HERBARIUMS AS BIG DATA SOURCES OF PLANT TRAITS

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Herbarium specimens have long been a cornerstone of taxonomic research but are only recently being recognized for their potential as a source of spatially and temporally extensive data on plant functional traits. Many researchers in trait-based disciplines, including functional ecologists and evolutionary biologists alike, remain surprisingly unaware of this powerful use of herbaria. This review brings together disparate studies to synthesize the past, current, and potential future uses of specimens as functional trait data sources, answering the following questions. First, what insights using specimens (including traits measured, approaches used, and research questions answered) have been made to date? Second, what new trait-based insights (including potential contributions to global trait databases and recent advancements such as machine learning and high-throughput phenotyping) can be made from herbarium specimens? And third, how can inherent limitations and collection biases be addressed when using specimens in unanticipated ways (including new analytical approaches and improved methods for collecting)? I conclude by identifying what is needed to foster the future of herbaria as big data sources of plant traits. Most notably, plant collecting must be continued, expanded beyond predominantly systematists, and intentionally revised with downstream trait measurements in mind. Furthermore, community-wide standards are needed to integrate otherwise disconnected data and directly link newly derived measurements back to specimen records. Specimens serve as reliable (and necessary) sources of phenotypic data, enabling us to answer questions across phylogenetic, temporal, and spatial dimensions that are otherwise not possible to answer. Herbaria should be embraced as centers for functional trait research.

Keywords: functional trait ecology, herbarium, museum digitization, natural history collections, phenomics, specimen.

Introduction: A New Relevance of Herbarium Specimens

More than 3000 active herbaria located across the world collectively serve as an enormous, shared, and increasingly connected scientific resource that documents botanical diversity through time and across space (Thiers 2021; fig. 1). With a staggering 396 million specimens (and counting), these collections represent all formally described plant species—an intense, ongoing effort of many thousands of botanists on every continent for more than four centuries. Each specimen contains not only the physical plant itself but also associated data on specimen labels, including collection location and notes made by the collector. The act of collecting from nature is an ancient practice, preserving what would otherwise be ephemeral as more permanent objects for admiration and study. With likely earlier roots, the mounting of dried, pressed plants to paper is attributed to have originated in Italy in the early sixteenth century, and the earliest existing collection dates to the sixteenth century (Lane 1996; Stefanaki et al. 2019). A growing interest in the natural world, in exploration, and in the development of the scientific method together contributed to rapid growth in the number of herbaria, many of which remain today (Funk 2018). Centuries later, the practice of plant collecting, curation, and specimen use continues, with an ever-increasing relevance to science and society (Heberling et al. 2019).

Historically, herbaria and other natural history collections were physical and intellectual spaces dominated by taxonomists. Understandably, collections-based research still emphasizes describing biodiversity: describing new species, resolving taxonomic relationships, and compiling species checklists to document what organisms have lived where and when (Funk 2018). The need for solid taxonomic research has only intensified in an era when the applied knowledge needed for effective biodiversity conservation is at an all-time high (Grace et al. 2021). The well-established conventional uses of herbaria can be placed into five non–mutually exclusive categories, as follows.

1. Taxonomy and systematics. Herbaria are essential as the foundation of taxonomic and systematic studies (Prather...
et al. 2004a; Wen et al. 2015), including the discovery and description of plant species, botanical nomenclature, and taxonomic monographs and revisions. Herbaria are where most plant species discovery and description occur, with estimations that most undescribed species are already sitting in herbarium cabinets awaiting study (Bebber et al. 2010). Any formal description of a new taxon must designate a type specimen that forever anchors that species name to a representative collection.
that can be referenced by future researchers. Taxonomic studies routinely include lists of specimens that were used to develop taxonomic circumscriptions and descriptions.

2. Floristics and biogeography. Herbarium record botanical biodiversity over space and time (Pyke and Ehrlich 2010). Herbarium specimens enable floristic inventories, as well as studies of distribution changes over time, species invasions, ecological patterns of biodiversity, and plant biogeography (Prather et al. 2004b; Lavoie 2013; Wen et al. 2015). This use of specimens has increased dramatically because of species distribution modeling (Soltis 2017), and many biogeographic studies rely not on the physical specimens themselves but on their associated metadata.

3. Species identification. With no specimens to reference, it is difficult or impossible to definitively confirm or reconsider a plant’s identity as taxonomic and nomenclatural knowledge increases (Goodwin et al. 2013).

4. Scientific vouchers. Voucher specimens serve as a record of the actual plants studied as opposed to simply their asserted identity in publications (Funk et al. 2005). Specimens are the primary plant biological data enabling verifiability and repeatability—of growing importance with the recent cultural shift toward “open science” (Schilthuizen et al. 2015).

5. Education. The long association of natural history collections with museums and universities has meant that since the inception of herbaria, plant specimens have played a role in education, including public education via exhibits and museum programming as well as direct classroom use. Educational use of specimens is growing rapidly because of increasing access to specimen data and images and the concomitant focus on inquiry-based and active learning (e.g., Cook et al. 2014; Monfils et al. 2017).

However, the scientific relevance of herbaria has diversified well beyond these core uses. Many herbarium uses that are now mainstream were completely unanticipated by plant collectors and curators just decades ago (Heberling and Isaac 2017). These uses include, for example, the extraction of genetic material from century-old specimens (Hart et al. 2016) and the quantification of changing plant-insect interactions (Meineke and Davies 2019). The realized importance of specimens is widening across the humanities and natural sciences alike. New uses for specimens continue to be actively explored.

Recently developed methods and tools have undoubtedly contributed to the diversification of herbarium use. These methodological advancements have deepened our ability to answer long-standing questions within historically herbarium-based disciplines (e.g., systematics) but have also enabled altogether new uses across fields. New molecular methods such as next-generation sequencing have made the extraction of genetic material from herbarium specimens possible—a developing field aptly named “museomics.” Such molecular advances have provided new phylogenetic insights into extinct species (e.g., Zedane et al. 2016) and have detected genetic changes to introduced species as they spread across the landscape over decades to centuries (e.g., Vandepitte et al. 2014). Other recent developments in modeling techniques, perhaps most notably species distribution/niche modeling using digitized specimen label data alone (Soltis 2017), have given newly perceived research value to herbarium use.

The motivating force behind most, if not all, of this new wave of herbarium use is the digitization of museum specimens. Although it started decades ago, specimen digitization has picked up steam within the past decade because of the birth of widespread nationally funded digitization initiatives across the world (Nelson and Ellis 2018), many of which are either ongoing or expanding in scope. Specimen digitization broadly includes (1) transcribing specimen label information to searchable databases, (2) georeferencing (assigning coordinates to specimen localities), and (3) creating high-resolution digital images of each specimen. The world’s collections are at various stages of digitization that are far from complete. Digitization is an ever-ongoing process, and the association of other metadata, such as relevant field notes, is very much in its infancy (Hedrick et al. 2020; Lendemer et al. 2020).

Museum digitization efforts have transformed how we access and engage with specimens (Soltis 2017; Hedrick et al. 2020). Rather than having to visit or request loans from collections individually, one can now make exhaustive searches across many collections simultaneously through online open-access consolidated data portals. Digitization makes specimens more findable. Second, high-resolution images further facilitate access to physical specimens and research uses for the digital images themselves. For example, more than 85 million plant specimens are now digitally available through the Global Biodiversity Information Facility (GBIF; https://gbif.org) alone, with roughly 40 million georeferenced and nearly 33 million with images (GBIF 2021b; fig. 1B). Many of these digitized data became available only in the past decade, being powerfully leveraged alongside observational data and community science programs (Heberling et al. 2021). Digitization of the world’s herbaria continues, with more and more data coming online each day. Burgeoning perspectives further expand these digitization efforts, recognizing the largely untapped value of other data streams collected alongside or otherwise adding context to specimens, such as field notes, ecological data, and associated climate data (Lendemer et al. 2020).

**Developments in Functional Trait Theory**

Meanwhile, independent of these developments unfolding in herbaria, the past 20 years have also witnessed a transformation in the use of plant functional traits to advance community ecology as a predictive mechanism-based discipline (McGill et al. 2006). Functional traits are defined as any morpho-physio-chemical-phenological characteristics that serve as proxies for understanding individual fitness (Violle et al. 2007). It is the indirect connection to performance and fitness via growth, reproduction, and survival that makes a trait “functional.”

Studying biodiversity and plant performance through functional traits has launched a new era of understanding plant strategy in the context of ecological, evolutionary, and physiological trade-offs. Notably, Wright et al. (2004) reported a global pattern of coordinated variation in leaf traits, the “leaf economics spectrum” (LES), which describes a general ecophysiological trade-off surface. Even with just a handful of relatively easy-to-measure traits, the LES describes a continuum from species with slow returns on resource investment (e.g., high leaf mass per area, high construction costs, low photosynthetic rates, and long leaf life span) to species with quick returns on investment at the opposite extreme. This main axis of variation runs from traits associated with resource acquisition (“fast”) to those
associated with resource conservation (“slow”; Reich 2014). Patterns that lie outside this trait trade-off surface are presumed to be maladaptive (selected against) or biophysically impossible (Reich et al. 1999). This “slow-fast” continuum is central to plant strategy theory, expanding toward a suite of traits that define species’ functions along trade-off spectra of whole plants and component tissues (e.g., leaves, wood, roots, flowers), as well as within species.

This new wave of functional trait studies shows that a few powerful traits can predict plant function and even scale to ecosystems (Westoby et al. 2002; Reich 2014). At their core, ecologists are increasingly measuring biodiversity not based on taxonomic identity and abundance alone but are rather using traits as the metrics to understand and predict population, community, and ecosystem processes. Plant strategies can be quantified by ecophysiological trade-offs that serve as axes of differentiation along a spectrum of coordinated trait variation.

**Bringing Together Functional Ecology and Natural History Collections**

Most of the foundational studies solidifying this functional trait perspective in plant ecology (e.g., Reich et al. 1997, 1999; Díaz et al. 2004, 2016; Wright et al. 2004) were possible only because of the compilation of many trait data sets collected from many sites and biomes across the world—a clear strength of herbaria (fig. 1B). Yet herbarium-derived trait data were scarcely used. Many functional trait ecologists simply remain unaware of the value that specimens can bring to their research questions. Conversely, many herbarium-based researchers are unaware of the functional trait literature and newly appreciated insights that can be gained from herbarium-derived trait measurements. Although specimens have received much attention for their potential as vast sources of genetic data (e.g., Hart et al. 2016) and in the context of global change biology (e.g., Meineke et al. 2018; Lang et al. 2019), little to no explicit attention has been paid toward specimens as primary sources of trait data (but see Queenborough 2017). A focused synthesis of realized and potential uses of herbarium specimens in plant trait research is needed to effectively foster the development of this wide-ranging and impactful use of specimens.

In this review, I integrate two areas of research developed by two mostly nonoverlapping groups of researchers—functional trait ecologists and collections-based biodiversity scientists. First, I describe the known value of herbaria in trait research through a compilation of studies that highlights questions asked and approaches used. Second, I explore the potential value of herbaria in trait research, including efforts toward the automation of trait measurements at a mass scale and the largely untapped potential contributions of herbaria to global trait databases. Third, I address the limitations of using herbarium specimens for trait research with possible ways to alleviate concerns leading to hesitation about their use. I conclude by looking to the future, proposing paths for improving trait and herbarium-based research, and embracing herbaria as centers of functional trait research.

As the functional roles of many traits may be assumed rather than tested, I use “functional trait,” “trait,” and “phenotype” interchangeably throughout this review, leaving debate as to the interpretive meaning of specific traits elsewhere. I limit the scope of this review to kingdom Plantae (mostly extant vascular plants) and exclude nonplant or fossil collections that are frequently curated under the umbrella of herbaria, such as fungi, lichen, diatom, and paleobotanical specimens. However, the themes in this review can be similarly extended to these and many other natural history collections.

**The Known Value of Herbaria for Functional Trait Research**

At face value, the notion of measuring traits from specimens is far from new. In a use ingrained since the very establishment of herbaria centuries ago, specimens were collected to provide identifying information. However, measurements were generally limited to visual descriptions, species-level means, or minimum/maximum ranges of trait values for identification purposes or for distinguishing taxa in the context of taxonomic or floristic study. For example, trait information listed in floras, taxonomic monographs, field guides, or dichotomous keys is mostly derived from the examination of many specimens collected across species’ ranges. However, in this context, trait information at the individual level is lost. Furthermore, the explicit connection back to the specimen(s) measured is rarely documented and is subsumed into species-level trait values included in formal taxonomic species descriptions. Although these secondary data in taxonomic treatments and floras can indeed provide useful trait summaries that permit quantitative analysis of certain questions (Cutts et al. 2021), the full value of specimens is not realized. The failure to record measured trait values linked to individual specimens is no fault of previous researchers. Instead, it is a product of the historically dominant motivation behind herbaria and specimen collection (e.g., taxon-level floristic study) and the fact that functional trait ecology as a discipline in its current form is far newer than herbarium practice. This use of specimens for functional trait data was unanticipated until recently (Heberling and Isaac 2017).

Influenced by developments in traits-based ecology and the advent of global change biology, there has been a recent surge in herbarium-based studies of phenotypic change through time and space. Although several early pioneering studies exemplified specimens as sources of functional trait data for analyzing change over time, space, and phylogeny (e.g., Woodson 1947; Desmarias 1952; McConnell and Russell 1959), the majority of these studies were published in the twenty-first century, motivated by recent developments in functional trait theory (e.g., Reich 2014).

Comprehensive, systematic review of specimen uses is difficult, as many studies do not cite herbarium use directly or at least not in an obvious way. The main reason that herbarium use for trait data often goes uncited is that it is simply expected (in the case of taxonomic studies) or the methods are often secondary (i.e., deemed too tangential to mention in study titles or abstracts). Specimen use becomes apparent only through careful reading of methods sections or is tucked away in supplemental information, thereby making literature keyword searches difficult and incomplete (Heberling et al. 2019). The uses of specimens as phenotypic data sources are broad, spanning a range of applications (e.g., ecology, evolution, anatomy, physiology, chemistry, and narrow subfields within). Therefore, these uses are widely equally spread across many topic areas and readerships of scientific journals.
Here, I consolidate these disparate uses of herbarium specimens in trait biology (table 1). I admit that this approach is far from systematic but rather has developed over years of ongoing compilation of herbarium-based studies that have emerged over the course of my own functional trait research. Table 1 serves as a near-comprehensive (although not exhaustive) list of herbarium-derived traits, providing citations to published studies that explicitly state herbarium-derived measurements in the main text or supporting information. Although some of these studies are well cited, the depth of the trait information that can be quantified and the questions asked using specimens are underappreciated. Below, I review these herbarium-based studies by trait categories, highlighting a subset of exemplars to showcase the known value of herbaria for functional trait research.

Phenology

Phenology, or the seasonal timing of life history events, has emerged as a major area of study. This rapid rise in phenological studies in recent decades is no doubt because phenology has been well demonstrated as especially sensitive to climate change, has clear implications scaling from individuals to species interactions, and is visually apparent to the broader public. Given the dynamic and multifaceted aspects of phenology, it is often treated as being conceptually distinct from other functional traits and therefore is not included or is treated separately in many functional trait reviews. However, phenology is included explicitly in the leading functional trait definition (Violle et al. 2007) and is of clear ecophysiologica relevance to contextualizing the functional value of other traits.

Herbarium specimens are now well recognized as sources of phenological data (Willis et al. 2017a), perhaps now even a leading use of specimens. With identification purposes in mind, botanists have long focused on collecting specimens that include reproductive parts (e.g., flowers and/or fruits), which since even before Linnaeus were regarded as critical to distinguishing species. After centuries of collecting, herbaria have become enormous unintentional repositories of phenological data. As indicated by the large number of phenology studies cited in table 1, the use of specimens in phenological research has received the most attention among all traits and remains an active area for specimen use. Unlike other traits, phenological research using herbarium specimens is extensively reviewed elsewhere (in particular, see Willis et al. 2017a; Jones and Daehler 2018). Therefore, I only briefly review these uses and emphasize more recent developments.

Mining herbarium specimens for phenological information in a broad sense is not new, but the way we extract and use this phenological information has drastically changed. Regional to global taxonomic treatments and field guides frequently include the flowering windows of many species (e.g., start and end months), presumably derived at least in part using herbarium references of specimens collected across the species’ ranges. However, in the context of climate change, herbaria have become recognized as a major source of historical data, that is, verifiable evidence for the flowering time of a plant at a given time and place. When paired with historical climate data, herbarium specimens enable analyses of species-level phenological sensitivities to temperature (i.e., the degree to which species shift flowering time; days per degree Celsius). In perhaps the earliest study to extract phenological data from specimens in this way, McConnell and Russell (1959) analyzed the response of flowering time to changes in photoperiod across the North American range of two widespread Viola species. This study is surprisingly undecited and is ripe for follow-up study with new analytical tools and specimen access through specimen digitization. It was not until decades later that specimens became appreciated for explaining mechanisms and impacts of phenological change across species through time and space.

Although earlier examples exist in the literature, the modern use of herbarium specimens as sources of phenological data was strongly inspired by an article by Primack et al. (2004), a landmark study that convincingly demonstrated the value of herbaria for understanding the impacts of climate change. Comparing the current timing of flowering in living plants with that assessed from herbarium specimens, they found that plants flowered an average of 8 d earlier over the past century in Boston, Massachusetts, which had increased in mean annual temperature by 1.5°C since 1900. A follow-up study further validated the herbarium approach by also supplementing the data set with historical photographs (Miller-Rushing et al. 2006). In addition to the Boston-based study, it was further validated that herbarium specimens can also be extended to much larger areas (Lavoie and Lachance 2006), as specimens are more intensively collected across the species’ range rather than repeatedly collected in the same location. Numerous herbarium-based phenological studies followed, and publication rates of herbarium-based phenological studies have only increased with time (table 1). A decade later, Davis et al. (2015) further validated the use of specimens not only to understand phenological responses to temperature across species and space but also to attribute these responses to specific phenological cuing mechanisms (e.g., spring forcing, winter chilling, photoperiod) at the species level. Statistical methods have even been developed to evaluate phenological responses in continuously flowering species (Daru et al. 2019; Lima et al. 2021). Quantifying the differences and understanding the ecological impacts of mismatches in species-level phenological responses to the environment remain active areas of research, with herbarium specimens at the forefront.

Most herbarium-based phenological studies focus on flowering time, but several recent studies have expanded into other areas of phenology, such as the timing of leaf out. Many deciduous woody species flower shortly before, during, or after leaf out. Since many specimens are purposefully collected in flower, these collections also uniquely capture early stages of vegetative phenology. As with many traits, this use was likely not necessarily the intent of the collector but is useful nonetheless. Everill et al. (2014) capitalized on this aspect of collecting behavior to study leaf out times of 27 woody species across a time span of 175 years in New England. Despite only 15% of the examined specimens having young leaves, the study demonstrated the vast potential of specimens as sources of historical leaf out data. Since then, surprisingly few studies have used herbarium specimens for leaf out data (table 1). However, given the critical importance of vegetative phenology to understanding individual performance and ecosystem carbon dynamics in light of global change factors, the use of specimens as data on the timing of leaf out will likely become more prevalent.

Likewise, many specimens are collected in fruit, making them amenable to explaining the drivers and consequences of fruiting
| Trait, unit                                      | Destructive sampling required? | Biological relevance* | Representative reference(s) using specimensb |
|------------------------------------------------|-------------------------------|-----------------------|-----------------------------------------------|
| **Whole-plant level:**                         |                               |                       |                                               |
| Plant height and internode length (mm)         | No                            | Plant strategy axis: competitive ability, stress tolerance, response to abiotic/biotic stressors | McGraw 2001; Law and Salick 2005; Ronse et al. 2010; Buswell et al. 2011; Leger 2013; Rollins et al. 2013; Dalrymple et al. 2015; Flores-Moreno et al. 2015; Sritharan et al. 2021 |
| Growth form and habit (categorical)            | No                            | Functional group adaptations | e.g., Engemann et al. 2016 |
| Pathogen/symbiont occurrence (presence/absence)| No/yes                        | Disease dynamics and susceptibility; associations with endophytes, mycorrhizal fungi, and other symbionts | White et al. 1992; Ristaino 1998; Koponen et al. 2000; Antonovics et al. 2003; Hood and Antonovics 2003; Alexander et al. 2007; Li et al. 2007; Malmstrom et al. 2007; Hood et al. 2010; Saville et al. 2016; Ingram et al. 2017; Heberling and Burke 2019; Smith et al. 2021 |
| Spinescence or armature (presence/absence)    | No                            | Herbivory defense | e.g., Xu et al. 2020 |
| Extralobar nectaries (presence/absence)       | No                            | Plant-insect interactions, defense | e.g., Weber and Keeler 2013 |
| **Stem level:**                                |                               |                       |                                               |
| Branch wood specific gravity (dimensionless)   | Yes                           | Wood economics strategy axis: structural investment | Perez et al. 2020 |
| Young stem thickness (cm)                     | No                            | Structural investment | Guzmán et al. 2018 |
| Domatia of stems or leaves (presence/absence, abundance) | No | Plant-insect interactions, defense | e.g., Mound 1993; Tillberg 2004; Romero et al. 2019 |
| **Leaf level:**                                |                               |                       |                                               |
| Leaf size or shape metrics:                   |                               |                       |                                               |
| Leaf area (mm²), leaf perimeter (mm), leaf width and length (mm), conifer needle length (mm), leaf length-to-width ratio, petiole, rachis length (mm), and other morphological metrics (e.g., multivariate geometric morphometrics; leaf margin: toothiness, dissection) | No | Plant strategy axis: light interception, water balance, nutrient status, thermoregulation | e.g., Woodson 1947; Desmarais 1952; Martin 1965; Backhaus et al. 2010; Knaus 2010; Buswell et al. 2011; Peppe et al. 2011; Blonder et al. 2012; Corney et al. 2012a, 2012b; Guerin et al. 2012; Schmerler et al. 2012; Dalrymple et al. 2015; Flores-Moreno et al. 2015; Onstein et al. 2016; Tomaszewski and Górzewska 2016; Beauvais et al. 2017; Stropp et al. 2017; Václavik et al. 2017; Guzmán et al. 2018; Petulañas and Gudžiūnės 2018; Smith et al. 2019; Borges et al. 2020; Buitrago Ariasitizabal et al. 2020; Weaver et al. 2020; Komineni et al. 2021 |
| Leaf compoundness or type (categorical)        | No                            | Light capture, structural investment | e.g., Lohbeck et al. 2013 |
| Leaf mass per area (mm² g⁻¹) = 1-specific leaf area (g mm⁻²) | Yes/No                        | Leaf economics: carbon investment, photosynthetic rate, leaf life span, construction cost | Peñuelas and Matamala 1990; Royer et al. 2010; Bonal et al. 2011; Buswell et al. 2011; Blonder et al. 2012; Queenborough and Porras 2014; Reef and Lovelock 2014; Dalrymple et al. 2015; Flores-Moreno et al. 2015; Perez et al. 2020 |
| Vein-related traits:                           |                               | Carbon economics: hydraulics and photosynthetic capacity | Walls 2011; Schneider et al. 2017, 2018 |
| Trait, unit | Yes/No | Representative reference(s) using specimens |
|-------------|--------|---------------------------------------------|
| Leaf thickness (mm) | Yes⁴ | Structural investments, leaf toughness, gas exchange, thermoregulation (Parkhurst 1978; Blonder et al. 2012; Perez et al. 2020) |
| Tissue chemistry: | | |
| Nutrients: | Yes | Nutrient-use strategy and/or nutrient availability (Peñuelas and Matamala 1990, 1993; Baddeley et al. 1994; Peñuelas and Estiarte 1997; Peñuelas and Fikl 2001; Wikon et al. 2009; Hietz et al. 2011; Delgado et al. 2013; Gritcan et al. 2016; Huang et al. 2016; DeLeo et al. 2020) |
| N, C, P, K (%), C:N and N:P ratios, other minerals (e.g., Al, Fe, Mg, Ca, Sr, S) | | |
| Heavy metals: | Yes | Plant hyperaccumulation, environmental pollution (Jaffre et al. 1979a, 1979b; Kersten et al. 1979; Herpin et al. 1997; Agnan et al. 2015; Rudin et al. 2017; Miller et al. 2020) |
| Pb, Zn, Ni, Cu, Cr, Co (%) | | |
| Other trace elements: | No | Estimate of directly measured similar chemical traits listed above (van der Ent et al. 2019; Gei et al. 2020) |
| Ni, Mn, Co, Zn, Hg (μg g⁻¹) via X-ray fluorescence “ionomics” | Yes | Water-use efficiency, past environmental conditions, photosynthetic pathway (CAM, C₃, C₄) (Peñuelas and Azcón-Bieto 1992; Peñuelas and Estiarte 1997; Peñuelas and Filella 2001; Pedicino and Leavitt 2002; Tice et al. 2002; Helliker and Griffiths 2007; Miller-Rushing et al. 2009; Wilson et al. 2009; McLauchlan et al. 2010; Bonal et al. 2011; Hietz et al. 2011; Tripp and Fatimah 2012; Delgado et al. 2013; Gritcan et al. 2016; Huang et al. 2016; Komer et al. 2016; Hobbie et al. 2017; DeLeo et al. 2020; Torres-Morales et al. 2020; Siniscalchi et al. 2021) |
| Stable isotopes: | Yes | Proxy for long-term shifts in carbon metabolism, photorespiration-to-photosynthesis ratio (Ehlers et al. 2015) |
| Δ¹³C, δ¹³C, δ¹⁵N, δ¹⁸O (%) | | |
| Deuterium isotopomers (D⁶/D⁶⁺ ratio) | Yes | Water-use efficiency, gas exchange regulation (Aalders and Hall 1962; Parkhurst 1978; Woodward 1987; Peñuelas and Matamala 1990; Beerling and Chaloner 1993; Beerling and Woodward 1993; Paolotti and Gellini 1993; Beerling and Kelly 1997; Chen et al. 2001; Tice et al. 2002; Kovenberg et al. 2003; Wagner et al. 2005; Miller-Rushing et al. 2009; Wagner-Cremer et al. 2010; Bonal et al. 2011; Tripp 2012) |
| Spectral reflectance (%) | No | Estimate of directly measured structural and chemical traits listed above (e.g., leaf mass per area, leaf N) (Costa et al. 2018; Kothari et al. 2021) |
| Macromolecules (%) | Yes | Protein, fatty acid, and amino acid composition (Tice et al. 2002; Miller et al. 2020) |
| Secondary metabolites: | | |
| Flavones (μg g⁻¹), pyrrolizidine alkaloids (μg g⁻¹), and glucosinolates (presence) | Yes | Defense against herbivory or ultraviolet damage (Ryan et al. 2009; Mithen et al. 2010; Colegate et al. 2014; Tasca et al. 2018) |
| Trichome density (hairs cm⁻²) and trichome length (cm) | No⁵ | Defense against herbivory or ultraviolet damage, water conservation (Goertzen and Small 1993; Steets et al. 2010; Václavik et al. 2017) |
| Stomata-related traits: | | |
| Density (no/mm²), abaxial-to-adaxial ratio, and stomatal size (μm²) | No/Yes | Water-use efficiency, gas exchange regulation (Aalders and Hall 1962; Parkhurst 1978; Woodward 1987; Peñuelas and Matamala 1990; Beerling and Chaloner 1993; Beerling and Woodward 1993; Paolotti and Gellini 1993; Beerling and Kelly 1997; Chen et al. 2001; Tice et al. 2002; Kovenberg et al. 2003; Wagner et al. 2005; Miller-Rushing et al. 2009; Wagner-Cremer et al. 2010; Bonal et al. 2011; Tripp 2012) |
| Trait, unit                                                                 | Destructive sampling required? | Biological relevance* | Representative reference(s) using specimens* |
|---------------------------------------------------------------------------|-------------------------------|------------------------|---------------------------------------------|
| **Herbivory/granivory damage (% tissue loss, presence/absence, sooty mold)**| No                            | Insect activity and plant susceptibility | Morrow and Fox 1989; Goertzen and Small 1993; Zangerl and Berenbaum 2005; Veenstra 2012; Youngsteadt et al. 2015; Schilthuizen et al. 2016; Beauvais et al. 2017; Meineke et al. 2018, 2019, 2020, 2021; Beaulieu et al. 2019; Meineke and Davies 2019; Moore et al. 2021 |
| **Leaf or stem domatia (presence/absence, abundance)**                   | No                            | Plant-insect interactions, defense | Mound 1993; Tillberg 2004; Romero et al. 2019 |
| **Flower, fruit, or propagule level:**                                    |                               |                        |                                             |
| Seed chemistry, for example, foranocoumarins (mg)                         | Yes                           | Secondary metabolites, lipid composition | Berenbaum and Zangerl 1998; Zangerl and Berenbaum 2005 |
| **Flower-, fruit-, or propagule-related morphometrics:**                  |                               |                        |                                             |
| Petal size (mm²), flower no., stamen anatomy, seed no. per fruit, seed mass (mg), fern spore size (mm), and other morphometrics | Yes/no*                       | Flower economics, reproductive output, plant-pollinator interactions, dispersal distance/colonization ability, seed output, seedling survival, ploidy level, pollination success | Barrington et al. 1986; Lambinos 2003; Carpenter et al. 2003; Knaus 2010; Bontrager and Angert 2016; Yu et al. 2016; Schenck and Saunders 2017; Chen et al. 2018; Guzmán et al. 2018; Sukhorukov et al. 2018; Duan et al. 2019; Kissing et al. 2019; McAllister et al. 2019; Buitrago Aristizábal et al. 2020; Kljuykov et al. 2020; Svoma et al. 2020 |
| Floral or fruit pigmentation (e.g., petal ultraviolet proportion, color)  | No                            | Plant-pollinator interactions, thermoregulation | Horovitz and Cohen 1972; Koski and Ashman 2016; Kissing et al. 2019; Koski et al. 2020; Sullivan and Koski 2021 |
| Pollen-related traits from anthers and/or stigmas:                       |                               |                        |                                             |
| Pollen identity, morphology, chemistry, and protein                      | Yes                           | Pollen transport networks, pollen limitation, food quality for pollinators | Tripp and Fatimah 2012; Ziska et al. 2016; Johnson et al. 2019; Torres-Montúfar et al. 2020 |
| Trait, unit | Destructive sampling required? | Biological relevance | Representative reference(s) using specimens |
|------------|-------------------------------|----------------------|---------------------------------------------|
| Phenology (timing of discrete events or continuous phenophases): | | | |
| Leaf out date (day of year) | No | Growing season length, understory light acquisition, responsiveness to environmental cues and changes, frost risk | Evenill et al. 2014; Zohner and Renner 2014; Ellwood et al. 2019; Zohner et al. 2020 |
| Fruit maturation (e.g., first, peak, and last fruit [day of year]) | No | Seed dispersal, frugivory, senescence in response to environment | Diskin et al. 2012; Barve et al. 2015; Munson and Sher 2015; Mulder et al. 2017; Willis et al. 2017; Gallinat et al. 2018; Ellwood et al. 2019; Love et al. 2019; Park et al. 2019; Lima et al. 2021; Miller et al. 2021 |
| Flowering date (e.g., first, peak, and last flower [day of year]) | No | Reproductive opportunity, plant-pollinator interactions, human allergens, responsiveness to environmental cues and changes, frost risk | McConnell and Russell 1959; Russell 1960; Borchert 1996; Carpenter et al. 2003; Primack et al. 2004; Bolmgren and Lonnberg 2005; Lavoie and Lachance 2006; Miller-Rushing et al. 2006; Houle 2007; Gallagher et al. 2009; Neil et al. 2010; von Holle et al. 2010; Robbirt et al. 2011; Zalamea et al. 2011; Diskin et al. 2012; Panchen et al. 2012; Calinger et al. 2013; Diez et al. 2013; Li et al. 2013; Hart et al. 2014; Barve et al. 2015; Berin 2013; Davis et al. 2015; Kharouba and Vellend 2015; Munson and Sher 2015; Park and Schwartz 2015; Pei et al. 2015; Rawal et al. 2015; Matthews and Mazer 2016; Park 2016; Yu et al. 2016; Mulder et al. 2017; Munson and Long 2017; Willis et al. 2017b; Berg et al. 2019; Daru et al. 2019; Ellwood et al. 2019; Park et al. 2019; Pearson 2019b; Kopp et al. 2020; Song et al. 2020; Neto-Bradley et al. 2021; Park et al. 2021; Renner et al. 2021 |

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*a Some examples of proximate biological functions are given here for context, but traits need not be “functional” (i.e., correlated to fitness) to be useful for taxonomic research (e.g., taxon delimitation and descriptions) and comparative biology (e.g., trait discriminant analyses).

*b This is intended as a useful, near-comprehensive bibliography highlighting studies that derive trait data from specimens. However, the list is not exhaustive, especially for more commonly measured traits, such as phenology, or for studies in which herbarium use was less obvious.

*c The use of standard digitized specimen images is sufficient for accurate measurement.

*d Tissue removal from the specimen is required for measurement(s), but it can be returned after measurement (remounted or placed in a fragment packet).
phenology. Fruit windows are generally much longer than those of flowers, with complete fruit maturation taking up to several months or more before seeds are dispersed. However, given the large number of specimens that include fruit, estimating the timing of first, peak, and last fruit is possible. Gallinat et al. (2018) used herbarium specimens to assess fruiting patterns across native and invasive species in New England, finding later fruiting times in invasive species, which suggests that migratory birds may consume these seeds later in the year.

Another emerging aspect of herbarium-based phenological research is investigating phenological change at continental scales and, within that, testing for population-level or ecotypic regional variation. This macroecological perspective is made possible only through specimens and their digitization. This fact is perhaps best epitomized by an impressive phenological analysis of 842,392 digitized specimen records, among the largest such study to date (Park and Mazer 2018). Beyond species-level analyses, intraspecific geographic variation in phenological responses to warming temperatures may also be important. In other words, do species’ phenological sensitivities vary across populations or latitudes, thereby making some parts of their range more vulnerable to climate change? A recent analysis using herbarium specimens collected from 30 species across the eastern United States highlighted the potentially large role of intraspecific variation in explaining geographic patterns in phenological responses to climate, with plants showing greater phenological responses to warming at southern locations (Park et al. 2019). Herbarium specimens are well suited for examining largely untested important questions on ecotypic variation. Within-species geographic variation in phenological responses is an active area of research, with studies on this theme rapidly emerging (Kopp et al. 2020; Song et al. 2020; Zohner et al. 2020).

Whole-Plant Level

It is often unclear what traits will be important for taxonomic identification purposes, so specimens are intentionally collected to include as much material as possible. It is unknown what may be of use for confirming the species level or even infraspecific levels (e.g., varieties, forms). Leaves and reproductive structures are often the focus, making specimens excellent sources of phenotypic data at those levels (described in the next sections). However, long-standing best practices in plant collecting indicate collecting the entire plant, including roots, stems, leaves, and reproductive organs. Of course, collecting an entire plant is simply not always possible (e.g., trees), but many plants, particularly herbaceous species, easily fit on standard herbarium sheets. This aspect of collecting practice has made herbaria vast repositories for whole-plant-level trait information.

For species that fit on an herbarium sheet, a major trait that can be measured is plant height, which relates to many aspects of plant strategy, such as competitive ability (light), stress tolerance, and seed dispersal. Height is a major dimension of functional variation in many quantitative ecological strategy frameworks (Westoby et al. 2002; Díaz et al. 2016). Height is well captured in some specimens because many herbaceous species are collected at reproductive maturity and have maximum heights that are smaller than herbarium sheets. Although commonly measured in the field by trait ecologists (e.g., among the top 10 most common traits in the TRY trait database; Kattge et al. 2020), it is relatively uncommonly measured from specimens.

Several studies have measured height from herbarium specimens to analyze change within species over time, especially in the context of climate change and the human harvesting of ethnobotanically important species. McGraw (2001) measured 11 size-related traits, with height among them, of American ginseng (Panax quinquefolius L.), a species whose trade is regulated by CITES and that has a long history of human use and international market value. Using specimens collected from the early 1800s to recent times, the study found significant declines in plant height, with the strongest declines since 1900. A similar herbarium-based study found evidence for human-induced dwarfing of a species harvested for traditional medicine in Asia (Law and Salick 2005). Comparing species with differing regions and histories of human harvesting, the authors conclude that human harvesting plays a strong selective force in the contemporary evolution of these threatened species. Other studies have analyzed change in the context of climate change and variability, with one notable study of annual species exhibiting mostly decreases in plant size over a century but that species, even within functional groups, may respond to climate differently (Leger 2013). While most herbarium-derived height measurements are from smaller-statured species that fit onto an herbarium sheet, internode length has been used as a proxy for plant height (Dalrymple et al. 2015), especially in the case of vine and prostrate growth forms.

Beyond height, other whole-plant traits, many of which are categorical or indicate presence/absence, can also be assessed from herbarium specimens. Often at the species level, specimens can be used to efficiently classify a large number of species into growth forms (Engemann et al. 2016). Other functionally significant characters that can be derived from specimens include the presence, placement, and number of domatia (specialized structures that house insect associates; e.g., Romero et al. 2019), extrafloral nectaries (Weber and Keeler 2013), and physical defenses (e.g., thorns; Xu et al. 2020).

Leaf Chemistry

A rising use of herbarium specimens in functional trait research includes sampling for leaf chemistry (table 1). Unlike whole-plant traits, these traits require destructive sampling, although often only of a small fragment of tissue. Leaf nitrogen concentration, for instance, is a core leaf economic trait directly related to photosynthesis, with nitrogen allocation a major factor in plant growth in many systems. Herbarium specimens have been sampled for a wide variety of leaf chemicals, including elemental concentrations (e.g., leaf N, C, P), stable isotopes (e.g., δ13C, δ15N), and heavy metals (e.g., Pb).

Perhaps among the most noteworthy specimens of historical interest are in the Lewis and Clark Herbarium at the Academy of Natural Sciences of Drexel University (PH). These specimens were collected by Meriwether Lewis and William Clark on their famous expedition in the early 1800s. Well recognized for their historical and scientific value (especially taxonomically, with several type specimens), they are also unrivaled sources of leaf chemical data, as they are among the earliest plant collections from northwestern North America. Teece et al. (2002) measured leaf fatty acid and stable carbon isotope composition in 11 specimens.
collected during this famous transcontinental expedition. By allowing for comparison of these trait values with those of modern specimens, these historic specimens serve to provide important baseline information on these traits from a time before widespread industrialization and the European-American colonization of the interior of North America. Given the exceptionally unique nature of these specimens, which invoke unrivaled scientific value and cultural heritage, this pioneering study provides an important case study for herbarium-based trait research, including a thoughtful narrative on the decision process for partially destructive sampling of specimens.

Stable isotope compositions can also be reliably measured from herbarium leaves, providing insights into eco-physiology across time, geography, and phylogeny. In particular, $\Delta^{13}$C measures the discrimination by photosynthesis of a heavier, less common stable isotope, $^{13}$C, compared with $^{12}$C. Carbon isotope composition in leaves is a well-demonstrated metric of time-integrated plant water-use efficiency, as well as a means of assessing photosynthetic pathways (Pérez-Harguindeguy et al. 2013). Relatedly, nitrogen isotopes in herbarium leaves can also provide important biogeochemical insights into historical nitrogen availability. McAulachlan et al. (2010) found decreasing trends in leaf nitrogen and $^{15}$N values across 24 plant species in the central North American grasslands over the past century, indicating declines in N availability in this ecosystem despite anthropogenic N deposition. Looking within a single species, DeLeo et al. (2020) powerfully leveraged specimens to measure a range of leaf chemical traits associated with the LES in the model organism Arabidopsis thaliana, linking responses to climate and geographic variation over 200 years and across its native range. Isotopic composition in algal specimens has also been used to reconstruct past marine environments (Miller et al. 2020). Isotopic studies of herbarium specimens provide both ecosystem-level insights related to biogeochemistry and plant performance and direct insights into plant function (e.g., water-use efficiency, photosynthetic pathway).

Other chemicals not traditionally associated with plant strategy schemes have also been measured using specimens, with much room for further development. Herbarium specimens can provide information on which species are heavy metal accumulators and can allow for analysis of changes in the heavy metals in leaf tissue as a result of anthropogenic activities (Rudin et al. 2017). Furthermore, herbarium specimens can be measured for secondary metabolites, including pyrrolizidine alkaloids in specimens in the milkweed family (Apocynaceae) collected more than 150 years ago (Tasca et al. 2018) and ultraviolet-B–protecting flavonoids produced in Antarctic mosses before and after stratospheric ozone depletion (Ryan et al. 2009). Another study used dried seeds on specimens to measure the long-term change of furanocoumarins, a class of organic compounds produced by certain plant families, providing strong evidence for coevolution and the evolutionary arms race between an introduced plant species and its associated insect herbivore (Berenbaum and Zangerl 1998).

**Leaf and Floral Morphology**

Morphological traits have been at the core of herbarium-based research for decades, most strongly in the context of taxonomic study. However, herbarium-based morphological measurements analyzed at the individual level in the context of functional trait theory have only recently come to the forefront. Morphological traits measured from specimens range from continuous to categorical traits and are measured at the level of leaves to reproductive structures. These morphometric studies include straightforward traits, such as leaf size, or more complicated multivariate quantifications of shape, such as geometric morphometrics. Given that herbarium specimens are pressed and (mostly) two-dimensional, they are well suited for morphometric analysis.

In one of the earliest uses of specimens for functional traits in the current sense, Woodson (1947) measured leaf shape in herbarium specimens to make “phenocontour” maps to show leaf shape patterns across spatial gradients. The study examined specimens of three subspecies of butterfly weed (Asclepias tuberosa L.) across their range, devised a new morphometric based on two leaf angles, and reported clines in leaf shape. These visually striking phenocontour maps showing spatial variation in functional traits within and across species remain uncommon, despite the remarkable developments in geographic information system and related tools for improved visualizations in recent years. With increased digitization and computational advancements permitting high-throughput measurement, similar herbarium-derived functional trait maps across species’ ranges might be reborn and become widespread.

Although several studies have measured morphological patterns across spatial scales using specimens since Woodson’s (1947) study, the use of herbarium specimens for plant morphological data did not become widespread in trait ecology until many decades later. Although many morphological studies using specimens remain taxonomically focused (e.g., distinguishing species or infraspecific taxa; Buitrago Aristizábal et al. 2020), an increasing number examine morphological trait shifts in the context of global change. To test whether evolutionary shifts are common in introduced plant species, Buswell et al. (2011) measured a variety of functional traits, including plant height, specific leaf area, leaf area, and leaf shape (length-to-width ratio) in 23 species introduced to New South Wales, Australia. Incredibly, they found that 75% of these species exhibited significant change in the 150 years since their introduction. Other studies have analyzed morphological shifts in the context of climate change for leaves (e.g., Guerin et al. 2012; Stropp et al. 2017; Sritharan et al. 2021) and floral traits (e.g., Bontrager and Angert 2016; Yu et al. 2016). Paleobotanists commonly measure leaf morphological traits, such as leaf size, shape, and serration, to estimate past temperatures from plant fossils (e.g., Pepe et al. 2011). These traits are similarly available in herbarium specimens, and in many ways, they can be treated as very well-preserved fossils.

**Specific Leaf Area**

Specific leaf area (inverse of leaf mass per area) is central to many functional trait schemes, including the LES. Being relatively easy to measure (a “soft” trait) with clear functional relevance, specific leaf area is frequently measured by functional ecologists (Pérez-Harguindeguy et al. 2013). With the exception of one earlier study (Peñuelas and Matamala 1990), herbarium specimens were not recognized as sources of specific leaf area data until recently (table 1). This specimen use will likely increase.
as more functional trait ecologists become aware of herbarium specimens as sources of trait data. However, only modified metrics of specific leaf area can be directly measured from specimens because the trait is typically calculated using the leaf area of fresh leaves (see “Limitations of Herbarium Specimen Use and How to Overcome Them,” below, on herbarium-derived trait protocols).

Leaf Stomata

Leaf stomata are well preserved on herbarium specimens and are especially poised for measurement. Standard specimen preparation protocol includes mounting specimens to sheets such that the adaxial side of some leaves and the abaxial side of other leaves are exposed for measurement. Parkhurst (1978) used specimens to assess which species have stomata on one or both sides of leaves, exploring the adaptive significance of this trait across phylogenies and environmental contexts. Similarly, a classic study by Woodward (1987) measured the stomatal density of seven woody species in Europe, reporting strong declines in stomatal numbers as a result of atmospheric CO₂ increases, a phenomenon that has since been repeated across many studies. Of special interest are the historical specimens measured for stomatal traits, with findings of inverse correlations with CO₂ levels similar to those found by Woodward (1987). These include specimens collected by Lewis and Clark in North America in the early 1800s (described above with leaf chemistry traits; Teece et al. 2002) and by Joseph Banks and David Solander during James Cook’s voyage to the South Pacific in 1769 (Large et al. 2017). The trait has even been used to reconstruct several millennia of CO₂ levels from ancient Egypt to today using preserved olive leaves dating to 1327 BCE from King Tutankhamun’s tomb alongside a chronosequence of traditional herbarium specimens (Beering and Chaloner 1993). More commonly, paleobotanists now routinely rely on both fossils and herbarium specimens (Beerling and Chaloner 1993). More commonly, paleobotanists now routinely rely on both fossils and herbarium specimens, alongside living material, to assess the functional significance of stomatal density and index in reconstructions of paleoenvironments (Hu et al. 2019).

Species Interactions and Extended Phenotypes

Herbarium specimens capture not only traits of the plants themselves but also their interactions with other species. For example, specimens provide information on the presence of and susceptibility to disease (Hood et al. 2010), as well as on leaf herbivory (Meineke et al. 2019) or granivory (Moore et al. 2021), and, in some cases, even include insects themselves unintentionally pressed among leaves (Whitehead 1976). Combined with specimen-derived traits, these interactions captured in herbaria provide insight into the interplay between traits and community context. In an early example, Morrow and Fox (1989) dug into the historic specimen record to estimate levels of herbivory between trees of Australia and North America, finding that higher rates of herbivory in Australia are not due to European colonization. Decades later, Meineke et al. (2019) developed an elegant grid system to reliably quantify levels of insect damage on specimens of four trees in the northeastern United States, finding that specimens collected in recent years with climate change display higher levels of leaf damage than those from the early 1900s. The same research group expanded this study across continents (Europe and the United States) and combined it with phenological data to demonstrate that plant species that are better at tracking climate by leafing out earlier during warm years are also more prone to higher rates of herbivory, an unexpected consequence of climate change (Meineke et al. 2021). Another study used specimens to find increases in different types of insect herbivory of an introduced plant over a century of invasion as assessed by distinct signatures of specific leaf damage, powerfully testing long-term impacts of biocontrol agents (Beaulieu et al. 2019). In addition to insect interactions, herbarium specimens may also provide information on trait shifts resulting from mammal herbivory. Using specimens to quantify the impact of deer on leaf area, Beuvais et al. (2017) compared specimens of a browse-sensitive understory herb species collected before deer became overabundant with modern data from areas with high deer densities or without deer. Herbarium specimens clearly show great promise for uncovering the impacts of co-evolved species interactions under global change (Meineke and Davies 2019), and more studies are needed to further connect these plant-herbivore and plant-disease interactions to plant phenotype dynamics.

Herbaria Are Poised for New Insights into Trait Biology

The known uses of herbaria as data sources for traits are diverse and well demonstrated (table 1). However, herbarium-derived traits generally, as well as their application to specific research areas, are very much in their infancy, with relatively few citations. Herbarium-based trait studies tend to be small scale, tapping into only a small fraction of the data that could be extracted from the world’s 396 million specimens (fig. 1). Most studies include few species or are restricted to local or regional scales. Although herbarium-based phenological studies are now widespread and mainstream, the application of other specimen-based trait scoring methods is still in the early phases of development. The first passes at standardized protocols have been developed, with just a few traits and data standards only recently published (see Yost et al. 2018 for herbarium phenology scoring protocol). There are tantalizing hints toward large-scale automated phenological scoring of specimen images (Pearson et al. 2020). We are only at the cusp of realizing the full value of herbarium specimens in functional traits research.

Potential Contributions to Global Trait Databases

The development and rapid growth of global trait databases have played a pivotal role in the emergence of functional trait perspectives. With millions of trait records compiled from the existing literature and directly submitted by hundreds of researchers, trait databases have enabled hundreds of publications on the inter- and intraspecific variation of traits at local to global scales (Kattge et al. 2020). Mostly within the past 20 years, large trait data sets and databases have contributed to our core understanding of the ecology and evolution of plant trade-offs, with major developments in trait theory based on these data. These databases take different forms ranging from species-level aggregated data to individual-level (or intraindividual-level) disaggregated data (König et al. 2019). Although many trait data initiatives exist, among the two largest and most used are TRY (initiated in 2007; Kattge et al. 2020) and BIEN (initiated in 2016 and also...
Herbarium specimens have been suggested as a source to fill the data voids in global trait databases (Queenborough and Porras 2014; Queenborough 2017; Perez et al. 2020). Yet to date, specimen-derived data make up a negligible source for TRY. In fact, the latest upcoming release of TRY (ver. 6) includes only four separate data sets with herbarium-derived trait values (J. Kattge, personal communication, January 18, 2021). As a very conservative estimate, if only a single trait could be measured from each of the estimated 396 million specimens (Thiers 2021), it would increase the database by >3400%. If digitized records on GBIF alone are compared with those on TRY, herbarium specimens far outnumber trait database records by orders of magnitude in terms of total number (fig. 2A), number of taxa covered (interspecific variation; fig. 2B), and number of records per species (intraspecific variation; fig. 2). The benefits of herbarium-derived data go beyond filling taxonomic voids in trait database coverage. Most trait data included in these databases are limited to recent years, while plant collecting is a centuries-old continuous practice done by many thousands of people distributed across the world (fig. 1B). Therefore, herbarium-derived traits also provide decades of data to test questions that it is not possible to test with current data in trait databases. One exception is a recent case study that measured leaf sizes of >32,000 leaves using >11,000 specimen images of seven species across four centuries (Kommineni et al. 2021). This impressive herbarium-derived data set is openly available on TRY, but these trait data are not directly connected to specimen records in collection databases. Although methodological and infrastructural considerations are needed for the full inclusion of herbarium-derived trait data alongside existing data streams (covered below in this review), the potential contributions of specimens to global trait databases are immense and well within reach.

**Herbarium-Derived Traits in the Digital Era**

The time and effort required to manually extract trait data from each specimen are major limitations of their large-scale measurement and contribution to global trait databases. For some traits, like leaf N, the physical specimen will always be needed for measurement (see table 1 for traits that can use images alone). Although certainly possible, it is difficult to scale up beyond a single to a few species or regions with handheld calipers or a ruler. Fortunately, recent and ongoing digitization projects across the world have changed the way traits can be gathered from specimens. Specimens are easier to search for and find across literally thousands of collections across the world. Digitized specimen label data enable biogeographic studies at large scales, such as species distribution modeling and, by extension, the potential to use biogeographic information as a proxy for the physiological tolerance of species (e.g., thermal optima) from biogeographic information (Perez and Feeley 2021). Beyond data accessibility, the widespread availability of digital specimen images permits detailed analysis not possible from physical specimens alone. While digitization of specimens within natural history collections is very much still ongoing, we have also entered a new era of digitization coined “digitization 2.0” — that is, new approaches that rely on the digitized products themselves (Hedrick et al. 2020). Digitization

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**Fig. 2** Number of trait records in the global plant trait database TRY (ver. 5, accessed January 20, 2021; https://try-db.org; Kattge et al. 2020) and the number of herbarium specimens accessible through the Global Biodiversity Information Facility (GBIF; GBIF 2021a). Comparison by the total number of available trait records and herbarium specimens (A), the number of species (B; broadly defined, including infraspecific taxa), and the number of individuals per species in each database (C; boxplots show the median in a thick black line, boxes denote the interquartile range, whiskers extend to 1.5 times the interquartile range, and outliers are not plotted).
Frontiers of Herbarium-Derived Traits

The specimen-derived traits highlighted in the section above are only a subset of those listed in table 1, merely scratching the surface of an ever-expanding list. As digitization continues and digitization 2.0 gains momentum, new approaches to specimen emerge. These approaches include modified techniques to more effectively measure well-established traits, as well as to realize altogether new traits that can be measured from specimens.

Newly developed methods for spectral trait estimation provide a promising avenue for herbaria. Although mostly applied more broadly to date, spectral methods are especially exciting for herbarium specimen trait research. A reflectance spectrum is a measure of light reflectance across a range of wavelengths. Reflectance spectroscopy powerfully provides integrated measurements of the chemical and structural composition of plants, which captures many aspects of plant phenotype and phylogenetic history (Meireles et al. 2020). In their most common application in herbaria so far, leaf optical spectra have been used as a method to discriminate species identity, with remarkable accuracy even among closely related and diverse tropical species (e.g., Lang et al. 2017) or, incredibly, even among populations within species (Cavender-Bares et al. 2016). Plant traits have also been estimated using optical spectra of dried, pressed leaves (Costa et al. 2018). Kothari et al. (2021) applied this technique to herbarium specimens, comparing measurements of pressed, ground, and fresh leaves, as well as relationships to leaf chemical (e.g., leaf N) and structural (e.g., specific leaf area) traits. This approach could transform herbarium-derived trait research, demonstrating the accurate estimation of plant function through reflectance spectra.

Nondestructive specimen measurements of trace elements have also been made using X-ray fluorescence, a field newly named “herbarium X-ray fluorescence ionomics” (van der Ent et al. 2019). Using a handheld X-ray fluorescence analyzer on pressed specimens, studies have screened species for trace metal hyperaccumulation using specimens (van der Ent et al. 2019; Gei et al. 2020). Mobile digitization units that will rapidly perform fluorescence spectroscopy measurements at the same time as specimen digitization are under development. Including trait measurements in digitization workflows may be one approach to efficient trait measurements at large scales.

Few herbarium studies have examined plant roots, and none have been published on the soil adhered to these roots. Linking these data to plant traits can provide important insight into individual and species responses to change. Broadly, root trait ecology is well behind leaf traits conceptually, being harder to measure, and is therefore less represented in functional trait literature and in trait databases (Freschet et al. 2021). It is standard practice to collect the entire plant, including roots, when feasible, and this is especially common for herbaceous plants. Herbaria are untapped repositories of not only roots but also their associated microbes and even the soil adhered to roots. Herbarium specimen roots have been recently used to quantify mycorrhizal communities as old as 137 years (Heberling and Burke 2019). However, to date, I am not aware of any herbarium studies measuring root traits. One trait that it might be possible to measure is specific root length (ratio of root length to dry mass). Although many specimen roots may not be suited for this measurement (e.g., incomplete or shriveled from pressing), the possibility remains unexplored. Species with thick fleshy roots, common in many temperate forest understory herbaceous perennial species, may be the most amenable to such measurements. If possible, as with leaf traits, specimens might valuably contribute to global root trait databases (Iversen et al. 2017; Guerrero-Ramírez et al. 2021), which fall well behind leaf traits in spatial and taxonomic coverage.

Another category of traits underexplored in herbaria is that of color. Perceived color in the human visible spectrum is preserved inconsistently in specimens, depending on many factors. Some colors preserve well, while others either do not or depend on how quickly specimens were dried and their storage conditions. However, information on labels can provide some insight because of the long-standing practice of collectors recording flower or fruit color. Floral color on labels was used in a recent analysis reporting within-species changes in pigmentation over time and as a function of abiotic conditions and climate change (Sullivan and Koski 2021). While visible color may not be well preserved in physical specimens themselves, patterns in the ultraviolet spectrum, as perceived by pollinators, can be well preserved. With an ultraviolet camera filter, herbarium specimens have been used to quantify ultraviolet reflectance across species and even as a diagnostic character to distinguish morphologically similar species (Horovitz and Cohen 1972). A recent study extended this technique further, measuring ultraviolet-absorbing floral pigmentation in specimens across the world and invoking long-term temporal shifts as a result of ozone depletion and climate change (Koski et al. 2020).
**Integrating Herbaria with Other Natural History Collections**

Herbaria are not isolated but are part of a centuries-long scientific culture of collecting that extends well beyond plants. A growing number of studies mine specimens for data on historical species interactions, an exciting and powerful area of novel specimen use. However, few studies actively integrate data from across different natural history collections. In particular, insect collections can provide information on long-term, abiotic, and spatial patterns of plant-insect interactions, including herbivory and pollination (Kharouba et al. 2019; Meineke and Davies 2019). Coupling phenological data with related data from other natural history collections is a promising avenue of research, although it remains uncommon, with few examples. Some studies have combined herbarium-derived plant phenological data with insect pollinator flight times using entomological collections (Kharouba and Vellend 2015; Hutchings et al. 2018). Boyle et al. (2019) used herbarium and butterfly collections to conclude that the declines in milkweed species predated the planting of genetically modified crops (but see Meineke and Daru 2021 and “Limitations of Herbarium Specimen Use and How to Overcome Them,” below, for discussion of biases in opportunistic collections). Similar studies could be conducted along those lines for functional traits, comparing traits across related taxa in the context of factors through time, space, or phylogeny. Government- and museum-sponsored historical expeditions often included collecting across organismal groups, and collecting holistically across taxa will hopefully become widespread in the next generation of collecting efforts (Schindel and Cook 2018).

**Integrating Genotypic Information with Phenotype**

Herbarium specimens have received far more attention as potential sources of genetic information (Buerki and Baker 2016), but this current review strongly indicates that specimens are becoming more widely appreciated for phenotypic information (e.g., table 1). However, few studies, if any, have extracted phenotypic and genetic data together from specimens in a synthetic analysis. With methodological developments in both genetic and phenotypic measurement methods, the time is ripe for such integrative analyses.

**Limitations of Herbarium Specimen Use and How to Overcome Them**

Modern uses of herbarium specimens are increasingly opportunistic, testing hypotheses for which the underlying data were not originally intended (Heberling and Isaac 2017). Because of this simple fact, herbarium specimens are often quickly discounted as potential sources of “new” data, including functional traits, because they are presumably riddled with caveats precluding their reliable measurement. The uses summarized in table 1 were not envisioned by the founders of these institutions, the curators who managed them, or the collectors who filled their cabinets with specimens. As a result, major concerns about specimen use include assertions that reliable measurements cannot be made post hoc from collected material, that biases in collecting effort create noise that overpowers true patterns, and that methods of pressing or possible degradation from long-term preservation is too damaging. While strong skepticism toward nontraditional specimen use is well warranted and necessary, the past decade of collections use has taught us that we cannot assume the limits of herbaria without trying. Preconceived assumptions about data suitability for use can stifle innovation, especially by external user groups new to herbaria. Yet these concerns often need not preclude their use altogether but instead are caveats to consider in study design and analysis. In some cases, recent studies have validated these concerns for some measurements or research questions, but in many other cases, it has become more apparent that herbaria are reliable and powerful data sources for functional traits. Retroactive approaches that explicitly consider specimen caveats, including new methodology and statistical tools to assess bias, have transformed their use (Meineke and Daru 2021). Proactive approaches include improved methods for specimen collecting to better capture phenotypic variation from the start. This section covers both retroactive and proactive solutions to potential limitations of herbaria as functional trait data sources.

**Addressing Collector Bias (and Bias about Bias)**

A false impression widely current among non-taxonomists is to the effect that herbarium specimens usually are collected because of some abnormality which attracts the fancy of a collector. The accusation reveals such prejudice that one is baffled for an effective retort. (Woodson 1947, p. 364)

An underlying assumption behind many herbarium-based trait studies and even herbarium studies generally is that a given specimen is in some way representative of the species. This assumption often goes a step further: that the specimen represents the mean trait value of the sampled population. For instance, are four-leaf clovers more prevalent in collections than in the wild? Perhaps, but that is an extreme case. Do some botanists focus on collecting certain species groups? Almost certainly. Are there “odd” specimens in herbaria? Of course. But as the quote above indicates, many of these cases are the minority. Woodson (1947) later goes on to suggest that the opposite may be the problem, that the “chief danger in plant collecting” is preferentially sampling too many “normal” specimens.

Potential collection biases and inherent data use limitations have long been recognized (Merrill 1916; Anderson and Turrill 1935; Fogg 1940; Fernald 1950), and recent analyses with digitized collections have shown that herbaria are indeed not random samples (Daru et al. 2018). These “biases” are often intentional, with field botanists and ecologists often interested in different types of questions and using different methods of surveying or collecting (Alba et al. 2021). While it is not possible to definitively know the motivation or sampling strategy of each collector, there are well-established approaches to addressing these potential biases (table 2). Many uses of specimens that are now mainstream (e.g., phenology) were undoubtedly met with skepticism that hindered the progress of methodological development before they became an accepted specimen use. Newly realized herbarium specimen uses push these limits, enabling new insight into old specimens.

Many of these limitations often depend on how the research questions are framed. Many biases can be addressed statistically or through study design (table 2). Biases in herbarium collections
## Table 2
Potential Biases and Limitations Associated with the Use of Herbarium-Derived Trait Data, including Proposed Solutions and Published Examples

| Source of bias or error, approach to address bias                                                                 | Example publication(s)                                                                 |
|------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------|
| **Spatial/temporal:**                                                                                                                                                        |
| Variable collection effort:                                                                                         |                                                                                       |
| Include complementary data sources (e.g., photographs, field notes)                                                | Miller-Rushing et al. 2006; Panchen et al. 2012; Spellman and Mulder 2016              |
| Design study as “before versus after” or “historic versus recent” comparisons                                     | Calinger 2015                                                                          |
| Supplement with contemporary field sampling                                                                       |                                                                                       |
| Analyze with statistical tests for and/or explicit acknowledgment of bias (sensitivity analyses, null models)     | Delisle et al. 2003; Kadmon et al. 2004; Case et al. 2007; Feeley and Silman 2011; ter Steege et al. 2011; Lavoie et al. 2012; Schmidt-Lebuhn et al. 2013; Yang et al. 2014; Hyndman et al. 2015; van Proosdij et al. 2016; Wolf et al. 2016; Antunes and Schamp 2017; Daru et al. 2018 |
| **Environmental:**                                                                                                  |                                                                                       |
| Unknown microsite conditions of whole plant or plant parts (e.g., unclear whether sun or shade leaves collected)    | Woodson 1947                                                                           |
| Ensure large sample size                                                                                           |                                                                                       |
| Use habitat information on labels                                                                                   | Hanan-A. et al. 2016                                                                   |
| Deliberate species selection (e.g., only open shaded habitat species; include species-level habitat affinities in analysis) | Koski et al. 2020                                                                       |
| Trait shifts over time may arise from acclimation (phenotypic plasticity) and/or evolution (adaptation):         | Case et al. 2007; Flores-Moreno et al. 2015                                             |
| Compare focal species with null control congeners or ecological analogues                                           |                                                                                       |
| Include ancillary data (e.g., historical climate records) in analysis                                              | Buswell et al. 2011                                                                   |
| Compare responses in home and away ranges (in case of invasion studies)                                            | Buswell et al. 2011                                                                   |
| Use specimens collected repeatedly from the same individual in botanical gardens                                   | Miller-Rushing et al. 2009                                                             |
| Conduct common-garden work with known germplasm accessions to link genotype to phenotype                           | Exposito-Alonso et al. 2018                                                            |
| Extract genetic data from specimens to corroborate evolutionary shift                                             | Lamar and Partridge 2020                                                               |
| **Curatorial:**                                                                                                    |                                                                                       |
| Specimen misidentification:                                                                                       |                                                                                       |
| Continued support for basic curation and collection annotation                                                    | Goodwin et al. 2015                                                                   |
| Georeferencing error and/or imprecise collection localities:                                                        |                                                                                       |
| Standardized protocols for specimen georeferencing, with accounting for precision of localities                   | Bloom et al. 2018; Chapman and Wieczorek 2020                                          |
| **Intrinsic:**                                                                                                     |                                                                                       |
| Specimens not representative of population and/or collected intentionally as outliers with unique morphology,     |                                                                                       |
| phenotype, and so on:                                                                                            |                                                                                       |
| Site-intensive collecting (“mass collections”)                                                                    | Woodson 1947                                                                          |
| Collect across life history stages                                                                                  |                                                                                       |
| Treat suspected variable of concern (e.g., collector) as covariate in models, use weighted averages, or analyze trait extremes intentionally (e.g., first leaf out date) | Anderson and Turrill 1935; Anderson 1941; Desmarais 1952; e.g., Buswell et al. 2011; Meineke et al. 2019 |
| Interpret results in context (e.g., specimens as conservative, down biased estimates of herbivory)              |                                                                                       |
| Specimen drying, pressing, age, and storage conditions may affect trait measurement values:                       |                                                                                       |
| Limit analysis to only herbarium-derived traits or compare herbarium-derived and non-herbarium-derived trait measurements on proportional change (i.e., measurement precision robust, accuracy may differ) | Many studies                                                                          |
| Experimentally simulate storage or preparation conditions to quantify potential effects                          | Miller et al. 2020                                                                    |
| Compare herbarium-derived traits with standard protocols and apply necessary correction factors                   |                                                                                       |

* These are not necessarily trait-based studies but can be similarly applied.
can be categorized into several groups, among them temporal, spatial, taxonomic, and phylogenetic biases (Daru et al. 2018), as well as intrinsic concerns dealing with tissue degradation or distortion on specimen preparation and storage. These biases do not necessarily mean that collections data must simply be disregarded. Rather, most specimens were merely collected for different purposes, as specimens for taxonomic use may not be appropriate for use in biogeographic analyses. Determining data fit for use is highly dependent on study goals and context, including the scale and resolution of the research questions. Various approaches exist to directly address or overcome these potential limitations, including statistical methods, complementary data sources, study design (including species selection and determining sample size), and data interpretation (table 2). In many cases, with careful considerations, the advantages provided by specimens far outweigh their limitations (also see Diskin et al. 2012 for a well-articulated overview).

Despite excellent summaries of biases in collecting effort across space, time, and phylogeny (Schmidt-Lebuhn et al. 2013; Daru et al. 2018; Panchen et al. 2019), few studies actively test for explicit bias by collectors in specimen selection—that is, what individual or plant fragment makes it on the herbarium sheet. This decision becomes especially pertinent in trait studies. On one hand, herbaria are intentional repositories of trait variation, including extremes. These records are important for documenting morphological diversity and distributional outliers that provide new insight into biodiversity and biodiversity change. In a recent survey of collectors, Pearson and Mast (2019) reported that a majority of collectors responded that they note outlier observations on specimen labels. These outliers are important contributions that are not biases per se but rather documentations of natural variation. On the other hand, collector bias is not always documented or intentional. A recent example has emerged for herbarium-based studies of leaf herbivory. Kozlov et al. (2020) compared student herbarium collections with simultaneous ecological surveys by the authors and concluded that collectors and curators intentionally select undamaged specimens. However, a reanalysis of these data with adequate sample sizes shows that field estimates and herbarium samples are indeed highly correlated (Meineke et al. 2021b). A related study asked whether herbarium specimens show systematic differences through time due to changes in plant collection practices (Kozlov et al. 2021). Comparing specimens of European trees collected from 1558 to 2016, they concluded that the average number of leaves increased through time and that the number of leaves correlated with maximum leaf length. However, with no consideration of covarying factors beyond the date of collection, it is unclear whether these patterns were indeed due to shifting collection practices or were due to biological responses as a product of collection localities (e.g., climate) or time (e.g., climate change), as leaf size has been shown to be affected by climate (Guerin et al. 2012). Further, maximum leaf size was the only characteristic considered that is directly relevant to trait studies. Assuming that the trait shifts they reported were due to shifting collection practices, it is unclear whether the temporal pattern would be robust to mean leaf length, which is more commonly measured in practice than maximum leaf length. Kozlov et al. (2021) also surveyed scientists to assess “scientific value” and artists to assess “aesthetic value.” Only one very old collection (from before 1600) was ranked as of lower scientific value, which is not surprising given the age and quality of such specimens. Interestingly, aesthetic value was remarkably consistent regardless of specimen age. These studies on collector behavior and bias, including surveys, are needed to account for biases within and across collections. However, most trait studies leverage many specimens to test the effects of climate, space, or species, not time, on traits, and therefore, systematic shifts in collection practices may add noise to statistical models but remain robust to false conclusions.

**Validating Herbarium-Derived Trait Measurements**

Separate from collector bias, additional considerations are needed to assess whether traits themselves can in fact be reliably measured from specimens. In other words, does the process of specimen drying, pressing, and storage affect trait values? Functional trait protocols have been well standardized in recent decades, with many traits requiring fresh tissues for accurate measurement (Pérez-Harguindeguy et al. 2013). Despite the dozens of published herbarium-based trait studies across many traits (table 1), few tests directly compare trait values measured from dried, pressed specimens with those measured using fresh collected specimens. A well-referenced trait protocol handbook by Pérez-Harguindeguy et al. (2013) that is used by functional trait ecologists provides standardized measurement protocols for 44 functional traits, of which only three traits mention herbarium specimens as a potential source of data. However, 17 of the 44 traits covered in the handbook have been measured using specimens, making up a subset listed in table 1. Explicit tests across species and traits are needed to assess the reliability of herbarium-derived traits, as well as modifications to existing protocols describing additional considerations for specimens.

Several traits have been well validated for herbarium-based measurement. The most studied is leaf shrinkage after drying, a concern for any traits invoking leaf area in ecological and palaeoecological research (Blonder et al. 2012; Queenborough and Porras 2014). However, leaf area shrinkage can be predicted by other morphological traits and varies by species (Blonder et al. 2012). Dried leaf area can be used with caution as a reliable proxy for fresh leaf area, especially if leaf area shrinkage is relatively minor for the focal species (Queenborough and Porras 2014). Leaf rehydration may also provide improved estimates for certain species (Blonder et al. 2012) or specimens with wrinkled leaves (Woodson 1947). Extending these studies, Perez et al. (2020) measured three traits (specific leaf area, leaf thickness, and branch wood specific gravity) of 28 woody species using plant tissues dried in a plant press and compared those with traits measured from fresh tissue of the same plants using standard trait protocols. In addition to interspecific comparisons, close correlations of dry- and fresh-measured leaf thickness were found in one species, which suggests that herbarium specimens may provide reliable intraspecific measurements of some traits across environment and time. Herbarium-derived trait values were highly correlated to those using fresh tissues. Therefore, the use of species-level correction factors could be applied in cases where herbarium-derived measurements are compared with measurements using fresh tissues. Onstein et al. (2016) found measurement error to be relatively consistent within a family, justifying the application of a single correction factor at the family level. In other cases, species-level correction factors may be needed, especially if leaf habit and structural traits are highly variable within a family. Even if herbarium-derived trait
measurements diverge from those of fresh specimens, all is not lost. Functional trait studies can restrict analysis to only herbarium-derived traits (Tomaszewski and Górzkowska 2016). Relative trends, not the absolute trait values, are often of interest. However, measurement protocols and data sources should be explicitly included in metadata to be included in aggregated global trait databases. Some species and traits may be less amenable to reliable herbarium measurement and dependent on the scale of the research question. For example, species with high intraspecific variation in leaf water content across environments or time may exhibit different leaf shrinkage after drying. Therefore, intraspecific trait validations and caution interpreting trends within species are needed.

Last, the effects of long-term storage and specimen preparation on nutrient chemistry are largely untested but are likely accurately preserved in specimens. One study reported no meaningful differences in amino acids, heavy metals, and stable isotopes (Miller et al. 2020) between macroalgae pressed using historical and modern (acid-free) paper. Similar studies are needed for other species.

**Addressing Effects of Microsite Variation**

Many species exhibit a high degree of phenotypic plasticity, with large variation in functional trait values depending on microsite conditions. For example, sun leaves and shade leaves of trees collected from the same population or even the same individual are often significantly different. Microsite details specific to individual branches are unfortunately rarely captured by most herbarium specimens. However, this situation is not unique to herbarium-derived traits, with environmental context unclear in many data sets in global trait databases (Keenan and Niinemets 2017). In some cases, traits may be robust to such microsite differences but may require tests in the field. For example, Large et al. (2017) found no difference in stomatal densities between sun and shade leaves measured in the field, thereby alleviating that concern in their herbarium results for the same species.

Information on specimen labels can provide important environmental context, although it is not well standardized (Merrill 1916). For instance, label metadata about bark and trunk characteristics, growth form, and height can be important information for the identification of woody species. Although few examples exist, ecological studies have used habitat descriptions from specimen labels, including documenting invasive species’ habitat affinity patterns (Huebner 2003; Hanan-A. et al. 2016). Similar approaches could be extended to functional trait studies that include species that differ in habitat or individuals collected across habitat types. Beyond habitat, herbarium data can also provide important community-level context. Specimens of different species that were collected together could be compared or considered in analyses. Similarly, “associated species” are frequently provided by collectors on specimen labels (Landrum and Lafferty 2015; Pearson 2018). These metadata are mostly unused.

**Capturing Within-Specimen Variation**

Depending on the species, some traits vary strongly within individuals. Therefore, individual trait values are not single values but instead mean values of multiple measurements used (Pérez-Harguindeguy et al. 2013). Similarly, multiple leaves per specimen can be measured to account for variation within specimens, and analyses might focus on multiple dimensions, including minimum, maximum, median, and mean values, as well as metrics of variance. Specimen values might be weighted by standard deviation to account for this intra-individual variation. Furthermore, specimens of smaller-statured species often include multiple individuals, which can be similarly weighted in analysis to account for nonindependence (e.g., Buswell et al. 2011).

Capturing a single value from a specimen to quantify phenology is similarly challenging, as many species display multiple phenophases along a continuum at any given time (e.g., open flowers and ripe fruits). Although fine-scale phenological data may not be necessary for some questions (Ellwood et al. 2019; Pearson 2019a), continuous metrics accounting for within-specimen variation can in some cases improve model fits and enable new questions to be asked. The use of continuous phenological metrics allows every relevant specimen to be included in a given analysis (i.e., specimens that were collected outside peak flowering are included). Such metrics also enable the investigation of phenological shifts across stages. Love et al. (2019) developed such a quantitative metric calculated from counts of reproductive structures at different stages (e.g., buds, flowers, fruits), along with a protocol for their measurement. This metric has also been used to combine field and herbarium data (Mulder et al. 2017). Similar protocols to effectively capture within-specimen variation should be developed for other functional traits.

**Archiving Within-Population Variation: Proactive Solutions to Collecting**

The standard herbarium specimen does not capture within-population variation, at least not in a complete or transparent way. As demonstrated by the trait studies reviewed above, this limitation is clearly not restrictive. Herbaria capture intraspecific variation that existing trait databases do not (fig. 2).

This shortcoming of herbaria in documenting population-level variation was first discussed by Anderson and Turrill (1935) and was later formalized in a method referred to as “mass collections” (Anderson 1941). The approach documents the relative frequency of trait variation in a population with physical vouchers, which enables many downstream taxonomic and ecological studies. Furthermore, the mass collections approach directly addresses the assumption that specimens are representative of the population, thereby minimizing uncertainty in collector bias. Later renamed “local population samples” (Woodson 1947), the method as initially described consisted of collecting a standard herbarium specimen along with a random sample of plant material collected across the population through a transect. The sampled material depends on the characteristics of the species. If a species is small statured, the entire individual could be the unit of sampling. However, the sampling unit would more often be a single leaf or reproductive structure from different individuals. Anderson (1941) envisioned each collection of a given population as not taking up much more space than a standard specimen, comprising a standard herbarium specimen mounted to a sheet in an enclosed folder (similar to those used to store types or palm specimens), along with unmounted labeled plant material documenting individual morphological variation. Although few, examples of mass collections exist (e.g., fig. 3; Fassett 1941; GBIF 2021d). In an
impressive study demonstrating the value of the approach, Desmarais (1952) collected 22,718 leaves from 465 populations between 1935 and 1948 in a comprehensive morphological study of sugar maple (*Acer saccharum* Marshall sensu lato).

The concept of mass collections or local population samples never became widespread. It is unclear whether any specimens as described in Anderson (1941) still exist or were ever even archived. For example, I could not locate any examples of the mass collections described by Anderson (1941) or any of the thousands of specimens collected by Desmarais (1952). It is possible that these specimens have been discarded over the years. With many herbaria confronting space limitations, curating population-level collections may simply not have been a priority. Furthermore, this method perhaps failed to gain widespread appreciation because it makes the already time-intensive activity of plant collecting even more time intensive. Mass collections introduce new curatorial challenges to storage (loose-leaf unmounted material) and cataloging (many individuals of possibly different taxonomic forms included). Without mention of the technique advocated only a decade earlier, Anderson (1952) described a new approach he coined as “inclusive herbaria.” Anderson’s research focused on species of cultivation, which he felt were not well archived in standard herbarium specimens for many reasons, including their size, morphology, and high variation, which is unlike that of wild species. Anderson’s inclusive herbaria consisted of single herbarium sheets with photographs, figures, and other measurement data. Highly unconventionally even today, many specimens did not even include biological material. This method was also never widely adopted, likely for similar reasons as mass collections (effort required) as well as because of its nonconventional form. In many ways, this approach is very much being resurrected in modern initiatives to connect disparate data with specimens (Lendemer et al. 2020).

Decades later, another problem in herbaria became apparent: specimens rarely document ontogenetic trait variation. Mature reproductive plants are frequently collected, but for most species, other life history stages are nearly virtually absent in herbaria. A possible solution is life history series vouchers, which are specimens holistically collected across all life history stages, from seedlings to reproductive adults (Utech et al. 1984; fig. 4).

Future Needs for Herbaria as Centers for Trait Research

Making a good herbarium record . . . is something like trying to stable a camel in a dog kennel. (Anderson 1952, p. 47)

Archiving trait variation is hard but well worth the investment. Specimens preserve multiple aspects of phenotypes that can provide new insights into long-standing questions at scales that field data alone cannot. Perhaps even more importantly, specimens are critical to the verifiability and repeatability of the plant sciences, including functional trait biology. Despite their demonstrated value, herbarium-derived traits and plant collecting are not yet embraced by the functional traits research community. Many are simply unaware of the broad relevance of herbaria, let alone their newfound value as sources of trait data. Herbaria have a history of being perceived as silos where taxonomists work, sometimes with relatively little overlap with
other research areas. In recent decades, herbaria have suffered from declines in funding and attention, in large part because of shifts from taxonomy, organismal biology, and natural history toward molecular, computational, and theoretical biology. Local plant collecting is on the decline (Prather et al. 2004a), as demonstrated by the necessity of some long-term phenological studies to supplement an herbarium-based analysis with more recent data from photographs or new field observations. Alarms have even
been sounded that the decline of collections might lead to the “end of botany” (Crisci et al. 2020). However, collections are receiving a renewed appreciation as the foundation of biodiversity science. New roles for herbaria in functional trait research will play a core part in this rebirth. In order for herbaria to become effective centers for functional trait research, we need to revisit the way we manage and engage with existing specimen data, as well as how we collect new specimens.

**Big Informatics Problem: How to Archive Trait Data?**

Museum digitization has necessitated a new cyberinfrastructure and the emergence of biodiversity informatics. Key among these developments is a shared set of explicitly defined terminology to facilitate the integration of billions of biodiversity records (Darwin Core; Wieczorek et al. 2012) that continue to evolve to meet community needs. Adding yet another layer to the already complex puzzle of biodiversity informatics, herbarium-derived data pose even further specialized challenges to their integration into the larger landscape of global biodiversity and trait data portals (Schneider et al. 2019).

Best practices for digital taxonomic annotations of specimens are well established in museum data workflows, but other types of specimen annotations, including specimen-derived trait data, are largely unresolved. For example, when a researcher measures leaf area from a specimen, there is no best practice or consensus as to how that data should best be archived for future use. Even in this simple example, the situation quickly becomes complicated when considering that multiple leaves and multiple traits may have been measured. The situation becomes further tangled when attempting to assign the individual leaves of a specimen to their respective trait values, how the traits were measured, what the units of measurement were, and so on. All these specimen-derived trait data would ideally become permanently archived with that specimen’s record, as well as deposited in an open-access online repository that enables future researchers to use these data alongside many other data sources. However, trait data are rarely available in digital herbarium records and, despite their contribution, are rarely deposited in global trait databases. Many collections-based studies deposit trait data in supplemental information or in external data repositories such as MorphoBank, a platform common in evolutionary studies that provides a digital object identifier (DOI) that could then become part of each specimen’s record (O’Leary and Kaufman 2011). While enabling data reproducibility, these approaches do not feed into aggregated databases, making them less accessible for future analysis.

The paucity of herbarium-derived trait data in trait databases and in museum databases is no fault of individual researchers but is indicative of community needs. First, most herbaria are not equipped to handle new data streams because of the lack of digital data curation infrastructure and the expertise required. Collection managers have become de facto data curators, and the new responsibilities resulting from specimen digitization alone are overwhelming. Museums are stretched thin, and managing new data streams generated by outside researchers is a challenge. Second, and perhaps more prohibitive, museum standards for archiving such data are virtually absent. Most progress has been made toward herbarium-derived phenological data (Yost et al. 2018); they are even beginning to be ingested into existing global phenological databases (Brenskelle et al. 2019). However, the pipeline from trait measurement to data archiving is in its infancy. Yost et al. (2018) proposed including phenological annotations in the Darwin Core Extended MeasurementOrFact extension. With difficulties in standardization, usability, and other practical logistics, this practice remains far from common. Similar proposals have yet to be even made, let alone implemented, for other functional traits. The functional trait community should work together with collections-based biodiversity scientists to actively develop these infrastructural needs to move herbaria and functional trait research forward.

Another approach to this informatics bottleneck for herbarium-derived trait data might be not to archive these data with the specimen record itself but instead to include stable links that connect the specimen record to external global trait databases. Herbarium-derived measurements are a negligible minority of global trait records to date, but if realized, they would substantially increase coverage (fig. 2). Although some data repositories provide DOIs for archived data sets from individual studies (e.g., MorphoBank, Dryad), many global trait databases (e.g., TRY, BIEN) do not. Linking specimen records directly with global trait data initiatives would ensure that herbarium-derived trait data are widely accessible alongside other data sources. Furthermore, connecting to existing trait data initiatives would be more efficient, as standards are already developed or underway in the functional trait community (Schneider et al. 2019; Gallagher et al. 2020; Kattge et al. 2020).

**Traits as the Heart of the “Extended Specimen Network”**

New collections-based initiatives that expand the successful digitization efforts of the past two decades to include additional data connected to specimens, including traits, are underway. The future of collections digitization lies in the connection of currently not well-integrated data streams: genetic, environmental, and phenotypic. The US-based Extended Specimen Network aims to develop this new infrastructure (Lendemer et al. 2020). Synergistic efforts are underway through the “Digital Specimen” initiative of the EU-supported Distributed System of Scientific Collections (Lannom et al. 2020).

The Extended Specimen Network holds great promise for making trait data from specimens more widely known and usable, from protocols to access to data use and archiving. The Extended Specimen Network builds on the concept of the extended specimen introduced in reference to ornithological collections by Webster (2017). The extended specimen concept not only includes the physical specimen at its core but also integrates the multidimensional aspects of the phenotype, genotype, species associations, distributional data, and related ancillary abiotic data relating to the specimen, which extend further into the community context in which the individual specimen was sampled. The Extended Specimen Network lays a framework to meet the community needs for maximal implementation of these ideas, including new approaches toward specimen collection, digitization, data integration, education, and their long-term sustainability across the world’s collections. With the rise of trait-based ecology coupled with increasing attention to herbarium-derived functional trait use, these initiatives will maximize herbaria as a data source of plant traits. However, the active participation of the functional trait research community is needed to realize this vision.

The Extended Specimen Network and related initiatives also provide a framework to digitally connect specimens and their
derived data to specific studies. Physical annotation labels are commonly added to herbarium specimens to note specimen use (i.e., stating who sampled material and when for genetic or chemical analysis), new taxonomic identification, or citation in a peer-reviewed publication. However, this practice is often incomplete for publication citations that relied on the specimen, as studies may not be published until years later, often unknown to herbarium staff, and these annotation labels are never added. Furthermore, many studies now use specimen data completely digitally, often as occurrence data in large distributional analyses. In the digital age of collections, these annotations can be added digitally. Since 2016, GBIF has provided researchers with a citable DOI with each digital download. Best practices are to cite these data DOIs in publications, such that the study is linked back to the specimens. In 2019 alone 723 GBIF-mediated studies, of which 38% cited a data DOI (Heberling et al. 2021), were published. Mechanisms should be resolved such that data DOIs connect published studies and their data back to individual specimen records.

**Herbaria and Open Science**

Herbaria have been practicing open science since long before the current shift in norms toward increased data transparency and access that is now widespread across science (Wilkinson et al. 2016). Specimens have been curated and archived in nonprofit museums and universities for centuries, continuing a long-standing tradition in open specimen access for the greater scientific good. The organism itself is the primary data source of biology (Fosberg 1946), thereby making herbarium specimens critical to data verifiability and the repeatability of science.

The role of voucher specimens is well recognized in taxonomy and systematics (Funk et al. 2018) but less appreciated in ecology and functional trait research (Schilthuizen et al. 2015). Of journals that do not regularly publish in the area of taxonomy and systematics, few, if any, require vouchers, especially ecological journals (only 4% “encourage” vouchers; Salvador and Cunha 2020). Many ecologists are simply unaware of the practice altogether. It is paradoxical that in an era with expectations for open-access deposition of data sets underlying each functional trait study, there is scarcely such a requirement for the foundation of those very data—specimens themselves. There have been recent calls for ecologists to regularly deposit voucher specimens (Schilthuizen et al. 2015) and, more broadly, for specimens to play a stronger and central role in the open science movement (Colella et al. 2021). While collecting a specimen for every functional trait measurement in the field is usually impractical for many ecological studies, at least one representative voucher should be collected per site-species combination, with associated trait data linked to the specimen. Although the ideal is physical vouchering, this goal may not be logistically, ethically, or financially possible for every trait measurement, but in many cases, images can be archived. Ideally, specimens that cover a range of trait variation should be collected (e.g., Anderson 1941; see next section). This connection between measurements in the field and specimens will further integrate herbaria and functional trait biologists. Furthermore, general collecting should also be stressed. Specimens collected for the purposes of the general documentation of biodiversity are all the more critical in an era of rapid biodiversity change, and their downstream uses, including trait measurement, are many.

As herbarium data become mobilized through digitization, the management of these data is increasingly guided by findability, accessibility, interoperability, and reusability data principles (Wilkinson et al. 2016). Specimen-derived data, including functional trait measurements, should be similarly open and accessible. However, as described above, there are additional hurdles before specimen-derived data can meet the standards. To facilitate this transition, herbarium-based scientists should engage in the broader community of traits researchers, including the Open Traits Network (Gallagher et al. 2020), a decentralized global community for the standardization and integration of trait data. The Open Traits Network does not explicitly consider herbarium-derived data, many of which require additional validation, modified protocols for measurement, or careful consideration when merging into databases of field-measured traits (e.g., applying correction factors). Herbaria should be an active part of that ongoing conversation about trait standards and open trait data integration.

**Rethinking the Specimen: A Call for a New Culture of Collecting and Collections**

To foster herbaria as sources of functional trait data, the status quo is not enough. Although herbaria have served their purpose well for centuries, we must rethink how we curate and collect specimens. New methodological developments have given existing collections new life, maximizing the data at hand despite their potential biases and limitations. These retroactive approaches are useful for existing collections, but plant collections must also continue to grow to remain relevant in an era of rapid environmental change. Rather than throw our hands up in the air and declare specimens as imperfect data, we can be proactive and reform collecting practices to ensure that these established uses become more effective and make new uses possible. New collections provide opportunities to revise how we collect in light of specimens as sources of functional trait data.

As described above in this review, some proactive collecting approaches have already been proposed but have failed to become widely implemented. We must ask how herbaria can better address the needs of new and unanticipated specimen uses. What information do we wish that collectors a century ago had provided with their specimens? Do we fully steward the information we have? Can we anticipate what future researchers will demand? Do we provide that desired information with recent specimens?

Despite dramatic shifts in data use, the scientific process of plant collecting has changed surprisingly little over the past century. Best practices for collecting do not exist in any formalized way. Bias is well acknowledged in existing collections, yet no concerted efforts have been made to revise our practices for future use. I propose an open reevaluation of the very collection event. Equipped with new tools in an increasingly digital landscape, historical approaches to archiving trait variation in specimens should be revisited and revised. New specimens should be born “extended” (Lendemer et al. 2020), not made so many years later in a forensic effort.

As described above, Anderson (1941) suggested that an ideal collection should include a typical herbarium specimen, along with a sample of leaves to document variation. I recommend that
protocols be developed that combine mass collections with life history vouchers (Utech et al. 1984), including multiple life history stages of the “standard” specimen(s), with multiple leaves collected in a randomized way to archive the relative frequency of variation in the population. With small but impactful modifications in the age of digitization, this relatively simple approach could transform herbaria into data centers for trait research.

Nature is more than what fits on an herbarium sheet. Plant collecting methods should be updated to seamlessly combine physical specimens with digital information. One recent approach leverages the community science platform iNaturalist to facilitate collecting in the field as a method to record specimen metadata digitally, as well as to enable new downstream uses by connecting digital images from the field to the physical specimen (Heberling and Isaac 2018). With specimens collected in this way, an herbarium researcher can gain instant access to high-resolution photos from the field, providing critical context and traits that might not be well preserved in specimens. Efforts should be made to standardize these photos, such as documenting the individual, population, and community context. Individual field images could document, with a length and color scale, morphological features for later analysis against a common background. Such standardization could also enable efficient high-throughput and machine learning approaches. Including abiotic data, such as light environment or soils, should become standard practice.

The metadata collected with specimens should be standardized and revisited. More than a century ago, Merrill (1916) made the case that many specimens lack any additional data beyond Latin names, locality, data, and collector—a deep-rooted practice that goes back to Linnaeus. The taxonomic identification, although of course useful, is perhaps the least important thing to be provided by the collector, as names can be added later but additional site-specific data cannot. In an age of species distribution modeling, the label data have become as valuable as the specimen itself. Relatedly, Fogg (1940) gave suggestions for better documentation, listing what biological aspects should be collected for specific plant families (e.g., roots, floral scent, multistemmed at the base, etc.). Such resources for species-specific best practices have never been extended at a meaningful scale. The botanical community should provide a globally accessible working database stating taxon-specific information that should be captured in collections, ensuring that they are maximally useful. Furthermore, standardization is needed for specimen metadata. This concern is one not of biodiversity informatics but of biology. Generally speaking, the data fields are well standardized (Wieczorek et al. 2012), but what information ends up in them is not. Many “gold standard” specimens exist, with impressive labels documenting exhaustive descriptions of the plant itself, the population, associated species, habitat, and more. While these labels provide valuable information, the lack of standardization makes it challenging to compare across specimens. Even for seemingly routine metadata fields, such as habitat, the lack of standardization makes these descriptions have less value without a shared thesaurus of habitat definitions. Plant collectors can be effective at detecting and documenting outliers, but the information is rarely recorded with specimens (Pearson and Mast 2019). Information behind the motivation of the individual specimen collection could also be informative for downstream use, highlighting specimens for further study or caveats for later trait study. For example, was the specimen collected because it was unusual in some way? The answer is often known only to the collector.

In addition to including a defined set of field images and other metadata, information relevant to traits could be digitally connected to physical specimens. It is commonplace for functional ecologists to digitally image many leaves of an individual and population to calculate leaf area. Imaging leaves could become part of the specimen preparation process and could be added to the digital specimen record. A subset of physical leaves (or other material) could also be archived with the specimen, similar to the process for mass collections (Anderson 1941). When vouchering additional leaves is impractical, digital images or scans of additional leaves connected to a traditional physical voucher can serve as an alternative. As many downstream trait and genetic analyses require destructive sampling (table 1), including additional unmounted leaves in fragment packets fixed to every new specimen for this purpose should become the norm.

Implementing these changes in the collection practices outlined above is not trivial. Herbarium culture and practices are deeply rooted. It is unrealistic to place the highest standards on every new specimen collected. Demanding new types of specimens may in fact lead to further declines in specimen collecting, as including more information with specimens will require more investment at a time when encouraging general voucher collection is already a struggle and museum staff are stretched thin (Ward et al. 2015). Furthermore, a sudden expectation for the adoption of these practices may also further the already existing disparities among countries (high and low income), herbaria (large and small), or researchers (funded and unfunded) with very different resources available. However, there should be a community-standard approach such that a given collector could collect a minimum baseline while also having the framework in place to collect more data-intensive specimens that would be maximally useful. Accessible best practices and methods for intensive collections will empower more biologists to collect.

Implementation of these changes requires new curatorial and financial investments. Many herbaria must charge curation fees to deposit specimens for the long-term preservation of voucher specimens. Other herbaria may simply not be equipped to accept a high volume of new specimens and novel specimen types. These costs must be built into a new culture of collection and explicitly embraced by institutional and governmental funding initiatives in collections infrastructure. Requirements are needed by funding agencies for researchers to explicitly account for specimens and the associated costs for their digitization, curation, and long-term care, as has been recommended for the US National Science Foundation through specimen management plans as a standard part of grant proposals (National Academies of Sciences, Engineering, and Medicine 2020). Such requirements increase awareness of the importance of voucher specimens and the recognition of specimens as a necessary part of research budgets. Journals should require or encourage voucher specimen deposition in their data availability statements (Salvador and Cunha 2020), many of which already require open data archiving. As science becomes more open, with increased data transparency, infrastructure and costs associated with voucher specimens must be included, beyond the current focus on long-term data archiving.

Revising collection practices provides an opportunity to grow and diversify a new herbarium community. My suggestions above are only just the start of a much larger conversation that is needed,
one that should include a diversity of perspectives from inside and outside museum walls. Ecologists and taxonomists measure biological diversity in very different but complementary ways (Alba et al. 2021). Similar to herbaria, living collections in botanical gardens have been shown to hold great promise as sources of trait data (Perez et al. 2018), and these institutions should work together to advance functional trait ecology, with particular promise for living collections providing material for herbarium trait protocol validations (Perez et al. 2020). Earth scientists should compare methods with botanists and determine what information could be collected for the betterment of both fields. Entomologists could provide information on how to best archive plant-insect interactions and foster new collaborations. Techniques well developed in paleobotany can be applied to herbarium specimens. Engaging a broader audience will also serve to promote the wider value of collections. An intentional process of inclusive community feedback, development, and support is needed for the development and implementation of a new culture for collections.

Conclusion: Maximizing the Potential of Collections

Clearly, in the realm of big data, herbaria provide intra- and interspecific trait information across phylogenetic, temporal, and spatial scales that it would otherwise not be possible to ascertain. However, many are unaware of the potential of specimens as sources of trait data. This review synthesizes the known value of specimens for functional trait biology and demonstrates their untapped potential to contribute to new insights and expand the coverage of global trait databases. Newly developed methods will continue to reveal unanticipated specimen uses, overcoming perceived biases and the shortcomings of existing collections. Plant collecting must also continue and expand beyond traditionally collections-based researchers. In an era of technology and newly realized uses of specimens, we must rethink herbarium practices, modifying existing methods to best archive phenotype variation for the future. Collaboration among diverse researchers across disciplines and institutions is needed to develop the next generation of collections.

Many new collections practices, several of which may be controversial or dismissed as wishful thinking and infeasible (e.g., space constraints, financial limitations, staff time), were encouraged or proposed in this review. However, without stating the research community needs for fully realizing herbaria in functional trait research, solutions will never be found. These changes are not trivial and will require a fundamentally new scientific culture surrounding herbaria with significant digital, physical, and human resource infrastructural investment for transformative change. Best practices for plant collecting are needed in light of new approaches for specimen use. In summary, community-wide considerations for new collections to advance functional trait research include the following.

1. Archiving population-level variation. More specimens are needed that capture population-level trait variation archived in an unbiased way through mass collection–inspired approaches (Anderson 1941). These specimens may integrate physical specimens with digital images of leaves from the population.

2. Archiving ontogenetic variation. More specimens are needed that capture variation across life history stages through life history series vouchers (Utech et al. 1984).

3. Effectively capturing environmental context. More specimens are needed that include environmental context (biotic and abiotic), such as habitat descriptions, associated species, soil conditions, and light environment. A standardized vocabulary for collectors is needed.

4. Implementing the extended specimen. More specimens are needed that are born extended (Lendemer et al. 2020)—that is, disparate data streams, such as those relating to the specimen itself (e.g., traits measured, field images), related collections (e.g., DNA samples), related observational data (e.g., iNaturalist record of specimen and associated species; Heberling and Isaac 2018), the environment (e.g., environmental measurements), or the collection event (e.g., other specimens collected or recorded), are connected on collection or shortly thereafter. Trait data derived from the specimen should be archived in trait databases and directly linked to the specimen’s digital record. Establishing community best practices for permanently linking trait data to specimen records is needed.

5. Anticipating future use. Including additional plant material with the specimen for destructive sampling, such as silica-dried leaves unmounted in fragment packets for future trait measurements, should become common.

6. Documenting change. Intentional plans for long-term collecting are important steps to enable unbiased trait comparisons in an era of global change. These plans may include scheduled repeated collections of individual plants over time (e.g., tagged plants in botanical gardens) or repeated collections of the same populations (sites). While general collecting and taxon-specific targeted collections must continue, we must also be intentional in our collecting efforts.

It is an exciting time for collections. Bolstered by more than a decade of digitization and emerging initiatives, the role of herbaria in modern research should only strengthen. Pleas have been made for modern plant collections to include “DNA-friendly” material (Gaudeul and Rouhan 2013). Similarly, this review validates the need for similar calls for “trait-friendly” specimens. Recent efforts have developed efficient pipelines for phylogenomic data extraction from specimens (Folk et al. 2021), and the extraction of trait data should be integrated into these workflows and projects. Herbaria should be embraced as centers for functional trait research, with their uses as diverse as the specimens they house.

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