한국생태학회지 27(2): 79～86, 2004 Korean J. Ecol.

Comparing Plant Species Diversity of Mountainous Deserts －Successes and Pitfalls[†]

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ABSTRACT : An extensive study of the vegetation characteristics of the Hamersley Ranges, a mountainous desert area of north-west Australia, facilitated the comparison of plant species diversity measures with mountainous deserts of other parts of the world. Alpha diversity was defined as the number of species co-existing at local scales and was found to average 18 species per 0.1 ha for the Hamersley Ranges. This was found to be similar to seven other mountainous deserts in North and South America, and southern Africa. Variation in alpha diversity between these deserts was found to considerably lower than within deserts, suggesting that local processes control species richness at local scales. Beta diversity, defined here as turnover in species composition at various spatial scales, can be measured in many ways. For the Hamersley Ranges, Wilson's β ranged from 1.2 to 1.6 for five sites along a topographic gradient, whereas Whittaker's β between different plant communities was found to average 0.93. Comparable data was not found for other desert areas, but comparisons to non-desert areas suggest beta diversity within landscapes is relatively high and is likely to reflect the considerable landform heterogeneity of the Hamersley Ranges. 55~70% of species were shared between different landscapes of the Hamersley Ranges; comparisons to other regions suggest beta diversity at this scale is relatively low. Gamma diversity, the number of species over large spatial extents, was successfully compared using regression analysis of the log-log species － area relationship. This revealed that the northern Sonoran desert has significantly less species than the Nama (inland) Karoo and Hamersley Ranges over medium spatial extents, but species numbers were similar at a regional scale. Several constraints to the valid comparison of species diversity were identified, including lack of standardisation of sampling techniques, the wide range of measures employed, general lack of published data, and the influence of the various components of spatial scale on most diversity measures. Recommendations on how to improve future comparative work are provided.

Key words : Community ecology, Desert ecology, Ecological comparisons, Species diversity, Vegetation

INTRODUCTION

Although numerous definitions of deserts abound in the literature, they are defined here, as per Evenari *et al.* (1985), as areas with Thornthwaite moisture index of －40 or less, with the mean temperature of the warmest month above 20℃, and with high to extreme year-to-year rainfall variability. Mountainous deserts then are such areas with marked topographic relief of at least 500 m; these have been mapped at a global scale (Fig. 1). These areas tend to have characteristic landforms such as uplands, pediments, bajada slopes and alluvial flats (Cooke *et al.* 1993).

Although vegetation studies of mountainous deserts are numerous (Goodall and Perry 1981, Evenari *et al.* 1985), little attempt has been made to compare ecological characteristics of the vegetation between deserts. Such comparisons appear limited to comparisons of the Karoo of southern Africa to other deserts (chiefly those of North America) in terms of: dynamics, plant life-forms and community structure (Esler *et al.* 1999); plant species diversity and endemism (Cowling *et al.* 1998, Cowling and Hilton-Taylor 1999); and ecosystem function and structure (Whitford 1999). As a result of the US-IBP program between 1965~74, aspects of plant species diversity, turnover and composition have been compared between the Sonoran and Monte deserts of North and South America respectively (Solbrig *et al.* 1977). Most comparisons between deserts are concentrated at an organism and species level (e.g. identifying convergent evolution), rather than at a community and landscape level of ecology (Whitford 1999). This contrasts with some other biomes where comparisons at such levels have been extensive and rigorous - a good example being Mediterranean shrublands (e.g. Naveh 1967,

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[†] This article was presented at the INTECOL meeting (Seoul, August 2002).

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Kalin Arroyo *et al.* 1995, Cowling *et al.* 1996, Rundel *et al.* 1999).

An extensive study of the vegetation of the Hamersley Ranges, a mountainous desert area of north-west Australia (Fig. 1b), was conducted throughout the 1990's (van Etten 2000). Measures and descriptions of the vegetation characteristics gained from this study enabled a comparison with others area. This was particular important given the lack of comparative work for Australian deserts and the proposition by Stafford Smith and Morton (1990) that Australia's arid zone is ecologically distinct from those elsewhere. The Hamersley Ranges consists of a series of ranges with broad intervening valley systems. Rainfall varies considerably from year to year (coefficient of variability is around 50%), but averages between 250~400 mm depending on locality, with 50~60% of this received during summer months on average. Deserts with similar physical environment include the Sonoran, northern Chihuahuan, Monte, Thar, northern Karoo and southern Kalahari deserts (Fig. 1).

The diversity of species is an important ecological characteristic of plant communities and localities. Convergence in species diversity is taken as strong evidence that the number and types of species in a community or habitat are determined by local, rather than regional, processes (Ricklefs and Schluter 1993). Comparisons of species diversity between similar but separate areas has been attempted numerous times, but is beset with numerous logistic and methodological difficulties (Westoby 1993). This paper compares various measures of species diversity measured for the Hamersley Ranges with deserts of similar physical environment in other parts of the world. The ecological implications and constraints to successful, rigorous comparisons are then described.

METHODS

A plethora of different types of diversity have been recognised. In this study, three types of diversity, commonly known as alpha, beta and gamma diversity, originally recognised by Whittaker (1972), were employed. Alpha (α) diversity is defined as local species diversity and was measured by counting the number species in 0.1 ha plots, 139 of which were randomly placed throughout the Hamersley Ranges within each main landform type. Total alpha diversity was divided into the richness of various life-forms. The data was then compared to published studies elsewhere which employed similar sampling protocol.

Beta (β) diversity is defined as turnover in species composition irrespective of spatial scale. Consequently a number of measures were used. Comparison of species composition between different plots, communities and landscapes of the Hamersley Ranges were performed using the Sorenson Index (Jongman *et al.* 1995). Where a series of plots were orientated along a particular ridge-top to valley floor toposequence, turnover was calculated by the number of species gained or lost along the toposequence divided by twice the mean species richness of plots, here called Wilson's β (Wilson and Shmida 1984). In addition, the ordination score from a one-dimensional solution of multi-dimensional scaling of such plots was plotted against distance along toposequence. Another measure was Whittakers β, calculated from $S/\alpha - 1$, where S = the total number of species found in a community (or area) and α = mean number of species found in each of the samples (e.g. α diversity in 0.1 ha plots) or units (e.g. plant communities).

Gamma (γ) diversity, the number of species occurring over regions or large areas (say greater than 100 km^2) was estimated for various areas of the Hamersley Ranges and similar deserts from flora surveys which were deemed to be comprehensive, thorough and overseen by experienced botanists. Linear regression of the log-log species-area relationship were conducted for different desert regions and the intercepts and slopes compared using *t*-tests. Mean gamma diversity was also compared between different deserts using analysis of covariance with area of survey used as the co-variable (Cowling *et al.* 1998).

RESULTS AND DISCUSSION

Alpha diversity

Alpha diversity, as measured in plots 0.1 ha in size, averaged 18 perennial species for the Hamersley Ranges. This is remarkably similar to the mean alpha diversity of other mountainous deserts with similar rainfall characteristics (Table 1). Each of the desert areas demonstrated a large range in alpha diversity across the landscape, with variability within areas far exceeding that between areas (Table 1). Most desert areas had sites with alpha diversities below 10 as well as sites where it exceeded 30. In the Hamersley Ranges, alpha diversity was highest in rocky uplands and dense shrublands/woodlands on alluvial flats, and lowest on pediment and bajada slopes. Albeit limited in that only eight studies are used, this comparison represents strong evidence for convergence in species diversity at local scales between similar, but widely separated, environments. As such it supports the notion that diversity at this scale is the outcome of local processes such as competition, within-habitat heterogeneity, and disturbance (Schulter and Ricklefs 1993). Indeed the alpha diversity was highest within the Hamersley Ranges where within-habitat heterogeneity was greatest (i.e. rocky areas and dense shrublands), a phenomenon often reported for mountainous deserts (e.g. Noy-Meir 1973, Olsvig-Whittaker *et al.* 1983, Ezcurra *et al.* 1987, Wierenga *et al.* 1987, Parker 1991). Using plots of 0.1 ha creates problems in this regard as it is not possible to separate the contribution that heterogeneity over this area makes toward spe-

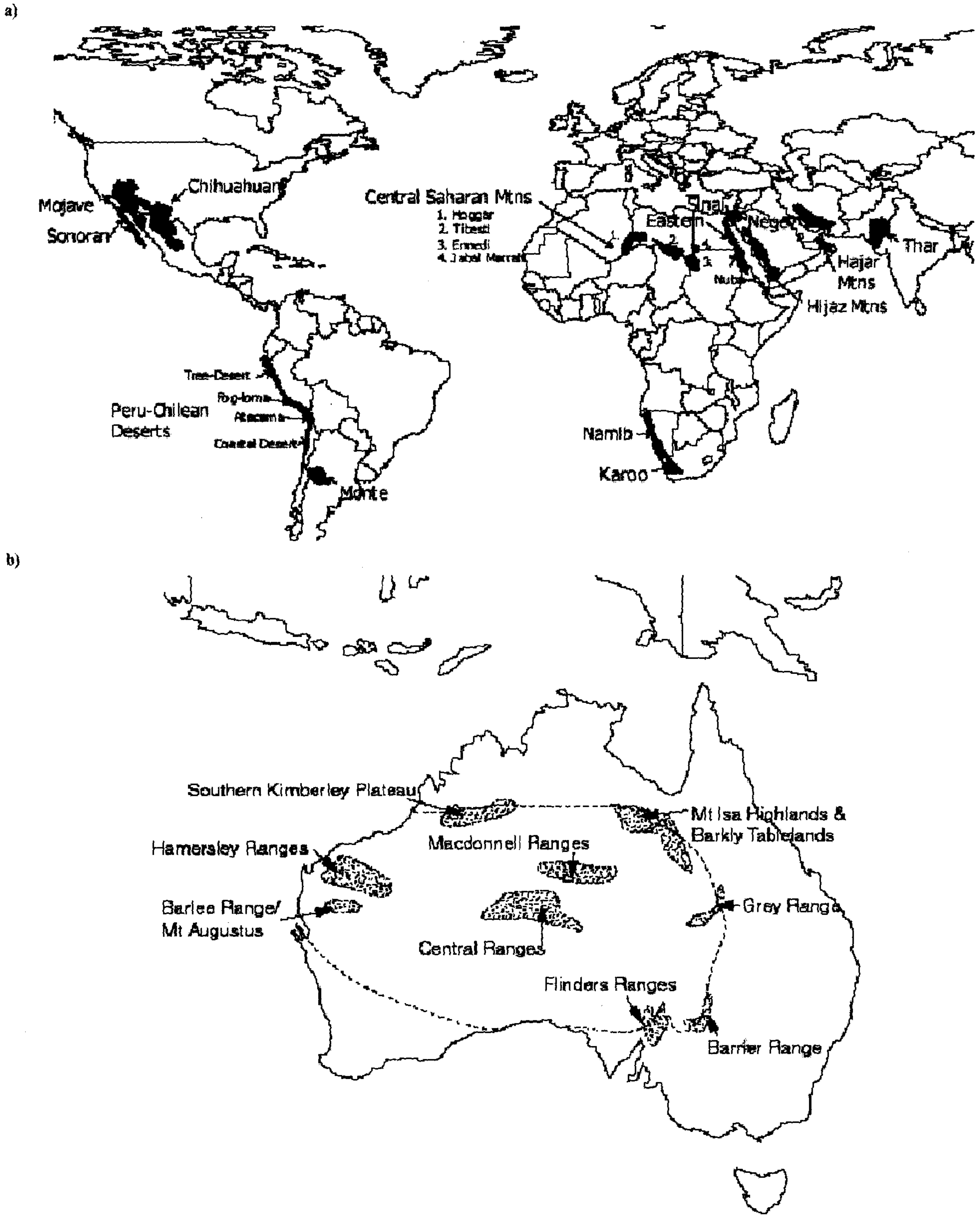

Fig. 1. Maps showing mountainous, warm/hot deserts of: **a)** the world outside of the Australian region; and **b)** the Australian region.

cies numbers from that of finer-scale processes such as competitive exclusion (Tilman and Pacala 1993). Nonetheless 0.1 ha plots have been widely used in studies of desert vegetation as they are effective in capturing the bulk of species present at sites where plant densities may be low (Fox 1981). The eight studies used for comparison followed a reasonably rigorous search of the literature. It is likely that much suitable data remains unpublished or is not clearly documented and the author is keen to hear of such work. Many studies were excluded from the comparison either because of their limited scope and number of replicate plots (a problem given the likely high variability in alpha diversity), or because they used a different plot size. One solution to fairly compare different size plots, as well as to potentially separate the influence of heterogeneity from other local processes, is to compare characteristics of species ?area curves over local scales (Rosenweig 1995).

The comparison is also limited to perennial species. This was because sampling of the Hamersley Ranges occurred over a number of years and seasons, with the number of annual/ephemeral species varying from zero to around thirty per 0.1 ha, depending primarily on the amount of rainfall in the months preceding sampling. At sites where ample pre-sampling rainfall was received, the average richness of annual/ephemeral was 13 per 0.1 ha. Limiting comparisons to perennial species highlighted other difficulties in comparing data. Firstly, some studies couldn't be used because they did not adequately differentiate between perennial and annual species. Secondly, of those that did, problems arose regarding inconsistencies in defining and differentiating perennial species. Some equated them with woody species only, whilst others included short-lived species that can survive longer than a year provided consistent rainfall and soil moisture over such a period (species sometimes known as semi-perennials). Commonly, researchers do not clearly differentiate between life-forms, a difficult issue in itself given that some desert species can, facultatively, change life-forms depending on rainfall patterns (Whittaker and Niering 1965). The third issue relates to the fact that pre-sampling rainfall also influences the number of perennial species present at a site. This was shown for the Hamersley Ranges where rainfall in the three months before sampling was strongly correlated ($r^2 = 0.55$; $p = 0.012$) to perennial species richness (van Etten 2000). In addition to perennial species numbers declining in drought and increasing during fluvial periods, other disturbances, such as fire and wind-storms, would also be likely to influence alpha diversity.

Beta diversity

As previously mentioned, various measures of beta diversity were obtained for the Hamersley Ranges, each with different spatial attributes. Firstly, turnover of species between different patches of the one community across the landscape varied from 0.27 to 0.58 using Whittaker's measure of β diversity. This suggests that from one quarter to just over one half the species found at one site within a community were different at another site of this community, on average. The only other study found which characterised turnover in this way was Cowling (1990), who reported an average within-community turnover of 0.68 for species-rich heathland of the Cape

Table 1. Mean, range and standard deviation of alpha diversity (measured by counting number of perennial plant species in *ca.* 0.1 ha plots) for various mountainous desert areas where n refers to the number of plots

Locality	Mean	Std. Dev.	Range	n	Habitat / Landform
Central Hamersley Ranges, Australia	18	8	4~50	139	All (uplands to basins)
McDonnell Ranges, Australia[1]	17	8	10~34	230	All (uplands to basins)
Murchison Catchment, Australia[2]	17	4	7~30	~150	Wash plains only
Silver Bell, Arizona[3]	13	8	3~31	17	Bajada slopes only
Organ Pipes NM, Arizona[4]	17	5	6~31	100	All (uplands to basins)
Sanpete County, Utah[5]	18	9	11~33	20	Montane slopes only
Joyango, Monte, Argentina[6]	13	6	3~24	11	Bajada slopes only
Nama Karoo, South Africa[7]	23	10	11~50	21	All (uplands to basins)

Sources: 1 = Griffin and Duguid 1997 ; 2 = Curry *et al.* 1994; 3 = Lowe *et al.* 1973; 4 = Parker 1991; 5 = Harner and Harper 1976; 6 = Solbrig *et al.* 1977; 7 = Cowling and Hilton-Taylor 1999.

Botanical Province of South Africa.

The second type of turnover relates to that from one community to another within a given landscape. Here Whittaker's β was 0.93 suggesting a near complete turnover in perennial species from one community to another, on average. This figure was calculated from an overall turnover across the study area of 15 divided by the number of communities delineated (16). No comparative data was found, although the fact that the degree of abstraction in terms of the number of communities delineated is likely to vary between different studies, making comparisons between regions difficult. The overall turnover of 15 (or 0.07 per site) was found to compare favourably to an overall turnover of 9.2 or 0.04 per site (260 × 100 m^2 samples) found by Hopkins and Griffin (1984) for the Mt Lesueur area on the northern coastal sandplains of southwestern Australia. No comparable data was found for desert areas, although, again, it is likely that such data exists in unpublished works or could be readily calculated from existing data sets.

Turnover from one community to another can also be characterised along geographic or environmental gradients. Floristic differences (such as using ordination scores) can be plotted against distance along transect, which characterises transitions between communities as well as their relative differences. There are some examples of this for mountainous deserts (e.g. Ezcurra *et al.* 1987. Phillips and MacMahon 1978), however comparison between regions is difficult. Wilson's β measure attempts to standardise such changes in floristics along gradients. For the Hamersley Ranges Wilson's β was between 1.2~1.6 for 5 sites along gradient from ridge top to valley floor. This is slightly higher than for 5 sites along a major topo-moisture gradient (of 500 m elevation and 300 mm average annual rainfall) within the Nama (inland) Karoo (Palmer and Cowling 1994). Cowling *et al.* (1989) also found a Wilson's β of around 1.5 for 4 sites within the Succulent Karoo, but over a horizontal distance of just 100 m. These turnovers seem small compared to a Wilson's β of 3.1 to 3.8 for 5 sites along soil fertility gradients in the south-western Cape Floristic Region (Cowling *et al.* 1992).

Finally, species turnover was characterised for different landscapes within the Hamersley Ranges region. The three surveyed landscapes were relatively close to one another (60~100 km apart) and similar in terms of geomorphology and vegetation, in that each were ironstone ranges with intervening broad valley systems (Fig. 2). The area furthest south (West Angelas) had 30% or so more species than the others; it was however larger in size and may therefore have sampled a wider variety and/or larger number of habitats and communities. The proportion of shared species (Sorenson Index) was relatively high (55~70%). Most (> 80%) of the species found at the smaller Marandoo and Yandicoogina sites were found at West Angelas indicating a relatively small degree of turnover with distance south (Fig. 2). Cowling *et al.* (1992) reported Sorenson similarities of around 45%~50% for floras of several areas within the Cape Floristic Region. Lamont *et al.* (1984) report a 34% Sorenson Index between two floras 60 km apart and located in healthland of south-west coast Australia. Turnover between landscapes in the Hamersley Ranges seems therefore to be considerably less than these Mediterranean ecosystems. Again, more widespread comparisons are constrained by lack of published data (Cowling *et al.* 1992).

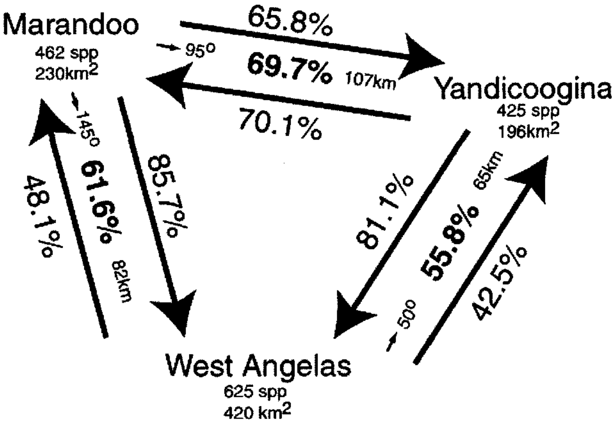

Fig. 2. A comparison of species richness between three landscapes within the central Hamersley Ranges. The number of species ad the area of survey are given under the names of the localities. Figures between arrows refer to the Sorensen Index (%) for the two respective localities, as well as the distance (km) and the direction (deg.) between them. Numbers associated with arrows refer to the percentage of species of one locality (start of arrow) found at the other (end of arrow).

Many ecologists over the years have attempted to better define and measure the turnover component of species diversity. This has led to a wide variety of terminology, approaches and measures (see Wilson and Mohler (1983) for quantitative data; Wilson and Shmida (1984) for qualitative data). Consequently, it can be difficult to find two studies which have measured turnover in exactly the same way. It is obvious that many of the differences between measures of turnover relate to differences in scale. Some authors have proposed different terms to delineate turnovers at different scales, such as beta, gamma, delta and even epsilon diversity (Bond 1989). As these terms do not appear to be standardised, β diversity has been used here to describe all types of turnover irrespective of scale. Table 2 attempts to clarify some of the approaches used to measure turnover in terms of the three main components of scale - that is grain (sample size), sampling intensity and extent (study limits).

Gamma diversity

A similar linear relationship between the log of species number

Table 2. Components of scale for some commonly used measures of species turnover. HC refers to half-change in species composition; plot refers to area used to sample species richness at a site; α refers to mean species richness per plot

Measure	Reference	Description	Measure	Extent	Sampling Intensity	Grain
β	Whittaker (1960)	Turnover between communities	$S/\alpha - 1$	Study area, variable but typically landscape	No. of plots in each community	Community
β	Wilson & Mohler (1983)	Turnover b/n sites along gradient	Rate of change or HC	Transect length; one to many community patches	No. transects	Site
γ or δ	Cody (1986) Whittaker (1972)	Turnover between sites within one community	Sorenson Index or similar	Community type within landscape	No. plots in each community patch	Site
δ	Bond (1989)	Turnover within one community between landscapes	Sorenson Index	Community type within Region	No. community patches	Community
ε	Walker (1989)	Turnover between landscapes in a region	Sorenson Index of 2 or more floras	Region	Variable; typically collation of many surveys	Landscapes

and log of area was found for the three desert regions (Fig. 3). Analysis of covariance (with $\log_{10}$(area) as the concomitant variable) demonstrated that the mean of the logarithm of the number of species was not significantly different between the three regions (F= 2.39; df=2; p=0.114). Indeed, for the whole Sonoran, Nama Karoo and Hamersley Ranges regions, species numbers were all similar, with *ca.*2000 species for 180~200 thousand square kilometres (Fig. 3). t-tests showed that the slope of regression lines were not significantly different from one another (Table 3) despite the slope for the Sonoran being greater than the other two regions (Fig. 3). t-tests comparing the intercept however showed that there was a significant difference in the intercept of the regression line of the Hamersley Ranges and the Sonoran (Table 3). Being a log-log relationship, differences in intercept can mean quite dramatic differences in species numbers. The k ratio of the two intercepts is 2.24. Therefore, in real terms, the relationship predicts that for a similar sized area, there will be just over twice as many species in the Hamersley Ranges compared to the Sonoran. This difference would be more common over medium-sized areas (i.e. 100~1,000 km^2) than at the regional scale given the greater steepness of the Sonoran relationship (Fig. 3). The Sonoran data was derived from plots centred around Arizona. This area of the desert is known to contain fewer species than the Mexican sections further south and west (MacMahon and Wagner 1985). Cowling *et al.* (1998) demonstrated, using similar regression analyses, that deserts with 100~400 mm rain per year and predominantly winter rainfall generally have around one-and-a-half times as many species as those with summer rainfall dominance. Of the winter-rainfall deserts in their data set, the Succulent Karoo of southern Africa is in a league of its own with respect to species numbers (Cowling *et al.* 1998, Esler *et al.* 1999). Without this region, the differences in diversity between summer- and winter-rainfall deserts appear slight.

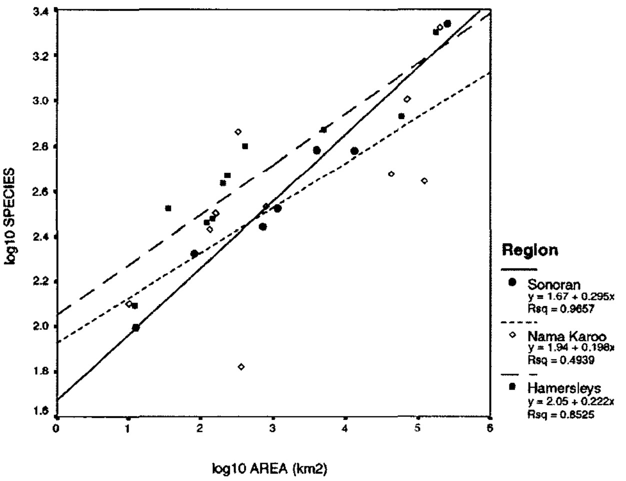

Fig. 3. Species - area relationships for three desert regions following logarithmic transformations of both species number and area. Linear regression line and equation are given for each region.

Table 3. t-tests comparing slope and intercepts of regression lines for the log-log relationship between species and area

Region		Hamersley Ranges			Nama Karoo		
		t	df	p	t	df	p
Nama Karoo	Intercept	0.415	16	0.6	-	-	-
	Slope	0.294	16	0.7	-	-	-
Sonoran	Intercept	2.92	13	0.018*	0.993	13	0.3
	Slope	1.74	13	0.1	1.28	13	0.2

This study has confirmed that regression equations for the log-log species-area relationship are a convenient and insightful way to compare the gamma diversity of arid lands. It also confirms that the Hamersley Ranges harbours about the number of species expected from a region with a mean of *ca.*300 mm rainfall. Rosenweig (1995) recommends that areas used for such regression analysis be spatially nested within one another. This criterion was not always followed in this study, given the difficulties in finding adequate data, which also appears to be the case for data used by Cowling *et al.* (1998). Species richness data for large areas are generally difficult to obtain and are derived either from exhaustive surveys of large areas or regional compilations where much botanical work has been conducted. Consequently sufficient data to analyse species-area relationships are only available for deserts of more developed countries (South Africa, Israel and middle east, North America). This unfortunately limits more detailed and wider comparisons.

CONCLUSION

This paper has highlighted considerable difficulties in fairly and rigorously comparing species diversity between localities and regions. Prime amongst these difficulties is the influence of spatial scale on species numbers. Comparing the relationship between species numbers and area of sample was successful over larger areas here and in and other studies, and could also be employed over finer scales (Rosenweig 1995, Cowling *et al.* 1998). Other components of scale (such as resolution and sampling intensity) can influence diversity measures, particularly beta diversity, and should be standardised for valid comparisons. Pursuing published literature has resulted in limited data for valid comparisons mainly because the primary objectives of much of this research lie elsewhere. Consequently, authors are not always explicit in terms of techniques and definitions of key terms. Perhaps a better approach is sharing raw data amongst researchers with a common aim of comparing diversity measures.

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(*Received December 30, 2003; Accepted April 2, 2004*)