

1 **NextGeneration specimen digitization:**  
2 **The international herbarium community goes spectral!**  
3

4 Jeannine Cavender-Bares<sup>1\*</sup>  
5 Dawson M. White<sup>1</sup>  
6 Natalie Iwanycki Ahlstrand<sup>2</sup>  
7 Matthew W. Austin<sup>3</sup>  
8 Denis Bastianelli<sup>4</sup>  
9 Samantha Bazan<sup>4</sup>  
10 Khalil Boughalmi<sup>5</sup>  
11 Warren Cardinal-McTeague<sup>6</sup>  
12 Eduardo Chacón-Madrigal<sup>7</sup>  
13 Thomas L.P. Couvreur<sup>5</sup>  
14 Charles Davis<sup>1</sup>  
15 Flávia M Durgante<sup>8,9</sup>  
16 Olwen M. Grace<sup>10</sup>  
17 J. Antonio Guzmán Q.<sup>1</sup>  
18 Kimberly Hansen<sup>11</sup>  
19 M.S. Hernández-Leal<sup>1</sup>  
20 Mike John Gilbert Hopkins<sup>9</sup>  
21 Rykkar Jackson<sup>6</sup>  
22 Shan Kothari<sup>12</sup>  
23 Aaron K. Lee<sup>13</sup>  
24 Étienne Lévillé-Bourret<sup>14</sup>  
25 Jesús Pinto-Ledezma<sup>15</sup>  
26 Natalia L. Quinteros Casaverde<sup>16</sup>  
27 Jose Eduardo Meireles<sup>17</sup>  
28 Barbara Neto-Bradley<sup>18</sup>  
29 Cornelius Onyedikachi Nichodemus<sup>17</sup>  
30 Michaela Schull<sup>1</sup>  
31 Douglas E. Soltis<sup>19</sup>  
32 Pamela S. Soltis<sup>19</sup>  
33 Hanna Tuomisto<sup>20,21</sup>  
34 Susan Ustin<sup>21,22</sup>  
35 Caroline C. Vasconcelos<sup>9</sup>  
36

37 \*jcavender@fas.harvard.edu  
38 <sup>1</sup>Harvard University Herbaria and Department of Organismic and Evolutionary Biology, Harvard  
39 University, Cambridge MA 02138, USA  
40 <sup>2</sup>Natural History Museum of Denmark, University of Copenhagen, Copenhagen, 1154, Denmark  
41 <sup>3</sup>Herbarium, Missouri Botanical Garden, 4344 Shaw Blvd, St. Louis MO 63110  
42 <sup>4</sup>CIRAD, Umr Selmet, Montpellier, France, UMR SELMET, F-34398 Montpellier, France.  
43 <sup>5</sup>DIADE, Univ Montpellier, CIRAD, IRD, Montpellier, France  
44 <sup>6</sup>Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, BC, V6T  
45 1Z4, Canada  
46 <sup>7</sup>Herbario Nacional, Departamento de Historia Natural, Museo Nacional de Costa Rica & Herbario Luis  
47 Fournier Origgí, Centro de Investigación en Biodiversidad y Ecología Tropical (CIBET),  
48 Universidad de Costa Rica, Costa Rica  
49 <sup>8</sup>Department of Wetlands Ecology, Karlsruhe Institute of Technology, KIT, Germany.  
50 <sup>9</sup>Herbário, National Institute of Amazonian Research, INPA, Brazil.  
51 <sup>10</sup>Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh EH3 5LR, United Kingdom  
52 <sup>11</sup>Field Museum of Natural History, 1400 S. DuSable Lake Shore Dr., Chicago, IL 60625, USA  
53 <sup>12</sup>Department of Renewable Resources, University of Alberta, Edmonton, AB T6G 2E3, Canada  
54 <sup>13</sup>Department of Plant and Microbial Biology, University of Minnesota, 1479 Gortner Ave, Saint Paul,  
55 MN 55108, USA  
56 <sup>14</sup>Département de sciences biologiques, Institut de recherche en biologie végétale (IRBV), Université de  
57 Montréal, Montréal, QC H1X 2B2, Canada  
58 <sup>15</sup>Department of Ecology, Evolution and Behavior, University of Minnesota, 1479 Gortner Ave, Saint  
59 Paul, MN 55108, USA  
60 <sup>16</sup>Biospheric Science Lab, NASA Goddard Space Flight Center, Greenbelt MD 20771, USA  
61 <sup>17</sup>School of Biology and Ecology, University of Maine, Orono, ME 04469, USA  
62 <sup>17</sup>School of Biology and Ecology, University of Maine, 5793 Hitchner Hall, Orono, Maine 04473, USA  
63 <sup>18</sup>Department of Plant Sciences, University of Cambridge, Cambridge CB23EA, UK  
64 <sup>19</sup>Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA  
65 <sup>20</sup>Department of Biology, Section of Ecoinformatics and Biodiversity, Aarhus University, Aarhus,  
66 Denmark  
67 <sup>21</sup>Department of Biology, University of Turku, Turku, Finland  
68 <sup>22</sup>Institute of the Environment and Department of Land, Air and Water Resources, University of  
69 California Davis, Davis, CA 95616, USA  
70

71 **Abstract**

72

- 73 1. Spectral reflectance measured from herbarium specimens represents a vast source of plant  
74 phenotypic and functional trait data.
- 75 2. The potential to capture data from specimens to enhance knowledge of plant function and taxon  
76 identification has inspired many laboratories worldwide to initiate next-generation spectral  
77 digitization from specimens.
- 78 3. Combining these datasets into a coordinated global database would enable prediction of traits  
79 from the world's plants and allow novel, impactful scientific questions to be addressed at global  
80 scale. These novel data streams will generate new capacity to model plant traits globally, enabling  
81 connection with remote sensing and ecological and biosphere models and to reconstruct their  
82 evolutionary history.
- 83 4. Coordination is needed to avoid downstream problems in data aggregation due to variation in data  
84 standards and technical specifications of the instruments, optical setups, or measurement  
85 protocols. The International Herbarium Spectral Digitization (IHerbSpec) working group has  
86 initiated a globally collaborative program, outlining the central issues to address in establishing  
87 protocols, standards, and best practices, and next steps. This collaborative effort will allow  
88 generation of replicable spectral reflectance data from plant specimens housed in herbaria around  
89 the world within ongoing digitization programs following community-defined standards and  
90 Findable, Accessible, Interoperable and Reusable (FAIR) principles.

91

92 **Keywords:** methodological standards, collection management, plant functional traits, spectral reflectance,  
93 next-generation digitization, global herbarium

94

95

96 **Introduction**

97 In an era of rapid global change and biodiversity loss, safeguarding our knowledge of plant diversity is  
98 essential. Herbaria serve as foundational repositories for this knowledge, both through their traditional  
99 applications to document species morphology, distribution, use, and phenology (National Academies of  
100 Sciences and Medicine 2020, Heberling et al. 2021, Davis 2023, Mandrioli 2023). Advancing  
101 technologies have now enabled investigations that apply whole-genome sequencing and metabolomic  
102 methods of herbarium specimens that are up to hundreds of years old (Burbano and Gutaker 2023, Davis  
103 2023, Medeiros et al. 2024, Davis and Knapp 2025). These advances are now routinely used in  
104 macroecological and biogeographical studies providing a vast botanical record of species distributions in  
105 space and time relevant to monitoring biodiversity change in the Anthropocene (Willis et al. 2008,  
106 Meineke et al. 2018a, Meineke et al. 2018b). We broaden the extended specimen concept, which  
107 reenvision the role of specimen data as a vast, connected repository of information about individual  
108 organisms (Webster 2017, National Academies of Sciences and Medicine 2020), to include spectral  
109 reflectance from dried plant specimens. A wealth of information about plant chemistry, function, structure  
110 can be inferred from plant reflectance spectra—the pattern of light’s reflectance from plant tissues across  
111 wavelengths (Elvidge 1990, Gitelson and Merzlyak 1994, Sims and Gamon 2002, Ustin et al. 2004, Asner  
112 and Martin 2011, Serbin et al. 2014b, Cavender-Bares et al. 2017, Chlus and Townsend 2022, Wang et al.  
113 2023). Spectra can provide information about taxonomic identity (Durgante et al. 2013), phylogenetic  
114 placement (Meireles et al. 2020a), defense chemistry in diverse genera (Fine et al. 2021), and phenotypic  
115 variation linked to genetic or phylogeographic variation (Cavender-Bares et al. 2016b, Deacon et al.  
116 2017a, Stasinski et al. 2021, Hernandez-Leal et al. 2025). The contribution of spectral information to  
117 obtaining both functional and phylogenetic information in plants centers reflectance spectra as a critical  
118 data type in the plant sciences with high potential to integrate information about plant diversity across  
119 scales, from leaves to ecosystems and the biosphere (Cavender-Bares et al. 2017, Cavender-Bares et al.  
120 2025, Wang et al. 2022, National Academies of Science and Medicine 2025).

121 Advances in spectroscopic technology and analytical approaches across scales that have enabled  
122 spectral data capture across scales (Jetz et al. 2016b, Jacquemoud and Ustin 2019, Serbin and Townsend  
123 2020, Wang et al. 2023) have led to the development of the growing field of spectral biology. This field  
124 enables trait models and methods of taxonomic identification from spectral measurements of fresh or  
125 dried, pressed leaves (Durgante et al. 2013, Meireles et al. 2020a, Kothari et al. 2023), including actual  
126 herbarium collections (Kühn et al. 2025, Neto-Bradley et al. 2025, White et al. 2025), to address myriad  
127 questions in ecology, evolution, taxonomy, phylogeography, historical biogeography, biochemistry, and  
128 related realms of inquiry. When combined with even a fraction of the world’s 400 million herbarium  
129 specimens (Thiers 2024), reflectance spectroscopy provides a new means to extend our inferences of  
130 plant phenotypic and functional variation across space and time – and across the entirety of plant  
131 taxonomic and phylogenetic diversity.

132 As with digitization standards for herbarium imaging over the past 25 years (Nelson et al. 2015,  
133 Hedrick et al. 2019, Davis et al. 2021), similar consensus on protocols and standards is now needed to  
134 incorporate spectral data in the ‘global metaherbarium’ (Davis 2023). Standardized workflows for  
135 spectral data and metadata collection will enable integration across herbarium collections, linking trait  
136 estimates to individual specimens and the time, place and environment in which they were collected  
137 (Davis et al. 2015, Willis et al. 2017, Meineke et al. 2018a, Meineke et al. 2018b, Pearson et al. 2020).

138 *This article documents the purpose and vision of the newly established international herbarium*  
139 *spectral digitization (IHerbSpec) working group, our progress to date in advancing spectral digitization*  
140 *within herbaria across all green plant groups as a scalable tool for biodiversity science. We describe*  
141 *the nature of spectra, the prospect of measuring them in the world’s herbaria, highlight the benefits of*  
142 *this massive effort, and address key challenges and next steps.*

143

#### 144 **The expanding use of plant traits in ecology and evolution**

145 Extensive work has been carried out by plant systematists to describe new species based on plant traits,  
146 often in conjunction with genetic and genomic data. Plant traits have become fundamental to  
147 understanding ecological processes such as interactions with the abiotic environment, interactions with  
148 herbivores and pollinators, growth responses to resource availability, community assembly processes, and  
149 the contributions to ecosystem and biosphere functions (Lavorel and Garnier 2002, Violle et al. 2007,  
150 Cavender-Bares et al. 2016a, Funk et al. 2017, Shipley et al. 2017, Dechant et al. 2024). Traits provide  
151 key insights into consistent patterns of resource acquisition and ecological functions across the green  
152 plant tree of life, termed the Leaf Economics Spectrum (Wright et al. 2004, Díaz et al. 2016). These  
153 patterns influence species distributions across environmental gradients and inform models of community  
154 assembly, vegetation dynamics, and biosphere function (Cavender-Bares et al. 2016a). Consequently,

155 significant effort has been invested in developing global plant trait databases (e.g., TRY (Kattge et al.  
156 2020), BIEN (Enquist et al. 2016), AusTraits (Falster et al. 2021, Wenk et al. 2024)), and scaling plant  
157 traits to global maps to model biosphere dynamics (Dechant et al. 2024). Frequently collected functional  
158 traits for leaves include nitrogen and other nutrients, leaf mass per area, cellulose, lignin, pigments, stable  
159 carbon isotopies, and other biochemical compounds, such as carbohydrates, proteins, lipids, and  
160 secondary metabolites (**Fig. 1**). Plant functional traits are well-studied and measured in temperate and  
161 arctic regions in well-resourced, easily accessible regions of North America, Europe, China, and  
162 Australia, but are undersampled in tropical regions (Bjorkman et al. 2018, Jetz et al. 2016). Common and  
163 widespread species are much better represented in plant functional trait databases than rare species,  
164 seasonally ephemeral species and species from understudied biogeographic regions. Given that herbaria  
165 provide access to plant specimens collected by generations of botanists, they offer a means to  
166 systematically obtain trait data from plants in taxa that are rare and/or occur in ecosystems or regions of  
167 the world that are difficult to access, filling in global gaps in plant functional traits of the known plant  
168 species and lineages (Heberling 2021). Although sampling biases also exist within herbaria (Daru et al.  
169 2018), their coverage is better than that of trait databases.

170

### 171 **What are reflectance spectra?**

172 Reflectance spectra are observations of the interaction of electromagnetic radiation (light) with get  
173 reflected from surfaces resolved to narrow wavelength bands representing a few nanometers each (**Fig. 1**).  
174 Plant tissues from across the tree of life have various structural, anatomical, organellar and biomolecular  
175 compositions that influence their spectral properties. As a result, spectral data can be used to estimate a  
176 wide array of plant traits, including structural, chemical, and physiological properties (Ustin et al. 2009,  
177 Serbin et al. 2014a, Féret et al. 2017), and provide a holistic view of plant phenotypes (Kothari and  
178 Schweiger 2022). Reflectance spectra spanning visible, near-infrared and short-wave infrared light (400 -  
179 2500 nm) from freshly-harvested leaves differ from those obtained from pressed and dried leaves because  
180 of changes in water content, pigments and structure during drying (**Fig. 1**). Spectra from fresh leaves can  
181 provide accurate estimates of plant pigments, traits related to water content, and mobile, degradable or  
182 small molecular weight carbon compounds (Wang et al. 2023). Dry leaves often provide more accurate  
183 prediction of macronutrients, micronutrients and carbon or nitrogen stable isotopes (Chlus and Townsend  
184 2022, Kothari et al. 2023) but are unsuitable for predicting water-related traits and some pigments that  
185 degrade during drying (Ustin et al. 2009). Spectra also vary with changes in environmental conditions,  
186 including light, water availability, carbon dioxide, temperature and soil conditions (Cavender-Bares et al.  
187 2016b, Jacquemoud and Ustin 2019, Kühn et al. 2025, Stefanski et al. 2025).

188           Given their utility in detecting variation in plants, reflectance spectra are widely used in applied  
189 contexts. High throughput methods of spectral detection are increasingly used in plant breeding programs  
190 to detect phenotype variation (e.g., Ge et al. 2016, Meacham-Hensold et al. 2019). Spectral signatures of  
191 plants are also used to detect heavy metals and other environmental contaminants in plant tissues (Zhang  
192 et al. 2022), to scale up detection of pathogen infections via remote sensing (e.g., Fallon et al. 2020, Sapes  
193 et al. 2024) and for detection of invasive species (e.g., Dao et al. 2021, Mallmann et al. 2023). Currently,  
194 major efforts are underway to scale up spectral data from plants for biodiversity monitoring (Jetz et al.  
195 2016a, Cavender-Bares et al. 2020, Wang et al. 2020, Williams et al. 2021, Cavender-Bares et al. 2022,  
196 Blanchard et al. 2024, Dechant et al. 2024, Hadlich et al. 2025).

197

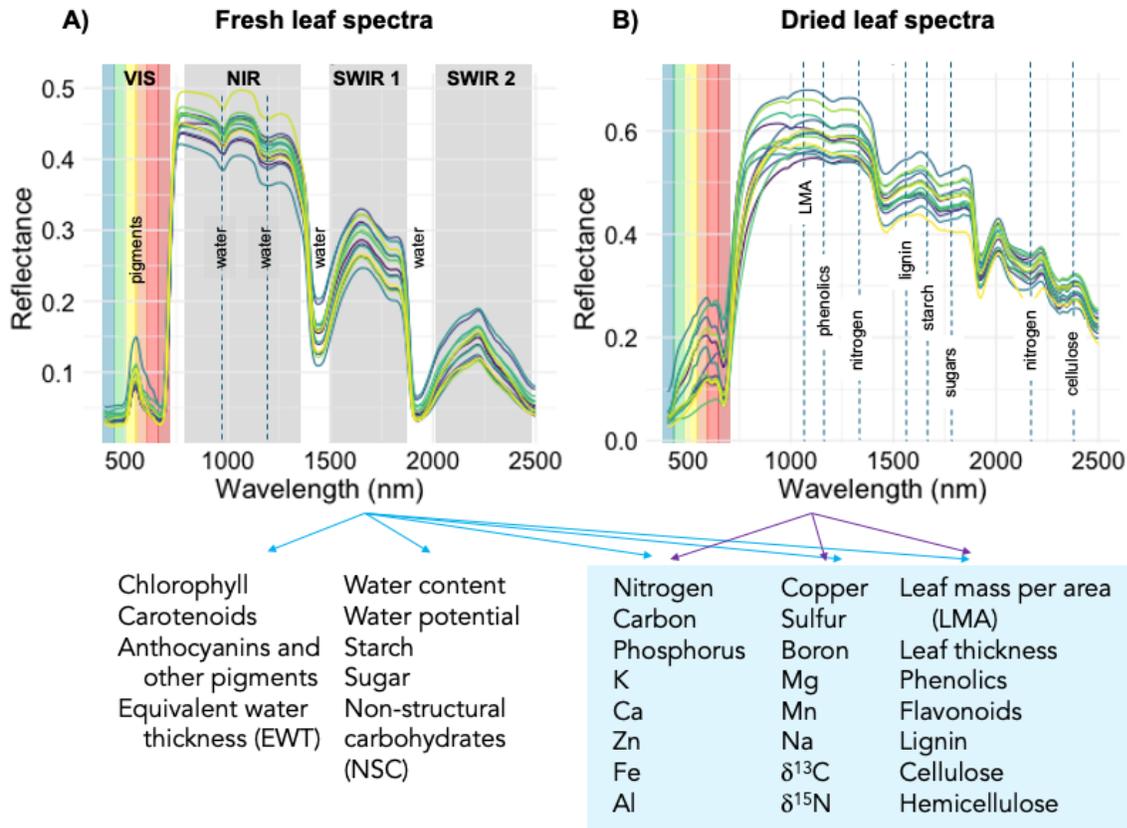
### 198 **Estimating plant traits from spectra of herbarium specimens**

199 Advancing technologies and a suite of studies over the past decade have set the stage for applying spectral  
200 biology to herborized specimens to predict plant function (**Fig. 1**). Some of the first spectral studies of  
201 dried leaves were conducted in the early 1990s and contributed to early vegetation index-based or  
202 radiative transfer model-based approaches to linking spectra with traits (Elvidge 1990; Fourty et al. 1996).  
203 More recently, Costa et al. (2018) showed the potential of using machine learning models trained on  
204 spectra on silica-dried leaves to predict traits of tropical tree species. Building on this work, Kothari et al.  
205 (2023) showed similar results for a wide range of traits in a large data set of unmounted pressed leaves  
206 from temperate forest species; indeed, for most chemical traits, spectra of pressed leaves performed better  
207 than the more conventional approach of using spectra of fresh leaves. Sampling the same species as  
208 Kothari et al. (2023), White et al. (2025) subsequently showed that spectral models trained using detached  
209 leaves from decades-old herbarium specimens accurately predicted key traits such as leaf mass per area.  
210 Kühn et al. (2025) applied a spectral model to 20th-century herbarium specimens to show temporal trends  
211 in leaf carbon, nitrogen, and phosphorus content associated with intensifying agricultural practices in  
212 Germany.

213

214 **Figure 1.** Plant traits derived from full-range spectral reflectance (400 - 2500 nm) from fresh leaf tissue  
215 (A) and dried, pressed leaves (B). Spectral regions can be characterized into the visible range (VIS, 400-  
216 700 nm, shown in rainbow colors in both A and B), the near infrared (NIR, ~700-1100), and the short-  
217 wave infrared (SWIR1 ~1100-2000, and SWIR2, ~2000-2500, shown by the gray shaded areas in (A)).  
218 Plant pigments (chlorophyll a and b, carotenoids, anthocyanins), traits related to water content and water  
219 potential, including leaf dry mass concentration (LDMC), equivalent water thickness (EWT), and mobile,  
220 degradable or small molecular weight carbon compounds (sugars, nonstructural carbohydrates) can be  
221 derived from spectra in fresh leaves. In dry leaves, water-related and pigmentation traits may not be  
222 reliably derived due to degradation. In both fresh and dry leaves, it may be possible to estimate  
223 macronutrients (nitrogen (N), carbon (C), phosphorus (P), potassium (K)) and micronutrients (calcium  
224 (Ca), zinc (Zn), iron (Fe), copper (Cu), sulfur (S), boron (B), magnesium (Mg), manganese (Mn),  
225 aluminum (Al), sodium (Na)), as well as large stable carbon-based molecules (phenolics, lignin, cellulose  
226 or hemicellulose), defense compounds (phenolics, flavonoids) and stable isotopes ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ). Indeed,

227 they may be more accurately detected from dried tissue due to the absence of water. Water absorbs energy  
 228 throughout the spectral range shown, but particularly in the bands indicated in A. Some of the spectral  
 229 features that are important for predicting traits are indicated in B, adapted from Cavender-Bares et al.  
 230 2025.



231

232

233 **Box 1 Brief glossary of terminology applied to plant reflectance**

234 **Band** - a range of wavelengths within a spectrum for which the radiation is detected.

235 **Bandwidth** - the range or span of the spectral band.

236 **Dark current** - the small electric current that flows through a spectroradiometer even in the absence of incident  
 237 light.

238 **Electromagnetic spectrum** - Wavelengths of electromagnetic radiation that span short wavelength (high frequency)  
 239 to long-wavelength (low frequency) wavebands.

240 **Fiber optic** - strands of glass or plastic (optical fibers) used to transmit light, for example as reflectance from a leaf  
 241 to an instrument detector.

242 **Full range spectrum** - Spectroradiometers used for foliar spectroscopy commonly span the range of 400 - 2500 nm  
 243 covering the visible (VIS), near-infrared (NIR) and shortwave infrared (SWIR), which is considered full  
 244 range (VIS-NIR-SWIR) wavelengths. Alternately, some instruments only span 400-1000 nm, which covers  
 245 only the visible and near-infrared.

246 **Herbarium specimen** - a specimen with associated taxonomic, geographic, temporal and other collection metadata  
 247 stored in an herbarium, for which we might not know how it was dried or conserved

248 **Hyperspectral** - Spanning the visible to near-infrared or shortwave infrared measuring narrow wavelength bands  
249 every 3 to 5 nm.

250 **InGaS sensor** - photodiodes for near-infrared (NIR) and short wavelength infrared (SWIR) regions.

251 **Near-infrared (NIR)** - the range of electromagnetic spectrum from 700 - 1100 nm.

252 **Partial Least Square Discriminant Analysis (PLS-DA)** - a machine learning approach used for the classification  
253 of high-dimensional datasets such as spectral data. PLS-DA utilizes spectral phenotypic data to create a  
254 simplified classification method to distinguish among taxonomic or functional groups.

255 **Pressed plant** - a controlled dried specimen that was pressed flat to dry

256 **Partial Least Square Regression (PLSR)** - is a statistical method (multivariate regression) used to model the  
257 relationship between X (predictor) and Y (response) variables. In spectral biology, PLSR is used to  
258 estimate foliar traits due to its ability to handle multicollinearity and reduce the dimensionality of spectral  
259 data.

260 **Radiative transfer models (RTM)** - physical models using computer programs to simulate the reflectance,  
261 transmittance, and absorption of solar radiation in various media, including leaves. Governed by physical  
262 laws, RTMs can operate in forward mode to predict spectral responses of leaves based on material  
263 characteristics or in backward mode to infer material properties from leaf spectra. These models vary in  
264 complexity, balancing computational demand, accuracy, and scalability. The number of traits that can be  
265 simultaneously identified is limited. For remotely sensed imagery, inputs such as solar radiation and  
266 elevation angle, and parameters like leaf angle distribution and leaf area index help to solve the radiative  
267 transfer equation in optical or thermal domains.

268 **Reflectance standards** - A reflectance standard is a physical reference sample that includes ratio values between the  
269 total amount of radiation, as of light, reflected by a surface, and the total amount of radiation incident on  
270 the surface across the measured spectrum. Reflectance standards are used for the calibration and  
271 verification of spectrometers.

272 **Spectral reflectance** - Reflectance expressed as a function of wavelength (i.e., as a spectrum). Spectral reflectance  
273 is the fraction of the incident radiant flux that is reflected as a function of wavelength

274 **Short wave infrared (SWIR)** - The range of the electromagnetic spectrum between 1100 and 3000 nm.

275 **Spectral biology** -The study of biological processes and biodiversity using spectral resolved observations of light's  
276 interaction with biological systems to reveal plant chemistry, structure, and function across scales, from  
277 genomes to ecosystems.

278 **Spectroradiometer** -A device designed to measure electromagnetic radiation across a range of wavelengths; a  
279 radiometrically calibrated spectrometer (c.f. spectrometer).

280 **Spectroscopy** - The study of interactions between electromagnetic radiation and matter, used in imaging to measure  
281 reflected radiation from image pixels that is used to analyze the properties of leaves, canopies, ecosystems,  
282 and landscapes over time and space.

283 **Spectral resolution** - the measure of a sensor or spectrometer's ability to distinguish between closely spaced  
284 wavelengths within the electromagnetic spectrum. It is quantified by the width of the spectral bands, the

285 minimum resolvable wavelength interval, or, specifically for spectrometers, as the ratio of the measured  
286 wavelength to the full width at half maximum (FWHM) of a spectral peak ( $R = \lambda/\Delta\lambda$ ). Higher spectral  
287 resolution, characterized by narrower bands or smaller FWHM values, allows for finer discrimination of  
288 spectral features and thus, more detailed identification of materials.

289 **Spectral range** - Span between the smallest and largest wavelengths that a sensor or system can detect.

290 **Taxon discrimination methods** - analytic methods aimed at classifying unidentified samples into taxonomic  
291 categories, or clustering samples according to taxonomic affinities.

292 **Trait models** - physical, statistical or machine learning models used to predict foliar traits from leaf spectra

293 **Visible range (VIS)** - the range of electromagnetic spectrum from 400 - 700 nm.

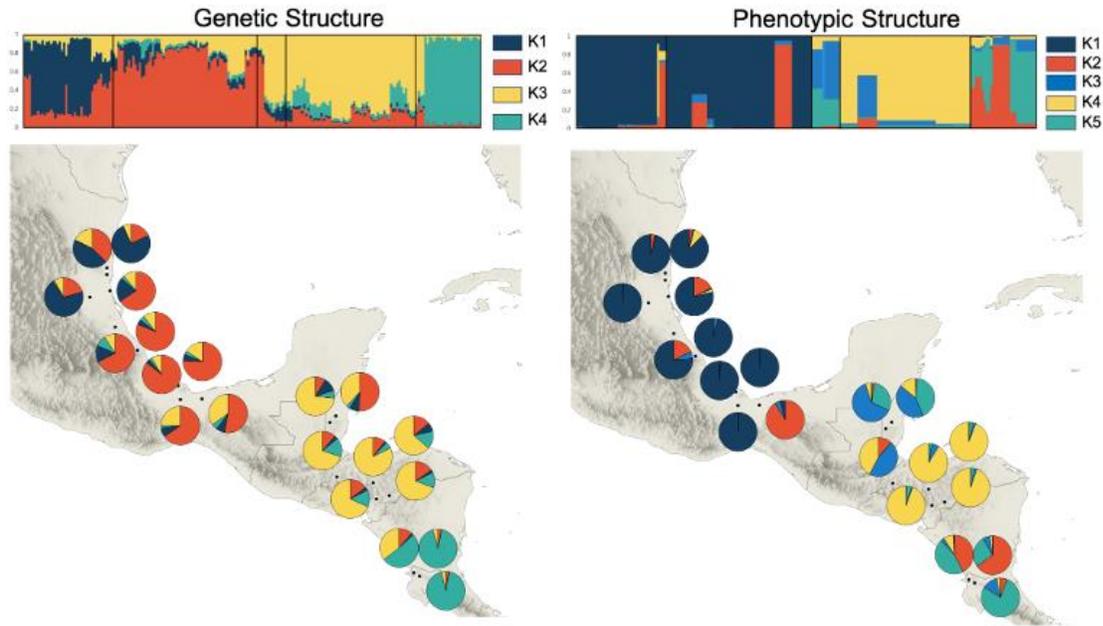
294

---

295

## 296 **Applying spectral signatures to phenotype-genotype associations and evolutionary models**

297 Spectroscopy provides a source of phenotypic data that can be measured on samples across the plant tree  
298 of life and coupled with genetic and genomic information (**Fig. 2**) or to scale up the study of phenotypic  
299 variation across large spatial, temporal, and phylogenetic scales from variation within species to the plant  
300 tree of life (Meireles et al. 2020, Cavender-Bares et al. 2025). Integrating spectra with genomic data  
301 allows researchers to determine factors and evolutionary processes involved in shaping underlying traits  
302 (Matsuda et al. 2012; Čepl et al. 2018). For example, spectral data can reveal variations in traits relevant  
303 to ecological niches, while genomic data provides insight into the genetic architecture underlying these  
304 traits (Blonder et al. 2020; Madritch et al. 2014). Together, these kinds of datasets can reveal how  
305 populations adapt to environmental pressures (Ge et al. 2019, Galan et al. 2020). Such integration  
306 revolutionizes our understanding of how adaptation unfolds at both microevolutionary and  
307 macroevolutionary scales. By comparing spectral data with genomic markers, it is possible to identify  
308 genetic loci associated with key traits, such as cold tolerance or drought resistance, and assess how these  
309 loci vary across populations (Madritch et al. 2014, Cavender-Bares et al. 2016b, Czyż et al. 2020). This  
310 integration illuminates the demographic history and selective pressures driving adaptation. For instance,  
311 closely related species of *Quercus* subsection *Virentes* exhibit various forms of evolutionary divergence,  
312 including sympatry, allopatry, and parapatry (Cavender-Bares et al. 2015). These species show spectral  
313 phenotypic divergence associated with specific microhabitats, shaped by local adaptation to ecological  
314 variation (Hernandez-Leal et al., 2025). This example highlights how demographic processes and  
315 selective pressures differ across spatial scales. Phenotype-genotype associations offer a robust framework  
316 for uncovering the interplay between natural selection, demographic processes, and adaptation (Kokaly et  
317 al. 2009, Cavender-Bares et al. 2016b, Deacon et al. 2017b, Blonder et al. 2020, Stasinski et al. 2021,  
318 Hernandez-Leal et al. 2025). Coupling spectral data with genomic and genetic information expands  
319 opportunities for understanding evolutionary processes across the plant tree of life (Ge et al. 2016).

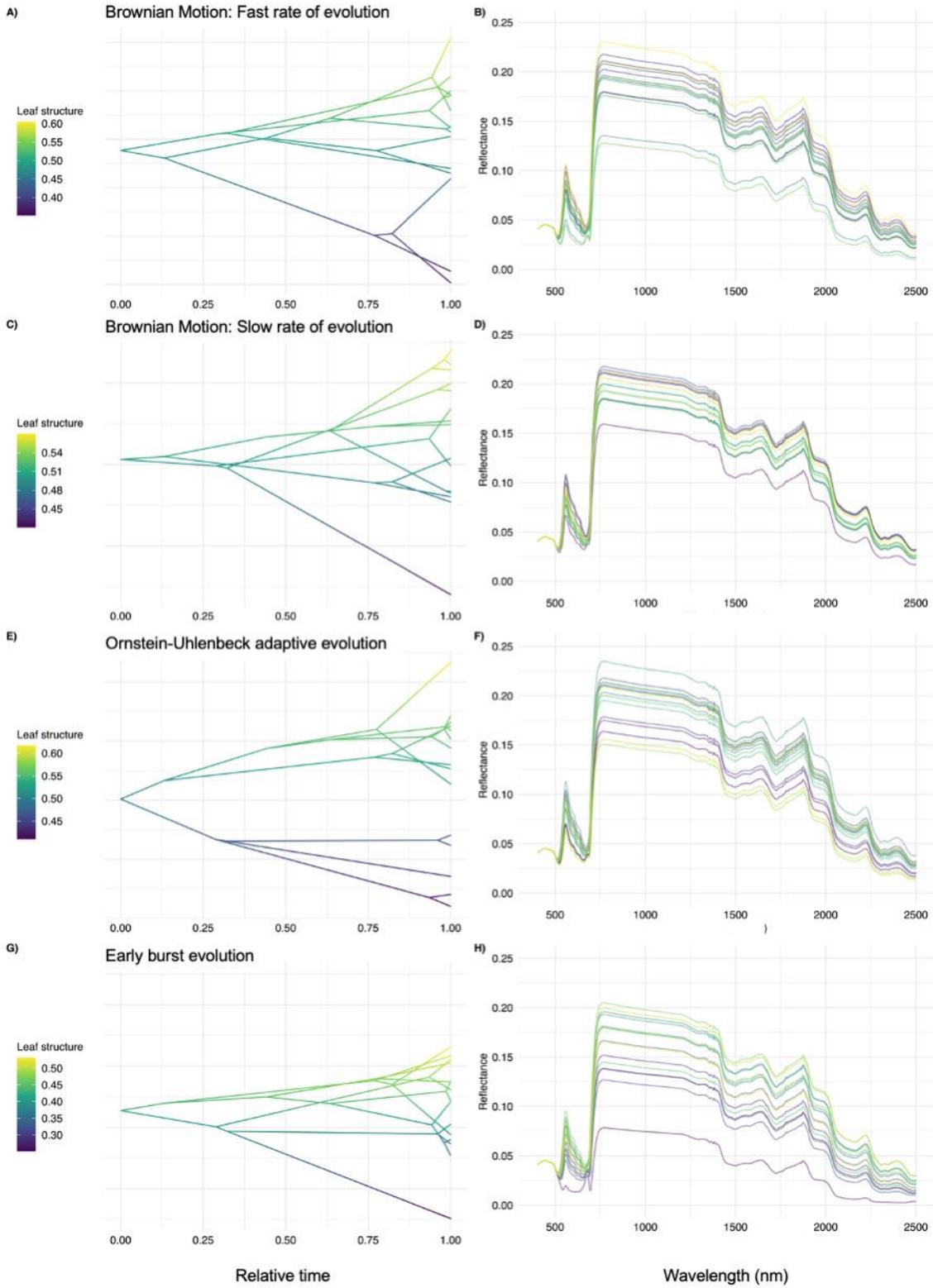


320

321 **Figure 2.** An example of combining genotypic and phenotypic data derived from pressed leaf spectra.  
 322 The spatial distribution of genetic (left) and phenotypic (right) variation in *Quercus oleoides*. Four genetic  
 323 groups were identified using STRUCTURE (Pritchard 2000) from 123 individuals and five phenotypic  
 324 groups identified by GENELAND (Guillot et al., 2009) using six spectrally derived leaf traits (leaf mass  
 325 area, thickness, solubles, hemicellulose, cellulose, lignin) derived from dried leaf spectra from all  
 326 individuals. The percentage assignment to genetic or phenotypic groups is represented at both the  
 327 individual tree level (upper bar plots) and subpopulation level (pie charts). Genetic data are from  
 328 Cavender-Bares et al. 2015. Figure is adapted from Hernandez-Leal et al. 2025.

329 Spectral data can also be used to model species traits on phylogenetic trees using comparative  
 330 methods (Harvey and Purvis 1991, Cavender-Bares 2019, Meireles et al. 2020a). Traits derived from  
 331 spectra, or spectral indices and variables themselves, can be used to model evolutionary rates, constraints  
 332 and selection when spectra are consistently measured across species. In a simulation exercise, we show  
 333 how dried leaf spectra are expected to evolve according to four models of evolution, Brownian motion  
 334 random walk model with fast and slow rates of evolution, a single-optimum Ornstein-Uhlenbeck model of  
 335 adaptive evolution, and an Early Burst model with declining rates of evolution through time (**Fig. 3**). A  
 336 major challenge, however, is the high dimensionality of full-range spectral data, which are comprised of  
 337 hundreds of interdependent variables per measurement. Incorporating this high-dimensionality within a  
 338 phylogenetic comparative framework is challenging both statistically and computationally because of the  
 339 high number of coevolving traits in a lower number of taxa (Clavel et al. 2019). Novel comparative  
 340 methods such as penalized likelihood approaches can now be applied to spectral data in phylogenetic  
 341 frameworks (Clavel et al. 2015, Clavel et al. 2019).

342



345 **Figure 3.** Simulated evolution of leaf structure (i.e., numbers of cell layers, N) under three models of  
346 evolution and the corresponding dried leaf spectra predicted from leaf traits using the PROSPECT D  
347 radiative transfer models (Féret et al. 2017) following Meireles et al. (2020a). Each row represents one  
348 model: Brownian motion with fast (A, B) or slow (C,D) evolutionary rates, a single-optimum Ornstein-  
349 Uhlenbeck adaptive evolution process (E,F), and an Early Burst process with declining rates over time  
350 (G,H). The graphs on the left show phylogenetic trees through relative time (x-axis) with y-values and  
351 branch colors indicating simulated leaf structure values. The graphs on the right show simulated  
352 reflectance spectra (400–2500 nm) for the final trait values of each lineage. (Starting values for the traits  
353 in the models are as follows: N=0.5, chlorophyll, Cab=10; carotenoids, Car=12.0; LMA/leaf dry matter  
354 content, Cm = 0.0005; water, Cw=0; leaf structure; sigma value for N= 0.1.)  
355

356

### 357 **Taxon discovery and discrimination**

358 Spectral data have become a valuable tool for evaluating and refining taxonomic hypotheses, enabling  
359 rapid, non-destructive assessment of phenotypic cohesion and differentiation among taxa (2024). Across  
360 taxonomic ranks, spectra from dry leaves have been used to supplement DNA-based methods and support  
361 systematic studies, particularly in morphologically complex clades. In the Amazon, researchers have  
362 analyzed spectral absorption profiles with a Fourier-transform near-infrared (FT-NIR) spectrometer on  
363 unmounted leaf samples to distinguish closely related species within the genus *Eschweilera*  
364 (Lecythidaceae) (Durgante et al. 2013) as well as among different developmental stages of species in the  
365 Burseraceae (Lang et al. 2015). Paiva et al. (2021) applied spectroscopy to pressed fern fronds to classify  
366 species in the genus *Microgramma* with over 90% accuracy Both Prata et al. (2018) and Damasco et al.  
367 (2019) integrated DNA and spectral data to suggest taxonomic solutions in species complexes, including  
368 the reestablishment of *Protium cordatum* (Burseraceae) to species rank (Damasco et al. 2019).  
369 Spectroscopy is now being used to support new species hypotheses based on morphological and  
370 morphometric characteristics (Vasconcelos et al. 2020, da Cruz Vasconcelos et al. 2021, Gaem et al.  
371 2022, Costa et al. 2025) or to differentiate hybrids from parental species (Deacon et al. 2017a).

372 Applications of these approaches to herbarium specimens are more recent. White et al. (2025)  
373 showed that spectral models from herbarium specimen leaves of diverse ages and sources (with a median  
374 age of 91 years) could classify specimens to species with up to 74% accuracy and genera up to 84%  
375 accuracy. In a broad study of stone oak (*Lithocarpus*) specimens from across Asia, Neto-Bradley et al.  
376 (2025) found that machine learning models trained on spectra work nearly as well as those from digitized  
377 images for identifying taxa. They concluded that spectra may be particularly important for identifying  
378 incomplete specimens of historical significance that may otherwise only be identified to family. In the  
379 future, it should be possible to combine digital images with spectral profiles to increase our power of  
380 discrimination at different taxonomic levels.

381           These studies highlight the feasibility of using spectra from herbarium specimens for species  
382 delimitation, taxonomic revision, and the detection of cryptic diversity. Discriminatory models offer an  
383 additional dimension of variation—rooted in chemistry and structure—that can complement morphology  
384 and genetics. Moreover, spectral classification can serve as a test of taxonomic validity, revealing whether  
385 phenotypic variation aligns with expected groupings. High within-taxon variation or convergent  
386 phenotypes can reduce accuracy, while informative spectral regions may shed light on the evolutionary  
387 processes shaping trait divergence.

388           For plant systematists, these advances represent a major opportunity to re-explore herbarium  
389 collections with new eyes. Spectral profiles can uncover consistent differences in chemical and structural  
390 traits in specimens that may not be evident through morphology. This offers an additional dimension of  
391 variation for species delimitation, taxonomic revisions, and the identification of cryptic diversity,  
392 especially in groups with limited diagnostic characters or incomplete material. As the number of spectral  
393 studies increases, the development of shared protocols and metadata standards will be essential to ensure  
394 reproducibility and cross-study comparability, enabling broader synthesis and integration into taxonomic  
395 workflows.

396           Operational workflows in botanical taxonomy are advancing rapidly, driven by the robustness  
397 and consistency of the results achieved across diverse taxonomic groups. This momentum will be further  
398 amplified by the development of compact handheld and benchtop spectrometers that have the potential to  
399 greatly expand the use of spectroscopy in herbarium collections worldwide. These devices enable  
400 individual herbaria to conduct spectral analysis of type specimens and other restricted materials,  
401 overcoming common barriers such as loan limitations and fragility of historical collections. Yet there are  
402 challenges to every aspect of this work, which if not addressed will make using the data collected  
403 difficult. Through an international collaborative working group, Meireles et al. (2020a) combined spectral  
404 data from fresh leaves collected from three different instrument models in different parts of the world by  
405 different investigators. By reconciling the instrument-specific variation and converting the data to a  
406 common format, they showed that reflectance signatures show phylogenetic signal and are tightly coupled  
407 to the tree of life with the capacity to reveal evolutionary history. This effort demonstrated both the  
408 difficulty and the benefits of aggregating data.

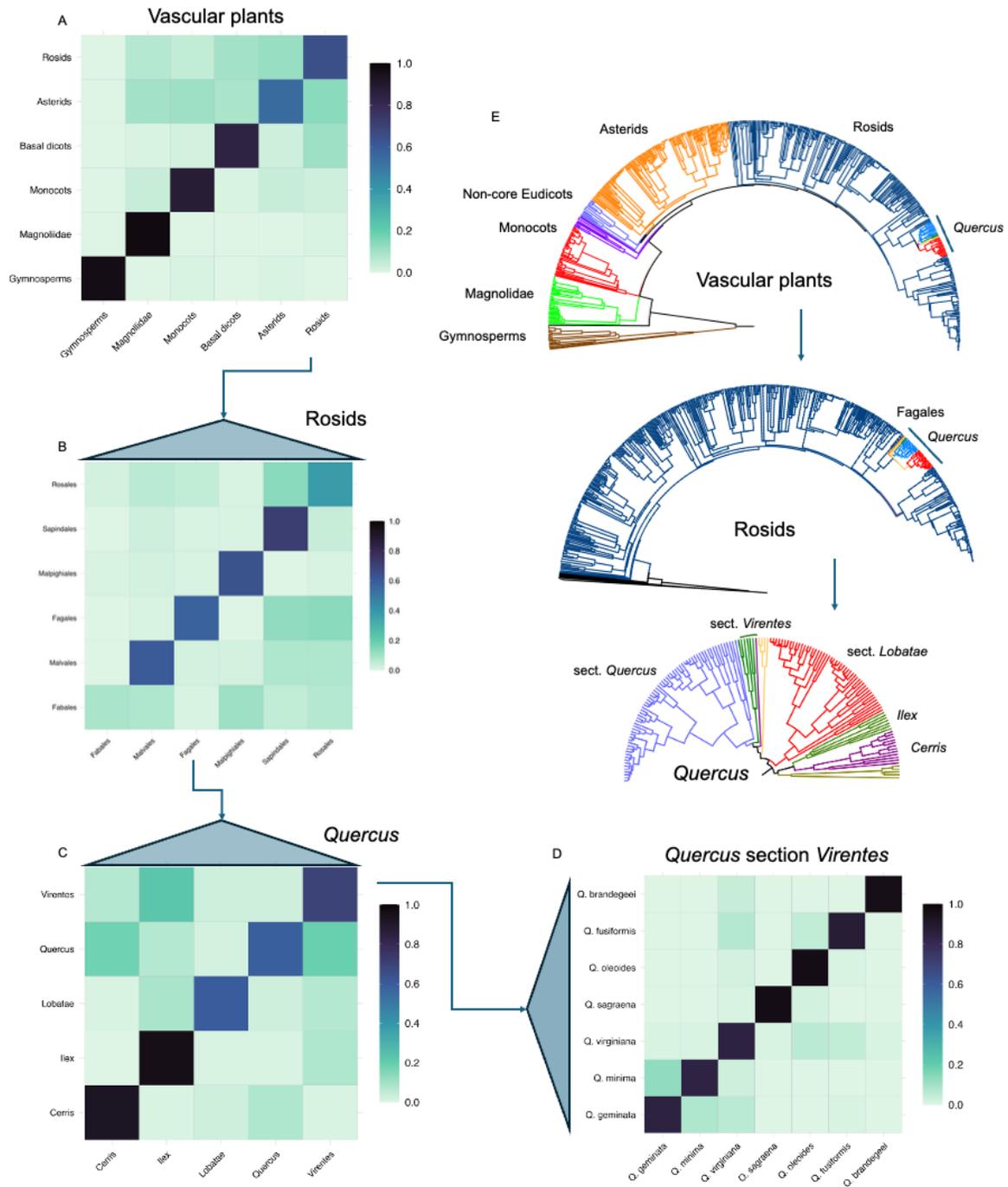
409           Generating spectral measurements from specimens of known identity will enable the  
410 development of reference datasets for identification purposes and may help to provide a preliminary  
411 taxonomic classification of the multitudes specimens in herbaria that have not been identified because  
412 they lack diagnostic structures, or have not yet been studied by sufficiently knowledgeable experts (Neto-  
413 Bradley et al. 2025). Fresh leaf spectra show promise for classifying species to all taxonomic ranks  
414 (Meireles et al. 2020b, Mallmann et al. 2023, Blanchard et al. 2024, Hadlich et al. 2025), and dried leaf

415 spectra may show even greater promise because the removal of the water absorption bands in the SWIR  
416 may reveal more unique absorption features (Kothari et al. 2023). Stepwise hierarchical approaches for  
417 classifying taxa first to broader and then narrower clades is a promising approach to accelerate the  
418 identification of undetermined (dried) herbarium material (**Fig. 4**). Such an approach would get around  
419 the problem of computational limits and reduced accuracy when large numbers of classes are  
420 discriminated among. To achieve high accuracies, highly populated spectral libraries at each phylogenetic  
421 scale would be necessary.

422           The success of taxonomic discrimination depends on the similarity of leaf and other plant part  
423 morphologies within each of the assigned taxa – and can be interpreted as a test of cohesion within groups  
424 and distinction between them. As such, an application of taxonomic discrimination models can be used to  
425 test the taxonomy itself. If there is nearly as much phenotypic variation within as between taxa, or if  
426 phenotypes evolve convergently, the success of taxonomic discrimination may be limited. Discriminatory  
427 models can potentially reveal the spectral regions that can best distinguish taxa, which may contribute to  
428 deciphering how taxa have diverged or converged and the evolutionary forces that have shaped their  
429 phenotypes.

430

431 **Figure 4.** Stepwise hierarchical approach to taxon classification to place specimens within the plant tree  
432 of life. Classification algorithms, such as partial least squares discriminant analysis (PLSDA), are limited  
433 by statistical power in the number of entities they can accurately discriminate between. One possible  
434 solution is a nested approach where spectral signatures are used to differentiate broad clades within the  
435 vascular plants, and stepwise within increasingly smaller clades, such as orders, families, genera—or  
436 increasingly narrow phylogenetic lineages. Shown are confusion matrices from broad to increasingly  
437 narrow taxonomic groups, starting with A) broad clades in the vascular plants, including the Rosid clade,  
438 B) orders within the Rosids, including the Fagales, C) sections of the genus *Quercus* within the Fagales,  
439 and D) species within *Quercus* section *Virentes*. Correct assignments are on the diagonal, incorrect  
440 assignments are in the off-diagonal cells. Data used in A and B and the vascular plant phylogeny are from  
441 Meireles et al. 2020; spectral data used C are from Cavender-Bares et al. 2016, spectral data in D are from  
442 Hernandez-Leal et al. 2025. The *Quercus* phylogeny is from Hipp et al. 2020.

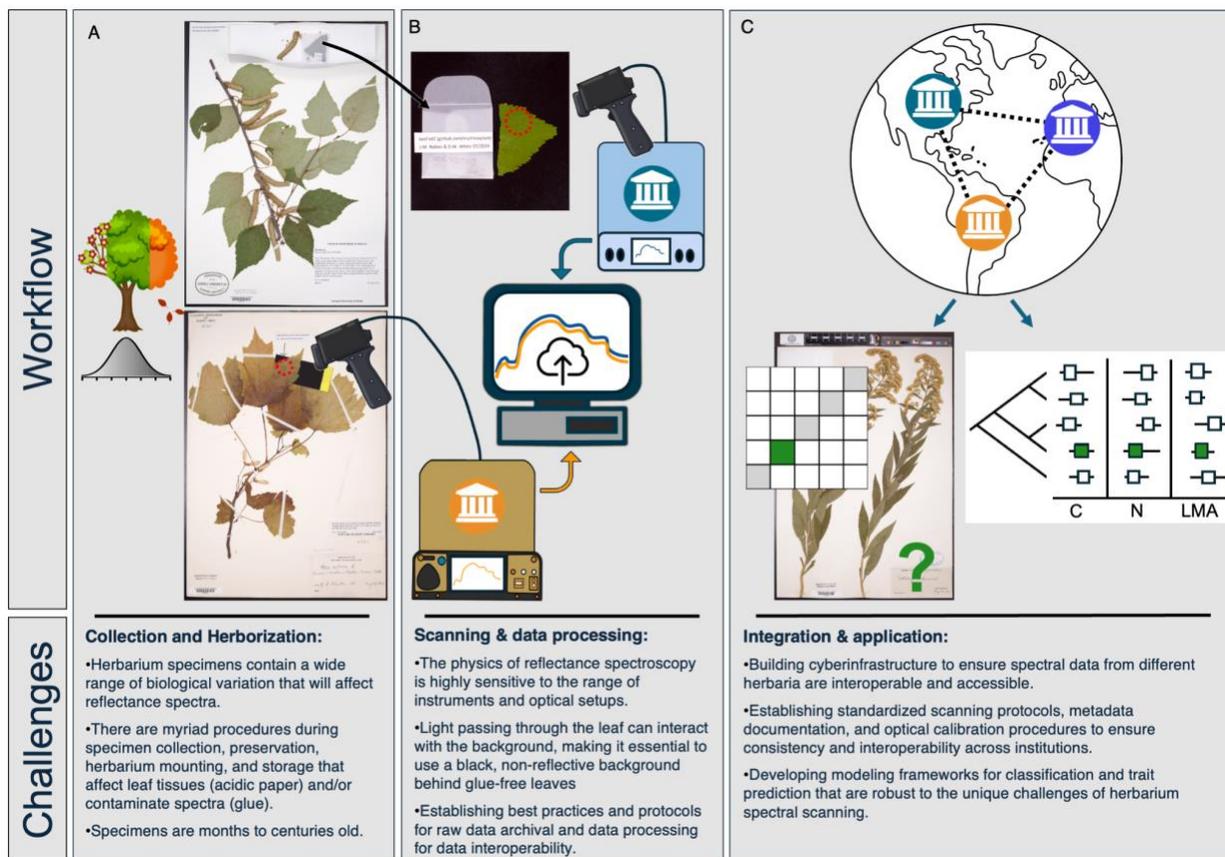


443

444 **Benefits and challenges to aggregating and scaling spectral data**

445 The beauty of the ‘global metaherbarium’ lies in its ability to connect a wide array of data types that  
 446 together comprise the extended specimen (Webster 2017, Lendemer et al. 2020, National Academies of  
 447 Sciences and Medicine 2020, Davis 2023, Davis and Knapp 2025). These include not only the physical  
 448 specimen itself, but also associated data such as digital images, species distribution models (SDMs), DNA  
 449 sequences, and ecological trait measurements (Webster 2017, Lendemer et al. 2020) promising layers of

450 information that can significantly enhance the value of the specimen and the power of global-scale  
 451 analyses if consistent or interoperable approaches can be established. While there is considerable  
 452 excitement for the application of spectrometry in herbaria, a series of methodological, material, and data  
 453 processing challenges must be addressed. Differences in instrumentation, specimen preservation, and data  
 454 processing pipelines introduce variability that complicates large-scale data aggregation and cross-  
 455 institutional compatibility (Fig. 5, (White et al. 2025)). These issues were encountered and overcome by  
 456 the NIMBioS (National Institute for Mathematical and Biological Synthesis) working group (Meireles et  
 457 al. 2020c), which aggregated and harmonized spectral data collected from fresh leaves using different  
 458 instruments and protocols around the world. Their work demonstrated both the promise and difficulty of  
 459 harmonizing spectral data, given that spectra can vary significantly based on optical system design and  
 460 measurement conditions. A further set of challenges arises from the varied nature of how herbarium  
 461 specimens are treated upon intake, their age, their storage conditions, the impact of chemical additives  
 462 such as glues, pest prevention treatments, and other specimen conservation factors (Kühn et al. 2025,  
 463 White et al. 2025). To maximize the utility of spectral data in functional trait estimation, taxonomic  
 464 classification, and evolutionary modeling, standardized measurement protocols across institutions, data  
 465 quality controls, and robust correction methods are critical.



466

467 **Figure 5.** The herbarium spectral digitization workflow from specimen collection to global integration,  
468 and challenges. A) Variation in specimen condition and mounting methods, including changes in leaf  
469 preservation quality, use of adhesives or sewing, and presence of detached leaves in packets. B) Spectral  
470 digitization process using different spectroradiometers, with emphasis on black background placement  
471 and data upload; differences in instruments, optics, and data processing. C) Global integration of spectral  
472 data across herbaria, linked to specimen records and trait data such as carbon (C), nitrogen (N), and leaf  
473 mass per area (LMA).  
474

#### 475 *Spectral regions to measure*

476 Spectroscopy has been widely used to analyze fresh leaf tissue in the range of 400-2500 nm to obtain  
477 information about plant function and phenotype (Table S1). The visible range (400 - 700 nm) is strongly  
478 associated with chlorophyll, carotenoids, anthocyanins and other pigments (Gitelson et al. 1998, Gamon  
479 and Surfus 1999). Chlorophyll is partially degraded when exposed to light and may be reduced in  
480 herborized leaves, but it can still be detected. Spectral information related to carotenoids, flavonoids,  
481 lignin, and other chemical compounds remain readily detected and may be less susceptible to degradation.  
482 In the near-infrared-region (NIR, 1000-2500 nm), vibration frequencies associated with molecular  
483 functional groups (-CH, -NH, -OH) show features of primary metabolites (carbohydrates, lipids, and  
484 proteins) as well as of secondary metabolites (phenolic compounds, terpenoids, and alkaloids) (Türker-  
485 Kaya and Huck 2017, Jacquemoud and Ustin 2019, Ustin and Jacquemoud 2020). Spectral regions  
486 beyond 2500 nm reveal additional information. In the mid- and long-wave infrared regions (2500-25000  
487 nm), for example, detailed chemical identification is possible, particularly for pure chemical compounds,  
488 (Türker-Kaya and Huck 2017), providing opportunities to detect ecologically and evolutionarily  
489 important differences among organisms, even when we do not have their taxonomic names.  
490

491 *Variation in foliar phenotypes.* Spectral data capture variation in leaves due to a multitude of factors,  
492 including leaf developmental and ontogenetic stage, light exposure and environmental conditions during  
493 growth, and a range of other factors (Fajardo and Siefert 2016). Exposure of the foliar tissue to a range of  
494 environmental conditions within a single tree canopy, across environmental gradients or in response to  
495 temperature, water availability or CO<sub>2</sub> concentrations can modify tissue properties (Stefanski et al. 2025)  
496 and thus influence the reflection of light. Spectral properties and traits change over the lifecycle of the  
497 leaf (e.g., Fajardo and Siefert 2016, Chlus and Townsend 2022). Within a single leaf, tissue properties  
498 will change from the edges to the vascular tissue. With age, leaves add secondary cell wall material,  
499 cuticles become more structurally complex and thicker, and concentrations of biochemical compounds  
500 change, including compounds that are upregulated or produced in response to stress. Herbarium  
501 specimens representing species with asynchronous flowering or fruiting may disproportionately contain  
502 young, developing leaves or reproductive structures, leading to spectra that do not adequately represent

503 mature leaves (**Fig. 6**). Predictive models show promise in accommodating such biological variation as  
504 long as models are trained to “see” the full range of variation (Lang et al. 2015, Wang et al. 2023).

505

506 *Adaxial and abaxial leaf surfaces.* Adaxial and abaxial surfaces on vascular plants are often distinct.

507 Given that leaf spectroscopy is often used to ground-truth remote sensing measurements, many protocols

508 only involve measuring the adaxial surface of the leaf, which is the side most likely to be observed from

509 above. Measurements of herbarium specimens have different goals, however, and the option is available

510 to measure both leaf surfaces. The abaxial surface may contain important features for taxonomic

511 identification, including pubescence or differing pigmentation. Whether both leaf surfaces should be

512 measured as standard is an area for further investigation and discussion. In any case, it is important to

513 document the leaf surface measured, given their spectral signatures are different (Ustin et al. 2001).

514

515 *Leaf size.* Small leaves present challenges to spectral measurement because they require adaptations to

516 optical detection arrangements, such as fine leaf probes, small radius fiber optic cables, and/or small

517 detection windows, which can reduce the signal-to-noise ratio and quality of the reflectance signal.

518 Conifer needles, vascular plants with tiny leaves, and non-vascular plants such as mosses and lycopodia,

519 can be difficult to measure due to their small size and the fact that many of them do not lie flat (**Fig. 6**).

520 When leaves are not flat, the 'geometry' or angle of the light source relative to the surface of the leaf often

521 varies from one measurement to the next, influencing the specular component of reflectance. When

522 possible, it may help to measure the flattest parts of the leaves. Alongside these challenges, lichens also

523 pose challenges due to their changing form and physiology when they dehydrate.

524

525 *Specimen age.* Over time specimens may undergo chemical or even structural degradation due to

526 exposure to environmental factors. Although some aspects of this process have been documented,

527 including the breakdown of chlorophyll and accumulation of brown pigments (Fourty et al. 1996), in

528 general little is known about the suite of changes through time and the factors that slow or accelerate

529 them. White et al. (2025) found that older specimens exhibit a slight decline in correct classification

530 probability from spectra. The potential influences of degradation on spectra reinforces the need for careful

531 specimen selection and possibly data filtering strategies that account for specimen age and preservation

532 history when integrating spectral datasets (Durgante et al. 2013, Lang et al. 2015).

533

534 **Figure 6.** Variation in the challenges of measuring reflectance spectra on mounted specimens. A) An  
535 example of a relatively straightforward measurement of a specimen leaf against a black background using  
536 a one-sided leaf clip with a fiber optic probe that is smaller diameter than the leaf laminar surface area.

537 Isotypes of (B) *Restio arcuatus* and (C) *Vulpia microstachys* are taxa with small leaves. D) *Abies*

538 *balsamea*, a conifer with typical narrow needles that is taped to the herbarium sheet but has also been  
 539 glued, evidenced by the discolored glue indicated with the arrow. A fully taped *Salix arctica* (E) specimen  
 540 from the Botanical Museum of Copenhagen with conspicuously gray discoloration representing  
 541 variability in preservation techniques and quality. An herb (F) with delicate, thin leaves that are fully  
 542 glued to the sheet with no packet containing extra material to measure. A *Sticta* lichen (G) with a non-flat  
 543 thallus that will distort optical geometry. Circles on the top left demonstrate various aperture sizes (mm)  
 544 typical of different optical instruments. For comparison, scale bars are shown in B, C and F, with a 2 cm  
 545 bar in B.



546  
 547  
 548 *Variation in preservation among specimens in herbarium collections.*  
 549 Herbarium collections are generally curated to maximize the taxonomic and/or geographical diversity of  
 550 specimens for given regions, and may represent centuries of collection efforts across biomes. The  
 551 historical and biogeographic breadth has led to heterogeneity in specimen preservation techniques.  
 552 Variability in storage conditions among herbarium facilities compounds the variation due to preservation  
 553 methods. The most significant factors affecting specimen degradation and quality are the protocols  
 554 implemented to initially press and dry the plant collection in the field. The best case scenario would be  
 555 that a collected specimen is immediately pressed inside acid-free paper and dried with forced-air at  
 556 ambient temperatures. However, this practice is rarely followed, and specimens, especially in the humid

557 tropics, are usually sealed in a bag containing 60-95% ethanol to kill fungus and prevent rotting. In all  
558 latitudes, pressed specimens are routinely dried using industrial ovens.

559         Glue is a particularly significant contaminating source for herbarium spectra due to its potential  
560 for direct contamination. For example, White et al. (2025) found that glue reduced the probability of  
561 correct species identification from spectra. Sewing specimens to the herbarium sheets or using archival  
562 grade mounting tape, both durable and secure mounting practices commonly used in European and South  
563 American herbaria, can avoid this problem. However, it is highly labor-intensive and has not been a  
564 standard practice in many herbaria. Consequently, glues are the most widely used adhesive in North  
565 America. The leaves of some specimens may contain multiple layers of different adhesives. Other  
566 common historical practices that may have resulted in the contamination of spectra include methyl  
567 bromide fumigation (now banned) and the sprinkling of diatom powder and various poisons such as  
568 arsenic or naphthalene. Efforts to ‘unmix’ or ‘subtract’ the glue or paper spectra from the leaf using  
569 spectral libraries of these contaminants have not yet yielded solutions to isolating the leaf signal from a  
570 spectral profile that contains these extra materials (A. Guzmán, B. Neto-Bradley, JE Meireles,  
571 unpublished data). Although many large herbaria in well-funded institutions can maintain temperature  
572 and humidity controls, humidity fluctuations remain a significant challenge worldwide, potentially  
573 accelerating specimen degradation.

574  
575 *Instruments and optics.* Variation in detectors and optical setups among instruments create differences in  
576 spectral signatures, adding complexity to the use of herbaria for spectral data collection (**Fig. 5, Table 1**).  
577 The signal-to-noise ratio, field-of-view, and spectral resolution and range are inherent instrument  
578 variables that can influence optimal measurements on specimens. Standardization of spectral digitization  
579 protocols and proper documentation is thus crucial for ensuring interoperability among spectral  
580 digitization efforts and integration into broader analytical frameworks. The signal-to-noise ratio (SNR),  
581 for instance, determines the quality and reliability of the measurements, where higher values mean clearer  
582 and more precise spectral data. SNR has a major effect on the comparison of measurements between  
583 instruments and, thus, the transferability of potential models derived from them. SNR is mostly  
584 influenced by light detector sensitivity (particularly affecting the wavelengths near the edges of the  
585 detector's spectral range) and light source intensity. Inappropriate selection of integration times, incorrect  
586 calibration, or variation in viewing and illumination angles can impact the SNR. The removal of bands  
587 with low SNR at the edge of the spectral range can help integrate data from different instruments into  
588 models (White et al. 2025). However, removing bands should not be a default approach and should be  
589 carefully considered in relation to project goals.

590 The field-of-view (FOV) – the angular extent of the observable area that can be seen through  
591 foreoptics or lenses – is another variable that often differs between instruments and influences how well  
592 specimens are captured in a single measurement. A wider FOV allows for the capture of a larger portion  
593 of the specimen, thereby increasing the representation of intraspecific variability. However, wider FOVs  
594 are usually associated with lower SNR measurements and are not ideal for small leaves and make it  
595 difficult to target specific leaf regions such as the blade rather than the central vein. Additionally, some  
596 instruments present a non-uniform FOV due to the optical fiber bundle and its integration with the light  
597 detector, which does not uniformly cover the viewing area (Lévesque et al. 2014). Using instruments with  
598 a narrow or non-uniform FOV might require several measurements of a leaf specimen to adequately  
599 capture the variability of optical information.

600 The spectral range and resolution are additional instrument variables inherent in instrument  
601 design. The spectral range of instruments is distinct from spectral resolution and is commonly used to  
602 differentiate between VIS-NIR spectrometers (e.g., 350 – 1000 nm), VIS-SWIR spectrometers (e.g., 350  
603 – 2500 nm; also known as 'full range'), MIR (2.5-6.0  $\mu\text{m}$  and and TIR spectrometers (e.g., 6.0 – 16  $\mu\text{m}$ )  
604 because these detect photons in different regions of the electromagnetic spectrum. Although VIS-NIR  
605 spectrometers are less expensive than full-range spectrometers, some studies on dried leaves have begun  
606 to suggest that full-range spectra perform better for trait prediction (Kothari et al. 2024; White et al.  
607 2025). Moreover, the spectral resolution of many full-range instruments varies within instruments because  
608 there are usually two or more light detectors, a silicon sensor (VIS and NIR) and an InGaAs (indium  
609 gallium arsenide) detector for the 1000–1700 nm wavelength region (e.g, Spectral Evolution) or an  
610 extended InGaAs covering the spectrum to 2500 nm (NIR and SWIR), each with distinct sensitivity and  
611 band sampling. Due to a trade-off between sensitivity and signal availability (i.e., light), silicon detectors  
612 designed for VIS-NIR wavelengths (e.g., 400 – 1000 nm)–where halogen bulbs generate peak irradiance–  
613 have high wavelength resolution. Consequently, they often achieve higher spectral resolution than  
614 detectors that span NIR-SWIR wavelengths (e.g., 1000 – 2500 nm). Instruments commonly report data  
615 output in 1-nm increments for spectral sampling of bandwidths 3 to 6 nm wide. Given the variation in  
616 design among instruments, the scanning interval (band center and band width) at different spectral ranges  
617 should be recorded in the metadata (see below).

618 Additional factors influencing the quality of spectral measurement data include the sensitivity of  
619 fiber optics, quality of standards, viewing and illumination angles, and the intensity of light sources  
620 (Grant 1987). Variations in fiber optic alignment can impact the signal-to-noise ratio, requiring careful  
621 handling and regular replacement (manufacturer maintenance should confirm whether all fibers are  
622 functional or, if not, determine the percentage of remaining fibers and their locations in the cluster). Use  
623 of a standardized leaf probe with integrated illumination avoids problems with the positioning of the

624 lights and the spectrometer. Regular replacement of calibration standards and routine instrument  
 625 maintenance, such as cleaning and recalibrating sensors, are essential for maintaining instrument  
 626 performance. The proper selection of light source intensity along with optimized integration times is  
 627 critical to avoiding heat effects on specimens, which can alter both their optical properties and integrity.  
 628 Lamps should be operated on direct current, not alternate current power supplies.

629  
 630 **Table 1. Challenges to aggregating spectral data across specimens and institutions and potential**  
 631 **solutions.**

<b>Challenge</b>	<b>Description</b>	<b>Mitigation Strategy</b>
Variation in leaf phenotypes due to environment	Environmental variation (light, temperature, CO <sub>2</sub> , nutrients) can influence spectra. Variation within a leaf	Collect spectra on specimens across a range of conditions to capture the full variation; avoid midrib and leaf edges, avoid leaves with herbivory and pathogens.
Variation in leaf phenotypes due to leaf age/development stage	Spectral properties and traits change over the lifecycle of the leaf	Capture information about leaf age in the metadata
Specimen age	Chemical degradation, pigmentation loss, and exposure to environmental factors over time can influence spectral signatures	Collect spectra on specimens across a range of ages to capture the full variation. When possible, conduct analyses on specimen age effects. Effects may not be large. Metadata should include date that specimen was acquired and location.
Preservation and storage variation	Drying, decontamination methods, adhesives, and storage environments can influence spectra	Standardize methods for incoming specimens. Conduct analyses on preservation and storage effects to determine if effects are large or small. Increase sample size to capture range of preservation methods.
Adhesives	Glues contaminate the reflectance spectrum	Prioritize leaves (or other tissues) without adhesives.
Leaf size	Small leaves are difficult to measure with standard set-ups	Fine leaf probes, narrow fiber optic cables, small detection windows
Leaf surface	Adaxial and abaxial surfaces differ	Measure both sides of the leaf. Capture metadata on which side(s) was/were measured
Measuring plant surfaces beyond leaves	Flowers, stems and other organs are also important	Measure on a project-by-project basis or using criteria at individual herbaria
Specimen geometry	Non-flat foliar surfaces generate specular influences on reflectance spectra (“noisy spectra”)	Prioritize flat tissues. Increase sample size. Use probe with a small optical aperture.
Instruments and optics	Different instruments give different spectral reflectance signatures. Optical setups also influence spectra.	Adhere to agreed upon protocols, instrument setup and metadata standards. Establish interconversion

		methods. Use the same reflectance standards across all labs
Reflectance background	White mounting paper introduces artefacts into the reflectance spectrum	Use a black non-reflective background on detached leaves or insert under a mounted leaf that is loose
Measurement settings and protocols	Sample count, leaf surface choice, integration times and other user-defined parameters influence SNR, data comparability and the time it takes to measure a specimen	Develop minimum sample counts and data standards across herbaria that can be surpassed for specific purposes and/or within individual herbaria
Destructive sampling for traits	Validation of models for many functional traits (N, P, cellulose, etc.) requires destroying leaf tissue to make direct observations.	Models may be generated from pressed leaves or tissues will need to be sampled ethically and in a coordinated manner.
Metadata collection and access	Data incompatibility due to the range of variables affecting herbarium spectral measurements	Establish metadata standards, similar to Darwin Core format, agreed upon, recorded and shared by all institutions.

632

633 **Considerations for standardization of protocols and metadata**

634 While detailed protocols and metadata standards remain to be established and agreed upon across  
635 institutions, it is important to provide some guidance at this stage, given the rapid increase in the use of  
636 spectroscopy for plant studies (Cavender-Bares et al. 2025). Here we make a series of recommendations  
637 and pose questions for consideration. Standardizing spectral digitization setups—including light source  
638 positioning, spectral calibration, and reference materials—will be essential to ensure compatibility  
639 between datasets collected using different instruments and workflows. Standardization of measurement  
640 protocols and metadata will be critical to maintaining consistency across instruments, collections, and  
641 institutions.

642

643 *Sampling.* We recommend sampling the variation among leaves on a specimen as well as variation within  
644 a single leaf, avoiding leaves with blemishes, contaminants or pathogens (unless these are relevant to the  
645 objectives of the study). When selecting among specimens for sampling, prioritizing those that have  
646 leaves where a black, non-reflective background can be readily inserted under the leaf will enable  
647 aggregation of data. Measuring sufficient leaf area to ensure that the spectra are representative of the  
648 variation within the specimen should be balanced against the care required to ensure non-destructive  
649 sampling. Taking 3-5 measurements across the leaf and 3-5 leaves per specimen can help capture relevant  
650 variation, but one fully expanded leaf per specimen may be a sufficient compromise to save time and  
651 avoid damage.

652

653 *Reflectance standards.* Given the variation in instrument and optical arrangements across institutions,  
654 regular measurement of standard cards of known reflectance using a set of certified reflectance standards  
655 ranging from black to gray to white provides a means to standardize data, making them comparable. A  
656 rare earth panel can be used to confirm wavelength calibration, especially if the instrument is returned for  
657 manufacturer recalibration infrequently. The black and gray standards would be measured regularly, such  
658 as once daily during measurement sessions. The white standard should be measured with each specimen,  
659 or at least every two to three specimens if spectral measurements are taken very rapidly.

660

661 *Reflectance background.* Background effects also play a critical role in spectral consistency across  
662 institutions. Light transmitted through leaves may reflect from the background (glue, paper, and even lab  
663 benches), which ‘contaminates’ the spectrum. The degree of contamination depends on the optical  
664 thickness of the leaves, which governs how much light is transmitted. Measuring leaves against a non-  
665 reflective black background to avoid contamination from other reflective surfaces is critical. This may  
666 create challenges for some specimens, which are often affixed to paper. If the specimen has been sewn or  
667 taped, it should be possible to slide a thin black sheet between the attached leaf and the paper. Herbarium  
668 specimens with loose leaves available in packets may be selected, and those leaves checked for glue  
669 before measuring them against a black background. A contact probe or modified leaf clip with the bottom  
670 portion removed will facilitate measurements. The importance of using a non-reflective black background  
671 will likely prevent automation through conveyor belts, as has been used for digitization of specimen  
672 images.

673 The selection of non-reflective black backgrounds is a critical component of standardization. A  
674 rule of thumb is that the background should have less than 4% reflection. EVA foam, black plastic, black  
675 card stock painted with Krylon® Camouflage Matte Black spray paint, and SpectralBlack® foil, or black  
676 backgrounds of manufacturer leaf clips for portable spectroradiometers (Malvern Panalytical [ASD],  
677 Spectra Vista Corporation, Spectral Evolution) are among the materials that have been used. It is  
678 worthwhile collecting a spectrum (or spectra) of the non-reflective black material to have as a reference if  
679 there are questions about the leaf measurements later. The identification and adoption of a universal  
680 background standard is an important objective of protocol development.

681 However, as noted above, vast portions of specimens already present in collections have been  
682 mounted with glue, such that using a non-reflective black background is not a feasible solution in all cases  
683 (Neto-Bradley et al., 2025). The extent to which measurements on mounted leaves should still be  
684 collected is an open area of discussion.

685

686 *Metadata standards.* Metadata standardization is critical for harmonizing datasets, as it facilitates the  
687 integration of phenomic data with associated specimen metadata, such as taxonomy, collection locality,  
688 and ecological context. Metadata will also provide users critical data on specimen preservation method,  
689 and potential artefacts due to glues or reflective backgrounds, that can inform aggregation and integration  
690 efforts. By adopting common metadata schemas and persistent identifiers (DOIs), researchers can link  
691 spectral data directly to digital databases, fostering seamless collaboration and data reuse. Experience  
692 gained from successful protocol standardization and data aggregation initiatives (e.g. Darwin Core and  
693 iDigBio; (Wieczorek et al. 2012, Soltis 2017) can be leveraged to implement a strategy for herbarium  
694 spectroscopic data. Recording metadata for instrument type, including the spectrometer brand and model,  
695 date of last maintenance and calibration by the manufacturer, whether the instrument is internally  
696 calibrated, as well as the spectral resolution and wavelength interval the instrument actually measures.  
697 The setup and standard measurements across a set of standard reference cards (white, gray, black) will be  
698 essential for aggregation. Also important is recording developmental, phenological, and ecological factors  
699 that influence leaf structure and physiology, as these are critical to untangling the effects of specimen  
700 processing and storage. Effective metadata curation and cyberinfrastructure development will be critical  
701 for integrating herbarium spectral data into global biodiversity platforms. Standardizing metadata fields  
702 for specimen age, preservation method, mounting medium, and measurement conditions will facilitate  
703 dataset comparison and allow researchers to apply appropriate quality control measures. Advances in  
704 spectral data repositories, such as linking reflectance data to GBIF, *speciesLink* and iDigBio records, will  
705 enhance accessibility and ensure that spectral datasets are fully interoperable with existing biodiversity  
706 databases (Heberling 2021, Davis 2023) and further enhance the extended specimen concept (Lendemer  
707 et al. 2020).

708  
709 *Data processing.* Raw data should be stored as collected directly from the instrument to avoid artifacts in  
710 the data that cannot be undone, e.g., resampling or binning bands to achieve higher SNR. Processed data  
711 may also be included. There are various approaches to processing raw spectra through resampling and  
712 normalization or transformation using derivatives or continuous wavelet transforms (CWT) to standardize  
713 datasets from different instruments. Band resampling at a higher resolution than the true resolution could  
714 introduce artificial data to the spectrum but resampling to reduce the number of bands is common. A  
715 resampling interval of 5 nm is reasonable for accommodating the differences in spectral resolution  
716 between instruments (e.g., Spectral Evolution NaturaSpec, PSR+, or SVC HR-1024i). Resampling  
717 reduces the number of correlated bands for predictive models. Although small absorption features may be  
718 perceived as insignificant or as noise, they may be important for taxonomic classification, and binning or  
719 resampling to lower resolution could result in loss of information. If the raw spectral data is preserved,

720 any loss of information can be assessed by comparison to the raw data. In full-range instruments, the  
721 350–400 nm and 2,400–2,500 nm regions are often trimmed due to the low signal to noise ratio in those  
722 regions. Reflectance values at the wavelengths where the silicon and InGaAs sensors meet need to be  
723 joined consistently. R packages like spectrolab (Meireles et al. 2017) have options for resampling,  
724 trimming, and joining data between the silicon and InGaAs sensors.

725 The success of aggregating herbarium reflectance spectra will depend on practices that ensure  
726 consistency, interoperability, and accessibility across institutions. Data quality controls must be ensured  
727 to include careful adherence to measurement protocols. It should also involve the preprocessing of  
728 spectral datasets to remove spectra of low quality. Routine validation processes will ensure that data  
729 meets the necessary standards for reproducibility and analysis. Finally, implementing analysis engines  
730 capable of handling high-dimensional datasets will be transformative. These engines should integrate  
731 spectral data with complementary datasets, such as genomic or spatial data, and provide tools for  
732 advanced modeling and visualization. Open-source analysis platforms with user-friendly interfaces will  
733 democratize access to these tools and foster collaboration across disciplines.

734

735 *Fitting appropriate functional trait models to specimens.* A key consideration is the transferability of  
736 spectral models between fresh, pressed, and herbarium specimens. While recent studies have confirmed  
737 that these specimen types are all informative for functional trait prediction and taxonomic classification  
738 (Wagner et al. 2019, Kothari et al. 2023), accounting for minor spectral shifts due to aging and  
739 preservation during model building will be important. Spectral models trained on recently pressed  
740 specimens may perform well on herbarium specimens, but in some cases where degradation will likely  
741 bias trait modeling (e.g., chlorophyll). Developing correction factors and harmonization techniques for  
742 cross-specimen spectral applications will be necessary to expand the utility of herbarium spectral  
743 databases. When seeking to apply a trait model, it is critical to collect some ground-truth data to ensure  
744 that it can yield accurate predictions for a particular class of specimens, based on taxa sampled, the  
745 herborization process, and instrumental set up. Without validation, there is no basis for ensuring that  
746 models developed for one set of specimens will accurately predict traits in another set of specimens.

747

#### 748 **Database sufficiency**

749 The development of cyberinfrastructure has been pivotal in enabling large-scale aggregation of  
750 spectral data. Platforms like iDigBio, *speciesLink* and GBIF provide centralized repositories for  
751 biodiversity data, but dedicated cyberinfrastructure for spectral datasets, integrated with existing  
752 platforms, will be essential for advancing collections-based research. These systems should support real-  
753 time synchronization of available data from herbarium institutions, cross-referencing, and retrieval for

754 global accessibility. Any dedicated spectral cyberinfrastructure platforms will require Application  
755 Programming Interfaces (APIs) to enable researchers to query, retrieve, and contribute spectral datasets  
756 programmatically; facilitating the large-scale synthesis of data. While several cyberinfrastructure  
757 platforms have been developed specifically for spectral data and models, such as EcoSIS and EcoSML  
758 (Wagner et al. 2019), they are not appropriate or sufficient for capturing taxonomic information required  
759 in biodiversity collections. A more efficient solution will be to ensure that the databases from natural  
760 history museums can incorporate spectral data and the critical associated metadata.

761  
762 *Darwin Core*. The Darwin Core (DC) standard is a compendium of terms and definitions that describe the  
763 observation of an organism at a particular time and space (Wieczorek et al. 2012). Broadening the Darwin  
764 Core to incorporate herbarium reflectance spectroscopy will enable data sharing across existing  
765 biodiversity informatics platforms (e.g., GBIF, *speciesLink*) and the use of spectral information in  
766 biodiversity research and conservation. In addition, extending DC for spectroscopy will supply new  
767 means for sharing protocols and practices for data aggregation that are critical for improving the quality  
768 of the herbarium reflectance data collection, storage, and distribution.

769

### 770 **Effective, Equitable and Ethical Sampling**

771 Herbarium users and stewards must balance innovation with preservation. Guidelines for the effectiveness  
772 and ethics of these global biodiversity heritage have been recently formalized to provide a path to better  
773 utilize and steward these collections to safeguard their continued use (Davis et al. 2025). Many of these  
774 guidelines have already been in place for decades and are often included in institutional policies that have  
775 been deliberated by stewards and shared with users (Richard et al. 2019, Shah 2023). The herbarium and  
776 Natural History Museum community has become increasingly aware of what we call the ‘destructive  
777 sampling conundrum’: how to foster innovative research that includes destructive sampling of specimens  
778 that are meant to be protected permanently (Davis et al. 2025). We additionally recognize that herbaria  
779 are differentially concentrated around the world, especially the global north (Heberling et al. 2019, Park et  
780 al. 2023), and are of different sizes and face a range of operating circumstances and challenges.

781         The effective implementation of spectroscopic sampling and measurement strategies requires  
782 meticulous consideration of both the specimen's characteristics and the preservation and repair methods  
783 that the world’s herbaria employ. Under ideal conditions, spectral digitization provides a non-destructive  
784 alternative to traditional trait measurements, allowing researchers to infer key plant traits without  
785 physically altering specimens (White et al. 2025). By non-destructive, we mean the specimen is left the  
786 way it was previously with no trace of tissue removal (Davis et al. 2025). Spectral data can be collected  
787 non-destructively when either detached leaves are available or when some leaves on a specimen are not

788 fully glued. Damage or removal of specimen tissue for spectroscopy efforts are likely to occur if non-  
789 destructive protocols are not enforced. While spectral measurements can be made non-destructively, if  
790 trait prediction is the ultimate goal, some amount of trait validation is necessary to improve the accuracy  
791 of trait prediction. Trait validation will require the destructive use of tissue from similar taxa ideally with  
792 similar herborization processes. The high performance of trait models from pressed leaves (Kothari et al.  
793 2023) applied to herborized specimens (White et al. 2025) indicates that pressed leaves of the same taxa  
794 can probably be used for validation rather than herbarium specimens. If tissue removal from specimens is  
795 required, it should be absolutely minimal, avoiding key features for identification or possible future use,  
796 and documenting what was removed. It is crucial to seek permission for these efforts. To minimize the  
797 need for destructive sampling, unwanted duplicates could be retained for spectroscopic and destructive  
798 trait measurements for calibration of trait models. Alternatively, excess duplicate specimens could be set  
799 aside and offered to the network of herbarium spectroscopy researchers, advancing the development of  
800 spectroscopic libraries for trait estimation. Adhering to non-destructive measurement approaches should  
801 be strongly encouraged to maintain the structural and historical integrity of the specimens. Researchers  
802 should obtain explicit permission before conducting studies and ensure that their methodologies align  
803 with the conservation objectives of the hosting institutions.

804 Finally, it is important that any databased content or spectral signatures harvested be offered as  
805 shared data to the host institution as part of the global metaherbarium, making the data available  
806 immediately. Doing so will help to avoid duplication of efforts with the same collection at other  
807 institutions. Finally, it is essential to promote collaboration, including by recognizing herbaria scholars,  
808 staff, and scientists formally as contributors, collaborators, funded partners, and coauthors (Edwards et al.  
809 2024, Davis et al. 2025) following practices that require extraction of tissue or other alterations to  
810 herbarium specimens (e.g., Burbano and Gutaker 2023, Davis 2023, Davis and Knapp 2025). Establishing  
811 clear guidelines for sampling ensures that scientific investigations do not compromise the preservation of  
812 these collections. For example, the American Society of Plant Taxonomists has outlined best practices  
813 that emphasize the importance of minimizing physical alterations to specimens. By adhering to such  
814 protocols, researchers can foster trust and facilitate ongoing access to these vital resources. All of these  
815 considerations are paramount in the application of leaf spectroscopy to herbarium specimens and for  
816 effective, equitable, and ethical sampling strategies (Davis et al. 2025). Sharing findings and derivative  
817 data with the broader scientific community will promote transparency and collective advancement of the  
818 plant sciences.

819

820 **Next Steps**

821 In closing, we declare that the international herbarium spectral digitization (IHerbSpec) working group is  
822 ready to go spectral! We acknowledge that we have considerable work to do as a community to ensure  
823 that data can be aggregated and to ensure fair and equitable practices. Our next step is to develop agreed  
824 upon protocols and metadata standards for the community. We pledge to be collaborative, inclusive and  
825 equitable in our work and to generate data from the world's herbaria to advance understanding and  
826 protection of the world's biodiversity.  
827

828 **Acknowledgements**

829 We thank Jorge Robles for contributions to Figure 5. For funding, we thank the US NSF Biology  
830 Integration Institute ASCEND, Advancing Spectral biology in Changing Environments to understand  
831 plant Diversity (DBI: 2021898) to JCB, the Harvard University Herbaria, iDigBio (NSF DBI-2027654) to  
832 PSS and NSF grant DBI-1930007 to DES and PSS, Canadian NSERC Discovery Grant, support from the  
833 Missouri Botanical Garden’s Revolutionizing Species Identification project. TLPC and KB are supported  
834 by funding from the European Research Council (ERC) under the European Union’s Horizon 2020  
835 research and innovation program (grant agreement No. 865787).

836

837 **Author contributions**

838 All authors contributed intellectually to the manuscript, including the writing, editing and tables. JCB,  
839 JPL, DW, MHL, JEM and BNB prepared or contributed to the figures. JCB organized and led the writing  
840 process with help from DW.

841

842

843 **References Cited**

- 844 Asner, G., and R. Martin. 2011. Canopy phylogenetic, chemical and spectral assembly in a lowland  
845 Amazonian forest. . *New Phytologist* **189**:999-1012
- 846 Blanchard, F., A. Bruneau, and E. Laliberté. 2024. Foliar spectra accurately distinguish most temperate  
847 tree species and show strong phylogenetic signal. *American Journal of Botany* **111**:e16314.
- 848 Blonder, B., B. J. Graae, B. Greer, M. Haagsma, K. Helsen, R. E. Kapás, H. Pai, J. Rieksta, D. Sapena, C.  
849 J. Still, and R. Strimbeck. 2020. Remote sensing of ploidy level in quaking aspen (*Populus*  
850 *tremuloides* Michx.). *Journal of Ecology* **108**:175-188.
- 851 Burbano, H. A., and R. M. Gutaker. 2023. Ancient DNA genomics and the renaissance of herbaria.  
852 *Science* **382**:59-63.
- 853 Cavender-Bares, J. 2019. Diversification, adaptation, and community assembly of the American oaks  
854 (*Quercus*), a model clade for integrating ecology and evolution. *New Phytologist* **221**:669-692.
- 855 Cavender-Bares J, Gonzalez-Rodriguez A, Eaton DAR, Hipp AAL, Beulke A, Manos PS. 2015.  
856 Phylogeny and biogeography of the American live oaks (*Quercus* subsection *Virentes*): a  
857 genomic and population genetics approach. *Molecular Ecology* **24**(14): 3668-3687.
- 858 Cavender-Bares, J., D. Ackerly, S. Hobbie, and P. Townsend. 2016a. Evolutionary legacy effects on  
859 ecosystems: Biogeographic origins, plant traits, and implications for management in the era of  
860 global change. *Annual Review of Ecology, Evolution, and Systematics* **47**:433-462.
- 861 Cavender-Bares, J., J. A. Gamon, S. E. Hobbie, M. D. Madritch, J. E. Meireles, A. K. Schweiger, and P.  
862 A. Townsend. 2017. Harnessing plant spectra to integrate the biodiversity sciences across  
863 biological and spatial scales. *American Journal of Botany* **104**:1-4 doi: 10.3732/ajb.1700061.
- 864 Cavender-Bares, J., A. Gonzalez-Rodriguez, D. A. R. Eaton, A. A. L. Hipp, A. Beulke, and P. S. Manos.  
865 2015. Phylogeny and biogeography of the American live oaks (*Quercus* subsection *Virentes*): a  
866 genomic and population genetics approach. *Molecular Ecology* **24**:3668-3687.
- 867 Cavender-Bares, J., J. E. Meireles, J. J. Couture, M. A. Kaproth, C. C. Kingdon, A. Singh, S. P. Serbin,  
868 A. Center, E. Zuniga, G. Pilz, and P. A. Townsend. 2016b. Associations of leaf spectra with  
869 genetic and phylogenetic variation in oaks: prospects for remote detection of biodiversity.  
870 *Remote Sensing* **8**:221-238.
- 871 Cavender-Bares, J., J. E. Meireles, J. Pinto-Ledezma, P. B. Reich, M. C. Schuman, P. A. Townsend, and  
872 A. Trowbridge. 2025. Spectral biology across scales in changing environments. *Ecology* **in press**.
- 873 Cavender-Bares, J., F. Schneider, M. Santos, A. Armstrong, A. Carnaval, K. Dahlin, L. Fatoyinbo, G.  
874 Hurtt, D. Schimel, and P. Townsend. 2022. Integrating remote sensing with ecology and  
875 evolution to advance biodiversity conservation. *Nature Ecology & Evolution* **1**:1-14.
- 876 Cavender-Bares, J., P. A. Townsend, and J. A. Gamon. 2020. *Remote Sensing of Plant Biodiversity*.  
877 Springer International Publishing.
- 878 Chlus, A., and P. A. Townsend. 2022. Characterizing seasonal variation in foliar biochemistry with  
879 airborne imaging spectroscopy. *Remote Sensing of Environment* **275**:113023.
- 880 Clavel, J., L. Aristide, and H. Morlon. 2019. A Penalized Likelihood Framework for High-Dimensional  
881 Phylogenetic Comparative Methods and an Application to New-World Monkeys Brain Evolution.  
882 *Systematic biology* **68**:93-116.
- 883 Clavel, J., G. Escarguel, and G. Merceron. 2015. mvmorph: an r package for fitting multivariate  
884 evolutionary models to morphometric data. *Methods in Ecology and Evolution* **6**:1311-1319.
- 885 Costa, D. d. S., E. F. S. Rossetto, and L. L. Giacomini. 2025. *Neea contracta* (Nyctaginaceae), a New  
886 Species from Amazonia. *Systematic Botany* **49**:743-748.
- 887 Czyż, E. A., C. Guillén Escribà, H. Wulf, A. Tedder, M. C. Schuman, F. D. Schneider, and M. E.  
888 Schaeppman. 2020. Intraspecific genetic variation of a *Fagus sylvatica* population in a temperate  
889 forest derived from airborne imaging spectroscopy time series. *Ecology and Evolution* **10**:7419-  
890 7430.

891 da Cruz Vasconcelos, C., I. D. K. Ferraz, M. U. Adrianzén, J. L. C. Camargo, and M. H. Terra-Araujo.  
892 2021. *Chromolucuma brevipedicellata* (Sapotaceae, Chrysophylloideae), a new tree species from  
893 central Amazonia, Brazil. *Brittonia* **73**:211-219.

894 Damasco, G., D. C. Daly, A. Vicentini, and P. V. A. Fine. 2019. Reestablishment of *Protium cordatum*  
895 (Burseraceae) based on integrative taxonomy. *Taxon* **68**:34-46.

896 Dao, P. D., Y. He, and C. Proctor. 2021. Plant drought impact detection using ultra-high spatial resolution  
897 hyperspectral images and machine learning. *International Journal of Applied Earth Observation*  
898 and *Geoinformation* **102**:102364.

899 Daru, B. H., D. S. Park, R. B. Primack, C. G. Willis, D. S. Barrington, T. J. S. Whitfeld, T. G. Seidler, P.  
900 W. Sweeney, D. R. Foster, A. M. Ellison, and C. C. Davis. 2018. Widespread sampling biases in  
901 herbaria revealed from large-scale digitization. *New Phytologist* **217**:939-955.

902 Davis, C. C. 2023. The herbarium of the future. *Trends in Ecology & Evolution* **38**:412-423.

903 Davis, C. C., J. A. Kennedy, and C. J. Grassa. 2021. Back to the future: A refined single-user photostation  
904 for massively scaling herbarium digitization. *Taxon* **70**:635-643.

905 Davis, C. C., and S. Knapp. 2025. Exploring biodiversity through museomics. *Nature Reviews Genetics*  
906 **26**:149-150.

907 Davis, C. C., E. Sessa, A. Paton, A. Antonelli, and J. K. Teisher. 2025. Guidelines for the effective and  
908 ethical sampling of herbaria. *Nature Ecology & Evolution* **9**:196-203.

909 Davis, C. C., C. G. Willis, B. Connolly, C. Kelly, and A. M. Ellison. 2015. Herbarium records are reliable  
910 sources of phenological change driven by climate and provide novel insights into species'  
911 phenological cueing mechanisms. *Am J Bot* **102**:1599-1609.

912 Deacon, N. J., J. J. Grossman, A. K. Schweiger, I. Armour, and J. Cavender-Bares. 2017a. Genetic,  
913 morphological, and spectral characterization of relictual Niobrara River hybrid aspens (*Populus* ×  
914 *smithii*). *American Journal of Botany* **104**:1878-1890.

915 Deacon, N. J., J. J. Grossman, A. K. Schweiger, I. Armour, and J. Cavender-Bares. 2017b. Genetic,  
916 morphological, and spectral characterization of relictual Niobrara River hybrid aspens (*Populus* ×  
917 *smithii*). *American Journal of Botany* **104**:1878-1890.

918 Dechant, B., J. Kattge, R. Pavlick, F. D. Schneider, F. M. Sabatini, Á. Moreno-Martínez, E. E. Butler, P.  
919 M. van Bodegom, H. Vallicrosa, T. Kattenborn, C. C. F. Boonman, N. Madani, I. J. Wright, N.  
920 Dong, H. Feilhauer, J. Peñuelas, J. Sardans, J. Aguirre-Gutiérrez, P. B. Reich, P. J. Leitão, J.  
921 Cavender-Bares, I. H. Myers-Smith, S. M. Durán, H. Croft, I. C. Prentice, A. Huth, K. Rebel, S.  
922 Zaehle, I. Šimová, S. Díaz, M. Reichstein, C. Schiller, H. Bruelheide, M. Mahecha, C. Wirth, Y.  
923 Malhi, and P. A. Townsend. 2024. Intercomparison of global foliar trait maps reveals  
924 fundamental differences and limitations of upscaling approaches. *Remote Sensing of*  
925 *Environment* **311**:114276.

926 Díaz, S., J. Kattge, J. H. C. Cornelissen, I. J. Wright, S. Lavorel, S. Dray, B. Reu, M. Kleyer, C. Wirth, I.  
927 Colin Prentice, E. Garnier, G. Bönsch, M. Westoby, H. Poorter, P. B. Reich, A. T. Moles, J.  
928 Dickie, A. N. Gillison, A. E. Zanne, J. Chave, S. Joseph Wright, S. N. Sheremet'ev, H. Jactel, C.  
929 Baraloto, B. Cerabolini, S. Pierce, B. Shipley, D. Kirkup, F. Casanoves, J. S. Joswig, A. Günther,  
930 V. Falczuk, N. Rüger, M. D. Mahecha, and L. D. Gorné. 2016. The global spectrum of plant form  
931 and function. *Nature* **529**:167-171.

932 Durgante, F. M., N. Higuchi, A. Almeida, and A. Vicentini. 2013. Species Spectral Signature:  
933 Discriminating closely related plant species in the Amazon with Near-Infrared Leaf-  
934 Spectroscopy. *Forest Ecology and Management* **291**:240-248.

935 Edwards, E. J., B. D. Mishler, and C. D. Davis. 2024. University herbaria are uniquely important. *Trends*  
936 *in Plant Science* **29**:825-826.

937 Elvidge, C. D. 1990. Visible and near infrared reflectance characteristics of dry plant materials.  
938 *International Journal of Remote Sensing* **11**:1775-1795.

939 Enquist, B. J., R. Condit, R. K. Peet, M. Schildhauer, and B. M. Thiers. 2016. Cyberinfrastructure for an  
940 integrated botanical information network to investigate the ecological impacts of global climate  
941 change on plant biodiversity. *PeerJ Preprints* **4**:e2615v2612.

942 Fajardo, A., and A. Siefert. 2016. Phenological variation of leaf functional traits within species.  
943 *Oecologia* **180**:951-959.

944 Fallon, B., A. Yang, C. Lapadat, I. Armour, J. Juzwik, R. A. Montgomery, and J. Cavender-Bares. 2020.  
945 Spectral differentiation of oak wilt from foliar fungal disease and drought is correlated with  
946 physiological changes. *Tree Physiology* **40**:377-390.

947 Falster, D., R. Gallagher, E. H. Wenk, I. J. Wright, D. Indiarito, S. C. Andrew, C. Baxter, J. Lawson, S.  
948 Allen, A. Fuchs, A. Monro, F. Kar, M. A. Adams, C. W. Ahrens, M. Alfonzetti, T. Angevin, D.  
949 M. G. Apgaua, S. Arndt, O. K. Atkin, J. Atkinson, T. Auld, A. Baker, M. von Balthazar, A. Bean,  
950 C. J. Blackman, K. Bloomfield, D. M. J. S. Bowman, J. Bragg, T. J. Brodribb, G. Buckton, G.  
951 Burrows, E. Caldwell, J. Camac, R. Carpenter, J. A. Catford, G. R. Cawthray, L. A. Cernusak, G.  
952 Chandler, A. R. Chapman, D. Cheal, A. W. Cheesman, S.-C. Chen, B. Choat, B. Clinton, P. L.  
953 Clode, H. Coleman, W. K. Cornwell, M. Cosgrove, M. Crisp, E. Cross, K. Y. Crous, S.  
954 Cunningham, T. Curran, E. Curtis, M. I. Daws, J. L. DeGabriel, M. D. Denton, N. Dong, P. Du,  
955 H. Duan, D. H. Duncan, R. P. Duncan, M. Duretto, J. M. Dwyer, C. Edwards, M. Esperon-  
956 Rodriguez, J. R. Evans, S. E. Everingham, C. Farrell, J. Firn, C. R. Fonseca, B. J. French, D.  
957 Froud, J. L. Funk, S. R. Geange, O. Ghannoum, S. M. Gleason, C. R. Gosper, E. Gray, P. K.  
958 Groom, S. Grootemaat, C. Gross, G. Guerin, L. Guja, A. K. Hahs, M. T. Harrison, P. E. Hayes,  
959 M. Henery, D. Hochuli, J. Howell, G. Huang, L. Hughes, J. Huisman, J. Ilic, A. Jagdish, D. Jin,  
960 G. Jordan, E. Jurado, J. Kanowski, S. Kasel, J. Kellermann, B. Kenny, M. Kohout, R. M.  
961 Kooyman, M. M. Kotowska, H. R. Lai, E. Laliberté, H. Lambers, B. B. Lamont, R. Lanfear, F.  
962 van Langevelde, D. C. Laughlin, B.-A. Laugier-Kitchener, S. Laurance, C. E. R. Lehmann, A.  
963 Leigh, M. R. Leishman, T. Lenz, B. Lepschi, J. D. Lewis, F. Lim, U. Liu, J. Lord, C. H. Lusk, C.  
964 Macinnis-Ng, H. McPherson, S. Magallón, A. Manea, A. López-Martinez, M. Mayfield, J. K.  
965 McCarthy, T. Meers, M. van der Merwe, D. J. Metcalfe, P. Milberg, K. Mokany, A. T. Moles, B.  
966 D. Moore, N. Moore, J. W. Morgan, W. Morris, A. Muir, S. Munroe, Á. Nicholson, D. Nicolle,  
967 A. B. Nicotra, Ü. Niinemets, T. North, A. O'Reilly-Nugent, O. S. O'Sullivan, B. Oberle, Y.  
968 Onoda, M. K. J. Ooi, C. P. Osborne, G. Paczkowska, B. Pekin, C. Guilherme Pereira, C.  
969 Pickering, M. Pickup, L. J. Pollock, P. Poot, J. R. Powell, S. A. Power, I. C. Prentice, L. Prior, S.  
970 M. Prober, J. Read, V. Reynolds, A. E. Richards, B. Richardson, M. L. Roderick, J. A. Rosell, M.  
971 Rossetto, B. Rye, P. D. Rymer, M. A. Sams, G. Sanson, H. Sauquet, S. Schmidt, J.  
972 Schönenberger, E.-D. Schulze, K. Sendall, S. Sinclair, B. Smith, R. Smith, F. Soper, B. Sparrow,  
973 R. J. Standish, T. L. Staples, R. Stephens, C. Szota, G. Taseski, E. Tasker, F. Thomas, D. T.  
974 Tissue, M. G. Tjoelker, D. Y. P. Tng, F. de Tombeur, K. Tomlinson, N. C. Turner, E. J.  
975 Veneklaas, S. Venn, P. Vesk, C. Vlasveld, M. S. Vorontsova, C. A. Warren, N. Warwick, L. K.  
976 Weerasinghe, J. Wells, M. Westoby, M. White, N. S. G. Williams, J. Wills, P. G. Wilson, C.  
977 Yates, A. E. Zanne, G. Zemunik, and K. Ziemińska. 2021. AusTraits, a curated plant trait  
978 database for the Australian flora. *Scientific Data* **8**:254.

979 Féret, J. B., A. A. Gitelson, S. D. Noble, and S. Jacquemoud. 2017. PROSPECT-D: Towards modeling  
980 leaf optical properties through a complete lifecycle. *Remote Sens. Environ.* **193**:204-215.

981 Fine, P. V. A., D. Salazar, R. E. Martin, M. R. Metz, T. M. Misiewicz, and G. P. Asner. 2021. Exploring  
982 the links between secondary metabolites and leaf spectral reflectance in a diverse genus of  
983 Amazonian trees. *Ecosphere* **12**:e03362.

984 Funk, J. L., J. E. Larson, G. M. Ames, B. J. Butterfield, J. Cavender-Bares, J. Firn, D. C. Laughlin, A. E.  
985 Sutton-Grier, L. Williams, and J. Wright. 2017. Revisiting the Holy Grail: using plant functional  
986 traits to understand ecological processes: Plant functional traits. *Biological Reviews* **92**:1156-  
987 1173.

988 Gaem, P. H., A. Andrade, F. F. Mazine, and A. Vicentini. 2022. Tree species delimitation in tropical  
989 forest inventories: Perspectives from a taxonomically challenging case study. *Forest Ecology and*  
990 *Management* **505**:119900.

991 Gamon, J., and J. Surfus. 1999. Assessing leaf pigment content and activity with a reflectometer. *New*  
992 *Phytologist* **143**:105-117.

- 993 Ge, Y., G. Bai, V. Stoerger, and J. c. Schnable. 2016. Temporal dynamics of maize plant growth, water  
 994 use, and leaf water content using automated high throughput RGB and hyperspectral imaging.  
 995 Comput. Electron. Agric. **127**:625-632.
- 996 Gitelson, A. A., C. Buschmann, and H. K. Lichtenthaler. 1998. Leaf chlorophyll fluorescence corrected  
 997 for re-absorption by means of absorption and reflectance measurements. J. Plant Physiol.  
 998 **152**:283-296.
- 999 Gitelson, A. A., and M. N. Merzlyak. 1994. Spectral reflectance changes associate with autumn  
 1000 senescence of *Aesculus hippocastanum* L. and *Acer platanoides* L. leaves. Spectral features and  
 1001 relation to chlorophyll estimation. . Journal of Plant Physiology **143**:286–292.
- 1002 Grant, L. 1987. Diffuse and specular characteristics of leaf reflectance. Remote Sensing of Environment  
 1003 **22**:309-322.
- 1004 Guillot G, Santos F. 2009. A computer program to simulate multilocus genotype data with spatially  
 1005 autocorrelated allele frequencies. Molecular Ecology Resources 9: 1112-1120.
- 1006 Hadlich, H. L., J. Schöngart, F. Wittmann, C. C. Vasconcelos, C. L. Mallmann, M. L. G. Conde, P.  
 1007 Amaral de Sá, L. O. Demarchi, G. B. Mori, M. T. F. Piedade, and F. M. Durgante. 2025. Scaling  
 1008 up tree diversity inventories across Amazonian ecosystems using field spectroscopy.  
 1009 bioRxiv:2025.2003.2026.645444.
- 1010 Harvey, P. H., and A. Purvis. 1991. Comparative methods for explaining adaptations. Nature **351**:619-  
 1011 624.
- 1012 Heberling, J. M. 2021. Herbaria as Big Data Sources of Plant Traits. International Journal of Plant  
 1013 Sciences **183**:87-118.
- 1014 Heberling, J. M., J. T. Miller, D. Noesgaard, S. B. Weingart, and D. Schigel. 2021. Data integration  
 1015 enables global biodiversity synthesis. Proceedings of the National Academy of Sciences  
 1016 **118**:e2018093118.
- 1017 Heberling, J. M., L. A. Prather, and S. J. Tonsor. 2019. The Changing Uses of Herbarium Data in an Era  
 1018 of Global Change: An Overview Using Automated Content Analysis. BioScience **69**:812-822.
- 1019 Hedrick, B., M. Heberling, E. Meineke, K. Turner, C. Grassa, D. Park, J. Kennedy, J. Clarke, J. Cook, D.  
 1020 Blackburn, S. Edwards, and C. Davis. 2019. Digitization and the future of natural history  
 1021 collections.
- 1022 Hernández-Leal MS, Guzmán Q. JA, González-Rodríguez A, Cavender-Bares J. 2025. Foliar spectral  
 1023 signatures reveal adaptive divergence in live oaks (*Quercus* section *Virentes*) across species and  
 1024 environmental niches. EcoEvoRxiv <https://ecoevorxiv.org/repository/view/9054/>:  
 1025 <https://doi.org/10.32942/X32942BK32990>.
- 1026 Hipp AL, Manos PS, Hahn M, Avishai M, Bodénès C, Cavender-Bares J, Crowl AA, Deng M, Denk T,  
 1027 Fitz-Gibbon S, et al. 2020. Genomic landscape of the global oak phylogeny. New Phytologist  
 1028 **226**(4): 1198-1212.
- 1029 Jacquemoud, S., and S. Ustin. 2019. Leaf Optical Properties. Cambridge University Press, New York.
- 1030 Jetz, W., J. Cavender-Bares, R. Pavlick, D. Schimel, F. W. Davis, G. P. Asner, R. Guralnick, J. Kattge, A.  
 1031 Latimer, P. Moorcroft, M. E. Schaepman, and S. L. Ustin. 2016a. Monitoring plant functional  
 1032 diversity from space. Nature Plants **2**.
- 1033 Jetz, W., J. Cavender-Bares, R. Pavlick, D. Schimel, F. W. Davis, G. P. Asner, R. Guralnick, J. Kattge, A.  
 1034 M. Latimer, P. Moorcroft, M. E. Schaepman, M. P. Schildhauer, F. D. Schneider, F. Schrod, U.  
 1035 Stahl, and S. L. Ustin. 2016b. Monitoring plant functional diversity from space. Nature Plants  
 1036 **2**:16024.
- 1037 Kattge, J., G. Bonisch, S. Diaz, S. Lavorel, I. C. Prentice, P. Leadley, S. Tautenhahn, G. D. A. Werner, T.  
 1038 Aakala, M. Abedi, A. T. R. Acosta, G. C. Adamidis, K. Adamson, M. Aiba, C. H. Albert, J. M.  
 1039 Alcantara, C. C. Alcazar, I. Aleixo, H. Ali, B. Amiaud, C. Ammer, M. M. Amoroso, M. Anand,  
 1040 C. Anderson, N. Anten, J. Antos, D. M. G. Apgaua, T. L. Ashman, D. H. Asmara, G. P. Asner,  
 1041 M. Aspinwall, O. Atkin, I. Aubin, L. Baastrop-Spohr, K. Bahalkeh, M. Bahn, T. Baker, W. J.  
 1042 Baker, J. P. Bakker, D. Baldocchi, J. Baltzer, A. Banerjee, A. Baranger, J. Barlow, D. R.  
 1043 Barneche, Z. Baruch, D. Bastianelli, J. Battles, W. Bauerle, M. Bauters, E. Bazzato, M.

1044 Beckmann, H. Beeckman, C. Beierkuhnlein, R. Bekker, G. Belfry, M. Belluau, M. Beloiu, R.  
 1045 Benavides, L. Benomar, M. L. Berdugo-Lattke, E. Berenguer, R. Bergamin, J. Bergmann, M. B.  
 1046 Carlucci, L. Berner, M. Bernhardt-Romermann, C. Bigler, A. D. Bjorkman, C. Blackman, C.  
 1047 Blanco, B. Blonder, D. Blumenthal, K. T. Bocanegra-Gonzalez, P. Boeckx, S. Bohlman, K.  
 1048 Bohning-Gaese, L. Boisvert-Marsh, W. Bond, B. Bond-Lamberty, A. Boom, C. C. F. Boonman,  
 1049 K. Bordin, E. H. Boughton, V. Boukili, D. Bowman, S. Bravo, M. R. Brendel, M. R. Broadley, K.  
 1050 A. Brown, H. Bruelheide, F. Brunnich, H. H. Bruun, D. Bruy, S. W. Buchanan, S. F. Bucher, N.  
 1051 Buchmann, R. Buitenwerf, D. E. Bunker, J. Burger, S. Burrascano, D. Burslem, B. J. Butterfield,  
 1052 C. Byun, M. Marques, M. C. Scalon, M. Caccianiga, M. Cadotte, M. Cailleret, J. Camac, J. J.  
 1053 Camarero, C. Company, G. Campetella, J. A. Campos, L. Cano-Arboleda, R. Canullo, M.  
 1054 Carbognani, F. Carvalho, F. Casanoves, B. Castagneyrol, J. A. Catford, J. Cavender-Bares, B. E.  
 1055 L. Cerabolini, M. Cervellini, E. Chacon-Madrigal, K. Chapin, F. S. Chapin, S. Chelli, S. C. Chen,  
 1056 A. P. Chen, P. Cherubini, F. Chianucci, B. Choat, K. S. Chung, M. Chytry, D. Ciccarelli, L. Coll,  
 1057 C. G. Collins, L. Conti, D. Coomes, J. H. C. Cornelissen, W. K. Cornwell, P. Corona, M. Coyea,  
 1058 J. Craine, D. Craven, J. Cromsigt, A. Csecserits, K. Cufar, M. Cuntz, A. C. da Silva, K. M.  
 1059 Dahlin, M. Dainese, I. Dalke, M. Dalle Fratte, T. D. L. Anh, J. Danihelka, M. Dannoura, S.  
 1060 Dawson, A. J. de Beer, A. De Frutos, J. R. De Long, B. Dechant, S. Delagrange, N. Delpierre, G.  
 1061 Derroire, A. S. Dias, M. H. Diaz-Toribio, P. G. Dimitrakopoulos, M. Dobrowolski, D. Doktor, P.  
 1062 Drevojan, N. Dong, J. Dransfield, S. Dressler, L. Duarte, E. Ducouret, S. Dullinger, W. Durka, R.  
 1063 Duursma, O. Dymova, A. E-Vojtko, R. L. Eckstein, H. Ejtehadi, J. Elser, T. Emilio, K.  
 1064 Engemann, M. B. Erfanian, A. Erfmeier, A. Esquivel-Muelbert, G. Esser, M. Estiarte, T. F.  
 1065 Domingues, W. F. Fagan, J. Fagundez, D. S. Falster, Y. Fan, J. Y. Fang, E. Farris, F. Fazlioglu,  
 1066 Y. H. Feng, F. Fernandez-Mendez, C. Ferrara, J. Ferreira, A. Fidelis, B. Finegan, J. Firn, T. J.  
 1067 Flowers, D. F. B. Flynn, V. Fontana, E. Forey, C. Forgiarini, L. Francois, M. Frangipani, D.  
 1068 Frank, C. Frenette-Dussault, G. T. Freschet, E. L. Fry, N. M. Fyllas, G. G. Mazzochini, S.  
 1069 Gachet, R. Gallagher, G. Ganade, F. Ganga, P. Garcia-Palacios, V. Gargaglione, E. Garnier, J. L.  
 1070 Garrido, A. L. de Gasper, G. Gea-Izquierdo, D. Gibson, A. N. Gillison, A. Giroldo, M. C.  
 1071 Glasenhardt, S. Gleason, M. Gliesch, E. Goldberg, B. Goldel, E. Gonzalez-Akre, J. L. Gonzalez-  
 1072 Andujar, A. Gonzalez-Melo, A. Gonzalez-Robles, B. J. Graae, E. Granda, S. Graves, W. A.  
 1073 Green, T. Gregor, N. Gross, G. R. Guerin, A. Gunther, A. G. Gutierrez, L. Haddock, A. Haines, J.  
 1074 Hall, A. Hambuckers, W. X. Han, S. P. Harrison, W. Hattingh, J. E. Hawes, T. H. He, P. C. He, J.  
 1075 M. Heberling, A. Helm, S. Hempel, J. Hentschel, B. Herault, A. M. Heres, K. Herz, M. Heuert,  
 1076 T. Hickler, P. Hietz, P. Higuchi, A. L. Hipp, A. Hiron, M. Hock, J. A. Hogan, K. Holl, O.  
 1077 Honnay, D. Hornstein, E. Q. Hou, N. Hough-Snee, K. A. Hovstad, T. Ichie, B. Igc, E. Illa, M.  
 1078 Isaac, M. Ishihara, L. Ivanov, L. Ivanova, C. M. Iversen, J. Izquierdo, R. B. Jackson, B. Jackson,  
 1079 H. Jactel, A. M. Jagodzinski, U. Jandt, S. Jansen, T. Jenkins, A. Jentsch, J. R. P. Jespersen, G. F.  
 1080 Jiang, J. L. Johansen, D. Johnson, E. J. Jokela, C. A. Joly, G. J. Jordan, G. S. Joseph, D. Junaedi,  
 1081 R. R. Junker, E. Justes, R. Kabzems, J. Kane, Z. Kaplan, T. Kattenborn, L. Kavelenova, E.  
 1082 Kearsley, A. Kempel, T. Kenzo, A. Kerkhoff, M. I. Khalil, N. L. Kinlock, W. D. Kissling, K.  
 1083 Kitajima, T. Kitzberger, R. Kjoller, T. Klein, M. Kleyer, J. Klimesova, J. Klipel, B. Kloeppe, S.  
 1084 Klotz, J. M. H. Knops, T. Kohyama, F. Koike, J. Kollmann, B. Komac, K. Komatsu, C. Konig, N.  
 1085 J. B. Kraft, K. Kramer, H. Kreft, I. Kuhn, D. Kumarathunge, J. Kuppler, H. Kurokawa, Y.  
 1086 Kurosawa, S. Kuyah, J. P. Laclau, B. Lafleur, E. Lallai, E. Lamb, A. Lamprecht, D. J. Larkin, D.  
 1087 Laughlin, Y. Le Bagousse-Pinguet, G. le Maire, P. C. le Roux, E. le Roux, T. Lee, F. Lens, S. L.  
 1088 Lewis, B. Lhotsky, Y. Z. Li, X. E. Li, J. W. Lichstein, M. Liebergesell, J. Y. Lim, Y. S. Lin, J. C.  
 1089 Linares, C. J. Liu, D. J. Liu, U. Liu, S. Livingstone, J. Llusia, M. Lohbeck, A. Lopez-Garcia, G.  
 1090 Lopez-Gonzalez, Z. Lososova, F. Louault, B. A. Lukacs, P. Lukes, Y. J. Luo, M. Lussu, S. Y.  
 1091 Ma, C. M. R. Pereira, M. Mack, V. Maire, A. Makela, H. Makinen, A. C. M. Malhado, A. Mallik,  
 1092 P. Manning, S. Manzoni, Z. Marchetti, L. Marchino, V. Marcilio-Silva, E. Marcon, M.  
 1093 Marignani, L. Markesteijn, A. Martin, C. Martinez-Garza, J. Martinez-Vilalta, T. Maskova, K.  
 1094 Mason, N. Mason, T. J. Massad, J. Masse, I. Mayrose, J. McCarthy, M. L. McCormack, K.

- 1095 McCulloh, I. R. McFadden, B. J. McGill, M. Y. McPartland, J. S. Medeiros, B. Medlyn, P.  
1096 Meerts, Z. Mehrabi, P. Meir, F. P. L. Melo, M. Mencuccini, C. Meredieu, J. Messier, I. Meszaros,  
1097 J. Metsaranta, S. T. Michaletz, C. Michelaki, S. Migalina, R. Milla, J. E. D. Miller, V. Minden, R.  
1098 Ming, K. Mokany, A. T. Moles, V. A. Molnar, J. Molofsky, M. Molz, R. A. Montgomery, A.  
1099 Monty, L. Moravcova, A. Moreno-Martinez, M. Moretti, A. S. Mori, S. Mori, D. Morris, J.  
1100 Morrison, L. Mucina, S. Mueller, C. D. Muir, S. C. Muller, F. Munoz, I. H. Myers-Smith, R. W.  
1101 Myster, M. Nagano, S. Naidu, A. Narayanan, B. Natesan, L. Negoita, A. S. Nelson, E. L.  
1102 Neuschulz, J. Ni, G. Niedrist, J. Nieto, U. Niinemets, R. Nolan, H. Nottebrock, Y. Nouvellon, A.  
1103 Novakovskiy, K. O. Nystuen, A. O'Grady, K. O'Hara, A. O'Reilly-Nugent, S. Oakley, W.  
1104 Oberhuber, T. Ohtsuka, R. Oliveira, K. Ollerer, M. E. Olson, V. Onipchenko, Y. Onoda, R. E.  
1105 Onstein, J. C. Ordonez, N. Osada, I. Ostonen, G. Ottaviani, S. Otto, G. E. Overbeck, W. A.  
1106 Ozinga, A. T. Pahl, C. E. T. Paine, R. J. Pakeman, A. C. Papageorgiou, E. Parfionova, M. Partel,  
1107 M. Patacca, S. Paula, J. Paule, H. Pauli, J. G. Pausas, B. Peco, J. Penuelas, A. Perea, P. L. Peri, A.  
1108 C. Petisco-Souza, A. Petraglia, A. M. Petritan, O. L. Phillips, S. Pierce, V. D. Pillar, J. Pisek, A.  
1109 Pomogaybin, H. Poorter, A. Portsmouth, P. Poschlod, C. Potvin, D. Pounds, A. S. Powell, S. A.  
1110 Power, A. Prinzing, G. Puglielli, P. Pysek, V. Raavel, A. Rammig, J. Ransijn, C. A. Ray, P. B.  
1111 Reich, M. Reichstein, D. E. B. Reid, M. Rejou-Mechain, V. R. de Dios, S. Ribeiro, S.  
1112 Richardson, K. Riibak, M. C. Rillig, F. Riviera, E. M. R. Robert, S. Roberts, B. Robroek, A.  
1113 Roddy, A. V. Rodrigues, A. Rogers, E. Rollinson, V. Rolo, C. Romermann, D. Ronzhina, C.  
1114 Roscher, J. A. Rosell, M. F. Rosenfield, C. Rossi, D. B. Roy, S. Royer-Tardif, N. Ruger, R. Ruiz-  
1115 Peinado, S. B. Rumpf, G. M. Rusch, M. Ryo, L. Sack, A. Saldana, B. Salgado-Negret, R.  
1116 Salguero-Gomez, I. Santa-Regina, A. C. Santacruz-Garcia, J. Santos, J. Sardans, B. Schamp, M.  
1117 Scherer-Lorenzen, M. Schleuning, B. Schmid, M. Schmidt, S. Schmitt, J. V. Schneider, S. D.  
1118 Schowanek, J. Schrader, F. Schrod, B. Schuldt, F. Schurr, G. S. Garvizu, M. Semchenko, C.  
1119 Seymour, J. C. Sfair, J. M. Sharpe, C. S. Sheppard, S. Sheremetiev, S. Shiodera, B. Shipley, T. A.  
1120 Shovon, A. Siebenkas, C. Sierra, V. Silva, M. Silva, T. Sitzia, H. Sjoman, M. Slot, N. G. Smith,  
1121 D. Sodhi, P. Soltis, D. Soltis, B. Somers, G. Sonnier, M. V. Sorensen, E. E. Sosinski, N. A.  
1122 Soudzilovskaia, A. F. Souza, M. Spasojevic, M. G. Sperandii, A. B. Stan, J. Stegen, K.  
1123 Steinbauer, J. G. Stephan, F. Sterck, D. B. Stojanovic, T. Strydom, M. L. Suarez, J. C. Svenning,  
1124 I. Svitkova, M. Svitok, M. Svoboda, E. Swaine, N. Swenson, M. Tabarelli, K. Takagi, U.  
1125 Tappeiner, R. Tarifa, S. Tauougourdeau, C. Tavsanoglu, M. te Beest, L. Tedersoo, N. Thiffault, D.  
1126 Thom, E. Thomas, K. Thompson, P. E. Thornton, W. Thuiller, L. Tichy, D. Tissue, M. G.  
1127 Tjoelker, D. Y. P. Tng, J. Tobias, P. Torok, T. Tarin, J. M. Torres-Ruiz, B. Tothmeresz, M.  
1128 Treurnicht, V. Trivellone, F. Trolliet, V. Trotsiuk, J. L. Tsakalos, I. Tsiripidis, N. Tysklind, T.  
1129 Umehara, V. Usoltsev, M. Vadeboncoeur, J. Vaezi, F. Valladares, J. Vamosi, P. M. van  
1130 Bodegom, M. van Breugel, E. Van Cleemput, M. van de Weg, S. van der Merwe, F. van der Plas,  
1131 M. T. van der Sande, M. van Kleunen, K. Van Meerbeek, M. Vanderwel, K. A. Vanselow, A.  
1132 Varhammar, L. Varone, M. Y. Valderrama, K. Vassilev, M. Vellend, E. J. Veneklaas, H.  
1133 Verbeeck, K. Verheyen, A. Vibrans, I. Vieira, J. Villacis, C. Violle, P. Vivek, K. Wagner, M.  
1134 Waldram, A. Waldron, A. P. Walker, M. Waller, G. Walther, H. Wang, F. Wang, W. Q. Wang,  
1135 H. Watkins, J. Watkins, U. Weber, J. T. Weedon, L. P. Wei, P. Weigelt, E. Weiher, A. W. Wells,  
1136 C. Wellstein, E. Wenk, M. Westoby, A. Westwood, P. J. White, M. Whitten, M. Williams, D. E.  
1137 Winkler, K. Winter, C. Womack, I. J. Wright, S. J. Wright, J. Wright, B. X. Pinho, F. Ximenes,  
1138 T. Yamada, K. Yamaji, R. Yanai, N. Yankov, B. Yguel, K. J. Zanini, A. E. Zanne, D. Zeleny, Y.  
1139 P. Zhao, J. M. Zheng, J. Zheng, K. Ziemska, C. R. Zirbel, G. Zizka, I. C. Zo-Bi, G. Zotz, C.  
1140 Wirth, and N. Nutrient. 2020. TRY plant trait database - enhanced coverage and open access.  
1141 *Global Change Biology* **26**:119-188.  
1142 Kokaly, R., G. Asner, S. Ollinger, M. Martin, and C. Wessman. 2009. Characterizing canopy  
1143 biochemistry from imaging spectroscopy and its application to ecosystem studies. *Remote*  
1144 *Sensing of Environment* **113**:S78-S91.

- 1145 Kothari, S., R. Beauchamp-Rioux, E. Laliberté, and J. Cavender-Bares. 2023. Reflectance spectroscopy  
 1146 allows rapid, accurate and non-destructive estimates of functional traits from pressed leaves.  
 1147 *Methods in Ecology and Evolution* **14**:385-401.
- 1148 Kothari, S., and A. K. Schweiger. 2022. Plant spectra as integrative measures of plant phenotypes. *Journal*  
 1149 *of Ecology* **110**:2536-2554.
- 1150 Kühn, P., R. Umazekabiri, C. Römermann, H. Bruelheide, and K. Wesche. 2025. Nitrogen content of  
 1151 herbarium specimens from arable fields and mesic meadows reflect the intensifying agricultural  
 1152 management during the 20th century. *Journal of Ecology* **113**:555-569.
- 1153 Lang, C., F. R. C. Costa, J. L. C. Camargo, F. M. Durgante, and A. Vicentini. 2015. Near Infrared  
 1154 Spectroscopy Facilitates Rapid Identification of Both Young and Mature Amazonian Tree  
 1155 Species. *Plos One* **10**:e0134521.
- 1156 Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem  
 1157 functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* **16**:545-556.
- 1158 Lendemer, J., B. Thiers, A. K. Monfils, J. Zaspel, E. R. Ellwood, A. Bentley, K. LeVan, J. Bates, D.  
 1159 Jennings, D. Contreras, L. Lagomarsino, P. Mabee, L. S. Ford, R. Guralnick, R. E. Gropp, M.  
 1160 Revelez, N. Cobb, K. Seltmann, and M. C. Aime. 2020. The Extended Specimen Network: A  
 1161 Strategy to Enhance US Biodiversity Collections, Promote Research and Education. *BioScience*  
 1162 **70**:23-30.
- 1163 Madritch, M. D., C. C. Kingdon, A. Singh, K. E. Mock, R. L. Lindroth, and P. A. Townsend. 2014.  
 1164 Imaging spectroscopy links aspen genotype with below-ground processes at landscape scales.  
 1165 *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **369**.
- 1166 Mallmann, C. L., W. Pereira Filho, J. B. B. Dreyer, L. A. Tabaldi, and F. M. Durgante. 2023. Leaf-Level  
 1167 Field Spectroscopy to Discriminate Invasive Species (*Psidium guajava* L. and *Hovenia dulcis*  
 1168 Thunb.) from Native Tree Species in the Southern Brazilian Atlantic Forest. *Remote Sensing*.
- 1169 Mandrioli, M. 2023. From Dormant Collections to Repositories for the Study of Habitat Changes: The  
 1170 Importance of Herbaria in Modern Life Sciences. *Life (Basel)* **13**.
- 1171 Meacham-Hensold, K., C. M. Montes, J. Wu, K. Guan, P. Fu, E. A. Ainsworth, T. Pederson, C. E. Moore,  
 1172 K. L. Brown, C. Raines, and C. J. Bernacchi. 2019. High-throughput field phenotyping using  
 1173 hyperspectral reflectance and partial least squares regression (PLSR) reveals genetic  
 1174 modifications to photosynthetic capacity. *Remote Sensing of Environment* **231**:111176.
- 1175 Medeiros, L. S., S. M. Q. Lima, M. d. Pinna, I. C. A. Souto-Santos, S. Pirro, and W. M. Berbel-Filho.  
 1176 2024. Whole-Genome Sequencing of Two *Listrura* and Five *Microcambeva* Species  
 1177 (*Trichomycteridae*, *Siluriformes*), Rare and Threatened Catfishes from the Atlantic Forest.  
 1178 *Biodiversity Genomes* **December**.
- 1179 Meineke, E. K., T. J. Davies, B. H. Daru, and C. C. Davis. 2018a. Biological collections for  
 1180 understanding biodiversity in the Anthropocene. *Philosophical Transactions of the Royal Society*  
 1181 *B: Biological Sciences* **374**:20170386.
- 1182 Meineke, E. K., C. C. Davis, and T. J. Davies. 2018b. The unrealized potential of herbaria for global  
 1183 change biology. *Ecological Monographs* **88**:505-525.
- 1184 Meireles, J. E., J. Cavender-Bares, P. A. Townsend, S. Ustin, J. A. Gamon, A. K. Schweiger, M. E.  
 1185 Schaepman, G. P. Asner, R. E. Martin, A. Singh, F. Schrod, A. Chlus, and B. O'Meara. 2020a.  
 1186 Leaf reflectance spectra capture the evolutionary history of seed plants. *New Phytologist*  
 1187 **228**:485-493.
- 1188 Meireles, J. E., B. O'Meara, and J. Cavender-Bares. 2020b. Linking leaf spectra to the plant tree of life.  
 1189 Pages 155-172 *in* J. Cavender-Bares, J. A. Gamon, and P. A. Townsend, editors. *Remote Sensing*  
 1190 *of Plant Biodiversity*. Springer.
- 1191 Meireles, J. E., B. O'Meara, and J. Cavender-Bares. 2020c. Linking Leaf Spectra to the Plant Tree of  
 1192 Life. Pages 155-172 *in* J. Cavender-Bares, J. A. Gamon, and P. A. Townsend, editors. *Remote*  
 1193 *Sensing of Plant Biodiversity*. Springer International Publishing, Cham.
- 1194 Meireles, J. E., A. K. Schweiger, and J. M. Cavender-Bares. 2017. spectrolab: Class and Methods for  
 1195 Hyperspectral Data. R package version 0.0.2.

- 1196 National Academies of Sciences, E., and Medicine. 2020. Biological Collections: Ensuring Critical  
 1197 Research and Education for the 21st Century. The National Academies Press, Washington, DC.
- 1198 Nelson, G., P. Sweeney, L. Wallace, R. Rabeler, D. Allard, H. Brown, R. Carter, M. Denslow, L.  
 1199 Ellwood, C. Germain-Aubrey, E. Gilbert, E. Gillespie, L. Goertzen, B. Legler, T. Marsico, A.  
 1200 Morris, Z. Murrell, M. Nazaire, and A. Mast. 2015. Digitization Workflows for Flat Sheets and  
 1201 Packets of Plants, Algae, and Fungi. *Applications in Plant Sciences* **3**.
- 1202 Paiva, D. N. A., R. d. O. Perdiz, and T. E. Almeida. 2021. Using near-infrared spectroscopy to  
 1203 discriminate closely related species: a case study of neotropical ferns. *Journal of Plant Research*  
 1204 **134**:509-520.
- 1205 Park, D. S., X. Feng, S. Akiyama, M. Ardiyani, N. Avendaño, Z. Barina, B. Bärtschi, M. Belgrano, J.  
 1206 Betancur, R. Bijmoer, A. Bogaerts, A. Cano, J. Danihelka, A. Garg, D. E. Giblin, R. Gogoi, A.  
 1207 Guggisberg, M. Hyvärinen, S. A. James, R. J. Sebola, T. Katagiri, J. A. Kennedy, T. S. Komil, B.  
 1208 Lee, S. M. L. Lee, D. Magri, R. Marcucci, S. Masinde, D. Melnikov, P. Mráz, W. Mulenko, P.  
 1209 Musili, G. Mwachala, B. E. Nelson, C. Niezgodá, C. Novoa Sepúlveda, S. Orli, A. Paton, S.  
 1210 Payette, K. D. Perkins, M. J. Ponce, H. Rainer, L. Rasingam, H. Rustiami, N. M. Shiyan, C. S.  
 1211 Bjorå, J. Solomon, F. Stauffer, A. Sumadijaya, M. Thiébaud, B. M. Thiers, H. Tsubota, A.  
 1212 Vaughan, R. Virtanen, T. J. S. Whitfeld, D. Zhang, F. O. Zuloaga, and C. C. Davis. 2023. The  
 1213 colonial legacy of herbaria. *Nature Human Behaviour* **7**:1059-1068.
- 1214 Pearson, K. D., G. Nelson, M. F. J. Aronson, P. Bonnet, L. Brenskelle, C. C. Davis, E. G. Denny, E. R.  
 1215 Ellwood, H. Goëau, J. M. Heberling, A. Joly, T. Lorieul, S. J. Mazer, E. K. Meineke, B. J.  
 1216 Stucky, P. Sweeney, A. E. White, and P. S. Soltis. 2020. Machine Learning Using Digitized  
 1217 Herbarium Specimens to Advance Phenological Research. *BioScience* **70**:610-620.
- 1218 Prata, E. M. B., C. Sass, D. P. Rodrigues, F. M. C. B. Domingos, C. D. Specht, G. Damasco, C. C. Ribas,  
 1219 P. V. A. Fine, and A. Vicentini. 2018. Towards integrative taxonomy in Neotropical botany:  
 1220 disentangling the *Pagamea guianensis* species complex (Rubiaceae). *Botanical Journal of the*  
 1221 *Linnean Society* **188**:213-231.
- 1222 Guillot G, Santos F. 2009. A computer program to simulate multilocus genotype data with spatially  
 1223 autocorrelated allele frequencies. *Molecular Ecology Resources* **9**: 1112-1120.
- 1224 Richard, K. R., T. S. Harlan, T. Barbara, L. A. Prather, A. M. James, P. L. Laura, C. M. Lucas, and J. F.  
 1225 Carolyn. 2019. Herbarium Practices and Ethics, III. *Systematic Botany* **44**:7-13.
- 1226 Sapes, G., L. Schroeder, A. Scott, I. Clark, J. Juzwik, R. A. Montgomery, J. A. Guzmán Q, and J.  
 1227 Cavender-Bares. 2024. Mechanistic links between physiology and spectral reflectance enable  
 1228 previsual detection of oak wilt and drought stress. *Proceedings of the National Academy of*  
 1229 *Sciences* **121**:e2316164121.
- 1230 Serbin, S. P., A. Singh, B. E. McNeil, C. C. Kingdon, and P. A. Townsend. 2014a. Spectroscopic  
 1231 determination of leaf morphological and biochemical traits for northern temperate and boreal tree  
 1232 species. *Ecological Applications* **24**:1651-1669.
- 1233 Serbin, S. P., A. Singh, B. E. McNeil, C. C. Kingdon, and P. A. Townsend. 2014b. Spectroscopic  
 1234 determination of leaf morphological and biochemical traits for northern temperate and boreal tree  
 1235 species. *Ecological Applications* **7**:1651-1669.
- 1236 Serbin, S. P., and P. A. Townsend. 2020. Scaling functional traits from leaves to canopies. *in* J. Cavender  
 1237 Bares, G. JA, and P. A. Townsend, editors. *Remote Sensing of Plant Biodiversity*. Springer, New  
 1238 York.
- 1239 Shah, T. 2023. *The Herbarium Handbook*. Kew Publishing.
- 1240 Shipley, B., M. Belluau, I. Kuhn, N. A. Soudzilovskaia, M. Bahn, J. Penuelas, J. Kattge, L. Sack, J.  
 1241 Cavender-Bares, W. A. Ozinga, B. Blonder, P. M. van Bodegom, P. Manning, T. Hickler, E.  
 1242 Sosinski, V. D. Pillar, V. Onipchenko, and P. Poschlod. 2017. Predicting habitat affinities of plant  
 1243 species using commonly measured functional traits. *Journal of Vegetation Science* **28**:1082-1095.
- 1244 Sims, D. A., and J. A. Gamon. 2002. Relationships between leaf pigment content and spectral reflectance  
 1245 across a wide range of species, leaf structures and developmental stages. *Remote Sensing of*  
 1246 *Environment* **81**:337-354.

- 1247 Soltis, P. S. 2017. Digitization of herbaria enables novel research. *Am J Bot* **104**:1281-1284.
- 1248 Sousa da Silva, G., and M. J. G. Hopkins. 2024. Utilização da espectroscopia do infravermelho próximo
- 1249 (NIRS) como ferramenta na discriminação de espécies do gênero *Dimorphandra* Schott
- 1250 (Leguminosae: Caesalpinioideae). *Scientia Plena* **20**.
- 1251 Stasinski, L., D. M. White, P. R. Nelson, R. H. Ree, and J. E. Meireles. 2021. Reading light: leaf spectra
- 1252 capture fine-scale diversity of closely related, hybridizing arctic shrubs. *New Phytologist* **n/a**.
- 1253 Stefanski, A., E. E. Butler, L. J. Williams, R. Bermudez, J. A. Guzmán Q., A. Larson, P. A. Townsend, R.
- 1254 A. Montgomery, J. Cavender-Bares, and P. Reich. 2025. All the light we cannot see: Climate
- 1255 manipulations leave short and long-term imprints in spectral reflectance of trees. *Ecology* **in**
- 1256 **press**.
- 1257 Thiers, B. M. 2024. Strengthening Partnerships to Safeguard the Future of Herbaria. *Diversity*.
- 1258 Türker-Kaya, S., and C. W. Huck. 2017. A Review of Mid-Infrared and Near-Infrared Imaging:
- 1259 Principles, Concepts and Applications in Plant Tissue Analysis. *Molecules*.
- 1260 Ustin, S. L., A. A. Gitelson, S. Jacquemoud, M. Schaepman, G. P. Asner, J. A. Gamon, and P. Zarco-
- 1261 Tejada. 2009. Retrieval of foliar information about plant pigment systems from high resolution
- 1262 spectroscopy. *Remote Sensing of Environment* **113**:S67-S77.
- 1263 Ustin, S. L., and S. Jacquemoud. 2020. How the Optical Properties of Leaves Modify the Absorption and
- 1264 Scattering of Energy and Enhance Leaf Functionality. Pages 349-384 *in* J. Cavender-Bares, J. A.
- 1265 Gamon, and P. A. Townsend, editors. *Remote Sensing of Plant Biodiversity*. Springer
- 1266 International Publishing, Cham.
- 1267 Ustin, S. L., S. Jacquemoud, and Y. Govaerts. 2001. Simulation of photon transport in a three-
- 1268 dimensional leaf: implications for photosynthesis. *Plant, Cell & Environment* **24**:1095-1103.
- 1269 Ustin, S. L., D. A. Roberts, J. A. Gamon, G. P. Asner, and R. O. Green. 2004. Using Imaging
- 1270 Spectroscopy to Study Ecosystem Processes and Properties. *BioScience* **54**:523-534.
- 1271 Vasconcelos, C. C., M. U. Adrianzén, J. L. C. Camargo, and M. H. Terra-Araujo. 2020. *Pouteria*
- 1272 *kossmanniae* (Sapotaceae): a new species from Central Amazonia, Brazil. *Phytotaxa* **447** 265–
- 1273 275.
- 1274 Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the
- 1275 concept of trait be functional! *Oikos* **116**:882-892.
- 1276 Wagner, E. P., J. Merz, and P. A. Townsend. 2019. EcoSIS: A Spectral Library and the Tools to Use It.
- 1277 American Geophysical Union, Fall Meeting 2019, abstract #B11F-2396
- 1278 **2019AGUFM.B11F2396W**.
- 1279 Wang, R., J. A. Gamon, and J. Cavender-Bares. 2022. Seasonal patterns of spectral diversity at leaf and
- 1280 canopy scales in the Cedar Creek prairie biodiversity experiment. *Remote Sensing of*
- 1281 *Environment* **280**:113169.
- 1282 Wang, Z., A. Chlus, R. Geygan, Z. Ye, T. Zheng, A. Singh, J. J. Couture, J. Cavender-Bares, E. L.
- 1283 Kruger, and P. A. Townsend. 2020. Foliar functional traits from imaging spectroscopy across
- 1284 biomes in eastern North America. *New Phytologist* **228**:494-511.
- 1285 Wang, Z., J.-B. Féret, N. Liu, Z. Sun, L. Yang, S. Geng, H. Zhang, A. Chlus, E. L. Kruger, and P. A.
- 1286 Townsend. 2023. Generality of leaf spectroscopic models for predicting key foliar functional
- 1287 traits across continents: A comparison between physically- and empirically-based approaches.
- 1288 *Remote Sensing of Environment* **293**:113614.
- 1289 Webster, M. S. 2017. *The Extended Specimen: Emerging Frontiers in Collections-Based Ornithological*
- 1290 *Research* (1st ed.). CRC Press.
- 1291 Wenk, E. H., H. Sauquet, R. V. Gallagher, R. Brownlee, C. Boettiger, D. Coleman, S. Yang, T. Auld, R.
- 1292 Barrett, T. Brodribb, B. Choat, L. Dun, D. Ellsworth, C. Gosper, L. Guja, G. J. Jordan, T. Le
- 1293 Breton, A. Leigh, P. Lu-Irving, B. Medlyn, R. Nolan, M. Ooi, K. D. Sommerville, P. Veski, M.
- 1294 White, I. J. Wright, and D. S. Falster. 2024. The AusTraits plant dictionary. *Scientific Data*
- 1295 **11**:537.

1296 White, D. M., J. Cavender-Bares, C. Davis, J. A. G. Q., S. Kothari, J. Robles, and J. E. Meireles. 2025.  
1297 Seeing herbaria in a new light: leaf reflectance spectroscopy unlocks predictive trait and  
1298 classification modeling in plant biodiversity collections. *EcoEvoRxiv*:1-41.

1299 Wieczorek, J., D. Bloom, R. Guralnick, S. Blum, M. Döring, R. Giovanni, T. Robertson, and D. Vieglais.  
1300 2012. Darwin Core: an evolving community-developed biodiversity data standard. *Plos One*  
1301 7:e29715.

1302 Williams, L. J., J. Cavender-Bares, P. A. Townsend, J. J. Couture, Z. Wang, A. Stefanski, C. Messier, and  
1303 P. B. Reich. 2021. Remote spectral detection of biodiversity effects on forest biomass. *Nature*  
1304 *Ecology & Evolution* 5:46-54.

1305 Willis, C. G., E. R. Ellwood, R. B. Primack, C. C. Davis, K. D. Pearson, A. S. Gallinat, J. M. Yost, G.  
1306 Nelson, S. J. Mazer, N. L. Rossington, T. H. Sparks, and P. S. Soltis. 2017. Old Plants, New  
1307 Tricks: Phenological Research Using Herbarium Specimens. *Trends in Ecology & Evolution*  
1308 32:531-546.

1309 Willis, C. G., B. Ruhfel, R. B. Primack, A. J. Miller-Rushing, and C. C. David. 2008. Phylogenetic  
1310 patterns of species loss in Thoreau’s woods are driven by climate change. *Proceedings of the*  
1311 *National Academy of Sciences of the United States of America* 105:17029 - 17033.

1312 Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T.  
1313 Chapin, J. H. Cornelissen, and M. Diemer. 2004. The worldwide leaf economics spectrum.  
1314 *Nature* 428:821-827.

1315 Zhang, J., M. Wang, K. Yang, Y. Li, Y. Li, B. Wu, and Q. Han. 2022. The New Hyperspectral Analysis  
1316 Method for Distinguishing the Types of Heavy Metal Copper and Lead Pollution Elements. *Int J*  
1317 *Environ Res Public Health* 19.

1318

1319

1320

1321

1322 **Supplemental Tables**

1323 Table S1. Previous studies using dry-leaf spectra.

1324

<b>Application (dry leaves)</b>	<b>Spectral Range</b>	<b>Author</b>
C, N, P, K, micronutrients, leaf pigments, d13C (see Fig. 1)	VIS-NIR: 400-2500 nm	Elvidge 1990, Fourty et al. 1996, Serbin et al. 2014, Prananto et al. 2020, Chlus and Townsend 2022, Chen et al. 2002, Kothari et al. 2023, 2024, Wang et al. 2023, Kühn et al. 2025
Nutrient contents and leaf traits	NIR: 1000-2500 nm	Prananto et al. 2021, Costa et al. 2018, Kothari et al. 2024
Species identification	VIS-NIR: 400-2,500 nm	Meireles et al. 2020; Vasconcelos et ali. 2025
Species identification	NIR: 1.000-2.500nm	Durgante et al. 2013; Lang et al. 2015;Paive et al. 2021; Vasconcelos et al. 2020, 2021
Species identification	IR: 1.250-25.000nm	Kim et al. 2004; Krajsek et al. 2008
Species characterization and chemical properties	Thermal IR: 2.5 - 20 $\mu$ m	Elvidge 1990; Richardson et. al. 2000

1325

1326