

Collections-based Studies of Plant Functional Traits

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Abstract

Herbaria may be collections of dead plants, but the information these collections provide is very much alive and growing, allowing a host of questions to be addressed, from a fuller description of the nature and distribution of diversity to a deeper understanding of plant evolution and adaptation. The use of herbarium specimens allows species-level functional trait data to be estimated for a much broader range of species that would otherwise be very time-consuming or difficult to collect from new specimens in the field. Fundamental traits such as leaf area and specific leaf area (SLA) can be easily collected from herbarium specimens. However, questions remain regarding the comparability between the trait data from live specimens versus herbarium samples, and there have been few attempts to quantify these differences. Other traits can also be collected from herbarium specimens, allowing new questions to be quickly answered. Basic traits might include leaf shape or margin type, while more detailed traits could indicate leaf venation patterns or the presence of extra-floral nectaries. Linking these trait data with plant distribution and biophysical data (climate, soils, etc.), as well as plot-level population dynamics data allows us to ask, for example, whether drip-tips are adaptations to high rainfall, what the abiotic drivers of leaf size are, or how fruit type is related to spatial pattern and life history. Thus, collecting functional trait information from plant herbarium specimens opens up a rich vein of new data with opportunities to verify old questions and expand into new areas of inquiry.

Key Words: Herbarium, specimen, databases

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The study of functional traits underpins investigations of plant resource use and life-history strategies because these two research areas characterize the fundamental trade-offs that determine the ecological roles of species (Grime 2006; Tilman 1988; Westoby & Wright 2006). By replacing species names with the quantitative values of physical traits, analysis of these traits from the individual level to the community-level allows us to step back from the specific identity of individuals and ask what factors drive their response to environmental variation, their influence on ecosystem

processes and services, and the structure and function of ecological communities (Wright *et al.* 2004; Reich *et al.* 2007; Kleyer *et al.* 2008; Suding & Goldstein 2008; Suding *et al.* 2008; Swenson *et al.* 2012). As such, functional traits can provide the basis for an ecology and global change science that is more quantitative and predictive than has been possible in the past (Lavorel & Garnier 2002; Westoby & Wright 2006; McGill *et al.* 2006; Cavender-Bares *et al.* 2009; Webb *et al.* 2010).

Functional traits of plants include the morphological, anatomical, biochemical, physiological, and phe-

nological features measurable at the individual level (Cornelissen *et al.* 2003). These traits reflect the outcome of evolutionary and community assembly processes in response to abiotic and biotic environmental constraints, and are evidence of trade-offs in structure, function, and resources within organisms. The trade-off between seed number and seed size illustrates this point (Leishman 2001; Coomes & Grubb 2003; Muller-Landau 2010). Plants devote finite resources to reproduction, resources which can be allocated among few large seeds or many small seeds (or some combination along this continuum). Large seeds give rise to large seedlings capable of surviving in sites of low resources and high competition; in contrast, small seeds require high resources and low competition to survive – their success lies in the higher chance of dispersal to such sites. Seed size is an easily-measured functional trait that informs our understanding of the relative quality of competition and dispersal of different species.

The development of standardized protocols for measuring individual functional traits (Cornelissen *et al.* 2003; Pérez-Harguindeguy *et al.* 2013) has driven efforts to compile these data into large functional trait databases, either with direct contributions from researchers or extracting data from existing literature (Chave *et al.* 2009). These varied databases are impressive. The TRY Plant Trait Database (<https://www.try-db.org/>; Kattge *et al.* 2011) contains more than 5 million trait records for 1100 traits of 2.2 million individual plants, representing 100,000 plant species. Half the data are geo-referenced, from over 12,000 measurement sites. The Global Wood Density database contains 16,500 data entries for 8412 species (<http://www.datadryad.org/handle/10255/dryad.235>; Zanne *et al.* 2009). Kew's Seed Information Database v.7.1 contains seed mass, dispersal, oil content, and other data on 33,346 taxa (<http://data.kew.org/sid/>).

Notwithstanding these impressive feats, trait databases have two main flaws. First, the values included in or extracted from such databases are often average values and generally not from the specific location(s) or even habitats of the study that uses them second-hand (Cordlandwehr *et al.* 2013). There are many

well-documented causes of intraspecific variation in plants (Albert *et al.* 2012), but the question remains as to how this variation affects the value and utility of trait databases (Albert *et al.* 2012; Violle *et al.* 2015).

Second, trait databases remain for many individual traits, woefully incomplete, highly skewed toward common species, and with trait values for rare species often biased by low sampling effort (Violle *et al.* 2015; Sandel *et al.* 2015). Given this issue is more of a problem for rare species, the impact of this flaw will vary according to the study. For instance, missing or erroneous values for rare species might not affect estimates of mean trait values at the community level.

The only way to address these two problems is to collect new trait data for each study, to ensure that data are appropriate to the question in hand. However, an apparently overlooked method that could rapidly and cheaply address the issues of both intraspecific variation and undersampling of live plants is to extract functional trait data from preserved and curated herbarium material. Using herbarium material ensures that trait data are linked to individual plants and opens up a greater sample size from which to measure traits, as well as other advantages detailed below.

The use of herbaria to add value to other scientific fields has been explored for many years (Smith 1956; Funk 2003), from making additional collections to examine population-level variability (Anderson & Turritt 1935; Anderson 1941), to studies of biogeography (Holland 1975), invasions (Lavoie *et al.* 2007), migrations (Feeley 2012), and phenology (Calinger *et al.* 2013). Thus, there should be no a priori reason to discount their use for studies of functional traits as well.

Sources of Trait Data

Functional trait data can be sourced from a variety of plant material. Trait data are best obtained from fresh material collected in situ (Cornelissen *et al.* 2003; Pérez-Harguindeguy *et al.* 2013). However, other options are available: In extremis, living collections could replace wild-collections; published species descriptions, floras and monographs contain data on life form, life history, size, and reproductive structures;

importantly, there is also a vast wealth of data in the dried plant collections in herbaria from which a number of significant traits could be determined, especially for species that are rare, or located in hard-to-reach or difficult collecting environments.

Living wild plants in situ

These plants will be acclimated to local climate and abiotic conditions and should therefore reflect the adaptive strategy that maximizes fitness. Because many plant species are plastic, traits should be measured on robust, healthy, mature plants, located in well-lit environments, unless specific goals suggest otherwise (Cornelissen *et al.* 2003). Collecting sun leaves is particularly important for some leaf traits that are known to be very plastic in response to light (Markesteijn *et al.* 2007; Rozendaal *et al.* 2006).

Living collections

Many botanical institutions have living collections in their greenhouses and gardens, often numbering tens of thousands of individuals (e.g. the Royal Botanic Gardens, Kew (K) has an estimated 19,000 species from 178,000 accessions; The Royal Botanic Garden Edinburgh (E) 15,000 species; The New York Botanical Garden (NY) has over 1 million accessions), many of which are available for research purposes (Dosmann 2007). Taking trait data from living collections is not ideal, in large part because of plants' high plasticity. In contrast to herbarium specimens, the whole plant is available for study, but many species will adapt in physiology and morphology to local growing conditions, which are often quite different from those experienced in their natural environment. As such, living collections are more akin to the 'common garden experiments' often run by evolutionary ecologists to determine the relative contribution of genes versus habitat on phenotype (Goldberg & Barton 1992). With little knowledge of the intra-specific variation in each trait of a particular species, the use of these data for large-scale comparative functional trait studies is not recommended.

Literature and descriptions

All descriptions of new species, as well as many floras and monographs, contain data that could contribute to trait databases (e.g. Croat 1978). These descriptions are written by taxonomists and systematists and based on observations of many fresh and dried specimens. As such, and depending on the author, the descriptions will generally reflect average values for quantitative traits such as seed, fruit and leaf size; qualitative traits such as life form, seed and fruit type, and dispersal mode, are likely to also be presented.

Herbarium specimens

After fresh, wild-collected specimens, herbarium specimens may be the next-best source of material for extracting functional trait data (for the parts that are collected, often limited to leaves, stems, flowers, and fruits). This is largely because these specimens are already collected, often from locations that would be difficult or expensive for trait ecologists to visit specifically to collect trait data (Mann 1997; Funk 2003). Further, as with fresh plant material, these data will be linked to individual specimens, and any errors or changes are much easier to correct than if using aggregated data from the literature.

Collecting Trait Data from Herbarium Specimens

Advantages of herbarium specimens

Using collections increases species coverage – By definition, herbarium specimens include all species ever described. As such, it is theoretically possible to sample all these specimens to build a complete picture of intra- and interspecific variation in trait data. Further, one can access a far greater range of species and range of variation in a herbarium than is possible at a single field site, depending on the quality and nature of the collections. Large botanical institutions, in particular, have millions of specimens and many thousands of

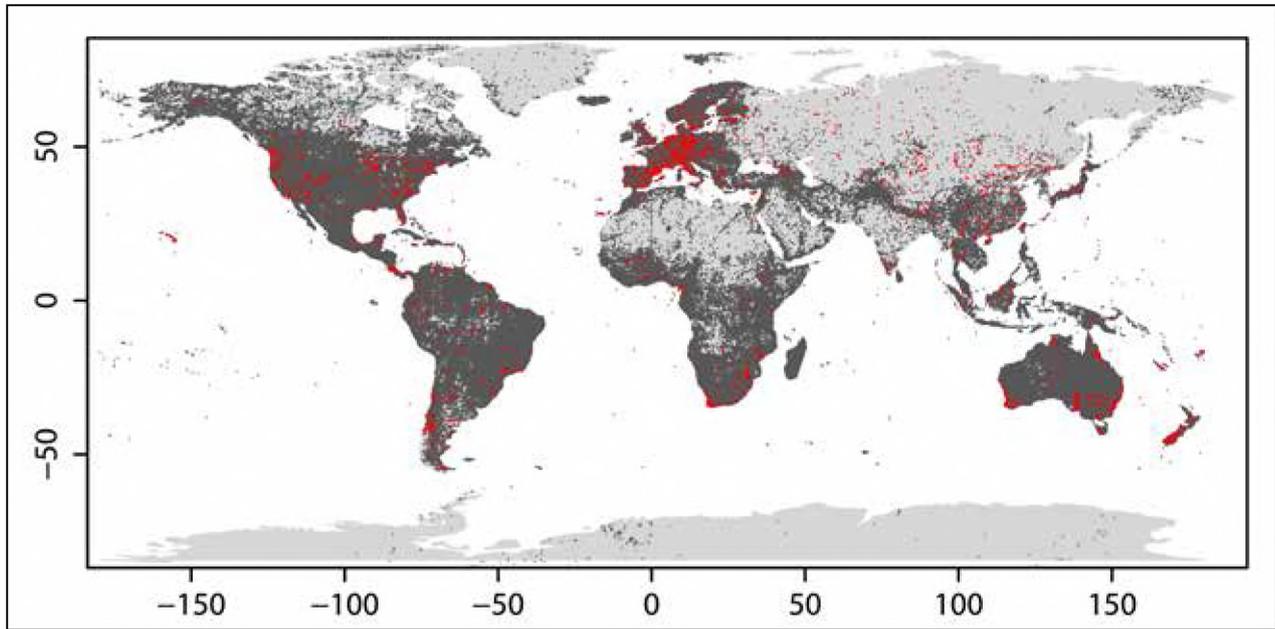


Fig. 1. A comparison of sites where plant trait data have been measured (red; geo-referenced measurement sites in the TRY database) with the location of all angiosperm herbarium specimens recorded in GBIF (grey; Global Biodiversity Information Facility, <http://www.gbif.org>).

specimens that could be accessed easily and cheaply for their existing trait data.

This advantage is highlighted when we compare the distribution of sites and ecosystems from which trait data has been sampled (e.g. Kattge *et al.* 2011). In general, functional data for traits such as specific leaf area and leaf nitrogen content remains a very small part of the total geographical and biome hyper-space that has been sampled as herbarium specimens (comparing the distribution of specimen data in GBIF with the trait data in TRY, Fig. 1). This situation is exacerbated in the tropics because most trait data comes from the temperate grasslands of Europe, North America, South Africa and Australia. The use of herbarium data would quickly and dramatically improve data coverage of areas and biomes that are under-represented in trait databases.

Historical and geographic record of trait variation, within and between species – Along with the variety of species present, many herbaria also have considerable historical collections going back over hundreds of years. These specimens can provide valuable data on how

traits may have changed over time, especially with regards to phenology and leaf-level traits (see examples below). Such trait data are invaluable. Given that we cannot go back in time to collect fresh trait material, herbarium specimens are likely the sole manner from which we can obtain information on trait values in the past.

Likewise, because many different plant collectors contribute duplicate specimens to multiple herbaria, these repositories have accumulated specimens from a wide range of geographical locations (local, regional, and global), often much wider than a single researcher could visit over the duration of a project. Determining the temporal and spatial nature of trait variation is a key issue to understanding the ecology and evolution of plant communities.

Trait data are linked to individual curated specimens – A major advantage of obtaining trait data from a herbarium specimen is the fact that the data are then linked to a specific enumerated and curated sample (assuming adequate records by the plant collector, herbarium, and trait researcher). While this system

may seem a constraint, it permits much flexibility in the future. First, it allows easy access to these specimens by taxonomic specialists to ensure that the determination of the specimen is correct; single trait-based specimens or samples for trait analysis stored in the researcher's laboratory are often inaccessible to taxonomists to complete this task – and ecologists are sometimes bad taxonomists! (Gotelli 2004; Bortolus 2008; Dexter *et al.* 2010; Gomes *et al.* 2013). Second, if the determination is incorrect, the system permits the name to be changed and for this name change to propagate through to any second-level datasets and analyses based on this specimen; if trait data are based on species names and those names change, there is no way to know if any particular datum from a researcher-collected specimen should also be reassigned a different taxonomic identity.

Following this advantage, it is recommended that voucher specimens be made from all field-collected data specimens (in line with all plot-based research), and duplicates deposited in international herbaria and sent to specialists for confirmation of their identity.

Herbarium specimens are already collected – A final advantage of using herbarium specimens is that they are already collected, avoiding the need for expensive and lengthy field excursions (Mann 1997). The researcher can get straight to work collecting and analyzing the trait data itself.

The combination of advantages listed above suggests that the use of herbarium specimens should open up a wide field of trait research that will rapidly produce results and insights. Unfortunately, there are a number of caveats to this exciting possibility.

Disadvantages of herbarium specimens

Herbarium specimens are collected already – Despite the time and financial advantages that having ready-collected specimens can provide, this benefit also has a disadvantage. The trait researcher is generally unsure if the herbarium specimens were collected according to standard trait protocols (see Living Wild Plants, above), unless the specimen label provides this information. Ideally, trait data should be collected from

mature, fully-expanded, healthy sun-lit plants (Cornelissen *et al.* 2003) – but many collected specimens were growing in no such state, especially the specimens that exist in historical collections. The question remains as to whether the benefits of using herbarium specimens outweigh the increased trait variance from using non-standard samples.

It should be noted, however, that many trait researchers who use wild living plants do not use 'ideal' samples because the nature of their studies renders prohibitive collecting such samples (Pérez-Harguindeguy *et al.* 2013). Tall rain forest trees are one such life form where climbing all of the 1000 species found in a large forest plot would almost certainly restrict trait-based research in such environments, and so data from saplings are frequently used instead (Kraft *et al.* 2008). As in all studies, the nature of the question should drive the data collected, and trait data from saplings for 1000 species may provide better answers than trait data sampled from the canopies of 10 species.

Biased collecting and sampling of the natural world – While ecologists may be less-than-perfect taxonomists, plant collectors are not immune to the bias of a particularly pretty flower or easily accessible tree. Ideally, we would sample the world at random. However, many studies have demonstrated the biased nature of taxonomic collecting, with more collections and higher species richness of focal taxa around taxonomic centers (Dennis & Thomas 2000; Dennis *et al.* 1999; Beck & Kitching 2007), and greater numbers of specimens collected from alongside roads and rivers (Funk *et al.* 1999; Kadmon *et al.* 2004).

As with the previous disadvantage, some data may be better than none, but the fact remains that rare and disturbed ecosystems such as rivers and roads are sampled with much higher intensity than continuous tracts of forest or grassland, especially in the tropics (Fig. 2). Traits may differ between these environments, and again, the variance in herbarium samples may be greater than that found between species, rendering the data less useful. At the same time, traditional trait researchers should also be warned that their field sampling schema may result in biased esti-

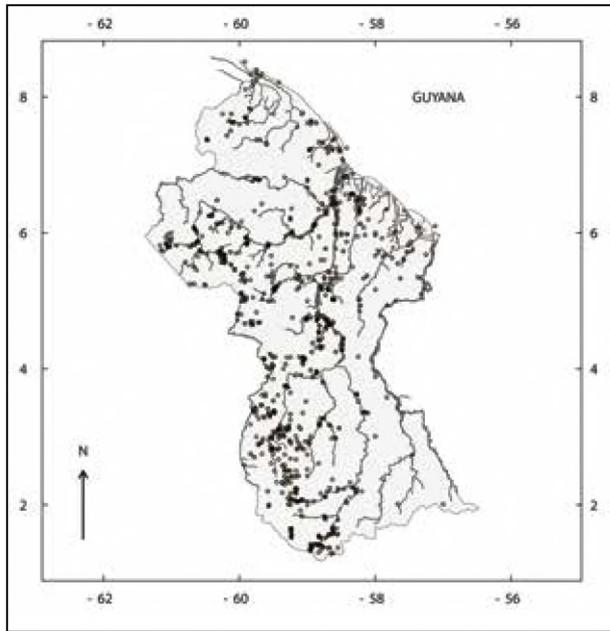


Fig. 2. Highlighting the biased nature of sampling from the natural world. Map of Guyana with main rivers, showing higher intensity of sampling near the rivers than elsewhere. Each dot represents at least one collection of Fabaceae registered in GBIF. Figure based on Funk *et al.* (1999) with additional data from GBIF.

mators of reality and to guard against this issue (Baraloto *et al.* 2010).

Specimens may have incorrect labels – Despite being the place where names are bestowed, herbaria often contain errors (Allen 1981; Bisang & Urmi 1994; Ahrends *et al.* 2011). In many cases, these errors reflect name changes that curators and specialists have yet to update. In other cases, the plant collector may have erred in the original label name. In taxonomically difficult groups, material essential for accurate determination, such as flowers or fruits, may not even be present within the specimen.

However, at least when a name is associated with a herbarium specimen it can be verified (too many field identifications in ecology, without a voucher, are not even available for verification). Many of these errors may be corrected in time, and as stated above, the advantage of linking data to specimens is that name changes can easily propagate throughout data sets if they are designed and managed correctly.

Drying and pressing changes specimens – The final, and most important, disadvantage is that the actual process of collecting and preserving may alter the specimen to a point where accurate trait data is impossible to obtain (Pérez-Harguindeguy *et al.* 2013). For many historical collecting trips, preservation in alcohol was the only way to ensure that specimens survived the climate of their origin and the journey back to the herbarium (Mori *et al.* 2011) – drying in situ was not an option. Even today, this technique may be the best choice in remote tropical locations. However, most taxonomists can now rely on returning to a semi-permanent field site where specimens can be dried and pressed quickly in drying ovens, packed, and transported rapidly to secure and dry herbaria for curation. This process does not leave the specimen unaltered, with several recent studies showing changes in leaf shape or proportion (Queenborough & Porras 2013), as well as documented changes in color that occur in several families (Gentry 1996; Pérez-Harguindeguy *et al.* 2013). From these observations, it appears that drying-induced changes in leaf (and other organ) morphology are primarily related to the structure of the organ. Tougher leaves hold their shape better, giving similar results for measures such as specific leaf area (area/dry mass) when calculations are performed on the same leaf when fresh or dry; fleshier leaves tend to shrink more and may undergo other internal changes (Queenborough & Porras 2013). Thus, care must be taken when taking trait data from dried samples. Ideally, before undertaking such a project, researchers should conduct some preliminary analyses, examining the mean and variance in trait data from samples they collect and prepare from both fresh and dried material for their trait/s of interest. They will then be in a position to decide whether or not to use herbarium material.

Linking trait data to other data types

The power of functional trait data lies in linking it with other data in order to examine patterns and processes of ecology and evolution at various levels and scales (McGill *et al.* 2006; Westoby & Wright 2006). Currently, these linkages are made through the key of

the species name (i.e. genus and specific epithet). Various resources are available to update and resolve nomenclatural issues, such as the Taxonomic Name Resolution Service (<http://tnrs.iplantcollaborative.org/>), the Plant List (<http://www.theplantlist.org/>) and others. None of these online services can ensure that the name matches the underlying sample or specimen in hand. This issue applies to all species-level data, trait or otherwise, and guidance is needed for what researchers should do if species names change, are split, or combined. Ideally, all trait data would be backed up with a valid voucher specimen that could be referred to in the event of such discrepancies, linked to in the trait database within which the data reside.

Collecting data from specimens sidesteps this issue, because it is the specimen itself that comes first. Thus, it is already collected and curated. Data taken from the specimen need to be linked back to it to allow any name changes to propagate through the databases and analyses. Any analysis based on these data might then calculate species-level means ‘on demand’ and then archive and reference the version of the database used. The wide availability of scripted programming and statistical software, version control software, and supplementary or archival websites make this issue trivial in terms of its technical nature, but likely would require a non-trivial change in the workflow of many researchers.

Tropical versus temperate collections

Many of the above issues equally apply to the use of collections from the tropics and the temperate zones. However, given the two issues of how collecting in alcohol in the tropics might impact functional trait data and just how many more collections exist from the temperate zone, there may be benefits to trialing large-scale extraction of traits from temperate specimens. Contrary to this recommendation, however, is the fact that the most extensive collections of tropical plants often reside in the temperate zone. It may, therefore, make more sense to trial data collection from a group of related taxa that are found throughout the world.

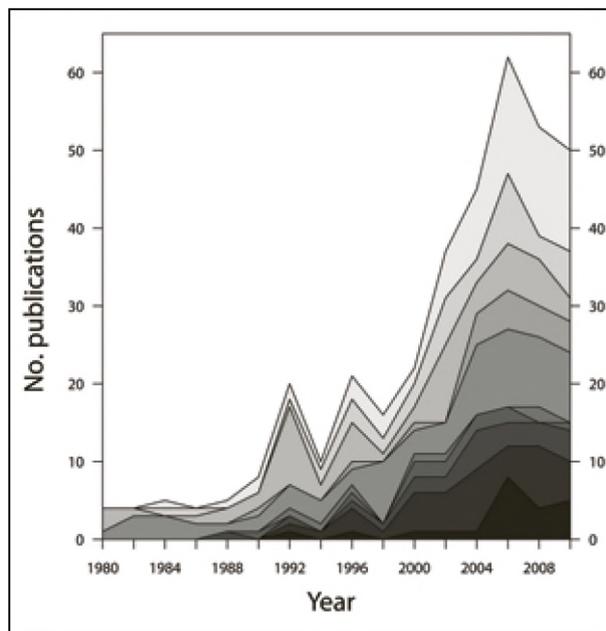


Fig. 3. Trends in publications using herbarium data, 1980–2010. The figure shows the number of publications every two years from 1980, in ten categories from bottom to top: biases associated with herbarium specimens, biogeographical patterns, plant diseases, historical floristic assessments, plant invasions, plant phenology, pollution (including carbon dioxide), rare or declining plant species, and multiple or other topics (including climate change and distribution range of plants and conservation priorities). Data from Lavoie (2013).

Examples of herbarium-based trait analysis

Given the advantages and challenges of working with this data source, increasing numbers of ecological and evolutionary studies are making use of herbarium specimens (Fig. 3; Lavoie 2013). Most of this work is not trait-based, but instead focuses on species distribution modeling (Loiselle *et al.* 2008; Elith & Leathwick 2007; Phillips & Dudík 2008; Feeley & Silman 2011) and investigations of invasive species (Delisle *et al.* 2003; Peterson *et al.* 2003). These studies make extensive use of only the species identity and location data associated with collections, and many trait analyses make use of field-collected trait databases (e.g. Wright *et al.* 2004; Poorter & Bongers 2006; Edwards *et al.* 2007). However, researchers are increasingly us-

ing information from actual specimens to answer not only intriguing biological questions but scientific questions of global importance.

Phenotypic change over time

As discussed above, collections of the same species from similar locations provide a time series of data that can be used to ask whether these populations have changed, and also to investigate the drivers of that change, for example in terms of phenology (see below) as well as other aspects of plant phenotype. Plant size, particularly of annuals, is especially amenable to study. In contrast to animals, little is known about changes in plant body size over the last 100 years. Leger (2013) measured herbarium specimens of seven species of small annual plants from the Great Basin-Mojave Desert floristic province in the western USA collected between 1893 and 2011. Most species were found to decrease in height and leaf size, with no obvious climatic driver. A limitation of using herbarium specimens for this kind of study, however, is deter-

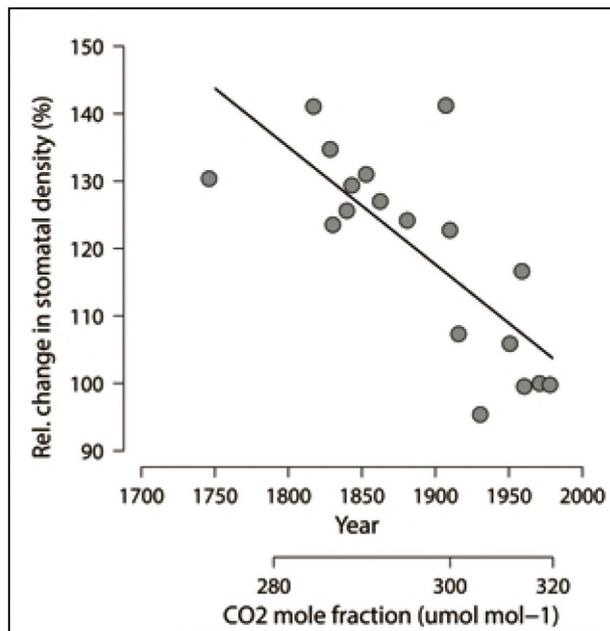


Fig. 4. Stomatal densities of herbarium stored leaves of eight species of temperate forest trees, and reconstructed atmospheric CO₂ based on ice cores. Data from Woodward (1987: Fig. 1).

mining if these changes are plastic responses to climate variation or a product of evolution in response to climate or another factor.

Historical CO₂ and stomatal density

Herbarium specimens collected over historical time were put to innovative use by Woodward (1987). He examined specimens of eight temperate tree species from the University of Cambridge's Department of Botany herbarium that had been collected between 1750 and 1981, and calculated stomatal density of these samples. Some attempt was made to use ideal full-sunlight leaves by only using samples from reproductive shoots. He found a convincing strong negative correlation between stomatal density and estimated atmospheric CO₂ concentration (from ice-core data) (Fig. 4) - and confirmed this result experimentally, suggesting that climate change was already having an effect on vegetation before recent shifts in species distributions were observed. Further studies corroborated this investigation (Beerling *et al.* 1991, 1993; McElwain *et al.* 1995), many even using fossil collections to demonstrate the effect of CO₂ on leaf stomata (Royer 2001).

Phenological change in response to climate

The study of plant phenology (the timing of life events such as reproduction) has traditionally been undertaken solely in the field at single intensively monitored sites (Fitter & Fitter 2002; Miller-Rushing & Primack 2008), or via networks of volunteers or citizen scientists (Dickinson *et al.* 2010, 2012; Miller-Rushing *et al.* 2012). The use of herbarium specimens permits analyses over much wider geographic ranges and time-scales. For example, several recent studies have linked reproductive trait data from herbarium specimens with historical temperature or rainfall data to examine the impact of climate change on phenology. Using the collection dates of reproductive specimens as a proxy for flowering time and with sufficient numbers of specimens, patterns and changes in phenology can be accurately calculated. This approach has been used successfully for single locations

(Primack *et al.* 2004; Lavoie & Lachance 2006; Robbirt *et al.* 2011; Panchen *et al.* 2012) and over wide geographical areas (Zalamea *et al.* 2011; Calinger *et al.* 2013; Hart *et al.* 2014; Park & Schwartz 2015).

Harvesting and artificial selection

Paleontological collections can obviously be used to examine the evolution of plants over deep time, as in the case of leaf stomata referred to above (Royer 2001). However, plants can also evolve rapidly and historical collections provide a snapshot or sample of populations that can be compared to more recent collections or fresh material. This approach can be especially useful when determining the effects on populations of harvesting by humans, because collecting based on certain traits may unintentionally select against that trait in the remaining population. For example, Law & Salick (2005) used historical herbarium samples and compared them to plants recently collected for the medicinal trade, showing that the medicinal snow lotus (*Saussurea laniceps*, Asteraceae) had reduced in size over the last 100 years, whereas its less-used sister taxon (*Saussurea medusa*) remained the same size. In passing, it should be noted that scientific collecting, at least from trees, generally has little impact on the individual or population (Phillips *et al.* 1998).

Adaptive variation of plant traits

Exciting developments in understanding questions of evolutionary adaptation are being realized with the combination of herbarium data and traits with large-scale vegetation plot networks. The advantage of plots over specimen collections is that in addition to incidence (i.e. whether the species is present or not), plots also provide quantitative information on the abundance of each species – species may be uniformly common or rare, or vary in abundance throughout their range (ter Steege *et al.* 2013). Using species-average trait values allows researchers to compare how the mean and variance in plot-level trait values (in terms of both species or individuals) vary over wide geographic ranges, climates, and soils. For example, Mal-

hado *et al.* (2009, 2012) used the RAINFOR network of over one hundred 1-ha tree plots to determine that larger leaves tend to be found in drier areas and leaves with drip-tips are more common in wetter areas, suggesting a strong role of water in driving the structure and function of leaves even in generally wet environments as tropical forest.

In addition to incidence and abundance, many vegetation plots are censused numerous times, allowing the inclusion of demographic data in the analysis. Muchleisen *et al.* (2016) used a mixture of field collections, herbarium specimens, scanned herbarium specimens and previously collected data to analyse the distribution and demographic correlates of extra-floral nectaries – nectar-producing glands on the leaves or stems of plants that attract ants, often hypothesized as a defensive strategy. Despite the wide distribution of extra-floral nectaries on the phylogeny, they found little evidence of an effect of extra-floral nectaries on the performance of mature trees, suggesting that examining seedlings and sapling might be where any fitness and/or performance benefit would be found.

Future Directions

There is important potential for large datasets from herbaria to expand our knowledge of how ecological systems interact and change over global scales. The goals of a quantitative and predictive ecology and global change science might be characterized as follows (McGill *et al.* 2006; Lavorel & Garnier 2002): (i) To determine the adaptive nature and/or fitness of plant traits; (ii) To understand the determinants of past and present plant diversity, distribution and abundance; (iii) To predict how species and vegetation will respond to future climate change. Attaining these goals will require the dynamic linking of numerous sources of data, from vegetation plot and demographic data to field-collected trait data as well as herbarium specimen location and trait data, and molecular phylogenetic data.

Several traits could very easily and quickly be collected from herbarium specimens. These are largely restricted to leaf traits, such as leaf size, shape, and

margin type, as well as specific leaf area and even nitrogen content. Flower and fruit traits could also be determined from herbarium sheets or carpological collections. For many such traits, access to a virtual herbarium is all that is required, because leaf area, shape and margin can all be measured visually (M. Sullivan & S. Queenborough, *unpublished data*). Indeed, it may even be possible to automate the collection of some of these traits, allowing entire (virtual) herbaria to be measured remotely (Belhumeur *et al.* 2008; Cope *et al.* 2012).

In conclusion, there are sound biological, theoretical, and financial reasons to explore the use of herbarium specimens in trait research. Initial studies comparing traits from herbarium to fresh specimens suggest that, with care, certain traits can certainly be used. Given the rapidly changing nature of the global climate, it behooves researchers to use creative methods to understand how plant community structure and function were driven by past climate and how they will likely respond to new and future climates.

Acknowledgements

I would like to thank Henrik Balslev and Ib Friis for the kind invitation to speak in Copenhagen at the symposium *Tropical Plant Collections: Legacies from the past? Essential tools for the future?* and the other attendees for interesting comments and discussion throughout the meeting. Erin Beasley and two anonymous reviewers made valuable suggestions on the manuscript.

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