Bryophyte specimen organization and storage systems: A comparative assessment of staff practices and user preferences

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Abstract. Discussions of curation practices for bryophyte collections have a long history in the literature dating back to the 19th and 20th centuries. This study aims to 1) document and synthesize the range of bryophyte storage and organization systems staff report using in European and North American herbaria, as well as the rationale behind these practices; 2) compare/contrast these practices and rationale with the curation preferences and rationale of active herbarium users; and 3) facilitate further discussion regarding practices for curating bryophyte collections. We collected survey data regarding staff curation practices at and user curation preferences for bryophyte collections in Europe and North America. We used regression models and thematic analysis to analyze our quantitative data and qualitative data, respectively. We found that institutional demographics, such as geographic location, institution type, and total herbarium size are significant predictors of bryophyte specimen storage and organization practices, and that user demographics, such as age, active bryology research agenda, and current primary title were significant predictors of the storage preferences of herbarium users. The most common theme that emerged in the practice/preference explanations of staff members and herbarium users was *convenience/accessibility*. Other prevalent themes in staff and user explanations for their bryophyte curation practices/preferences include *physical factors*, *inherited tradition*, *lack of expertise,* and *phylogenetic/taxonomic concerns*. Our findings also suggest the context in which members of the bryological community operate plays a significant role in shaping individuals' curation practices/preferences, including both institutional and user demographics. We conclude by offering a discussion of recommendations for bryophyte specimen storage and organization at herbaria.

Keywords. Bryophyte collections, curation practices, herbaria, natural history collections, survey research.

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In comparison to vascular plant herbaria, best practices for storing and organizing bryophyte herbaria are not as well-documented (British Columbia Ministry of Forests 1996; Savile 1962), and methods used in preparing vascular plant specimens are not directly transferable to the curation of bryophyte specimens (British Columbia Ministry of Forests 1996; Fish 1999; Smith 1965; Victor et al. 1994). For instance, while vascular plants are often mounted flat onto a standard herbarium sheet, Fish (1999) thought that affixing bryophytes directly to paper with such substances could irreversibly damage the specimens. Meanwhile, the British Columbia Ministry of Forests (1996) and Gilbert (1904) argued that storing bryophytes attached directly to sheets can also make them more challenging to examine. Similarly, while vascular plant specimens are typically stored horizontally (Bridson & Forman 1998), bryophytes in packets can be stored either horizontally or vertically with the packets either being attached to standard herbarium sheets or stored loose (Glime & Wagner 2013; Horton 2003; Salick & Solomon 2014; Savile 1962). In terms of their organization, vascular plant specimens are most often arranged phylogenetically by family or genus, whereas bryophytes are more

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often arranged alphabetically by genus (British Columbia Ministry of Forests 1996) due to the perception that vascular plant phylogenies are more stable than bryophyte phylogenies (Smith 1965; Tocci 2019). In more recent years, some bryophyte collections have begun to adopt phylogenetic and/or hybrid organization systems (Glime & Wagner 2013; Tocci 2019). Given these important differences in storage and organization systems, a thorough review of the herbarium curation practices literature is warranted in order to better understand the unique history of curating bryophyte specimens.

Curation Methods in Bryophyte Collections: A Literature Review

With regard to bryophyte collections specifically, methods for storing (mounting) bryophyte specimens have been a consistent topic of conversation in the curation literature since the mid- to late-1800s. Nave & Spicer (1867) reported attaching some species of bryophytes directly to paper (see also Smith 1965). Grout (1900), by comparison, asserted that "the most artistic way of mounting mosses is to glue them to small cards" (p. 7), while simultaneously conceding that gluing bryophytes directly to full herbarium sheets may prove "more satisfactory" (p. 7; see also Chemberlain 1903; Franks 1965). Yet, it is also Grout (1900) who first documented the emergence of a third storage option for bryophyte specimens in the literature: packets (envelopes) attached to standard herbarium sheets. Over the course of the next six years, *The Bryologist* published a series of opinion pieces discussing how best to attach the packets with Grout (1900), Chemberlain (1903), Gilbert (1904), and Collins (1906) supporting the use of glues/adhesives, pins, pockets/brackets, and gummed wafers, respectively. While the use of pins or gummed wafers for affixing specimen packets to herbarium sheets received little to no additional attention in the subsequent bryophyte curation literature, Dore (1953) and Savile (1962) both reported finding the pockets/brackets technique to be a suitable means for storing bryophytes. One of the less often mentioned storage techniques is offered by Ogden (1945), who suggested that bryophyte packets should be constructed of transparent material, at least in part, so that the specimen itself is more visible to those using the collections. Despite advocating for a different type of packet, Ogden (1945) remained committed to the idea that packets should be attached to a standard herbarium sheet, albeit with staples instead, a sentiment echoed 20 years later by Schuster (1966).

The bryophyte curation literature first mentioned storing bryophytes in loose packets filed vertically in boxes or drawers in the mid-20th century. In their report relaying the findings of a special committee of the Sullivant Moss Society that was tasked with surveying its membership on best practices for curating bryophyte collections, Flowers et al. (1945) explicitly recommended filing packets "in boxes, card catalog fashion" (p. 199). Moreover, they asserted that, should an institution elect to attach packets to sheets, they should limit the number of specimens to only one per sheet. Gier (1952) appeared to take both of the special committee's suggestions to heart, reporting that he attached packets to smaller pieces of herbarium paper and then filed the specimens upright in boxes. Fosberg (1946) and Savile (1962), by comparison, took a more neutral stance as to which storage technique is best, remarking that both methods remain common in bryophyte collections. By the mid- to late 1990s, bryophyte storage preferences again shifted away from packets attached to sheets with Victor et al. (1994), British Columbia Ministry of Forests (1996), and Fish (1999) all indicating that bryophyte specimens should be stored upright in boxes or drawers. One notable exception to what appears to be a burgeoning consensus on best practices for bryophyte storage methods in the literature was Bridson and Forman (1998), who argued that large herbaria store their specimens in packets attached to sheets while also noting that other institutions stored loose packets vertically instead. Several publications from the early 2000s concurred with Bridson & Forman's assessment of the most common storage methods in bryophyte collections, including Horton (2003), Glime & Wagner (2013), Salick & Solomon (2014), and Smith & Chinnapa (2015), who concluded that attaching packets to sheets and filing loose packets upright in boxes or drawers both remain suitable storage options for most bryophyte specimens.

How best to organize (arrange) bryophyte collections has received even less attention in the literature. One notable exception, however, were the recommendations for moss preparation and care put forth by a special committee of the Sullivant

Moss Society in 1945. In this paper, Flowers et al. (1945) indicated that bryophyte specimens may be arranged phylogenetically (systematically) by family and genus or, alternatively, alphabetically by genus. They then recommended arranging species alphabetically within each genus, regardless of the system used to organize the specimens at the family and/or genus levels. Flowers et al. (1945) also suggested that one should sort the specimens in a given species group by geography. Several decades later, Glime & Wagner (2013) affirmed that both phylogenetic and alphabetical organization systems remain popular for bryophyte collections while indirectly suggesting that hybrid systems, which consist of a combination of phylogenetic and alphabetical sorting, are becoming more widespread (see also Bridson & Forman 1998). In a notable departure from the 1945 special committee recommendations, British Columbia Ministry of Forests (1996) stated that bryophytes "are often filed alphabetically by genera without the familial arrangement used for vascular plants" (p. 26). Tocci (2019), by contrast, offered a different perspective as to whether families are utilized in the organization of bryophyte specimens, suggesting that some collections still organize specimens alphabetically by family and then genus.

While this comprehensive literature review provides many valuable insights into the most common bryophyte curation methods (storage/organization) across space and time, the vast majority of these publications, particularly those from the 19th and 20th centuries, could be characterized as anecdotal opinion pieces conveying a *single* individual's preferences for curating bryophyte specimens (e.g., Collins 1906; Chemberlain 1903; Clarke 1903; Gilbert 1904; Grout 1900; Ogden 1945). The literature reviewed above reveals that uniform curation standards for bryophyte collections have yet to emerge in the bryological community with some members preferring certain curation practices over others. Therefore, this study aims to: 1) document and synthesize the range of bryophyte storage and organization systems staff report using in European and North American herbaria, as well as the rationale behind these practices; 2) compare/contrast these practices and rationale with the curation preferences and rationale of active herbarium users; and 3) facilitate further discussion regarding the curation of bryophyte collections.

Materials & Methods

Study population. In 2016, there were 2,962 active herbaria in the world, housing an estimated 381,308,064 plant specimens (Thiers 2017). Just over half of these institutions (51.1%) were located in one of two geographic regions—Europe or North America—where an estimated 69.9% of the world's herbarium specimens are housed (Thiers 2017). As such, our study population includes individuals working at European and North American herbaria ('herbarium staff'), as well as individuals who utilize bryophyte collections at these 1,487 herbaria ('herbarium users').

In 2016, there were approximately 4,882 staff members at the 1,487 active European and North American herbaria (Thiers 2017), which comprises our 'herbarium staff' study population. Using the 2016 staffing estimates from Index Herbariorum, the 695 European herbaria reported an average of 3.9 staff members per herbarium, whereas North America's 792 herbaria reported an average of 2.7 staff members per herbarium (Thiers 2017). European herbaria housed a total of 176,631,607 specimens with 254,147 specimens per institution on average, while North American herbaria contained 90,232,239 specimens with an average number of 113,930 specimens per institution in 2016 (Thiers 2017).

With regard to herbarium users, there are approximately 1,300 bryologists worldwide who subscribe to the Bryonet-L listserv (J. Glime, pers. comm., 16 March 2017). This is our best estimate of the number of bryologists worldwide since the majority of people with bryological research interests likely subscribe. Given that European and North American herbaria are home to 266,863,846 specimens, we assume that many (if not a majority) of these bryologists have utilized, are currently utilizing, or may one day utilize bryophyte specimens held by these institutions. As such, these bryologists constitute the 'herbarium users' portion of our study population.

Data collection and participant recruitment. We collected data using two surveys: one for staff working with bryophyte herbaria and the other for users of bryophyte herbaria. Both survey instruments consisted of a mixture of close-ended (predefined response categories) and open-ended (free response) questions. Our staff survey included a

total of 44 content questions divided into four subsections: a) respondent demographics, b) herbarium basics, c) specimen organization and storage practices, and d) specimen loan information. Our herbarium user survey was of a similar length (47 content questions) but divided into five subsections: a) respondent demographics, b) bryological interests and training, c) bryophyte collection practices, d) herbarium visit preferences, and e) bryophyte loan practices. These two survey instruments, as well as our other study protocols, were reviewed and approved by the Institutional Review Board (IRB) at Hobart and William Smith Colleges (Application #17-47).

Participant recruitment for the staff and user surveys began in 2017 and 2018, respectively, with both surveys closing on 31 August 2019. These surveys were circulated on two professional listservs to which a large number of herbarium staff and users subscribe, Herbaria (https://www.nacse.org/mailman/listinfo/herbaria; sponsored by the American Society of Plant Taxonomists and the Society of Herbarium Curators) and Bryonet-L (https://bryology.org/ bryonet/; sponsored by the International Association of Bryologists). We also recruited study participants via social media, during in-person site visits to herbaria in North America and Europe, and while attending scientific conferences such as the Botanical Society of America annual meeting.

Data analysis. In preparation for our analyses, we first removed duplicate staff responses submitted for the same Index Herbariorum (IH) code, retaining only the most recent survey response. In those instances in which a staff member reported that their institution housed more than one herbarium (with multiple IH codes), we split the data into separate responses, each associated with one IH code. With regard to incomplete surveys, we elected to retain these responses in our dataset as respondents could skip any question(s) while completing the surveys.

Next, we began to thematically analyze our survey data, focusing primarily on study participant responses to our open-ended survey questions. Thematic analysis is "a method for identifying, analyzing, and reporting patterns (themes)" (Braun & Clarke 2006, p. 79) across a dataset. We first read through participant responses, making note of recurrent words, phrases, and ideas. Once we had a sense of potential patterns in our dataset, we began qualitatively coding the data using an inductive approach as "a way of opening up [further] avenues of inquiry" (Emerson et al. 2011, p. 175). We continued coding our survey data until no new qualitative codes emerged. Having reached a saturation point in the coding process, we then transitioned into a code consolidation phase in which we combined similar codes into larger categories called 'themes' (**Table 1**). For instance, when coding staff explanations for their preferred organization system(s) for arranging bryophyte specimens, responses such as "easier for non-specialist curatorial staff," "lack of knowledge of phylogenetic relationships," and "we have no active bryologist on staff" were coded under the theme of *lack of expertise* (**Table 1**). Often a single response contained more than one idea and thus was coded under more than one theme. We then sorted our survey data by theme in order to identify "the most salient 'constellations' of meanings" (Neuendorf, 2019, p. 213, citing Joffe 2012) evident within each thematically coded set of responses. With the most meaningful patterns within the data now identified, we calculated the prevalence (frequency) of each theme across our dataset, paying specific attention to the frequencies at which each theme occurred in herbarium staff versus user responses to our survey questions. In this final phase of our qualitative analyses, we also determined the keyness (utility) of each theme in addressing our research questions. Comparative analyses between theme frequencies in the herbarium staff and user explanations for their storage and organization practices/preferences were carried out using chi-squared tests in R 3.0.2 (R Core Team 2020) and RStudio 1.0.143 (RStudio Team 2020).

In preparation for our quantitative analyses, we converted participant responses to our open-ended survey questions regarding organization and storage practices/preferences into quantitative counts by placing them into categories based on the content of their answers. We grouped responses for organization practices/preferences based whether or not bryophyte specimens were sorted 1) into taxonomic divisions (i.e., mosses, liverworts, and hornworts); 2) alphabetically or phylogenetically at the family and/or genus levels; and 3) geographically above the family and/or below the genus levels. While our storage practice/preference questions were not open-ended, we also grouped the responses to these

Table 1. Descriptions of the themes evident in staff and herbarium users' explanations of their bryophyte curation practices/preferences.

Theme	Description
Analogous curation methods	Curation of bryophyte specimens in a manner similar to how other plant groups (e.g., lichens and/or vascular plants) are curated
Bryophyte collection size	Matters related to the size of a given institution's bryophyte collection(s)
Convenience/accessibility	Matters related to the convenience and/or ease with which specimens can be accessed
Copied/familiar/learned	Curation preferences developed during the course of one's education and/or career
Geographic significance	Concerns related to the geographic significance of specimens
Inherited tradition	Curation practices established by and/or preferred by previous staff members at a given institution
Lack of expertise	A lack of institutional and/or personal expertise related to bryophytes
Mixup/loss concerns	Concerns related to specimens being mixed up and/or lost while being used by herbarium staff and/or users
Phylogenetic/taxonomic concerns	Concerns related to the need to annotate and/or rearrange specimens as the result of nomenclature changes, shifting bryophyte phylogenies, etc.
Physical factors	Related to the amount and/or quality of the physical resources (e.g., space) an institution has to store its bryophyte specimens
Resource constraints	Concerns related to a dearth of resources such as the number of available staff, how staff time is allocated, and/or money to purchase new cabinetry, folders, packets, etc.
Specimen significance	Concerns related to the significance of the specimens
Specimen wear & tear	Concerns related to the physical integrity of bryophyte specimens such as those related to potential damage from being compressed while being stored
Speed/efficiency	Matters related to the speed at and/or efficiency with which specimens can be handled

survey questions into the following categories: 1) whether specimens placed in packets are stored loose or attached to full herbarium sheets and 2) whether those specimens placed in loose packets are stored vertically or horizontally.

We then analyzed these quantitative data using logistic regression models for binary response variables. With regard to bryophyte curation practices of herbarium staff, we examined the influence of the main effects of geographic location (binary), total herbarium size (continuous), bryophyte collection size (continuous), institution type (categorical), and affiliation type (categorical) on the response variables of specimen organization and storage system practices in bryophyte collections. For herbarium user curation preferences, the main effects of duration of bryological interest (continuous), age in years (ordered categorical), formal training in bryology (ordered categorical), current primary title (categorical), and current bryology research (binary) on the response variables for organization and storage systems used in the bryophyte collections they visit were examined. Starting with a full model, which included all of the predictor variables outlined above, we then ran stepwise regression algorithms in R and RStudio to determine which variables had a significant effect on the response variables.

Results

Sample population. We received 117 responses from staff at herbaria in North America and Europe and 85 responses from bryophyte herbaria users around the world. Once we removed duplicate responses from our staff dataset, we had responses from 94 staff members representing 96 unique herbaria to analyze. While some respondents opted to skip a question or two on the survey, we included all 85 herbarium user responses in our dataset. Due to the ability of respondents to skip questions, the numbers reported below often diverge from the total number of respondents listed above.

For the staff survey, 48 responses were from North American herbaria and 48 were from European herbaria. The vast majority of the North American herbaria were located in the United States ($N = 43$). By comparison, European herbaria were broadly distributed across continental Europe and the British Isles. We used data from Index Herbariorum (http://sweetgum.nybg.org/science/ih/) to classify the herbaria based on total herbarium size, institution type, and affiliation type (Thiers 2017). Total herbarium size, which includes the total number of specimens from all plant and fungal groups, ranged from 5,000 to 7,800,000 specimens (**Fig. 1A**), whereas bryophyte collection sizes ranged from 500 to 800,000 specimens. Among these

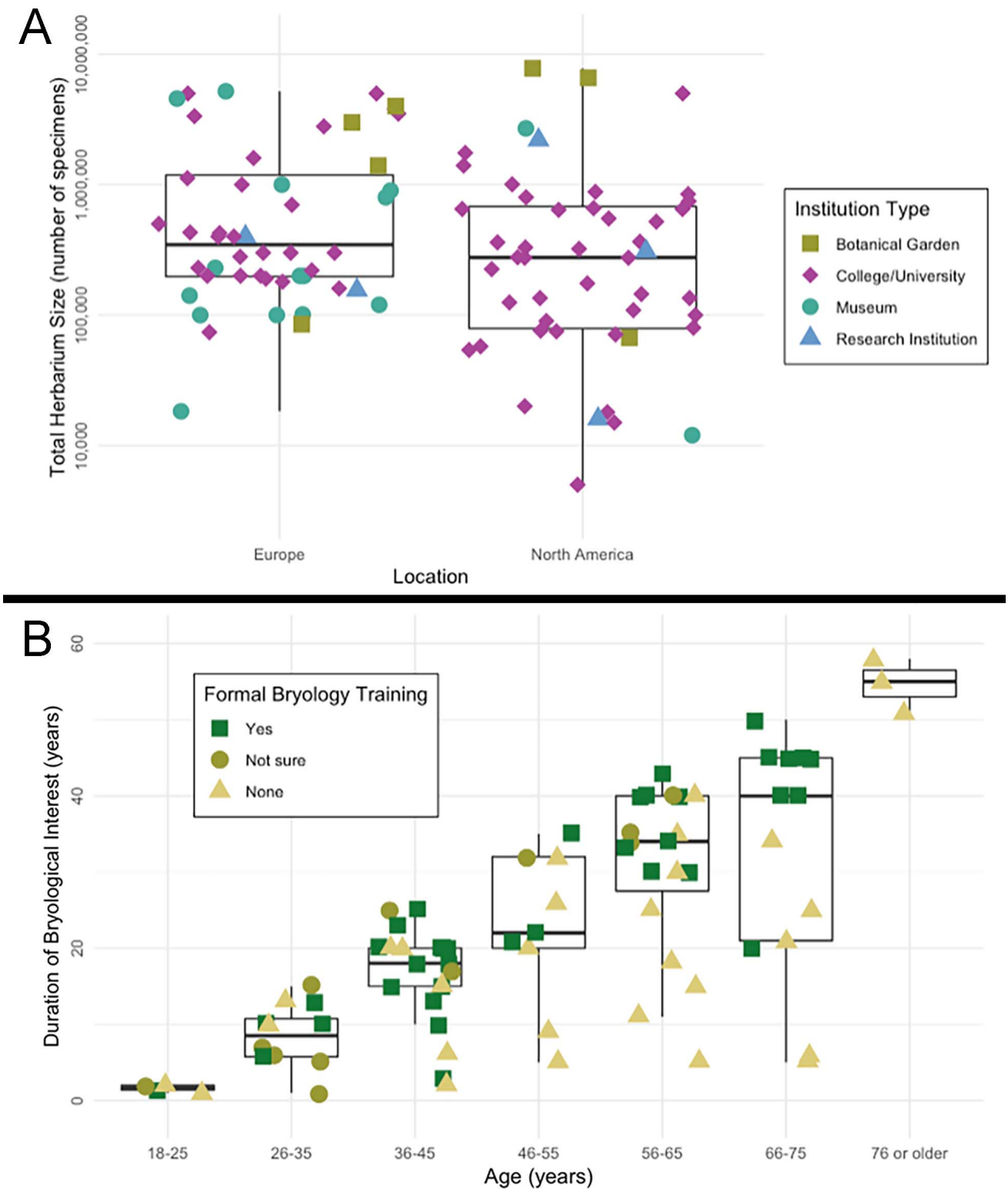

Figure 1. Sample populations from our surveys of herbarium staff and users. **A.** Institution type and total herbarium size, which includes the number of specimens from all plant and fungal groups, are based on data from Index Herbariorum (Thiers 2017). Forty-eight herbaria were located in North America and 48 were located in Europe. Institution types included botanical gardens ($N = 7$), colleges/universities ($N = 68$), museums ($N = 16$), and research institutions ($N = 5$). **B.** Users classified themselves into one of the following age cohorts: 18–25, 26–35, 36–45, 46–55, 56–65, 66–75, and 76 years or older. Respondents also reported their duration of bryological interest from 1 to 58 years. Thirty-nine respondents indicated that they have had formal bryology training with 12 indicating they were unsure, and 30 indicating they had no formal bryology training.

Table 2. Majority bryophyte storage practices reported by staff for the herbaria where they work ($N = 91$) and bryophyte storage preferences reported by herbarium users for the institutions whose collections they visit ($N = 67$).

Storage system	Frequency of staff practices	Frequency of user preferences
Direct to sheet	1.1% ($N = 1$)	—
A single packet attached to a full herbarium sheet	4.4% ($N = 4$)	—
Multiple packets attached to a full herbarium sheet	20.9% ($N = 19$)	14.9% ($N = 10$)
Loose packets stored vertically in filing cabinets	9.9% ($N = 9$)	7.5% ($N = 5$)
Loose packets stored vertically in boxes placed in herbarium cabinets	40.7% ($N = 37$)	44.8% ($N = 30$)
Loose packets stored horizontally in palm folders	14.3% ($N = 13$)	19.4% ($N = 13$)
Other	8.8% ($N = 8$)	13.4% ($N = 9$)

herbaria, the institution types included are botanical gardens ($N = 7$), colleges/universities ($N = 68$), museums ($N = 16$), and research institutions ($N = 5$) with a diversity of affiliation types including city ($N = 9$), government ($N = 23$), national/federal ($N = 11$), private ($N = 12$), and state/provincial ($N = 41$).

For the user survey, 38 of the respondents were from North America, 22 from Europe, 4 from outside of North America and Europe, and 21 did not respond to this question. The vast majority of the North American responses were from the United States ($N = 32$). European responses were broadly distributed across continental Europe and the British Isles. Thirty-four respondents identified as female, 50 as male, and one as non-binary. Respondents classified themselves into one of the following age cohorts: 18–25 ($N = 4$), 26–35 ($N = 12$), 36–45 ($N = 22$), 46–55 ($N = 10$), 56–65 ($N = 19$), 66–75 ($N = 14$), 76 years or older ($N = 4$; **Fig. 1B**). Respondents reported their duration of bryological interest, which ranged from 1 to 58 years with an average of 22.4 years (**Fig. 1B**). Thirty-nine respondents indicated that they have had formal bryology training with 12 indicating they were unsure and 30 indicating they had not had formal bryology training (**Fig. 1B**). Seventy respondents provided details on their current primary title. Respondents included people who self-identified as collections managers/curators ($N = 24$), postdocs ($N = 5$), professors/lecturers ($N = 16$), professional society members ($N = 1$), researchers ($N = 16$), students ($N = 7$), or volunteers ($N = 1$). Sixty-nine respondents reported they are currently affiliated with an institution, while 15 individuals reported being unaffiliated at present. Respondents indicated diverse bryological interests with 46 interested in all groups of bryophytes, 11 in both mosses and liverworts, 1 in both liverworts and hornworts, 15 in mosses only, and 8 in liverworts only. Of the 85 respondents to the user survey, 70 respondents (82.4%) indicated that they have an active bryological research agenda.

Specimen storage: Herbarium practices reported by staff. Staff members indicated the storage method for the majority of the bryophyte specimens at their herbarium with the most frequently reported method being loose packets that are kept vertically in boxes placed in herbarium cabinets (**Table 2**). Fewer staff members indicated that they place the majority of their bryophyte specimens in packets that are attached to a full herbarium sheet with multiple packets per sheet and an even lower frequency of staff reported that their herbarium uses loose packets that are filed horizontally in palm folders as its majority bryophyte storage method (**Table 2**). We analyzed these data to determine which institutional demographics are the strongest predictors of bryophyte specimen storage practices. Examining the predictors for collections that store bryophytes in packets attached to full herbarium sheets ($N = 23$) versus those that store specimens in loose packets ($N = 59$; binary response variable), we determined that total herbarium size, which includes the total number of specimens from all plant and fungal groups, was the strongest and only significant predictor in a full model ($F_{1, 63} = 4.07$, $P = 0.048$). Herbaria with specimens attached to sheets had a larger total herbarium size with an average of 1,553,791 specimens, whereas herbaria with specimens in loose packets were smaller with an average total herbarium size of 781,403 specimens (**Fig. 2A**).

Next, focusing on only the 59 herbaria that store bryophyte specimens in loose packets, we examined the predictors for whether they store these packets vertically ($N = 46$) versus horizontally ($N = 13$; binary response variable). In a full model, geo-

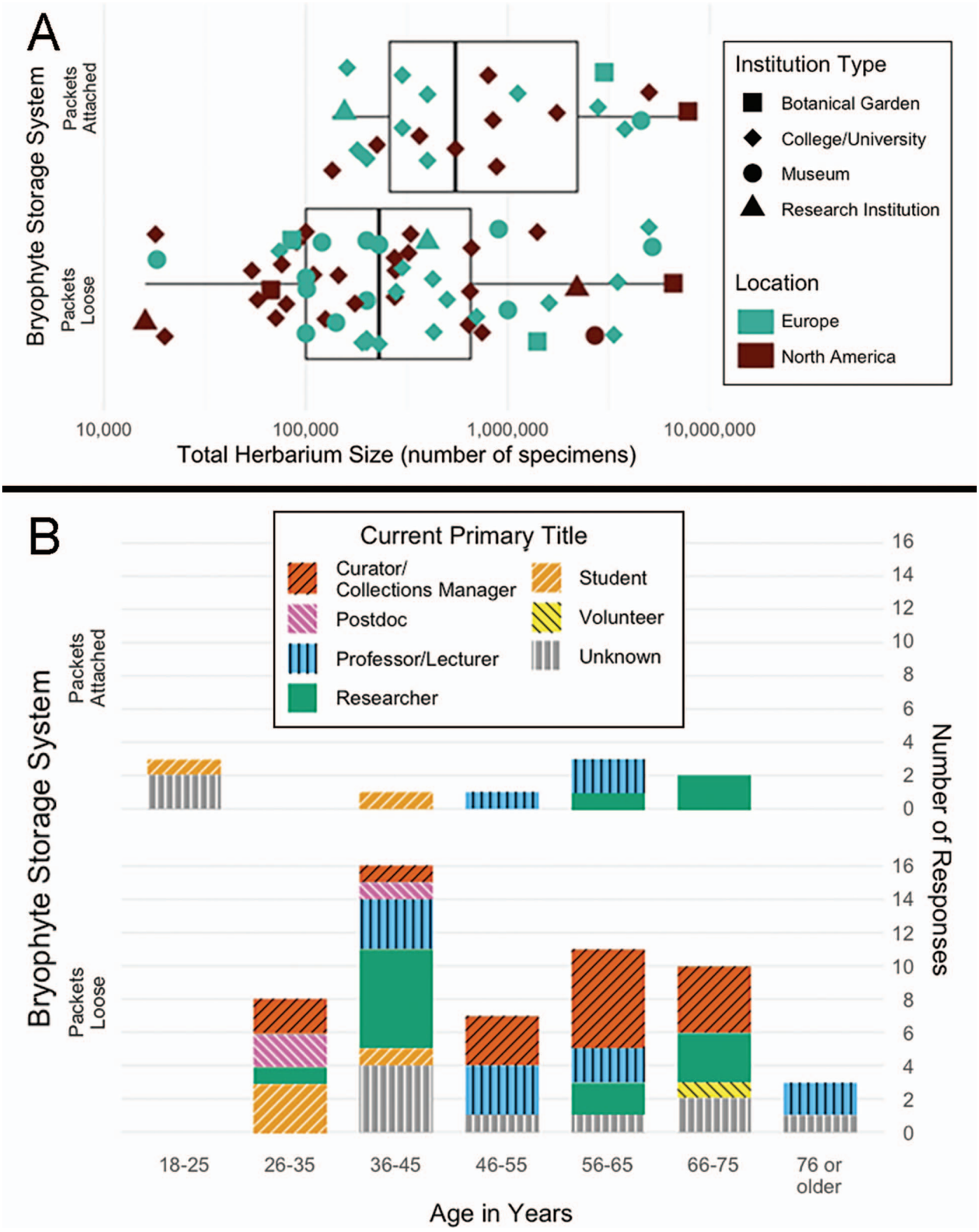

Figure 2. Bryophyte specimen storage systems. **A.** Practices reported by staff for their herbarium's majority storage system coded as either packets attached to full herbarium sheets or loose packets. Institution type is based on data from Index Herbariorum (Thiers 2017). **B.** Responses from bryophyte herbarium users regarding their preferences as to whether the bryophyte collections they visit store specimens in packets attached to full herbarium sheets versus loose. Respondents classified themselves into one of the following age cohorts: 18–25, 26–35, 36–45, 46–55, 56–65, 66–75, and 76 years or older and also reported their current primary title.

Table 3. A comparison of the frequency of themes observed in staff explanations for their herbarium's majority bryophyte storage method ($N = 85$) versus those evident in herbarium user explanations for their preferred bryophyte storage method ($N = 63$). Chi-squared tests examine whether are not there is a significant difference in the proportion of themes between the staff and user explanations for their bryophyte storage practices/preferences. Themes with statistically significant differences ($P < 0.05$) between the staff and user frequencies are in bold.

Theme	Staff frequency	Users frequency	Chi-squared	Degrees of freedom	p-value
Convenience/accessibility	**38.8%**	**82.5%**	**24.48**	**1**	**7.52E-07**
Physical factors	**31.8%**	**15.9%**	**4.06**	**1**	**0.044**
Inherited tradition	**30.6%**	**0.0%**	**21.31**	**1**	**3.90E-06**
Copied/familiar/learned	10.6%	17.5%	0.93	1	0.33
Specimen wear and tear concerns	10.6%	15.9%	0.49	1	0.48
Phylogenetic/taxonomic concerns	9.4%	9.5%	6.48E-31	1	1
Not sure/do not know	9.4%	0.0%	3.77	1	0.052
Analogous curation methods	8.2%	0.0%	3.77	1	0.052
Resource constraints	8.2%	3.2%	0.44	1	0.51
Speed/and efficiency	5.9%	11.1%	0.72	1	0.40
Mixup/loss concerns	3.5%	4.8%	4.21E-31	1	1
Specimen significance	1.2%	0.0%	6.79E-32	1	1
Geographic significance	0.0%	1.6%	0.023	1	0.88
Lack of expertise	0.0%	1.6%	0.023	1	0.88
Other	0.0%	1.6%	0.023	1	0.88

graphic location was the strongest and only significant predictor ($F_{1,\ 42} = 4.35$, $P = 0.043$). Herbaria located in North America store their loose bryophyte packets vertically at a higher frequency (93.1%), compared to Europe where only 63.3% of herbaria store their loose packets vertically.

We subsequently analyzed the themes evident in staff member explanations of why their herbarium stores the majority of its bryophyte specimens in the manner that it does. Of the 91 staff members who indicated how their herbarium stores the majority of its bryophyte specimens, 93.4% explained why they store bryophytes the way they do with a total of 12 themes observed in these explanations (**Table 3**). The average number of reasons an individual staff member provided in their bryophyte storage method explanations was 1.7 reasons with a range of one to five reasons per herbarium.

Across all storage types, the most common theme in staff explanations for their herbarium's majority bryophyte storage method was *convenience/accessibility* (**Table 3**). Nearly 70.0% of these 33 staff members discussed their herbarium's majority storage method in terms of bryophyte specimens to be "easy/easier" or "(more) convenient" to "access," "file," "handle," "manage," "reorganize," and/or "transfer." Notably, staff who reported storing bryophyte specimens in loose packets were more than twice as likely to cite *convenience/accessibility* in their written explanation for their herbarium's majority storage method than those who reported utilizing packets attached to sheets (44.1% versus 17.4%, respectively). Staff members who indicated that their herbarium places bryophyte specimens in loose packets stored vertically cited *convenience/accessibility* at a similar rate as staff who indicated that their herbarium places bryophyte specimens in packets that are stored horizontally (46.2% and 43.5%, respectively).

The second most frequent theme in staff explanations for their herbarium's bryophyte storage system was *physical factors* (**Table 3**). Among the 27 staff members who discussed *physical factors*, 63.0% described "space" as shaping their herbarium's storage approach with the majority of these respondents indicating that the storage system employed at their herbarium "save[d] space" and/or was otherwise more "efficient" than other possible storage methods. Meanwhile, 25.9% of these 27 staff members discussed how cabinetry influences their herbarium's majority bryophyte storage method, often specifically referencing "available cabinet[s]" as playing a role in how their institutions approach the storage of bryophyte specimens. Staff at herbaria that store bryophytes in packets attached to sheets and those at herbaria

that store such specimens in loose packets discussed *physical factors* at comparable frequencies (30.4% and 28.8%, respectively). On the other hand, the frequency at which staff working at herbaria that store bryophytes in loose packets vertically cited *physical factors* in their storage explanations exceeded those of staff whose herbarium's majority bryophyte storage method was loose packets stored horizontally (30.4% versus 23.1%, respectively).

The third most common theme in staff explanations for their herbarium's majority bryophyte storage method was *inherited tradition* (**Table 3**). A little more than a quarter of these 26 staff (26.9%) referenced a previous staff member who they viewed as being responsible for the majority bryophyte storage system currently in use at their herbarium. Just under half of staff explanations that we coded under the theme of *inherited tradition* (46.2%), by comparison, cited "tradition" and/or "history" as driving their herbarium's majority bryophyte storage practice, articulating sentiments such as "this is what was being used at the time," "[the storage system] predated my arrival," or "legacy/historical storage." Those staff who indicated that their herbarium stores the majority of its bryophyte specimens in packets attached to herbarium sheets cited *inherited tradition* as playing a role in shaping their storage approach at a slightly higher rate than those who reported that their herbarium utilizes a loose packet approach (34.8% versus 27.1%, respectively). Among the staff who reported that their herbarium stores bryophyte specimens in loose packets, those herbaria that store these packets vertically were slightly more likely to reference *inherited tradition* than their counterparts who store such packets horizontally (28.3% versus 23.1%, respectively).

Specimen storage: Herbarium user preferences for the herbaria they visit. Slightly more than half of herbarium users indicated a preference for storing bryophyte specimens in loose packets vertically in boxes stored in standard herbarium cabinets (**Table 2**). The second and third most commonly preferred storage methods (i.e., loose packets stored horizontally in palm folders and multiple attached bryophyte packets per herbarium sheet, respectively) were each preferred by less than one fifth of herbarium users (**Table 2**). Responses placed in the 'other' category included five herbarium users who described unique storage preferences for the herbaria they visit, as well as four users who reported preferences for more than one storage type (**Table 2**).

We then analyzed these data to determine what herbarium user demographics are the strongest predictors of their bryophyte storage preferences for herbaria they visit. We examined the predictors for user preferences for specimens in packets attached to full herbarium sheets ($N = 10$) versus loose packets ($N = 55$; binary response variable). We determined that current primary title ($F_{5,\ 38} = 6.74$, $P < 0.001$), active bryology research agenda ($F_{1,\ 38} = 5.11$, $P = 0.030$), and age in years ($F_{6,\ 38} = 4.88$, $P < 0.001$) were the strongest predictors in a full model (**Fig. 2B**). Users who preferred packets attached to full herbarium sheets often described their current primary title as student, researcher, or professor/lecturer, have an active bryology research agenda, and had an average age of 47.5 years. In comparison, users who preferred loose packets had a wider array of job titles, including curator/collections manager, postdocs, and volunteers and were less likely to have an active research agenda and slightly older with an average age of 52.0 years (**Fig. 2B**). We then focused on only the users who expressed a preference for loose specimen packets by examining the predictors for loose packets stored vertically ($N = 40$) versus horizontally ($N = 13$; binary response variable). Two of the responses were excluded due to a lack of preference for either vertical or horizontal storage. We found that none of the predictors were significant in either the full or reduced models.

Next, we analyzed the themes evident in herbarium users' explanations for their bryophyte storage method preferences. Of the 67 herbarium users who indicated their preferred bryophyte storage methods for herbaria they visit, 92.5% explained these preferences using a total of 11 different themes in their explanations (**Table 3**). The average number of reasons that an individual herbarium user included in their preferred bryophyte storage method explanation was 1.7 reasons with a range of one to four reasons per person.

Across all storage types, the most common theme in herbarium user explanations for their preferred bryophyte storage method was *convenience/accessibility* (**Table 3**). Approximately 79.0% of the 52 herbarium users who included variations of the word "ease" and/or "convenience" in their explanations often did so by referencing their ability

to "search [for]," "find," "locate," "pull," "handle," "sort," "examine," "manipulate," and/or otherwise "use" and/or "work with" bryophyte specimens at the herbaria they visit. Notably, the theme of *convenience/accessibility* appeared in 72.7% of the storage preference explanations provided by herbarium users who prefer bryophyte specimens stored in loose packets, while this particular theme was present in only 50.0% of the explanations provided by those users who prefer packets attached to sheets. Several herbarium users who prefer loose packets articulated that they find attached packets to be "difficult to use" and/or otherwise a "pain." Among herbarium users who indicated a preference for loose packets, those users who prefer loose packets stored horizontally cited *convenience/accessibility* at a comparable rate as those individuals preferring loose packets stored vertically (46.2% versus 43.5%, respectively).

The second most frequent theme evident in herbarium user explanations for their bryophyte storage system preferences was *copied/familiar/learned* (**Table 3**). In this instance, 72.3% of these 11 herbarium users indicated their bryophyte storage preference(s) were the result of the storage method(s) with which they were already "familiar," often framing their preferences in terms of "what I know."

The next two most frequently cited themes evident in user storage preference explanations were *physical factors* and *specimen wear and tear concerns* (**Table 3**). For the ten individuals who described *physical factors* in their explanations of their preferred storage method, 60.0% mentioned "boxes" and/or "compactors" as shaping their storage preferences and 30.0% of these herbarium users made note of "space" and/or "cabinetry" in their explanations. Meanwhile, 90.0% of the ten herbarium users explaining their storage preferences in terms of *specimen wear and tear concerns* discussed their preferred storage method as "preserv[ing]" and/or "protect[ing]" specimens from potential "damage" resulting from the "pressure" and/or "compression" to which other storage methods might subject specimens. This sentiment was particularly evident in the explanations provided by herbarium users who prefer loose packets stored vertically with 23.1% of these users mentioning *specimen wear and tear concerns*, whereas herbarium users who prefer loose packets stored horizontally mentioned this theme at a lower rate (10.0%).

Specimen storage*: *Thematic comparison of staff practices and herbarium user preferences. We then conducted chi-squared tests to compare the frequencies of the 15 themes we identified in staff and herbarium user explanations for their storage system practices/preferences (**Table 3**). We observed statistically significant differences between the frequencies at which *convenience/accessibility*, *physical factors*, and *inherited tradition* occurred in the staff and user populations. Although *convenience/accessibility* is the most frequent theme evident in both datasets, herbarium users included this theme in their bryophyte herbarium storage preference explanations at a significantly higher rate than staff (**Table 3**). In contrast, staff explained their herbarium's rationale for their bryophyte storage system in terms of *physical factors* and *inherited tradition* at significantly higher rates than users (**Table 3**). None of the remaining ten themes occurred at significantly different rates in the staff and herbarium user explanations for their storage system practices/preferences (**Table 3**).

Specimen organization*: *Herbarium practices reported by staff. Out of the 92 herbaria whose associated staff described their current herbarium organization methods, approximately one-third indicated sorting their bryophytes by division ($N = 33$), with either mosses, liverworts, and hornworts filed separately or mosses and hepatics (i.e., liverworts and hornworts) filed separately. Irrespective of divisional sorting, 46 herbaria reported organizing their specimens solely by genus with 92.3% of these herbaria indicating that they organize bryophyte genera alphabetically (**Table 4**). Thirty staff members reported organizing bryophyte specimens using both family and genus level sorting with more than half of these herbaria organizing both of these levels alphabetically (**Table 4**). All 56 herbaria whose staff mentioned species level organization indicated using alphabetical sorting at this level.

We then analyzed these data to determine which institutional demographics are the strongest predictors of bryophyte specimen organization practices. We categorized the responses into those that described phylogenetic sorting as part of the organization system ($N = 19$) versus those that did not report phylogenetic sorting but included

Table 4. Majority bryophyte organization practices reported by staff for the herbaria where they work ($N = 92$) and bryophyte organization system preferences reported by herbarium users for the herbaria whose bryophyte collections they visit ($N = 64$).

Family Level	Genus Level	Staff practices	User preferences
Alphabetical	Alphabetical	$N = 17$	$N = 6$
Absent	Alphabetical	$N = 44$	$N = 31$
Alphabetical (level unclear)		$N = 7$	$N = 9$
Total with alphabetical sorting		**73.9% ($N = 68$)**	**71.9% ($N = 46$)**
Phylogenetic	Alphabetical	$N = 9$	$N = 11$
Phylogenetic	Phylogenetic	$N = 4$	—
Phylogenetic	Absent	—	$N = 1$
Absent	Phylogenetic	$N = 2$	—
Phylogenetic (level unclear)		$N = 4$	$N = 2$
Total with phylogenetic sorting		**20.6% ($N = 19$)**	**21.9% ($N = 14$)**
Organization type and level unclear or no preference		**5.4% ($N = 5$)**	**6.3% ($N = 4$)**

alphabetical sorting instead ($N = 68$; binary response variable; **Table 4**). None of the predictor variables were significant in a full model. However, in a reduced model in which total herbarium size was the sole predictor, this predictor was significant ($F_{1, 85} = 8.04$, $P = 0.0057$). Herbaria with bryophyte organization systems that include phylogenetic sorting were larger on average (total herbarium size of 1,995,579 specimens) than those with alphabetical organization systems that lack phylogenetic sorting (total herbarium size of 742,854 specimens; **Fig. 3**; **Table 4**).

Of the 92 staff responses that described the organization system utilized in their herbarium's bryophyte collections, 51.1% reported that they include geographic sorting. Of these herbarium staff responses, seven reported that the geographic sorting occurred only above the family level, 37 reported organizing bryophyte specimens by geography exclusively below the genus level, and three

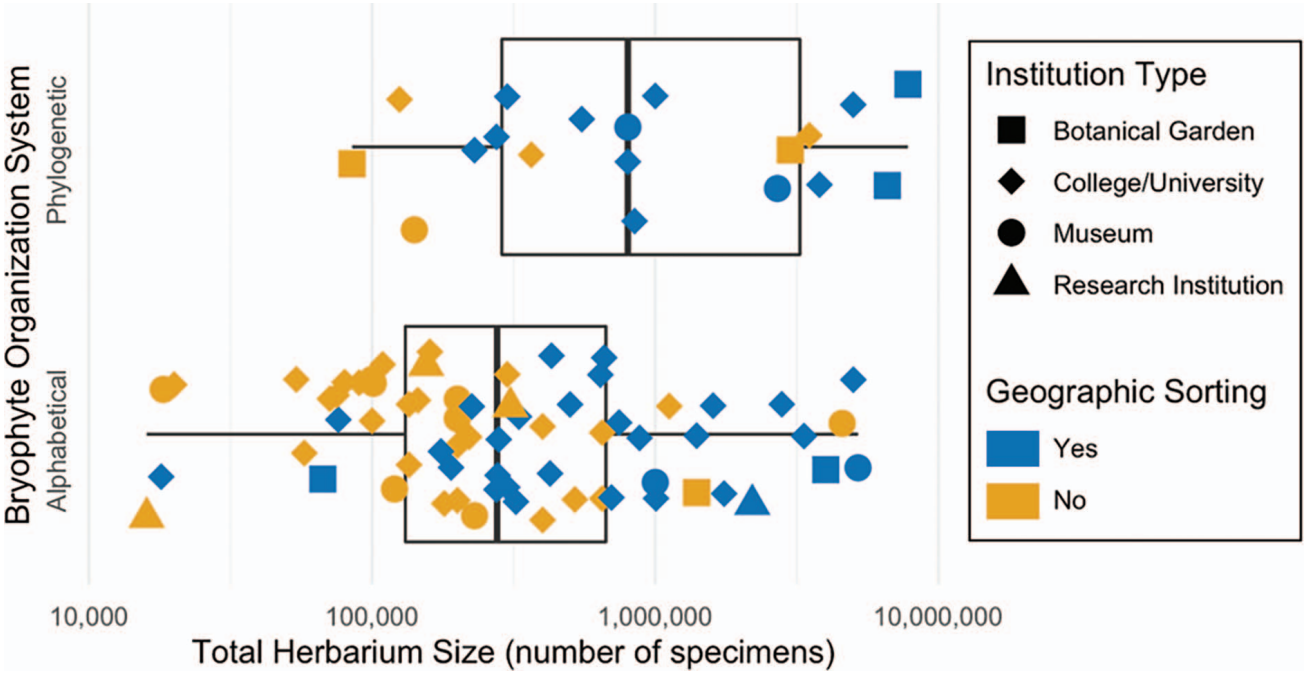

Figure 3. Bryophyte specimen organization systems reported by herbarium staff across Europe and North America. Responses were coded into those that described phylogenetic sorting as part of the bryophyte organization system versus those that did not and instead included alphabetical sorting (Table 4). Responses were also categorized into either systems that included geographic sorting or those that did not. Institution type and total herbarium size, which includes the number of specimens from all plant and fungal groups, are based on data from Index Herbariorum (Thiers 2017).

Table 5. A comparison of the frequency of themes observed in staff explanations for their herbarium's approach to organizing its bryophyte specimens ($N = 87$) and those evident in herbarium user explanations for the bryophyte organization system they prefer the herbaria they visit utilize ($N = 60$). Chi-squared tests examine whether are not there is a significant difference in the proportion of themes between the staff and user explanations for their bryophyte organization practices/preferences. Themes with statistically significant differences ($P < 0.05$) between the staff and user frequencies are in bold.

Theme	Staff frequency	Users frequency	Chi-squared	Degrees of freedom	p-value
Convenience/accessibility	48.3%	63.3%	2.67	1	0.10
Inherited tradition	**29.9%**	**0.0%**	**19.78**	**1**	**8.69E-06**
Lack of expertise	23.0%	13.3%	1.57	1	0.21
Phylogenetic/taxonomic concerns	**10.3%**	**45.0%**	**26.65**	**1**	**2.44E-07**
Copied/familiar/learned	9.2%	11.7%	0.044	1	0.83
Unsure or do not know	**9.2%**	**0.0%**	**4.18**	**1**	**0.04**
Analogous curation methods	4.6%	1.7%	0.25	1	0.62
Geographic significance	3.4%	8.3%	0.89	1	0.34
Collection size	3.4%	1.7%	0.019	1	0.89
Physical factors	3.4%	1.7%	0.019	1	0.89
Speed/efficiency	3.4%	3.3%	1.50E-30	1	1
Specimen wear and tear concerns	3.4%	1.7%	2.27E-32	1	1
Resource constraints	0.0%	5.0%	2.29	1	0.13
Other	2.2%	1.7%	9.25E-31	1	1

reported geographic sorting at both of these levels (**Table 4**). In order to determine which institutional demographics are the strongest predictors of staff organization practices, we categorized the responses into either systems that included geographic sorting ($N = 47$) or those that did not ($N = 45$; binary response variable). In a full model, the two strongest predictors that explained whether bryophyte collections include geographic sorting were institution type ($F_{3,\ 72} = 3.35$, $P = 0.024$) and the total herbarium size ($F_{1,\ 72} = 2.56$, $P = 0.114$). In our sample, 57% of botanical gardens, 54% of colleges/universities, 31% of museums, and 20% of research institutions reported geographic sorting. Additionally, herbaria that reported their bryophyte collections include geographic sorting were on larger on average (total herbarium size of 1,563,784 specimens) than herbaria that did not (total herbarium size of 475,692 specimens; **Fig. 3**).

We subsequently analyzed the themes evident in staff member explanations of why their herbarium organizes its bryophyte specimens in the manner that it does. Of the 92 staff members who provided details about their herbarium's approach to organizing bryophyte specimens, 94.6% explained why they utilize these systems using 13 different themes (**Table 5**). The average number of reasons an individual staff member provided in their explanation of their herbarium's bryophyte organization approach was 1.5 reasons with a range of one to four reasons per herbarium.

The most common theme among staff explanations for their herbarium's bryophyte organization system was *convenience/accessibility* (**Table 5**). Of these 42 staff members, 9.5% characterized their bryophyte organization system as being "logical" and/or "practical," which was a view exclusively expressed among staff working at herbaria with an organization system that included phylogenetic sorting. By comparison, 78.5% of these 42 staff members discussed the "accessibility," "convenience," and/or "ease" of "fil[ing]," "find[ing]," "locat[ing]," and/or "us[ing]" bryophyte specimens at their herbaria. This way of talking about *convenience/ accessibility* was a particularly common occurrence in the explanations provided by the 34 staff working at herbaria with alphabetical organization systems that lack any phylogenetic sorting with 81.1% of these staff members using such terms for discussing *convenience/accessibility*. Regardless of the specific language that staff used to describe their herbarium's approach to organizing its bryophyte specimens, staff whose herbaria use phylogenetic sorting to organize their bryophyte collections cited *convenience/accessibility* at a lower frequency than staff whose bryophyte organization systems are alphabetical and do not include phylogenetic sorting (31.6% versus 50.0%, respectively).

Inherited tradition was the second most frequently observed theme in staff explanations for their herbarium's approach to organizing its bryophyte specimens (**Table 5**). Half of these 26 staff explanations including this theme discussed their herbarium's bryophyte organization system in terms of "tradition" and/or "history." Moreover, 26.9% of staff whose explanations included the *inherited tradition* theme went on to identify a particular person and/or point in time as being the origin(s) of their herbarium's bryophyte organization system. Staff working at herbaria using a system that includes phylogenetic sorting cited *inherited tradition* at a higher frequency than those staff whose herbaria do not and instead utilize alphabetical sorting (36.5% versus 25.0%, respectively).

The third most common theme we identified in staff explanations of their herbarium's bryophyte organization system was *lack of expertise* (**Table 5**). Of these 20 staff members, half explained that their herbarium currently lacks institutional expertise in bryophytes. For example, several individuals reported that their herbarium "lack[s]...a bryophyte specific curator" and/or "ha[s] no active bryologist on staff." In some instances, they indicated that their herbarium had already gone "several decades without a dedicated [bryophyte] curator" and/or "it is unlikely we will [have such a specialist on staff] in the near future." In addition, 60.0% of these respondents, including some of those who identified a lack of institutional expertise, discussed *lack of expertise* in terms of their herbarium's organization system being "accessible" to "staff," "students," and/or "visitors" regardless of whether an individual has personal knowledge of and/or training in bryology. Staff working at herbaria with alphabetical organization systems that lack phylogenetic sorting cited *lack of expertise* at more than five times the frequency than staff whose collections included phylogenetic sorting (28.0% versus 5.3%, respectively).

Specimen organization: Herbarium user preferences for the herbaria they visit. Sixty-four of the 85 herbarium users responding to our survey indicated their preferred organization systems for the bryophyte collections they visit. A small number of users described their preferred systems as including a separation of specimens by division ($N = 3$). Seventeen users indicated a preference for collections using both family and genus level sorting with the majority reporting a preference for phylogenetic sorting of bryophyte families and alphabetical sorting of bryophyte genera (**Table 4**). Nearly double the number of users prefer the collections they visit to organize their specimens exclusively by genus with all of these respondents indicating a preference for alphabetical sorting of bryophyte genera. All 27 users who mentioned species-level organization reported a preference for alphabetical sorting.

We then analyzed these data to determine which user demographics are the strongest predictors of their bryophyte organization preferences. We categorized the responses into those that described phylogenetic sorting as part of the organization system ($N = 14$) versus those that did not report phylogenetic sorting but included alphabetical sorting instead ($N = 46$; binary response variable; **Table 4**). None of the predictors were significant in either the full or reduced models.

Of the 64 herbarium users who described their preferred bryophyte organization systems, 28.1% expressed a preference for geographic sorting of specimens with three of these users preferring geographic sorting above the family level and 15 of these users preferring geographic sorting below the genus level (**Table 4**). We analyzed whether any of the user demographic variables are strong predictors of user preferences for geographic sorting at herbaria they visit (including geographic sorting: $N = 18$; without geographic sorting: $N = 48$; binary response variable) and found that none of the predictors were significant in either the full or reduced models.

Next, we analyzed the themes evident in herbarium users' explanations for their preferred bryophyte organization systems. A total of 64 herbarium users provided details on how they prefer the herbaria they visit to organize their bryophyte specimens and 93.8% of these respondents went on to explain their bryophyte organization system preferences. Across these 60 explanations, 12 different themes emerged (**Table 5**). The average number of themes evident in an individual herbarium user's explanation of their preferred bryophyte organization system was 1.7 reasons with a range of one to four reasons per person.

Among herbarium users who explained their bryophyte organization system preferences, the most

frequent theme evident in their explanations was *convenience/accessibility* (**Table 5**). Of the 38 herbarium users whose explanations included the theme of *convenience/accessibility*, 72.4% discussed how their preferred organization system made it "easy/easier" for them to "find" or "locate" specimens of interest at the herbaria they visit. When comparing the relative frequencies of the *convenience/accessibility* theme by organization system preference, the frequency at which this theme occurs in the explanations provided by users who prefer phylogenetic sorting is lower than that of users whose prefer alphabetical sorting (42.9% versus 67.4%, respectively).

The second most common theme in herbarium users' preferred bryophyte organization system explanations was *phylogenetic/taxonomic concerns* (**Table 5**). Sixty percent of the 30 herbarium user explanations that we coded as *phylogenetic/taxonomic concerns* articulated that their organization system preferences are driven by the fact that bryophyte "taxonomy" and/or "phylogenies" are "unstable," "changing," and/or "evolving." One herbarium user who indicated a preference for alphabetical organization systems stated, for example, that "the phylogenetic system is not stable enough, is not universally accepted, and is more difficult to know when looking for specimens." Several others who also reported a preference for alphabetical approaches echoed this sentiment by stating that systems including phylogenetic sorting are "in constant need of updating and [are] likely to have at least some taxa filed in different families from the ones you expect." As such, finding specimens in such systems "requires more time." Herbarium users who prefer organization systems with phylogenetic sorting, by comparison, expressed fewer reservations about the fact that "taxonomy changes." One such individual articulated, "I find it fairly easy to keep up with where genera reside (which family they are currently in), so its [*sic*] easy to go to a family [and] then look for the genus alphabetically." Moreover, those herbarium users who prefer approaches to bryophyte organization systems that include phylogenetic sorting often described these systems as a "good compromise" because they include a "combination of evolutionary big picture plus convenience to find the material within families or genera." As such, herbarium users who prefer visiting herbaria with organization systems that include phylogenetic sorting cited *phylogenetic/taxonomic concerns* at a higher frequency than those who prefer an alphabetical sorting (71.4% versus 41.3%, respectively).

The third most frequent theme that we identified in the explanations that herbarium users provided for their preferred bryophyte organization system was *lack of expertise* (**Table 5**). Three-quarters of these eight herbarium users discussed *lack of expertise* in terms of the limits of their own "experience" with and/or "knowledge" of bryophyte "families" and/or "relationships." For instance, several herbarium users who reported a preference for alphabetical bryophyte organization indicated that they "know the genus but not necessarily what family it belongs to." The remaining 25.0% of users discussed *lack of expertise* in a broader manner, expressing sentiments such as their preferred organization system "does not require very much taxonomic expertise" or "it's [easier] for students who don't know bryophyte families." Overall, herbarium users who prefer that herbaria organize bryophyte specimens using phylogenetic sorting cited *lack of expertise* at a lower frequency than those users who prefer bryophyte organization systems that use alphabetical sorting (25.0% versus 36.5%, respectively; **Table 5**).

Specimen organization: Thematic comparison of staff practices and herbarium user preferences. Next, we compared the rates at which herbarium staff and user explanations for organization system practices/preferences include each of the 14 themes that we identified across our two datasets (**Table 5**). Similar to the herbarium storage rationale, *convenience/accessibility* was the most frequent theme identified in both staff and user organization system explanations (**Table 5**). However, herbarium staff and users did not discuss this particular theme at statistically different rates for the organization system rationale (**Table 5**). The frequencies at which staff and users discussed three other themes—*inherited tradition*, *phylogenetic/taxonomic concerns*, and *not sure/do not know*—were significantly different. Herbarium user explanations for their preferred bryophyte organization system included the theme of *phylogenetic/taxonomic concerns* at a significantly higher frequency than staff explanations for how their herbaria organizes its bryophyte specimens (**Table 5**). In the case of the *inherited tradition* and *not sure/do not know* themes, staff

explanations for organization system preferences included these themes at a significantly higher frequency than user explanations (**Table 5**).

Discussion

The bryological community has long wrestled with how best to store and organize herbarium specimens. Our study builds on these historical conversations by undertaking the field's first comprehensive study of bryophyte curation practices at herbaria across Europe and North America and then comparing these practices with the curation preferences of the individuals who utilize bryophyte collections at these herbaria. In doing so, we are able to advance the bryological community's understanding of the most commonly utilized/preferred bryophyte specimen storage and organization systems. In addition, we also draw attention to the reasons why herbarium staff utilize and users prefer particular bryophyte storage and organization systems, offering valuable insight into the various factors that shape the curation of bryophyte specimens at herbaria, as well as the curation preferences of the individuals who visit these collections.

Below, we outline three limitations to consider when interpreting the results of our study. First, by limiting the geographic scope of our study to Europe and North America, we cannot shed light on staff practices at and user preferences for bryophyte storage and organization at the 30.1% of herbaria located elsewhere in the world (Thiers 2017). Thus, we acknowledge that our findings may not be representative of the full range of curation practices/preferences and rationale evident within the worldwide bryological community. Second, our sample size is relatively small yet robust. While most previous bryophyte curation studies have reflected the opinions of a handful of experts (e.g., Kruse pers. comm. in Glime & Wagner 2013), our study participants include 94 staff members and 85 herbarium users. As a result, we are able to offer a more inclusive picture of the curation practices/preferences evident within the bryological community. Lastly, while approximately 56.0% of the 1,487 herbaria included in our study population are located at colleges/universities (Theirs 2017), 70.8% of our staff sample are from college/university herbaria. We therefore acknowledge that staff curation practices at college/university herbaria may be overrepresented in our sample. Despite these limitations, our research represents the most comprehensive and up-to-date synthesis of bryophyte organization and storage practices/preferences available. As such, our study is an important step forward in engaging the bryological community in critical and reflective dialogue regarding curation practices/preferences.

Common curation practices/preferences in the bryological community. Our study reveals that the most frequently used/preferred bryophyte storage method by staff and herbarium users alike is loose packets stored vertically in boxes placed in herbarium cabinets (**Table 2**). Our findings suggest that these members of the bryological community may have heeded the advice of Flowers et al. (1945), who advocated for storing bryophyte packets "in boxes, card catalog fashion" (p. 199; see also Bridson & Forman 1998). Yet, we note that more than half of both staff and herbarium users indicated that they use/prefer another type of bryophyte storage (**Table 2**). Thus, even though the topic was first discussed in the literature during the first part of the 20th century (e.g., Chemberlain 1903; Clarke 1903; Gilbert 1904; Grout 1900), the bryological community continues to have diverse practices/preferences for storing bryophyte specimens at herbaria. This finding echoes the conclusions of the informal survey of bryophyte curation methods conducted by Dale Kruse in 2008 (Kruse pers. comm. in Glime & Wagner 2013), suggesting that a wide range of bryophyte storage methods remain common.

With regard to bryophyte collection organization, an alphabetical approach that lacks phylogenetic sorting was the most popular with a majority of herbarium staff and users indicating this particular bryophyte organization practice/preference (**Table 4**). This finding confirms Kruse's conclusion that alphabetical organization systems were common within the bryological community (Kruse pers. comm. in Glime & Wagner 2013; see also British Columbia Ministry of Forests 1996). We found that organization systems including phylogenetic sorting are only used/preferred by approximately a fifth of staff and herbarium users (**Table 4**). Glime & Wagner (2013) stated that phylogenetic organization approaches are "in widespread use in the arrangement of bryophyte herbaria" (p. 3-1-15; see also Bridson & Forman 1998). Unfortunately, due to a lack of systematically collected historical

data on this topic, we cannot quantitatively evaluate whether or not bryophyte organization practices/preferences have shifted. Our study establishes a critical baseline for documenting changes in bryophyte curation practices/preferences over time.

Herbarium staff and user explanations for current curation practices/preferences. When examining our study participants' explanations for their bryophyte curation practices/preferences, we identified a number of important themes. Regardless of whether staff or herbarium users were explaining their storage or organization practices/preferences, *convenience/accessibility* was the most frequent theme in our dataset. While this particular theme was common in both the staff and user datasets, herbarium users referenced *convenience/accessibility* at a significantly higher frequency in their preference explanations than staff did when explaining their herbarium's current bryophyte storage practices (**Tables 3 & 5**). Moreover, the manner in which herbarium users discussed *convenience/accessibility* was markedly different from how herbarium staff approached this topic. Across storage and organization explanations alike, herbarium users frequently stressed how important it is for herbaria to store and organize their bryophytes in a manner that makes it "easy" or "easier" for visitors to "search [for]," "find," "locate," "pull," "handle," "examine," "manipulate," and/or otherwise "use" these specimens. In comparison, staff explanations tended to focus on the "ease" with which they themselves (rather than visitors) can "file," "find," "handle," "locate," "manage," "reorganize," and/or "transfer" specimens in their bryophyte collections. While there is some overlap in how staff and herbarium users conceptualize "ease," the two groups appear to diverge in which tasks they feel should be made "easy" or "easier." For staff, utilizing curation methods that allow for "easy" management of the bryophyte collection is a top priority. Herbarium users, by comparison, prioritize the "ease" with which visitors can use bryophyte collections at the herbaria they visit. Our review of the bryophyte curation literature indicated that the "ease" with which herbarium collections can be managed and utilized is a popular topic in the literature (e.g., Bridson & Forman 1998; Chemberlain 1903; Franks 1965; Funk 2003; Glime & Wagner 2013; Holmes 1899; Millsbaugh 1925; Nave & Spicer 1867; Salick & Solomon 2014; Tocci 2019). It is our assessment, however, that many of these studies focused exclusively on staff priorities and do not pay as much attention to the needs of herbarium users. For instance, while discussing cryptogam organizations systems, Tocci (2019) suggested that "if the staff can find the specimens, you win" (n.p.). Similarly, in their remarks on herbarium arrangement, Bridson & Forman (1998) stressed the "ease" with which staff alone can navigate different organization systems. One notable exception to the lack of user focus is the occasional reference in the literature to alphabetically arranged herbaria presenting "the user…[with] no difficulty" (Fosberg & Sachet 1965, p. 79; see also Bridson & Forman 2008).

With regard to bryophyte storage systems, herbarium staff and users often specified that *physical factors* also influence their curation practices/preferences with staff including this particular rationale in their explanations at a significantly higher frequency than herbarium users (**Table 3**). Staff explanations for their bryophyte storage practices frequently discussed *physical factors* in terms of "sav[ing] space" and/or otherwise making "efficient" use of the "space" and/or "cabinetry" available to them across the entire herbarium beyond just the bryophyte collection. In other words, staff explanations describe "space" as a limited resource in many herbaria. Herbarium user references to *physical factors*, in contrast, were more commonly focused on the advantages and disadvantages of using "boxes," "compactors," and/or "cabinets" to store bryophyte specimens. That is, herbarium users are more concerned with the amount of "space" taken by the common storage vessels used in bryophyte collections. As such, staff and herbarium users appear to conceptualize herbarium "space" differently. While the bryophyte curation literature does not specifically address the different conceptualizations of "space" evident in the bryological community, our study affirms the argument that "the normal activities and interests of many herbaria have been cramped and stifled by a lack of space" (Fosberg 1946, p. 433).

Regarding bryophyte organization systems, herbarium staff and users also drew attention to the ways in which a *lack of expertise* and *phylogenetic/taxonomic concerns* also affect their organization practices/preferences (**Table 5**). Overall, we observed that staff and herbarium users who indicated that they use/prefer an alphabetical approach to

filing bryophyte specimens more frequently discussed *lack of expertise* in their organization practice/preference explanations. In other words, staff and herbarium users who use/prefer alphabetical organization systems are more likely to discuss their practice/preference in terms of lacking the requisite "knowledge," "experience," and/or "expertise" to efficiently navigate organization systems that include phylogenetic sorting. This finding mirrors the conclusions of several prior studies that argued that alphabetical organization systems require less specialized knowledge and, as such, are easier for most individuals to navigate (Bridson & Forman 1998; Fosberg 1946; Franks 1965; Glime & Wagner 2013; Millsbaugh 1925; Tocci 2019). In contrast, herbarium staff and users reporting an organization practice/preference that includes phylogenetic sorting frequently discussed their practices/preferences in terms of *phylogenetic/taxonomic concerns* (**Table 5**). A subset of our study participants suggested that bryophyte phylogenies are too "unstable," particularly at the family level and, as such, often expressed skepticism about bryophyte collections that include phylogenetic sorting. However, the bryophyte curation literature does not specifically discuss the relationship between continuously updated phylogenetic relationships and its impact on bryophyte collection organization systems. In contrast, the community has long wrestled with how best to organize vascular plant specimens in light of evolving understandings of the relationships between species (Funk 2003; Millsbaugh 1925; Shetler 1969). Millsbaugh (1925) discussed that the challenge of utilizing a phylogenetic approach to organizing herbarium specimens lies in the fact that such systems "require changing with the issue of each new monograph" (p. 13; see also Shetler 1969). In an op-ed published 78 years later, Funk (2003) expressed a similar sentiment, noting that one of the most common complaints about phylogenetic organization systems is that they "ke[ep] changing with families splitting and small segregates being recognized, etc." (p. 131). For many scholars, the solution for overcoming such challenges is for herbaria to use an exclusively alphabetical approach when organizing specimens (Fosberg & Sachet 1965; Glime & Wagner 2013; Millsbaugh 1925; Salick & Solomon 2014; Shetler 1969); however, such an organization system does not eliminate the impacts of taxonomic revisions on specimen organization.

Another common theme in the curation practice/preference explanations provided by staff and herbarium users was *inherited tradition* (**Tables 3 & 5**). Staff members often discussed how the bryophyte storage and organization systems in use at their herbaria were established by previous staff at some time in the past. In other words, when prompted to explain their institution's curation practices, staff members often reported, "This is how we do it." As such, several herbarium staff were unable to offer other explanations for their bryophyte curation practices, suggesting that *inherited tradition* likely plays an important role in shaping how herbaria store and organize their bryophyte specimens. While Bridson & Forman (2008) acknowledged that, once an herbarium adopts a particular system, "it usually remains in use evermore" (p. 90; see also Jain & Rao 1977; Rabeler et al. 2019), this particular topic is not examined in-depth in the bryophyte curation literature. We therefore suggest that *inherited tradition* is an unspoken and often unacknowledged variable shaping curation practices at many herbaria and one worthy of further examination.

On occasion, herbarium user explanations for their bryophyte curation preferences also included a similar theme: *copied/familiar/learned* (**Tables 3 & 5**). These particular herbarium users discussed their curation preferences in similar terms as staff members, explaining that they prefer bryophyte curation methods that they "know," "are familiar with," and/or "comfortable with," particularly while citing their own prior "experience" and/or "training" as the source of their storage and organization preferences. Consequently, just as staff members embody institutional norms for bryophyte curation practices that are passed from one generation to the next, we conclude that herbarium users are also internalizing the bryophyte curation preferences of the individuals and/or institutions that they have encountered during their previous experiences with bryophyte collections. As a result, we draw attention to the pervasiveness of unspoken rules and norms within the bryological community, suggesting that some of these rules and norms are influencing the bryophyte curation practices/preferences of institutions and individuals.

While the bryophyte curation literature has yet to consider this topic, research in the field of science and technology studies suggests that members of the

same epistemic community, which Haas (1992) defines as a "network...of professionals with recognized expertise and competence in a particular domain" (p. 3), may adopt the community's rules and norms, often doing so without questioning their validity and/or origins (Knorr Cetina 1999). After all, it is common for newcomers to a field to seek guidance from those who may be more knowledgeable and/or experienced; such experts are thought to have "an authoritative claim to policy-relevant knowledge within that domain" (Haas 1992, p. 3). It is therefore not surprising that the practices/preferences of certain bryologists—particularly those individuals viewed as experts—linger at the herbaria where they worked and do so with reverberating effects on the entire bryological community. Yet the bryophyte curation literature does not frequently confront the fact that "the lives and whims of individuals" (Shetler 1969, p. 726) permeate herbarium collections and therefore influence curation practices/preferences. Science and technology studies researchers argue that such attempts to view science as an objective endeavor are misguided, as "science and the production of expert knowledge are inherently a social phenomenon" (Lewis 2011, p.56, citing Haas 1997; Latour 1987, 1999; Latour & Woolgar 1979; Sismondo 2004). In other words, while many scientists tend to remove themselves from the stories they generate, extricating oneself from one's work in this manner is neither attainable nor desirable (Haas 1997; Sismondo 2004). Our study, which acknowledges that herbarium curation practices/preferences are the product of "the 'machines of knowing' that govern the production, mobilization, and stabilization of knowledge" (Lewis 2011, p. 56, citing Knorr Cetina 1999) within the bryological community, is therefore an important first step in considering the 'human factor' shaping bryophyte curation practices/preferences.

Context matters: Demographic predictors of staff curation practices in bryophyte collections. While the herbarium curation literature occasionally includes general statements such as larger herbaria typically store their bryophyte specimens attached to sheets that "are arranged in systematic or sometimes alphabetical order" (Bridson & Forman 1998, p. 236), it is relatively silent on how institutional demographics influence staff curation practices at herbaria around the world. Our findings indicate that the bryophyte curation practices at herbaria in Europe and North America are predicted by three main factors: 1) geographic location, 2) total herbarium size, and 3) institution type.

In our study, geographic location is the strongest predictor of whether an herbarium stores its loose bryophyte specimens vertically or horizontally. North American herbaria are more likely to store their specimens vertically—in either filing cabinets or in boxes placed in standard herbarium cabinets—compared to European herbaria. European herbaria store their loose bryophyte specimens horizontally in folders more often in comparison to North American herbaria, which rarely use this storage method. Although the curation literature includes anecdotal opinions regarding bryophyte specimen storage, our study is among the first to document a clear difference in the herbarium curation practices between these two geographic regions. We suggest that such differences may be the product of the time periods in which herbaria developed in these regions. As Shetler (1969) notes, "the herbarium was an almost exclusively European institution for more than 200 years" (p. 700) with the earliest herbaria in Europe dating back to the 16th century (Cholewa 1997; Fosberg 1946; Shetler 1969; Thiers 2020). In North America, however, the vast majority of large herbaria "were founded in the mid-1800′s [*sic*]" (Funk 2017, p. 83) with the greatest advances occurring "over a 50-year period from 1925 to 1974" (Funk 2017, p. 85). Despite the fact that most (if not all) herbaria can trace their roots back to Europe, "the politics, traditions, and perspectives of each country give each herbarium origin story a distinct flavor" (Thiers 2020, p. 165). Thus, once imported from Europe, it is likely that North American herbaria continued to develop and diverge from these European traditions in order to meet the specific needs of the geographic contexts in which they are operating.

Total herbarium size, which includes all plant and fungal specimens, is a strong predictor in several of our models examining organization and storage practices at herbaria in Europe and North America. We found that larger herbaria are more likely to store bryophyte specimens attached to full herbarium sheets, while smaller herbaria are more likely to utilize loose packets for their bryophyte specimens. These results support Bridson & Forman (1998)'s conclusion that packets attached to sheets are a

commonly used bryophyte storage method at larger herbaria. One potential explanation for the prevalence of packets attached to sheets at these herbaria is a curatorial desire to store plant specimens in as uniform a manner as possible so that "standard herbarium cabinets, species covers, and genus covers" (Glime & Wagner 2013, p. 3-1-10) can be utilized. Additionally, attaching bryophyte packets to full herbarium sheets makes specimens physically larger, which could result in less damage (Glime & Wagner 2013). Large herbaria that attach multiple packets per sheet also have the advantage of decreasing the number of independent items within their collections. This practice may decrease the likelihood that individual specimens are misplaced and/or lost over time (Glime & Wagner 2013).

Total herbarium size also predicts the presence or absence of phylogenetic sorting, as well as the presence or absence of geographic sorting in bryophyte collections. Our findings confirm the conclusions of earlier researchers who argued that total herbarium size influences bryophyte organization practices (Bridson & Forman 1998; Franks 1965; National Park Service 1999; Rabeler et al. 2019; Shetler 1969; Tocci 2019). Specifically, we found that herbaria that include phylogenetic sorting in their bryophyte organization systems are larger than those that did not. The same is true for geographic sorting. One plausible explanation for the prevalence of such organizational practices at larger herbaria is that they have more specimens to curate and, as a result, these additional layers of sorting enable staff to organize their specimens more efficiently. For example, larger herbaria with many specimens of the same species may elect to sort specimens geographically below the species level (i.e., after the taxonomy has been fully resolved) in an effort to make it easier to locate these specimens. With regard to the presence of phylogenetic sorting specifically, another factor may be whether or not the herbarium currently has or previously had a dedicated bryophyte curator whose taxonomic expertise could have aided in setting up and/or transitioning to an organization system that includes phylogenetic sorting. However, these hypotheses remain unexplored and could be the focus of future research on specimen organization systems.

Institution type is another strong predictor of the presence or absence of geographic sorting in bryophyte collections. More than half of the herbaria at botanical gardens and colleges/universities reported geographic sorting, while other types of institutions reported geographic sorting at lower rates. Although it is difficult to ascertain why geographic sorting of bryophyte specimens is common at some institutions and not others, one possible explanation for the use of geographic sorting at botanical garden herbaria relates to design traditions at such institutions. According to Söderström (2008), botanical gardens "often mimic…naturally occurring ecosystems" (p. 495) and therefore arrange their living plant collections ecologically and/or geographically (see also Klemun 2019). Given the overlapping manners in which living and dried plant collections are used in botanical research, botanical garden staff may implement similar geographic sorting in each of the collections they curate. The presence of geographic sorting at college/university herbaria, by comparison, may be explained by the importance of these collections to the geographic areas where these herbaria are located. College/university herbaria often "specialize in local flora" (Gier 1952, p. 45) and therefore "function more as teaching tools" (Beaman 1965, p. 113; see also Rollins 1965). As a result, geographic sorting offers a means by which college/university herbaria can tailor their collections to their specific user groups.

Context matters: Demographic predictors of user curation preferences for bryophyte collections. Our review of the herbarium curation literature suggests that the needs and interests of herbarium users are typically only given passing consideration in many studies. For example, Holmes (1899) suggested that herbarium organization can be improved "to economise the time at the disposal of the visitor as well as the curator" (p. 63). Rabeler et al. (2019) discussed herbarium users in a similar vein, arguing that "no matter what filing system is used, it is critical that employees and visitors be able to locate specimens in an efficient manner" (p. 8). One notable exception that focused on herbarium users' needs and interests is Kruse's 2008 informal survey of the bryophyte storage preferences among Bryonet subscribers (see Kruse pers. comm. in Glime & Wagner 2013). Kruse employed targeted sampling and was able to document differences in the curation preferences of a handful of well-known bryologists (see Kruse pers. comm. in Glime & Wagner 2013). What this study did not investigate,

however, is whether the demographics of herbarium users influence their curation preferences. Our study, in contrast, takes a more systematic approach to studying curation practices/preferences with survey instruments that included both demographic and content questions.

We found that user preferences for bryophyte storage of loose versus attached packets is the only curation preference that is predicted by user demographics. Yet, in an effort not to stereotype members of the community, we have refrained from drawing any definitive conclusions about the nature of these relationships. Thus, we recommend that future studies delve more deeply into the curation preferences of herbarium users, paying specific attention to the ways in which an individual's lived experiences shape their curation preferences. We also encourage more frequent and sustained dialogue between herbaria and their constituents so that herbarium staff can help to educate users on practices that promote specimen preservation, while giving users more of a voice in how bryophyte collections are curated.

Reflections on bryophyte curation. Since we began this study in 2017, we are regularly asked by herbarium staff and researchers about the "best" way to store and organize bryophyte specimens. A number of factors must be considered when reflecting on this question. In addition to the institutional factors discussed above, another critical component is the people interacting with the specimens—both staff and users—at a particular herbarium. Greater discussion between these two stakeholder groups is important so that all types of specimen interactions can be considered. Although we do not think there is a 'one-size-fits-all' approach to bryophyte collection organization and storage systems, we discuss below the considerations and tradeoffs of different systems, paying particular attention to factors such as resources, potential specimen damage, levels of bryological expertise, ease of examination, and total herbarium size.

Opponents of the loose packet storage method express concerns about whether storing specimens in this manner leads to a higher rate of specimen loss over time (Glime & Wagner 2013). A number of our study participants argued that specimens stored in packets attached to sheets are less likely to be misplaced and/or lost. One possible explanation is that, when attached to a full herbarium sheet, bryophyte specimens are physically larger than those stored in loose packets. Accordingly, packets attached to sheets are easier to keep track of. Specimens stored in loose packets, by comparison, may be more easily misplaced "due to their small size" (Glime & Wagner 2013, p. 3-1-10).

A related concern for herbarium staff and users was the notion that the loose packet storage method may subject specimens to greater levels of wear and tear. Some authors have argued that storing bryophyte specimens vertically in loose packets can lead to soil collecting at the bottom of packets which, in turn, may damage the specimens (Glime & Wagner 2013; Victor et al. 1994). Other scholars, however, asserted that the downward pressure exerted on specimens when folders of specimens are stacked on top of one another can result in comparable amounts of damage (National Park Service 1999). Our review of the literature suggests that debate on the topic remains ongoing, but we acknowledge that no matter the storage method, the more tightly packed specimens are, the greater potential there is for damage.

The physical materials used for curation differ between storage types and can have direct impacts on the per specimen storage costs. Additional layers can be placed inside the archival packets, such as cardstock beneath the specimen or double packeting can be used. These techniques not only provide a mechanism for removing the specimen from the primary packet but can also provide additional layers of protection from damage that could be caused by packets bending or flexing (see also British Columbia Ministry of Forests 1996; Society of Herbarium Curators n.d.). These additional layers might be particularly helpful for protecting bryophyte specimens in loose packets, as these packets lack the extra support provided when primary packets are attached to a sheet of herbarium paper. Though cardstock and/or double packeting may be the best practice for protecting bryophyte specimens in packets, these layers of paper also add to curation costs, both in terms of purchasing supplies and the curational time needed to integrate them into already accessioned specimens or into existing curatorial practices. Outside of the primary packet, attaching packets to sheets requires herbarium paper as well as an attachment mechanism, which could consist of staples, double-

sided tape, or pins. Loose packets can be stored horizontally in folders, vertically in boxes that fit into an herbarium cabinet cubby, or vertically in the drawer of a card catalog style filing cabinet (see also British Columbia Ministry of Forests 1996; Glime & Wagner 2013; Graddstein et al. 2001; Horton 2003). Formal analyses of bryophyte specimen storage costs per packet and the impacts of storage methods on the space required to store these collections remain understudied. This topic represents an exciting avenue for future research, one that is likely to have significant implications for all types of plant and fungal specimens stored in packets.

Our findings indicate that a consideration for some herbarium users is whether or not they can easily examine bryophyte specimens under a dissecting microscope. In comparison to packets attached to full herbarium sheets, loose packets are physically smaller and therefore easier to position under a microscope (Bridson & Forman 1998; Glime & Wagner 2013). In addition, bryophyte specimens stored in loose packets may not require specimens to be removed from their packets in all instances, thereby decreasing the likelihood of potential specimen mixups and/or losses (Bridson & Forman 1998; Glime & Wagner 2013). Specimens glued directly to sheets are even more difficult to examine under a dissecting microscope as close examination of such specimens may require the physical removal of material from the sheet, thus subjecting the specimen to damage (Smith 1965), which has likely contributed to the decline in the number of bryophyte specimens stored in this manner.

Our findings support the idea that alphabetical organization systems are thought to be easier to navigate for herbarium staff and users alike, particularly for those individuals with limited to no bryological expertise. While the literature contains differing opinions regarding the level for organizing specimens alphabetically, a large number of the staff we surveyed report arranging bryophyte genera alphabetically without any family level organization (**Table 4**). Since alphabetical systems require lower levels of bryological expertise, they should be an easier organization system for herbarium staff to implement. Additionally, as the most frequently used/preferred bryophyte organization system in our study, alphabetical by genus is likely to be the system with which users are most familiar and thus are prepared to navigate.

Should the staff at and/or frequent users of an herbarium have higher levels of bryological expertise, a system that includes sorting specimens by division (i.e., mosses, liverworts, and hornworts) and/or organization at the family level may be more appropriate. These systems place more closely related taxa in physical proximity to one another (Fosberg & Sachet 1965; Funk 2003; Holmes 1899). This could be especially helpful for bryology researchers interested in a single bryophyte lineage (approximately a third of the users participating in our study), working on multiple genera in a family (Funk 2003; Tocci 2019), and/or for training students in bryophyte taxonomy and identification. That said, herbarium staff should consider the added complexities that phylogenetic sorting may present for staff, volunteers, students, and other users. Arranging families alphabetically only requires an herbarium to have a list of the genera included in each family, whereas arranging bryophyte families phylogenetically also requires a large-scale classification or phylogeny that can be used to define the sequence of the families. Both the lists of genera in a family and the sequence of the families are available in a number of recent publications (i.e., Crandall-Stotler et al. 2008; Goffinet et al. 2008; Goffinet & Buck 2021; Renzaglia et al. 2008; Söderström et al. 2016). Yet, many of our survey participants expressed concerns about how changes in the phylogenetic relationships make organization systems with phylogenetic sorting both more challenging to navigate and take additional time and resources to keep up-to-date, especially for users and/or staff who lack bryological expertise.

All collections—no matter their organization system—are impacted by taxonomic revisions that result in the need for curatorial updates (e.g., genera being split or combined and/or individual species being moved to another genus). For revisions involving closely related taxa, these updates may be more easily carried out in collections using phylogenetic sorting. In such instances, closely related taxa are already located in physical proximity to one another, compared to collections organized alphabetically. Regardless of the organization system used, if taxonomic revisions are not regularly integrated into curation practices, all collections

run the risk of becoming frozen in time and/or having a mixture of current and historical organization systems. As Sears (1967) articulated:

> The bewildering array of systems and partial systems in use among herbaria today, which often are long since outgrown or overgrown and of which no two seem to be alike, stand like ancient shipwrecks as mute testimony to the navigational errors of past curators who tried to keep pace with the times by arranging part or all of their collection according to current taxonomic concepts, only to have these concepts change faster than they could rearrange the specimens consistently (p.727).

When an herbarium also sorts its bryophyte specimens by geography, another layer of complexity emerges (Tocci 2019). Despite Flowers et al. (1945) having recommended geographic sorting of herbarium collections, we found that this particular organizational practice/preference was not consistently present among our study participants. Yet, we note that the presence of geographical sorting below the species level (i.e., after all taxonomy is resolved) allows researchers undertaking a worldwide study of a particular taxonomic group to more easily locate specimens from different parts of the world (Lawrence 1951; Massey 1974). Meanwhile, sorting geographically above the family level is helpful for researchers carrying out ecological studies in which they examine a range of different taxa from the same geographic area (Fosberg & Sachet 1965; Massey 1974). However, in sorting geographically above the family level, specimens of single genera and species may be located in two or more locations within the herbarium. As a result, any staff member or herbarium user interested in locating all members of a genus or species will have to look in multiple—and likely spatially separated—cabinets for these materials. Alternatively, placing the geographical sorting below the genus level, which was the most common system practiced by herbaria in our survey, means the specimens of a particular species are located physically closer together in the herbarium. Overall, geographic sorting may be more useful in larger collections. However, which geographic regions are used is often a placed-based decision that depends on an herbarium's "size, the area it serves, and the diversity of this area" (Bridson & Forman 1998, p.92; see also Fosberg & Sachet 1965).

Regardless of whether an herbarium sorts bryophyte families strictly alphabetically or includes phylogenetic sorting, it should prepare a guide for staff and herbarium users to consult when working in the collection (Franks 1965; Funk 2003; Glime & Wagner 2013; Holmes 1899; Macmillian 1968; Massey 1974). Such an herbarium guide should contain a list of the order of bryophyte families (Massey 1974), as well as a list of the genera included in each family (Holmes 1899). Geographic sorting guides, which typically include maps and color-coded keys, are another important resource that is helpful for navigating this additional level of sorting (Tocci 2019). Many of the herbarium users who participated in our study, particularly those without a clear bryophyte organization system preference, articulate the sentiment that, "as long as there is a guide," then the collection should be "easy enough" for most people to use. In summary, we recommend that any herbarium electing to sort its bryophyte specimens by family clearly document how it orders the families so that herbarium users can navigate the collection without occupying staff time (Massey 1974; Rabeler et al. 2019). We acknowledge, however, that organizing bryophyte specimens by family as described above could significantly increase the amount of staff time required to curate the bryophyte collection (Fosberg & Sachet 1965; Holmes 1899; Millspaugh 1925), especially if regular updates are to be made when the classification or phylogeny on which the bryophyte organization system is based changes.

Conclusions

Curation methods directly impact how we use natural history collection specimens. Examining, thinking about, and reflecting upon our curation practices/preferences is a useful endeavor to harness the experience and expertise of a broad community of researchers in order to move our natural history collections into the 21st century (Lendemer et al. 2020). With limited finances and time, herbaria must optimize the resources at their disposal. Enhancements to curation methods need to be executed in ways that are both financially effective and have the largest positive impact on the ability of

staff to curate the collection and the users to engage with the specimens in the collection. Establishing practices via a collaboratively developed vision will enable us to maintain and/or enhance the herbarium user experience so that the collections continue to be used and studied in both traditional and novel ways (Heberling & Isaac 2017). As the curators caring for and researchers using bryophyte herbaria, it is critical that we share our knowledge about the importance of these small, dry, and charismatic organisms with members of the public to engage them in the scientific process and institutional administrators to justify the continued allocation of space and resources to these collections (Thiers et al. 2021). We hope that this study serves as a model for collections communities beyond bryology to reflect on their curation practices and better understand the preferences of individuals using natural history collections.

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