

## Chapter 3: Floristics and Patterns of Plant Diversity.

### *Introduction*

Ultramafic areas have long been recognised because of often dramatic changes in vegetation (Proctor and Woodell, 1975). From the early 1900s a number of publications document serpentine (ultramafic) vegetation in various parts of the world (Proctor and Woodell, 1975). Studies in southern Africa are relatively recent, Wild published a paper on the flora of the Great Dyke of Zimbabwe in 1965 and it was only in 1989 that the Barberton Greenstone Belt ultramafics were investigated (Morrey et al., 1989).

### **Importance of ultramafic sites to plant diversity**

Ultramafic areas usually have unique combinations of plants and often have endemic species (e.g.s Changwe K. & Balkwill K., 2003; González-Torres L.R. *et al.*, 2004; Harrison S. 1999). Species that hyperaccumulate Ni have been found at a number sites (e.g.s Baker A.J.M. *et al.*, 1985; Baker A.J.M. *et al.*, 1992), and disjunct distributions have been reported (Kruckeberg, 2004). Plant cover and species richness of sites tend to follow the general trend of increasing richness towards the equator with some temperate sites described as “barrens” and New Caledonia and Cuba supporting a diverse flora with good plant cover.

The sites in Swaziland are situated in a botanically rich area, the Barberton Centre of Plant Diversity and Endemism and are adjacent to the Maputaland-Pondoland Region (Davis *et al.*, 1994). The area also has diverse topography, soil and climate and these factors together with the high regional diversity make it likely that the ultramafic flora would also be diverse and contribute the region’s plant diversity. Ultramafic patches in Swaziland are relatively small, the largest about 8 x 1.2 km, which would tend to favour “generalist” species (Harrison, 1999), endemic species having less probability of persistence on small habitat patches (Bruun, 2002). This does not preclude the possibility that some of the plants on the ultramafic soils are tolerant races of the species on surrounding soils as was the case, for example, for *Festuca rubra* (Johnston W.R. & Proctor J., 1981). This study will determine plant diversity and level of endemism.

Ultramafic sites in Swaziland are of particular interest because they include the highest altitude sites in southern Africa. These sites, with a temperate climate, are in close proximity to lower sites, with

a subtropical climate. Swaziland thus offers an opportunity to ascertain the effect of altitude on ultramafic vegetation.

## **Plant diversity and conservation**

The urgent need for action to preserve the biodiversity of the planet is recognised by a majority of biologists and many governments (South African Bill of Rights, 1996; Biodiversity Act, 2004). International agreements and summits have resolved that every effort should be made to preserve the biodiversity of earth. “Biodiversity, which plays a critical role in overall sustainable development and poverty eradication, is essential to our planet, human well-being and to the livelihood and cultural integrity of people. However, biodiversity is currently being lost at unprecedented rates due to human activities” (Report of the World Summit on Sustainable Development, Johannesburg, South Africa, 26 August - 4 September 2002). The current extinction rate is 1000 times the baseline rate for the past 65 million years (Raven, 1999), and natural areas are shrinking to a level that would support only 5% of plants and animals (Rosenzweig, 1999). It is therefore imperative that areas that will preserve the greatest diversity be identified as conservation priorities.

There are several reasons why the Swaziland ultramafic sites should be considered as possible conservation priorities. Relative to their comparatively small extent they contribute significantly to the number of endemics in the region. These soils are a source of plants pre-adapted to conditions on ultramafic mine tailings and could be important for restoration (Bradshaw A.D., 1997). Nickel hyperaccumulators have been used in remediation of soils and could be used for phyto-recovery of Ni (Brooks et al., 2001; Howes & Slatter, 1999).

## **Floristics**

A common feature of ultramafic vegetation is that many species of plant are excluded from this soil type. The question that arises is whether the ability to grow on ultramafic soils is more common in particular plant groups such as monocotyledons or dicotyledons or particular families or genera.

Some of the differences between monocotyledons and dicotyledons may be advantageous for particular soils or altitudes. If there is an advantage at this level of organisation one might expect a higher proportion of one or another group under conditions that favour that group. Some differences which may be relevant for survival on ultramafic soils are listed in Table 3.1.

**Table 3.1. Some monocotyledon and dicotyledon features which may affect growth on ultramafic soils.**

Monocotyledons	Dicotyledons	Comment
Fibrous root system.	Fibrous or tap root system Often tap root initially.	Robertson (1992) suggests that Ni effects on the root meristem may be more damaging to a taproot system.
Scattered vascular tissue.	Vascular tissue zoned.	Arrangement might affect Ni exclusion efficiency
Many taxa with indeterminate leaf growth, meristem basal.	Leaf growth determinate.	Indeterminate leaf growth may allow dilution of potentially toxic ions by extra growth or removal by death of the distal part.
C4 photosynthetic pathway more common for monocotyledons	C4 photosynthetic pathway less common in dicotyledons	The C4 pathway increases photosynthetic efficiency at low CO <sub>2</sub> levels reducing the need for gaseous exchange and the amount of transpiration. Reduced transpiration may be an advantage in reducing toxic ion uptake.

There are examples of traits or adaptations that are common in a particular family or genus such as the stem succulence of the Cactaceae, and examples of traits arising independently in more than one plant family. The cactus family and the euphorbia family both have members with succulent angled stems protected by thorns or spines. *Kleinia stapeliiformis* (E. Phillips) Stapf, a plant with stem succulence in the daisy family is so named because of a strong resemblance to *Stapelia* in the milkweed family. Giant *Lobelias* and *Dendrosenecio* from the high mountains of Africa and Silverswords from Hawaiian mountains are unrelated but have similar morphology.

Specialised traits and less common or uncommon combinations of traits might be expected to occur more frequently in some genera or families. The sparse and depauperate vegetation found on many ultramafic sites suggests that survival requires unusual attributes, and it is thus likely that tolerance may have arisen infrequently and tolerant taxa would be more likely to arise from other tolerant taxa than develop anew. Some evidence for genus level specialization on ultramafic soils can be found in that a number of genera have been found to have several Ni accumulating species for example 7 out of 16 taxa of *Homalium* (Flacourtiaceae) in New Caledonia (Baker *et al.*, 1985), 48 taxa of *Allysum* (Brassicaceae) (Reeves, 1992), three species of *Berkheya* (Asteraceae) in the Barberton Greenstone belt (Morrey *et al.*, 1992; Smith *et al.*, 2001) and two species of *Senecio* (Asteraceae) (Smith *et al.*, 2001). If the assumption that congeneric species are more alike in any measurable biological characteristic than are less closely related species, then metal tolerance by

mechanisms other than those resulting in hyperaccumulation may also be common in a genus or within a family.

In practice it is difficult to demonstrate a difference in taxonomic ratios because they depend on sample size (Gotelli & Colwell, 2001). Previous biological interpretations based on species to genus ratios were in effect based on a statistical artefact (Järvinen, 1982). It is unfortunately beyond the scope of this thesis to show whether species genus ratios indicate an increase in congeners on ultramafic soils because the probability calculations are very complex (Simberloff, 1970).

### *Plant diversity*

Biodiversity is generally used in the sense of “variety of life” and has been defined by various authors to encompass concepts including: number and frequency of species, genes and genetic diversity, ecosystems and ecological processes (Gaston, 1996). It is multifaceted with many interrelated aspects, to the extent that Hurlbert (1971) suggested abandoning the term because it was so ill-defined. Biodiversity has three interconnected components, a structural, a compositional and a functional component, each of which has various levels of organization (Noss, 1990). Whittaker (1972) defined three levels of diversity which he called alpha, beta and gamma diversity. Alpha diversity is diversity within a habitat or community. Beta diversity represents the species change or turnover along environmental gradients and gamma diversity is the diversity of an entire landscape or region.

Two important components of alpha diversity are the variety (species richness) and the relative abundance of species (evenness) (Magurran, 1983). A number of indices have been proposed to try and quantify diversity using both aspects. Different indices tend to emphasise different aspects of diversity and some indices discriminate between similar sample data better than others. Table 3.2 evaluates the strengths and weaknesses of some commonly used indices.

The number of species recorded is related to sampling effort, the more individuals that are sampled the more species will be recorded (Gotelli and Colwell, 2001; Fleishman *et al.*, 2005) and so care needs to be taken when diversity measures from one study are related to those of another. Species richness does not rate species, so two closely related species and two unrelated species add equal value to richness, as do a mature tree of one species and a small sapling of another (Peet, 1974). Indices which use some measure of the taxonomic difference between pairs of species have been

proposed to improve the value of species richness data for comparing areas (Ricotta & Avena, 2002). Accurate measurement of, or estimation of, species richness is critical if correct inferences or decisions are to be made regarding ‘hotspots’ and to calibrate background and current rates of extinction (Gotelli and Colwell, 2001).

Complete inventories of species for particular areas are costly in time and effort so relative species richness or an estimate of total species richness often has to suffice. Rarefaction techniques estimate the species richness which would be measured for a particular sample size or data collecting effort. They do not estimate the actual species richness (Gaston, 1996). A common mistake made by researchers is comparing numbers of species per unit area without referring to taxon sampling curves. Differences may indicate a difference in species richness, but may be due to a difference in the shape of the underlying relative abundance distribution or a difference in the number of individuals counted or collected. Valid comparisons can only be made when a clear asymptote has been reached in the accumulation or rarefaction curves, or failing that the curves themselves may be compared. (Gotelli and Colwell, 2001).

**Table 3.2. Summary of performance and characters of a range of diversity measures taken from Magurran (1983).**

	Discriminant ability	Sensitivity to sample size	Aspect of diversity measured
$\alpha$ (log series)	Good	Low	Richness
S (species richness)	Good	High	Richness
Shannon-Wiener $H'$	Moderate	Moderate	Richness
Simpson index $\lambda$	Moderate	Low	Dominance
Shannon evenness	Poor	Moderate	Evenness

The Shannon-Wiener Index is derived from a function originally used in information theory and describes the average degree of uncertainty of predicting the species of the next individual picked at random from a community. Simpson’s Index measures the probability that two individuals randomly selected from a sample will belong to the same species. This measure is usually transformed in some way such as the reciprocal,  $1/\lambda$  or  $1 - \lambda$  to give a number which increases as diversity increases. The function  $-\ln \lambda$  gives numbers of similar magnitude to those of the Shannon-Wiener Index.

## **Species turnover (◉ diversity)**

Beta diversity is defined as ‘extent of species replacement or biotic change along environmental gradients’ (Whittaker, 1972). It is an important component of overall diversity because it gives an indication of the habitat diversity and allows the comparison of different areas. It also shows to what extent habitats have been partitioned by species and is part of the overall diversity or biotic heterogeneity of an area (Wilson & Shmida, 1984). In the present study three main environmental gradients can be considered, an altitudinal gradient, a disturbance gradient and an edaphic gradient.

## **Effects of unfavourable soil conditions on diversity**

There are two processes which are likely to affect diversity on ultramafic soils. The number of species could be reduced, as those affected by high Ni would fail to establish or would not persist. This is documented for many ultramafic soils for example for New South Wales (Specht, 2001). The other process would tend to increase diversity by reducing competition. This has been found in experiments where nutrients are applied at various concentrations and diversity has decreased (Gough *et al.*, 2000). Species with lower competitive ability have been found at sites where plants are stressed by low fertility, shading or disturbance (Gurevitch, 1986). The Swaziland ultramafic soils may support species which would be out-competed on other soils if the superior competitors have reduced vigour or abundance on ultramafic soils.

## **Research Questions**

1. Do the proportions of monocotyledons and dicotyledons differ on ultramafic soils in Swaziland, as compared to non-ultramafic soils, indicating an uneven distribution of traits for survival on ultramafic soils between these major groupings?
2. In this study, were some genera and/or families relatively more common on ultramafic soils than on non-ultramafic soils?
3. Is species richness higher for Swaziland ultramafic sites than for Swaziland non-ultramafic sites, as would be expected for a reduction in competitive exclusion, or lower as would be expected if ultramafic soils exclude many taxa?
4. Are differences in diversity correlated with altitude differently for ultramafic and non-ultramafic soils?

## Methods and materials

A number of trips were made to Swaziland at different times of the year and fertile specimens were collected from ultramafic and non-ultramafic areas. These specimens are housed in the C. E. Moss Herbarium (J) with duplicates given to the Swaziland National Herbarium and duplicates of Malolotja specimens given to Malolotja Nature Reserve. Lists of these and specimens at (J) collected by other workers were retrieved from the computerised herbarium management system. Plant samples and specimens were also collected within modified Whittaker plots (Figure 3.1) and all additional species recorded were added to the checklist. The samples were identified by comparison with specimens in the C.E. Moss Herbarium and reference to taxonomic literature. Specimens which could not be identified were sorted and given the same working name for all plots. Microsoft Excel was used to manipulate the data to determine species richness, species overlap and to determine species composition on a site basis. Species abundance was estimated by arbitrarily laying a 50 m tape across the plot and recording the species intercepted every 10 cm.

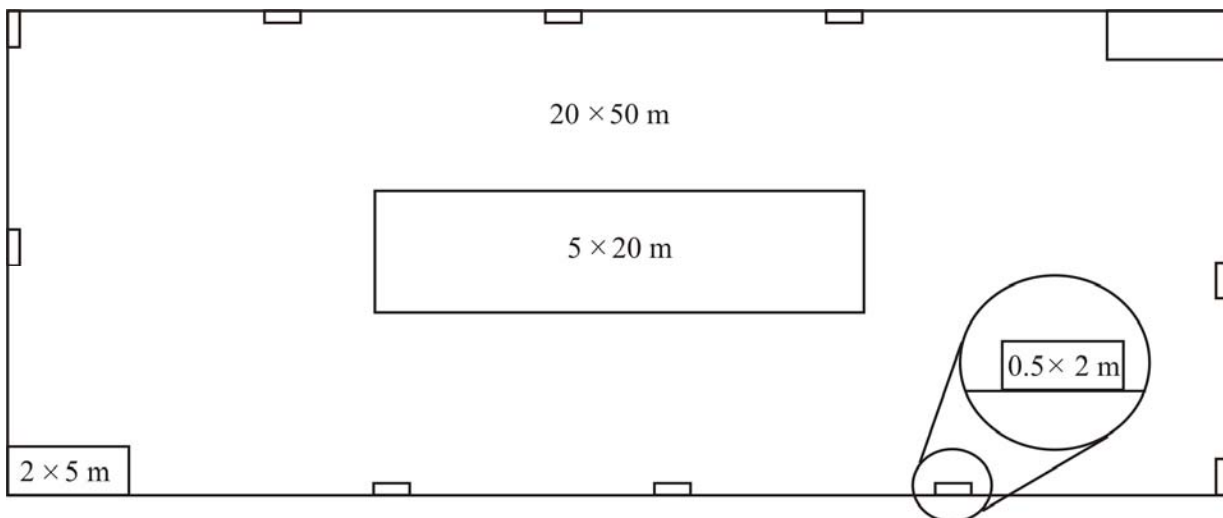


Figure 3.1. Whittaker nested plots as modified by Stohlgren *et al.*, 1995.

### Positions of sample plots

Plots were positioned according to the following criteria: they were at least 5 m from paths, fences or other sources of disturbance. The longer axis was perpendicular to the contours of the slope, giving the maximum altitudinal range for the plot size. Wooded stream banks were avoided. Plots were arbitrarily sited by throwing an object to mark a corner and then tossing a coin to determine if the corner was to be the lower left or lower right hand corner. Positions for plots were however chosen to ensure that slopes with different aspects were sampled and to sample as many ultramafic patches as possible (Figure 3.2).

The composition of the vegetation in this study is influenced by many factors in addition to the soil type. The positions of sample plots were chosen to match as many of these factors as possible for ultramafic and non-ultramafic plots in order to allow the effects of the soil to be separated from those of other environmental and anthropogenic effects. The area of Swaziland where the study took place is a densely populated rural area, and possible positions for sample sites were severely limited, hence the ideal was only partially achieved (Figure 3.3).

Ultramafic soils in Swaziland are derived from two rock sequences. One is a sequence of serpentinous and tremolitic schists and the other is described as serpentinite. Forbes Reef 6 was situated on the sequence of serpentinous and tremolitic schists and all the other ultramafic sample plots were situated on serpentinite (Figure 3.2).



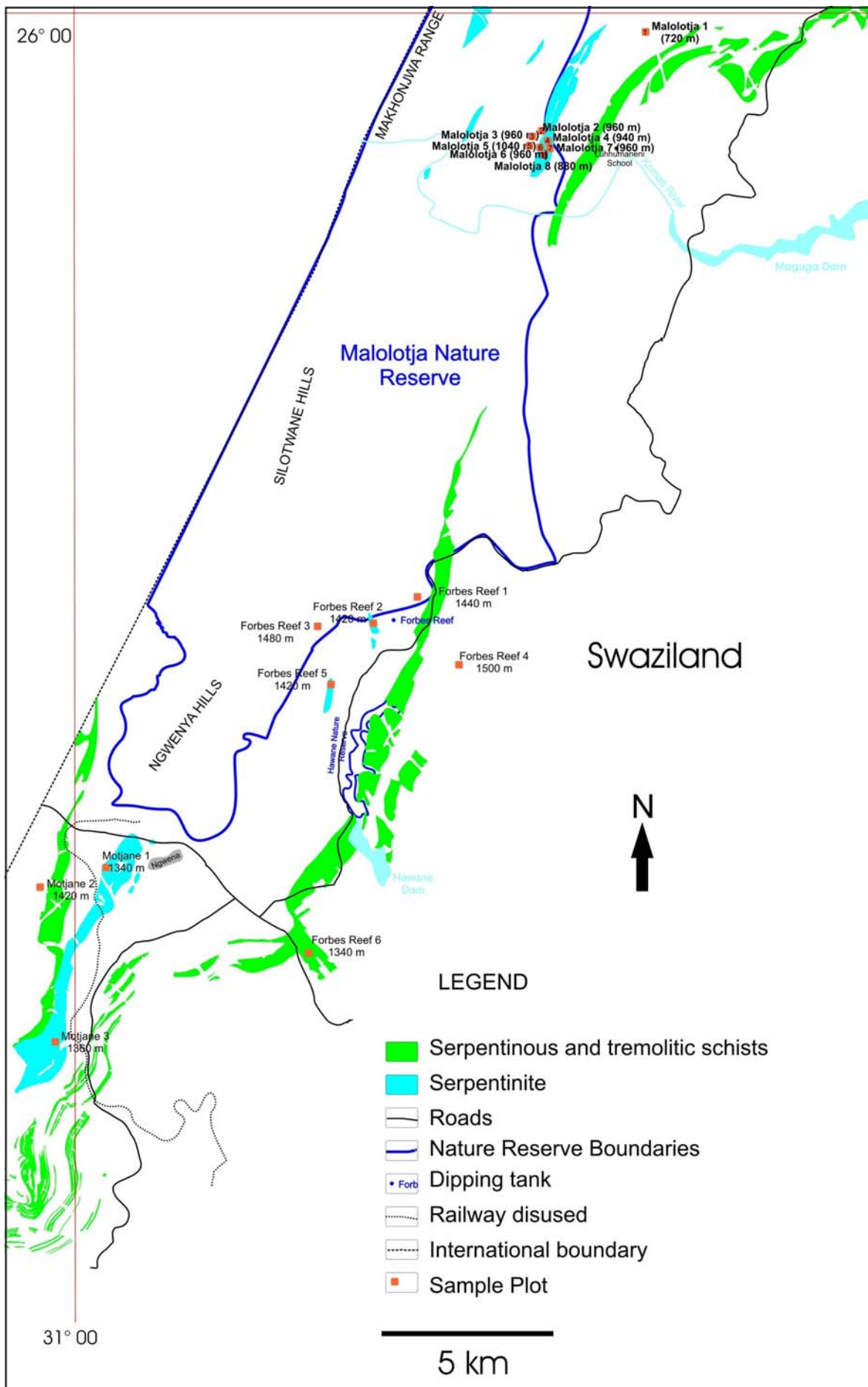


Figure 3.2. Map showing positions of sample plots.

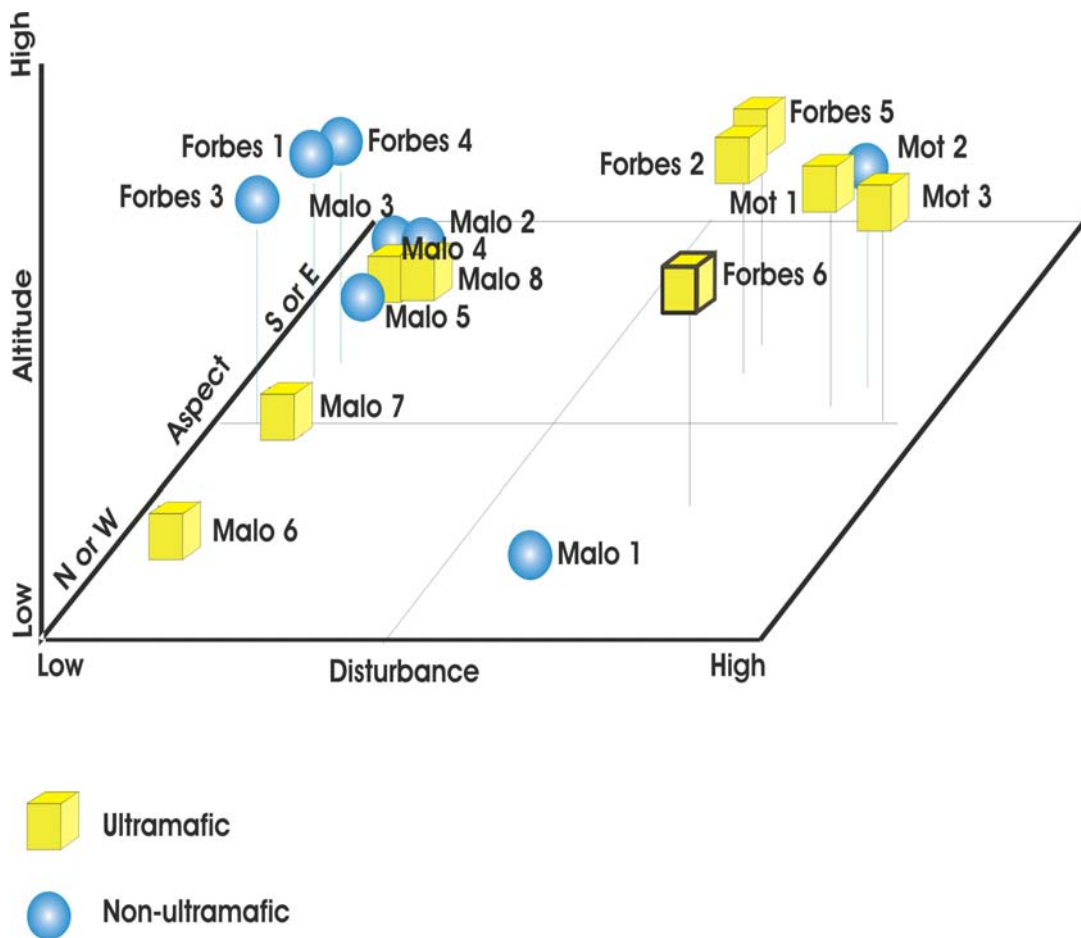


Figure 3.3. Diagram showing sample plots in relation to the most important gradients determining vegetation structure. Forbes Reef 6 was on serpentinous and tremolitic schists (indicated by heavy border around the symbol) and all other ultramafic plots were on serpentinite.

### The sites

Motjane is a relatively level site about 8 km long by up to about 1.2 km wide. It varies in altitude from approximately 1340 – 1360 m above sealevel. The site is heavily utilized for cattle grazing and the cultivation of crops, and only very rocky areas did not have signs of past cultivation. The southern side had large stands of *Acacia mearnsii* De Wild. surrounding and encroaching onto the site.

Forbes Reef consists of three separate sites all on communal land (Swazi Nation Land) used for cattle grazing. Two sites were small outcrops of serpentinite at an altitude of 1420 m, both about 1000 x 100 m, but one divided into two smaller parts by recent sediments. The sites were 1200 m

apart. The third site was on serpentinous and tremolitic schists on the south side of a site 18 x 1 km at the widest.

Malolotja is mainly within the Malolotja Nature Reserve with the part outside the reserve grazed by cattle and goats. The site is 5 x 0.5 km and is situated on a mountainside crossed by a number of streams with deep valleys. The altitude of the site ranges from 880 – 960 m above sea level.

### **Plant classification system followed.**

Families and genera are as recognized in Seed Plants of Southern Africa (Leistner, 2000) except in the case of the Scrophulariaceae where the circumscription of Judd *et al.* (1999) is used. Counts quoted from other sources have been adjusted to reflect this classification scheme (for example, the incorporation of Asclepiadaceae and Periplocaceae into Apocynaceae).

### **Hierarchical distribution**

The number of families, genera, species and infraspecific taxa for Swaziland were used to calculate an expected number at each rank for the plots using the number of species and infraspecific taxa recorded. A Chi-squared test was performed to find the probability of the observed result if there was no difference between plots and the Swaziland flora. In a similar way the totals for plots were used to calculate values expected if there was no difference and a Chi-squared test was performed to see if the difference between observed and expected numbers was significant.

### **Similarity**

Sørensen's Index (S.I.) was calculated to determine the similarity in species composition between various sites.

$$\text{Sørensen's Index} = \frac{2 \times \text{no. of taxa in common}}{\text{total in A} + \text{total in B}} \times 100$$

There were three times as many comparisons between plots on different soil types (ultramafic/ non-ultramafic) as there were comparisons between plots on the same soil type therefore a Kruskal-Wallis test was appropriate to determine if the difference in means of the Sørensen's Indices was significant.

## Diversity measures

EstimateS (Version 6.0b1), Copyright R. K. Colwell: <http://viceroy.eeb.uconn.edu/estimates> was used to estimate species richness and to calculate various diversity indices. Hill's Numbers and evenness measures were calculated from outputs from EstimateS. Coleman curves are almost identical to rarefaction curves, but are easier to calculate (Colwell, 2001). Table 3.3 expands on the various indices used. Although the Michaelis Menten Means gave the best estimate of richness in this study, the other richness estimators are included because they are used in other studies and, whilst differing in the number of species estimated, they show the same relationships between sites. A variety of diversity measures are given because they are used in the literature and measure different aspects of diversity.

**Table 3.3. Species richness, diversity and evenness estimators (Colwell and Coddington, 1995).**

Index/measure	Type of estimator	Description
Coleman	Rarefaction curve	Estimates sample species richness from pooled total species richness.
Jack 1	First-order Jackknife richness estimator	Based on the number of species occurring in only one sample.
Jack 2	Second-order Jackknife richness estimator	Based on the number of species occurring in only one sample, as well as those that occur in exactly two samples.
Bootstrap	Bootstrap richness estimator	Based on the proportion of samples containing each species
MM Means	Michaelis Menten Means richness estimator	Derived from the Michaelis Menton equation for enzyme kinetics, extrapolates to an expected richness.
Hill's Diversity Number N1 ( $e^{H'}$ )	Diversity index	Also used for calculating evenness measures
Hill's Diversity Number N2 ( $1/\lambda$ )	Diversity index	Also used for calculating evenness measures
E1 ( $H'/H_{max}$ )	Evenness measure	
E5 ( $(N2-1)/(N1-1)$ )	Evenness measure	

Evenness measures attempt to quantify how unequally species are represented relative to a hypothetical sample in which all species are equally abundant (Krebs, 1989). Two evenness measures were calculated to compare the sites. Shannon's evenness, E1 or J', is commonly used but is sensitive to sample size. E5 is not as sensitive to size sample and is recommended as least ambiguous (Ludwig and Reynolds, 1988). A value of 1 for E1 would represent a completely even distribution of species.

## **Beta diversity**

The measure of beta diversity proposed by Whittaker (1960) was calculated to determine community turnover between sites. The formula used is:

$$\beta_w = s / \bar{\alpha} - 1$$

where  $s$  is the total number of species recorded for the study and  $\bar{\alpha}$  is the average number of species within community samples. Diversity was calculated using the total number of species recorded in the study, sample plot data only and for ultramafic plots and non-ultramafic plots only to give beta diversity at various scales.

## **Bare Ground**

When measuring the abundance of species it was found that some points fell between plants, giving a measure of open ground. Bare ground is often a feature of temperate ultramafic sites, and bare ground could be a measure of how unsuitable the soil is for plant growth. No measurements were made for Motjane and Malolotja 4. Results for Malolotja 1 have not been used as this site was very disturbed and all the other Malolotja sites were in the nature reserve and not disturbed.

## *Results*

### **Floristic analysis**

There were 600 species and infraspecific taxa in 315 genera and 79 families on ultramafic soils in Swaziland as determined by vouchers in the C.E. Moss Herbarium and plants identified in Whittaker plots. Collections and plots on other soils near the ultramafic sites yielded 301 species and infra-specific taxa in 207 genera and 57 families. Appendix 1 is the checklist for the ultramafic flora of Swaziland. Appendix 2 tabulates presence and absence for Whittaker plots and incorporates additional records from vouchers housed in the C.E. Moss Herbarium and from the literature. The list covers plants from both ultramafic and non-ultramafic soils.

### **Major groupings – proportions of dicotyledons, monocotyledons and pteridophytes**

Dicotyledons were the predominant group with between 71% and 80% of the species and infraspecific taxa. Monocotyledons contributed the balance except for a small fraction (between 0.8% and 3%) contributed by pteridophytes. The estimated number of higher plant species for

Swaziland is 3400 (Dlamini and Dlamini, 2002), a marked increase from 2825 quoted by Kemp (1983). The older figure is used in Table 3.4 because no breakdown into major groups was given for the more recent estimate.

### **Number of species of dicotyledons, monocotyledons and pteridophytes for Swaziland flora, ultramafic plots and non-ultramafic plots.**

The observed difference in the proportions of the major groups for Swaziland and the sample plots and between ultramafic and non-ultramafic plots as a whole were not significant at the 95% confidence level but when the results of the two soil categories were split into higher and lower altitude sites, there was a significant difference (Table 3.4).

The high altitude sites had a greater proportion of monocotyledons than the total Swaziland flora and the low altitude sites. This difference was significant for ultramafic sites. For each lithology

**Table 3.4. Numbers and percentages of species and infraspecific taxa per major group for Swaziland, ultramafic and non-ultramafic plots. The total for Swaziland excludes 8 gymnosperms. Altitudes in bold font denote a significant difference in proportions of major groups from that of the Swaziland flora ( $P < 0.05$ ).**

		Altitude		Monocotyledons		Dicotyledons		Pteridophytes		Total
		number	%	number	%	number	%	number		
Ultramafic plots	<b>High</b>	67	34.18	126	64.29	3	1.53	196		
	Low	44	21.05	160	76.55	5	2.39	209		
	Total	91	26.84	242	71.39	5	1.47	338		
Non-ultramafic plots	High	50	25.77	138	71.13	6	3.09	194		
	<b>Low</b>	32	19.28	132	79.51	2	1.2	166		
	Total	71	23.20	228	74.51	7	2.29	306		
Swaziland	Total	723	25.59	2006	71.01	88	3.12	2817		

low altitude sites had a greater proportion of dicotyledons than that of high altitude sites, the difference was significant for non-ultramafic sites compared to the Swaziland flora, and to high altitude ultramafic soils. Grasses were probably under-recorded for the high altitude sites as fertile material was scarce and identification from vegetative plants was seldom possible. It is therefore likely that the difference in proportions is even greater than was measured.

### **Number of species by major grouping for various ultramafic sites**

There was no significant difference in the proportions of pteridophytes, dicotyledons and monocotyledons on ultramafic soils in Swaziland, South African sites on the Barberton Greenstone

Belt and on the Witwatersrand (Table 3.5). These proportions are typical of the grassland biome (Reddy *et al.*, 2001). There are very few pteridophytes in grasslands so 5 taxa approaches the maximum number of species that could be present.

**Table 3.5. Number of species and infraspecific taxa for pteridophytes, dicotyledons and monocotyledons for ultramafic sites on the Witwatersrand, Barberton Greenstone Belt and Swaziland. Differences in proportions are not significant ( $P > 0.05$ ). Sources of data: <sup>1</sup>Williamson, 1995, <sup>2</sup>Kidger, 1993, <sup>3</sup>Changwe & Balkwill, 2003, <sup>4</sup>Reddy *et al.*, 2001.**

	Swaziland		Agnes <sup>1</sup>		Kaapsehoop <sup>1</sup>		Diepgezet <sup>2</sup>		Dunbar <sup>3</sup>		Witwatersrand <sup>4</sup>	
	number	%	number	%	number	%	number	%	number	%	number	%
Monocotyledons	137	22.8	62	31.5	43	27.9	48	23.9	64	25.2	120	28.2
Dicotyledons	457	76.2	131	66.5	109	70.8	150	74.6	186	73.2	300	70.6
Pteridophytes	6	1.0	4	2.0	2	1.3	3	1.5	4	1.6	5	1.2
Total	600		197		154		201		254		425	

### Hierarchical distribution of taxa

Fewer genera than would be expected for the number of species occurred on the higher altitude ultramafic soils and more genera than would be expected for the number of species were recorded for the lower altitude non-ultramafic soils. These differences were not significant, but were based on simple calculations of the expected values. Accurate estimates of expected values are a statistical function of the number of species sampled and computationally difficult to determine (J...rvinen, 1982). No conclusions can therefore be drawn from these results.

**Table 3.6. Cumulative number of families, genera and species and sub-specific taxa for ultramafic and other soils in the study area. The values in the columns marked 'High' and 'Low' are counts recorded for sample plots from the higher altitude and lower altitude sites. 'All' is the pooled results from plots for the soil type indicated. The expected values were calculated from the lower and higher altitudes for ultramafic and non-ultramafic soils. The probability of getting the observed result if there was no difference is (Chi-squared = 596 \* ( $P < 0.60$ )) (two-tailed  $df = 6$ ).**

	Ultramafic					Non-ultramafic				
	High		Low		All	High		Low		All
	obs	exp	obs	exp		obs	exp	obs	exp	
Families	39	42.2	57	51.7	63	44	46.3	42	41.8	57
Genera	111	122.6	152	150.3	209	136	134.5	130	121.6	199
Species & infra-specific taxa	191	176.2	209	216	339	194	193.2	166	174.6	306
Species/Genus	1.7	1.44	1.4	1.44	1.6	1.4	1.44	1.2	1.44	1.5

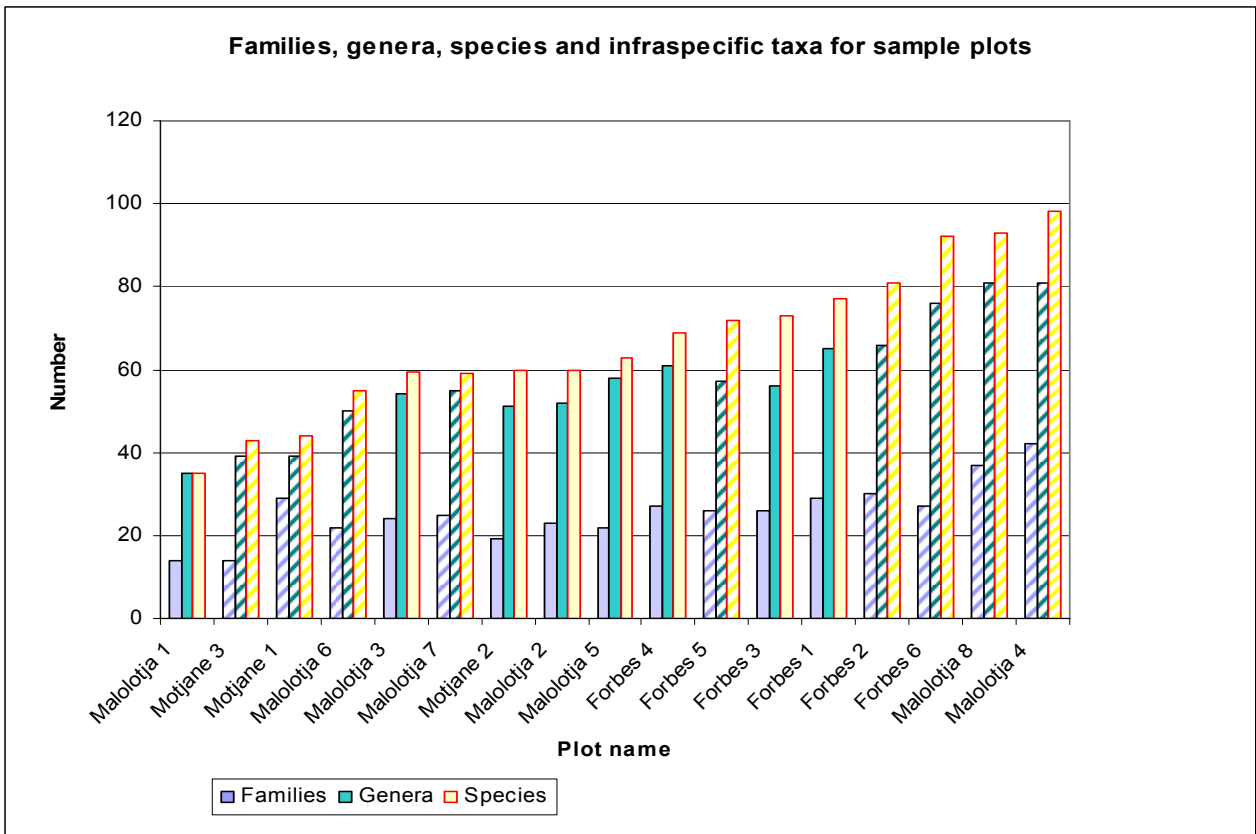


Figure 3.4. The number of families, genera, species and infraspecific taxa recorded for the sample plots. Diagonal hatching indicates ultramafic sites.

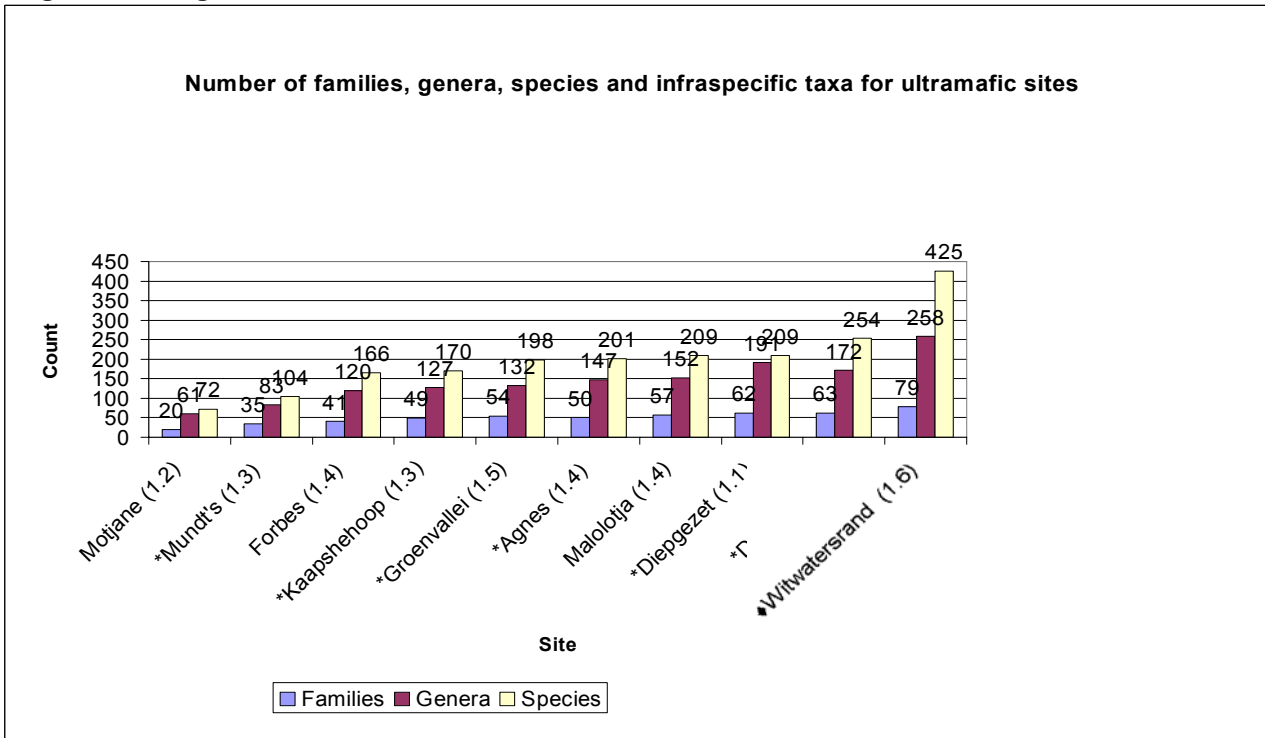


Figure 3.5. Families, genera and infraspecific taxa for various ultramafic sites in the Barberton Greenstone Belt and for the Witwatersrand. Numbers in parentheses after the site name are the species to genus ratio. Sources of data: ♦ Reddy *et al.*, 2001, \* Changwe and Balkwill (2003).



When the counts of families, genera and species for individual sample plots are ranked from most to fewest species and infraspecific taxa, there is no discernable pattern due to soil type or altitude (Figure 3.4). The species to genus ratio for Barberton Greenstone Belt and Witwatersrand ultramafic soils ranges from 1.1 to 1.7 and there is no trend to suggest that the type of soil may affect this ratio. When sites are ranked by species number the Swaziland sites are dispersed between the BGB sites. Witwatersrand numbers are the totals from nine sample plots and 4 sites, hence the higher numbers for all ranks are due to a larger sample (Figure 3.5). A plot of species vs genera (Figure 3.6) shows a close correlation between the number of species and the number of genera. The relationship between the number of genera and the number of families is not as strong (Figure 3.7). The correlation between the number of families and genera and the number of families and species is weaker for ultramafic soils than is the case for non-ultramafic soils (Table 3.7). Differences in the relationship between the different taxonomic ranks cannot be interpreted as having any biologically meaningful basis without ensuring that results are not a statistical artefact (J...rvinen, 1982).

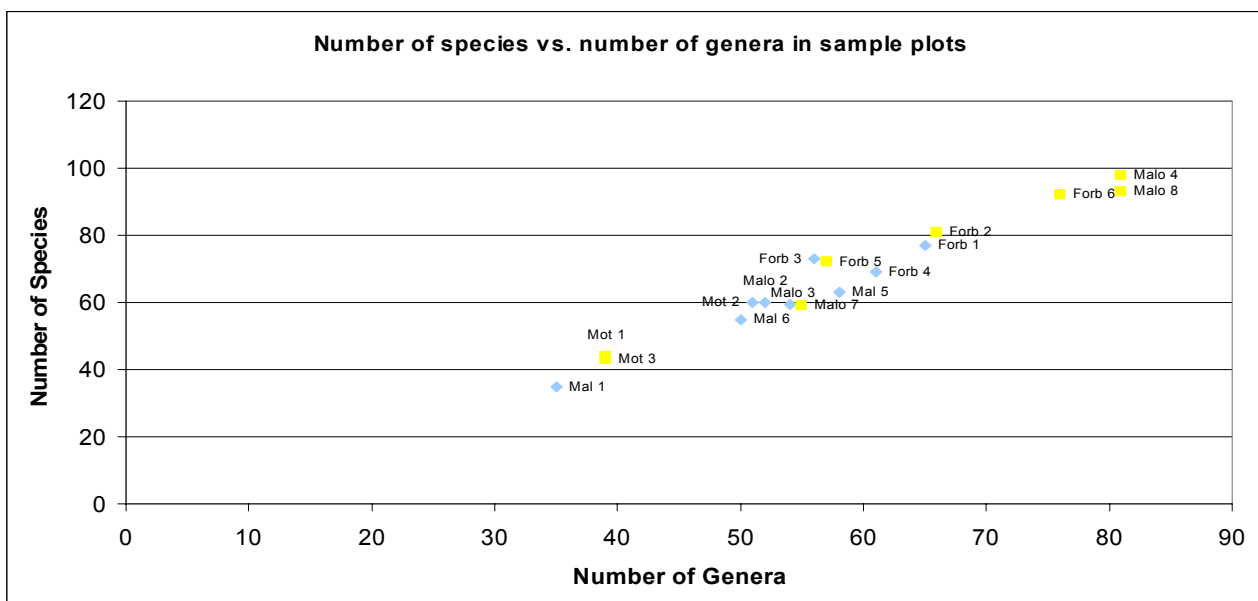


Figure 3.6. Numbers of species and infraspecific taxa vs. genera for sample plots. Yellow square = ultramafic plot, blue diamond = non-ultramafic plot.

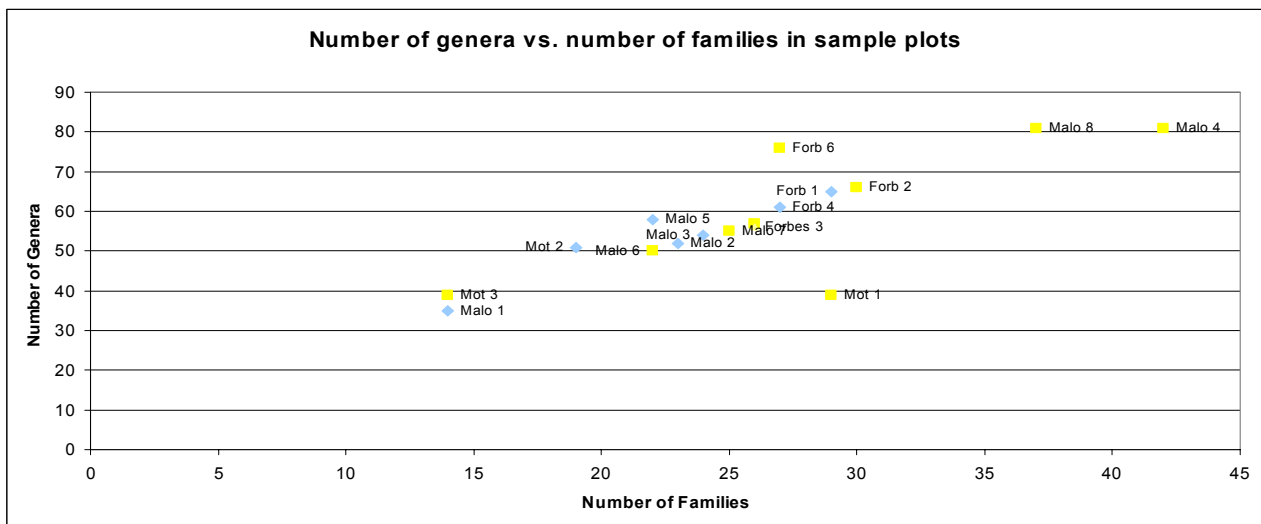


Figure 3.7. Numbers of families vs. genera for sample plots. Yellow square = ultramafic plot, blue diamond = non-ultramafic plot.

Table 3.7. Correlation coefficients for numbers of taxa at different ranks.

Comparison	Correlation coefficient		
	All plots	Ultramafic	Non-ultramafic
Families + Genera	0.82	0.77	0.84
Genera + Species	0.98	0.99	0.95
Families + Species	0.82	0.77	0.93

### Contribution by families

The relative importance of each family differed from plot to plot. The Poaceae contributed a much greater percentage of species for the Motjane plots than was the case for other plots and ranked first for ultramafic plots as a whole and second for non-ultramafic plots as a whole.

The families with the most species are listed in Table 3.8. The difference in the percentage contribution by the seventeen largest families for the two soil types was not significant.

**Table 3.8. The % of the total flora (mean  $\pm$  S.E.) for the families with the most species for ultramafic and non-ultramafic sites.**

Family	Ultramafic	Non-ultramafic
Asteraceae	19.43 $\pm$ 1.35	19.01 $\pm$ 1.61
Poaceae	20.85 $\pm$ 3.64	17.81 $\pm$ 2.31
Fabaceae	7.29 $\pm$ 1.31	11.54 $\pm$ 1.46
Rubiaceae	5.00 $\pm$ 1.06	6.80 $\pm$ 0.38
Acanthaceae	4.50 $\pm$ 0.79	2.05 $\pm$ 0.54
Cyperaceae	3.04 $\pm$ 0.87	2.26 $\pm$ 0.37
Euphorbiaceae	2.25 $\pm$ 0.76	3.31 $\pm$ 0.46
Lamiaceae	2.79 $\pm$ 0.52	3.54 $\pm$ 0.95
Apocynaceae	1.00 $\pm$ 0.31	1.38 $\pm$ 0.62
Anacardiaceae	1.16 $\pm$ 0.45	0.32 $\pm$ 0.32
Iridaceae	0.96 $\pm$ 0.32	1.26 $\pm$ 0.57
Orobanchaceae	0.98 $\pm$ 0.44	1.11 $\pm$ 0.46
Convolvulaceae	0.005	0.16 $\pm$ 0.16
Scrophulariaceae	0.005	0.33 $\pm$ 0.22
Hyacinthaceae	0.005	0.51 $\pm$ 0.25
Crassulaceae	0.005	0.35 $\pm$ 0.23
Orchidaceae	0.005	0.50 $\pm$ 0.36
Total	69.42	72.25

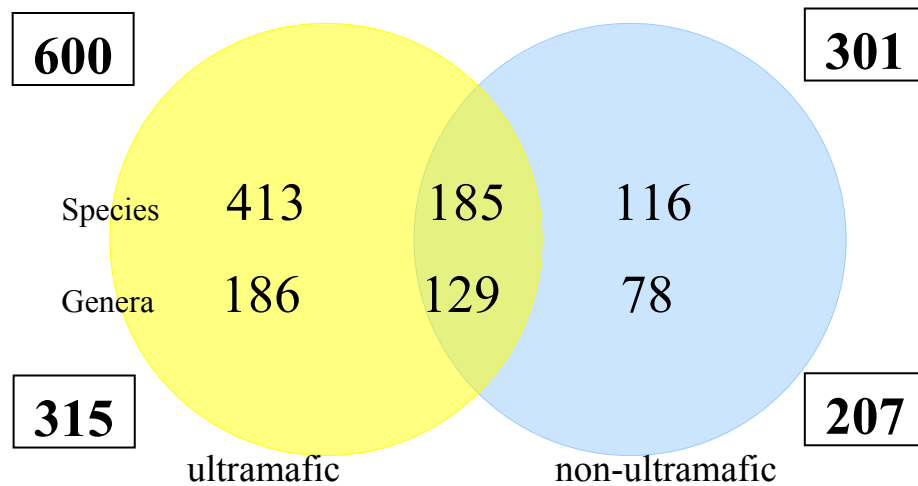
At the family level most families contributed one or a few species and a few families with many species predominate. The species to genus ratio is low in some families whilst others have a few genera with many species. Table 3.9 shows the largest families for various ultramafic sites. The Poaceae was the dominant family for the Motjane ultramafic site contributing 37.5% of species. Dunbar was the only other site where the Poaceae dominated, contributing 17.2 % of the total. The Asteraceae, with from 10.2 – 16.6 %, was the largest family in all the other sites. The Fabaceae ranked third for all except Motjane where its rank was 6<sup>th</sup> and Forbes Reef where 3<sup>rd</sup> rank was shared between Euphorbiaceae, Fabaceae and Rubiaceae. The Acanthaceae, Cyperaceae, Lamiaceae and Apocynaceae were the other large families.

Table 3.9. The largest families on Swaziland ultramafic sites, other Barberton Greenstone Belt sites and the Witwatersrand. Sources of data: ■ Leistner (2000), † Williamson (1995), ‡ Kidger (1993), ◆ Reddy et al. (2001) and \* Changwe and Balkwill (2003).

Family (species in southern Africa.■)	Agnest		Diepgezet†		Dunbar *		Kaapshoep†		Malolotja		Motjane		Forbes Reef		Swaziland Ultramafic		Non-Ultra Swaziland		Witwatersrand◆	
	#	%	#	%	#	%	#	%	#	%	#	%	#	%	#	%	#	%	#	%
Asteraceae (2305)	22	10.9	37	17.7	30	11.8	27	16.0	35	16.7	14	19.4	37	22.2	119	19.9	50	16.6	72	16.0
Poaceae (912)	20	10.0	34	16.3	44	17.2	16	9.5	16	7.7	27	37.5	30	18.0	51	8.5	46	15.2	54	12.0
Fabaceae (1705)	13	6.5	23	11.0	23	9.1	11	6.5	18	8.6	2	2.8	9	5.4	34	5.7	36	11.9	35	7.9
Lamiaceae (235)	10	5.0	8	3.8	7	2.8	10	5.9	6	2.9	2	2.8	4	2.4	27	4.5	6	2.0	9	2.0
Rubiaceae (228)	8	4.0	9	4.3	7	2.8	10	5.9	8	3.8	4	5.5	9	5.4	25	4.2	9	3.0	9	2.0
Cyperaceae (±400)	8	4.0	4	1.9	7	2.8	6	3.6	3	1.4	5	6.9	3	1.8	16	2.7	7	2.3	14	3.1
Acanthaceae (±350)	6	3.0	7	3.3	8	3.1	6	3.6	11	5.2	3	4.2	5	3.0	14	2.3	7	2.3	11	2.4
Apocynaceae (±696)	7	3.5	6	2.9	15	5.9	1	0.6	3	1.4	1	1.4	4	2.4	14	2.4	6	2.0	13	2.9
Euphorbiaceae (484)	6	3.0	7	3.3	11	4.3	6	3.6	5	2.4	1	1.4	9	5.4	12	2.0	9	3.0	6	1.3
Anacardiaceae (±110)	5	2.5	4	1.9	3	1.2	2	1.2	5	2.4	-	-	1	0.6	10	1.7	4	1.3	5	1.1
Apiaceae (152)	3	1.5	1	0.5	3	1.2	5	3.0	3	1.4	-	-	3	1.8	10	1.7	2	0.7	3	0.7
Iridaceae (1020)	8	4.0	3	1.4	1	0.4	6	3.6	2	1.0	-	-	1	0.6	9	1.5	5	1.7	4	0.9
Total number of species for site	201		209		254		169		209		72		167		598		302		449	

## Genera, species and infraspecific taxa

More genera and species were collected only on ultramafic soil than were collected only on non-ultramafic soil. Forty one percent of genera and 30.9% of species and infraspecific taxa collected on ultramafic soils were also collected on non-ultramafic soils compared to 61.46% of genera and 62.3% of species collected on non-ultramafic soils that were also collected on ultramafic soils. The species to genus ratios for ultramafic and non-ultramafic sites were 1.87 and 1.45.



**Figure 3.8. Genera and species and infraspecific taxa for ultramafic and non-ultramafic soils in the study area. The numbers in the blocks are the totals for the soil type.**

## Genera

The fifteen genera with the most species are tabulated in Table 3.10. Changwe and Balkwill (2003) found *Senecio* to be the most speciose genus for sites on the Barberton Greenstone Belt. In Swaziland it was second to *Helichrysum* which was also the most speciose genus for associated non-ultramafic sites. *Vernonia*, *Berkheya* and *Gnidia*, which are amongst the largest genera for Swaziland, are listed as well represented in the BGB. Genera which are less speciose in Swaziland than for the BGB are *Pearsonia*, *Acalypha* and *Eragrostis*. *Rhus*, *Indigofera*, *Wahlenbergia*, *Polygala*, *Conyza*, *Crassula*, *Hypoxis*, *Chaetacanthus*, *Rhynchosia* and *Digitaria* are all more speciose in Swaziland. The number of species for each genus for ultramafic and non-ultramafic sites does not differ significantly from the number expected if numbers are proportional to the total number of genera (Table 3.10).

**Table 3.10. Number of species in the most speciose genera. The expected values were calculated based on the proportions of ultramafic and non-ultramafic species making up the total number of species recorded in this study. A Chi-squared test showed no significant difference between the observed numbers and the calculated values.**

Genus	All collections	Ultramafic		Non-Ultramafic	
		Obs	Exp	Obs	Exp
<i>Helichrysum</i>	31	25	27	14	19
<i>Senecio</i>	18	17	17.1	7	8.6
<i>Vernonia</i>	11	10	10.7	5	5.4
<i>Rhus</i>	11	10	8.5	2	4.3
<i>Berkheya</i>	10	8	8.5	4	4.3
<i>Indigofera</i>	9	6	7.1	4	3.6
<i>Wahlenbergia</i>	8	6	7.1	4	3.6
<i>Polygala</i>	8	6	6.3	3	3.26
<i>Conyza</i>	7	6	5.0	1	2.56
<i>Crassula</i>	7	5	5.0	2	2.56
<i>Hypoxis</i>	7	6	5.0	1	2.56
<i>Chaetacanthus</i>	6	6	6.4	3	3.26
<i>Gnidia</i>	6	5	6.4	4	3.26
<i>Rhynchosia</i>	6	5	5.7	3	2.9
<i>Digitaria</i>	6	4	5.0	3	2.5

## Species

A total of 489 species and infraspecific taxa were recorded in the 17 modified Whittaker plots in this study (9 ultramafic, 8 non-ultramafic). Of these, more than half, (258) were recorded in a single plot only. A further 94 were collected in only 2 plots. Only 18 species occurred in more than half the sample plots. Of these, 6 were in the Poaceae and 6 were in the Asteraceae with the remaining 6 each in a different family (Table 3.10). All the species occurring in 9 or more plots (Table 3.11) occurred on both soil types. Malolotja 1 had the fewest species and infraspecific taxa and Malolotja 4 had the highest. Malolotja 1 was west-facing, on granite and there was evidence of previous disturbance in the form of an overgrown track and a trench dug to one side of the sample plot and an accumulation of rocks at the base of the hill where the plot was situated, possibly indicating cultivation in the past. This contrasts with Malolotja 4 which was on ultramafic soil on the south slope of a stream valley within Malolotja N.R., protected from cattle and with a slope so steep and rocky that past disturbance is highly unlikely.

**Table 3.11. Species recorded in 9 or more modified Whittaker plots.**

Species	Total # plots present	Ultramafic	Non-ultramafic
<i>Themeda triandra</i>	15	8	7
<i>Diheteropogon amplexans</i>	14	8	6
<i>Eragrostis racemosa</i>	12	6	6
<i>Loudetia simplex</i>	11	5	6
<i>Panicum natalense</i>	11	6	5
<i>Rhynchosia totta</i>	11	6	5
<i>Berkheya setifera</i>	10	5	5
<i>Bulbostylis schoenoides</i>	10	5	5
<i>Helichrysum pilosellum</i>	10	4	6
<i>Ledebouria revoluta</i>	10	6	4
<i>Oxalis obliquifolia</i>	10	6	4
<i>Aster harveyanus</i>	9	5	4
<i>Rothea hirsuta</i>	9	4	5
<i>Dicoma zeyheri</i>	9	7	2
<i>Helichrysum nudifolium</i>	9	5	4
<i>Monocymbium cerasiiforme</i>	9	3	6
<i>Polygala transvaalensis</i>	9	4	5
<i>Sonchus integrifolius</i>	9	4	5

### Species shared between plots

The similarity between plots was generally low whether comparing plots of the same soil type and altitude or plots from different soils and altitudes. Sørensen's Index (SI) of similarity ranged from 0% for Malolotja 1 and 2 (both non-ultramafic) to 54% for Malolotja 6 and 7 (both ultramafic). Malolotja 1 (low altitude, non-ultramafic) had very few species in common with any other plots, with SI ranging up to 10% for Forbes Reef 2 (high altitude, ultramafic). The Malolotja SI values for pairs of ultramafic plots ranged from 18% – 54%, pairs with an ultramafic and a non-ultramafic site ranged from 0% – 34% and pairs of non-ultramafic plots ranged from 5% – 37%. Motjane 2 and 3, non-ultramafic and ultramafic, were most similar with an index of 53%. The other ultramafic /non-ultramafic pair, Motjane 1 and 2, had an index of 29% and the ultramafic pair (MO1 and MO3) had a value of 34%. The similarity between plots at Forbes Reef was greater for plots of the same soil type than for plots of different soil type. The ultramafic plots had the highest number of shared species, around 40% and the non-ultramafic plots shared around 35% but only around 30% were common to both ultramafic and non-ultramafic sites. The Kruskal-Wallis Statistic gave a Chi-squared value of 9.74 ( $P < 0.0076$ , Table 3.12). There was a significant difference in

the number of shared species between like lithologies and unlike lithologies. The number of species shared between plots for the Malolotja and Motjane sites did differ significantly for plots of the same soil type or for plots of different soil types. Comparing the mean similarity

**Table 3.12. Table of Sørensen's Indices for Forbes Reef plots. The plot names are abbreviated to F for Forbes Reef followed by the plot number. ie F1 is Forbes Reef 1.**

Plots compared	Ultramafic/ ultramafic	Ultramafic/ non-ultramafic	Non-ultramafic/ non-ultramafic
F1 and F2		24%	
F1 and F3			37%
F1 and F4			25%
F1 and F5		26%	
F1 and F6		31%	
F2 and F3		30%	
F2 and F4		25%	
F2 and F5	38%		
F2 and F6	44%		
F3 and F4			35%
F3 and F5		36%	
F3 and F6		33%	
F4 and F5		28%	
F4 and F6		31%	
F5 and F6	38%		
Mean	40 ± 2%	29 ± 1.3%	36 ± 0.7%

between plots with similar soils to the mean similarity between plots with different soils for all plots gave no significant difference (Table 3.13b). When the similarity between plots at different altitudes was compared (Table 3.13a), plots of like altitude were more similar than plots of different altitude.



**Table 3.13. Sørensen indices of % similarity for sample plots. Plots grouped by altitude (A) and by soil type (B). One way ANOVA for altitude gave  $F = 17.88$  ( $p \leq 0.001$ ). The difference in species composition due to altitude is significant. An ANOVA for soil type gave no significance ( $p > 0.05$ ). Shading shows ultramafic plots in A, higher altitude plots in B. Highest similarities red, lowest blue.**

	F1	F2	F3	F4	F5	F6	MO1	MO2	MO3	MA1	MA2	MA3	MA4	MA5	MA6	MA7	MA8																	
F1		High vs. high $27.8 \pm 1.4$								High vs. low $16.7 \pm 0.9$								N																
F2	24																		U															
F3	37	30																		N														
F4	25	25	35																		N													
F5	26	38	36	28																		U												
F6	31	44	33	31	38																		U											
MO1	13	19	17	23	24	22																		U										
MO2	19	20	26	23	34	29	29																		N									
MO3	20	21	21	13	33	28	34	53																		U								
MA1	02	10	04	04	06	05	03	06	08																		N							
MA2	25	20	26	20	15	22	08	13	14	0																		N						
MA3	26	21	20	16	20	19	12	19	12	04	32																		N					
MA4	13	15	16	14	11	21	06	14	06	05	14	15																		U				
MA5	27	25	29	23	21	17	07	15	09	08	34	34	14																		N			
MA6	23	21	28	13	25	22	10	16	12	07	19	18	18	36																		U		
MA7	24	23	26	17	21	21	14	15	10	06	20	20	22	34	54																		U	
MA8	28	25	27	16	38	28	07	14	13	05	22	37	32	29	24	24																		U
	Higher altitude plots									Lower altitude plots																								

**A**

	F2	F5	F6	MO1	MO3	MA4	MA6	MA7	MA8	F1	F3	F4	MO2	MA1	MA2	MA3	MA5																	
F2		Ultramafic vs. ultramafic $22.9 \pm 1.8$								Ultramafic vs. non-ultramafic $19.7 \pm 1.1$								H																
F5	38																		H															
F6	44	38																		H														
MO1	19	24	22																		H													
MO3	21	33	28	34																		H												
MA4	15	11	21	06	06																		L											
MA6	21	25	22	10	12	18																		L										
MA7	23	21	21	14	10	22	54																		L									
MA8	25	38	28	07	13	32	24	24																		L								
F1	24	26	31	13	20	13	23	24	28																		H							
F3	30	36	33	17	21	16	28	26	27	37																		H						
F4	25	28	31	23	13	14	13	17	16	25	35																		H					
MO2	20	34	29	29	53	14	16	15	14	19	26	23																		H				
MA1	10	06	05	03	08	05	07	06	05	02	04	04	06																		L			
MA2	20	15	22	08	14	14	19	20	22	25	26	20	13	0																		L		
MA3	21	20	19	12	12	15	18	20	37	26	20	16	19	04	32																		L	
MA5	25	21	17	07	09	14	36	34	29	27	29	23	15	08	34	34																		L
	Ultramafic plots									Non-ultramafic plots																								

**B**

## Species shared between sites and between soil types.

Swaziland ultramafic sites were most similar to non-ultramafic sites situated near them and distant sites differed more than closer sites regardless of soil type (Figure 3.9). There was no correlation between soil types and number of shared species and weak correlation between number of shared species and distance between sites (Figure 3.10).

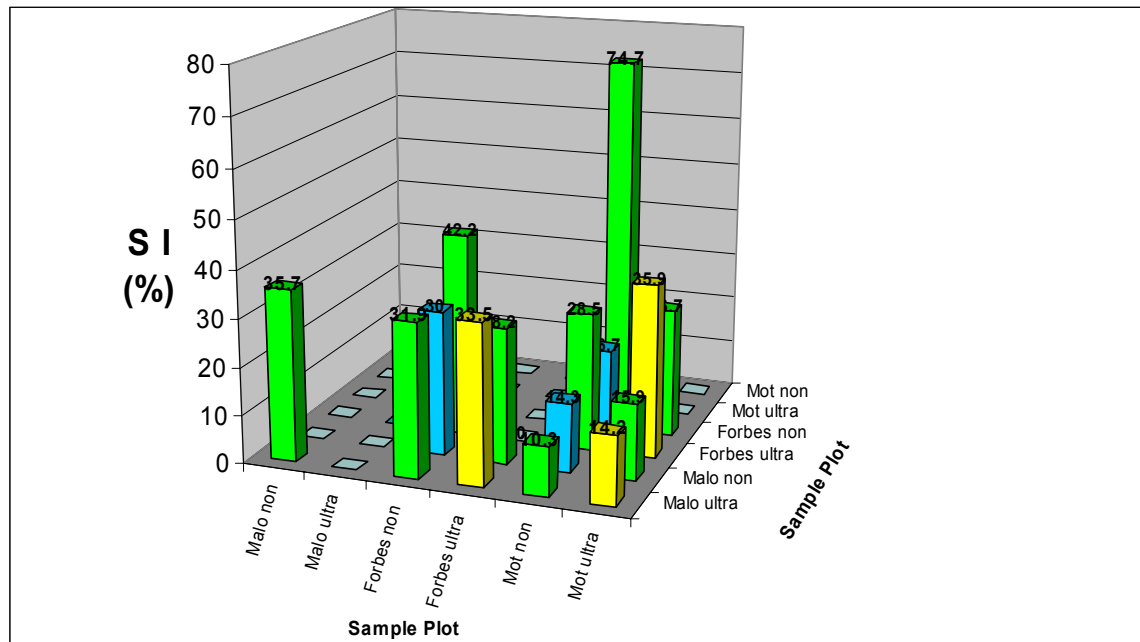


Figure 3.9. Sørensen indices for pairs of sites. ■ Ultramafic vs. ultramafic. ■ Ultramafic vs. non-ultramafic. ■ Non-ultramafic vs. non-ultramafic

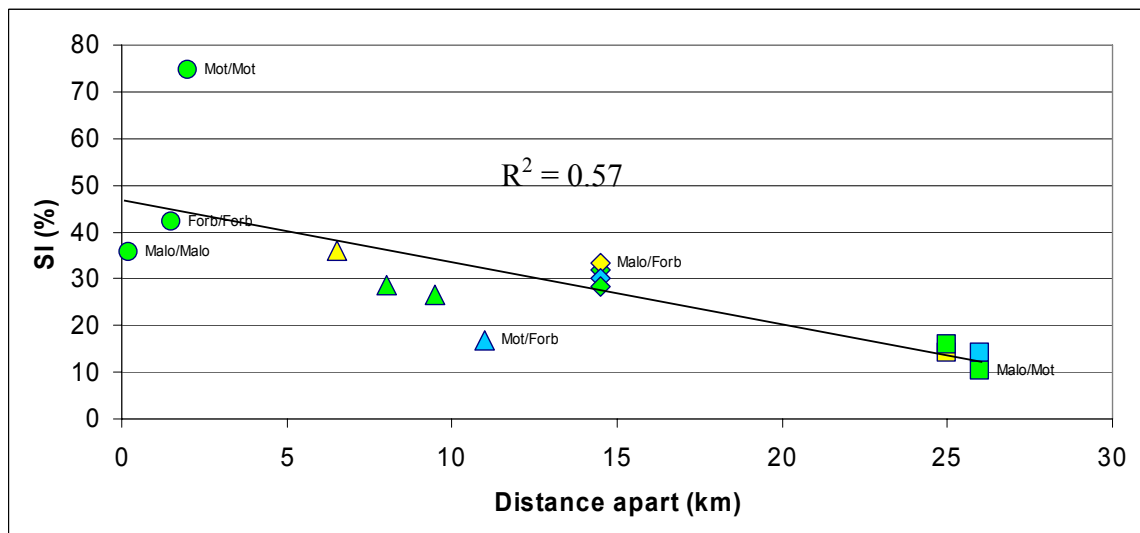


Figure 3.10. Scatterplot of Sørensen indices vs. distance apart for pairs of plots. ■ Ultramafic vs. ultramafic. ■ Ultramafic vs. non-ultramafic. ■ Non-ultramafic vs. non-ultramafic indicated by colours. Shapes indicate sites for the plot pairs. Squares Malo/Mot, diamonds Malo/Forb, triangles Mot/Forb and circles as labeled. If the Mot/Mot value is excluded then the level of correlation increases ( $R^2 = 0.72$ ).

Other Barberton Greenstone sites also had a higher similarity to surrounding non-ultramafic sites (Table 3.14).

**Table 3.14. Sørensen's indices of similarity (%) between ultramafic and non-ultramafic sites at Motjane (Mo), Rosentuin (RT), Sawmill (SM), Kalkloof (KL), Forbes Reef (FR), Groenvaly (GV), Mundt's Concession (MC), Malolotja (Ma), Magnesite (MM), Dunbar Valley (DV) and Core Zone (CZ). Motjane, Forbes Reef and Malolotja based on present study. Information for other sites from Changwe and Balkwill (2003).**

	Mo	RT	SM	KL	FR	GV	MC	Ma	MM	DV	CZ
SI(%)	74.7	<b>46.1</b>	<b>44.0</b>	<b>43.4</b>	42.2	<b>39.9</b>	<b>39.3</b>	35.7	<b>35.9</b>	<b>31.2</b>	<b>31.1</b>

When the Swaziland ultramafic flora as a whole is compared to the non-ultramafic Swaziland flora and to ultramafic sites elsewhere in southern Africa, there is a marked similarity to the associated non-ultramafic flora and similarity to other ultramafic sites is lower and ranges from 29.3% for the Witwatersrand to 5.6% for the Great Dyke (Table 3.15).

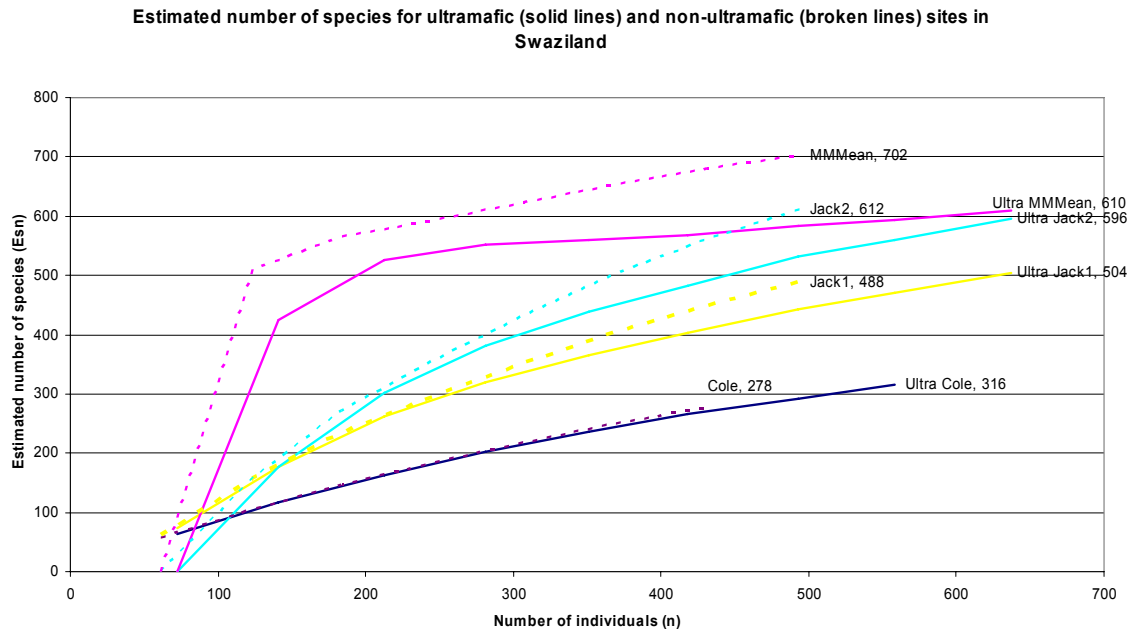
**Table 3.15. Sørensen's indices of similarity (%) between the Swaziland ultramafic flora and those of associated non-ultramafic sites (NU) and ultramafic sites in southern Africa. Witwatersrand (WWR), Dunbar Valley (DV), Agnes Mine (AM), Diepgezet (DG), Kaapsehoop (KH) and Great Dyke (GD) calculated from data in † Williamson (1995), ‡ Kidger (1993), ♦ Reddy et al. (2001), \* Changwe and Balkwill (2003) and ♠ Wild (1964).**

	NU	WWR♦	DV*	AM†	DG‡	KH†	GD♠
SI (%)	41.2	29.3	26.8	26.5	24.0	22.7	5.6

## Species richness

The rarefaction curve and curves for estimating total species richness for the pooled results for all ultramafic sites all lie below those for the same estimator for associated non-ultramafic sites, indicating that in this study ultramafic soils overall are not as species rich as non-ultramafic soils. The Michaelis Menten Means estimator (MM Means) and Jack knife 2 (Jack 2) give estimates for the ultramafic areas (609 and 596, respectively) close to the number of species collected on ultramafic soils in this study (598) (Figure 3.11). Of all the estimators the Michaelis Menton Means estimator is closer to an asymptote and the estimate of species richness is a reasonable expectation based on the number of species collected.

The differences in elevation, aspect, climate and level of disturbance between sites will provide a diversity of resources, and it is likely that the pools of species suited to the different situations will be different and the species richness is likely to differ. Figures 3.12, 3.13 and 3.14 compare ultramafic and non-ultramafic plots for each site.



**Figure 3.11.** Species richness estimation curves for species collected in ultramafic (solid lines) and non-ultramafic (broken lines) plots in Swaziland. The curves represent successively pooled and randomly ordered samples. The curves were computed using *EstimateS* (Colwell, 2001).

There is lower species richness for Forbes Reef ultramafic plots than for the associated non-ultramafic plots, as was the case for all Swaziland ultramafic plots vs. all non-ultramafic plots. The rarefaction (Coleman) and various estimated accumulation curves for ultramafic plots lie below the non-ultramafic curves. The number of plots at Motjane was too few to estimate species richness as may be seen from the steeply rising curves in Figure 3.12, but the slopes of all the estimators indicate that the curves would be below those of the non-ultramafic plots, and so species richness will be lower for ultramafic plots. Malolotja differs from the higher sites and has higher species richness for ultramafic sites than for surrounding non-ultramafic sites (Figure 3.14).

Estimates of number of species for Forbes Reef ultramafic (solid lines) and non-ultramafic sites (broken lines).

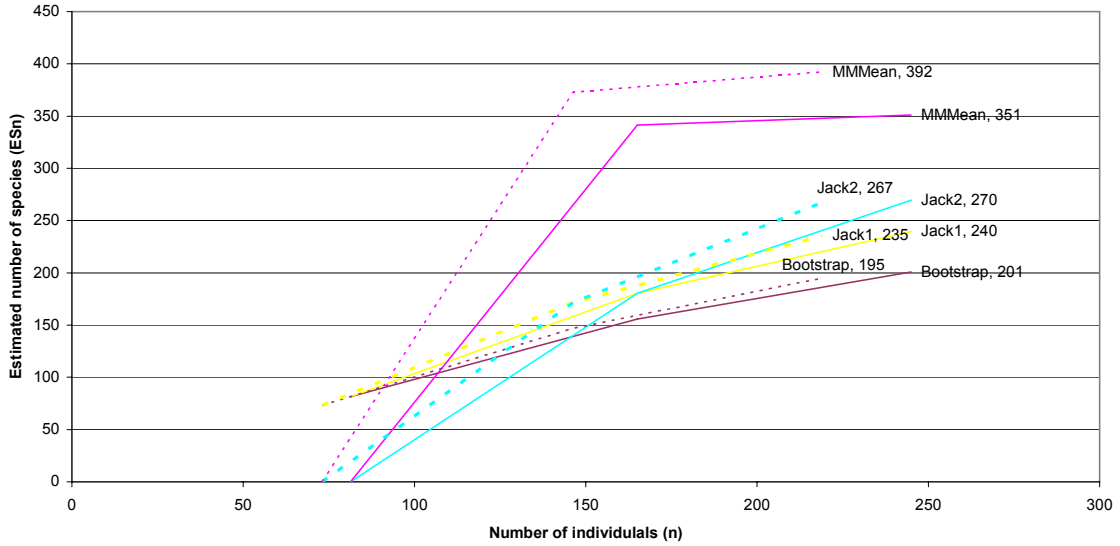


Figure 3.12. Species richness estimation curves for species collected on Forbes Reef ultramafic (solid lines) and associated non-ultramafic (broken lines) plots in Swaziland. The curves represent successively pooled and randomly ordered samples.

Estimates of the number of species for Motjane ultramafic (solid lines) and non-ultramafic (broken lines) sites.

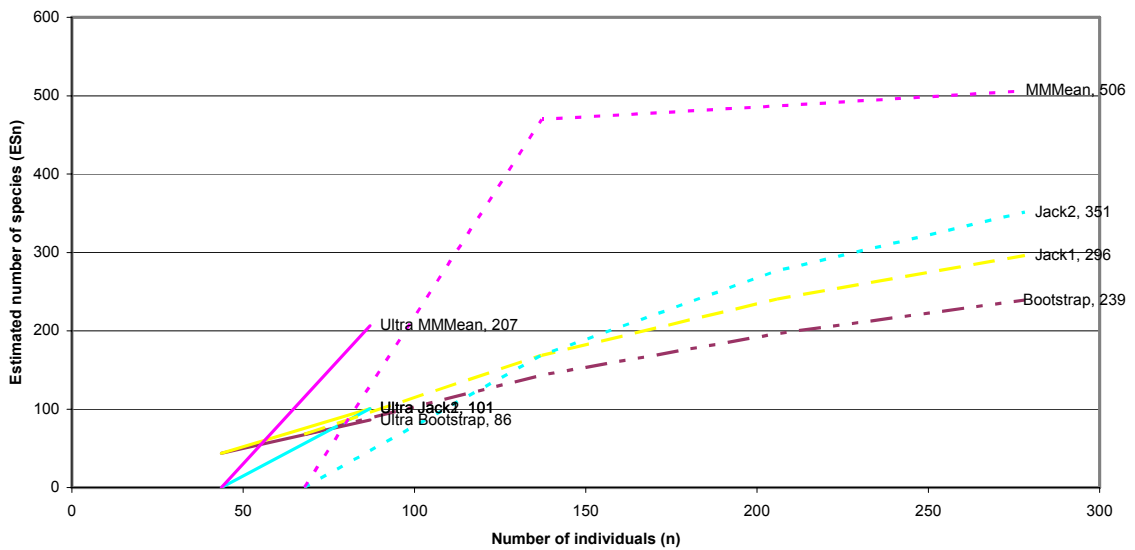


Figure 3.13. Species richness estimation curves for species collected on Motjane ultramafic (solid lines) and associated non-ultramafic (broken lines) plots in Swaziland. The curves represent successively pooled and randomly ordered samples.

Estimates of number of species for Malolotja ultramafic (ultra) and non-ultramafic sites.

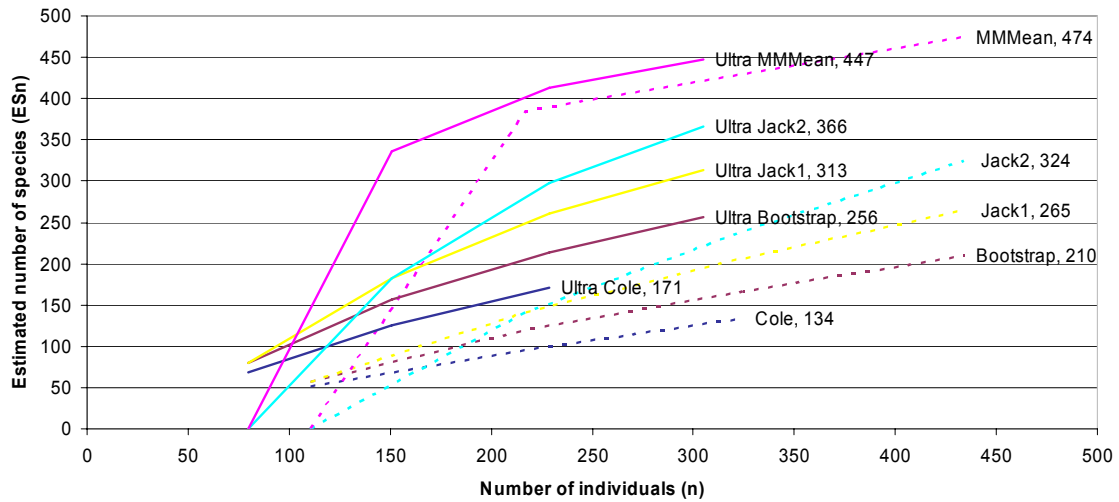


Figure 3.14. Species richness estimation curves for species collected on Malolotja ultramafic (solid lines) and associated non-ultramafic (broken lines) plots in Swaziland. The curves represent successively pooled and randomly ordered samples.

Estimates of number of species for Malolotja, Forbes Reef and Motjane ultramafic sites

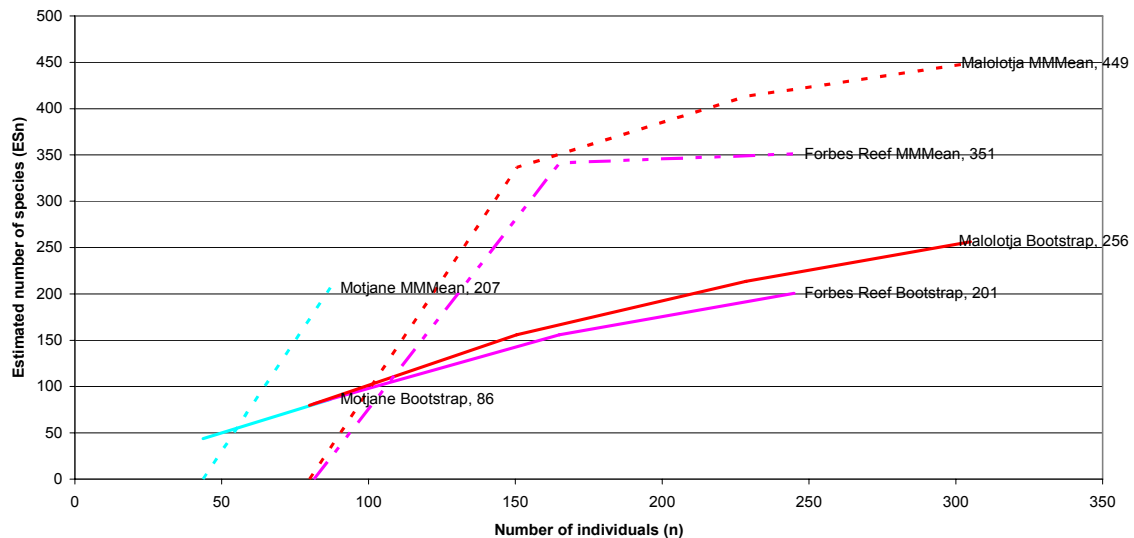


Figure 3.15. Species richness curves for species collected at Forbes Reef, Motjane and Malolotja ultramafic sites.

Species counts from 1000 m<sup>2</sup> sample plots for the three sites show Forbes Reef to have the highest species richness ( $81.7 \pm 5.8$ ) followed by Malolotja ( $76.3 \pm 11.2$ ) with Motjane having the lowest species richness ( $43.5 \pm 0.5$ ) (Table 3.17). Both bootstrap and MM Means species estimation curves however show a greater species richness for Malolotja (256 – 446) than for Forbes Reef (200 – 361) and the slopes of the Motjane curves parallel those of Malolotja, indicating the true species richness of these two sites may be similar.

## Species richness at other sites on the Barberton Green Stone Belt.

Forbes Reef serpentine ranks second in the Barberton Greenstone Belt for the number of species collected on a 1000 m<sup>2</sup> plot and Malolotja is in the more speciose half of the sites (Table 3.16).

**Table 3.16. Average species richness (i.e. number of species recorded per 1000 m<sup>2</sup>) on ultramafic and non-ultramafic sites. Forbes Reef, Motjane and Malolotja from present study; information for other sites from Changwe and Balkwill (2003). \* denotes significant difference (Student's t-test).**

Site	Ultramafic	Non-ultramafic	Probability of difference in richness	
Kalkloof	83.5 ± 6.6	81.5 ± 8.7	P > 0.05	n.s.
Forbes Reef	81.7 ± 5.8	73.0 ± 2.3	P > 0.05	n.s.
Groenvally	80.3 ± 6.8	73.5 ± 10.7	P < 0.05	*
Malolotja	76.3 ± 11.2	54.3 ± 6.5	P > 0.05	n.s.
Core Zone	75.5 ± 4.8	84.0 ± 5.2	P < 0.05	*
Sawmill	75.0 ± 5.8	78.5 ± 9.7	P > 0.05	n.s.
Magnesite	73.0 ± 6.6	54.3 ± 9.4	P < 0.05	*
Rosentuin	72.3 ± 11.7	69.0 ± 5.2	P > 0.05	n.s.
Mundt's Concession	65.0 ± 3.1	67.5 ± 4.7	P > 0.05	n.s.
Motjane	43.5 ± 0.5	59.0 single	P > 0.05	n.s.
Dunbar Valley	29.0 ± 4.3	31.7 ± 2.9	P > 0.05	n.s.

The differences in species count between ultramafic and non-ultramafic sites were not significant for any of the Swaziland sites.

## Diversity indices and Evenness

The Shannon-Wiener and Simpson's diversity indices have been widely used. The first is a measure of species richness and the second a measure of dominance (evenness). Forbes Reef and Malolotja ultramafic sites were more diverse than the corresponding non-ultramafic sites as determined by both the Shannon-Wiener and Simpson's indices. No abundance measure was made for the Motjane ultramafic plots due to the difficulty in identifying grasses from vegetative plants, consequently the Simpson's indices for that site are not very reliable estimates (Table 3.17). Malolotja ultramafic plots are much more diverse than the corresponding non-ultramafic plots. Swaziland sites are more diverse than Dunbar as determined by the Shannon-Wiener Index (Table 3.18).

**Table 3.17. Species diversity indices calculated for the ultramafic sites in Swaziland and associated non-ultramafic sites. N = number of species, n = number of sample plots.**

Index	Forbes Reef		Motjane		Malolotja	
	Ultra	Non-ultra	Ultra	Non-ultra	Ultra	Non-ultra
	n = 3 N = 168	n = 3 N = 160	n = 2 N = 72	Insufficient data	n = 4 N = 209	n = 4 N = 167
Shannon-Wiener H'	4.50	4.43	4.23		4.55	3.92
Simpson ( $\lambda$ )	0.021	0.021	0.0040		0.031	0.058
Simpson ( $-\ln \lambda$ )	3.88	3.85	5.51		3.50	2.84

**Table 3.18. Shannon-Wiener index (H') for ultramafic and non ultramafic sites at Forbes Reef, Motjane, Malolotja and Dunbar Valley. Figures for Dunbar Valley from Changwe and Balkwill (2003).**

Site	H' Ultramafic	H' Non-ultramafic
Forbes Reef	4.50	4.43
Motjane	4.23	4.23
Malolotja	4.55	3.92
Dunbar	2.63	2.89

**Table 3.19. Evenness measures calculated for Forbes Reef, Motjane and Malolotja. ♦ indicates no suitable data available to calculate evenness measure.**

Evenness measure	Forbes Reef		Motjane		Malolotja	
	Ultramafic	Non-ultra	Ultramafic	Non-ultra	Ultramafic	Non-ultra
E1 (J')	0.027	0.023	0.059	0.027	0.022	0.024
E5	0.530	0.552	♦	♦	0.339	0.325

The E5 evenness measure (Table 3.19) indicates Malolotja has greater dominance by some species than is the case for Forbes Reef where the distribution of species is more even. The Malolotja plots were dominated by *Themeda triandra* and *Loudetia simplex* with up to 50 % cover, and often with *Diheteropogon amplexens* and *Monocymbium ceresiiforme* as subdominants with around 10 – 15 % cover. Forbes Reef plots did not show such a clear dominance by any one species. Some plots had up to 15% cover for one or more species, but the more common species differed from plot to plot.

### Beta diversity

Beta diversity was examined at different scales for this study. The total number of species in the study gives a measure of how diverse each site is relative to the whole area. The beta diversity within soil types and the diversity by study site were also



determined (Table 3.20). For the latter, plot data only were used to remove the possible effect of differential sampling by soil type.

**Table 3.20. Whittaker's Beta diversity for sites compared with study area, total species counts for all plots and total species counts for soil type.**

	Average # species	Study area	Study area plots only	Ultramafic	Non-ultramafic	Forbes Reef	Mojane	Malolotja
S		776	488	338	274	167 160	73 91	210 166
F2								
F5	81.6	8.51	4.89	3.14	2.36	1.05		
F6								
MO1							0.68	
MO3	43.5	16.84	10.22	6.77	5.30			
MA4								
MA6	76.5	9.14	5.38	3.42	2.58			1.75
MA7								
MA8								
F1								
F3	73.0	9.63	5.68	3.63	2.74	1.19		
F4								
MO2	59.0	12.15	7.27	4.73	3.63		0.54	
MA1								
MA2	54.3	13.29	7.99	5.22	4.05			2.06
MA3								
MA5								

### **Bare ground**

The results in Table 3.21 show significantly more bare ground for Malolotja ultramafic site than for the corresponding non-ultramafic sites. There was no significant difference between ultramafic and non-ultramafic plots for Forbes Reef.

**Table 3.21. Estimate of bare ground (linear %) in plots. A tape was placed arbitrarily across the plot and the species present or lack of a plant was recorded every 10 cm for 100 points.**

Forbes Reef	Ultramafic	F2	23%	t(cal) = 0.154 N.S. (P>0.05)
		F5	13%	
		F6	0%	
	Non-ultramafic	F1	0%	
		F3	18%	
		F4	14%	
Motjane	Ultramafic	Mo1	-	
		Mo3	-	
	Non-ultramafic	Mo2	-	
Malolotja	Ultramafic	Ma4	-	t(cal) = 3.754 (P<0.05)
		Ma6	34%	
		Ma7	24%	
		Ma8	25%	
	Non-ultramafic	Ma1	-	
		Ma2	6%	
		Ma3	2%	
	Ma5	16%		

### *Discussion*

Biotic diversity is low towards the poles and high towards the equator (Gaston and Williams, 1996). This pattern seems to apply to plants on ultramafic soils, with only 20 tolerant species reported for northern Finland, 65° N (Brooks, 1987). Sites in Europe and North America are often referred to as 'barrens'. Eighty-two species on ultramafics in south Westland, New Zealand, 42° S, about 60 on Mt Yupari, Japan, 35° N (Brooks, 1987). The Woko and Glenrock ultramafics in New South Wales, 30° S, Australia, have 79 species (Davie and Benson, 1992). In contrast 920 ultramafic endemics are reported for Cuba, 22° N without counting the tolerant (bodenvag) species (Berazain Iturralde, 1979) and 1500 species, 900 of them ultramafic endemics, for New Caledonia, 21° S (Brooks, 1987). Information from the Malay Archipelago, 5° N, is scanty but it appears from the accounts in Brooks (1987) that the plant species richness is probably high. In California there is a decline in ultramafic endemics from north to south, which exceeds a similar trend that holds for plants in general (Harrison *et al.*, 2000). The ultramafic flora appears to show a more sensitive response to the rainfall gradient that is probably responsible for the reversed latitudinal trend (Harrison *et al.*, 2000).

In southern Africa, the Great Dyke has 322 species in an area of 3000 km<sup>2</sup>, low species richness for the size of the area – the Chimanimani mountains in the same region have 859

species in a 400 km<sup>2</sup> area (Brooks, 1987). Compared to the Great Dyke and other sites outside the tropics the ultramafic sites of the Barberton Greenstone Belt (BGB) are very species rich. In this study 600 species were collected from about 10 km<sup>2</sup> out of a total ultramafic area of 52 km<sup>2</sup>.

The natural vegetation surrounding the Great Dyke is woodland, but few trees occur on the Great Dyke and the few species which do occur are stunted (Robertson, 1992). The absence, reduction of numbers and/or stunting of trees has been reported for Queensland (Batianoff and Specht, 1992), Cuba (Borhidi, 1992) and North America (Brooks, 1987). The dwarf forest reported on ultramafic soils of Palawan Island appears to be connected to hydrology however, rather than soil (Proctor and Nagy, 1992) and rainforest occurs on some ultramafic sites, so the effect on trees is not universal. Robertson (1992) showed that exposure to Ni stopped root growth, and that small amounts of Mg or larger amounts of Ca allowed root growth to resume. He suggested that Ni may be at toxic concentrations in the soil for only brief periods, perhaps immediately after rain, with further rainfall diluting or leaching away some of the Ni. Plants with adventitious roots and those which produced roots readily would be at an advantage, whilst trees with a tap root and plants which do not produce numerous roots would be affected most. A recent study has shown that the production of adventitious roots on the primary roots of dicotyledons, including trees, is common and widespread (Paolillo Jr & Zobel, 2002). This root production ought to ameliorate the effects on the root system as a result of damage to root tips. If this is the case, the reduced number and vigour of trees on some ultramafic sites is more likely to be a result of establishment failure because of early damage to the root system before it is extensive enough to produce enough adventitious roots for adequate functioning, as the postulate that trees are not able to produce numerous roots appears to be unfounded.

In this study the species composition of ultramafic sites was most similar to that of non-ultramafic sites situated near them. The species richness of the surroundings will affect species richness on ultramafic soils because the surrounding soils are the main source of ultramafic tolerant species. The Swaziland ultramafic sites are situated in a species rich region and the pool of potentially ultramafic tolerant species is thus large.

The proportion of monocotyledons making up the vegetation sampled in the study area did not differ greatly from the proportion for the entire Swaziland flora (Table 3.4, 3.5) even though with few trees in the montane grassland, and with grass as the dominant element of the vegetation, an increased contribution to the vegetation by monocotyledons might have

been expected. When the proportions for monocotyledons on and off ultramafic soils were compared there was no significant difference (Table 3.4). There were significantly more monocotyledons on the higher altitude ultramafic sites and significantly fewer on the lower altitude non-ultramafic sites than there were in the whole Swaziland flora. The higher altitude sites had high levels of disturbance, so altitude and or disturbance combined with ultramafic soils resulted in a greater proportion of monocotyledons. The possibility of differences in response to similar grazing pressure, or of a preference by cattle for ultramafic sites, merits further investigation. Grazing can reduce species richness in nutrient poor systems (Proulx & Mazumder, 1998). Perhaps monocotyledons are better able to survive or regenerate (basal meristem in leaves perhaps important) under the dual pressures of grazing and ultramafic soils and the difference is more a result of a differential loss of species under disturbance than an increased 'fitness' for monocotyledons.

The relationship between the numbers of species and genera (or families) is statistically complex and simple projections of expected numbers cannot be used to determine if the number of genera is lower than expected (Järvinen, 1982). The alternative approach of comparing the most speciose genera on and off ultramafic soils and determining if there was any significant difference in the number of species indicated no difference.

The BGB sites are more speciose than temperate sites, but do not have the high levels of endemism of some tropical sites. In New Caledonia, 69% of plants on ultramafic soils are endemic to those soils (Brooks, 1987) and in Cuba there are 920 ultramafic endemics (Berazain Iturralde, 1979) but only 29 ultramafic endemics are known to occur on the BGB (Williamson and Balkwill, in edit). Outside the tropics, ultramafic sites often have considerably fewer species than the non-ultramafic surroundings. For example, Mt. Yupari, Japan had 60 species on ultramafic soils and 535 species on non-ultramafic soils; south Westland, New Zealand had 82 ultramafic species and 404 on other substrates and the ultramafic Mt. Rai-iz in the Urals has 91 species compared to 216 for nearby Mt. Slantsevaya (Brooks, 1987). In contrast sites of the BGB have species richness close to that of their surroundings (Table 3.16) with no significant difference in species numbers between soil types for eight sites, two sites with significantly lower species richness on ultramafic soils and one site with a significantly higher number of species on ultramafic soil.

The curves of the various estimators indicate a lower species richness relative to surrounding areas for Swaziland ultramafic sites as a whole, and for the Forbes Reef and Motjane sites, but for Malolotja (Figure 3.14) the estimator curves for ultramafic sites lie above those for

non-ultramafic sites, indicating higher species richness. Diversity indices show slightly higher diversity for ultramafic plots at Forbes Reef and much higher diversity for ultramafic plots at Malolotja. The Unified Neutral Theory of Biodiversity and Biogeography of Hubbell (2001) shows, using probability, how patterns of diversity can be explained by speciation, dispersal and extinction rates and that immigration rate and community size are the determinants of species richness. For small community size, the theory predicts that the common species will be more common and the rare species more rare than would be predicted from random sampling of the surrounding community (metacommunity) (Hubbell, 2001). This prediction suggests the possibility that more complete sampling of the vegetation may increase the number of species found on ultramafic soils more than the number found off ultramafic soils, and thus it is possible that ultramafic soils may be richer in species.

The high relative species richness on Swaziland ultramafic sites is probably because grassland plants have attributes which enable them to tolerate the ultramafic soils. The ability to regenerate roots and the possession of mechanisms to store water and nutrients for the dry season are common in grassland species and may be important for tolerance (Robinson, 1992). Given a high pool of species potentially able to tolerate ultramafic conditions, and relatively few endemics (ultramafic specialists), the less favourable conditions may reduce plant density or competitive exclusion, allowing more species the space to establish, as has been found for nutrient poor conditions. A number of studies have investigated the relationship between species richness and productivity (Gough *et al.*, 2000; Henry *et al.*, 1999; Proulx and Mazumder, 1998). When various plant communities were fertilized with N there was an increase in productivity and a decrease in species richness (Gough *et al.*, 2000). It has also been shown that the increase in plant density in response to fertilizer results in a decreased species richness (Henry *et al.*, 1999). In nutrient rich ecosystems grazing increased species richness, but the reverse was true for nutrient poor ecosystems (Proulx and Mazumder, 1998).

Malolotja ultramafic plots had significantly more bare ground and higher species richness than Malolotja non-ultramafic plots, results consistent with reduced plant density allowing space for additional species to establish. Lower species richness for ultramafic vs. non-ultramafic plots for Forbes Reef and Motjane may be a differential response to grazing, with species richness tending to be reduced on ultramafic soils under grazing. Ultramafic conditions result in slow regrowth of species and continued grazing may prevent sufficient growth to sustain some species (e.g. see *Kniphofia umbrina* in chapter 4).

## *Conclusions*

There is some evidence that useful survival traits for conditions in this study may occur more frequently in monocotyledons as a group than in dicotyledons as a group, as there was a significantly higher proportion of monocotyledons sampled on the higher altitude ultramafic sites in Swaziland than is found in the whole Swaziland Flora. As the result is for a combination of factors (altitude, ultramafic soil and disturbance level), it is not clear to what extent each of these individual factors contribute to the increased proportion of monocotyledons. The proportion of monocotyledons on the Great Dyke was 40% – 60% of species, a much greater proportion than found in this study (Proctor & Cole, 1992).

The species richness for ultramafic soils in Swaziland overall is less than that for non-ultramafic soils but high compared to many higher latitude sites where the species numbers on ultramafic soils are much lower than those of surroundings. Species were more evenly distributed for the higher altitude sites than for the lower site. The increased evenness could arise by the loss of rarer species. It is possible that the original diversity of some sites has been reduced by grazing and cultivation. *Kniphofia umbrina* is an example of a species threatened by grazing (Witkowski *et al.*, 2001). At Malolotja the ultramafic site was more speciose than the non-ultramafic site, possibly because of lower plant density that allows space for additional species. Species that are small or slow growing and usually easily overgrown by larger faster species, may persist better under reduced plant density or where competing plants are stunted.

The differences in diversity linked with altitude were of similar magnitude and direction for ultramafic and non-ultramafic soils. Ultramafic soils did not influence the effect of altitude and/or disturbance on diversity patterns. Ultramafic vegetation was similar to proximal non-ultramafic vegetation than distant vegetation of any soil type. Forbes Reef at higher altitude and Malolotja at lower altitude both had higher species richness than Motjane at higher altitude. The level of disturbance was much greater for Motjane than for the other sites and disturbance probably had the greatest negative effect on diversity. This contrasts with California where fire and grazing increased diversity (Safford & Harrison, 2003).