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Antje Burke

Biodiversity Patterns in Arid, Variable Environments

A Case Study of Namibian Inselberg and Mountain Floras

Despite its importance for tourism and rural development, the biogeographic status of semi-desert and savanna transition inselbergs and mountains in central Namibia is poorly known. This study therefore investigates 11 inselbergs and their mountain flora in the central Namib Desert with regard to biogeographic patterns. Variation between seasons in variable environments is one of the most critical factors biasing global biodiversity analyses, and often results in lack of biogeographic analysis in these areas altogether. This study shows that patterns in floristic measures were largely maintained when a subset of the data was analyzed that contained only perennial plants (which are visible at these sites also during a poor rainy reason). This approach may hence be adapted in other areas that experience similar problems in data coverage related to seasonal differences.

Keywords: *Biogeography; inselbergs; central Namib; sampling effort; savanna transition; southern Africa.*

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Introduction

The central Namib and semi-desert savanna transition inselbergs (isolated mountains), such as Spitzkoppe and the Brandberg, are among the most important tourism attractions in Namibia (Barnard 1998). The recent development of conservancies and associated tourism facilities have enabled rural communities to participate in income-generating opportunities linked to tourism. This can decrease rural populations' reliance on small stock farming, which is marginal and associated with degradation in some of these arid areas (Burke 2004). Despite these developments and their associated impacts, the conservation importance of these inselbergs is poorly known. One of the reasons is that good biological data coverage suitable for biogeographic analyses is only available for few sites.

Central to all biological fieldwork is the question of when to collect data—eg at what season—when assessing the abundance/presence of species (Eberhardt and Thomas 1991). In arid regions this question often has to be asked in relation to the number and quality of seasons covered by field surveys. Biomass and, in some instances, plant diversity are controlled by the timing and amount of rain received in a particular area, often over a longer time span than the rainy season in which surveys are undertaken (Huenneke et al 2002). Investigating floristic patterns in arid regions is hence always constrained by where, when, and how much rain falls during a particular study period (Günster 1995; Burke 1997). Implementing a sampling design that takes care of these unpredictable events becomes a difficult task and opportunistic sampling has to be applied. Biological data coverage is hence patchy in arid regions, which are often not included in biodiversity hotspot analyses.

As a result, some researchers have questioned global analyses and postulated that the lack of biodiversity hotspots in developing countries may well be the result of lack of data rather than a lack of hotspots per se (Cooper and du Plessis 1998). In other instances, local and regional biogeographic analyses are not carried out (Cowling 2002) owing to lack of adequate data. In this context the question arises whether it is mandatory to ensure that the full complement of all plants growing in a particular area has been recorded or whether using indicators may be adequate (eg Balmford 1998; Reid 1998; Slotow and Hamer 2000). Although biogeographic analyses based on incomplete data are carried out in many parts of the world (eg Lovett et al 2000), whether or not these analyses provide a fair reflection of the true situation has not yet been tested.

From a biogeographic perspective, it is important to understand floristic affinities and the factors that explain them. There is a large influence of scale on biogeographic analyses (Levin 1992, 2000), evidenced by the relationship between regional and local species pools (Caley and Schluter 1997). Investigating patterns at different scales may thus help to unravel important determinants (Gaston 2000; Kluth and Bruelheide 2004) and elucidate drivers of endemism (Green and Ostling 2003).

With the aim of investigating questions related to sampling in variable environments and biogeographic patterns, this study analyzed floristic data for central Namib granite inselbergs and granite mountains. Substrate and landforms were similar, and many of these sites were sampled repeatedly (Nordenstam 1974, 1982; Craven and Craven 2000) to ensure that a near-complete record of the flora was obtained at a particular site. The same questions were investigated with a data set that presented the nearly complete flora at a particular site, and a subset of these data confined to perennial plants that are always visible at these arid sites, even if the rains fail.

The overall objective of this study was to test the hypothesis that trends in biogeographic relationships of a flora are similar if investigated with a near-complete account of the flora or a subset of perennial plants. More detailed questions were: (1) What are the floristic

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affinities between granite inselberg and mountain flora in the central Namib? (2) Are floristic affinities between inselberg and mountain flora related to spatial distances between the sites? (3) How does this relationship vary with geographic scale?

Materials and methods

Study area

The study area is the central Namib Desert and semidesert and savanna transition zone in Namibia (Giess 1971). It includes granite inselbergs in the Tumas, Spitzkoppe, and Brandberg area, as well as the Erongo Mountains (Figure 1; center approximately at 21°30′ latitude South and 15°00′ longitude East). It stretches some 320 km from north to south. The Brandberg rises to 2573 m, with an elevation of approximately 1800 m above the surrounding plains. The Erongo Mountains' highest peak is 2319 m, rising some 1200 m above the plains at its western edge. The inselbergs range from 50 to 470 m in height above the surrounding plains (Table 1).

The study area lies in a transitional zone between the desert, a narrow strip of the Nama Karoo, and the savanna biome in Namibia (Irish 1994). Rainfall decreases from east to west, with a long-term annual average of 290 mm at Omaruru, east of the Erongo Mountains, 134 mm at Usakos at the edge of the desert, and decreasing to as little as 15 mm near the coast (Weather Bureau, Windhoek). Most rains fall in the late summer months (January–March) and rains are unpredictable, highly variable between years, and extremely patchy.

FIGURE 1 The study area and individual sites in Namibia. (Map by author, modified by Andreas Brodbeck)

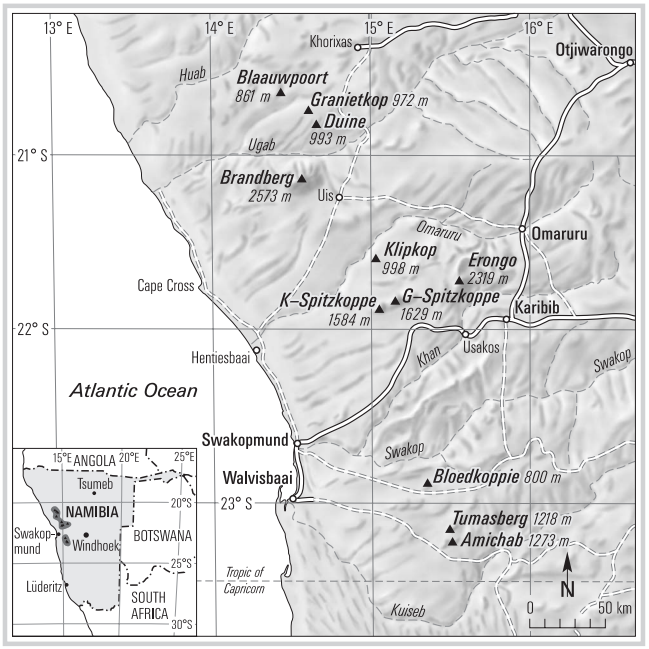
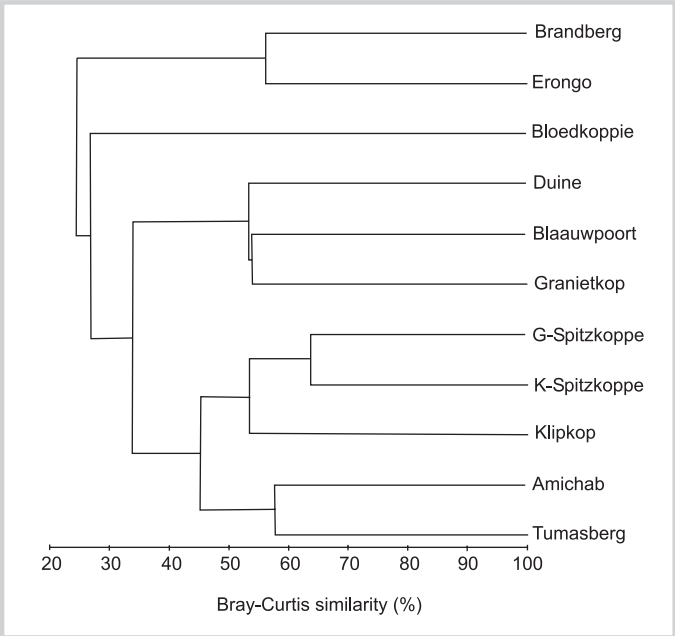


TABLE 1 Number of plant species (unique, frequency = 1) and topographic features of investigated inselbergs and mountains.

Site	Number of plant species			Height above surrounding terrain (m)	Altitude (m asl)	Base area (km²)
	All	Perennial	Unique			
Amichab	80	34	4	290	1273	3.79
Blaauwpoort	94	58	5	221	861	0.73
Bloedkoppie	46	34	1	50	800	0.51
Brandberg	501	205	167	1800	2573	658.98
Duine	80	44	1	100	993	0.99
Erongo	539	202	195	1200	2319	1509.99
G–Spitzkoppe	143	81	5	390	1629	6.85
Granietkop	108	55	3	130	972	5.25
K–Spitzkoppe	138	77	2	470	1584	8.24
Klipkop	101	52	2	220	998	0.73
Tumasberg	93	51	3	220	1218	3.65

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FIGURE 2 Bray-Curtis similarity coefficients for all species indicating floristic relationships between inselberg and mountain floras in the central Namib.



ite, while the Erongo Mountains are composed of a mix of granite and volcanic material, largely rhyolite and undifferentiated basalt lava flows (Geological Survey 1997).

The zonal vegetation in this area has been described as *Calicorema capitata* and *Euphorbia damarana* zone (Hachfeld 2000), with savanna species such as *Acacia reficiens* becoming more prominent towards the east.

Data analyses

Plant species lists were compiled for 11 sites using field data of inselbergs and the Erongo Mountains that were surveyed by the author during the period 1998 to 2004, as well as published data, and data from the Specimens Database of the National Botanical Research Institute of Namibia. The survey methodology has been described in detail by Burke (2002) and is here summarized briefly. To ensure the best coverage, field surveys were undertaken during an above-average season. Plant species abundance was recorded along transects from the bottom to the top of the inselberg or mountain under study, including species occurring nearby. The detailed information on plant species abundance was then summarized to obtain species lists per inselberg. A species list for the Brandberg was based on published information (Craven and Craven 2000), while a species list for the Erongo Mountains was generated using the author's own surveys and data from the Specimens Database of the National Botanical Research Institute. The nomenclature follows Craven (1999).

For the purpose of this study, perennial plants were defined as those that were always visible, even during a poor rainy season. This included all shrubs, trees and perennial succulents, but excluded herbs, geophytes, hemicryptophytes and grasses, some of which are strictly speaking perennials. Two plant species lists were then compiled for each site: one comprising all plant species, the second with perennials only. All analyses were carried out twice, once for all species and then for perennials only. Unique species were defined as those which were only reported once during this study (these are not necessarily endemic to these sites, but were not reported from other sites included in this study).

To investigate the floristic relationship between sites, similarity matrices of the flora data were prepared with the PRIMER computer program (Carr 1997) using the Bray-Curtis similarity index and 4th root transformation of the original data. In order to obtain some indication of surface area, perimeters of all inselbergs and mountains were determined based on topographic maps and then used to determine the (two-dimensional) base area of each inselberg and mountain. Although this is not equivalent to the surface area of an inselberg, it provides a comparative measure of size.

After testing the data for normality, the influence of distance between the sites was explored using linear regression analysis (Zar 1984). Two regression analyses were undertaken: (1) at the regional scale (all data) and (2) at the local scale (data <60 km distance, which excluded all distances beyond geographic areas). A 5% significance level was used in all statistical analyses.

Results

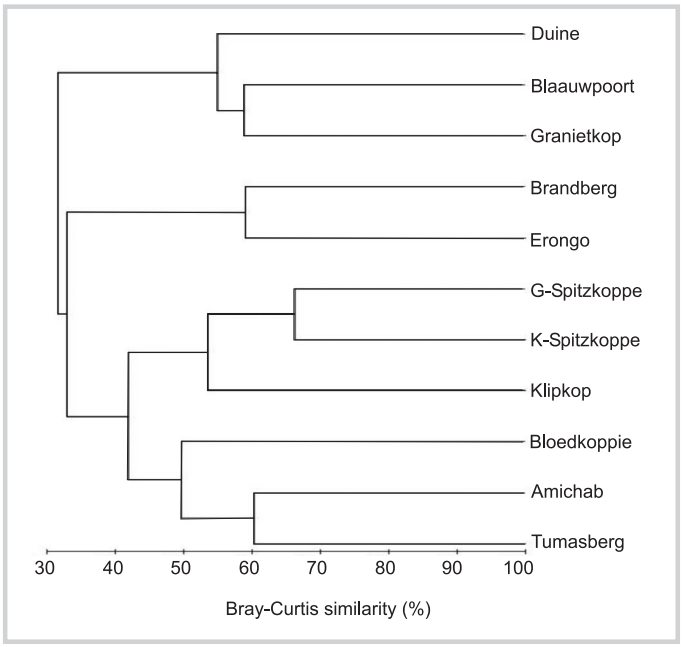
The complete data comprised 790 species of flowering plants, 307 of which were treated as perennials in this study (1982 records, 11 sites). The number of total species per site ranged from 46 to 539. The Erongo and Brandberg mountains showed by far the highest number of species only reported from these sites in this study (Table 1). The stem succulents *Commiphora glaucescens* and *Commiphora saxicola*, as well as the shrubs *Dyerophytum africanum* and *Polygala guerichiana,* were present at all sites, as was the short-lived herb *Forsskaolea candida*. Further frequent species which occurred at nearly all sites were the trees *Boscia albitrunca* and *Sterculia africana*, the stem-succulents *Commiphora virgata* and *Euphorbia virosa*, and the shrubs *Boscia foetida, Cryptolepis decidua, Monechma cleomoides* and *Solanum rigescentoides*. Very frequent short-lived components were *Euphorbia glandulosa, Trichodesma africana* and *Zygophyllum simplex*.

Floristic affinities

When all plant species were included in the analysis, the two large mountains, Brandberg and Erongo, were

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FIGURE 3 Bray-Curtis similarity coefficients for perennial species indicating floristic relationships between inselberg and mountain floras in the central Namib.



clearly separated from the granite inselberg floras, sharing just under 30% of their plant species with the inselbergs (Figure 2). With the exception of Bloedkoppie, the remaining inselbergs formed 3 distinct groups which clearly reflected their spatial relationship to each other. These patterns emerged even more clearly when only perennial plants were included in the analysis (Figure 3). Now there were 3 distinct inselberg groups based on geographic area, and one group comprising the large mountains. However, the hierarchy of these groups differed from that with the complete data. Most separated from other groups were the northernmost inselbergs (Duine, Blaauwpoort and Granietkop). The two large mountains (Brandberg and Erongo) were now only second in separation from the other groups. The hierarchies within groups remained the same, except for Bloedkoppie, which joined the group of the southernmost inselbergs (Amichab and Tumas). Another difference was that similarities were generally slightly higher, eg the most separate group shared more than 30% of its species with other groups.

Floristic affinities and distance between sites

Based on 55 observations, distances between the sites ranged from 9 to 318 km (mean 139.7, standard deviation 87.6) (Table 2). The Bray-Curtis similarity measures for all species ranged between 12 and 64% (mean 34.3, standard deviation 12.3), and for perennials from 19 to 66% (mean 35.6, standard deviation 11.2). The data were normally distributed. Comparing individual observations for all flora on the one hand, and for the perennial flora on the other, indicated that the slightly higher similarities for perennials were generally maintained. However, in some instances similarities of perennials were lower than for all plants (eg more than 1% lower: Amichab–Granietkop, Amichab–Klein Spitzkoppe, Amichab–Klipkop, Blaauwpoort–Klein Spitzkoppe, Duine–Klipkop, Gross Spitzkoppe–Granietkop, Granietkop–Tumasberg, Klein Spitzkoppe–Klipkop, Klein Spitzkoppe–Tumasberg). With the exception of Klein Spitzkoppe–Klipkop, these were all at distances >60 km, ie observations at the regional scale.

At the regional scale (ie when all distance data were included), although positive and significant ($p < 0.001$), the linear correlation between distances and the similarities of floras was very weak ($R^2 = 0.17$, $n = 55$). When only perennial plants were regressed against distances, a highly significant ($p < 0.0001$), positive, but still weak (Fowler and Cohen 1992) correlation was found ($R^2 = 0.36$, $n = 55$). At the local scale (<60 km distance, ie within geographic groups), the linear correlation was positive, significant ($p < 0.0001$), and modestly strong ($R^2 = 0.66$, $n = 15$) (Figure 4). This correlation remained positive and significant ($p < 0.001$), but was slightly lower when only perennials were investigated ($R^2 = 0.52$, $n = 15$).

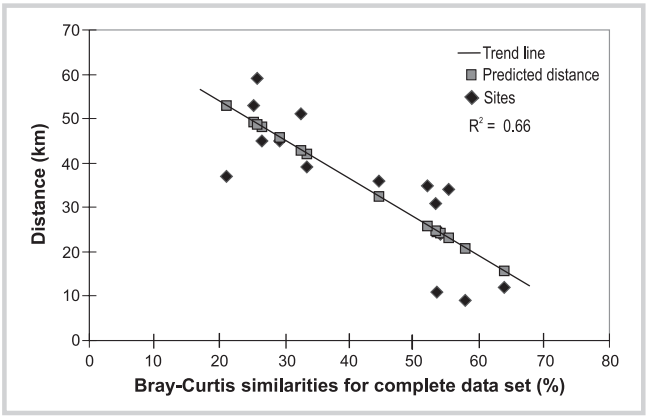
Discussion

Are biogeographic patterns of a complete flora satisfactorily indicated by a subset of the perennial flora in an arid area? Trends regarding floristic affinities were largely maintained; more detailed insights are discussed below.

Floristic affinities

Comparing the outcome of the complete and the perennial data indicated that the general patterns of

FIGURE 4 Distances plotted against Bray-Curtis similarities for sites within a 60-km radius (local level, complete data set).



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TABLE 2 Distances and Bray–Curtis similarity (BC) indices in percent for the complete data set (BC–all) and the perennial subset (BC–per).

From – to	Distance (km)	BC–all (%)	BC–per (%)
Amichab–Blaauwpoort	318	32.98	35.77
Amichab–Bloedkoppie	45	29.33	40.44
Amichab–Brandberg	258	20.29	21.65
Amichab–Duine	287	29.25	31.35
Amichab–Erongo	171	19.07	23.61
Amichab–G-Spitzkoppe	160	41.65	39.54
Amichab–Granietkop	299	31.99	30.06
Amichab–K-Spitzkoppe	159	38.21	36.32
Amichab–Klipkop	193	47.89	46.70
Amichab–Tumasberg	9	57.81	60.30
Blaauwpoort–Bloedkoppie	271	23.82	28.16
Blaauwpoort–Brandberg	59	25.74	36.98
Blaauwpoort–Duine	31	53.22	56.99
Blaauwpoort–Erongo	167	22.98	32.91
Blaauwpoort–G-Spitzkoppe	161	35.56	36.94
Blaauwpoort–Granietkop	24	53.95	58.85
Blaauwpoort–K-Spitzkoppe	160	38.27	35.58
Blaauwpoort–Klipkop	127	36.24	34.97
Blaauwpoort–Tumasberg	310	35.33	34.36
Bloedkoppie–Brandberg	215	13.89	23.43
Bloedkoppie–Duine	243	13.49	19.58
Bloedkoppie–Erongo	130	11.97	22.03
Bloedkoppie–G-Spitzkoppe	117	30.07	38.28
Bloedkoppie–Granietkop	254	16.50	19.98
Bloedkoppie–K-Spitzkoppe	115	29.79	38.28
Bloedkoppie–Klipkop	149	28.19	36.08
Bloedkoppie–Tumasberg	36	44.60	58.82
Brandberg–Duine	37	21.07	27.70
Brandberg–Erongo	120	56.35	58.97
Brandberg–G-Spitzkoppe	104	34.22	44.65
Brandberg–Granietkop	45	26.58	32.46
Brandberg–K-Spitzkoppe	101	32.88	43.86
Brandberg–Klipkop	70	26.18	33.89
Brandberg–Tumasberg	251	23.57	29.69
Duine–Erongo	135	23.63	32.04
Duine–G-Spitzkoppe	128	30.71	32.87
Duine–Granietkop	11	53.51	53.12
Duine–K-Spitzkoppe	129	32.97	31.63
Duine–Klipkop	96	33.21	29.30
Duine–Tumasberg	280	26.61	26.34
Erongo–G-Spitzkoppe	39	33.50	43.72
Erongo–Granietkop	148	27.16	33.57
Erongo–K-Spitzkoppe	51	32.52	42.95
Erongo–Klipkop	53	25.27	32.72
Erongo–Tumasberg	164	23.42	33.20
G-Spitzkoppe–Granietkop	140	37.52	35.46
G-Spitzkoppe–K-Spitzkoppe	12	63.74	66.34
G-Spitzkoppe–Klipkop	34	55.22	56.51
G-Spitzkoppe–Tumasberg	152	47.86	46.66
Granietkop–K-Spitzkoppe	141	37.49	34.15
Granietkop–Klipkop	108	38.41	38.07
Granietkop–Tumasberg	293	32.31	29.03
K-Spitzkoppe–Klipkop	35	51.94	50.51
K-Spitzkoppe–Tumasberg	151	45.47	42.14
Klipkop–Tumasberg	186	51.21	52.98

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floristic groupings were largely maintained and only their hierarchy was affected (Figures 2 and 3). At the regional scale of this analysis, floristic affinities based on perennial plants in this arid area hence provided a good indicator of biogeographic patterns. The change in hierarchy, however, may reflect a change in the relative contribution of explanatory variables, which are complex and likely represented by multiple interactive, abiotic and biotic variables (Huston 1997). For example, when all plants were included, the two large mountains, which provided the largest surface area and the highest altitudes, were clearly separated from the other groups, pointing towards surface area and altitude as critical, but likely not the only aspects controlling floristic relationships (Table 1). Using perennial plants only, the group of high altitude mountains became secondary in importance, and spatial relationships appeared to become more important as explanatory variables for these floristic patterns.

Not surprisingly, the most species-rich sites, Brandberg and Erongo, also showed the highest number of unique plants (ie species recorded only once during this survey). At the same time, these mountains also showed the highest altitude, greatest height above surroundings, and the greatest area (Table 1), indicating the importance of these abiotic variables as well as the conservation importance of these high mountains.

Floristic affinities and distance between inselbergs

Trends in floristic similarities were maintained between complete data and the perennial plant subset at the local level, but 8 sites in the regional distance category (>60 km) showed a reverse pattern. At regional scales there was a low statistical correlation between floristic similarities and distances, for both the complete data and the perennial subset. However, at local scales there was a modest, positive correlation and this was supported by both data sets—although there were slight differences in the strength of the correlation. The influence of scale on biogeographic questions has been demonstrated repeatedly (eg Clark et al 1999; Gaston 2000; Green and Ostling 2003) and was manifested in this study in the results of investigating the influence of distances on floristic relationships at different scales.

In contrast to expectations based on island biogeographic principles, which predict decreasing affinities with increasing distance (MacArthur and Wilson 1967), relationships became stronger with increasing distance between sites at the local level. This likely indicates the complex nature of the influence of abiotic and biotic variables on floristic affinities. There could be several reasons for this pattern: 1) the study area is heterogeneous and environmental variables not considered in this study, which could be called 'hidden treatments' (Huston 1997), were more important than distance; 2) floras within regions are fairly homogenous and the relationship between distance and floristic affinities within a geographic area is random, providing this seeming correlation by chance; or 3) the number of observations (15) may also have been too few to provide a conclusive answer. In fragmented landscapes, connectivity and appropriate corridors between habitat patches are important (eg Hanski et al 1996; Gonzalez et al 1998), more likely than distance between habitat patches per se.

Conclusion

The focus of this study was to find a reasonable surrogate for biogeographic patterns to assist with conservation priority selection at the regional level in a variable, arid environment. Perennial plants provided a fair reflection of biogeographic patterns at the regional scale in this arid area, but indicated that the importance of explanatory environmental variables may change, depending on whether or not a complete set or a subset of the flora was used. The emphasis in this study was, however, on timing and variability between seasons, and not on sampling effort per se. The latter is a question of 1) selecting the correct sampling design for a particular research question (Eberhardt and Thomas 1991) and 2) deciding whether a data set that has been collected for a different purpose is appropriate. Most general botanical collecting has a strong bias towards specific taxa and often reflects easy access to certain areas (Gibbs Russel et al 1984). Where this is the case, such data are of limited value for regional and local scale analyses, but may provide a reasonable indication at the national level.

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