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Review

Biological collections in an ever changing world: Herbaria as tools for biogeographical and environmental studies

Claude Lavoie*

École supérieure d'aménagement du territoire et de développement régional, Université Laval, Quebec City, Quebec G1A 0V6, Canada

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ABSTRACT

Plant specimens stored in herbaria are being used as never before to document the impacts of global change on humans and nature. However, published statistics on the use of biological collections are rare, and ecologists lack quantitative data demonstrating the relevance to science of herbarium specimens. I found 382 studies with original data that used herbarium specimens to document biogeographical patterns or environmental changes. Most studies are less than 10 years old, and only 1.4% of the herbarium specimens worldwide have been used to answer biogeographical or environmental questions. The vast majority (82%) of papers dealt with vascular plants, but some studies also used bryophytes, lichens, seaweeds and fungi. The herbarium specimens were collected from all continents, but most of the studies used specimens from North America (40% of studies) or Europe (28%). Many types of researches (conservation, plant disease, plant invasion, pollution, etc.) can be conducted using herbarium specimens. Climate change, and especially phenological reconstructions, are clearly emerging research topics. By group, small herbaria (<100,000 specimens) are consulted as often as very large herbaria (>1,000,000 specimens) for biogeographical and environmental research, but in most cases, only large facilities provide specimens collected worldwide. The median number of specimens per study in papers using computerized collections (15,295) was much higher than for papers that did not include electronic data (226). The use of molecular analyses to investigate herbarium specimens is still relatively unexplored, at least from biogeographical and environmental points of view. Combined with recently developed procedures to correct biases, herbarium specimens might provide in the near future exciting additional spatio-temporal insights that are currently unimaginable.

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* Tel.: +1 418 656 2131; fax: +1 418 656 2018.
E-mail address: claude.lavoie@esad.ulaval.ca

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Introduction

With the decline of interest in – or resources allotted to – systematics studies (Lee, 2000; Winston, 2007; Expert Panel on Biodiversity Science, 2010; Pyke and Ehrlich, 2010), several scientists and administrators have questioned over the last two decades the relevance of preserving biological collections of plants and animals, considering space and budget limitations. This questioning is not new: in 1969, Stanwyn Shetler, one of the curators of the Smithsonian Institution, was already complaining about the growing number of people who saw biological collections "*as an economic millstone and an intellectual dinosaur in the modern scheme of science*" or as "*an expensive, latter-day white elephant, which in terms of resources demanded is a facility that drains more than it adds to a modern science program*" (pp. 716, 731). Public and institutional budget crises of the 1990s and 2000s led to the closure of some collections and to severe resource reductions of others (Dalton, 2003; Gropp, 2003). Some botanists even suggested the destruction of herbaria and their replacement by electronic or printed files (Clifford et al., 1990). Moreover, declining plant and animal collecting, especially in North America and Europe (Winker, 1996; Prather et al., 2004; Rich, 2006; Boakes et al., 2010; Lavoie et al., 2012), have slowly but surely diminished the value of collections. As stressed by Winker (1996), "*how informative is a library that stops acquiring books?*" (p. 704).

These threats to the existence of biological collections are paradoxical, since plant and animal specimens are being used more than ever before to document the impacts of global change on humans and nature (Pyke and Ehrlich, 2010). Several scientists have recently reviewed the possible uses of these collections, such as the reconstruction of distribution ranges, habitat uses, morphological changes, pollution trends or population sizes, or the identification of pests and diseases threatening human health or agricultural activities (Shaffer et al., 1998; Suarez and Tsutsui, 2004; Rainbow, 2008; Newbold, 2010; Pyke and Ehrlich, 2010). These reviews are informative, but they have essentially focussed on animal collections. Herbaria are also important sources of information, with more than 350 million specimens stored worldwide (New York Botanical Garden, 2012).

Published statistics on the use of biological collections are rare, and ecologists lack quantitative data demonstrating the relevance to science of plant specimens. To remedy this problem, I reviewed all studies, published from 1933 up to February 2012, which used herbarium specimens as information sources for documenting biogeographical patterns or environmental changes. I collected statistics on the research topics, the study sites, the types of herbaria consulted, and the number of specimens used. I also investigated the impact of computerization on the use of herbaria. I answered the following questions: (1) to what extent are herbaria used for biogeographical and environmental studies; (2) what are the trending research topics associated with herbarium specimens; (3) are small and medium sized herbaria consulted as frequently as large facilities for biogeographical and environmental studies; (4) has the computerization of collections facilitated the use of specimens for documenting environmental changes; and (5) are biogeographers and ecologists studying herbarium specimens using molecular techniques.

Materials and methods

The literature review focussed exclusively on peer-reviewed journals. Other information sources (reports, online databases, etc.) can also provide important insights regarding the use of herbarium specimens. However, considering their sometimes limited distribution (especially of reports), it would have been impractical to conduct an international review within a reasonable time-frame. I first examined all papers found by the Web of Science^{SM} search engine (Thomson Reuters, 2012), with the keywords "collection" or "museum" or "herbarium" ("herbaria") in the headings "topic" or "title". Each paper identified was screened for its content: only papers presenting original data and explicitly using herbarium specimens for documenting biogeographical patterns or environmental changes were retained. Papers focussing exclusively on systematics, or using herbarium specimens only for mapping the distribution range of a plant without further spatial or temporal analysis were discarded. Although these papers reflect an extremely important use of herbaria, our focus was on studies presenting innovative or non-traditional uses of herbarium specimens. Additional papers (about 50% of the total) were subsequently found by reading the articles and screening the literature cited. The author of this paper can read English, French, Italian and Spanish, and collaborators provided papers in other languages (especially Chinese), but it is likely that several papers, especially those published in Russian, were missed.

Each paper was categorized according to the topics covered; papers could have more than one topic: (1) biases associated with the use of herbarium specimens (bias assessment or correction methods); (2) biogeographical patterns (plant distribution analyses); (3) conservation priorities (site selection for natural reserves); (4) historical floristic assessments (comparisons of floras over time); (5) impacts of climate change on plant distribution; (6) plant diseases; (7) plant invasions; (8) plant phenology (historical reconstructions or spatio-temporal distributions); (9) pollution trends (including carbon dioxide as a pollutant); (10) rare or declining plant species (population trends or spatial distributions); and (11) other topics (chemical ecology, insect outbreaks, pollination, etc.).

The following data were collected for each paper: (1) first author affiliation; (2) publication year; (3) journal name; (4) number of pages; (5) study site (country); (6) organisms studied (vascular plants, bryophytes, lichens, fungi, seaweeds); (7) number of herbarium specimens used; (8) herbarium/herbaria consulted; (9) whether or not a computerized database was used; and (10) whether or not molecular analyses were conducted on specimens. Additional data were collected for herbaria, i.e. (1) location (country) and (2) number of specimens stored (from New York Botanical Garden, 2012).

Results

Number of studies and spatial distribution of study sites

I found 382 studies with original data that used herbarium specimens to document biogeographical patterns or environmental changes (Appendix 1). These papers total 4620 pages and were

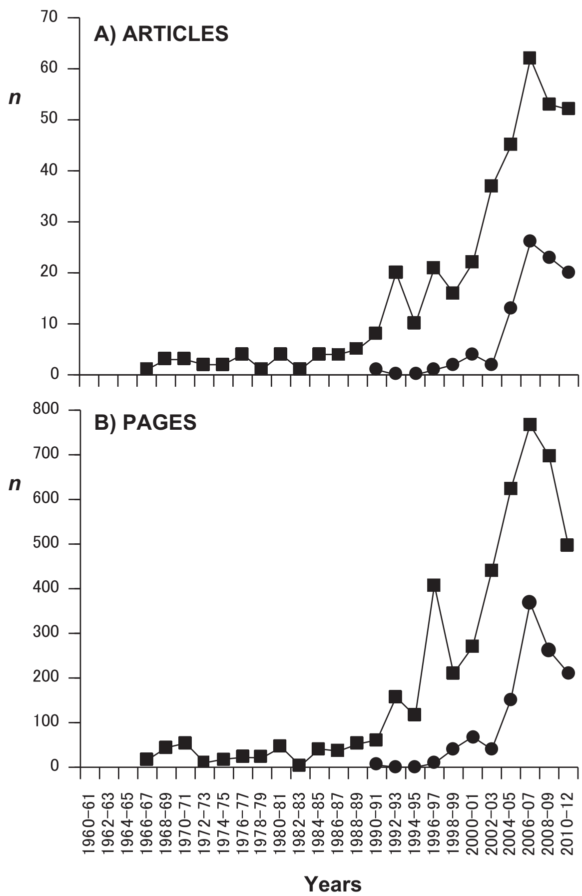

Fig. 1. Peer-reviewed articles with original data that used herbarium specimens for documenting biogeographical patterns or environmental changes and published from 1966 to February 2012. (A) Published articles per two-year period (January and February 2012 included in 2010–2011 data); (B) published pages per two-year period; squares: all articles (or pages); circles: only articles (or pages) with computerized collection(s) as information source(s) for herbarium specimens.

published in 130 journals from 1966 to 2012 (Fig. 1), with two exceptions published in 1933 (Fawcett and Jenkins, 1933; Jenkins and Fawcett, 1933). They came from 37 countries and 239 institutions, primarily universities or colleges (63%). Seventy one percent of the papers were published since 2000, and half since 2005 (Fig. 1; Table 1). This represents about two or three papers per month for the last seven years. The decline in the number of papers during the last four years is probably an artefact of the literature review: since about half the papers were discovered by screening the literature cited sections, recent papers were more difficult to detect because they have not yet been cited. The vast majority (82%) of papers dealt with vascular plants ($n = 317$), but some studies also used bryophytes ($n = 39$), lichens ($n = 16$), seaweeds ($n = 12$) and fungi ($n = 4$) as research material. The herbarium specimens were collected from all continents, including Antarctica (Table 2), but most studies used specimens from North America (40% of studies) or Europe (28%).

Table 2
Summary of peer-reviewed studies (per continent studied) with original data that used herbarium specimens for documenting biogeographical patterns or environmental changes from 1933 to February 2012. A study could span more than one continent.

Continent	Articles (n)	Pages (n)
North America (including Mexico)	151	1967
Europe	108	1219
South America	40	526
Oceania (including Australia and New Zealand)	38	453
Asia (including Middle East countries)	36	368
Africa	29	368
Central America (including Caribbean countries)	12	154
Antarctica	3	30

Research topics

Before the 1990s, herbarium specimens were used almost exclusively to reconstruct the spread of invasive plants or to document pollution trends (Table 1). Ronald Stuckey (Ohio State University) was a pioneer in this field: he published 11 historical reconstructions of exotic plant spread from 1966 (Stuckey, 1966) to 1985 (Les and Stuckey, 1985). Since then, herbarium specimens have been used to reconstruct habitat preferences of invasive plants (e.g. Pyšek and Prach, 1993; Lambrinos, 2001; Lavoie et al., 2007; Essl et al., 2009), document the impact of exotic species on the floristic composition of urban or natural areas (e.g. Lavoie and Saint-Louis, 2008; Dolan et al., 2011), and model the potential distribution of invaders (e.g. Arriaga et al., 2004; Mohamed et al., 2006; Barney et al., 2008). Following the pioneer works on lead pollution conducted by Åke Rühling and Germund Tyler at the University of Lund (1968, 1969), herbarium specimens have been used to study pollution caused by carbon dioxide (e.g. Woodward, 1987; Beerling et al., 1993; Miller-Rushing et al., 2009; Bonal et al., 2011), heavy metals (e.g. Lee and Tallis, 1973; Herpin et al., 1997; Peñuelas and Filella, 2002; Shotbolt et al., 2007), hydrocarbons (Foan et al., 2010), nitrogen (e.g. Pitcairn and Fowler, 1995; Solga et al., 2006; Wilson et al., 2009), and phosphorus (Peñuelas and Filella, 2001). They have also

Table 1
Summary of peer-reviewed studies (per topic) with original data that used herbarium specimens for documenting biogeographical patterns or environmental changes from 1933 to February 2012. A study could have more than one topic.

Topic	Articles (n)	Pages (n)	Earliest article (year)	Articles (% of the total) published since		Median number of herbarium specimens used per article
				2000	2005	
Plant invasions	98	1156	1966	60	45	277
Biogeographical patterns	71	1085	1990	86	59	3335
Biases associated with herbarium specimens	67	807	1985	87	72	4316
Pollution (including carbon dioxide)	65	588	1968	49	31	50
Rare or declining plant species	58	941	1985	78	55	351
Plant phenology	21	362	1991	86	76	1256
Historical floristic assessments	20	368	1989	70	45	2000
Plant diseases	18	146	1933	72	33	391
Conservation priorities	14	180	1998	93	64	2858
Climate change and distribution range of plants	11	120	1999	91	73	1075
Other topics	29	312	1976	79	66	926
All topics	382	4620	1933	71	51	486

Table 3
Summary of consultations of herbaria (according to the size of their collections) that were used to document biogeographical patterns or environmental changes in peer-reviewed studies published from 1933 to February 2012. International consultations (for specimens not collected in the country of the herbaria) are indicated. Consultations of computerized collections were not considered because in some cases they included data from several herbaria.

Herbarium size (*n* specimens)	Number of herbaria (% of the total)	Number of specimens stored (% of the total)	Consultations		
			Number (% of the total)	Mean number per herbarium	International (% of the consultations)
<100,000	407 (56)	13,359,040 (5)	805 (31)	2.0	6.5
100,000–999,999	263 (36)	84,220,778 (32)	1021 (39)	3.9	10.5
≥1,000,000	63 (9)	166,964,016 (63)	779 (30)	12.4	35.4
Total	733 (100)	264,543,834 (100)	2605 (100)	3.6	16.7

been used to evaluate the consequences of ozone-depleting substances on ultraviolet radiation (e.g. Huttunen et al., 2005; Lomax et al., 2008; Otero et al., 2009; Ryan et al., 2009). Bryophytes or lichens, used in 58% of the papers, were particularly important for pollution studies.

Although plant invasions and pollution are still studied using herbarium specimens, these research topics represent only a fraction of the types of studies that can be conducted with herbaria. For instance, herbarium material has been widely used to illustrate and explain phytogeographical patterns on all continents. Good examples (among many others) have recently been published for Africa (Linder et al., 2005; Parmentier et al., 2005; Schmidt et al., 2005), Antarctica (Peat et al., 2007), Asia (Hsu and Wolf, 2009; Raes et al., 2009), Australia (González-Orozco et al., 2011; Phillips et al., 2011), Europe (Otte et al., 2005; Wollan et al., 2008), North America (Villaseñor et al., 2007; Lindstrom, 2009; Santa Anna del Conde Juárez et al., 2009), and South America (Rovito et al., 2004; Murray-Smith et al., 2008).

Conservation biologists have used herbarium specimens to reconstruct population trends for rare or declining plants, or to assess the status of potentially threatened species (e.g. Farnsworth and Ogurcak, 2006; Case et al., 2007; Van den Eynden et al., 2008; Rivers et al., 2011). They have also used the spatial distribution of specimens to identify priority sites for protected areas, especially in Africa (e.g. Callmander et al., 2007; Droissart et al., 2011) and South America (e.g. da Costa and de Faria, 2008; Murray-Smith et al., 2008). Pathologists have frequently used herbarium specimens to study the origin, hosts, distribution or prevalence of plant pathogens, such as anther-smut disease and late blight (e.g. Ristaino et al., 2001; Hood et al., 2010), or barley yellow dwarf and tobacco mosaic viruses (Fraile et al., 1997; Malmstrom et al., 2007).

Newly emerging research topics include the impact of climate change on plant distribution (e.g. Gómez-Mendoza and Arriaga, 2007; Loarie et al., 2008) or plant phenology: about 75% of the papers dealing with these topics have been published since 2005. More specifically, the publication in the mid-2000s of a paper showing the relevance of herbarium specimens for reconstructing phenological changes associated with climate warming (Primack et al., 2004) rapidly stimulated the publication of 11 additional studies from a variety of habitats ranging from urban areas to deserts and mountains (e.g. Lavoie and Lachance, 2006; Neil et al., 2010; Robbirt et al., 2011). New techniques for studying herbarium specimens have been developed in the fields of chemical ecology (Zangerl and Berenbaum, 2005; Cook et al., 2009), insect outbreaks (Lees et al., 2011), and pollination ecology (Ollerton et al., 2009; Pauw and Hawkins, 2011).

There are several concerns regarding biases associated with herbarium specimens. At least 38 studies clearly illustrate these biases. For instance, botanists have often (1) focussed their specimen collection efforts on specific areas, especially in parks or near roads or university centres (Nelson et al., 1990; Kress et al., 1998; Parnell et al., 2003; Küper et al., 2006; Hopkins, 2007; Schulman et al., 2007; Tobler et al., 2007; Loiselle et al., 2008); (2) collected variable numbers of specimens over time (Prather et al., 2004; Rich, 2006; Hofmann et al., 2007; Lavoie et al., 2012); (3) misidentified specimens (Bisang and Urmi, 1994; Ahrends et al., 2011); (4) given imprecise or incorrect information on sampling location (Applequist et al., 2007; Miller et al., 2007); (5) deliberately avoided damaged plants (Abbott et al., 1999); (6) missed inconspicuous taxa (Urmi and Schnyder, 2000); or (7) oversampled rare species (Garcillán et al., 2008; Garcillán and Ezcurra, 2011).

Methods for correcting – or at least taking into account – these biases are presented in 29 studies. For instance, the data have been (1) compared to simulated data (Aikio et al., 2010a, 2010b); (2) weighted to take into account a variable sampling effort over space and time (Mihulka and Pyšek, 2001; Hedenäs et al., 2002; Delisle et al., 2003; Schmidt et al., 2005; Robertson and Barker, 2006; Hofmann et al., 2007; Jácome et al., 2007; Bergamini et al., 2009); (3) checked for location accuracy (Bowe and Haq, 2010; Feeley and Silman, 2010); or (4) incorporated into rarefaction analyses (Solow and Roberts, 2006; Grytnes and Romdal, 2008; Droissart et al., 2011).

Number of herbarium specimens used

To date, a total of 4,789,579 herbarium specimens have been used in studies documenting biogeographical patterns or environmental changes ($n = 251$ studies; this information was not provided in the rest of the studies), although some specimens were probably used more than once. The number of herbarium specimens used per study ranged from 2 (Sérgio et al., 1992) to 1,063,530 (Schulman et al., 2007), but overall, the median number of specimens – a better indicator than the mean because of extreme values – was about 500. The median number of specimens varied greatly among topics: from <300 for invasion and pollution studies to >2800 for studies dealing with biases, biogeographical patterns and conservation priorities (Table 1).

Herbaria consulted

A total of 733 different herbaria were consulted for these studies (Table 3). Together, these herbaria conserve about 265,000,000 specimens, i.e. 75% of the world total (New York Botanical Garden, 2012), and they were consulted 2605 times. Small (<100,000 specimens), medium sized (100,000–999,999) and large (≥1,000,000) herbaria were, by group, equally consulted, but on a per herbarium basis, large institutions were consulted three to six times more often than smaller ones. They also have a more international vocation (i.e. they were consulted for specimens not collected in the country of the herbarium) than small and medium sized herbaria.

The herbaria of some countries have a more international vocation than others. For instance, >90% of the consultations of Belgian or Dutch herbaria concerned specimens not locally collected, i.e. in Belgium or in The Netherlands (Table 4). This is also the case

Table 4
Number of consultations of the herbaria of specific countries that were necessary for documenting biogeographical patterns or environmental changes in peer-reviewed studies published from 1933 to February 2012. International consultations (for specimens not collected in the country of the herbaria) are indicated. Only countries with at least ten consultations for their herbaria are listed.

Country	Consultations (*n*)	International consultations (*n*)	% of consultations that were international
United States	1514	151	10.0
Canada	232	34	14.7
United Kingdom	86	68	79.1
Czech Republic	64	0	0
Germany	62	19	30.6
France	57	21	36.8
Switzerland	55	19	34.5
Australia	55	10	18.2
Mexico	48	0	0
Sweden	30	18	60.0
Republic of South Africa	25	7	28.0
Austria	25	6	24.0
China	25	0	0
The Netherlands	23	21	91.3
Belgium	19	19	100
Brazil	18	0	0
Finland	16	4	25.0
Italy	16	2	12.5
New Zealand	15	3	20.0
Argentina	15	0	0
Denmark	14	11	78.6
Spain	14	2	14.3
Japan	12	6	50.0
Norway	12	0	0

for about 80% of consultations of herbaria in Denmark and the United Kingdom. On the other hand, the herbaria of some countries, although widely used (e.g. China, Czech Republic, Mexico), have a more national vocation, at least for scientists conducting environmental studies. The United States is unique: the herbaria of this country were, by far, the most widely used for international studies; however the number of studies conducted nationally was so high that international consultations represent only 10% of the total.

The specimens of 14 herbaria were consulted at least 20 times (Table 5). All these herbaria have at least 500,000 specimens in their collections; 12 have more than 1,000,000. All were founded before the 20th century and are located in North America, with the exception of two British institutions: the herbarium of the Royal Botanic Garden at Kew (K) and the herbarium of the Natural History Museum of London (BM). These two herbaria have an essentially international vocation, providing scientists worldwide with specimens not collected in the United Kingdom. The four largest American herbaria respond both to national and international requests. The other herbaria have an essentially national vocation.

Computerized collections

Very few studies ($n = 10$) used computerized collections before 2004 (oldest: Rebelo and Cowling, 1991), but since then, 82 studies benefited from the computerization of collections (Fig. 1). Indeed, the median number of specimens per study rose from 226 (without the use of computerized collections) to 15,295 (with the use of computerized collections). The TROPICOS database of the Missouri Botanical Garden herbarium (MO) was the most widely used database by far ($n = 17$), notably to extract information from a large number (>90,000) of specimens (Schulman et al., 2007; Loiselle et al., 2008; Ahrends et al., 2011). Other databases (e.g. Australia's Virtual Herbarium, Global Biodiversity Information Facility, PRÉCIS Information Database) were also frequently consulted.

Molecular studies

A small number of biogeographical and environmental studies ($n = 17$) used herbarium specimens with molecular analyses; the earliest was published in 2001 (Ristaino et al., 2001). Polymerase

Table 5
Herbaria of the world that were consulted at least 20 times for documenting biogeographical patterns or environmental changes in peer-reviewed studies published from 1933 to February 2012. International consultations (for specimens not collected in the country of the herbaria) are indicated. Numbers include consultations of herbaria that were subsequently integrated into a larger institution (acronyms indicated). Data on herbaria (including acronyms) are from New York Botanical Garden (2012).

Herbarium	Country	Foundation (year)	Specimens (*n*)	Consultations	
				Total (*n*)	International (% of the total)
Missouri Botanical Garden (MO)	USA	1859	5,870,000	66	50.0
Harvard University (GH, including A, AMES, FH, NEBC, WELC)	USA	na	5,005,000	58	27.6
New York Botanical Garden (NY)	USA	1891	7,300,000	56	32.7
Smithsonian Institution (US)	USA	1848	4,340,000	43	32.6
Royal Botanic Gardens (K)	United Kingdom	1852	7,000,000	36	87.5
University of Michigan (MICH, including CUS)	USA	1837	1,700,000	36	11.1
Canadian Museum of Nature (CAN)	Canada	1882	588,000	34	11.8
Agriculture and Agri-Food Canada (DAO)	Canada	1886	1,035,000	30	6.7
The Natural History Museum (BM)	United Kingdom	1753	5,200,000	29	76.9
University of California (UC)	USA	1872	2,100,000	25	16.0
Field Museum of Natural History (F)	USA	1893	2,700,000	23	21.8
Ohio State University (OS, including OC)	USA	1891	500,000	22	4.5
Academy of Natural Sciences (PH, including PENN)	USA	1812	1,430,000	20	10.0
University of Wisconsin (WIS, including MAD, Y)	USA	1849	1,065,000	20	10.0

chain reaction (PCR), the most common DNA analysis technique, was particularly used to study plant pathogens (e.g. Ristaino et al., 2001; Bearchell et al., 2005; Li et al., 2007; Malmstrom et al., 2007; Hood et al., 2010) and the dispersal of plant or animal invaders (e.g. Saltonstall, 2002; Lelong et al., 2007; Provan et al., 2008; Okada et al., 2009; Lees et al., 2011).

Discussion

This literature review provides a good overview of the use of herbaria for studying biogeographical patterns and various environmental questions. It showed that the number of studies using herbarium specimens as research material has rapidly increased since the beginning of the 1990s, as is the case for studies using animal specimens (Pyke and Ehrlich, 2010). However, this research field is still in its infancy: most studies are less than 10 years old, and only 1.4% of the herbarium specimens worldwide have been used to answer biogeographical or environmental questions. The potential for further development is thus enormous.

To what extent are herbaria used and which are the emerging research topics?

Much research, both fundamental and applied, can be conducted using herbarium specimens. Some research topics, such as plant invasions, pollution and historical floristic assessments, have been well studied for nearly 50 years; the potential for further development is relatively limited. However, there is place for further development, as indicated by recent studies which used plant specimens to evaluate the consequences of ozone-depleting substances on ultraviolet radiation. Moreover, the high number of publications linking herbarium specimens to phenological changes clearly illustrates the potential of this emerging research field. For example, Lavoie and Lachance (2006) showed that earlier flowering in Quebec was only observed in cities, which questions the relative influence of global warming versus the urban heat island effect on plants. Kauserud et al. (2008) observed that mushroom fruiting in Norway was delayed with warming temperatures, which was a totally different response to global warming compared to vascular plants. These discoveries challenge perceptions regarding the impacts of climate change on vegetation. Other extremely promising avenues awaiting further exploration include the use of damaged herbarium specimens for studying insect outbreaks (Lees et al., 2011), the study of chemical compounds in plant specimens to determine variations in plant toxicity over space and time (Zangerl and Berenbaum, 2005; Cook et al., 2009), or the examination of pollen production structures for reconstructing pollination rates (Pauw and Hawkins, 2011). Combined with recently developed procedures to correct biases, herbarium specimens might provide in the near future exciting additional spatio-temporal insights that are currently unimaginable.

Are small and medium sized herbaria as consulted as large institutions?

Not surprisingly, small herbaria are less consulted on a per institution basis than large ones, but by group, they are equally consulted for biogeographical and environmental research though they hold only about 5% of the total number of specimens stored worldwide. Their role is thus non-negligible, especially from a national or local point of view. Smaller facilities typically have collections of historical interest that are not duplicated in larger herbaria (Snow, 2005). For instance, in their reconstruction of the spread of an invasive weed in France with herbarium specimens from 58 European herbaria, Chauvel et al. (2006) found that the four largest herbaria provided only 50% of the total information, and the ten largest 73%. Local herbaria provided a significant number of specimens that improved the quality of the reconstruction.

On the other hand, in most cases, only large herbaria can provide specimens that have been collected worldwide. For scientists conducting world- or continental-scale studies, large herbaria are essential because they contain many high quality specimens available at a much lower overall cost than retrieving the specimens individually from many small national institutions. This is particularly true for very large institutions (>5,000,000 specimens) and those located in European countries with a colonial past (Belgium, United Kingdom, France, The Netherlands, etc.). Some large institutions have also been involved in biodiversity inventory programmes in Africa, Asia and South America, and often have more important collections of plants from these continents than local herbaria located in developing countries.

Has the computerization of collections increased the number of specimens used?

The computerization of herbarium collections began in the 1970s (Crovello, 1972; Forero and Pereira, 1976; Wetmore, 1979). The first large-scale effort (PRÉCIS Information Database) was initiated in South Africa in 1974 (Morris and Glen, 1978), and now includes a total of 900,000 specimens (South African National Biodiversity Institute, 2012). Several other similar initiatives have since been developed (Smith et al., 2003; Graham et al., 2004; Nic Lughadha and Miller, 2009), but not without criticism. Some curators questioned the costs and benefits of internet access to museum data (Graves, 2000), or feared that computerized catalogues would prompt the closure of herbaria, the real specimens becoming obsolete (Lane, 1996; Krishtalka and Humphrey, 2000).

The reality is quite different: specimens that otherwise would have been ignored are now widely used to document biogeographical patterns or answer environmental research questions. The inclusion of thousands of specimens in a single study is now common since the advent of the internet in the 1990s – and this probably explains why very few studies with computerized collection data were published before the 2000s, although such data exist since the 1970s. Only a small fraction of the herbarium specimens of the world have been computerized to date (Nic Lughadha and Miller, 2009), and manual searches are thus still necessary, but even a small percentage (1–2%) of computerized specimens can save thousands of dollars of research costs and help scientists focus on collections likely to contain the most information-rich specimens (O'Connell et al., 2004).

A few years ago, Wheeler et al. (2004) severely criticized the emphasis put on the computerization of collections to the detriment of fundamental systematics research: "*Some naively see the information technology challenge as liberating data from cabinets. The reality is that for all but a few taxa, much data is outdated or unreliable. Many specimens represent undescribed or misidentified species. Rapid access to bad data is unacceptable; the challenge is not merely to speed data access but to expedite taxonomic research*" (p. 285). I do not share the opinion that much data is "outdated or unreliable", but Wheeler et al. (2004) were correct that quality control must be addressed, especially for specimens at risk of misidentification due to storage in institutions without the relevant taxonomic expertise. Two recent studies clearly illustrate the dangers associated with the use of computerized collections (here, the Global Biodiversity Information Facility) without careful data filtering. Feeley and Silman (2010) showed that georeferencing errors can cause an overestimation of the area occupied by a species by an average of 52%. In some cases, they estimated that georeferencing artefacts were so great that it was impossible to predict whether a species range would increase or decrease under global warming scenarios. Yesson et al. (2007) found that 16% of records of Fabaceae were geographically invalid (mainly located in the ocean), and that there were serious problems of uneven coverage between species and areas for this group of plants. This does not invalidate the use of this database – after all, 84% of records were correctly georeferenced – but rather cautions against using computerized collections without any form of quality control.

Are biogeographers and ecologists using molecular techniques with herbarium specimens?

The potential of herbarium specimens for molecular analysis has been known for more than two decades (Taylor and Swann, 1994), and appropriate DNA extraction and amplification protocols have been published since the early 2000s (Drábková et al., 2002). DNA from herbarium specimens is widely used in phylogenetic studies, but to date, few scientists have used ancient DNA to elucidate biogeographical or environmental questions. In a recent review, Gugerli et al. (2005) found 57 plant studies that had used ancient DNA – not extracted from herbarium specimens for the most part – but this represented only 7% of all studies (including animals and microorganisms) that used ancient DNA as research material. It is possible that the low level of polymorphism present in chloroplast and mitochondrial DNA, and the limited number of markers readily available, restricted the use of plant specimen DNA for environmental studies (Gugerli et al., 2005), but Wandeler et al. (2007), in another review, nevertheless qualified as "puzzling" the lack of plant studies with ancient DNA. This research field clearly merits further investigation, especially given the falling costs of molecular analyses.

Conclusion

In 1969, Stanwyn Shetler advocated a solid alliance between taxonomists and ecologists. The ecosystem taxonomist, he wrote, "*will be less concerned with (...) identifications (...) and more concerned with the general, statistical patterns of distribution as they correlate with environmental factors, including pollutants; he will also be concerned (...) with the interrelationships and coevolution of different plants and of plants and animals, including man. Thus he will need a much more flexible access to the data locked up in the herbarium than we now have*" (p. 729). To what extent this alliance has been achieved remains to be defined, but this visionary botanist clearly saw – decades in advance – the vast potential of herbaria for biogeographical and environmental studies. Furthermore, in the context of global environmental change, the value of these institutions is clearly increasing (Johnson et al., 2011; Lister and Climate Change Research Group, 2011). With almost 400 studies demonstrating the potential, more than 350 million plant specimens awaiting examination and internet access to a growing number of specimens, there are no longer any excuses for not exploiting this invaluable resource.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ppees.2012.10.002.

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