

How well do herbarium data predict the location of present populations? A test using *Echinacea* species in Missouri

WENDY L. APPLEQUIST^{1,*}, DANIEL J. MCGLINN²,
MICHELE MILLER^{3,4}, QUINN G. LONG^{3,5} and JAMES S. MILLER¹

¹William L. Brown Center for Plant Genetic Resources, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166-0299, USA; ²Botany Department, Oklahoma State University, 117 LSE, Stillwater, OK 74078, USA; ³Division of Biological Sciences, 105 Tucker Hall, University of Missouri – Columbia, Columbia, MO 65211-7400, USA; ⁴Current address: Kansas Migrant Education Program, 231 E. Madison, P.O. Box 97, Gardner, KS 66030, USA; ⁵Current address: Department of Ecology and Evolutionary Biology, 2041 Haworth Hall, 1200 Sunnyside Ave., The University of Kansas, Lawrence, KS 66045, USA; *Author for correspondence (e-mail: wendy.applequist@mobot.org; phone: +1-314-577-0267; fax: +1-314-577-0800)

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Abstract. The four native Missouri taxa of *Echinacea* were used as a model to test the predictive value of herbarium data with regard to present-day distribution. Specimens with label data considered potentially adequate to relocate the population were databased and the sites in question were visited. Most of the historical populations were not relocated, although a greater percentage of those collected post-1980 were found to still exist. Time since collection significantly affected the probability of relocation of *E. purpurea* and *E. pallida* var. *pallida*, the two native taxa commonly harvested for medicinal products. The collection rate for *E. pallida* var. *pallida* remained high over time. However, the collection rate for *E. purpurea* has been much reduced in recent decades. Few of the historical populations were relocated, and located populations on unprotected public land were very small, perhaps indicating that habitat loss or human activity is causing a decline in Missouri populations of *E. purpurea*.

Introduction

In floristic and taxonomic studies, the distribution of a plant species is typically plotted from locality data on herbarium specimens, which usually provide the best available information regarding distribution. Herbarium specimens are also frequently used to track changes, usually expansions, in the range of a species over time (e.g., Stuckey 1980; Pyšek 1991; Weber 1998; Delisle et al. 2003), to study the distribution and prevalence of plant pathogens (e.g., Ristaino 1988; Koponen et al. 2000; Antonovics et al. 2003), and sometimes to identify temporal changes in phenotype, genotype or phenology within a specified range (e.g., Parkhurst 1978; Saltonstall 2002; Primack et al. 2004). In addition to these uses, herbarium records may play a critical role in assessing conservation status, conservation priorities, or changes over time in species

frequency (e.g., Burgman et al. 1995; MacDougall et al. 1998; Funk et al. 1999; ter Steege et al. 2000; Golding 2001; Hedenas et al. 2002; Schatz 2002; Willis et al. 2003; Ungricht et al. 2005). However, it has been found that floristic records provide limited accuracy in predicting distribution, as many populations may have been overlooked due to inadequate geographic coverage or various collection biases (e.g., Rich and Woodruff 1992; Heyligers 1998; MacDougall et al. 1998; Ungricht et al. 2005). An additional source of error may be that previously documented populations are no longer present; Kropf and Bernhardt (2004) found that of 13 Austrian populations of *Anthyllis montana* subsp. *jacquinii*, documented by 305 herbarium collections, seven were apparently extinct. As the assumption may be made by potential end users that a dot map based on herbarium specimens represents current presence at the indicated localities, especially for conservation purposes it would be valuable to have some estimate of the validity of historical data in predicting current distributions.

The fact that a species has not been collected recently from a particular area certainly does not indicate that it is no longer present, as many regions are very sparsely collected. Moreover, even if a formerly present species does not occur in later collections from the same locality, this may indicate not genuine loss of the population but chance failure to relocate it, collection at the wrong time of the year, etc. Nilsson and Nilsson (1983) determined that the apparent rate of species turnover on six carefully surveyed small islands was up to three times the actual rate, with the excess being due to sampling error, and one might assume that sampling error would be greater in larger areas that are more diverse and less thoroughly studied.

The central purpose of the present study was to test the predictive value of herbarium collections by attempting to relocate historical populations of *Echinacea* that were documented in herbarium collections from the state of Missouri. *Echinacea* is endemic to North America; the most recent revision (Binns et al. 2002) recognized four species, most including multiple varieties that correspond to the nine species in the treatment by McGregor (1968). Thus, the four taxa native to Missouri are *E. atrorubens* (Nutt.) Nutt. var. *paradoxa* (J. B. Norton) Cronq., *E. pallida* (Nutt.) Nutt. var. *pallida*, *E. pallida* var. *simulata* (McGregor) Binns, and *E. purpurea* (L.) Moench. according to Binns et al.'s (2002) classification, but *E. paradoxa* (J. B. Norton) Britton, *E. pallida*, *E. simulata* McGregor, and *E. purpurea* according to McGregor's (1968) classification, which remains the more commonly used at present. *Echinacea pallida* var. *pallida* and *E. purpurea* are in commercial demand for their medicinal value, and harvest usually involves collection of the roots; thus, these species are of conservation concern as it is not clear that the level of harvesting in some regions is sustainable. Another rationale for selecting *Echinacea* as a model was that it often grows in fairly open areas and is conspicuous when in flower. Thus, if the locality is sufficiently well defined, geographically limited, and accessible, it is frequently possible for the observer to declare with relative certainty that the plant is or is not present, which is not the case for smaller, less conspicuous plants growing in less open habitats.

Methods

The herbaria at the Missouri Botanical Garden (MO) and University of Missouri – Columbia (UMO), which represent two of the largest holdings of Missouri collections, were inventoried for *Echinacea* specimens from Missouri. Specimens were found of the four taxa native to Missouri, including *E. atrorubens* var. *paradoxa* (J. B. Norton) Cronq., *E. pallida* (Nutt.) Nutt. var. *pallida*, *E. pallida* var. *simulata* (McGregor) Binns, and *E. purpurea* (L.) Moench. *Echinacea atrorubens* var. *paradoxa* was collected from the southwestern quadrant of Missouri, and *E. pallida* var. *simulata* from the southeastern quadrant. *Echinacea purpurea* and *E. pallida* var. *pallida*, the two native taxa used in commercial botanical products, were widely distributed (see Figure 1). There were 4 specimens identified as *E. pallida* var. *angustifolia* (DC.) Cronq. and 27 initially identified as *E. pallida* var. *tennesseensis* (Beadle) Binns, which were generally either collected from cultivation, obviously introduced, or misidentified as in the case of most older collections supposed to be var. *tennesseensis*. These varieties are not believed to occur naturally in Missouri, and neither was observed in the field. Because *E. pallida* var. *pallida* and var.

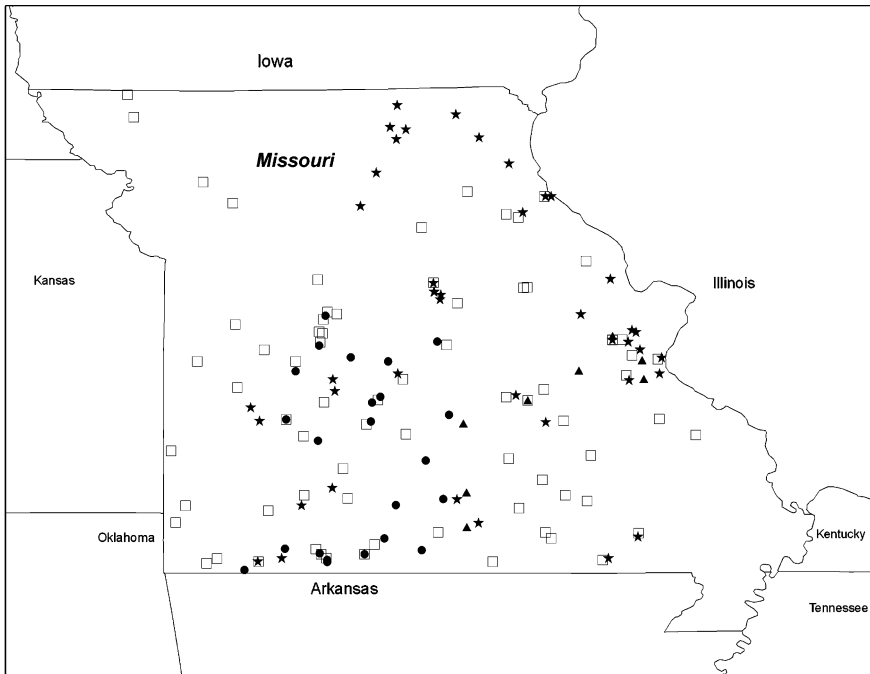


Figure 1. Dot map of the state of Missouri showing distribution of native *Echinacea* taxa, based on historical collections from MO and UMO having adequate label data to permit georeferencing. ● = *E. atrorubens* var. *paradoxa*; □ = *E. pallida* var. *pallida*; ▲ = *E. pallida* var. *simulata*; ★ = *E. purpurea*.

simulata have somewhat different ranges, and because the very broad species concepts recognized by Binns et al. (2002) are still controversial, these two taxa were treated separately rather than being grouped as '*E. pallida*.'

Locality data from these specimens were entered into the Missouri Botanical Garden's TROPICOS database. Certain collections from markets and from the Missouri Botanical Garden's St. Louis grounds were considered not to genuinely represent Missouri localities and were excluded. Label data were compiled by county, and approximate latitude and longitude of localities with sufficient label data were obtained from a gazetteer. Multiple collections of a single taxon that were clearly collected from a single place were combined into a single locality. Localities were classified as potentially locatable or unlocatable, with a bias toward the former category, given that the sites had not been observed at the time of classification; for example, 'Rocky hillside, Meramec Spring' and 'State Hwy. 42, west of Doniphan' were counted as potentially locatable, whereas 'vicinity of Columbia,' a sprawling large town, was counted as unlocatable. A number of collections that were clearly on private property and probably of planted horticultural material were classified as unlocatable to avoid the difficulties of gaining access to those sites.

In late summer, we traveled to potentially locatable sites and attempted to relocate the expected species or varieties of *Echinacea*. During the course of field work, some sites were discovered to be inaccessible by road or otherwise unable to be reached without excessive effort, thus were excluded from the analyses as unlocatable. Presence or absence of the expected taxon was recorded for each accessible site. In some cases, the locality was reached and *Echinacea* was not observed, but such factors as terrain or the size of the potential collecting area prevented an exhaustive search, so the locality was scored as 'unknown' rather than indisputably 'absent.' Voucher specimens were collected from relocated populations whenever possible; in some instances, populations were on private property and permission to collect could not be obtained. Any obvious threats to the population, such as grazing or development, were recorded.

For purposes of discussion, specimens were divided into three age categories: pre-1950, 1950–1980, and post-1980 (up to 2002). This division was made arbitrarily; as *Echinacea* species are perennials that may live for decades if undisturbed, it was felt that specimens from the last 20 years or more might plausibly be considered recent. Also, those break points were convenient in that no potentially locatable specimens were collected during the selected years. Notably, there was a distinct drop in collection activity throughout the 1940s and early 1950s, so that no potentially locatable specimens were dated between 1944 and 1950, possibly due in part to sociopolitical events including World War II.

We performed two separate analyses: one analysis treated 'unknown' scores as 'absent' scores, while a second analysis excluded 'unknown' sites and analyzed only data points scored as 'present' or 'absent'. We built logistic regression models (Quinn and Keough 2002) with date of collection as

the independent variable to test the null hypothesis that the probability of reoccurrence did not change through time. All analyses were performed using the statistical software system R (R Development Core Team 2004).

Results

The surveyed herbaria contained 51 collections of *E. atrorubens* var. *paradoxa*, the oldest dating to 1897, representing 25 unique and potentially locatable sites (date range 1926–1996); 131 collections of *E. pallida* var. *pallida*, the oldest dating to 1865, representing 74 potentially locatable localities (date range 1904–2000); 12 collections of *E. pallida* var. *simulata*, representing 8 potentially locatable localities (date range 1928–2000); and 123 collections of *E. purpurea*, the oldest dating to 1878, representing 42 potentially locatable localities (date range 1915–1999). These collections were categorized by age (Table 1), divided into the categories of pre-1950; 1951–1980; and post-1981. Across the four native taxa, 24% of the pre-1950 collections represented unique, potentially

Table 1. Numbers of unique, potentially locatable collecting localities and total collections for the four native species of *Echinacea* in Missouri, in total and broken into predetermined age categories, with collecting date ranges for locatable collections and the number and percentage of visited localities at which the population was found to be present, absent or unknown.

Taxon	#Locatable/ Total	Date range ^a	Present # (%)	Absent # (%)	Unknown ^b # (%)
<i>E. atrorubens</i> var. <i>paradoxa</i>	25/51	All	13 (52)	8 (32)	4 (16)
early	9/25	1926–1937	4 (44)	3 (33)	2 (22)
middle	7/12	1951–1978	2 (29)	4 (57)	1 (14)
recent	9/14	1981–1996	7 (78)	1 (11)	1 (11)
<i>E. pallida</i> var. <i>pallida</i>	74/131	All	27 (36)	37 (50)	10 (14)
early	12/52	1904–1940	2 (17)	8 (67)	2 (17)
middle	27/35	1954–1979	4 (15)	17 (63)	6 (22)
recent	35/44	1981–2000	21 (60)	12 (34)	2 (6)
<i>E. pallida</i> var. <i>simulata</i>	8/12	All	5 (63)	2 (25)	1 (13)
early	1/3	1928		1 (100)	
middle	3/4	1969–1978	3 (100)		
recent	4/5	1989–2000	2 (50)	1 (25)	1 (25)
<i>E. purpurea</i>	42/123	All	5 (12)	24 (57)	13 (31)
early	17/82	1915–1943		11 (65)	6 (35)
middle	19/24	1954–1979	3 (16)	10 (53)	6 (32)
recent	6/17	1988–1999	2 (33)	3 (50)	1 (17)

^aDate ranges are broken into early (pre-1950), middle (1950–1980) and recent (post-1980) ranges; dates given in table represent actual dates of specimen collection.

^bUnknown = not found but still potentially present.

locatable localities, compared to 75% of the 1951–1980 collections and 68% of the post-1981 collections. Table 1 shows for each taxon the number and percentage of potentially locatable sites, broken down by date range, for which the target taxon was present, absent, or unknown (the last representing sites at which the taxon appeared to be absent but its presence could not be excluded with certainty).

Both age and taxon appeared to affect the probability of relocation of a taxon at potentially locatable sites. While 36% of *E. pallida* var. *pallida* populations were present at the original sites, only 12% of *E. purpurea* populations were present; 52% of *E. atrorubens* var. *paradoxa* populations were present and 63% of *E. pallida* var. *simulata* populations, although the latter in particular had few and primarily recent collections. Within *E. pallida* var. *pallida*, only 17% and 15% respectively of populations from the first two date ranges were relocated, vs. 60% of the post-1980 date range; within *E. purpurea*, no pre-1950 populations were relocated, vs. 16% and 33% respectively of potentially relocatable populations from the two later date ranges. No correlation between geography and the probability of recollection was apparent; collections from the northernmost counties of Missouri appeared less likely to be recollected, but these collections were older than average, as recent collections from that region are sparse.

Logistic regression curves created using only ‘present’ and ‘absent’ data points are displayed in Figure 2. Model chi-square tests (Table 2) indicated that the probability of relocation varied significantly in relation to the time of collection for *E. pallida* var. *pallida* ($p = 0.004$) and in *E. purpurea* ($p = 0.015$), but not in *E. pallida* var. *simulata* ($p = 0.338$), for which only a handful of data points were available, nor in *E. atrorubens* var. *paradoxa* ($p = 0.737$). Results were similar if ‘unknown’ data points were counted as absent (Table 2), with the probability of relocating a taxon being lowered in certain cases (notably in *E. atrorubens* var. *paradoxa* and in recent collections of *E. purpurea*). The probability curves for *E. atrorubens* var. *paradoxa* and

Table 2. The results of the logistic regression models for each taxon.

Taxon	Analysis	Years considered	Number of records	χ^2	p^a
<i>E. pallida</i> var. <i>pallida</i>	Unknowns included	1904–2000	74	10.408	0.001
	Unknowns excluded	1904–2000	65	8.424	0.004
<i>E. purpurea</i>	Unknowns included	1915–1999	42	5.986	0.014
	Unknowns excluded	1932–1996	29	5.934	0.015
<i>E. atrorubens</i> var. <i>paradoxa</i>	Unknowns included	1926–1996	23	0.918	0.762*
	Unknowns excluded	1926–1996	18	0.113	0.737*
<i>E. pallida</i> var. <i>simulata</i>	Unknowns included	1928–2000	8	0.455	0.500*
	Unknowns excluded	1928–2000	7	0.919	0.338*

Date of collection was used to predict reoccurrence in each model.

^aProbabilities (p) are for model χ^2 tests evaluating whether the null hypothesis of zero change in the probability of reoccurrence through time was rejected. Bold lettering identifies those p values that are significant (≤ 0.05).

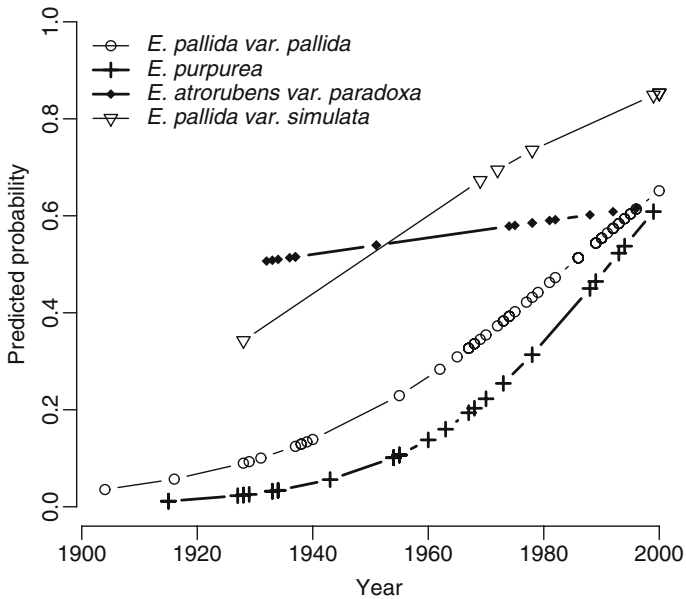


Figure 2. Logistic regression curves showing relationship between time since collection and predicted probability of relocation for all four native *Echinacea* taxa in Missouri, with 'unknown' data points excluded.

E. pallida var. *simulata* are less reliable because very few data points were available for the analysis of these taxa.

Discussion

In attempting to locate populations from herbarium data, two types of errors are possible: false positives, in which the population located is present at or near the original locality but is not the same population, and false negatives, in which the population is still present but is not located. False positives may result from inadequate label data, allowing too broad an area to be searched, although a false positive of this nature would still demonstrate the continuing presence of the plant in the near vicinity. False positives may also result from planting or replanting of cultivated material. Many *Echinacea* populations in Missouri are along roads, where they are sometimes planted. In several cases, the expected species of *Echinacea* was not found at a locality but another was; it is possible that the original population died out or was destroyed and was later replanted (although previous sympatry, with one taxon now locally extinct, would present the same appearance). Had the population been replaced with plants of the same variety, the historical discontinuity would not have been observable.

False negatives, like false positives, may result from inadequate label data, so that the field collector has too large a potential area to cover and is unable to find the population. In this study, such instances probably occurred, as locatability was generously assessed in order to maximize the number of localities included, although the category of 'unknown' as opposed to 'absent' was introduced to acknowledge the potential for such errors and the primary statistical analysis conservatively excluded 'unknown' data points. Some plants are difficult to locate even when the locality is well specified, because they are rare, inconspicuous, and/or found in habitat that is difficult to search thoroughly (e.g., ginseng or goldenseal). *Echinacea* populations are fairly conspicuous, and false negatives of this type were assumed to be minimal. Error rates are therefore not likely to have been high enough to significantly bias the conclusions of this study.

We expected that a lower percentage of older collections would be counted as potentially relocatable, even under a generous standard, and likewise that a lower percentage of the potentially locatable older collections would be relocated, both because the label data were of poorer quality and because more time had passed in which population extinction might occur. This proved to be the case (Table 1); in the two widespread taxa, *E. pallida* var. *pallida* and *E. purpurea*, the effect of time was significant and the predicted probability of relocation drops below 50% after 20 years or less (Figures 2). Older populations were usually absent from the sites where they had been collected. Of course, we have no means of estimating the rate at which new populations have come into being. The apparent loss of many historical populations cannot, therefore, be taken as evidence that the total number of populations in Missouri has decreased. Furthermore, some populations may undergo apparent extinction and later re-emerge from a persistent seed bank, or may exist as shifting metapopulations in which individual localities within a region are repeatedly recolonized following local extinction (Freckleton and Watkinson 2002).

There were differences among species in collection frequency as well as relocation rates over time. The collection rate of *E. purpurea* has dropped (82 collections before 1943, 24 between 1954 and 1979, vs. 17 after 1985; moreover, a disproportionate number of the post-1985 collections were cultivated in inaccessible private gardens and the like, so that only 6 of 17 were counted as locatable). This could be attributed simply to reduced botanical collection in recent decades (e.g., Delisle et al. 2003). However, the collection rate of *E. pallida* var. *pallida*, which like *E. purpurea* is widely distributed in Missouri, has increased and remains steady (52 collections before 1940 and 35 collections between 1954 and 1979, vs. 44 after 1981). This may indicate that relatively fewer populations of *E. purpurea* are now accessible to field collectors. Relative collections of *E. pallida* may also have increased because it is more frequently found along roadsides, where it may be conveniently collected. Six extant populations of *E. purpurea* were observed during the course of this study (including one not documented by a previous collection). The two populations

seen on unprotected public land were both very small (ca. 12–20 mature individuals), indicating potential threat to those populations.

Given the fact that a sizeable majority of the older populations were not recollected, it is worth enquiring into the characteristics of the relocated populations that enabled them to survive for extended periods of time. Six populations of *E. pallida* var. *pallida* dating between 1904 and 1979 were relocated, and three populations of *E. purpurea* dating between 1954 and 1979. These populations of *E. pallida* var. *pallida* were located on publicly accessible, state-owned or otherwise protected land, four of them along roadsides. While state protection may have preserved these populations, such populations may also be replanted if necessary as part of a beautification program, increasing the likelihood that the populations collected may not in fact have been the original populations. Two older *E. purpurea* populations were entirely or primarily located in privately owned woodlands; another was along the edge of a wood near a county road, and included only about 20 mature flowering plants.

The findings that *E. purpurea* collections have decreased in number relative to collections of the other widespread taxon, that historical populations are less likely to be relocated than those of other species, and that surviving populations are sometimes very small, together provide cause for concern that *E. purpurea* in Missouri may be facing unsustainable pressures resulting in a long-term decline in numbers. There has been concern about the effects of excessive wildcrafting on populations of *E. purpurea*, which has been favored over *E. pallida* in the medicinal plants trade because some believe it to be more potent, and perhaps because it is larger and provides more usable material per plant. Moreover, *E. purpurea* is often found in woodland glades, a habitat that is probably more threatened in Missouri than the open areas preferred by *E. pallida*. Encroachment of woody cover into glades, resulting from often human-influenced processes such as fire suppression, can choke out herbaceous species; Kimmel and Probasco (1980) found that open space in Missouri glades, as assessed by aerial photography, diminished from 50% in 1938 to 16% in 1975. At least one *E. purpurea* population in such a glade was observed to have near-total shade cover over about 50% of the population, with woody plants encroaching on the remaining 50%. Long-term research plots should be set up and maintained to directly examine the effect of habitat degradation, harvesting, and other environmental pressures on population viability of *Echinacea purpurea* in Missouri.

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References

- Antonovics J., Hood M.E., Thrall P.H., Abrams J.Y. and Duthie G.M. 2003. Herbarium studies on the distribution of anther-smut fungus (*Microbotryum violaceum*) and *Silene* species (Caryophyllaceae) in the eastern United States. *Am. J. Bot.* 90: 1522–1531.
- Binns S.E., Baum B.R. and Arnason J.T. 2002. A taxonomic revision of *Echinacea* (Asteraceae). *Syst. Bot.* 27: 610–632.
- Burgman M.A., Grimson R.C. and Ferson S. 1995. Inferring threat from scientific collections. *Conserv. Biol.* 9: 923–928.
- Delisle F., Lavoie C., Jean M. and Lachance D. 2003. Reconstructing the spread of invasive plants: taking into account biases associated with herbarium specimens. *J. Biogeogr.* 30: 1033–1042.
- Freckleton R.P. and Watkinson A.R. 2002. Large-scale spatial dynamics of plants: metapopulations, regional ensembles and patchy populations. *J. Ecol.* 90: 419–434.
- Funk V.A., Zermoglio M.F. and Nasir N. 1999. Testing the use of specimen collection data and GIS in biodiversity exploration and conservation decision making in Guyana. *Biodivers. Conserv.* 8: 727–751.
- Golding J.S. 2001. Southern African herbaria and Red Data Lists. *Taxon* 50: 593–602.
- Hedenas L., Bisang I., Tehler A., Hamnede M., Jaederfelt K. and Odelvik G. 2002. A herbarium-based method for estimates of temporal frequency changes: mosses in Sweden. *Biol. Conserv.* 105: 321–331.
- Heyligers P.C. 1998. Some New South Wales coastal plant distributions: a comparison of herbarium records with transect survey data. *Cunninghamia* 5: 645–664.
- Kimmel V.I. and Probasco G.E. 1980. Change in woody cover on limestone glades between 1938 and 1975. *Trans. Mo. Acad. Sci.* 14: 69–74.
- Koponen H.S., Hellqvist H., Lindqvist-Kreuzer H., Bang U. and Valkonen J.P.T. 2000. Occurrence of *Peronospora sparsa* (*P. rubi*) on cultivated and wild *Rubus* species in Finland and Sweden. *Ann. Appl. Biol.* 137: 107–112.
- Kropf M. and Bernhardt K.-G. 2004. The historical distribution of *Anthyllis montana* subsp. *jacquini* (Fabaceae) in Austria: insights from herbarium material. *Planta Europaea*, 4th European Conference on the Conservation of Wild Plants, 17–20.09.2004, Valencia, Spain. Available on the World Wide Web at http://www.nerium.net/plantaeuropaea/Download/Proceedings/Kropf_Bernhart.pdf [sic; accessed 2 May 2005].
- MacDougall A.S., Loo J.A., Clayden S.R., Goltz J.G. and Hinds H.R. 1998. Defining conservation priorities for plant taxa in southeastern New Brunswick, Canada using herbarium records. *Biol. Conserv.* 86: 325–338.
- McGregor R.L. 1968. The taxonomy of the genus *Echinacea* (Compositae). *Univ. Kansas Sci. Bull.* 68: 113–142.
- Nilsson S.G. and Nilsson I.N. 1983. Are estimated species turnover rates on islands largely sampling errors? *Am. Nat.* 121: 595–597.
- Parkhurst D.F. 1978. The adaptive significance of stomatal occurrence on one or both surfaces of leaves. *J. Ecol.* 66: 367–383.
- Primack D., Imbres C., Primack R.B., Miller-Rushing A.J. and Del Tredici P. 2004. Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. *Am. J. Bot.* 91: 1260–1264.

- Pyšek P. 1991. *Heracleum mantegazzianum* in the Czech Republic: dynamics of spreading from the historical perspective. *Folia Geobotanica et Phytotaxonomica* 26: 439–454.
- Quinn G. and Keough M. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge, UK.
- R Development Core Team 2004. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Rich T.C.G. and Woodruff E.R. 1992. Recording bias in botanical surveys. *Watsonia* 19: 73–95.
- Ristaino J.B. 1988. The importance of archival and herbarium materials in understanding the role of oospores in late blight epidemics of the past. *Phytopathology* 88: 1120–1130.
- Saltonstall K. 2002. Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. *Proc. Natl. Acad. Sci. USA* 99: 2445–2449.
- Schatz G.E. 2002. Taxonomy and herbaria in service of plant conservation: lessons from Madagascar's endemic families. *Ann. Mo. Bot. Gard.* 89: 145–152.
- Stuckey R.L. 1980. Distributional history of *Lythrum salicaria* (purple loosestrife) in North America. *Bartonia* 47: 3–20.
- ter Steege H., Jansen-Jacobs M.J. and Datadin V.K. 2000. Can botanical collections assist in a National Protected Area Strategy in Guyana? *Biodivers. Conserv.* 9: 215–240.
- Ungricht S., Rasplus J.-Y. and Kjellberg F. 2005. Extinction threat evaluation of endemic fig trees of New Caledonia: priority assessment for taxonomy and conservation with herbarium collections. *Biodivers. Conserv.* 14: 205–232.
- Weber E. 1998. The dynamics of plant invasions: a case study of three exotic goldenrod species (*Solidago* L.) in Europe. *J. Biogeogr.* 25: 147–154.
- Willis F., Moat J. and Paton A. 2003. Defining a role for herbarium data in Red List assessments: a case study of *Plectranthus* from eastern and southern tropical Africa. *Biodivers. Conserv.* 12: 1537–1552.