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Vegetation response to clearing of exotic invasive plants along the Sabie River, South Africa

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2007-02-26T12:52:33Z
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CHAPTER 6

DIFFERENCES IN SPECIES COMPOSITION, RICHNESS AND DIVERSITY IN RESPONSE TO INVASION AND CLEARING

6.1 Introduction

Communities may be seen as consisting of a number of individuals of different species, with interactions between individuals and their environment, and between themselves. The diversity-stability hypothesis predicts that complex trophic systems will be more stable than simple ones, or, in general, that more diverse communities will be more stable than less diverse ones and several studies have demonstrated that with a loss in diversity, community function becomes less stable (Shugart & Seagle 1985; Petraitis *et al.* 1989; Tilman & Downing 1994). Although this has been demonstrated, it is also evident that there is no simple relationship between species diversity and stability in ecological systems (Goodman 1975).

In the past, changes in species diversity and species richness have been illustrated where communities have been altered (MacDonald & Richardson 1986; Henderson & Wells 1986; Hobbs & Huenneke 1992). The changes to diversity resulting from the removal of a species or group of species from the community are varied, and may also depend on species interactions and the duration of this "disturbance" (Lewis *et al.* 1988). Potentially every alteration to a community poses the possibility of a "loss or gain of species" and hence an alteration to species richness and diversity.

One such factor, introduction of exotic species, may influence the community by changing its overall structure and thus proportional abundance of species in the community. It may also change functional relationships within the community such as those between pollinator and plant or seed dispersal agent and plant (Breytenbach 1991). The application of clearing programs and the invasion of communities in the eastern escarpment will undoubtedly have also resulted in some alteration to the community. The extent of those alterations and the effect that these would have on the community species composition is yet unknown.

6.1.1 Invasion by exotic species

Impacts have been defined as a change to the ecosystem, community or population process caused by an alteration to the physical or biophysical environment. Exotic species, once they have invaded the community fall within this category. The most obvious impact caused by exotic species invasion is the partial to complete replacement of indigenous communities, thereby reducing species richness and

altering the appearance and character of the landscape (Gause 1934; Crombie 1947; Hutchinson 1961; Miller 1967; Huston 1979; Henderson & Wells 1986; Hansen *et al.* 1991). A local example of this can be seen in the Tzaneen (South Africa) area where invasion by *S. mauritianum* has resulted in a species poor system (Dean 1985).

This decrease in plant diversity and loss of species 'before and after' invasion and with forest and range management practices is well documented (Henderson & Wells 1986; MacDonald & Richardson 1986; Lewis *et al.* 1988) and may be a consequence of interacting factors within the community, such as overtopping and shading by exotic invasive species causing modifications to distributions of species of shorter life form (Midgley *et al.* 1992). Alternatively, the opposite may occur with invasion by exotic vegetation causing an increase in species richness and diversity through the creation of establishment opportunities for "other" species. This is more likely to occur if the disturbance caused by the invading species is of an intermediate nature to the community (Hobbs & Huenneke 1992).

The outcome of interactions between exotic species and the existing community will determine if the exotic will "fit in" or "repel" indigenous ecosystem processes, composition and structure. Stabilization of the community may occur, with the community being a single or near single species stand (Cronk & Fuller 1995), or a dynamic multi-species community (MacDonald & Richardson 1986).

Exotic species introduction may have other side effects besides the spread of the introduced species. Propagation of exotic species may, besides affecting the species content of the community, modify the habitat in such a manner as to facilitate the further dispersal and establishment of its own and other exotic invader species both in the modified community and the surrounding communities. This occurs in the same manner as explained by Island Biogeography and a good example of just such an occurrence is found in KwaZulu-Natal, where a number of problematic invader species are escapees of timber plantations (MacDonald & Jarman 1985). Timber plantations tend to form seed source centers, especially for species, which are dispersed by bird (eg. *S. mauritianum*), and it follows that areas close and adjacent to plantations may be regarded as areas of high invasion threat/potential (MacDonald & Jarman 1985).

6.1.2 Clearing of invasive species

Clearing of invasive species, although a selective process, tends to result in disturbance to the affected community. The removal of species will thus result in a certain amount of change or alteration to the community or community environment. Theoretically, the removal of 1 or 2 species or individuals from the community will result in a minor change in the species richness and diversity measure. On the

contrary, excessive disturbance caused by the removal process may result directly in loss of community diversity and structure (Breytenbach 1991; Petraitis *et al.* 1989).

There are also secondary disturbance effects caused by species removal from the community. These are seen through vegetation structure, species interactions and environmental modifications (Vitousek 1990). Removal of species from the community manifests itself in spatial and temporal "gaps" in the vegetation which can be vital to the regeneration of vegetation by allowing "new" species to enter the community (Shugart & West, 1977; Sousa 1984; Shugart & Seagle 1985; Everard *et al.* 1995). "New" individuals, either of existing indigenous or exotic species may take up this opportunity to "enter" a community (Geldenhuys *et al.* 1985).

In this chapter, variables relating to biodiversity and species richness were measured and evaluated in order to determine the relationship and species composition of species richness and diversity to exotic species invasion prior to and after clearing. This will enable better understanding of the effects of species removal on the community species composition, diversity and richness. It will also focus on the impacts of invasion on species richness and diversity in order to better explain the changes occurring in riverine communities of the eastern escarpment under the current management regime.

6.2 Materials and Methods

6.2.1 Field sampling & identification

Data collection

Data collection for species diversity parameters was undertaken during January 1997. Voucher plant specimens for all species encountered were collected and pressed in the field for later identification. Specimens were keyed out and identified using the University of the Witwatersrand Charles E. Moss Herbarium specimen sheets and library with the assistance of Prof. K. Balkwall, herbarium curator. All specimens were identified to the genus level and where possible, to species level. Species were classed as invasive or indigenous using the WWP list of problem species for Mpumalanga (Table 6.1.). Different growth forms of the species were identified in the field and verified once the species had been identified.

In the field, species were identified and counted at each quadrat size within the modified nested plot (i.e. quadrat sizes 1 m^2, 10 m^2, 100 m^2 and 1000 m^2). The number of individuals for all species was determined for only the 1 m^2 and 10 m^2 quadrats. The number of individuals for each woody species was also determined in the 100 m^2 quadrats. Presence or absence data for all species was determined for all four quadrat scales.

Species area curves

Due to the large data set collected, it was decided to focus on the optimum quadrat size as spatial scope and "grain of resolution will affect richness measures" (Willis & Whittaker 2002). This was determined using species area curves. Species richness was calculated for indigenous and total species composition at all sites and all quadrat sizes. From species richness data collected for each quadrat size within sample plots, species area curves were plotted, and the optimum quadrat size for diversity analysis was determined. This was done for two of the different growth forms encountered (herbaceous/grass species and woody species of trees and shrubs) in the field, in order to cater for the obvious size differences of plant growth forms which quadrat size was thought to bias.

Species richness – total and indigenous species

Comparisons between cleared and uncleared plots of both high and low invasion for both altitudes were made using a two way ANOVA for total species richness and indigenous species richness for all experimental categories. This was done using only the optimal quadrat size determined from the species richness curves.

Species richness - growth forms

A number of different vegetation growth form classes were recognized in this study. These were defined for ease of use and to be as close to the working definitions found in the literature as possible. The different growth forms identified in the project were: single stemmed trees, multi-stemmed trees, single stemmed shrubs, multi-stemmed shrubs, erect herbs/forbs, prostrate herbs/forbs and tufted and stoloniferous grasses.

- Trees were defined as a perennial woody plant with a distinct upper crown and of a height of at least 2 m (Van Wyk & Van Wyk 1997).
- Shrubs were defined as a perennial woody plant with multi- or single stems arising from or near the ground; differs from a tree in that it is smaller and does not have a trunk or a bole (van Wyk & Van Wyk 1997).
- Herbs/Forbs were defined as a plant whose stem is not woody or persistent normally with an annual life cycle.
- Grasses as used in this study included the group known as sedges or Cyperaceae (Van Oudtshoorn 1992).

Comparisons were made between the species richness for each of the different growth forms within each experimental category using a one-way ANOVA for each growth form. It was found, using the

species richness curves, that the best measures of species richness for woody growth forms was for the 100 m^2 quadrats, and for herbaceous growth forms the 10 m^2 quadrats.

6.2.2 Plant diversity

Plant diversity was measured using the optimum quadrate size as determined from species richness curves. Total and herbaceous alpha diversity was calculated on the 10 m^2 and tree alpha diversity on the 100 m^2 quadrat size.

Alpha diversity

Simpsons index for alpha diversity was the index used to measure the diversity of species independently for each plots within the experimental design. This index is as follows:

$$D_a = 1 - \Sigma \{[n_i (n_i - 1)]/[N (N - 1)]\}$$

D = Alpha diversity

n_i = Number of individuals of species I

N = Total sample size

The reason for using Simpsons index over other indices was for two fundamental reasons:

(a) Simpsons index is a widely used medium of comparison for biodiversity in the literature and;

(b) It is one of the commonly employed indices that can use density data, as opposed to cover abundance data.

Simpsons index was calculated for all species from the 10 m^2 quadrat and trees from the 100 m^2 quadrat. The alpha diversity indices obtained from each quadrat were then statistically compared for plots between altitude, invasion intensity and clearing using a three way ANOVA and Ryan's Q post hoc test.

Beta diversity

Beta diversity was calculated for sites separated by altitude, invasion intensity and clearing treatments. Beta Diversity was calculated for plot management/treatments using Sorenson's (1948) coefficient of community.

$$CC = 2 S_s / (S_j + S_k)$$

CC = Beta diversity

S_s = Number of species shared by both samples;

S_j = Number of species present in sample 1;

S_k = Number of species present in sample 2;

This index was calculated for all pair-wise comparisons of all pooled sampled sites for high and low altitudes, cleared and uncleared categories. This was then used to complement the statistical comparisons made between treatments/management categories using Simpson's measure of diversity and compared to other measures in the literature. A larger value means that the sites are more similar in their diversity.

6.2.3 Multivariate analysis

Constrained Canonical Analyses (CCA) were done using 0.002 ha (2 * 10 m^2 quadrats) within each plot in the high and low altitude divisions. This was done with species presence and absence data obtained in the field using the multivariate package called CANOCO.

Similar to the multivariate analysis done for the Environmental Modification data in Chapter 3, the analysis was repeated for both high and low altitude divisions with each being treated as a separate data set. The reasons for the altitudinal separation/divisions of data was that different biological processes, and different rates of these processes, occur at different altitudes. It was reasoned that altitudinal differences were not the focus of the study and hence they were largely ignored for the sake of simplicity of explanation (T.G. O'Connor, *pers. comm.* 1997).

6.3 Results

6.3.1 Species richness

Species area curves

The species area curves for all sites (Figure 6.1) illustrated the optimum sampling scale for riverine forest vegetation to be the 10 m^2 and 100 m^2 plot sizes. Considering the different growth forms encountered within the study, it was decided to cater for species richness for each of the growth forms. The reason for this is that the number of infrequently encountered species and the size of larger vegetation growth forms could bias the results obtained. It was thus determined that the optimum species richness measure falls into the 100 m^2 and 10 m^2 quadrat scales for the larger and smaller growth forms respectively (Figure 6.1). For this reason these two quadrat sizes were focused on for all interpretation in order to remove confusion of quadrat size on results.

Species Richness

Three-way ANOVA statistical comparisons of the species richness of total species for the 1 m^2, 10 m^2 and 100 m^2 quadrat size illustrated that species richness was significantly higher under low invasion categories than under high invasion categories (Table 6.1 & 6.2). Significant differences were also

found for species richness between high altitude and low altitude sites although low altitude sites tended to have a higher species richness (Table 6.1 & 6.2). Only at the 1000 m^2 were significant differences found between cleared and uncleared sites at both invasion intensities (Table 6.1).

Comparisons of species richness for the 10 m^2 plots did not show significant differences between sites for cleared and uncleared (MAN) categories at $P < 0.05$, (Table 6.1). There was however a tendency for clearing of low invasion sites to result in an increase in species richness (Table 6.2).

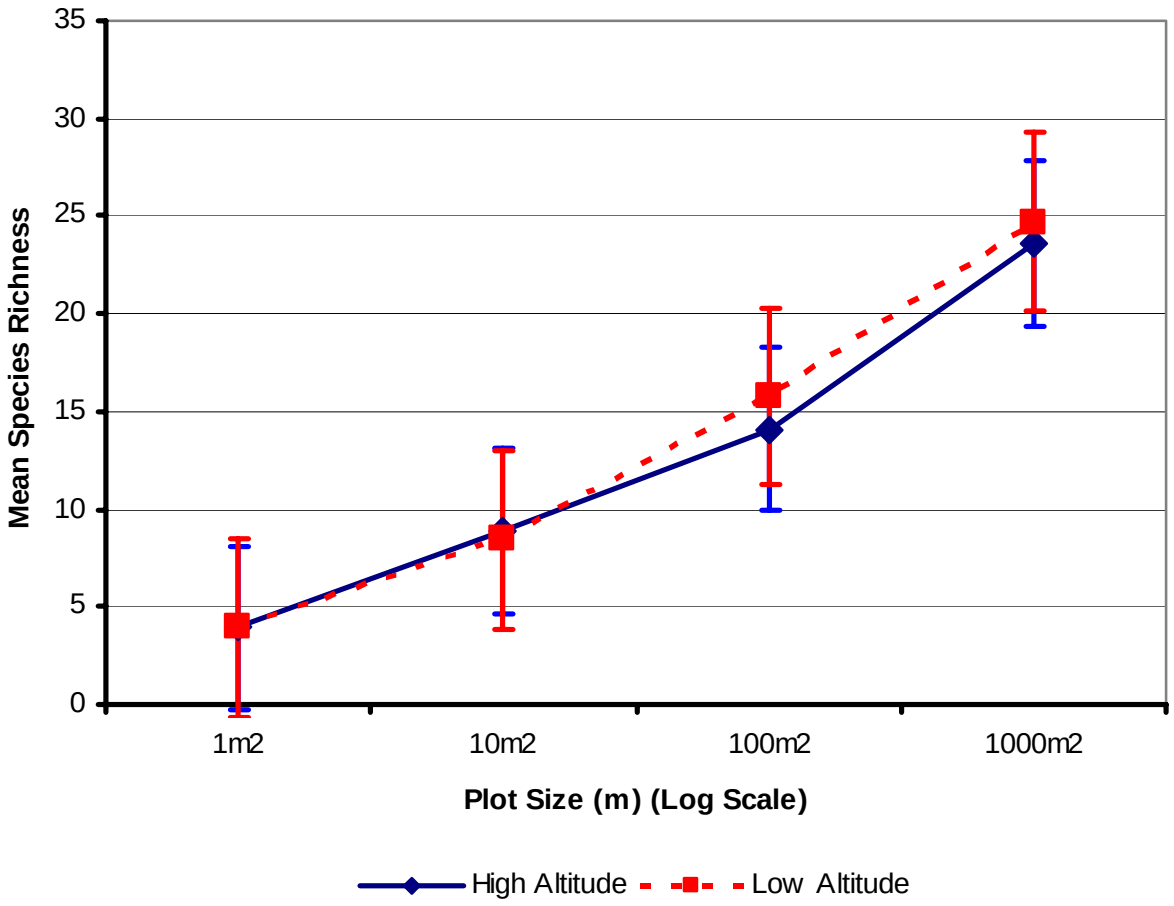


Figure 6.1 Species richness as a function of plot sizes (log scale), including 1 m^2 (200 plots at each altitude), 10 m^2 (40 plots at each altitude), 100 m^2 (20 plots at each altitude) and 1000 m^2 (20 plots at each altitude & includes all species found within smaller plots) (mean ± S.E.) for both high and low altitudes.

The regression analyses of species richness with invasion intensity illustrated only a weak negative relationship of species richness with invasion intensity for only the uncleared sites at the 100 m^2 quadrat size (Figures 6.2 & 6.3 respectively). This relationship corroborated the ANOVA analysis for species richness differentiations with invasion and clearing.

Table 6.1 Plant species richness significance values for three-way ANOVA's of altitude (ALT), invasion intensity (INV) and management / clearing treatment (MAN) for quadrat sizes 1 m^2, 10 m^2, 100 m^2 and 1000 m^2. *d.f.* = 1,32 for all main effects and interaction terms. Bold text indicates $P < 0.05$.

Quadrat Size	ALT	INV	MAN	ALT*INV	ALT*MAN	INV*MAN	ALT*INV *MAN
1 m^2	0.971	**0.003**	0.184	0.385	0.196	0.468	0.295
10 m^2	0.444	0.237	0.056	0.798	**0.047**	0.798	0.496
100 m^2	0.181	**< 0.001**	0.208	0.307	0.538	0.967	0.902
1000 m^2	0.460	**< 0.001**	**0.043**	0.893	0.348	0.686	0.099

6.3.2 Plant species diversity

Plant alpha diversity was calculated (Table 6.3) and these values were compared for differences at the 1 m^2, 10 m^2, and 100 m^2 scale (data was to variable for 1000 m^2 scale data) (Table 6.4). Plant alpha diversity (Simpson's Index) was found to have an average of 0.41 for all sites sampled at the 100 m^2 quadrat size. This is marginally higher than that found in some grassland areas but is similar to the diversity found in the savanna biome (0.15 – 0.30).

Comparisons of plant species diversity illustrated that alpha diversity was significantly different for the high and low altitude sites (Table 6.4). Similarly, there were significant differences in plant diversity between high and low invasion categories (Table 6.4). Some significant differences were found for the ALT*INV, ALT*MAN and INV*MAN interactions at the 1 m^2 scale of sampling. This was attributed to the scale of the quadrat and the bias towards smaller growing species such as herbs and grasses, which would more readily reflect the disturbance caused by clearing.

Table 6.2 Mean and standard error for plant species richness. Values with the same superscript letter within rows are not significantly different using Ryan's Q multiple comparison test ($P < 0.05$).

Treatment	High Altitude				Low Altitude			
Variable	High Invasion		Low Invasion		High Invasion		Low Invasion	
	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
1 m^2	4.0 ± 0.67^{a}	2.78 ± 0.14^{a}	4.62 ± 0.19^{b}	4.38 ± 0.42^{b}	3.58 ± 0.15^{a}	3.66 ± 0.33^{a}	4.3 ± 0.51^{b}	4.2 ± 0.32^{b}
10 m^2	8.9 ± 0.45^{ab}	8.3 ± 1.29^{ac}	8.9 ± 0.48^{ab}	9.4 ± 1.02^{ac}	6.7 ± 0.49^{ab}	9.3 ± 0.51^{ac}	7.8 ± 1.08^{ab}	9.9 ± 0.76^{ac}
100 m^2	12.8 ± 1.88^{a}	11.8 ± 1.74^{a}	16.2 ± 1.77^{b}	15.6 ± 1.54^{b}	13.8 ± 1.02^{a}	11.6 ± 0.51^{a}	20 ± 2.21^{b}	17.6 ± 2.23^{b}
1000 m^2	20.4 ± 2.50^{ac}	19 ± 2.21^{ad}	31.2 ± 2.69^{bc}	23.6 ± 1.12^{bd}	22.4 ± 1.89^{ac}	18.8 ± 1.20^{ad}	28.6 ± 2.29^{bc}	28.8 ± 2.15^{bd}

Table 6.3 Mean and standard error for plant species alpha diversity using Simpson's Index. Values with the same superscript letter within rows are not significantly different using Ryan's Q post-hoc multiple comparison test ($P < 0.05$).

Treatment	High Altitude				Low Altitude			
Variable	High Invasion		Low Invasion		High Invasion		Low Invasion	
	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
1 m^2	0.50 ± 0.10	0.63 ± 0.04	0.49 ± 0.04	0.49 ± 0.08	0.52 ± 0.09	0.48 ± 0.07	0.51 ± 0.04	0.48 ± 0.05
10 m^2	0.50 ± 0.24	0.52 ± 0.24	0.19 ± 0.07	0.27 ± 0.12	0.37 ± 0.16	0.28 ± 0.04	0.14 ± 0.57	0.24 ± 0.11
100 m^2	0.50 ± 0.21^{ac}	0.52 ± 0.21^{ac}	0.19 ± 0.16^{ad}	0.27 ± 0.20^{ad}	0.37 ± 0.20^{bc}	0.28 ± 0.07^{bc}	0.14 ± 0.19^{bd}	0.24 ± 0.22^{bd}

Table 6.4 Total plant species alpha diversity (Simpsons Index) significance values for three-way ANOVA's of altitude (ALT), invasion intensity (INV) and management / clearing treatment (MAN) for quadrat sizes 1 m^2, 10 $m^2$and 100 m^2. *d.f.* = 1,32 for all main effects and interaction terms. Bold text indicates $P < 0.05$.

Quadrat Size	ALT	INV	MAN	ALT*INV	ALT*MAN	INV*MAN	ALT*INV *MAN
1 m^2	0.216	0.111	0.636	0.140	0.053	0.200	0.162
10 m^2	0.983	0.643	0.966	0.835	0.274	0.661	0.244
100 m^2	**0.021**	**<0.001**	0.587	0.123	0.664	0.171	0.419

The three-way ANOVA analysis with a Ryan's Q post-hoc test indicated that alpha diversity of species increased with invasion (Table 6.3).

Plant diversity – growth forms

Woody plant species alpha diversity at all quadrat sizes were found to be significantly different between altitude categories (Table 6.5), with a lower diversity occurring at high altitude. Both the 100 m^2 and 1000 m^2 quadrat size was found to be significantly different between Invasion categories (Table 6.5). A Tukey post-hoc test (Appendix 17) indicated that invasion intensity detrimentally affected the woody plant species alpha diversity. No significant differences were noted for the management / clearing treatments (MAN) for any of the quadrat size for woody plant species alpha diversity.

Table 6.5 Woody plant species alpha diversity (Simpsons Index) significance values for three-way ANOVA's of altitude (ALT), invasion intensity (INV) and management / clearing treatment (MAN) for quadrat sizes 1 m^2, 10 m^2, 100 m^2 and 1000 m^2. *d.f.* = 1,32 for all main effects and interaction terms. Bold text indicates $P < 0.05$.

Quadrat Size	ALT	INV	MAN	ALT*INV	ALT*MAN	INV*MAN	ALT*INV *MAN
1 m^2	**0.007**	0.122	0.513	0.793	0.242	0.361	0.513
10 m^2	**0.012**	0.254	0.254	0.254	0.869	1.000	1.000
100 m^2	**0.002**	**0.005**	0.519	0.138	0.201	0.091	0.519
1000 m^2	**0.001**	**0.001**	0.058	0.058	0.918	0.187	0.187

A regression of the total plant species alpha diversity against invasion intensity for the 100 m^2 quadrat size indicated a weakly positive logarithmic relationship for uncleared categories that was marginally significant ($P < 0.10$) (Figure 6.4 & Appendix 15). This indicated that an increase in invasion results in a marginal increase in species alpha diversity. At the 100 m^2 scale, a positive linear relationship between invasion intensity and species alpha diversity was obtained for cleared sites indicating a greater alpha diversity occurs with clearing of high invasion categories (Figure 6.5), corresponding with the expected increase in shorter growth forms (i.e. herbaceous species).

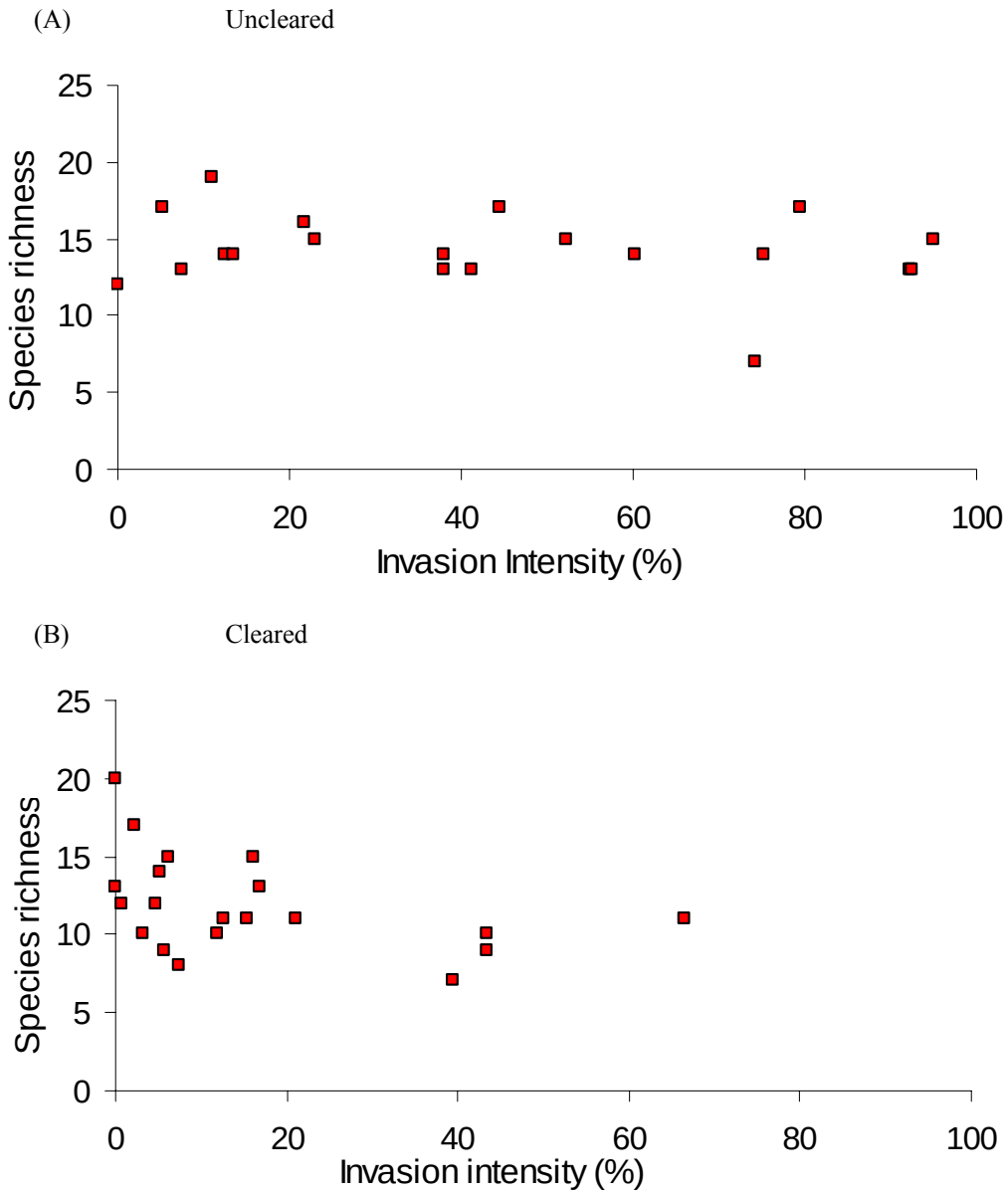


Figure 6.2 The relationship between plant species richness and invasion intensity (% aerial cover of exotic plants as calculated in section 4.4.2 of the Vegetation Chapter) at the low altitude sites for (A) uncleared ($r^2 = 0.06$; $P > 0.05$) and (B) cleared plots ($r^2 = 0.25$; $P > 0.05$) at the 10 m^2 quadrat scale.

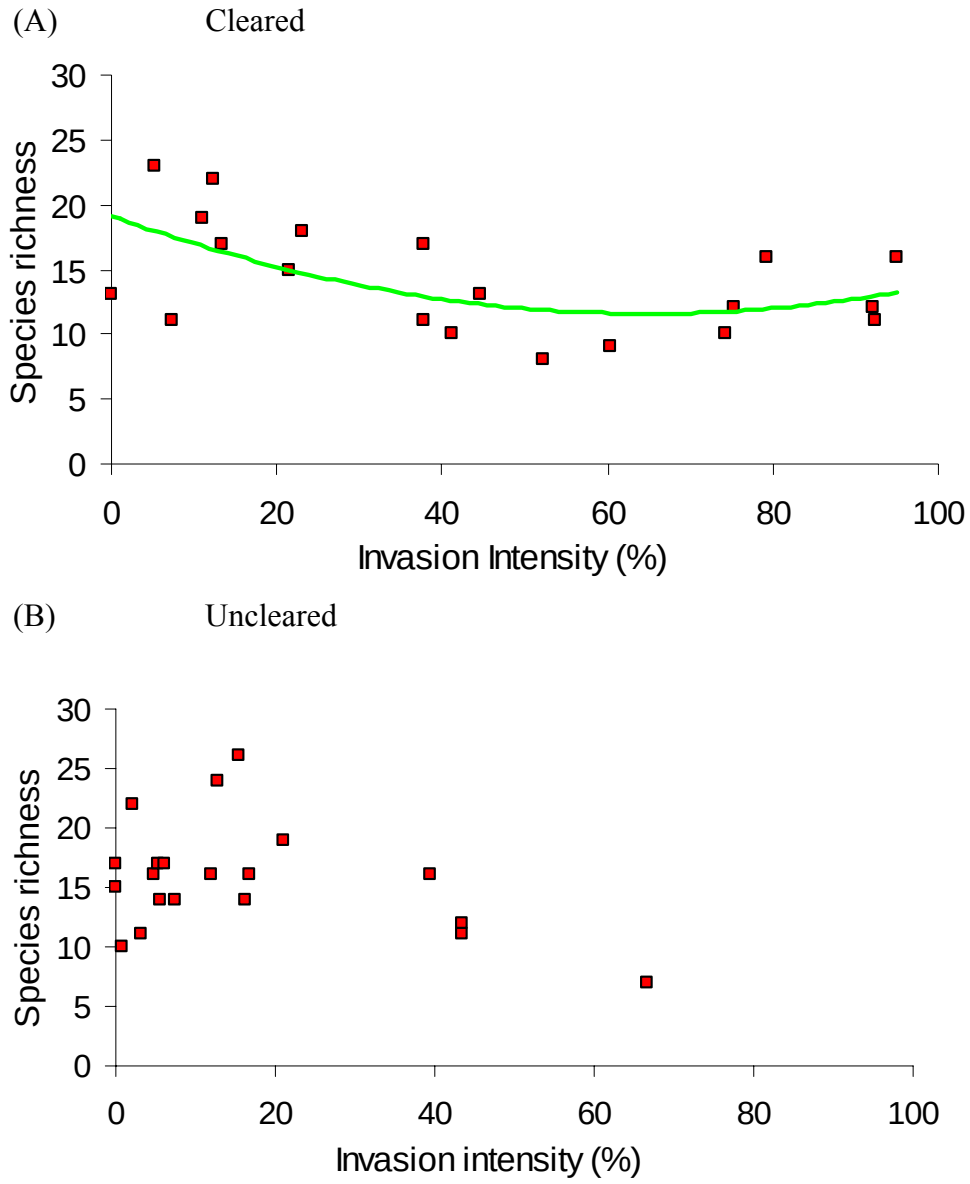


Figure 6.3 The relationship between plant species richness and invasion intensity (% aerial cover of exotic plants as calculated in section 4.4.2 of the Vegetation Chapter) at the high altitude sites for (A) uncleared ($r^2 = 0.32$; $P < 0.05$) and (B) cleared plots ($r^2 = 0.24$; $P > 0.05$) at the 100 m^2 quadrat scale. Regression relationship for uncleared plots is as follows: $Y = 0.0018x2 - 0.233x + 19.158$

Table 6.6 List of plant species with author citations and taxonomic family for grass, herbaceous, shrub and tree growth forms found in riverine habitats along the Sabie River (Germishuizen & Meyer 2003). Presence (1) and absence of species for each different experimental categories is given (invasion (INV), altitude (ALT) and management/clearing treatment (MAN). * denotes Category 1 weed species; ** denotes Category 2 weed species; *** denotes Category 3 weed species as per the National Water Act of 1998; and ◙ denotes weed species not declared.

Species	Author citations	Family	High altitude				Low Altitude			
			High Invasion		Low Invasion		High Invasion		Low Invasion	
			Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
Grasses and Sedges										
Bothriochloa radicans	(Selum) A.Camus	Poaceae					1		1	
Brachiaria deflexa	(Schumach.) C.E.Hubb.	Poaceae	1	1	1	1	1	1	1	1
Cymbopogon validus	(Stapf) Stapf ex Burtt Davy	Poaceae			1					
Cyperus esculentus	L.	Cyperaceae	1		1	1	1		1	1
Hemarthria altissima	L.	Poaceae	1			1				
Hyparrhenia dichroa	(Steud.) Stapf	Poaceae	1	1	1	1				1
Ischaemum fasciculatum	L.	Poaceae			1	1	1			1
Kyllinga erecta	L.	Cyperaceae	1		1				1	1
Panicum aequinerve	Nees	Poaceae		1		1				
Panicum maximum	Jacq.	Poaceae			1					
Paspalum urvillei	Steud.	Poaceae	1		1	1	1			1
Pennisetum macrourum	Leeke	Poaceae	1						1	
Phragmites australis	(Cav.) Steud.	Poaceae	1	1	1		1	1	1	1
Setaria incrassata	(Hochst.) Hack.	Poaceae	1	1	1	1	1	1	1	1
Setaria megaphylla	(Steud.) Dur. & Shinz	Poaceae	1	1	1	1	1	1	1	1
Sorghum bicolor	L.	Poaceae	1		1		1			
Sporobolus consimilis	Fresen	Poaceae			1					
Themeda triandra	Forssk.	Poaceae		1	1	1				
Unknown Grass sp.		Poaceae	1						1	
Total number of grass species	**19**		**12**	**7**	**14**	**10**	**9**	**4**	**9**	**9**

Species	Author citations	Family	High altitude				Low Altitude			
			High Invasion		Low Invasion		High Invasion		Low Invasion	
			Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
Table 6.6 Continued……										
Herbaceous species										
Acalypha caperonioides	Baill.	Euphorbiaceae	1							
Acalypha villicaulis	Hochst.	Euphorbiaceae		1	1	1			1	1
Achyranthes aspera*	L.	Amaranthaceae		1					1	
Adenocline acuta	(Thunb.) Baill	Euphorbiaceae		1						
Adiantum poiretii	Wikstr.	Adiantaceae			1					
Anomatheca laxa	(Thunb.) Goldbl.	Iridaceae	1							
Anthospermum welwitschii	Hiern	Rubiaceae				1			1	1
Asclepias physocarpa	(E.Mey.) Schltr.	Asclepiadaceae	1	1	1					
Asparagus cooperi	(Bak.)	Liliaceae			1					
Bidens pilosa◙	L.	Asteraceae	1	1	1	1	1		1	1
Cheilanthes viridis	(Forssk.) Swartz	Adiantaceae	1	1	1		1	1	1	1
Chenopodium schraderianum	schult.	Chenopodiaceae	1	1	1	1		1	1	
Convolvulus arvensis*	L. Field	Convolvulaceae	1	1	1	1	1	1	1	1
Conyza aegyptiaca◙	(l.) Ait.	Asteraceae	1							
Conyza albida◙	Spreng	Asteraceae	1	1	1	1	1			1
Corchorus asperifolius	Burch.	Tiliaceae	1						1	
Cucumis zeyheri	Sond.	Cucurbitaceae	1	1	1	1	1	1	1	1
Cynoglossum lanceolatum	Forssk.	Boraginaceae	1		1				1	1
Desmodium repandum	(Vahl) DC.	Fabaceae		1	1					
Dietes iridioides	(L.) Sweet ex Klatt	Iridaceae					1	1	1	
Eriosema pauciflorum	Notzsch	Fabaceae			1		1			
Eriosema psoraleoides	(Lam.) G. Don.	Fabaceae	1	1						
Foeniculum vulgare◙	Mill.	Apiaceae	1		1					
Gladiolus dalenii	Van Geel	Iridaceae	1	1	1	1	1		1	1
Helichrysum ruderale	Hilliard & Burtt	Asteraceae	1	1	1	1				
Helichrysum acutatum	DC.	Asteraceae			1	1				

Species	Author citations	Family	High altitude				Low Altitude			
			High Invasion		Low Invasion		High Invasion		Low Invasion	
			Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
Table 6.6 Continued……										
Helichrysum revolutum	(Thunb.) Less.	Asteraceae					1			
Helichrysum sp.	Mill.	Asteraceae	1	1	1	1	1		1	1
Helichrysum rugulosum	Less.	Asteraceae								
Hydrocotyle americana	L.	Apiaceae	1	1		1	1		1	1
Hypoestes forskaolii	(Vahl) R. Br.	Acanthaceae					1		1	1
Hypoxis rigidula	Bak.	Hypoxidaceae	1	1	1					
Hypoxis sp.	L.	Hypoxidaceae	1							
Indigofera swaziensis	H. Bol.	Fabaceae				1			1	1
Ipomoea cairica◙	(L.) R. Br.	Convolvulaceae					1	1	1	1
Ipomoea purpurea* **	(L.) Roth	Convolvulaceae		1		1				
Lagenaria siceraria	(Malina) Standl.	Cucurbitaceae	1							
Mariscus congestus	(Vahl) C.B.Cl.		1		1	1	1	1	1	1
Medicago hispida◙	Gaertn.	Fabaceae			1					
Mentha longifolia	(L.) Hudson	Labiatae	1							
Myrsiphyllum volubile	(Thunb.) Oberm.	Liliaceae		1	1					
Nepeta cataria	L.	Lamiaceae				1	1	1		1
Oxalis corniculata	L.	Oxalidaceae	1							
Oxalis latifolia	H.B.K.	Oxalidaceae	1	1	1	1	1			1
Passiflora edulis◙	L.	Passifloraceae		1			1	1	1	
Passiflora sp.*	L.	Passifloraceae		1	1	1	1	1	1	1
Pentodon pentandrus	(Schumach. & Thonn.) Vatke	Rubiaceae				1		1		1
Physalis angulata	L.	Solanaceae			1					
Protasparagus exuvialis	(Burch.) Oberm.	Asparagaceae		1	1					
Pseudarthria hookeri	Wright & Arn.	Fabaceae				1	1			1
Pseudognaphalium luteo-album	(L.) Hilliard & Burtt.	Asteraceae	1			1				
Pteridium aquilinum	(L.) Kuhn	Dennstaedtiaceae	1	1	1	1	1	1	1	1

Species	Author citations	Family	High altitude				Low Altitude			
			High Invasion		Low Invasion		High Invasion		Low Invasion	
			Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
Table 6.6 Continued……										
Rhynchosia galpinii	Bak. f.	Fabaceae					1			
Rhynchosia hirta	(Andr.) Meikle & Verde.	Fabaceae		1						1
Rumohra adiantiformis	(G. Farst.) Ching	Polypodiaceae	1	1	1	1	1	1	1	1
Scadoxus multiflorus	(Martyn) Raf.	Amaryllidaceae		1	1					
Selago transvaalensis	Rolfe	Seligeraceae				1				
Senecio affinis	DC.	Asteraceae	1							
Senecio conrathii	N.E. Br.	Asteraceae	1							
Senecio coronatus	(Thunb.) Harv.	Asteraceae			1	1				1
Senecio graminifolius	(Thunb.) DC.	Asteraceae		1			1	1	1	
Senecio poseideonis	Hilliard & Burtt.	Asteraceae	1		1					
Senecio quinquelobus	(Thunb.) DC.	Asteraceae	1	1	1					
Senecio serratuloides	DC.	Asteraceae		1	1					
Senna septemtrionalis	(Viv) Irwin & Barnebg	Fabaceae					1		1	
Smilax anceps	Willd.	Smilacaeae	1	1	1	1	1	1	1	1
Solanum nigrum	L.	Solanaceae	1		1	1				
Solanum sisymbrifolium*	Lam.	Solanaceae			1					
Stephania abyssinica	(Dill. & Rich) Walp.	Menispermaceae	1		1	1	1	1	1	1
Thelypteris pozoi	Schmidel	Thelypteridaceae	1	1	1	1		1	1	
Toddalia asiatica	(L.) Lam.	Rutaceae						1	1	
Thunbergia natalensis	Hook.	Thunbergiaceae	1	1	1			1		
Wahlenbergia undulata	(L.f.) A. DC.	Campanulaceae			1					
Total number of herbaceous species	**74**		**37**	**33**	**40**	**29**	**26**	**21**	**27**	**26**
Shrub species										
Ageratum houstonianum*	Mill	Asteraceae			1					
Antidesma venosum	E.Mey. ex Tul.	Euphorbiaceae								1
Artemisia afra	Jacq. ex Willd.	Asteraceae		1	1	1				

Species	Author citations	Family	High altitude				Low Altitude			
			High Invasion		Low Invasion		High Invasion		Low Invasion	
			Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
Table 6.6 Continued……										
Brachylaena discolor	(Phill. & Schweick) J. Paiva	Asteraceae					1		1	
Caesalpinia decapetala*	(Roth) Alston	Caesalpiniaceae	1		1	1		1		1
Cassinopsis ilicifolia	(Hochst.) Kuntze	Icacinaceae	1		1				1	
Clausena anisata	(Willd.) Hook. f. ex Benth.	Rutaceae			1					
Cliffortia linearifolia	Eckl. & Zeyh.	Rosaceae				1				
Clutia affinis	Sond.	Euphorbiaceae			1	1		1	1	1
Clutia monticola	S.Moore	Euphorbiaceae			1					
Dalbergia armata	E.Mey.	Fabaceae	1	1	1	1	1	1	1	1
Diospyros galpinii	(Hiern) De Winter	Ebenaceae		1			1	1	1	1
Diospyros lycioides	Desf.	Ebenaceae					1			
Diospyros whyteana	(Hiern) F. White	Ebenaceae						1	1	
Endostemon obtusifolius	(E.Mey. ex Benth.) N.E. Br.	Lamiaceae				1				1
Englerophytum magalismontanum	(Sond.) Heine & J.H. Hemsl.	Sapotaceae		1						1
Euclea crispa	(Thunb.) Guerke	Ebenaceae			1	1	1	1	1	1
Euclea natalensis	DC.	Ebenaceae	1			1				1
Flemingia grahamiana	Wight & Arn.	Papilionoidae					1			
Gymnosporia mossambicensis	(Klotzsch) Blakelock	Celastraceae				1		1	1	1
Hymenodictyon parvifolium	Oliv.	Rubiaceae								1
Indigofera daleoides	Benth. ex Harv.	Papilionoidae	1		1					
Keetia gueinzii	(Sond.) Bridson	Rubiaceae		1		1			1	
Lantana camara*	L.	Verbenaceae	1	1	1	1	1	1	1	1
Leucosidea sericea	Eckl. & Zeyh.	Rosaceae			1					
Leonotis sp.	(Pers.) R. Br.	Lamiaceae		1	1					
Lippia javanica	(Burm. f.) Spreng.	Verbenaceae	1		1			1	1	1
Maesa lanceolata	Forssk.	Myrsinaceae					1		1	1

Species	Author citations	Family	High altitude				Low Altitude			
			High Invasion		Low Invasion		High Invasion		Low Invasion	
			Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
Table 6.6 Continued……										
Gymnosporia polyacantha	(Wight & Arn.) Benth. & Hook. f.	Celastraceae	1				1			
Passerina filiformis	L.	Thymelaeaceae				1				1
Pavetta gracilifolia	Brem.	Rubiaceae					1	1	1	1
Pavonia burchellii	(DC.) R.A. Dyer	Fabaceae		1						
Plectranthus laxiflorus	Benth.	Lamiaceae	1	1	1	1	1	1	1	1
Plectranthus sp.	Th. Fr. Jr.	Lamiaceae	1	1	1	1	1	1	1	1
Rhamnus prinoides	L' Hérit.	Rhamnaceae	1	1	1					
Rhoicissus tomentosa	(Lam.) Wild & Drum.	Vitaceae		1		1				1
Rhoicissus tridentata subsp. cuneifolia	(L.f.) Wild & drum.	Vitaceae	1		1				1	
Rhus dentata	Thunb.	Anacardiaceae	1		1	1	1		1	1
Rhus discolor	E. Mey. ex Sond.	Anacardiaceae			1	1	1		1	1
Rubus cuneifolius*	Pursh	Rosaceae	1	1	1	1	1	1	1	1
Solanum mauritianum*	Scop.	Solanaceae	1	1	1		1	1	1	1
Toddalia asiatica	(L.) Lam.	Rutaceae		1					1	1
Trimeria grandifolia	(Hochst.) Warb.	Flacourtiaceae		1	1					
Verbena bonariensis◙	L.	Verbenaceae	1		1		1	1	1	
Total number of shrub species	**44**		**16**	**16**	**24**	**18**	**17**	**15**	**22**	**24**
Tree species										
Acacia ataxacantha	DC. Benth.	Fabaceae	1	1	1		1	1	1	1
Acacia mearnsii	De Wild.	Fabaceae				1		1		
Acacia melanoxylon*	Benth.	Fabaceae		1			1	1	1	1
Apodytes dimidiata subsp. *dimidiata*	E.May. ex Arn.	Icacinaceae		1	1		1	1	1	1
Breonadia salicina	(Vahl) Hepper & Wood	Rubiaceae						1		1
Buddleja auriculata	Leeuwenberg	Buddlejaceae	1		1	1		1		1
Buddleja salviifolia	(L.) Lam.	Buddlejaceae	1	1	1	1		1	1	1

Species	Author citations	Family	High altitude				Low Altitude			
			High Invasion		Low Invasion		High Invasion		Low Invasion	
			Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
Table 6.6 Continued……										
Cephalanthus natalensis	Oliv.	Rubiaceae							1	
Combretum celastroides	Welw. ex Laws.	Combretaceae								1
Combretum fragrans	Loefl.	Combretaceae			1	1			1	
Combretum kraussii	Hochst.	Combretaceae	1	1	1	1	1	1	1	1
Cussonia paniculata	Eckl. & Zeyh.	Araliaceae		1	1					
Cyathea dregei	Kunze	Cyatheaceae			1					1
Dombeya rotundifolia	(Hochst.) Planch	Sterculiaceae								1
Eucalyptus grandis**	W. Hill ex Maiden	Myrtaceae	1	1	1	1	1	1	1	1
Ficus sur	Forssk.	Moraceae		1	1					
Grevillea robusta***	A.Cunn. ex R.Br..	Proteaceae	1	1						
Grewia occidentalis	L.	Tiliaceae		1	1			1	1	1
Halleria lucida	L.	Scrophulariaceae								1
Ilex mitis	(L.) Radlk.	Aquifoliaceae		1						
Musa lanceolata	Forssk.	Myrsinaceae							1	
Pinus patula**	Schlechtd. & Cham.	Pinaceae		1		1		1	1	1
Prunus persica◙	(L.) Batsch	Rosaceae					1	1	1	1
Rawsonia lucida	Harv. & Sond.	Flacourtiaceae			1		1	1		
Sequoia sp.◙	(Taxod.)	Taxodiaceae				1				
Syzygium cordatum	Hochst.	Myrtaceae							1	
Tricalysia capensis	(Meisn. ex Hochst.) Sim	Rubiaceae		1					1	1
Zanthoxylum davyi	(Verdoorn) Waterm.	Rutaceae							1	
Ziziphus mucronata	Willd.	Rhamnaceae						1	1	1
Total number of tree species	**29**		**6**	**13**	**12**	**8**	**7**	**14**	**17**	**15**
Total species number	**164**		**71**	**69**	**90**	**65**	**59**	**54**	**75**	**74**

6.3.3 Beta Diversity - Sorenson's coefficient of community

The Sorenson's coefficient of community indicates the similarity between different sites (a larger value indicates a greater similarity). Sorenson's coefficient of community (plant species beta diversity) between sites illustrated that the lowest community similarity occurred between the low altitude low invasion sites and the high altitude high invasion cleared sites (Table 6.7). Low altitude, low invasion cleared and uncleared sites were highly similar in their community composition (Table 6.7), indicating very little disturbance to the community caused by low invasion and the clearing there-of.

High altitude, high invasion intensity sites uncleared of exotic vegetation had a high community difference with clearing (CC = 0.29). It is interesting to note that the lowest community similarity was found between the high invasion uncleared sites of the two different altitudes (Table 6.7). This indicates that altitudinal differences played a considerable role in community composition. In contrast, the second highest similarity was also found between altitudes but with the low altitude high invasion uncleared site being similar to the high altitude low invasion cleared site (Table 6.7). This could indicate that the changes brought on by clearing and invasion can result in a similar community composition (i.e. uncleared high invasion communities at low altitude are similar to low invasion cleared communities at high altitude).

6.3.4 Site associations by species composition

Canonical Analysis

It is evident for low altitude that sites can be clearly distinguished on the basis of their species composition (Figure 6.6). The Constrained Canonical Analyses (CCA) of species data illustrates the distribution of species and sites through ordinal space based on study site species presence or absence (Figure 6.6 & 6.7). From the 1st and 2nd axis plot of the low altitude sites in Figure 6.6, it is evident that there is a high-low invasion division present, with indigenous species being closely associated with low invasion (lower left quadrant of the plot). The species, *S. mauritianum,* however was found to straddle this division illustrating the high degree of proliferation in both high and low invasion sites (Figure 6.6). There were no distinguishable species groupings for low altitude plots (Figure 6.6) associated with different category sites, indicating species composition did not clearly change with clearing of exotic species. For the high altitude sites however, there was a definite grouping of species associated with different study sites from the different categories (Figure 6.7). Most exotic species were closely associated with high invasion sites in the high altitude plots (Figure 6.7).

Table 6.7 Matrix of Sorenson's coefficient of community for sites in each experimental category at the 10 m^2 quadrat scale. Red – Low community similarity (< 0.30); Green – High community similarity (> 0.50).

			High Altitude				Low Altitude			
			High Invasion		Low Invasion		High Invasion		Low Invasion	
			Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
High Altitude	High Invasion	Cleared		0.29	0.32	0.28	0.48	0.37	0.27	0.27
		Uncleared			0.50	0.78	0.45	0.24	0.39	0.39
	Low Invasion	Cleared				0.40	0.33	0.65	0.46	0.45
		Uncleared					0.31	0.29	0.27	0.32
Low Altitude	High Invasion	Cleared						0.60	0.46	0.55
		Uncleared							0.48	0.43
	Low Invasion	Cleared								0.60
		Uncleared								

Problematic invasive species with high growth rates and resprouting vigor, such as *Lantana camara, Caesalpinia decapetala* and *S. mauritianum,* were closely associated with both high and low invasion sites, and all cleared sites. These species were generally found in all experimental categories (Table 6.2).

Unlike low altitude sites, the CCA showed that high altitude cleared study sites had poor separation on the basis of species composition (Figure 6.7), and there were no distinct groupings, but rather close associations between sites of the same experimental category (Figure 6.7). Cleared sites tended to be more closely associated on the 1st axis while the 2nd axis illustrated the variation, which separates the high invasion, uncleared and low invasion uncleared sites (Figure 6.7). Exotic species such as *P. patula* were once again associated with the low invasion uncleared category, while *E. grandis* was associated with high invasion uncleared sites (Figure 6.7). *S. mauritianum* was closely associated with high invasion uncleared sites and some of the low invasion cleared sites. Overall, *S. mauritianum* is found in the center of the cleared grouping which indicates an association of this species with clearing and the successful regeneration of this species (Figure 6.7).

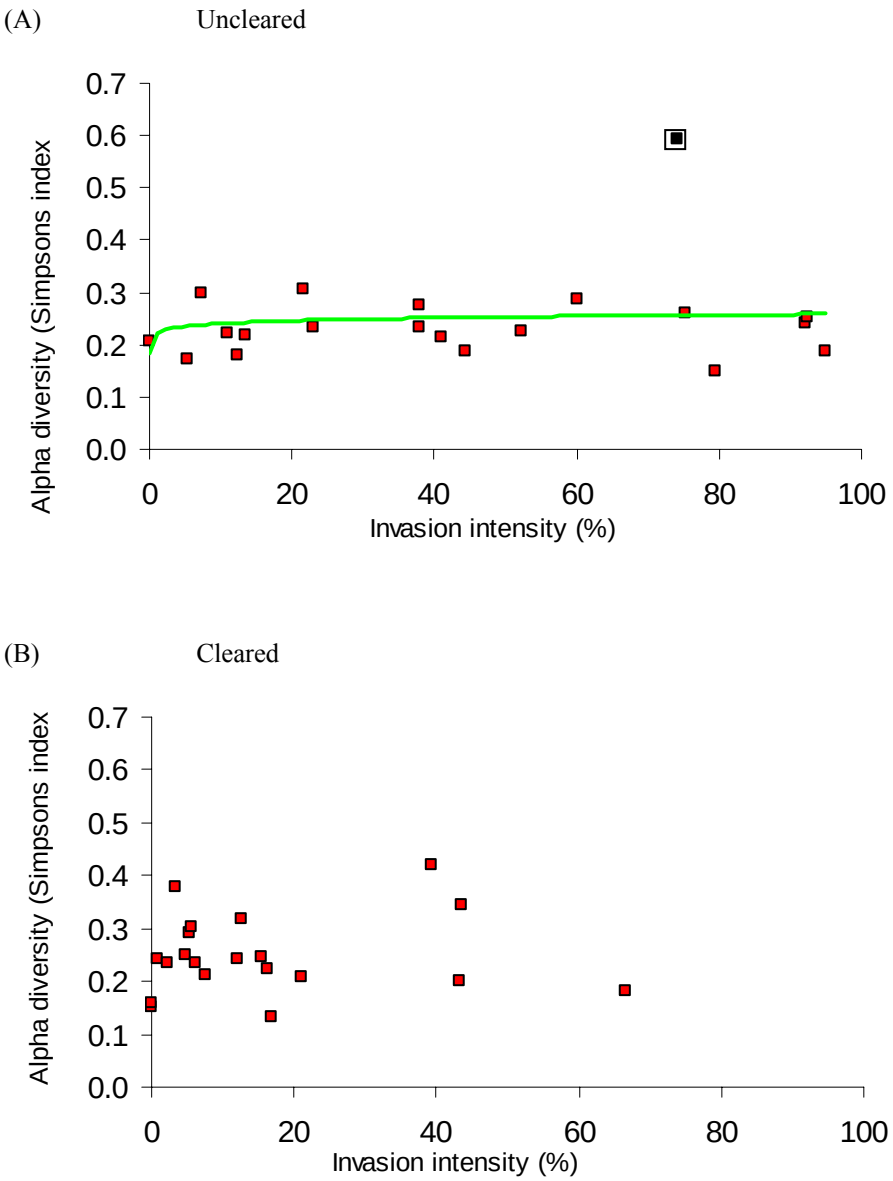


Figure 6.4 The relationship between plant species alpha diversity and invasion intensity (% aerial cover of exotic plants as calculated in section 4.4.2 of the Vegetation Chapter) for (A) cleared (r^2 = 0.15; $P < 0.10$) and (B) uncleared plots ($r^2 = 0.04$; $P > 0.10$) at the 10 m^2 quadrat scale. Regression relationship for uncleared plots is as follows: $Y =$ 0.2294527 + 0.00569029 * LOG(X). ▣ indicates outliers not included in regression calculation.

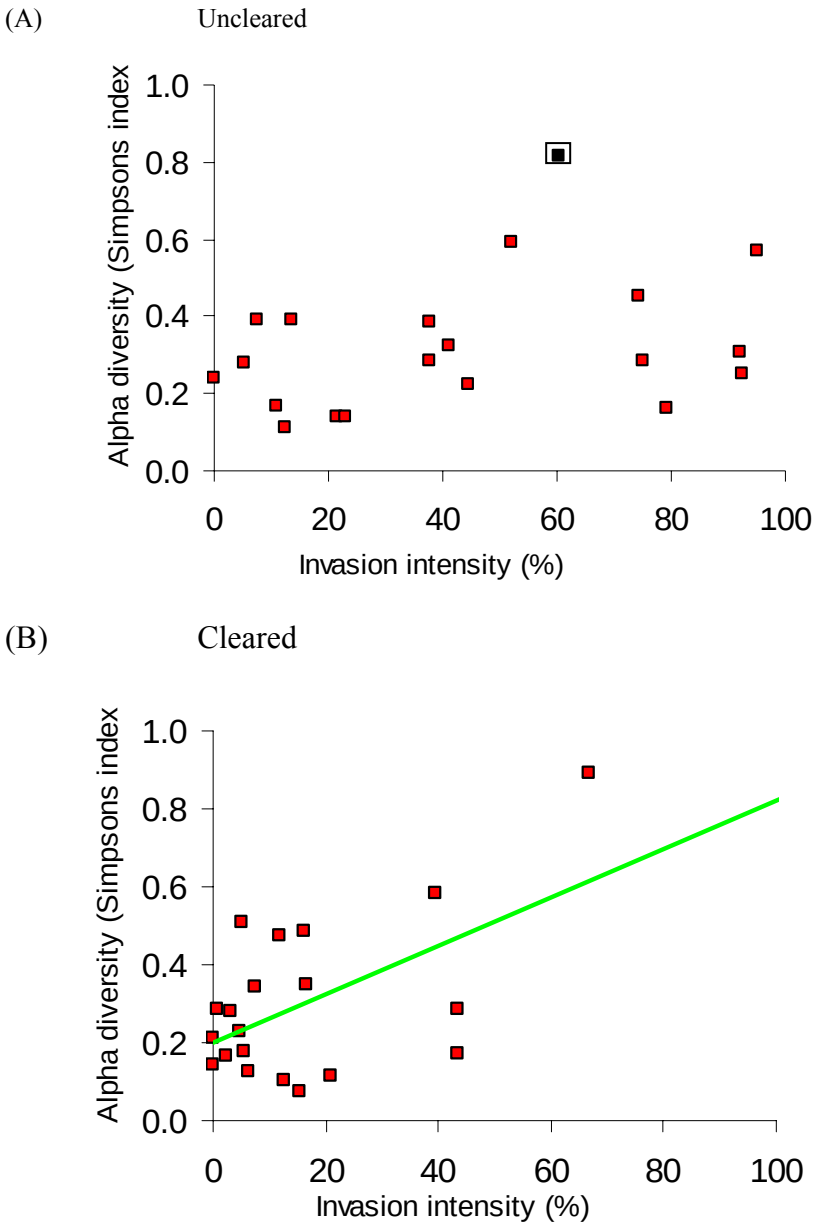
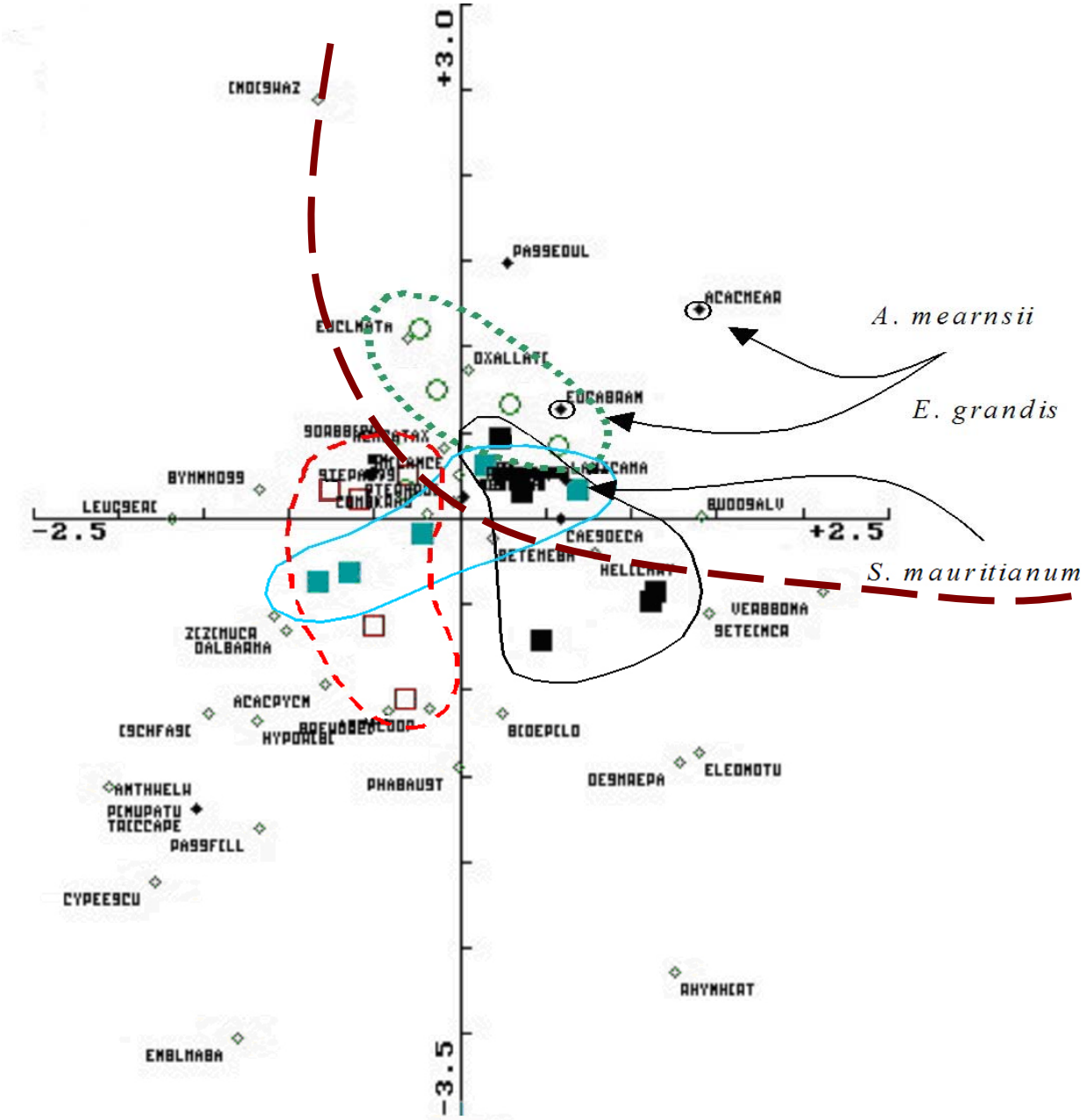


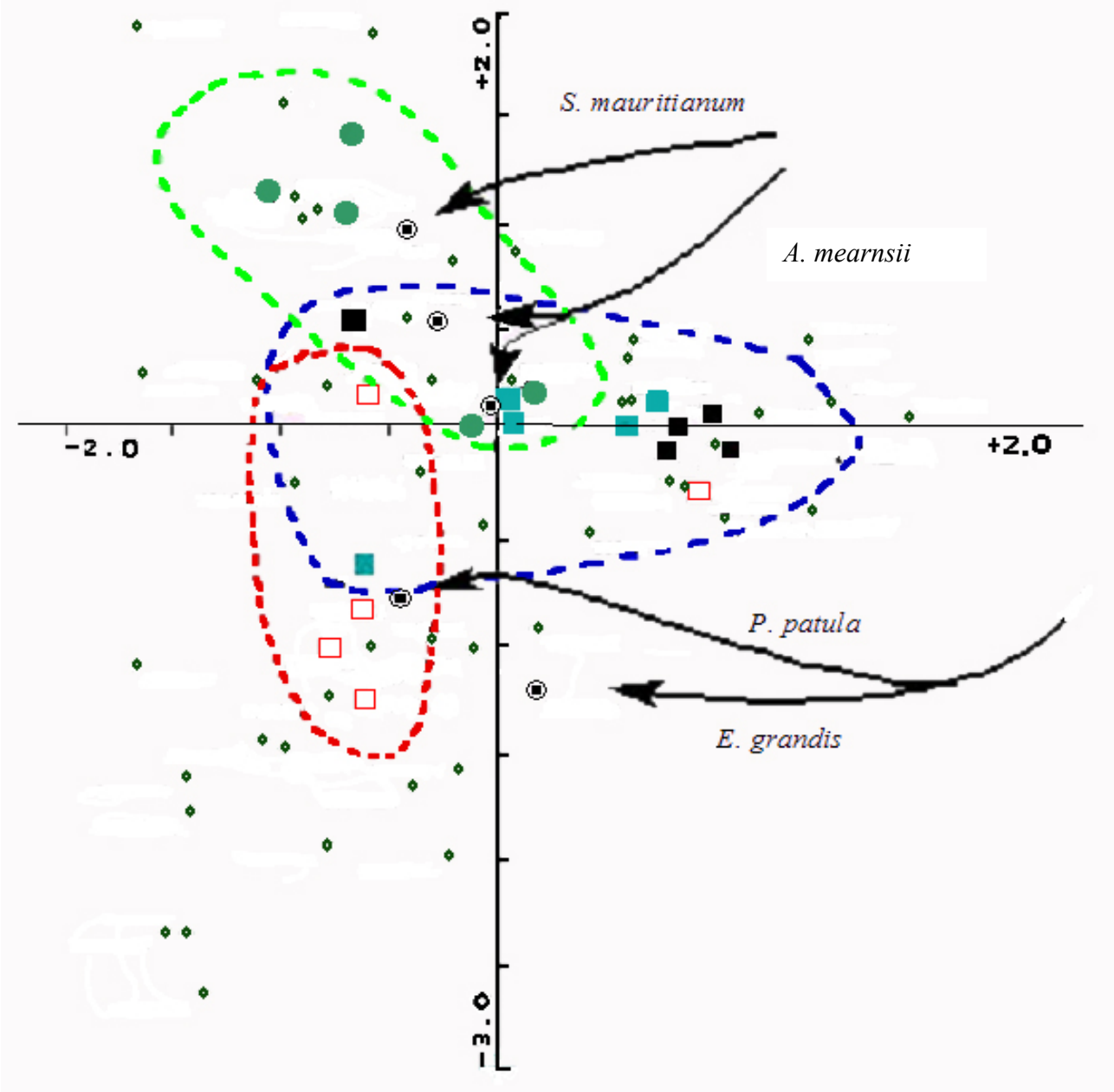
Figure 6.5 The relationship between woody plant species alpha diversity and invasion intensity (% aerial cover of exotic plants as calculated in section 4.4.2 of the Vegetation Chapter) for (A) cleared ($r^2 = 0.12$; $P > 0.05$) and (B) uncleared plots ($r^2 = 0.31$; $P < 0.05$) at the 100 m^2 quadrat scale. Regression relationship for cleared plots is as follows: $Y = 0.1992874 + (0.006228929 * X)$. ▣ indicates outliers not included in regression calculation. Outlier in uncleared regression (A) is the same site as outlier in Figure 6.4.



Key:

High Invasion Cleared Sites	■	Indigenous Species	◊
High Invasion Uncleared Sites	○	Exotic Species	♦
Low Invasion Cleared Sites	■	Low Invasion Uncleared Sites	□

Figure 6.6 Constrained Canonical Analyses (CCA) of low altitude plots using symmetric scaling. Species were separated into exotic and indigenous based on the Mpumalanga Working for Water list of unwanted exotic species (Table 1.1). Black arrows point to predominant exotic species in relation to site categories. The brown line depicts a indigenous/exotic species division. The four experimental groupings: Red – Low Invasion Uncleared Sites; Black – High Invasion Cleared Sites; Blue – Low Invasion Cleared Sites; and Green – High Invasion Uncleared Sites (Refer to Appendix 17 for species label codes).



Key:

High Invasion Cleared Sites	■	Indigenous Species	◊
High Invasion Uncleared Sites	○	Exotic Species	▣
Low Invasion Cleared Sites	■		
Low Invasion Uncleared Sites	□		

Figure 6.7 Constrained Canonical Analyses (CCA) of high altitude plots using symmetric scaling. Species were separated into exotic and indigenous based on the Mpumalanga Working for Water list of unwanted exotic species (Table 1.1). Black arrows point to predominant exotic species. The experimental categories are highlighted as groupings: Red – Low Invasion Uncleared Sites; Blue – Low Invasion Cleared Sites; and Green – High Invasion Uncleared Sites (Refer to Appendix 16 for species label codes).

For high altitude sites, species found positively associated with high invasion were *Trimeria grandifolia, Tricalysia capensis, E. grandis, L. camara* and *Cheilanthes viridis.* Those species found negatively associated with high invasion intensity were *P. patula, Rhus discolor, Setaria megaphylla, Eriosema psoraleoides* and *Anthospermum welwitschii,* which were (excluding *P. patula*) all indigenous species.

6.4 Discussion

6.4.1 Species richness

Optimum quadrat size

As experienced in other studies, quadrat size does play a role in species richness measurement (Stohlgren *et al.* 1995; Willis & Whittaker 2002). In accordance with observations in other studies the vegetation type and morphology determined optimum quadrat size for measurement. This was found to be unique in the riverine bushveld biome due to the wide range of growth forms (grasses through to large woody tree species). For the study, the decision was made to focus on the 10 m^2 and 100 m^2 quadrat sizes (based on species area curves), but to also investigate the 1 m^2 and 1000 m^2 quadrat data where possible. Results of the species area curves indicate that this would be a wise approach for any future studies in order to reduce sampling time and optimize results.

Altitude

Altitudinal differences between the high and low altitude sites within the project were in the region of 1500 m. In line with the multivariate analysis assumption that different altitudes have different biological processes and community composition, the two altitudinal ranges had varied plant species richness and alpha plant species diversity. Generally, high plant species richness occurred at the low altitude sites relative to their corresponding experimental regime at high altitude. The higher altitude sites are located in the grassland biome and the low altitude sites located in the savanna biome. Typically, the plant species richness differences seen could be inherent in the two different biomes, which occur in this project layout. This was beyond the scope of the study but further investigation in this area could explore the extent of this variable with interactions of invasion and clearing treatment on species richness.

Invasion intensity

A general decrease in plant species richness occurred with increased invasion intensity of uncleared sites. This was supported by both the univariate and multivariate analysis of the vegetation where separation of experimental categories based on invasion intensity was observed. Reasons for this were attributed to morphological and physiological effects of the taller growing weed species

shading out indigenous species as was observed by Rutherford *et al.* (1991). This was particularly evident in the extremely high invasion sites where a plantation type effect was observed with very little understorey vegetation occurring. This exclusion of plant species from high invasion sites was however, not as extreme as was seen in Tzaneen by Dean (1985).

Clearing of exotic species

Plant species richness showed that clearing of exotic plant species from the community generally resulted in an overall increase in plant species richness although this was not found to be significant. This lack of change was attributed to the different growth forms within the community reacting to the clearing disturbance in different manners and resulting in a poor overall net change to the plant species richness. This follows observations that communities are dynamic systems and are all spatially heterogeneous (Sousa 1984). Disturbance caused by clearing of exotic vegetation is a major source of temporal and spatial heterogeneity in the structure and dynamics of the communities. Hence, clearing of exotic vegetation allows for a wide range of species establishment (this includes species typically excluded from established communities such as herbs and grasses) and re-establishment. These “new” species add to the overall plant species richness of the site. Alternatively, the clearing of exotic species reduces the number of taller woody species through collateral damage of indigenous species and the removal of exotic plant species, hence reducing the overall plant species richness. This was also complicated by the different community responses seen at the different altitudes observed in the study.

The total plant species richness generally decreased with clearing at low altitude sites. However, following Lewis *et al.’s* (1998) paper on species richness after a disturbance event, for a short period there will be an increase/elevated species richness can be expected due to the establishment of individuals into the disturbed environment. Species richness, at least in the herbaceous vegetation category, should increase with clearing, and the high altitude study sites conformed to this observation. Low altitude sites did not exhibit this richness “behavior”, but could be explained by the high herbaceous species richness inherent at the low altitude sites before clearing or that the clearing was done at an earlier stage and already plant species exclusion due to competition was in effect. In addition to this, clearing also did not eradicate all of the targeted weed species and individuals of eucalyptus and *S. mauritianum* were still found in the community, especially the low altitude sites, after clearing. Field observations indicated that these were already playing a role in limiting light to shorter height growth forms in addition to adding to the total plant species richness.

Low invasion intensity sites, both cleared and uncleared, were similar in species richness, indicating that at low invasion intensity, clearing does not result in large changes to the species composition. In terms of the diversity/stability hypothesis (Goodman 1975), this would indicate that the disturbances caused by low invasion and/or clearing of low invasion does not significantly alter the species richness and diversity, and hence affect community stability. This statement may however have a flaw, as should annual plant species be included in the calculation a false sense of stability may be read into the alpha diversity of a community disturbed by either invasion or clearing.

For those sites with a low impact caused by invasion or clearing it was observed that in terms of growth form, plant species richness appeared to be comprised more or less evenly of herbaceous and woody species. It was also noted that for high invasion categories, a high number of woody species and a low herbaceous species number occurred. This indicates the dominance of the taller exotic woody plant species in the invaded community and the subsequent shading out of shorter (height) growing species.

6.4.2 Plant species Alpha Diversity – Simpson's Index

Plant species alpha diversity was relatively low for the communities within the study area when compared to the species rich fynbos biome. Plant species alpha diversity did fall within the values identified for savanna type biomes.

Herbaceous species

Invasion of communities did have a negative impact on the alpha diversity of herbaceous species. This was expected due to the shading out and physical modifications caused by high invasion intensity (high litter cover, low light conditions). Clearing of invasive vegetation from communities generally resulted in an increase in the herbaceous plant alpha diversity. This is attributed to the disturbance created by clearing, which opens areas for pioneer and new species establishment.

This is an important point for the management of clearing operations as there should be some means in determining the level of weed control and the "cut-off line" between maintaining the current plant alpha diversity and the high financial cost implications experienced by clearing operations. Once a decision has been made on the level of "acceptable invasion" this method could be used to prioritize areas, which need to be cleared (Pringle & Hopkins 2004).

Woody plant species

Clearing of invasive woody species had a non-significant detrimental effect on woody plant species alpha diversity mainly evident for the high invasion category. This was due to high invasion intensity site species composition being mainly comprised of exotic species, which were selected for by the clearing process. The damage caused by the clearing process on surrounding indigenous woody species also played a role in reducing the total woody plant species diversity. The tree species removed from uncleared sites were typically eradicated from the site and hence did not contribute to the cleared site species list at the time of sampling.

The woody species composition of low invasion sites was not as detrimentally affected by the clearing of invasive species due to: a) The uncleared sites not being dominated by exotic vegetation and holding a high indigenous species number and abundance, and b) clearing was not as intrusive on the indigenous vegetation when under low invasion intensity. This observation is corroborated by the significant difference found in species diversity of invaded and un-invaded sites.

Total species Alpha Diversity

Similar to plant species richness, plant species alpha diversity was different between the different altitudes. This was attributed to the study being sited at different altitudes and being located in different biomes, namely the grassland and savanna biomes.

High invasion intensity results in a decrease in the plant species alpha diversity of the community. This is caused mainly through the loss of herbaceous and short (small) growing plant species from the community due to habitat modifications (Shugart & Seagle 1985). Low invasion intensity does not have the same significant negative implications for the plant species alpha diversity. In cases with low invasion intensity, the presence of exotic vegetation does not dominate the indigenous plant species and hence does not reduce the diversity of indigenous vegetation. The exotic species under these low invasion conditions can be seen as additional species adding to the plant species alpha diversity of the community. This is where the observations by Sousa (1984) on species diversity being an indicator of community stability are poorly founded.

Clearing of invasive vegetation only had a significant impact on the alpha diversity of the community when under high invasion intensity. Under high invasion intensity the indigenous vegetation diversity has already been detrimentally impacted by the presence of exotic species in uncleared sites and removal of

these exotic species only exacerbates the loss of alpha diversity, at least within the time-scale of this study. This however, occurs for only a short period after the clearing process. After this an increased alpha diversity comprised of pioneer species establish, which result in an increased alpha diversity with clearing.

From a practical application of exotic vegetation control, this means that clearing of high invasion sites has a positive result for biodiversity. However, it must be noted that this could be relatively short term if the invasive species again re-establish into the community.

6.4.3 Beta Diversity - Sorenson's coefficient of community

Using Sorenson's coefficient of community as a measure of plant species beta diversity, illustrated that changes between the study categories were present and were complex (Macdonald 2004). Generally, the different altitudes had a low community similarity. This did not contradict the observations made using other indicators of species diversity (plant species richness and alpha diversity).

Generally, the community similarity was lowest for sites that were from high invasion cleared relative to high invasion uncleared. This would be indicative of the establishment of new species into the communities with the disturbance after clearing. Hence, clearing of sites, increased the species turnover and hence the beta diversity. This trend was however contradicted by the high similarity found between low altitude sites with high invasion, which had been cleared or uncleared. This may be explained by the period of time after clearing that the sampling for this data was done. Further investigation into this is needed, however.

The complexity of the Sorenson's coefficient of community results relates to the modification of environmental variables discussed in Chapter 3, where the impact of invasion is a disturbance to the community & environment but the subsequent clearing of the invasion has additional implications to what is essentially an already disturbed community. With invasion of the community being the primary or initial disturbance to the community and this then being added to by clearing of exotic species from the community, the sites that have been both invaded and cleared would have been subject to the largest disturbance to the community in terms of vegetation structure and environmental modification. It would be expected that the species turnover would also be the highest for these categories of the study design but this is complicated by the intensity of the invasion.

6.5. Conclusion

The initial aim of determining and studying species richness and diversity as a function of alien plant invasion and its subsequent clearing has been discussed. There are species richness, alpha and beta diversity relationships with invasion specifically, and weaker relationships for clearing of invasive vegetation. This agrees with the observations made by Latimer *et al*. (2004) where it was found that forestry and invasive alien plants influence species in direct proportion to their prevalence. Typically plant species alpha diversity decreases with increased invasion intensity while a weaker increase in alpha diversity occurs with clearing (the higher the invasion intensity, the higher the plant species alpha diversity). Most species richness and diversity changes were however, only statistically significant for the high invasion categories, where the modification to the environment and community play a large role in changing species composition.

Species diversity needs to be observed with a full understanding of which specific species are being lost from the system, and which are being re-established or invading for the first time. The alpha diversity and species richness numbers *per se* (or on their own) do not give a full indication of the changes to the community brought about by clearing and invasion. The interactions between clearing / invasion and biodiversity of plant species within a community remain a complex issue as was concluded by Macdonald (2004) in a recent review of research into the Working for Water Programme.