Botany Letters

ISSN: 2381-8107 (Print) 2381-8115 (Online) Journal homepage: http://www.tandfonline.com/loi/tabg21

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To cite this article: Guillaume Besnard, Myriam Gaudeul, Sébastien Lavergne, Serge Muller, Germinal Rouhan, Alexander P. Sukhorukov, Alain Vanderpoorten & Florian Jabbour (2018) Herbarium-based science in the twenty-first century, Botany Letters, 165:3-4, 323-327, DOI: 10.1080/23818107.2018.1482783

To link to this article: https://doi.org/10.1080/23818107.2018.1482783

Published online: 17 Oct 2018.

BOTANY LETTERS
2018, VOL. 165, NOS. 3–4, 323–327
https://doi.org/10.1080/23818107.2018.1482783

EDITORIAL

Herbarium-based science in the twenty-first century

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ARTICLE HISTORY Received 7 May 2018; Accepted 8 May 2018

Background and context

Herbarium collections are natural history collections and as such, are repositories of plant biodiversity and have been central to botanical knowledge for over four centuries. The Index Herbariorum lists 3001 herbaria worldwide, containing more than 387 million specimens (Thiers 2018). A herbarium specimen typically consists of dried plant material, its associated collection data and possible additional materials (e.g. drawings and photographs). Herbarium collections have traditionally served: (1) for systematics and taxonomy to describe and classify the dazzling diversity of plants; and (2) for botanical expertise to identify natural specimens relative to reference plant samples. The current use of herbaria reaches far beyond those originally anticipated uses, and new potential uses of herbarium specimens have emerged over time (Funk 2003; Mason Heberling and Isaac 2017), following scientific advances and societal priorities.

As a consequence, recently there has been growing interest for these new uses of herbarium specimens, along with rapid advances in genome sequencing and edition, imaging technology, and computing power. Such novel uses of herbarium have already shed new light on the mechanisms shaping species adaptation and diversification, and biodiversity patterns over space and time. Several methodological papers and reviews on the use of herbarium material have been published these last years, focusing on particular fields of research (e.g. Corney et al. 2012 [automatic phenotyping]; Lavoie 2013 [biogeography and environmental changes]; Meineke, Davis, and Davies 2018 [ecology and global changes]; Nualart et al. 2017 [conservation]; Wandeler, Hoeck, and Keller 2007 [population genetics]; Willis et al. 2017a [phenology]). In this Special Issue of *Botany Letters* we present a selection of original and state-of-the art studies, mini-reviews and technical notes, illustrating the ever-increasing diversity of uses of herbarium specimens. The first article of this Special Issue examines the research conducted on herbarium collections. It analyzes the array of uses of herbarium specimens as well as the profiles of the main users of herbarium collections (Carine et al. 2018). The remaining contributions cover two main topics: (1) systematics and patterns of biodiversity; and (2) lineage and trait evolution.

Systematics and patterns of biodiversity

Herbaria as repositories of biodiversity, a reference for systematics studies

Herbaria gather specimens that are snapshots of biodiversity sampled at different times and places (Le Bras et al. 2017), although sampling biases have to be acknowledged (Daru et al. 2018). This material is crucial for taxonomical studies, in particular when considering that a portion of these specimens is designated as types for taxon names, i.e. reference specimens generally cited in the original descriptions of species, with which other specimens have to be compared to be determined. Currently, mass digitization of herbarium specimens (Beaman and Cellinese 2012; Smith and Blagoderov 2012; Seregin 2016) triggers systematics studies and has a strong impact on the development of innovative methods of trait data extraction from image analysis, including machine learning algorithms (Younis et al. 2018; Schneider et al. 2018; Corney et al. 2012; Unger, Merhof, and Renner 2016; Reeb et al. 2018). Herbarium specimens can also be a convenient source of biological material (e.g. leaves, flowers, pollen grains, fruits and seeds) for studies on plant morphology and anatomy (Sukhorukov and Kushunina 2016) as well as plant chemical composition (e.g. isotopes, heavy metals, biochemical compounds) as shown for instance by Herpin et al. (1997), Körner et al. (2016) and Nielsen et al.

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Published online 17 Oct 2018

(2017). Two taxonomy-oriented works based on herbarium specimens are included in this Special Issue. Dentant, Lavergne, and Malécot (2018) conducted a thorough study of the taxonomy of rockjasmines (genus *Androsace*, Primulaceae), while Henning et al. (2018) introduce a workflow currently implemented on the EDIT Platform for Cybertaxonomy, which improves use and sustainable handling of specimen data. In addition, we also present a short review about the techniques used to prepare herbarium specimens for morphological and anatomical studies (Espinosa and Pinedo Castro 2018), and, to our knowledge, the first study investigating the morphological diversity of herbarium flowers using geometric morphometrics (Chen et al. 2018).

Ecology and distribution of taxa

Owing to the associated collection data, herbarium specimens, as occurrence records of taxa, are routinely used to reconstruct distribution maps and variation in species ranges through time (Joye, Castella, and Lachavanne 2002). Here we report a diachronic study of the distribution area of a species presenting perianth dimorphism, based on collections from ca. 40 herbaria (Damerval et al. 2018). This approach can be applied to study both the origin and expansion of invasive species (e.g. Lavoie 2013; Muller 2015), as well as temporal changes in traits during the course of geographic expansion (Buswell, Moles, and Hartley 2011). In turn, occurrence data extracted from herbarium specimens are crucial for analyzing the regression of some species and assessing their conservation status (Willis, Moat, and Paton 2003; Muller 2016; Nualart et al. 2017). Herbarium specimens can also allow the characterization of environmental modifications of territories (connected to local pollutions or global changes) as those of air quality (Woodward 1987; Herpin et al. 1997; Shotbolt, Buker, and Ashmore 2007; Ryan, Burne, and Seppelt 2009). When analyzed in relation to the phenological stage of the plant sample, they can contribute to studies on the effects of climate change on plant populations (Zohner and Renner 2014; Meineke, Davis, and Davies 2018; Willis et al. 2017b; Hufft et al. 2018). The availability of data is constantly increasing, with the ongoing digitization effort undertaken by many herbaria (including imaging, as well as transcription of collection data, accelerated thanks to participatory science programs [Hill et al. 2012; Rouhan et al. 2016; Ellwood et al. 2018]), facilitating such ecological and distributional studies (Soltis 2017).

Lineage and trait evolution

Molecular phylogenetics and biogeography

With the relatively recent development of DNA sequencing technologies, herbarium material is increasingly used in producing molecular phylogenies for systematic purposes, as well as in reconstructing the phylogeography of worldwide distributed species (e.g. Dunning et al. 2017; Martin et al. 2018). In particular, herbarium collections allow us to sample rare species, and even recently-extinct taxa that are impossible to collect in the field (e.g. Van de Paer et al. 2016; Welch et al. 2016). The sequencing of phylogenetic markers from DNA extracted from herbarium specimens thus allows researchers to reach appropriate sampling ratios and a suitable geographic coverage (Zecca et al. 2012), provided that some precautions are taken (Rogers and Bendich 1985). In this Special Issue, Wang recommends the best practices for DNA extraction from herbarium material, subsequent amplification and sequencing of phylogenetic markers, and discusses the impact of contaminant DNA sequences on the resulting molecular phylogeny (Wang 2018). Genomic data (i.e. nuclear genome data, complete plastome, mitogenome) extracted from herbarium material are also available (Bakker 2017) and, thus far, have allowed us to resolve challenging phylogenetic relationships (e.g. Rydin, Wikström, and Bremer 2017).

Evolutionary genomics of adaptation

Herbarium specimens serve not only to reconstruct lineage biogeographic history, but also to investigate their response to environmental changes at different space and time scales. Bieker and Martin (2018) make a significant contribution to this Special Issue by summarizing the major challenges associated with using historical plant DNA in evolutionary studies, and reviewing genetic studies integrating herbarium specimens. Once again, the availability of plant material collected from different provenances at different times, and the possibility to extract exploitable DNA from it, make herbarium specimens a suitable material to investigate the genomics of adaptive traits such as photosynthetic pathways (Lundgren et al. 2015; Besnard et al. 2018).

Conservation genetics and management of genetic resources of crops

The recent demography of species, a basic knowledge in biological conservation, can be inferred by population genetics analyses (e.g. Lande 1988). The study of individual species collected at different times may allow us to compare the recent population size fluctuation between endangered and low-concern species, or track colonization routes of invasive species (Wandeler, Hoeck, and Keller 2007; Matsuhashi et al. 2016). Herbarium collections are also the source of ancient, historical material recording the introduction or spread of cultivated plants and associated microbiome, for instance, potato from the Neotropics into Europe or sweet potato in Oceania, as well as crop pathogens (Li et al. 2007; Ames and Spooner 2008; Martin et al. 2013; Roullier et al. 2013).

Other uses and future prospects

In addition to the two main research areas listed here, many other fields of research can benefit from the use of herbarium specimens. Archaeobotanical and palaeobotanical studies might need plant samples previously collected for comparison or discussion purposes (e.g. Fuller and Murphy 2018). Also, herbarium material and the associated collection data are invaluable sources of information for researchers interested in the history of science and in reconstructing the history of past expeditions (e.g. Wolcott and Renner 2017).

We hope this Special Issue will fuel the discussions about current questions raised by collection managers, curators and botanists as a whole: How to better conserve the specimens in the long term? How to efficiently share the associated data in the long term? What will be the role of virtual herbaria in the future?

Acknowledgments

We thank Sophie Nadot and Elisabeth Dodinet for their assistance during the preparation of this Special Issue.

Disclosure statement

No potential conflict of interest was reported by the authors.

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Authors Contribution

For this editorial, GB and FJ wrote a first version of the manuscript, and all co-authors contributed to its final version.

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