries involving exceptionally large requests
490 should be vetted carefully by internal and, where appropriate, external stakeholders.
491 Moreover, material requests involving larger sampling efforts should be initiated as part of
492 a formal collaboration with associated MOUs, MTAs, and DUAs negotiated prior to the
493 onset of such efforts. These agreements also should include a clear statement of when the
494 data and metadata will be released and how aliquots will be archived and shared. As noted
495 earlier, herbaria should guard against being seen as a 'back door' to access the genetic
496 diversity of another country (see Best Practice #3 for Herbarium Users). Large requests for
497 sampling from a particular country should be directed first to its national institutions so
498 appropriate collaborations can be organized by the user. Whenever possible, all reasonable
499 efforts should be made to accommodate requests from in-country representatives to
500 sample their country's biodiversity. There may be additional rules restricting use of
501 collections from particular countries, and in all cases for country-focused studies,
502 collaboration with in-country partners must be the norm[56,57,59].
503
504 Finally, the primary voucher set of any such derivative collections (e.g., DNA aliquots)
505 should reside at the herbarium providing the samples. If adequate curation of such

derivative collections is not possible, a third-party institution should be designated, ideally another herbarium with appropriate domain knowledge and expertise. Similarly, following long-standing practice among herbaria to deal with physical specimens, large derivative sample sets should be dispersed to all collaborating institutions and institutional partners rather than to single individuals or labs to mitigate against loss.

6. Ensure proper institutional permitting is up to date, held, and available for inspection. This includes national level permits for CITES-listed plants, relevant import/export permits, permits for plants deemed illicit, and any additional permits required by sub-national jurisdictions. Sampling should be restricted wherever possible to specimens that can be clearly documented with all relevant permits. We recognize that this high standard is not always possible with older material, but it should be standard practice with newer collections, which are also preferable in terms of metabolites and DNA quality (see Best Practice #4 for Herbarium Users;[30])

7. Destructive sampling should coincide with barcoding and specimen digitization. Every specimen should be barcoded, imaged, and transcribed, ideally *prior* to destructive sampling. Users should be asked to support financially or, if staffing is unavailable, help input these data following institutional guidance and standards at the time of sampling. A visit is not considered complete until this essential bookkeeping is finished. Stewards should also expect that users will verify and update the taxonomic accuracy of each specimen sampled, which for some groups and regions of the world may be highly inaccurate[47]. Ensuring that researchers inform herbaria of newer, better determinations is critical to the vitality and continued relevance of herbaria.

Relatedly, stewards should coordinate with organizations, networks, and initiatives to provide greater access to herbarium resources (e.g., GBIF, iDigBio, DiSSCo, and BCoN), further extend specimen data, and grow the Global Metaherbarium[2,49]. Annotations of collections for multiomic sampling should be added to the digital specimen record with the associated researcher who collected the sample and the focal project (**Fig. 3**). These efforts should also be further coordinated with ongoing large efforts to sequence genomes across

the Tree of Life, such as the Earth Biogenome Project[60], the African Biogenome Project[61], and the 10,000 Plants Genome Project[62]. Multiomics data arising from the conducted research always should be made available in publicly accessible databases within a reasonable period regardless of its publication status. Herbaria should consider restricting sampling of their material if this is not the case.

8. Maintain thorough records and hold users accountable. Ideally, an institution should be able to link any specimen cited in a publication resulting from destructive sampling directly to an MTA or DUA certifying the researcher had permission to take that material and use it according to the reported methods. When researchers fail to honor the conditions of these agreements (e.g., deliberately sampling specimens not included in the MTA, using materials for different projects than the ones proposed, withholding data resulting from samples), they should be prevented from future access. Repeat offenders should be reported to their institutions and to the herbarium community so other collections can protect their specimens accordingly. Using material without permission is theft and makes the task of responsibly safeguarding collections impossible.

9. Destructive sampling requests should balance the importance of current discovery against future needs. This is complicated and potentially more subjective, but nevertheless important. Certain research questions and potential discoveries ensuing from them should be prioritized for destructive sampling, especially when rare or sensitive specimens are under consideration. This includes extinct species and populations, and species central to humankind, including not only crops and their wild relatives but also plants of medicinal and spiritual importance. At present, crops and their wild relatives are not well preserved in seed banks and germplasm resources[63]. However, when available, such material allows researchers to grow plants for study, thus obviating the need to sample herbaria and expanding their ability to conduct broader investigations. The same likely applies to other plants of human use. Herbaria offer another important and underused path to preservation of these groups and should be treated with great care and caution. Permission to sample these collections should be granted only in cases where research promises to add

567 significant additional value to the extended specimen and where we should do our very
568 best to facilitate these advancements for the benefit of humanity.
569
570 *10. Establish transparent policies for destructive sampling and treat them as 'living*
571 *documents.'* Biodiversity will continue to change. Similarly, new science will develop and
572 lead to new technologies. It is important that documentation on how specimens may be
573 sampled in herbaria also evolve. Herbarium steering committees, leadership teams,
574 curators, staff, researchers, and other stakeholders should work to keep these documents
575 current and relevant to facilitate responsible stewardship and support impactful science.
576 Although some amount of judgment by collections stewards will always be necessary,
577 guidelines for researchers about sampling policies should be as clear and consistently
578 applied as possible. Ideally, these policies should form part of the broader strategic plan for
579 any herbarium that explicitly balances preservation with use. Although institutions will
580 vary in their needs and resources and it is impossible to establish a one-size-fits-all policy,
581 there is value to both the herbarium community and its various users in having consistent
582 guidelines across institutions.
583
584 **Summary and conclusions**

585 New technologies have revolutionized the uses of herbarium specimens, yielding
586 invaluable insights into evolution, ecology, taxonomy, conservation, ethnobotany, history,
587 and the social sciences. Although these developments have been exciting and herbaria have
588 certainly benefited from a renewed global interest in their resources, a lack of clear
589 community guidelines and best practices for destructive sampling of irreplaceable
590 specimens risks the long-term sustainability of the only verifiable record of plant and
591 fungal life on Earth. The lack of best practices also places undue burdens on the stewards
592 and users of these collections, resulting in needless confusion and consternation.

593 We have outlined here what we hope will be a starting point for much-needed
594 conversations within and among herbaria and their associated research communities. The
595 more than 3,500 herbaria across the globe [1] are nearly as diverse as the specimens they

596 contain, so it is nearly impossible to write one-size-fits-all prescriptions. We hope the
597 recommendations presented here will be a useful framework for the community to begin to
598 clarify and create a path towards greater common understanding about how herbarium
599 specimens can be sampled sustainably and responsibly while continuing to expand our
600 knowledge and understanding of botanical diversity and preserve their use for generations
601 to come.

602 Although we have suggested separate recommendations for users and stewards, we feel
603 strongly that progress requires that both users and stewards better understand and
604 appreciate one another's needs and concerns. Taken collectively, our proposed best-
605 practices will help ensure that: i) physical collections will be preserved indefinitely and will
606 continue to grow for the benefit of future generations; ii) the expertise required to build
607 and maintain collections will be valued, recognized, and cultivated; iii) the rights of nations
608 and Indigenous communities for their biodiversity and knowledge will be respected; iv)
609 access to samples for research will be fair and equitable; and v) knowledge generated from
610 destructive sampling will build upon and complement the expanded specimen network,
611 creating a truly powerful, accessible, and comprehensive Global Metaherbarium.

612

613 **Author Contributions**

614

615 CCD, JT, AP, AA, and ES jointly conceived the premise of this paper. CCD wrote the paper
616 with key initial editorial input on the stewards and conclusions sections from JT. All
617 authors revised and approved the final text. Figures were coordinated and/or compiled by
618 CCD, Jackson Kehoe, Lucas Marino, and Megumi Kirby.

619

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621

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