The application of selected invertebrates as indicators of ecosystem change due to veld fires.

KM Botha BSc

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Promoter: Prof. H van Hamburg
Co-promoter: Dr. A. N. Andersen
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ABSTRACT

The quality of terrestrial invertebrates as indicators for the detection of ecological change associated with disturbance is widely acknowledged. Invertebrates, at the community level, are often more sensitive to changes than are plants or vertebrates. Both ants and beetles have been studied extensively; changes in ant community composition have been applied successfully as an indication of restoration success. Ants are ideal due to their high abundances and diversity, their ecological importance at all trophic levels, their relative sampling and sorting ease and their sensitivity to ecological change. A detailed understanding of community dynamics greatly facilitates the correct interpretation of signals provided by indicator taxa. Beetles to a great extent, are useful ecological or biodiversity indicators and have been adopted as suitable indicators in environmental monitoring and assessment, as well as to facilitate the evaluation of conservation of biodiversity in landscapes subjected to harvesting. It is well known that ground-dwelling beetle assemblages (especially ground and rove beetles) are sensitive to habitat structure, microclimate and biodiversity management strategies.

The use of bio-indicators with regard to land management is becoming increasingly common in ecological studies, because the results obtained can hopefully provide a framework of reference for the prediction of ecosystem response and the means to select the best land use practices. Such predictions will become useful when considering the consequences of ecological perturbations such as fire regimes, bush encroachment, grazing, mining activity, etc. The objectives of this particular study are to determine the effect that past fire treatments may have had on vegetation structure and how ant and beetle assemblages respond to such changes, and what such changes in habitat structure mean in terms of increased bush density. It is expected that the results obtained will provide an indication of the manner in which ecosystem change affects bio-indicator community assemblages, and how this can be applied with regard to future restoration efforts.

These organisms were sampled by means of pitfall traps placed within strategic sites varying in vegetation composition and sampled over a number of days. The contents of each trap was sorted to genus level, and where possible, to species level, and their species richness, abundance and composition determined. The data obtained was analysed statistically using STATISTICA, CANOCO, PRIMER and Microsoft Excel. Four sites with different burn histories were selected: an unburnt site, one burnt in 2002, one burnt in 1997, and one burnt in 1992. Soil characteristics were found to be relatively homogenous throughout all the sample sites, while each of the burn treatment replicates could be characterised by a particular plant structural arrangement.

With regards to the ant assemblages, both in terms of species composition and functional group composition, low species diversity appeared to segregate the 1997 burn treatment replicates markedly from the other three burn treatments, with a high degree of species dominance exhibited by Anaplolepis steingroeveri. The ants seem to indicate a higher species diversity in the burn treatment sites that had a more diverse vegetation structure. This occurrence however seems to alter over time after a fire incident, before returning to as close to its original state as possible. The beetles, however, displayed very haphazard assemblages, and did not show any discernable significant results that may be used to describe the environmental parameters in question.

The reaction of the ants seemed to occur over an extended period of time, with immediate effects of the burn being an increase in non-specialised and opportunistic species abundances, possibly due to a decrease in competition with other species and taxa. Changes in ant assemblages became more apparent after seven years of the burn incident, seemingly linked to structural changes in the plant community. Ant species diversity increased again at the twelve year recovery time, with and associated change in plant habitat structure. The ants thus, in conclusion, show significant results towards indicating a response to habitat change brought on by fire. It is a requirement that this experiment be replicated in order to establish more discernable patterns. Additional recommendations to improve on this study are also discussed.

Key words: ants; beetles; habitat change; plant structures; bun treatments; increased bush density.

OPSOMMING

Die effektiwiteit van terrestriële invertebrata as indikatore van ekologiese verandering geassossieer met verskeie tipes versteuring word wêreldwyd erken. Invertebrata, op gemeenskapsvlak, is heelwat meer sensitief vir ekosisteem veranderinge as plante of Vertebrata. Beide miere en kewers is internasionaal in hierdie verband nagevors; en veranderinge in mier-gemeenskapsamestelling is al heelwat toegepas as indikator van restourasiesukses. Miere is ideaal as gevolg van hul hoë getalle en diversiteit, hul belangrikheid op elke trofiese vlak, die relatiewe gemak van monsterneming en sortering en hul sensitiwiteit vir ekologiese verandering. 'n Goeie agtergrondskennis van gemeenskapsdinamika is belangrik om die inligting wat indikatortaksa verskaf, korrek te interpreteer. Kewers is tot 'n groot mate baie nuttig as ekologiese- of biodiversiteitsindikatore, en word algemeen aanvaar as geskik in omgewingsmonitering en –assessering, sowel as in die fasilitering van die evaluasie van biodiversiteitsbewaring in landskappe onderworpe aan benutting en eksploitering. Dit is bekend dat grondwonende kewersamestellings (veral grond- en roofkewers), sensitief is tot hul omgewing se struktuur, mikro-klimaat en bestuur.

Die gebruik van bio-indikatore in landbestuur word toenemend merkbaar in ekologiese studies, moontlik omdat die resultate 'n verwysingsraamwerk gee vir die voorspelling van hoe 'n ekosisteem sal reageer op verskeie versteuringstipes. Hierdie inligting stel ons in staat om die beste landverbruikmetodes te selekteer. Sulke voorspellings kan in die toekoms doeltreffend gebruik word om die gevolge van ekologies-veranderende aktiwiteite te oorweeg. Die doel van hierdie projek is om vas te stel wat die effek van vorige brandbehandelings op habitatstruktuur is, hoe mier- en kewersamestellings reageer op sulke veranderings, en wat sulke veranderinge in habitatstruktuur beteken ten opsigte van toenemende bosverdigting.

Die beste metode vir versameling van organismes is met putvalle wat in strategiese persele, gebaseer op plantgemeenskap-samestelling, geplaas word vir 'n paar dae. Die inhoud van elke putval word tot op genusvlak, en waar moontlik spesievlak sorteer. Die spesierykheid, spesiegetalle en gemeenskapsamestelling word dan vasgestel. Data wat verkry word, word statisties geanaliseer, met behulp van rekenaarprogramme soos bv. STATISTICA, CANOCO, PRIMER en Microsoft Excel. Vier persele, elk met 'n eie brandgeskiedenis, was geselekteer. Een was nie voorheen gebrand nie, die ander drie respektiewelik gebrand in 1992, 1997 en 2002. Grondeienskappe was relatief homogeen by al die persele, maar elk van die brandperseel-replikate kon volgens redelike spesifieke plantstruktuur- rangskikklings gekarakteriseer word.

Met betrekking tot die miersamestellings, beide in terme van spesiesamestelling en funksionele-groepsamestelling, was die 1997-brandherhaling betekenisvol onderskeibaar van die ander brandbehandelings op grond van 'n lae spesie-diversiteit en hoë spesiedominansie deur Anaplolepis steingroeveri. Dit blyk hierdie miere toon 'n positiewe korrelasie van groter diversiteit in brandbehandelings met 'n meer diverse habitatstruktuur, wat skyn om te verander met tyd na 'n brandinsident. Kewers, daarenteen, het wisselende samestellings getoon, en het nie enige beduidende resultate gelewer om die omgewingsparameters wat ondersoek is, te verduidelik nie.

Die reaksie van die miere vind oor 'n verlengde tydperk plaas, met die onmiddellike effek van die brand 'n toename in gespesialiseerde en oppertunistiese spesie-veelheid, heel waarskynlik as gevolg van 'n afname van kompetisie met ander spesies. Veranderinge in miersamestellings was meer opvallend sewe jaar na 'n brandinsident, moontlik weens strukturele veranderinge in die habitatstruktuur. Mierspesiediversiteit het weereens toegeneem in die herstelperiode tot by twaalf jaar na brand, geasossieer met veranderinge in plant habitatstruktuur. Die gevolgtrekking wat gemaak kan word, dui daarop dat die resultate ten opsigte van die miere beduidend reageer op habitatsveranderinge as gevolg van brandbehandelings. Dit is wenslik dat die eksperiment herhaal sal word om duidelike patrone te bevestig. Bykomende aanbevelings om die studie te verbeter word ook bespreek.

Sleutel-woorde: miere; kewers; habitat verandering; plant strukture; brand behandelings; toenemende bosverdigting.

LIST OF KEY ABBREVIATIONS

Ant Functional Groups Abbreviation Key	
HCS	Hot Climate Specialist
CCS	Cold Climate Specialist
GM	Generalised Myrmicinae
O	Opportunists
SC	Subordinate Camponotini
SP	Specialist Predator
Beetle Families Abbreviation Key	
CAR	Carabidae
CHR	Chrysomelidae
CUR	Curculonidae
HIS	Histeridae
MEL	Meloidae
MON	Monommatidae
NIT	Nitidinae
OTHER	Unknown group
SCA	Scarabaeidae
SIL	Silvanidae
TEN	Tenebrionidae
Plant Physiognomy Abbreviation Key	
G cm	Grass height in cm
S cm	Shrub height in cm
T cm	Tree height in cm
F cm	Forbe height in cm
G % cov	Percentage grass cover
S % cov	Percentage shrub cover
T % cov	Percentage tree cover
F % cov	Percentage forbe cover
Soil Characteristics Abbreviation Key	
P	Phosphorous
% C	Percentage Carbon
% Org ma	Percentage organic matter
Ca	Calcium
K	Pottasium
Mg	Magnesium
NO3-N	Soil Nitrate
pH	Soil acidity/alkalinity
Silt	Percentage Silt

Zn	Zinc
Fine Sand	Percentage Fine Sand
Clay	Percentage Clay
Coarse S	Percentage Coarse Sand
Med Sand	Percentage Medium Sand
Total sa	Total Sand

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CHAPTER 1: INTRODUCTION

1. 1 Context of and motivation for this study

1.1.1 Desert Margins Programme

This masters project has been executed as part of a collaboration of research initiatives for The Desert Margins Program (DMP), component 1: Ecological Monitoring and Assessment, which is aimed at improving knowledge about the physical processes leading to biodiversity loss in dry-lands, in particular the relative importance of human and climatic factors, the development of quantitative indicators of biodiversity loss, and improved monitoring techniques. The DMP was developed in response to a recommendation made to the international research community at the United Nations Conference on Environment and Development (UNCED) to consider specific contributions for implementation of the three International Conventions on Biodiversity, Climate Change, and Desertification.

The imperative for more effective utilization of resources to address common problems has brought together nine countries of sub-Saharan Africa: Kenya, Botswana, Burkina Faso, Mali, Namibia, Senegal, Niger, South Africa, and Zimbabwe into the Desert Margins Programme (DMP) with a basic premise to develop an integrated national, sub-regional, and international action programme for developing sustainable natural-resource management options to combat land degradation and loss of biodiversity.
Selected sites in SOUTH AFRICA are in the Northern Cape Province and the North West Province:
(1) Mier (Kalahari) Molopo Nature Reserve and adjacent Molopo Agricultural district as buffer area. Molopo is situated in the Kalahari Plains Thornveld and bordering Botswana.
(2) Paulshoek\Leliefontein in Namaqualand Lehurutshe (Agricultural district) – borders Botswana

(3) Suid Bokkeveld in the Hantam district, Northern Cape Kudumane (Agricultural district)

The DMP would build on the existing National Action Programs (NAPs) of the Convention to Combat Desertification (CCD) and involve both development and action-research efforts to unravel the complex causal factors of biodiversity loss through land degradation, and formulate and pilot appropriate solutions (GEF, 2002).

As previously stated, this project considers the first component of the DMP, which is concerned with Ecological Monitoring and Assessment, and thus aimed at improving knowledge about the physical processes leading to biodiversity loss in the drylands, in particular the relative importance of human and climatic factors, the development of quantitative indicators of biodiversity loss, and improved monitoring techniques. The focus of this project was the selection of indicators to assess specifically identified parameters of habitat change, namely fire and bush encroachment, in conjunction with habitat identification and quantification via vegetation structure and soil composition. The invertebrate indicators selected are ants and beetles, reasons for which will be discussed in upcoming sections.

1. 2 Ecosystem change

1.2.1 Factors involved in the dynamics of savannas

The co-existence of trees and grasses is a characteristic feature of all savannas. A complex set of factors, referred to as determinants, influences the balance between trees and grasses in savanna ecosystems. The principal determinants of savanna structure and functioning are soil moisture, soil nutrients, herbivory and fire (Walter 1971, Huntley 1982, Bourliere & Hadley 1983, Werger 1978, 1983, Sarmiento 1984, Tothill & Mott 1985, Walker 1987, Skarpe 1992, Frost 1996). The determinant that will be investigated here is fire, as well as its relationship with bush encroachment.

1.2.1.1 Fire

Fire is a major agent of ecological disturbance (Andersen *et al*, 2007; Whelan, 1995), and typically acts to simplify vegetation structure both in the short term, through direct consumption of plant biomass, and in the long term, through the effects of fire regimes on vegetation dynamics (Andersen *et al*, 2007; Bond & van Wilgen, 1996). Fire in savanna landscapes might thus be expected to have contrasting impacts on species occupying different parts of the habitat gradient (Andersen *et al*, 2007). Grass fires are characteristic of tropical savannas (Frost & Robertson 1987, Van Wilgen & Scholes 1997). They have been a feature of African savannas since the beginning of time (Scott 1970) and have been one of the factors attributed to the origins of savannas and the maintenance of the balance between trees and grasses in these ecosystems (Tainton 1981, Werger 1983, Singh *et al*.. 1985, Menaut *et al.* 1985). Both man and natural causes such as lightning can be the source of ignition of savanna fires. Historically both African pastoralists and hunter-gatherers set fires especially during the dry season in order to help maintain grass cover in savannas and prevent succession from developing into thickets which might be undesirable for savanna utilisation. Trees are favoured by the absence of fire to which they are sensitive during the early stages of establishment (Stocks *et al.* 1997, Van de Vijver 1999). Thus fire has been used, though at times unintentionally, in the control of bush encroachment in these ecosystems (Donaldson 1969, Trollope 1974) since savanna trees only recruit into the adult population once they escape the zone of influence of grass fires (Higgins *et al.* 2000). In moist savannas, fire can be used to control bush encroachment but in arid savannas it has the role of maintaining trees and shrubs at an available height and in acceptable state to browsers (Trollope 1980). This is so because in moist savannas rainfall is high enough to enable grass fuel to accumulate to support frequent enough fires to burn down tree seedlings and woody growth.

The occurrence of fire depends on several factors that include enough fuel to support the fire, the right climatic conditions, and a source of ignition. Above ground primary productivity, which provides fuel for fires, is largely determined by the amount of rainfall a site receives, as well as other savanna determinants. In general, fire, once started, cannot be maintained over extensive areas in climates with less than 300 mm annual rainfall, where the annual grass production falls below 1 ton per ha per year (Werger 1983).

Grazing reduces the standing crop of grasses and with this, fire intensity (Goldstein & Sarmiento 1987) thus reducing their effectiveness in controlling the establishment of woody vegetation. Modern range managers and researchers have realised the importance of fire in savanna management as it can readily be manipulated. Researchers in fire ecology have shown that fire is important and usually beneficial in maintaining the diversity, structure and functioning of savanna ecosystems (Frost 1984, 1985, Van de Vijver 1999). The effectiveness of fire in savanna range management depends on other interacting factors such as rainfall, herbivory and soil nutrient status. Even so the emphasis remains on fuel dynamics and fire suppression, with prescribed fire primarily considered in the context of managing fire hazard rather than biodiversity (Parr & Andersen, 2006; Kauffman 2004; Stephens & Ruth 2005), which is only just emerging as a major consideration (Parr & Andersen, 2006; Smucker *et al.* 2005). Fire-management strategies that aim to introduce increased fire variability into the landscape through the use of dynamic mosaics across space and time are often referred to as patch mosaic burning (PMB) (Parr & Andersen, 2006; Brockett *et al.* 2001), where fire variables are manipulated to create a mosaic of patches representative of a range of fire histories, so as to generate heterogeneity across space and time (Parr & Andersen, 2006; Parr & Brockett 1999). Although having its origins in Australia (Saxon 1984), PMB is has been implemented with greater ferver in southern African management plans, which embrace a robust system of adaptive management that incorporates detailed monitoring of fire patterns (Parr & Andersen, 2006; Brockett *et al.* 2001; Biggs 2002), towards a better understanding of fire and ecosystem dynamics.

1.2.1.1.1 Components of Fire Behaviour

Fires in savanna systems have been considered in terms of the four main components of the fire treatment; fire type, fire intensity, season of burning, and frequency of burning (Trollope; in Tainton, 1999).

- **Fire type.** The most common types of fires in savanna systems are surface fires burning as either head fires (fires burning with the wind) or back fires (fires burning against the wind). Crown fires will only occur with extreme fire conditions. Grass regrowth may be significantly depressed by back-fires, as opposed to head-fires; this is thought to result from the longer period during which temperatures remain above the threshold of approximately 95°C in back-fires, which release much of their heat at or near the soil surface. In head-fires much of the heat is carried upwards and away from the meristematic growing points of grass tillers. Woody savanna component will respond differently to type of fire as a function of the differences in vertical distribution of heat. Head-fires cause greater topkill of stems and branches of trees and shrubs than do back-fires because of their greater intensity, resulting in more heat being carried upwards into the canopies.

- **Fire intensity.** Head fires ranging in intensity between 925kJ/s/m and 3326 kJ/s/m do not significantly affect the recovery of the grass sward. Bush is considered extremely resistant to fire alone as low bush mortality rates have been recorded following intense fires in semi-arid savanna. Thus, while fires do not kill the majority of shrubs and trees, they do change the vertical positioning of subsequent growth. Topkill of trees and shrubs increases as fire intensity increases, and individuals may also become more tolerant of fire as their height increases.
- **Season of burning.** Fires in areas such as the area in this study tend to occur during late autumn, winter and spring (in Tainton, 1999)
- **Frequency of burning.** Two concepts need to be kept in mind when considering the frequency of burning: the number of times fire has taken place and the type of management experienced during intervals between fire occurrences. Frequent fires are normally inclined to improve the nutritional value of the forage produced in savanna areas. (Plowes 1957; West 1965; Tainton *et al* 1977b, Tainton 1999).The major influence that frequency of fire has on the bush component is the extent to which the coppicing (where young tree stems are cut down to a low level) individuals are able to recover during the interval between fires, and on the amount of grass fuel which accumulates during the inter-fire period. The absolute effect however has not yet been established definitely. Fire has been found to change the stature of woody species, in that coppice growth is prevented from gaining height, and thus savanna communities may be kept relatively open with repeated moderately intense fires.

1.2.1.1.2 Fire and invertebrates

The effects of fire on invertebrates operate through a variety of mechanisms, expressed at different temporal scales, in that they can have an immediate effect through direct mortality or through forced migration, or in the longer term, they may respond to the effects of fire on fundamental ecosystem processes such as nutrient cycling and primary production. In the shorter term, fire induced modifications to habitat can have crucial effects on foraging sites (Andersen 1988, Andersen *et al* 2003), food supplies (Benzie 1986, Andersen *et al.* 2003), microclimate (Samways 1990, Andersen, 1988, Andersen *et al.* 2003) and rates of predation (Knutson & Campbell, 1976; Andersen *et al.* 2003).

Given the range of possible fire types and the diversity of invertebrates and their ecological requirements, it is understandable that there will also be a great variety of responses of invertebrates to fires in grasslands and other habitats. (Andersen *et al.* 2003). Resilience in relation to fire has been shown at family level for large arthropod groups such as beetles (Collett, 2000; Andersen *et al.* 2003). The resilience of animal species in relation to fire can therefore be expected to vary according to their habitat preferences (Andersen *et al*, 2007; Andersen, 1988; Farji-Brener *et al.*, 2002; Parr *et al.*, 2004), with frequent fire-favouring species that prefer structurally simple habitats, and longer unburnt areas favouring species that prefer more complex environments (Andersen *et al*, 2007; Sackman & Farji-Brener, 2006).

Studies have shown that the vulnerability of taxa to the immediate effects of fire was related to their flying ability, in that those organism taxa that are capable of flying, show low mortality. The biomass of grass-layer invertebrates may also begin to increase soon after burning, but with changed community structure due to changes in the structure of the grass layer. Regular burning has shown inclinations towards marked reductions in the biomasses of detritivorous and predaceous soil arthropods, although groups such as ants seemed relatively unaffected (Gillon 1983; Andersen *et al.* 2003).

An interesting distinction can be made with regards to fire and arthropod dynamics; insect assemblages are reasonably resilient to fire in habitats where they reflect a long history of association with frequent fire, as opposed to resilience shown by insect assemblages to individual fires (Friend 1996; Andersen *et al* 2003) but not to frequent fire (York 1999a. b; Andersen *et al.* 2003). Fire affects 1) vegetation structure; 2) level of insolation from the ground (Andersen 1986a); 3) decomposition processes (Greenslade

1997); and 4) reducing the number of plants that are needed for shelter and food, which may be disadvantageous to invertebrates. For invertebrates in general the effect of fire in context of the afore-mentioned points has been found to be mainly short term and insignificant. Thus, although fire plays a role, seasonal and environmental conditions exert a greater influence (Greenslade 1997). This being said, studies have indicated that fire can significantly affect beetle assemblages but in the broader context of overall beetle dynamics, assemblages appear rather resilient to fire (Orgeas & Andersen 2001). Apigian *et al.* (2006) also discovered that fire changed overall beetle community composition over the long term, but remained diverse and abundant none the less. In a study conducted by Wikars and Schimmel (2001), it was found that sampling soon after fire occurrence indicated no differences, with such differences becoming more apparent with later sampling efforts. They had also observed the instantaneous colonization by fire-favoured beetles in their samples taken shortly after fire occurrence. These observations regarding immediate, short-term and long-term effects of fire pose very interesting questions.

Ants do tend to veer from the above generalizations associated with most invertebrates in that overall abundance, richness and composition vary fundamentally in relation to fire. Ants are largely protected from direct mortality during fire due to their colonial structure and nesting behaviour, but show much sensitivity to fire-induced modifications to habitat structure and micro-climate (Andersen 1991a; Andersen *et al.* 2003), as well as decreases in food supplies and the onset of interspecific competition by other ants and other taxa (Andersen 1991a). Many studies have shown that ants benefit from vegetation burning due to their preference for high temperatures and open spaces (Greenslade 1997), with additional benefits including seed rain, mobilization of nutrients and foraging obstruction clearing (Jackson & Fox, 1996). An increase in ant activity following burning may provide advantages with regard to their seed foraging rate and seed dispersal (Hosking & Turner 1997). Vanderwoude *et al* (1997) discovered that burning frequency may affect the dominance of specific functional groups, the use of which is strongly suggested by Andersen (1991a) when investigating the response of ants to fire because of the functional group differences to habitat requirements and their competitive interactions.

Andersen *et al* (2007) investigated the extent to which ant community divergence following fire exclusion varied between habitat strata. Their findings were that the number of ant species records was about twice as high in burnt compared with unburnt habitat. Forest ant faunas show very pronounced vertical stratification, with remarkably distinct communities occurring in leaf litter, on the ground, and in the canopy (Andersen *et al,* 2007; Brühl *et al.*, 1998). In contrast, savanna ant communities in Australia are overwhelmingly dominated by ground-nesting, epigaeic species, with few specialist cryptic or arboreal taxa (Andersen *et al,* 2007; Majer, 1990b; Andersen, 2000b).

Burning leads to the establishment of new habitats that are preferred by opportunistic and hot climate specialists (Jackson & Fox 1996). Specialist ant species are not favoured by burning due to their need for high vegetation cover, particular food and habitat requirements, and competition for resources by more competitive ant species. It is because of this sensitivity that ants may be a potentially useful indicator taxon (Andersen *et al* 2003) for assessing ecological responses to fire management (Vanderwoude 1997; Andersen *et al* 2003).

1.2.1.2 Woody Components of Savanna

1.2.1.2.1 Bush encroachment

One problem of savanna land use and management is that of bush encroachment. Bush encroachment is the phenomenon whereby trees and shrubs invade into open grassland or thicken up in already wooded areas (Trollope 1980). This woody plant encroachment has occurred in many parts of the world including North America (Archer 1989), Australia (Walker & Gillison 1982) and Africa (van Vegten 1983, O'Connor 1995).

In semi-arid savannas, the invasion of grassland by woody plants is a sign of ranch deterioration, which reduces grazing capacity (Jeltsch *et al* 1997), due to a decline in the productivity of grasses (Du Toit 1972, Dye 1983, Dye & Spear 1982). Bush encroachment may result in intensification in grazing pressure because farmers do not often destock in response to decreases in grass production caused by increased tree density (Scholes & Archer 1997). Research at various sites in Zimbabwe has shown that grass productivity increases by between 160 and 400% when trees are removed (Robinson & Robertshaw 1975, Barnes 1979). Partial clearing of trees may be beneficial in terms of grass productivity as grass yields have been found to be higher under the canopy of isolated trees as opposed to open areas because of a stable microenvironment and greater soil fertility (Kennard and Walker 1973, Belsky *et al.* 1989, Stuart-Hill & Tainton 1989).

Alternative means of controlling bush would be the combined use of browsers and fire, but this is only possible in areas where there is still enough grass fuel to support reasonably intense fires. The effect of fire on bush encroachment is therefore a habitat modification factor. In the past, researchers had to deal with the problem of bush encroachment when large tracks of savanna land already had mature trees and consequently research on bush encroachment has focused on grass versus adult-tree dynamics (Anon, 2004).

When bush encroachment occurs in the semi-arid regions of South Africa, multi-species grass swards in open savannas are replaced by virtually impenetrable thickets of a single species of thorn tree. These trees are not eaten by cattle and other grazing herbivores, and the thickets render remaining tufts of grass inaccessible to livestock (Ward, no date).

In open savannas, the natural balance between the ratio of trees to grasses can be affected by cattle and sheep which eat grass but seldom browse trees. Conventionally, it is considered that grasses, being fast-growing plants with roots in the upper layers of the soil, out-compete trees (which are slow-growing and have deeper root systems) for water and soil nutrients. When heavy grazing or overgrazing occurs, the grasses are removed, exposing water and soil resources for the trees to exploit. Tree seeds are then able to germinate in large amounts, creating an impenetrable thicket (Ward, no date).

1.2.1.2.2 Identified encroacher: Acacia mellifera

Acacia mellifera is a tall rounded shrub or small tree with a ball-shaped crown, reaching occasionally 9 m in height in the southern limit of its distribution. Branches are covered with very sharp, recurved thorns. The bark is smooth and grey with white lenticels on the young branches. Shoots carry leaves which have only 1-2 pairs of pinnae with 1-2 pairs of leaflets, obliquely ovate or obovate, i.e. quite asymmetrical. This shrub also simultaneously develops leaves and flowers in the early rainy season. Young leaves may, however, appear well before the onset of the rains; it then constitutes a most appreciated browse, especially to goats and camels. It is a gregarious species as it often occurs in almost pure, dense, impenetrable, even-aged thickets.

Acacia mellifera occurs in the rainfall belts between 400 and 800 mm MAR., but down to the 100 mm isohyet in the Rep. of Sudan along the drainage networks (e.g. Wadi al Milk, in Kordofan) and is usually found on clay soils, but can grow on most soils.

During times of drought, when the veld is already in a condition of stress, the most damage is caused through overgrazing. Symptoms of this damage are observed in the form of soil erosion and bush encroachment by *A. mellifera* . Bush encroachment is an exceptionally effective way of protecting the soil from the elements of nature, but offers little grazing (Van Oudtshoorn, 2002).

Ivens (1970) showed that A. mellifera is easily killed by stumping and cutting and repeated burning exerts a good deal of control. (Le Houérou; Dalziel 1955; Dale & Greenway 1961; Giffard 1966; Amin 1973; Geerling 1982/88; Von Maydell 1983/86; Baumer 1983; Wickens *et al.* 1995).

1.3 Invertebrates as indicators of ecosystem change

The concept of ecological disturbance was defined by Sousa (1984) as a "discrete, punctuated killing, displacement or damaging of individuals that directly or indirectly creates an opportunity for new individuals to become established". Either by killing individuals and/or by changing the environment to some degree, disturbance usually results in abrupt changes in community structure and can greatly modify species succession. The resulting development of the affected communities of either sessile or mobile organisms could depend on a number of characteristics of the disturbance, especially its rigorousness and consequential mortality rate of organisms, the heterogeneity and structure of the new environment and its level of connectivity to potential sources of pioneers (Sousa, 1984, Peltzer *et al.*, 2000; Spies & Turner, 2001). In order for any system to function on a self-sufficient level, be it natural or influenced by anthropogenic activity, it needs to display biological integrity. Biological integrity is "the ability to support and maintain a balanced, integrated, adaptive community of organisms having a species composition and functional organisation comparable to that of natural habitats in the region" (Frey, 1977; Karr, 1993).

Biological indicators are readily measured components of the biota that are employed to supply collective information regarding the complex ecosystems in which they occur, and in this, have a major function to perform in conservation planning, rehabilitation, monitoring and management. Bioindicators have long been applied with great success in aquatic systems to serve as a measure of ecosystem sustainability and viability based on the macroinvertebrate assemblage structure and composition. (Hellawell, 1978; Spellerberg, 1991; Andersen 1999). Many focuses however, have now aimed their attention towards the application of invertebrates as bioindicators in terrestrial ecosystems. (Greenslade & Greenslade, 1984; Rosenberg *et al.* 1986; Andersen, 1999). Biodiversity also includes diversity in biological structures (Jeltsch *et al.* 2003) and the impact of factors such as fires on habitat and bush structures is therefore important.

According to Noss, (1990); Goldsmith, (1991); Spellerberg, (1991); Pearson, (1994) and Baldi & Kisbenedek, (1997): the indicator should be (1) sensitive to changes; (2) widely distributed; (3) easily and cost-effectively measurable, collectable, and identifiable (stable taxonomy); (4) able to differentiate between natural and anthropogenic variations; (5) relevant to ecological phenomena; and (6) economically important. These criteria are applicable not only for monitoring programmes, but for many programmes addressing environmental questions.

Terrestrial invertebrates often respond rapidly to environmental changes and provide early detection of ecological changes (Kremen *et al.*, 1993). They fulfill a variety of roles in natural environments as decomposers, predators, parasites, herbivores, and pollinators, and they respond to various perturbations (Rosenberg *et al*, 1986; Price, 1988). Additionally, certain taxa (such as beetles, butterflies, and ants) respond in highly distinctive ways to effects of human or natural disturbance (Niemela *et al.* 1993; Singer & Thomas, 1996; Andersen, 1997; Blair, 1996; Spitzer *et al.* 1997; Rodriguez *et al.* 1998).

Disturbances from natural and anthropogenic origins bring about a variety of changes within ecosystems. Species within an ecosystem form an important component that can be used as ecological indicators. One cannot ignore the total species composition, especially within disturbed areas. With regards to present rehabilitation practices, only a small number of species establish, resulting in low biodiversity, and thus in effect, unstable ecosystems. (Bradshaw & Chadwick, 1980; Morgenthal *et al.* 2001). Due to the magnitude of complete biodiversity assays, the use of representative species has been and still is being investigated in order to determine whether entire ecosystems could be described based on indicator taxa. The search for dependable biological indicators of human disturbance in terrestrial environments continues on several levels (Blair 1996; Laurance & Laurance, 1996; Mason, 1996; Favila & Halffter, 1997; McGeoch, 1998). Terrestrial invertebrates are ideal candidates for biological indicators because they are omnipresent, diverse, easy to sample, and ecologically significant (Andersen, 1997; Disney, 1986 & Rosenberg *et al.* 1986).

1.3.1 Ants as Indicators of ecosystem change

1.3.1.1 Previous studies involving the use of ants

A number of studies have examined the effects of different habitat disturbances on ant communities, including changes after fire (Andersen & McKaige, 1987; Andersen, 1991a; Mahila *et al.*, 2001), mining (Majer, 1984, 1985; Majer *et al.*, 1984, Majer & Nichols, 1998, Mahila *et al.*, 2001), forest clear-cutting (Jennings *et al.*, 1986; Whitford & Gentry; 1981; Mahila *et al.*, 2001), soil-vegetation changes resulting from over-grazing and drought (Wisdom & Whitford, 1981; James *et al.*, 1999; Mahila *et al.*, 2001), clearing for agriculture (Lobry de Bruyn, 1993; Mahila *et al.*, 2001), and agricultural tillage practices, soil conditions, and insecticide use (Peck *et al.*, 1998; Mahila *et al.*, 2001).

Ants have been identified as a diverse, abundant and ecologically dominant faunal group in Australia (Andersen, 1995; Read & Andersen, 2000a). Their important ecological roles include those such as soil turnover (Lobry de Bruyn & Conacher, 1994; Read & Andersen, 2000), nutrient recycling (Lobry de Bruyn & Conacher, 1990; Read & Andersen, 2000), structuring invertebrate and plant assemblages (Greenslade, 1976; Read & Andersen, 2000; Buckley, 1982; Huxley & Cutler, 1991; Read & Andersen, 2000), and possibly forming the primary diet of a wide range of vertebrates (Pianka, 1986; Redford, 1987; Abensberg-Traun & Steven, 1997; Read, 1999; Read & Andersen, 2000). The diversity of these functional roles implies that ant communities may be likely to integrate many aspects of ecological change, and may thus provide valuable information as bioindicators in environmental monitoring programmes (Greenslade & Greenslade, 1984; Majer, 1983; Andersen, 1990; Read & Andersen, 2000).

Ants pose as good indicators of ecological condition and change because they are highly diverse, functionally important, are capable of integrating a variety of ecological processes, are sensitive to environmental change, and are relatively easily sampled (Greenslade & Greenslade, 1984; Brown, 1997; McGeogh, 1998; Andersen *et al.* 2002). Specifically in Australia, ants have frequently been adopted as bioindicators in land management (Majer, 1983; Andersen, 1997a; Andersen *et al.*2002), and have, in particular, been repeatedly applied in studies of mine sites as indicators of restoration success (Majer, 1983; Andersen, 1997b; Andersen *et al.*, 2002). Ant species richness and composition have been noted to show predictable colonisation patterns at mine sites undergoing rehabilitation (Andersen 1993; Majer & Nichols, 1998; Bisevac & Majer, 1999; Andersen *et al.* 2002; Van Hamburg *et al.* 2004), with these patterns often reflecting those of other invertebrate groups (Majer, 1983; Andersen 1997b; Andersen *et al.* 2002; Van Hamburg *et al.* 2004), and key ecosystem processes (Andersen & Sparling 1997; Andersen *et al.*, 2002).

Although this study bears some similarities to that of Parr *et al* (2002), it was thought necessary to expand on the methodology and extend the years of sampling beyond that explored in Pilanesberg. Thus, where Parr *et al* (2002) found that there was an overall increase in the diversity of ants with recovery after fire, extending the surveys beyond the recovery from fire in this project indicated different results. Due to the variability of the factors involved in determining any trends in this type of research, it is essential that such research be repeated in a variety of habitats as well as a range of fire recovery times and treatments in order to ascertain which trends are applicable across the board and those which may only represent once off occurrences.

1.3.1.2 The application of functional groups to assess ecological change

The use of bioindicators to gauge ecological change in relation to land use is most useful when supported by an extrapolative understanding of the organisation of bioindicator communities. This allows the impact of anthropogenic disturbance to be distinguished from inherent site variability. More generally, it guarantees correct interpretation of the "signal" provided by the bioindicator, especially considering the limited replication available for many impact studies (Reynoldson *et al.*, 1995, Wright 1995, MacNally 1996; Andersen, 1997c). Community ecologists regularly classify species into functional groups that transcend taxonomic boundaries, thereby reducing the obvious complexity of ecological systems and allowing comparisons between communities without the risk of falsely grouping species. In a bioindicator context, functional groups may provide an extensive, predictive understanding of community responses to disturbance (Andersen 1997a; Andersen, 1997c). In animal communities, functional groups are typically "guilds"; sets of species utilising common resources (Terborgh & Robinson 1986; Andersen, 1997c), usually trophically based. Most ant species have similar foraging requirements, thus trophically based guilds are of limited use in ant community studies (Andersen 1991a; 1997c).

Little is known of the species composition of most ant communities, let alone their dynamics. In most cases, extrapolative power is not possible at the species level, and will not be in the projected future. Extrapolative power is possible, however, at the functional group level. Ant functional groups have been identified, which vary predictably in relation to climate, soil, vegetation, and disturbance; these functional groups have formed the foundation of continental and global analyses of community composition (Andersen 1995a, 1997b, 1997c). In addition to biogeographic comparisons, this broadscale extrapolative power, in relation to environmental stress and disturbance, has been usefully applied to plot-scale studies, such as the identification of taxa most likely to be limited by competitive interactions (Andersen 1992; Andersen & Patel 1994; Andersen, 1997c), and the responses of local communities to disturbance (Andersen and McKaige 1987; Andersen 1991a, 1997c).

In a bioindicator context, the use of functional groups to provide universal predictive possibilities is primarily of value when the frequency of species-level identification is somewhat low. Mine site restoration serves as an example of this (Andersen 1997a, 1997c), because in these cases environmental disturbance has been extreme, and the objective of management is to produce self-sustaining ecosystems largely similar to, but not necessarily identical to, those occurring before the disturbance. Ant functional groups have shown lucid successional patterns relative to time since rehabilitation (Andersen 1993; 1997c). An additional example is that of the monitoring of ecological responses to contrasting fire treatments, which produce distinctly different profiles of ant functional groups (Andersen 1991a; Vanderwoude *et al.* 1997; Andersen, 1997c).

Functional group classifications designed to help interpret the dynamics of particular communities cannot necessarily be extrapolated to larger spatial scales. For example, ant ecologists often highlight the importance of competition to community structure, and focus their attention on the role of dominant species in communities (Andersen & Patel, 1994). On a local scale, whichever species that is abundant and tends to win competitive interactions with other species, is considered dominant. As a result, a diverse array of taxa has been described as dominant (Hölldobler & Wilson 1990). On a global scale, however, dominant species are highly competitive taxa having their maximum expression under conditions of low environmental stress (factors limiting productivity) and disturbance (factors removing biomass; Grime 1979). For ants, such conditions are represented by hot and open environments experiencing low to moderate levels of disturbance, and the behaviourally dominant taxa that reach their maximum abundance at such sites are exclusively members of the sub-family Dolichoderinae (Andersen 1995, 1997b).

Under low disturbance, the abundance of most functional groups is chiefly regulated by stress-factors relating to climate and habitat structure. Habitat disturbance has a negative influence on specialised ants, primarily through changes in habitat structure, micro-climate and food supplies (Andersen, 1995; 1997a). This in turn reduces the competitive pressure on Opportunists and Generalised Myrmicinae, which often flourish in disturbed environments (Andersen, 1997a).

Functional groups have been identified for ants based on Australian studies (Greenslade, 1978; Andersen 1995, 1997a, 2000a). Despite only being able to identify five in this study, there are seven such functional groups, namely:

1. Climate specialists: These taxa have distributions determined either by arid zones (hot climate specialists (HCS)), humid tropics (tropical climate specialists (TCS)), or cool temperate regions (cold climate specialists (CCS)). In Australia cold and tropical climate specialists are characteristic of habitats where the abundance of dominant dolichoderinae is low, and barring their habitat tolerances, are unspecialised ants. Hot climate specialists, however, are characteristic of sites where dominant dolichoderinae are abundant and they also possess a variety of physiological,

morphological and behavioural specializations regarding their foraging ecology, thus reducing their interaction with other ants (Andersen, 2000a).

2. Cryptic species (CS): These are small to minute species that nest and forage primarily within soil, litter, and rooting log material. They are most diverse and abundant in forested habitats and are a major component of leaf litter in rainforests (Andersen, 2000a).
3. Dominant Dolichoderinae (DD): From a global perspective, competitively dominant taxa are by definition those that predominate in environments experiencing low levels of stress and disturbance. Such areas, for ants, are those that are hot and open, and are more often than not dominated by this group, both in absolute and functional abundance. An important point however is to keep in mind that global dominance does not always imply universal dominance (Andersen 1997b, Andersen, 2000a). This group may often be completely absent from environments undergoing even the smallest amount of stress. However, this group is not applicable to Africa.
4. Generalised Myrmicinae (GM): Species within this group are ubiquitous members of ant communities throughout the warmer regions of the world, and they are often among the most abundant ants. Competitive tension often arises between this group and the dominant dolichoderines (Andersen, 2000a).
5. Opportunists (O): These are unspecialized, poorly competitive, ruderal species (Grime, 1979; Andersen, 2000a), whose distributions seem to be very strongly influenced by competition from other ants. They often have very wide habitat distributions, but predominate only at sites where stress or disturbance severely limit ant productivity and diversity, and therefore where behavioural dominance is low (Andersen, 2000a).
6. Specialist Predators (SP): This group comprises medium-sized to large species that are specialist predators of other arthropods. They include solitary foragers and group raiders. Except for direct predation, they tend to have little interaction with other ants owing to their specialized diets and typically low population densities (Andersen, 2000a).
7. Subordinate Camponotini (SC): This group is often diverse and abundant in rich ant communities. Most are behaviourally submissive to the previously discussed functional group, and many are ecologically segregated from them owing to their large body size and often nocturnal foraging (Andersen, 2000a).

1.3.2 Beetles as indicators of ecosystem change

1.3.2.2 Previous studies involving the use of beetles

Litter-dwelling (epigaeic) arthropods, which include beetles (Coleoptera: Carabidae and Staphylinidae) to a great extent, are useful ecological or biodiversity indicators (McGeoch, 1998; Dale & Beyeler, 2001; Erwin 1997), and these taxa have been adopted as suitable bioindicators in environmental monitoring and assessment (Rainio & Niemelä, 2003; Luff 1996; Desender & Bosmans 1998; Petit & Usher 1998; Rodriguez, Pearson & Barrera 1998), as well as to facilitate the evaluation of conservation of biodiversity in landscapes subjected to harvesting (Niemelä, 2000). It is well known that ground-dwelling beetle assemblages (especially ground and rove beetles) are sensitive to habitat structure, microclimate and management (Perner & Malt, 2003; Luff & Rushton, 1989, McFerran *et al.*, 1994, Ekschmitt *et al.*, 1997, Topping & Lovei, 1997, Dennis *et al.*, 1997 and Wardle *et al.*, 1999).

Staphylinidae (rove beetles) and Carabidae (ground beetles) are widely distributed but have shown distinct associations with specific habitat types. Many of these epigaeic taxa are also important predators of pest insects (Buddle *et al.*, 2005; Cameron & Reeves, 1990, DuDevoir & Reeves, 1990, Jennings *et al*, 1990, Mason *et al*, 1997; Raymond *et al.* 2002), and are tied to critical and disturbance-sensitive habitat features (Buddle *et al.* 2005; Hammond, 1997; Buddle, 2001; Grove, 2002).

Carabid beetles respond to agriculture, fire, and clearcutting (Kimberling *et al.* 2001; Refseth; Van Holliday & Niemela). Darkling beetles (Tenebrionidae) are primarily omnivorous scavengers; some studies have demonstrated the importance of soil type and shrub distribution in tenebrionid distribution patterns (Kimberling *et al.* 2001; Rogers *et al.*. 1978; Sheldon; Rogers *et al.*. 1988; Rogers & Stapp).

The Coleoptera comprises the largest of all insect orders, with more than 300 000 known species occurring in terrestrial and freshwater environments. Their size range is extensive, and their characteristic features are the hard cuticle and tough elytra that allow them to exploit a variety of habitats and environmental conditions. Adults are quite resistant to desiccation and as a result are capable of surviving drier conditions as opposed to other insects (Curry 1994). Due to the greatvariation in size, habits and activity patterns, little reliable data is available for total beetle populations in grassland habitats. Coleoptera exhibit a wide range of feeding habits; the phytophagous forms that feed on woody and herbaceous plants, dung beetles that feed on organic-matter, and predators (Carabidae and Staphylinidae) that feed on a range of soil and surface dwelling invertebrates. It is essential to note that differences in feeding habits may even occur within the various beetle families (Curry, 1994). Carabids are often used to characterise habitats because of their strong habitat-specificity (Lövei & Sunderland, 1996). They have different environmental requirements which are well known and which respond quickly to change (Thiele, 1977).

Among this diverse group of insects, the ground beetles (Coleoptera: Carabidae) are particularly well studied (Holmes *et al*.., 1993, Butterfield *et al*.., 1995, Jukes *et al*.., 2001; Eyre *et al*.., 2003, Heyborne *et al*.., 2003, Irmler, 2003; Vanbergen *et al*.., 2005; Chen *et al*., 2005). This is because carabids are abundant, exhibit high species diversity, and are functionally important (as predators) in ecosystems (Thiele, 1977, Niemelä *et al*.., 1993; Samways, 1994; Chen *et al*., 2005). Moreover, carabids are taxonomically stable and easy to collect with standardized methods, such as pitfall trapping (Niemelä *et al*.., 1993, Jukes *et al*.., 2001; Villa-Castillo & Wagner, 2002; Chen *et al*., 2005). Carabid beetles respond to agriculture, fire, and clearcutting (Niemela *et al*., 1993; Chen *et al*., 2005). It is often expected that Carabid taxon richness would decrease with disturbance because native predator–prey relationships might be disrupted, and in contrast, it's often predicted that some Carabids, the polyphagous taxa, would increase because of their opportunistic feeding habits and higher tolerance for disturbance (Niemela *et al*., 1993; Chen *et al*., 2005).

Tenebrionids (darkling beetles) are the fifth largest family of beetles usually occurring particularly in arid and semi-arid terrestrial ecosystems (Borror *et al*l.., 1989). In addition, they are quite mobile presumably for the purpose of seeking food, mates, or other resources as well as suitable habitats (Doyen & Tschinkel, 1974). These are primarily omnivorous scavengers; some studies have demonstrated the important effect of soil type and shrub distribution on Tenebrionid distribution patterns (Rogers *et al*.., 1978a; Sheldon, 1984; Rogers *et al*.., 1988; Rogers, 1978b and Stapp, 1997). Tenebrionid taxa richness decreases in habitats where there are fewer shrubs and greater disturbance (Rogers *et al*.., 1978a; Sheldon, 1984; Rogers *et al*., 1988; Rogers, 1978b and Stapp, 1997).

1. 4 Environmental factors influencing ant and beetle diversity

Factors that exhibit strong influences on the ability of ants and beetles to recolonise an area successfully include:

- Rehabilitation methods employed
- Climatic factors
- Ground insolation
- Presence of large logs
- Plant growth
- Inter ant/beetle species competition
- Establishment of a sufficient litter layer
- Plant species richness
- Vegetation structural diversity.

These factors, as described by Andersen (1997a) and Majer (1984a; 1990a), establish favourable micro-climates within the disturbed area, determining the availability of food, shelter and territory sites. Such conditions will favour the establishment of a richer beetle fauna which, as with ants, is most likely to be determined by climatic factors and micro-habitat structure (Majer 1984a). Depending on the type of disturbance which had occurred, the particular habitat response in question will vary, with areas experiencing a more favourable rainfall distribution exhibiting higher rates of beetle re-colonisation (Majer & De Kock 1992).

1. 5 Aims of the study

The objective of this study is to determine whether any patterns exist with regard to ant and beetle community assemblages and whether these patterns could serve as a possible indicator of habitat change brought on by fire. It was also an attempt of this study to investigate the effect of burning on invertebrate community assemblages in context of Molopo conditions and extended recovery after burning periods. Possible habitat change was measured in terms of vegetation structure and composition, the effect of bushes as well as the possible effect on soil structure and composition.

CHAPTER 2: MATERIALS AND METHODS

2.1 Study Site

The study was conducted during 2004 within the Molopo Nature Reserve (25° 52' 60" S; 25° 34' 0" E), North West Province, South Africa (Figures 2.1 & 2.2). The reserve is 24 000 hectares in extent and lies on the border with Botswana in the far west of the province, 250 km north of Vryburg and 7 km west of the village of Vostershoop. (http://www.tourismnorthwest.co.za/molopo/index.html)

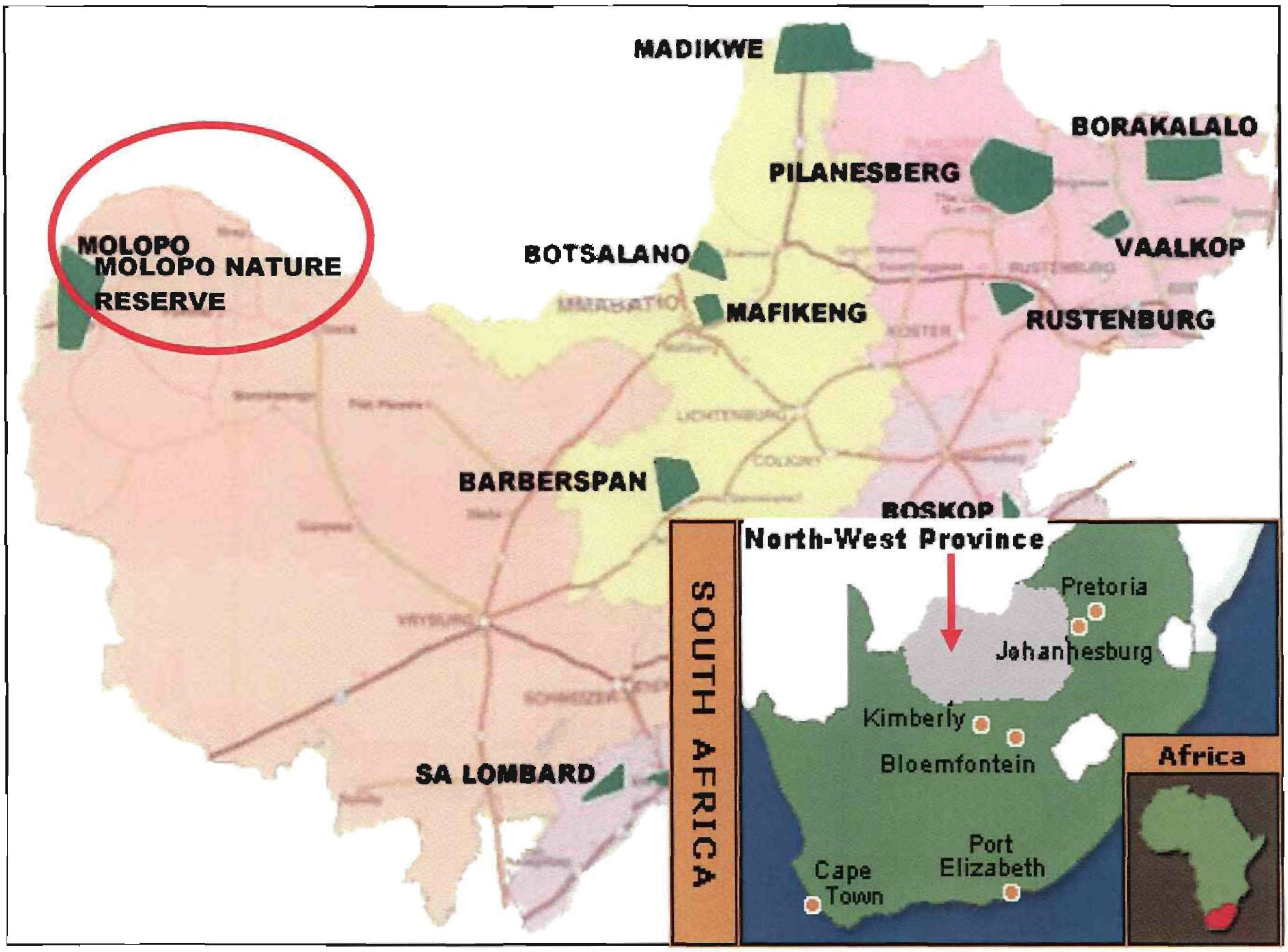


Figure 2.1: Location of the study site in South Africa.

Until the 1960´s, the study area was Bushmen (San) land (Godwin, 2001). As drilling techniques improved, deep groundwater became accessible and farmers began breeding cattle and game. Stocking rates are about one cattle per 13 to 15 hectares. Farm sizes range from about 3.500 ha up to 10.000 ha and more. The Molopo Nature Reserve consists of 9 former farmlands, which were operated until the early 1980´s for cattle breeding. The entire Reserve (240 km^2) is fenced and stocked with a variety of antelope, including grazers and browsers. Large predators like cheetah and leopard occur at low densities. Game stock is regulated by captures for other Reserves and Parks. Except occasional burning, no management is applied on the vegetation. (Meyer *et al.* 2004)

The Molopo Nature Reserve falls within the Kalahari Plains Thorn Bushveld biome, also known as Kalahari Thornveld (A16), as described in Low and Rebelo, 1996. This biome is found on deep, loose sand in the Bray, Vorstershoop and Pomfret areas, mostly in North-West Province, and also in the north-eastern part of Northern Cape. The area is characterised by undulating to flat sandy plains, at about 1 000 m altitude. The average annual rainfall is 300 mm, which falls in summer and early autumn. Temperatures vary between -9°C and 42°C, with an average of 18°C. Soils are deep sandy to loamy and of aeolian origin, underlain by calcrete. The vegetation of this biome is characterised by a fairly well-developed tree stratum with Camel Thorn Acacia erioloba and Shepherd's Tree Boscia albitrunca as the dominant trees, along with scattered individuals of Belly Thorn Acacia luederitzii and Silver Clusterleaf Terminalia sericea, which may be locally conspicuous. The shrub layer is moderately developed and individuals of Black Thorn Acacia mellifera, Weeping Candle Thorn A. hebeclada, Karee-thorn Lycium hirsutum, Grewia flava and Acacia haematoxylon dominate this layer. The grass cover depends on the amount of rainfall during the growing season. Grasses such as Lehmann's Lovegrass Eragrostis lehmanniana, Sour Bushmangrass Schmidtia kalahariensis and Silky Bushman grass Stipagrostis uniplumis are conspicuous. The vegetation type structure is very much influenced by the low rainfall on the sandy plains as well as the grazing by livestock. This area is currently described as being poorly conserved (Leistner, 1967; Bezuidenhout *et al.*. 1993; Low & Rebelo 1993; Bredenkamp *et al.*. 1996).

2.2 Site selection and experimental design

2.2.1 Fire treatment selection

Study sites were selected using burn history parameters, specifically sites that had burnt only once since the existence of the nature reserve in 1982. Four sites were selected, each having burnt at a different time prior to the study. The first site selected burnt in October 2002 and was recorded as a block or accidental fire, the second site in December 1997 as a result of lightning, the third site in September 1992, also recorded as a block or accidental burn, and the final site selected had, according to burn records for the reserve, not burned at all since its inception. (Figure 2.2.)

The three fires identified all occurred in the dry season of Spring and early Summer, hence the occurrence of only one lightning induced fire. It was ascertained during personal communication with Wendy Lloyd (deceased 2006), a former researcher with the Agricultural Research Council who studied fire behaviour in the Molopo Nature Reserve, that fires were mostly of a low intensity and short-lived duration.

2.2.2 Experimental layout at the four burn treatments to determine ant and beetle diversity and composition.

Three randomly located plots, 20m in width and 40m in length, were marked out in each of the four burn treatment sites. Pitfall traps with a 250ml volume and 60mm diameter, filled with 50 ml propylene glycol, were placed in the soil, 10 metres apart, surfaces flush with the ground surface, in grids of 3 x 5 pitfall traps. Traps remained active for a period of 48 hours during sampling in February 2004 and April 2004. With-in site replicates were far apart (+-2km) from each other, although pseudo-replication is still evident and must be taken into consideration. Replication under different circumstances and vegetation types should be considered after this initial study. According to Andersen (1990), a 24 hour sampling period is sufficient for sampling in hotter regions.

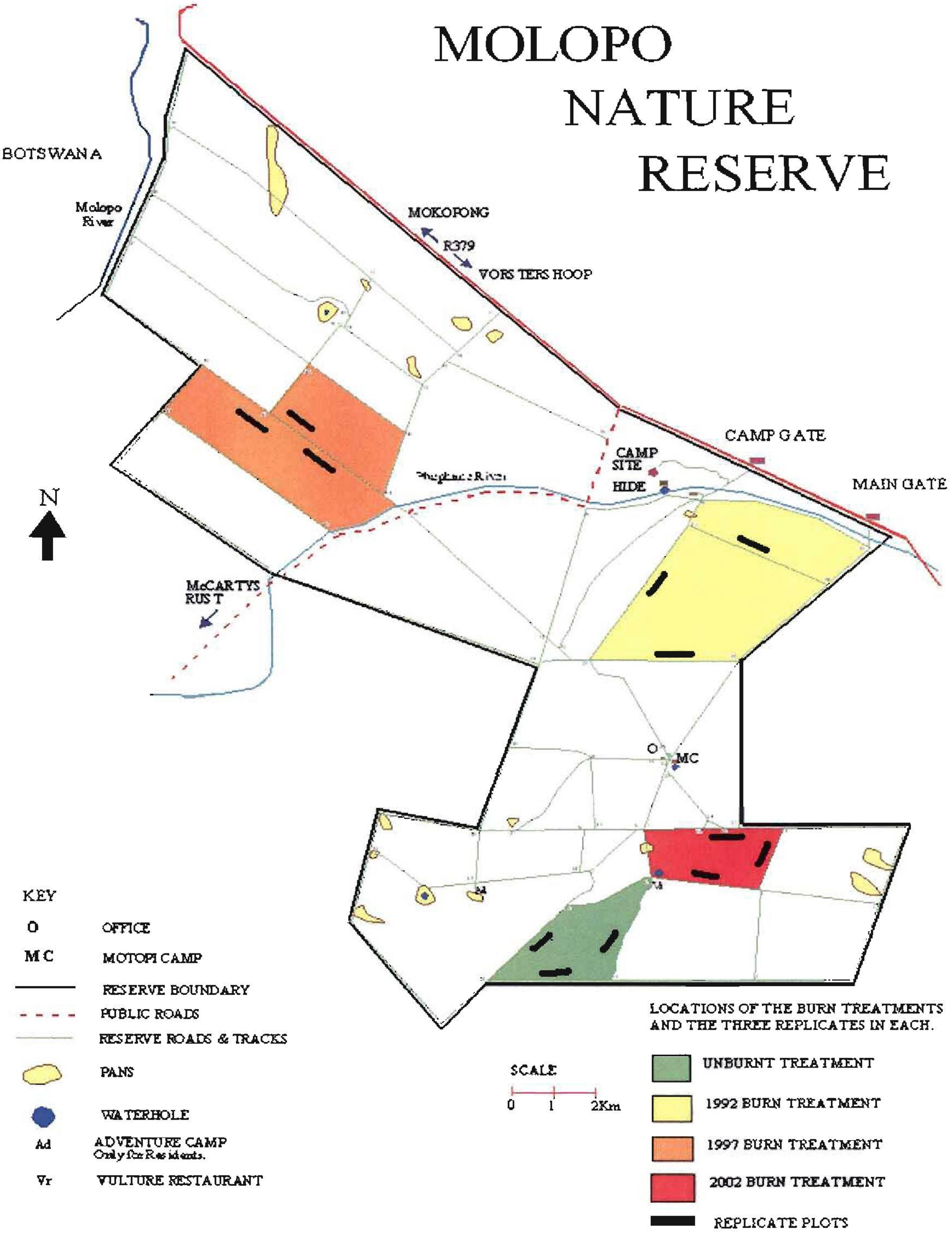


Figure 2.2: Map of the study site, indicating the positioning of each of the burn treatments and the three replicates in each.

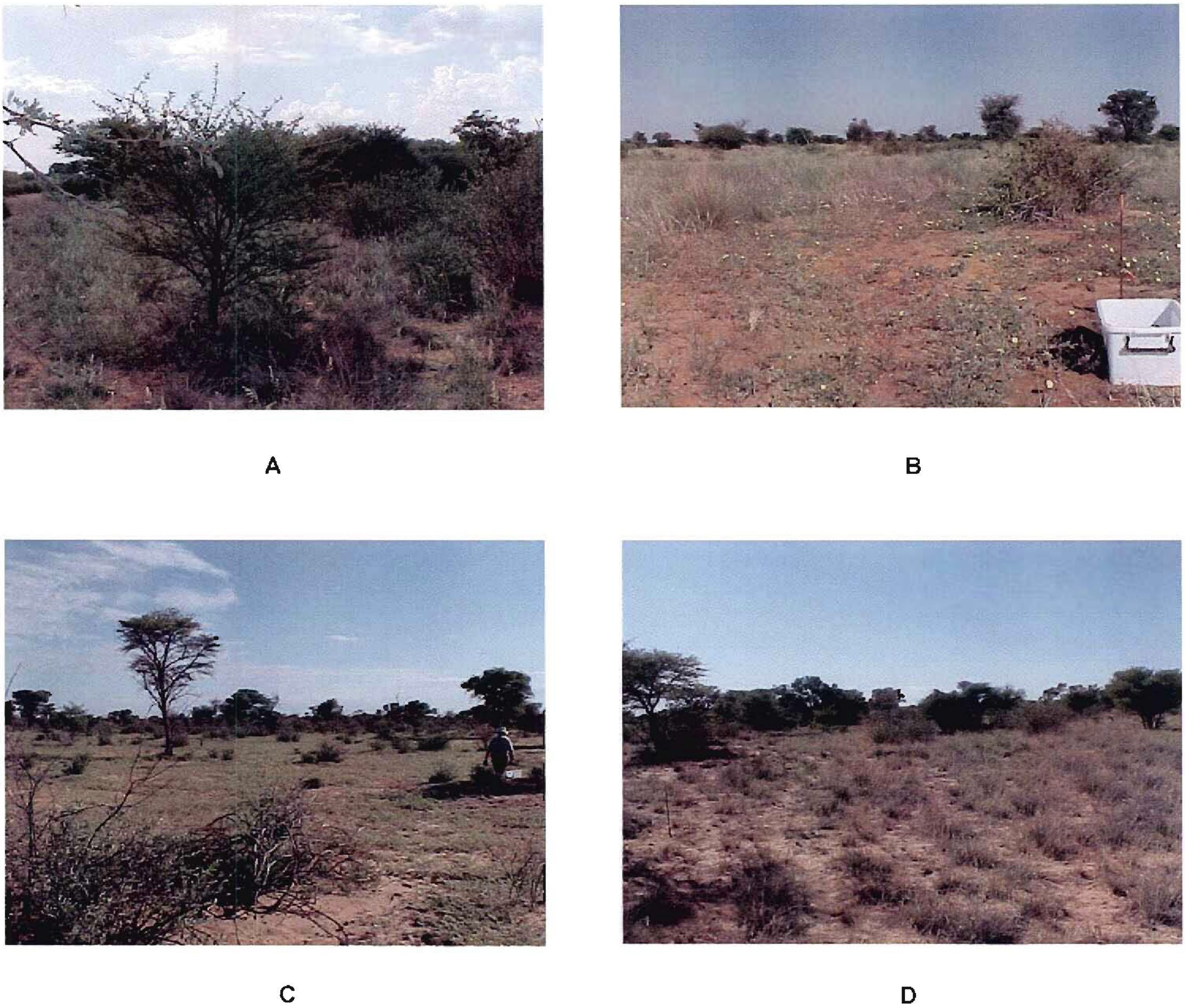


Figure 2.3: Photographic representation of the sites at each of the burn treatments. A: burnt in 1992; B: burnt in 1997; C: burnt in 2002; and D: unburnt.

2.2.3 Experimental design to determine the effect of Acacia mellifera bushes on ant and beetle diversity and composition.

Within each of the four burn regions, 10 like-sized Acacia mellifera plants were selected within clumps of this plant. One pitfall was placed beneath each bush, as well as three pitfalls at intervals of 1m, 2m, and 3m from the base of the bush. The aim of this survey was to determine the effect of bush encroachment on ant and beetle abundance and composition. Pitfall traps remained active for 48 hours before being collected.

2.3 Preservation, sorting and identification

Organisms collected were preserved in plastic specimen jars containing 70% ethanol and labeled according to a predetermined system. The ants and beetles were sorted from each sample and stored separately in labeled McCartney bottles. Ants and beetles in each pitfall trap were identified, numbered and counted, with these totals being documented in hardcopy tables and MS Excel software spreadsheets. Specimens representing each morphospecies for both the ants and beetles were mounted and are kept at the School of Environmental Sciences and Development, North-West University, Potchefstroom.

Dr. Alan Andersen of CSIRO, Tropical Environments Research Centre Winnelie, Australia compiled a preliminary species key for the ants which had been sampled in a pilot study aimed at determining possible ant diversity. Morphospecies for ants were classified to genus level, and where possible, to species level. Ant species that were subsequently added to the list were later verified by Dr. Andersen. Additional ant species identification and verification was undertaken in collaboration with Marisa Coetzee of the Agricultural Research Council, Potchefstroom.

R. Stals and E. Grobelaar at the Biosystematics division: Plant Protection Research Institute of the Agricultural Research Council in Pretoria identified the beetles, providing a detailed list of their known classifications, up to family and genus level, and where possible, species level.

2.4 Vegetation Surveys

To identify possible habitat changing effects due to the fire treatments, vegetation surveys were carried out within each of the replicate sites in each of the burn treatments. Cover abundance and identity of each species was estimated according to the Braun Blanquet cover abundance scale (Mueller-Dombois and Ellenberg, 1974) with the assistance of Jauné-Pierré Smith of the North-West University. The scale considers the percentage of ground cover, with the following scale intervals: 0–1, 1–5, 5–10, 10–25, 25–50, 50–75, 75–100%.

The physiognomy of the vegetation layer was recorded in terms of the height of each species, in centimeters, as well as in terms of estimated percentage cover abundance. The height of certain species was also used to determine whether they qualified as trees or shrubs.

2.5 Soil Analysis

Soil samples were collected at each of the sites in order to investigate degree of homogeneity of the soil at the burn treatments in the reserve. This was done to assess whether soil would be a cause of heterogeneity in vegetation composition and structure between the burn treatments. Soil from beneath the dominant woody component (Acacia mellifera) within each replicate of the different burn sites, as well as from the open herbaceous area, was sampled and analysed. At each replicate, eight samples of soil were sampled in four categories: two topsoil and two subsoil samples from the open herbaceous areas, and two topsoil and two subsoil samples from beneath the dominant woody components. Topsoil samples were taken to a depth of 25cm whereas subsoil samples were taken at a depth of approximately 50-75cm. Plant litter occurring in any of the samples was discarded.

Soil analyses were conducted by Dr. Dries Bloem of the Agricultural Research Council, Potchefstroom, making use of standard methods (The Non-Affiliated Soil Analyses Work Committee) (Coetzee, 2006)

- Soil pH was determined in a 1:2:5 soil to 1M KCl suspension.
- Calcium (Ca), Magnesium (Mg), potassium (K) and sodium (Na) were determined by atomic absorption after extraction in 1M ammonium acetate, making use of a soil to solution ratio of 1:10.
- Plant available phosphorous was extracted with the Bray 1 solution (0.025 mol/l HCl + 0.03 mol/l NH_4F) using a soil to solution ratio of 1:7:5.

- Cation exchange capacity (CEC) was determined by saturating the soil and displaced sodium concentration (by ammonium acetate), followed by atomic absorption spectrophotometry.
- The percentage carbon (C) was determined by wet oxidation-redox titration and standard methods
- Nitrate (NO_3) was determined by 1M KCl extraction and automatic flow system.
- Zinc (Zn) was extracted by 0.1M HCl on a 1:4 soil to solution ratio, and then determined by atomic absorption spectrophotometry.
- Particle size and composition of the soil were determined by the hydrometer method (The Non-Affiliated Soil Analyses Work Committee) (Coetzee, 2006).

2.6 Data analyses

2.6.1 Measurement of ant and beetle diversity

Available literature demonstrates the use of a variety of indices that may provide some indication of ecological status (Majer 1983).
The following indices were calculated for each burn treatment:

- Species richness (S): The total number of ant species per sampling unit. Species richness is however dependent on sample size.
- Species equitability (Pielou's eveness) (J'): this is an indication of how evenly the individuals are distributed between species.

$$J' = \frac{H'}{\ln S}$$

H' = Shannon-Wiener diversity index
lnS = natural log of the number of species

- Margalef richness index (d): a measure of the number of species present, making some allowance for the number of individuals caught. (sample size)

$$d = (S-1)/\mathrm{Log}(N)$$

S = Number of species
N = Number of individuals caught

The following indicators were also applied:

- Indicator species: individual species whose presence, absence or abundance is indicative of a particular factor.
- Indicator groups: groups such as functional groups or feeding guilds that are indicative of disturbance and perturbations based on their functions within a given ecosystem habitat.

2.6.2 Statistical analyses

All analyses were performed separately for the ants and beetles using Primer v. 5 (Clarke & Warwick 2004), Microsoft Excel, CANOCO 4 (Ter Braak & Smilauer, 1998) for PCA's and CCA's, and STATISTICA 5.1 The following procedures were executed:

- Similarity matrices were constructed in PRIMER using the mean Bray-Curtis similarities of each paired comparison. All Bray-Curtis similarities were log transformed before analysis. This similarity measure gives more weight to abundant than to rare species. Differences in similarities of assemblages of ants and beetles were thus tested between the different fire treatments.
- Relative abundances (%) of ant and beetle species were calculated by dividing the number of individuals of each species by the total number of individuals (n_i/N-100) for each transect.
- Ranked species abundance curves (dominance) and k-dominance curves.
- Multidimensional scaling (MDS) to establish outliers.
- Analysis of similarities (ANOSIM). One-way crossed to establish the existence of significant differences between the various fire treatments. A log transformation was applied to reduce the weighting of abundant species but preserves relative abundance information (Clarke, 1993). Anosim, analysis of similarities, allows for a statistical test of the null hypothesis that there will be no assemblage differences between groups of samples, defined a priori, using permutation methods on a similarity matrix of the selected samples. The statistical outcome is that of a global R value for the data defined, with the values being distributed

around zero. In the event of no differences between samples, then between group and within group similarities will be more or less equal, ideally never indicating a value higher then 0.15. R statistic values greater than this lead to a rejection of the null hypothesis at the 0.1% level.

- Simper breakdowns (Clarke, 1993) were conducted to determine which species were primarily responsible for the differences within and between fire treatments. Species typical of a given treatment are also indicated.
- Ordination of species compositional data for the different matrices, using Canonical Correspondence Analysis (CCA) and associated eigen values. The eigenvalue is a measure of importance of an ordination axis; it is the variance in the species data explained by the ordination axis, and is expressed as a fraction of the total variance (which is set to 1). Canoco for Windows 4.5 On-line Help, (c) 1997-2002 Biometris, Wageningen.
- Monte-Carlo permutation tests to establish the significance of species-environment relations for the first and second canonical axes.
- Unconstrained linear ordinations of the soil component, using Principal Components Analysis (PCA).
- Analysis of variance (ANOVA) was applied to investigate the possible presence of correlations between the two surveys, as well as to establish any significant variation trends between the different burn treatments. These results are represented in box and whisker graphs. The "whiskers" are indicative of the standard deviation from the average value for each of the burn treatments, the longer the whisker, the greater the variation in the standard deviation. The box represents the standard error, the bigger the box, the greater the variation in standard error.
- Tukey's test for significance was employed to determine if there was significant variation in the mean invertebrate species richness sampled within each of the different burn treatments. The Tukey tests performed are a statistical measure of the differences between sites, with values less than 0.05 ($p<0.05$) indicating a statistically significant difference for the variable in question.

These procedures aim to add, and provide solutions, to the "why" questions that arose from the research statement.

CHAPTER 3: RESULTS

3.1 Indicators of ecosystem change brought on by fire

3.1.1 Ants

3.1.1.1 Diversity and composition

In this study, a total of 54102 ants in 22 species were collected between February and April 2004 in the various open grassland burn treatments of the park A total of 40963 ants in 36 species were collected in Acacia mellifera dense areas of the same burn treatments. A total of 41 ant species were collected during the study. Both the open grassland replicates and the Acacia mellifera dense areas of the park showed large numbers of *Anaploolepis steingroeveri*, *Monomorium notulum, Monomorium* sp. C, *Monomorium* sp. A, *Ocymyrmex* sp. A and *Pheidole* sp. C. whilst *Monomorium rufulum* and *Lepisiota* sp. A were found in greater abundances within the Acacia mellifera dense areas. Table 3.1 indicates the relative abundance values of each of the ant species sampled within the burn treatment sites for the February survey, with Table 3.2 indicating the ant relative abundance values for April. Absolute ant abundances collected for the two surveys are summarised in appendix D.

Figure 3.1 illustrates a rank abundance curve of the ant data collected in February, showing high dominance and low species richness for the 1997 burn treatment, with the unburnt and 2002 burn treatment curves being flatter with lower dominance and higher species richness, and the 1992 treatment indicating an intermediary dominance pattern. A similar pattern is seen in Figure 3.2, a rank abundance curve of the ant data collected in April, with 1997 exhibiting high dominance when compared to the curves for the unburnt, 1992 and 2002 burn treatments. Ant species sampled in both February and April indicate lower species richness and eveness at the 1997 burn treatment, with species richness and eveness being more similar for the unburnt, 1992 and 2002 sites. This pattern is especially clear from the February data.

Table 3.1. Relative abundance values of the ant species occurring within the open grassland replicates of the different fire treatments for the February survey.

Species	**Burnt in:**			
	Unburnt	**1992**	**1997**	**2002**
Tapinolepis sp. A				
Tapinolepis sp. B	0.00	0.00	0.00	0.58
Anoplolepis steingroeveri	3.63	0.00	96.68	8.37
Camponotus sp. A (fulvopilosus group)	0.15	0.57	0.00	1.95
Camponotus sp. B	0.30	0.28	0.00	0.19
Camponotus sp. D	0.91	0.00	0.02	1.75
Meranoplus sp. A	3.02	1.00	0.04	0.39
Monomorium notulum	12.69	11.81	0.59	18.87
Monomorium sp. C	10.42	5.97	0.72	8.17
Monomorium sp. D	4.23	0.14	0.11	0.00
Monomorium sp. E	12.08	22.76	0.58	17.90
Myrmicaria	0.45	2.99	0.00	2.53
Ocymyrmex sp. A	11.78	12.66	0.88	14.01
Ocymyrmex sp. D	0.30	0.43	0.00	0.00
Opthalmopane berthoudi	0.45	0.14	0.01	0.78
Pheidole sp. C	34.29	37.84	0.16	16.73
Tetramorium sericeiventre	0.00	0.14	0.00	0.39
Tetramorium setuliferum	2.42	0.28	0.04	3.70
Tetramorium sp. A	0.30	0.14	0.00	0.78
Tetramorium sp. B	0.00	0.28	0.00	0.00
Tetramorium sp. C	2.42	2.28	0.11	1.95

Table 3.2. Relative abundance values of the ant species occurring within the open grassland replicates of the different fire treatments for the April survey.

Species	Unburnt	Burnt in: 1992	1997	2002
Anoplolepis steingroeveri	4.37	0.52	98.35	1.33
Camponotus sp. A (fulvopilosus group)	0.26	0.52	0.00	0.27
Camponotus sp. D	1.80	3.11	0.00	1.60
Crematogaster sp. B	0.00	0.52	0.00	0.00
Meranoplus sp. A	0.26	5.18	0.03	0.80
Meranoplus sp. B	1.54	0.00	0.00	3.72
Monomorium notulum	12.85	17.62	0.18	13.03
Monomorium sp. C	10.28	4.66	0.62	11.44
Monomorium sp. D	0.00	0.00	0.13	0.00
Monomorium sp. E	13.11	20.73	0.27	11.44
Myrmicaria	3.34	5.70	0.00	2.66
Ocymyrmex sp. A	3.34	5.70	0.12	3.46
Ocymyrmex sp. D	0.00	0.52	0.00	0.00
Opthalmopane berthoudi	2.57	2.59	0.02	2.66
Pheidole sp. C	37.53	18.13	0.17	33.78
Tetramorium sericeiventre	0.26	0.00	0.00	0.00
Tetramorium setuliferum	3.08	1.55	0.06	3.19
Tetramorium sp. A	0.00	2.07	0.00	0.00
Tetramorium sp. B	0.00	6.74	0.00	0.00
Tetramorium sp. C	5.40	4.15	0.04	10.64

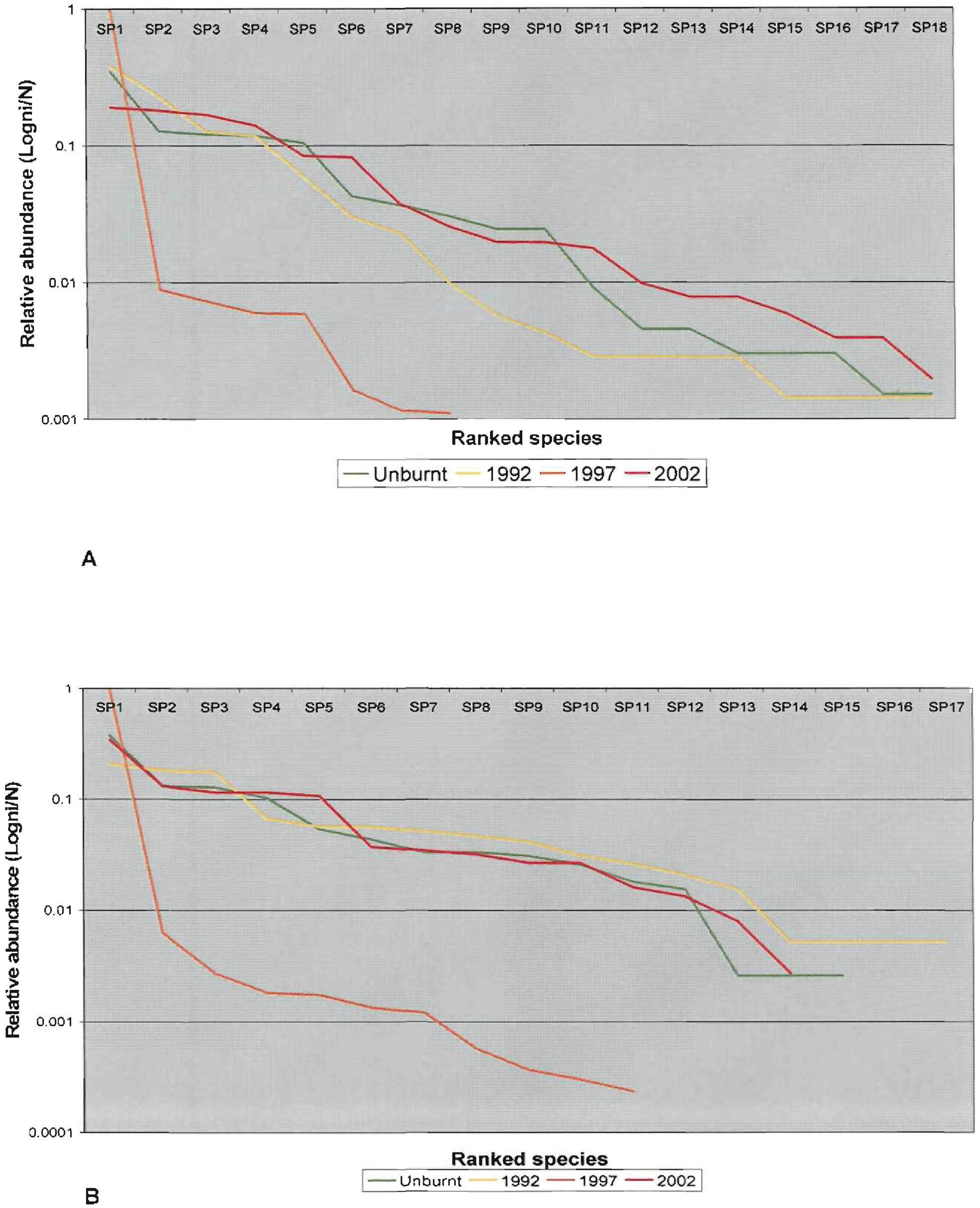


Figure 3.1. Ranked abundance curves illustrating the diversity in the ant assemblages within the open grassland replicates of each fire treatment (A: February and B: April).

Table 3.3. Diversity indices for the February and April ant surveys in the open grassland replicates of each fire treatment. (S- number of species; N- total abundance; d- Margalef; J'- Pielou's eveness.)

	Site	S	N	d	J'
February	Unburnt	18.0	662.0	2.6173	0.7181
	1992	18.0	703.0	2.5933	0.6160
	1997	13.0	20961.0	1.3065	0.0790
	2002	18.0	514.0	2.7234	0.7799
April	Unburnt	15.0	389.0	2.3476	0.7523
	1992	17.0	193.0	3.0403	0.8241
	1997	11.0	30166.0	1.1634	0.0450
	2002	14.0	514.0	2.7234	0.7799

Table 3.3 summarises the various diversity and richness indices for each of the burn treatments for both the February and April open grassland sampling efforts, and in both cases it is evident that the species richness and species eveness is lower in the 1997 burn treatment than in the unburnt, 1992 and 2002 burn treatments.

These findings suggest that burn treatment 1997 stands apart dramatically from the unburnt, 1992 and 2002 burn treatments. The possible reasons for this were investigated from a variety of angles in order to determine whether fire treatments may have had a significant effect via habitat changes. An ordination of ant absolute abundance was therefore carried out to determine grouping of treatment sites along the fire treatment gradient.

3.1.1.2 Ordination of ant species abundance along a burn gradient

The grouping of ant assemblages according to the burn treatments was determined by means of MDS (refer to methods), the results for the February and April survey illustrated in Figure 3.2.

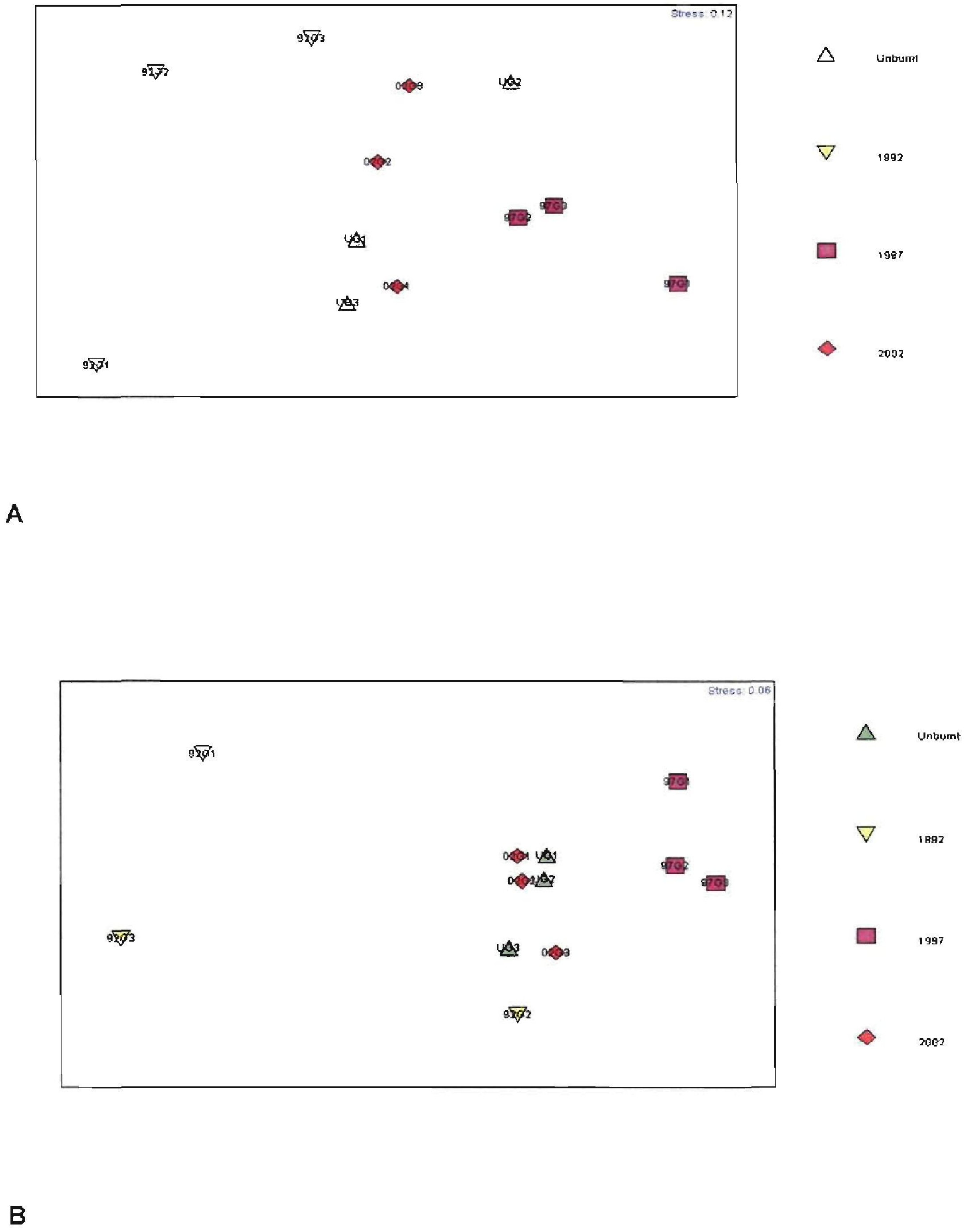


Figure 3.2. MDS (Multi-Dimensional Scaling) of the absolute abundance of ant species within each replicate of the different burn treatments (A: February and B: April).

The deletion of the 1997 data from the ordination did not lead to greater separation of the remaining burn treatment sites.

The Anosim results for the February and April ant surveys represented in Tables 3.4 and 3.5 respectively, with the R statistic in both cases being greater than 0.15, thus suggesting definite differences between the four burn treatments, with the greatest between site differences occurring in combinations with 1997, as summarised in Table 3.3.

The Anosim statistics show clear differences between the samples with regards to the ants, further identifying burn treatment 1997 as a comparably unique site. to determine which species primarily account for the observed differences, the SIMPER (similarity percentages) routine is used, which looks at the overall percentage contribution of each of the species to the dissimilarity between two sample groups, enabling the construction of a list of species in decreasing order of their importance in segregating two samples. These similarity and dissimilarity values are summarised in Table 3.4 for the February survey and Table 3.5 for the April survey. (Species names typed in plain text contributed towards the 1st sample group in each between group comparison, while those in bold contributed towards the 2nd sample group.)

The greatest between site ant diversity dissimilarity for both February and April is for the 1992 and 1997 burn treatments, whereas the smallest dissimilarities are exhibited between burn treatments unburnt and 2002, an observation already noted when discussing the distribution of ants with regard to their absolute abundance. In order to verify the stated research question, these data need to be considered in the context of environmental data, particularly that of habitat structure as defined by the vegetation and soil. This relationship will be dealt with in section 3.2.

Table 3.4. Anosim and Simper results indicating the greatest species contributions for absolute abundance of ants for each burn treatment in the open grassland areas during the February survey. (Values listed in bold in each column correspond with the first site, values in normal print correspond with the second site.)

Anosim Global R Statistic: 0.537						
Simper % dissimilarities between groups						
	Unburnt	**1992**	**1997**	**2002**		
Unburnt	**-**	**37.06**	**31.08**	**30.67**		
1992	**37.06**	**-**	**45.3**	**37.14**		
1997	**31.78**	**45.3**	**-**	**34.76**		
2002	**30.67**	**37.14**	**34.76**	**-**		
% Species Contributions	**Unburnt/1992**	**Unburnt/1997**	**Unburnt/2002**	**1992/ 1997**	**1992/ 2002**	**1997/ 2002**
Cam A	-	-	-	-	-	6.01
Mer A	**4.4**	**6.35**	**2.64**	-	-	-
Mon C	**6.18**	5.19	**5.05**	5.92	-	5.62
Mon D	**7.92**	-	**9.41**	7.07	-	**9.71**
Mon E	7.12	3.03	-	**5.09**	**7.04**	-
Mon not	-	3.84	-	5.25	6.55	-
Myr sp	6.71	-	-	**6**	**5.64**	7.42
Ocy A	10.73	12.14	-	5.55	**6.93**	**5.61**
Phe C	3	**9.14**	**5.15**	**7.67**	**5.27**	4.89
Tap ste	**10.75**	23.24	6.23	25.75	11	**20.54**
Tet set	**6.4**	-	-	-	**7.32**	-

Table 3.5. Anosim and Simper results indicating the greatest species contributions for absolute abundance of ants for each burn treatment in the open grassland areas during the April survey. (Values listed in bold in each column correspond with the first site, values in normal print correspond with the second site.)

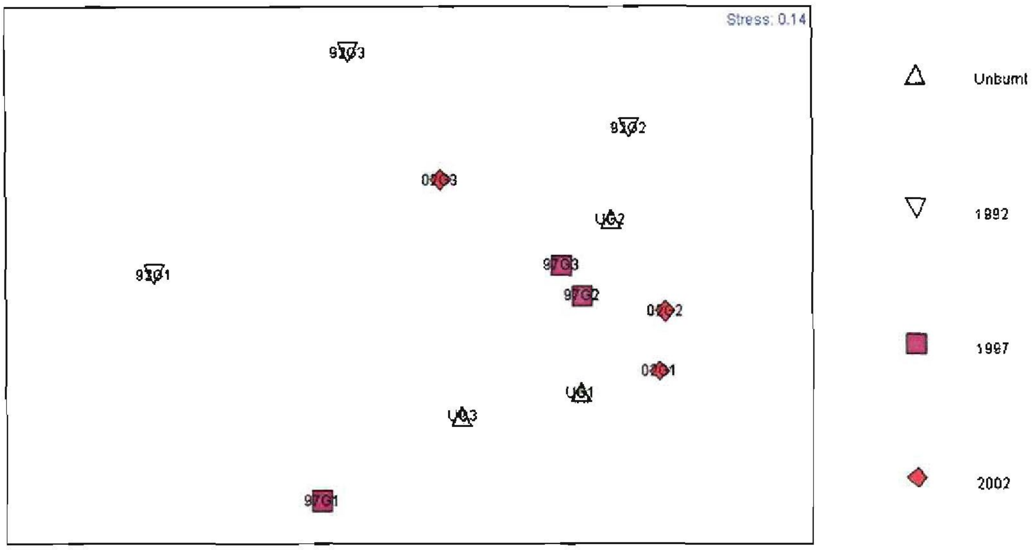
Anosim Global R Statistic: 0.394				
Simper % dissimilarities between groups				
	Unburnt	**1992**	**1997**	**2002**
Unburnt	**-**	**42.92**	**36.5**	**23.68**
1992	**42.92**	**-**	**54.01**	**43.98**
1997	**36.5**	**54.01**	**-**	**37.53**
2002	**23.68**	**43.98**	**37.53**	**-**

% Species Contributions	**Unburnt/1992**	**Unburnt/1997**	**Unburnt/2002**	**1992/ 1997**	**1992/ 2002**	**1997/ 2002**
Mon C	**9.97**	6.88	-	11.83	9.61	**6.22**
Mon D	-	12.15	-	9.39	-	**11.56**
Mon E	-	3.71	6.27	3.32	4.27	-
Mon not	**4.66**	-	5.89	3.28	4.89	3.2
Ocy A	-	5.4	9.14	4.88	6.58	-
Phe C	**13.83**	**4.66**	**3.09**	-	12.04	3.61
Tap ste	**8.16**	25.24	-	24.46	5.46	**25.14**
Tet C	**4.78**	-	-	-	-	4.35

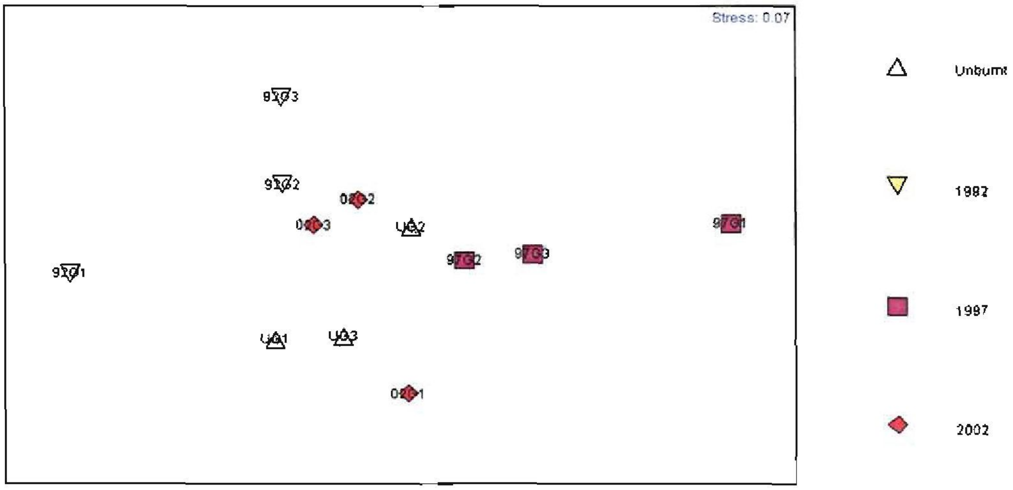
The species tabulated here are those that contribute the greatest percentage dissimilarity between each of the samples compared, but are not the only species that occurred within each burn treatment. The above species are repeated in different sequences and percentages throughout all of the between sample comparisons, providing an idea of the manner in which ant communities may be assembled within each burn treatment. In order to understand how ant community assemblages function, it is useful to consider them in context of their functional groups. It is then also more applicable to mention the rarer species percentage contributions to between sample dissimilarities in order to define each burn treatment in context of the specific species occurring there, irrespective of their percentage contribution. This follows in the next section.

3.1.1.3 Ordinations of Ant Functional Groups

MDS ordinations were constructed to provide an indication of the manner in which the ant functional groups are assembled at each of the burn treatment sites, as such groups are believed to respond to the structure and functioning of their respective habitats at a given time. The ant functional group assemblages were represented in terms of the number of species occurring per ant functional group, and then also in terms of the abundance of organisms occurring per ant functional group. Figure 3.3 represents the MDS for the number of species per ant functional group (A), and the abundance per ant functional group (B) for the February data, whilst the same is illustrated in Figure 3.4 for the April data.



A



B

Figure 3.3. MDS (Multi-Dimensional Scaling) of A: the number of species per ant functional group and B: the abundance per ant functional group within each replicate of the different burn treatments for the February survey.

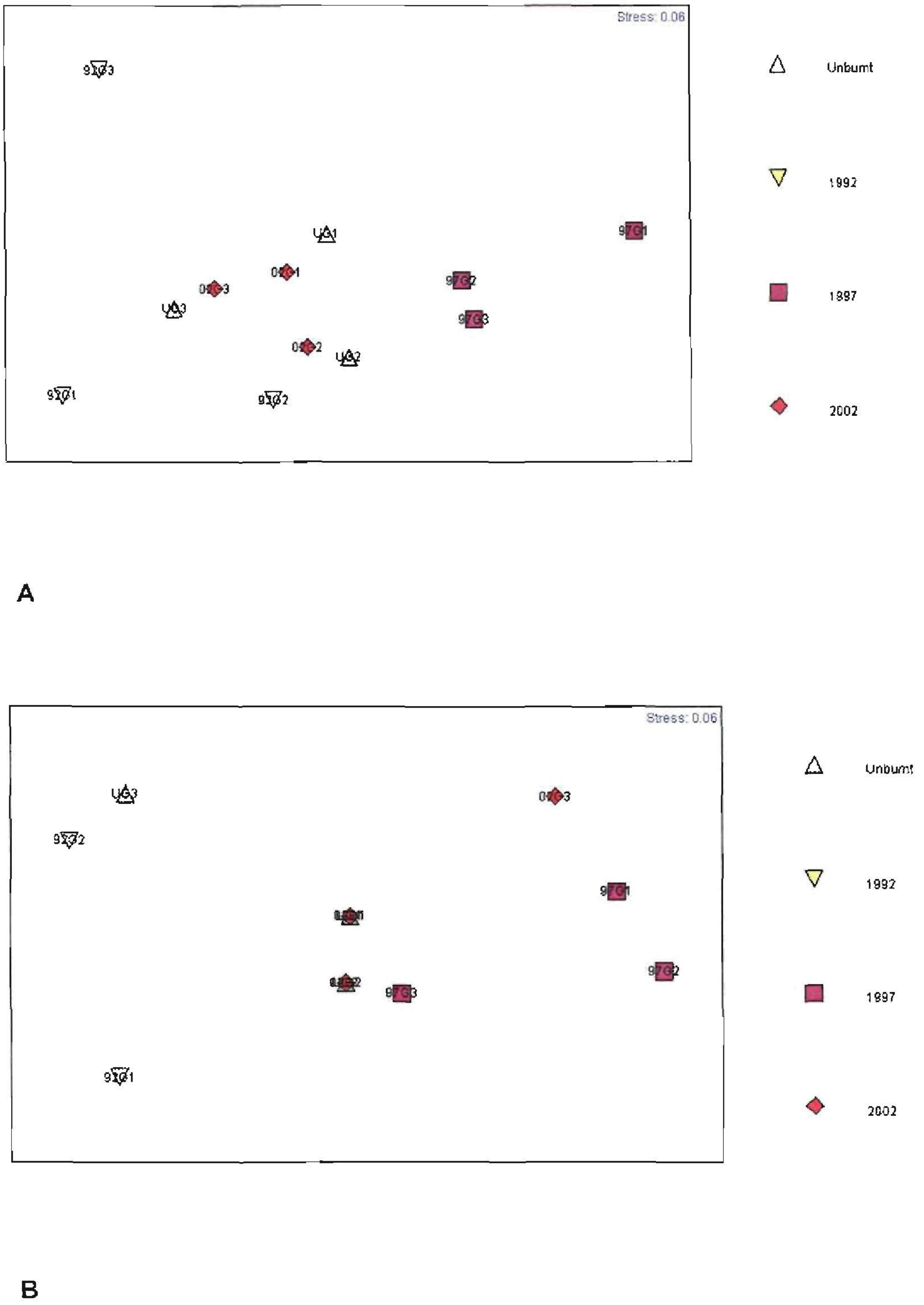


Figure 3.4. MDS (Multi-Dimensional Scaling) of A: the number of species per ant functional group and B: the abundance per ant functional group within each replicate of the different burn treatments for the April survey.

With regards to **ant functional groups** MDS Figures 3.3 and 3.4 illustrate that it is clear that the functional group assemblages did differ for each burn treatment regarding number of species as well as abundance per ant functional group with 1997, once again, separating from the remaining treatment replicates mainly due to the dominance of cold climate specialists.

As stated in the research question, it is hypothesised that fire caused alterations within the ecosystem habitat, resulting in the restructuring of the then present ant community. Previous studies (Andersen, 1991a; Andersen *et al.* 2003; Greenslade, 1997; Hosking and Turner, 1997; Jackson & Fox, 1996) have indicated that ant communities do not tend to show immediate responses to fire within the given habitat, thus meaning that changes within ant community structures will become more apparent over time, after which communities may begin to normalise in the direction of the community structures existing prior to burning. The same was found by Andersen *et al.* (2007) and Andersen, (1991b), in that the observations of their research is consistent with an indirect effect of fire, with the response being a result of longer-term habitat simplification caused by repeated fires. The abundance of highly active thermophilic savanna ant species is known to be promoted by the reduced tree and shrub cover that typically results from frequent fire.

Anosim and Simper tests were carried out to obtain statistical quantification for the above MDS observations, as can be seen in Tables 3.6 and 3.7 for February and April respectively. The Simper test again provides a more statistical break down of functional group contributions to each burn treatment.

Table 3.6. Anosim and Simper results indicating the greatest functional group contributions for the abundance of ants for each burn treatment in the open grassland areas during the February survey. (Values listed in bold in each column correspond with the first site, values in normal print correspond with the second site.)

Anosim Global R Statistic: 0.307				
Simper % dissimilarities between groups				
	Unburnt	**1992**	**1997**	**2002**
Unburnt	**-**	**23.11**	**24.07**	**16.52**
1992	**23.11**	**-**	**33.32**	**24.34**
1997	**24.07**	**33.32**	**-**	**24.2**

2002	**16.52**	**24.34**	**24.2**	-		

% Func. Group Contributions	**Unburnt/1992**	**Unburnt/1997**	**Unburnt/2002**	**1992/ 1997**	**1992/ 2002**	**1997/ 2002**
CSS	9.7	54.85	10.62	63.24	-	**52.35**
GM	-	-	**12.3**	-	**10.43**	-
HCS	**13.57**	**7.81**	14.29	-	17.28	12.01
O	-	-	12.29	-	-	7.15
SC	-	17.8	**27.7**	17.8	**19.61**	**14.2**
SP	**34.86**	-	22.8	**6.02**	33.44	7.16

Table 3.7. Anosim and Simper results indicating the greatest functional group contributions for the abundance of ants for each burn treatment in the open grassland areas during the April survey. (Values listed in bold in each column correspond with the first site, values in normal print correspond with the second site.)

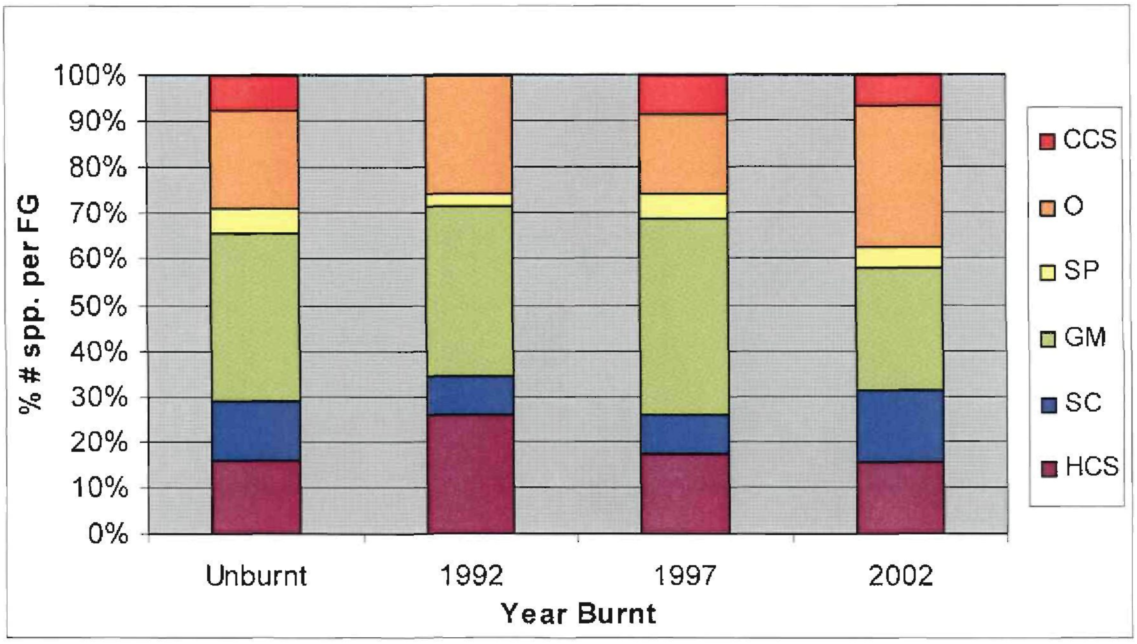
Anosim Global R Statistic: 0.296

Simper % dissimilarities between groups

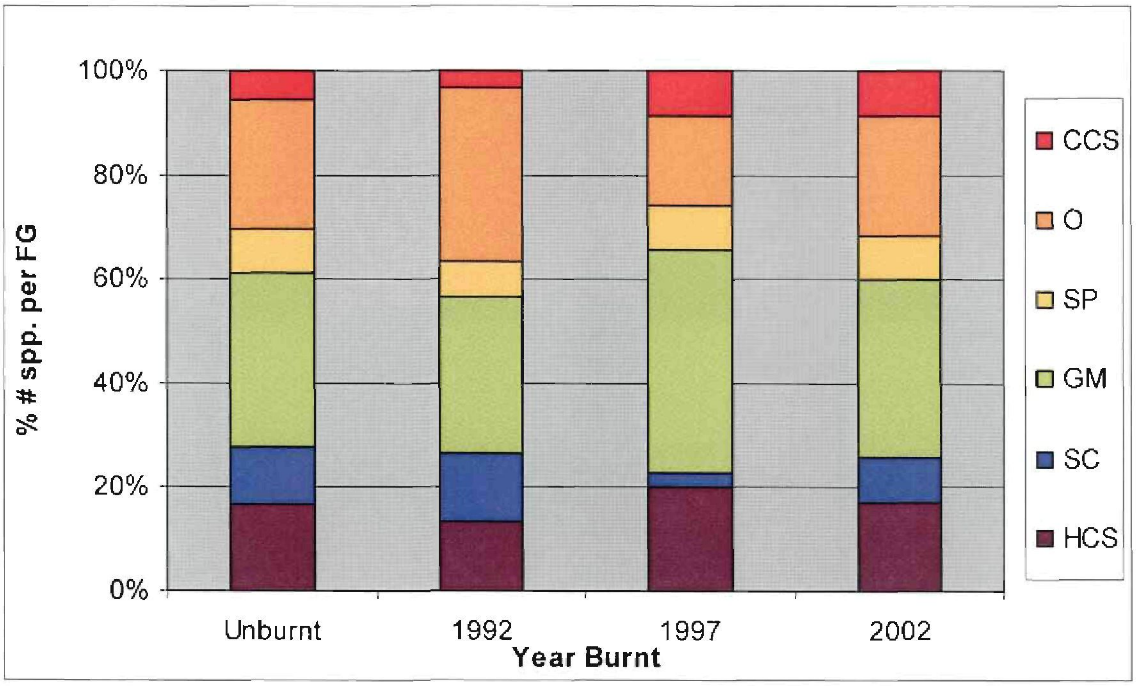
	Unburnt	1992	1997	2002
Unburnt	-	25.29	**28.49**	**16.98**
1992	**25.29**	-	-	**23.26**
1997	28.49	39.95	-	**29.77**
2002	16.98	23.26	**29.77**	-

% Func. Group Contributions	**Unburnt/ 1992**	**Unburnt/ 1997**	**Unburnt/ 2002**	**1992/ 1997**	**1992/ 2002**	**1997/ 2002**
CSS	**24.92**	56.8	**25.47**	56.84	13.52	**60.66**
GM	**18.83**	-	-	12.26	19.66	-
HCS	19.7	12.03	19.92	11.9	21.95	7.78
SC	-	**10.24**	**18.03**	-	-	9.58
SP	**14.42**	-	-	-	-	-
O	**11.51**	**7.09**	11.94	-	14.53	8.45

The bar graphs in Figure 3.5 represent the percentage number of species per ant functional group present in the open grassland areas of each of the burn treatments (A: February and B: April). Figure 3.6 represents the abundance per ant functional group present in the open grassland areas of each of the burn treatments (A: February and B: April).

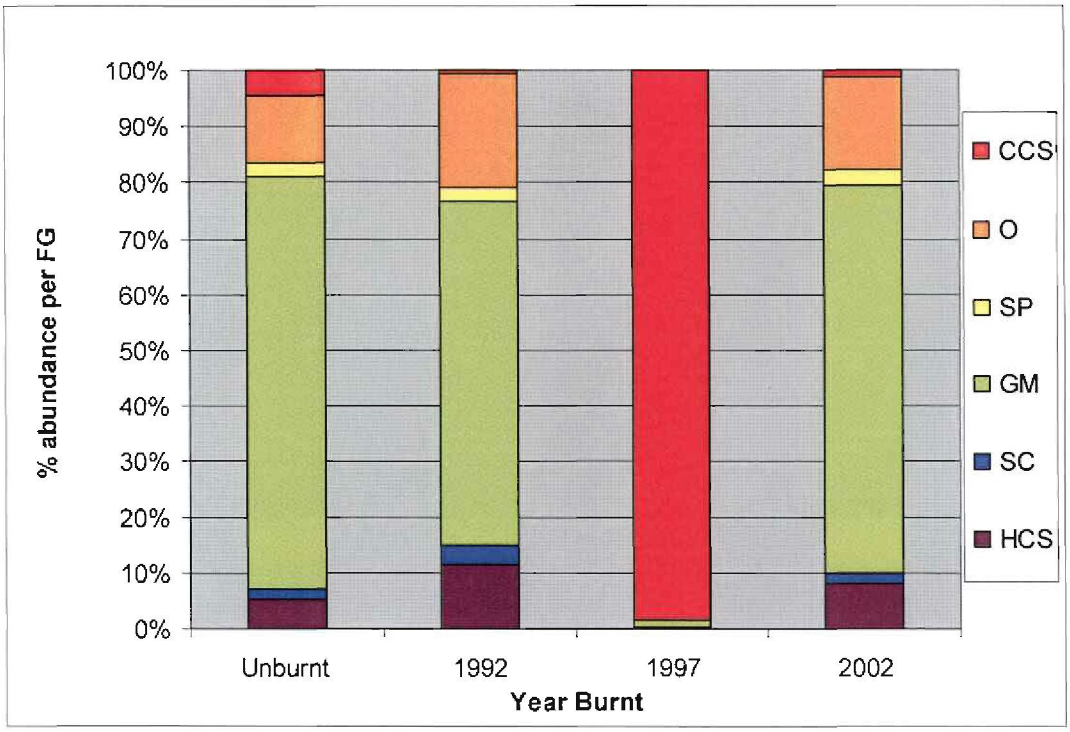


A



B

Figure 3.5. Histograms representing the percentage number of species per ant functional group present in the open grassland areas of each of the burn treatments (A: February and B: April).



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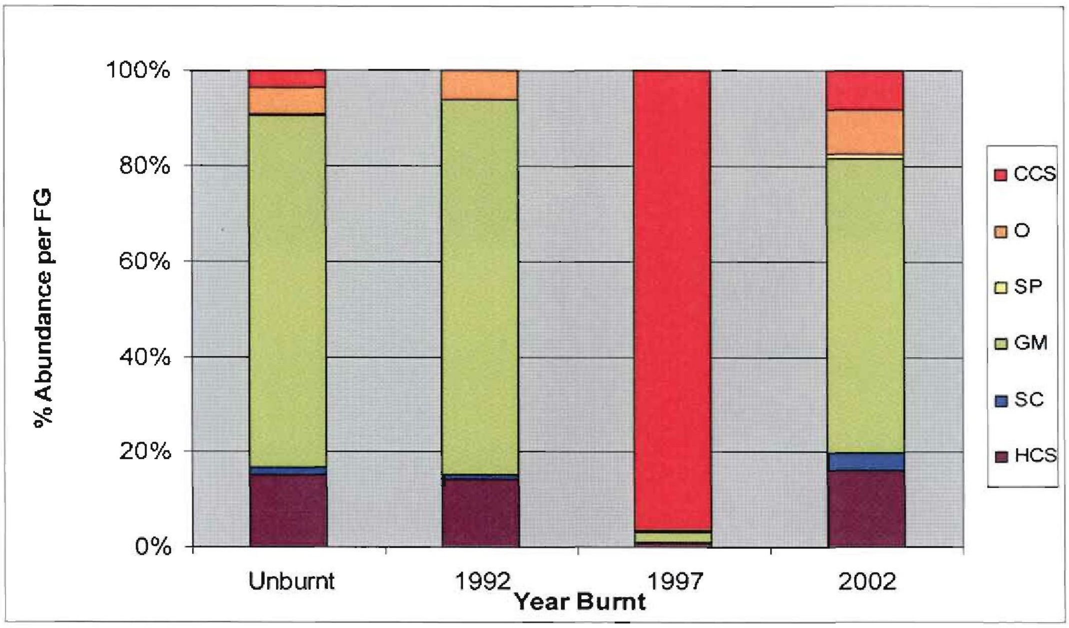


B

Figure 3.6. Histograms representing the abundance per ant functional group present in the open grassland areas of each of the burn treatments (A: February and B: April).

Figures 3.5 and 3.6 represent the percentage distribution of the abundance of ants per functional group for each treatment in February and April respectively. The differences between the sites cannot be accounted for by the number of functional groups occurring within each treatment, and thus it seems more appropriate to compare the number of species occurring per functional group per burn treatment for both the February and April surveys.

The Subordinate Camponotini make a reasonable appearance in most of the burn treatments, but are far less represented in diversity for the 1997 burn treatment of the February and April survey. According to Andersen (2000a) this group is somewhat behaviourally submissive to the Dominant Dolichoderinae, but due to their absence, pose no threat. This group is often diverse and abundant in rich ant communities, and according to the diversity data of the previous section, burn treatments 1992, 2002 and unburnt do exhibit greater diversity than 1997 and thus this group seems to support that 1997, with respect to ant assemblages, indicates a greater degree of stress. One would expect the opportunists to be abundant in the 1997 burn treatment, however, this not being the case may be explained by the total dominance of the Generalised Myrmicinae in relation to other functional groups.

Opportunists are considered to be poorly competitive, and their distributions will be strongly influenced by competition from other ants, in this case the Generalised Myrmicinae. The fact that the Opportunists do, however, occur at the burn treatment replicates indicates varying degrees of environmental stress, as hypothesised, possibly due to fire. Specialist predators make a relatively consistent appearance throughout all the burn treatments for both surveys, barring burn treatment 1997 of the February survey. Due to their specialised diets and typically low population densities, (Andersen, 2000a), this group has very little interaction with other ants, explaining their presence and distribution not being affected.

The Hot climate specialists make an interesting appearance throughout the burn treatments, particularly the hot February survey. This could be as a result of their high level of specialisation with regards to their foraging ecology, limiting their interaction with other ants. The Cold Climate Specialists exhibit a low, though even, distribution throughout the burn treatments for February and April. Being unspecialised, apart for their habitat tolerances, one may expect to observe them in lower densities due to the dominance of the Generalised Myrmicinae.

The cold climate specialists show a clear dominance in 1997, due to the abundance of *Anoplolepis steingroeveri*, with hot climate specialists being evenly distributed over the remaining treatments. The same is true for the subordinate camponotini and opportunists, with the specialist predators making an appearance in reasonable numbers at unburnt, 1992 and 2002. Despite these groups showing representation in terms of number of species as seen in Figure 3.5 in the 1997 replicates, their overall abundances are much lower when compared to unburnt, 1992 and 2002. Once again, unburnt and 2002 seem to reflect similar patterns, with 1992 showing some differences, and 1997 grouping apart with a high degree of dominance by the vast abundance of Cold Climate Specialists.

A different invertebrate group, namely beetles, was selected to identify the impact of the burn treatments on their abundance and distribution. The beetles (Coleoptera), and their presence within each of the burn treatments was determined in the same manner as for the ants, in order to make effective comparisons. The results follow in the next section.

3.1.2 Beetles

3.1.2.1 Diversity and composition

A total of 1904 beetles of 32 species were collected between February and April 2004 in the various open grassland burn treatments of the park with vast abundances of Zophosis burkei, Silvinidae sp. Indeterminate and Saprininae Hypocacculus sp., Passalidus fortipes, Zophosis subaenea and Onthophagus sp. Tables 3.8 and 3.9 indicate the relative abundance values of each of the beetle species sampled within the burn treatment sites for the two surveys. The absolute abundances are summarised in appendix E, and a complete species list appears in Appendix B.

Table 3.8. Relative abundance values of the beetle species occurring within the open grassland replicates of the different fire treatments for the February survey.

Species	**Burnt in:**			
	Unburnt	**1992**	**1997**	**2002**
Scarabaeus flavicomis	0.80	2.03	0.86	8.78
Atractonotus mulsanti	0.00	0.00	0.00	0.27
Brachycerus	0.27	0.68	0.29	0.27
Carabidae Gen. et spec. indet	0.00	0.00	0.86	0.00
Hypocacculus sp.	0.00	5.41	0.29	2.93
Macrocoma/ Pseudocolaspis sp. 2	0.27	0.68	0.29	1.06
Metacatharsius	1.33	0.00	0.57	1.06
Mimaulus papulosus	0.00	0.68	0.00	2.13
Monommatidae Gen. et spec. indet 1	6.63	1.35	3.16	0.27
Onthophagus	0.00	3.38	0.29	0.80
Passalidius fortipes	2.39	2.70	2.30	0.27
Phanerotomea	0.00	0.68	0.00	0.00
Prionolytta binotata	0.00	0.00	0.00	17.55
Psammodes sp.	0.00	0.00	0.29	0.00
Psammodes vialis	0.00	0.68	1.72	0.00
Scarabidae Gen. et spec. indet 1	0.27	0.00	0.00	0.00
Silvanidae	9.55	10.81	0.57	0.27
Spartecerus cf. rudis	0.00	0.00	0.57	1.06
Spartecerus sp.	0.00	0.00	0.29	0.27
Zophosis boei	3.18	2.70	3.45	5.32
Zophosis burkei	55.44	50.68	68.97	55.85
Zophosis subaenea	19.89	17.57	15.23	1.86

Table 3.9. Relative abundance values of the beetle species occurring within the open grassland replicates of the different fire treatments for the April survey.

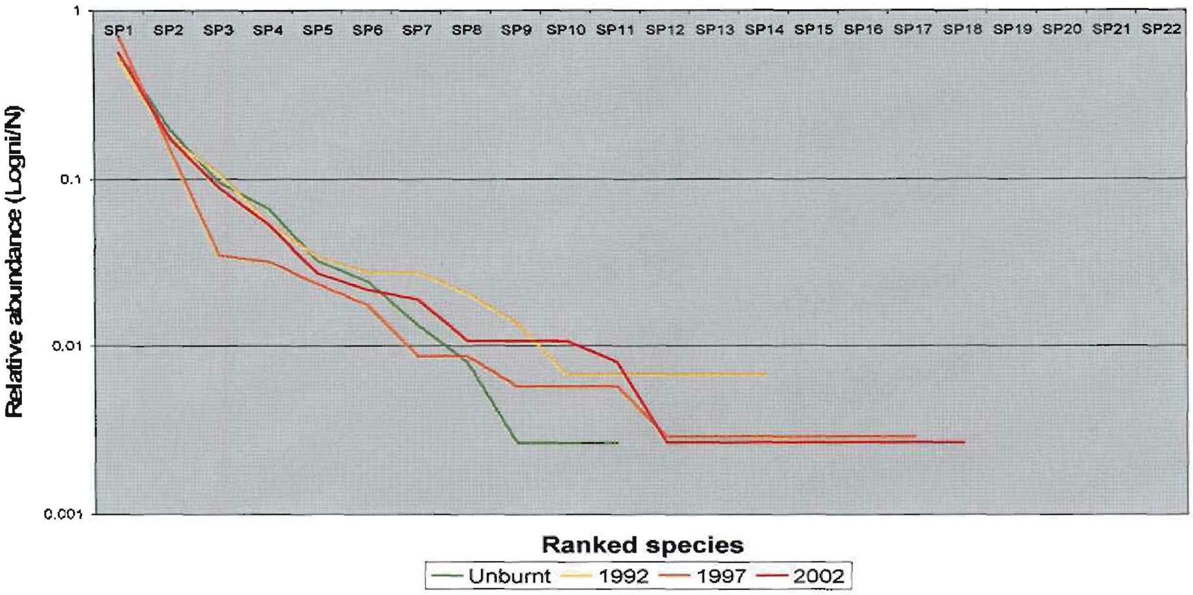
Species	**Burnt in:**			
	Unburnt	**1992**	**1997**	**2002**
Atractonotus mulsanti	**0.00**	**0.00**	**1.34**	**0.00**
Boeomimetes ephippium	1.41	0.00	0.00	0.71
Carabidae Gen. et spec. indet	2.11	8.70	0.67	0.00
Chrysolina vigintiquatuorsignata	2.11	3.48	1.34	2.84
Crepidogaster sp.	0.00	0.87	0.00	0.00
Cylas sp.	0.00	1.74	0.67	0.00
Gonopus deplanatus	0.70	1.74	0.67	1.42
Graphipterus amabilis	0.00	0.00	1.34	0.00
Hypocacculus sp.	10.56	10.43	23.49	8.51
Macrocoma/ Pseudocolaspis sp. 1	0.70	0.00	0.00	2.13
Macrocoma/ Pseudocolaspis sp. 2	0.70	0.00	1.34	0.71
Metacatharsius	0.00	0.00	0.67	0.00
Monommatidae Gen. et spec. indet 1	0.70	0.87	1.34	0.00
Onthophagus sp. 1	19.72	7.83	2.01	12.77
Onthophagus sp. 2	0.00	0.87	0.00	0.00
Pachylomerus femoralis	1.41	0.00	0.00	0.71
Passalidius fortipes	7.75	20.87	3.36	0.71
Phanerotomea	0.70	0.87	0.67	0.00
Prionolytta binotata	0.00	0.00	0.00	2.13
Psammodes sp.	0.00	0.00	0.67	0.00
Psammodes vialis	0.70	0.00	2.01	0.71
Scarabaeus flavicomis	17.61	10.43	14.09	38.30
Scarabaeus sp.1	0.70	0.87	0.00	0.71
Scarabidae Gen. et spec. indet 1	1.41	0.87	1.34	2.13
Scarabidae Gen. et spec. indet 2	2.11	0.87	2.01	0.00
Silvanidae Gen. et spec. indet 1	0.70	0.00	28.19	0.00
Sp U 12	1.41	0.00	0.00	0.00
Spartecerus sp. 1	0.00	0.00	0.00	0.71

Xeloma maura	0.70	0.00	0.00	2.13
Zophosis boei	7.75	9.57	1.34	2.13
Zophosis burkei	10.56	10.43	5.37	19.86
Zophosis subaenea	7.75	8.70	6.04	0.71

The values represented in these Tables are better understood when considered in conjunction with Figure 3.7, and Table 3.10. Figure 3.7 shows the ranked abundance curves for the February (A) and April (B) beetle data.

Differences within the February and April beetle data may be better understood in context of their species composition and community structure. Table 3.10 summarises the different diversity and richness indices. No clear trends could be identified along the burn gradient.

Although eveness and dominance appear to be relatively similar for the February and April ranked abundance curves illustrated in Figure 3.7 the February unburnt site shows low species richness with the 1997 and 2002 sites being the highest. For the April survey, higher species richness was found compared with the February survey. The high dominance and low diversity that was found for the ant data in the 1997 burn treatment for both surveys was not reflected by the beetle data (Table 3.10). In fact, the opposite trend was found to occur with a tendency of higher beetle species diversity in disturbed situations (if we assume that the 1997 site was more negatively affected by fire). This trend was also found in former studies (Van Hamburg *et al.* 2004).



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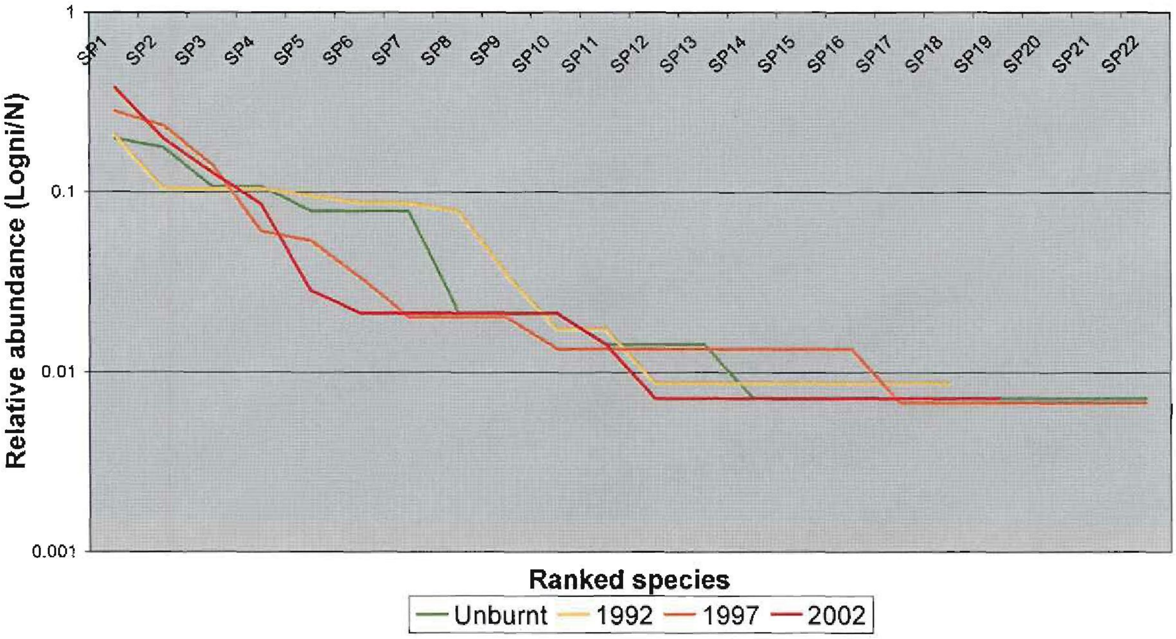


B

Figure 3.7. Ranked abundance curves illustrating the diversity in the beetle community within the open grassland replicates of each fire treatment (A: February and B: April).

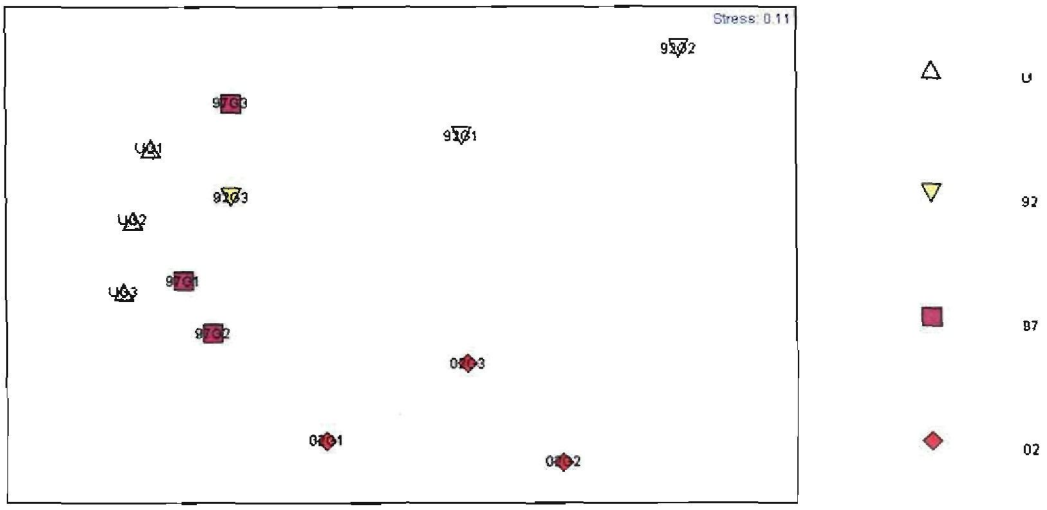
Table 3.10. Diversity indices for the February and April beetle surveys in the open grassland replicates of each fire treatment. (S- number of species; N- total abundance; d- Margalef; J'- Pielou's eveness.)

	Site	S	N	d	J'
February	Unburnt	11.0	754.0	1.6603	0.5595
	1992	14.0	296.0	2.4603	0.5632
	1997	17.0	696.0	2.5973	0.4468
	2002	18.0	752.0	2.7179	0.4981
April	Unburnt	23.0	284.0	4.0715	0.6105
	1992	18.0	230.0	3.3100	0.6480
	1997	22.0	298.0	3.8616	0.5809
	2002	19.0	282.0	3.3677	0.5673

3.1.2.2 Ordinations of beetle species abundance along a burn gradient

The grouping of beetle assemblages according to the burn treatments was determined by means of MDS (refer to methods). Figure 3.8 illustrates the abundance of beetle species within each replicate of the different burn treatments (A: February and B: April). Apart from the grouping of the 2002 treatment on the second axis in the February data, no satisfactory pattern is reflected.

Beetle data was analysed using the Anosim and Simper procedures (refer to methods), to determine whether the beetle diversity indices indicate any between treatment dissimilarities, and the species that accounting for these. Table 3.11 summarises the February data and Table 3.12 summarises the April data. No notable trends could be identified apart from the vast survey assemblage differences, which may be seasonal.



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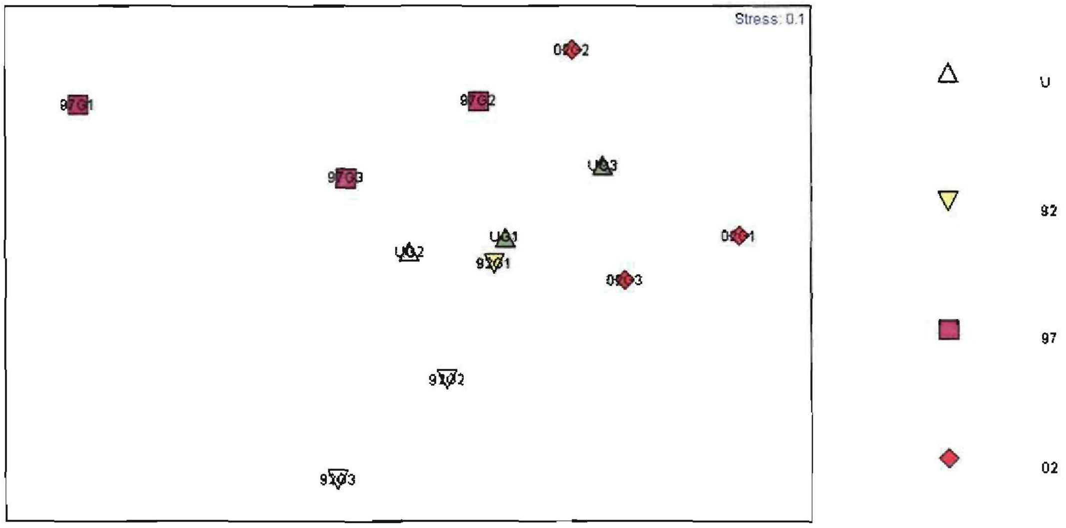


B

Figure 3.8. MDS (Multi-Dimensional Scaling) of the absolute abundance of beetle species within each replicate of the different burn treatments (A: February and B: April).

Table 3.11. Anosim and Simper results indicating the greatest species contributions for absolute abundance of beetles in the open grassland areas during the February survey. (Values listed in bold in each column correspond with the first site, values in normal print correspond with the second site.)

Anosim Global R Statistic: 0.407						
Simper % dissimilarities between groups						
	Unburnt	**1992**	**1997**	**2002**		
Unburnt	-	**50.96**	**37.59**	**55.71**		
1992	**50.96**	-	**49.23**	**54.09**		
1997	**37.59**	**49.23**	-	**50.67**		
2002	**55.71**	**54.09**	**50.67**	-		
% Species Contributions	**Unburnt/1992**	**Unburnt/1997**	**Unburnt/2002**	**1992/ 1997**	**1992/ 2002**	**1997/ 2002**
Mon ind	**11.13**	**10.9**	-	-	-	-
Pas for	-	-	-	8.12	-	**5.95**
Pri bin	-	-	14.86	-	17.69	16.37
Sca fla	-	-	7.78	-	-	7
Sil ind	**11.77**	**15.84**	**10.22**	**9.36**	**7.98**	-
Zop boe	-	11.99	8.7	-	9.41	-
Zop bur	**7.92**	**8.83**	-	7.52	**6.92**	**6.02**
Zop sub	**16.47**	**5.39**	**10.35**	**16**	**7.94**	**10.39**

Table 3.12. Anosim and Simper results indicating the greatest species contributions for absolute abundance of beetles in the open grassland areas during the April survey. (Values listed in bold in each column correspond with the first site, values in normal print correspond with the second site.)

Anosim Global R Statistic: 0.417						
Simper % dissimilarities between groups						
	Unburnt	**1992**	**1997**	**2002**		
Unburnt	-	**50.91**	**61**	**51.5**		
1992	**50.91**	-	**66.51**	**65.38**		
1997	**61**	**66.51**	-	**67.28**		
2002	**51.5**	**65.38**	**67.28**	-		
% Species Contributions	**Unburnt/1992**	**Unburnt/1997**	**Unburnt/2002**	**1992/ 1997**	**1992/ 2002**	**1997/ 2002**
Mon ind	-	-	-	**5.92**	**6.36**	-
Ont sp	**18.03**	**14.64**	**17.29**	**3.83**	8.09	8.41
Pas for	11.72	-	6.98	**12.59**	14.54	-
Pri bin	-	-	-	-	-	-
Sca fla	13.63	11.46	23.17	-	24.46	20.42
Sil ind	-	20.65	-	21.19	-	19.35
Zop boe	-	**5.34**	-	5.64	5.55	-
Zop bur	**9.16**	**6.24**	11.56	**5.85**	-	11.32
Zop sub	**5.24**	-	-	-	**5.57**	**4.33**

The beetle data is in contrast to that of the ant data in that the SIMPER percentage trends are opposite to one another, and in that where the February and April data for the ants show the same trends, they do not for the beetle data.

Dominating the species percentage contribution for the February beetle survey are Silvinidae species indeterminate, Zophosis burkei and Zophosis subaneae at the unburnt treatment, and Prionolytta binotata, Scarabaeus flavicomis, Zophosis boei, Zophosis burkei and Zophosis subaenea at burn treatment 2002. For the April survey, the dominating species percentage contributions were Ontophagus spp., Scarabaeus flavicomis, Zophosis burkei and Zophosis subaenea at burn treatment 2002, Silvinidae species indeterminate at 1997, and Monommatidae General et species indeterminate at 1992. Based on this, no apparent distinctive patterns seem to associate the February and April surveys with one another with regards to beetle species composition.

3.1.2.3 Ordinations of Beetle Families

Although beetle species composition differs to a great extent between the February and April surveys, there is a possibility that potential patterns exist in the beetle community structures, with the equivalent focus of ant functional groups being beetle families. Species that attribute differences may still all be from a defined group or family, thus possibly reflecting patterns at family level, and thus applicable to their function in the given ecosystem (refer to Table 3.10). To determine whether the February and April surveys indicate any similarities with regard to number of species per family, MDS graphs were created as illustrated in Figure 3.9. Additional MDS graphs were created to determine any possible patterns with regards to total abundances per family as illustrated in Figure 3.10. No significant grouping was found to indicate an effect of burn treatments, barring a slight grouping of the 1997 burn treatment on the second axis in the April MDS.

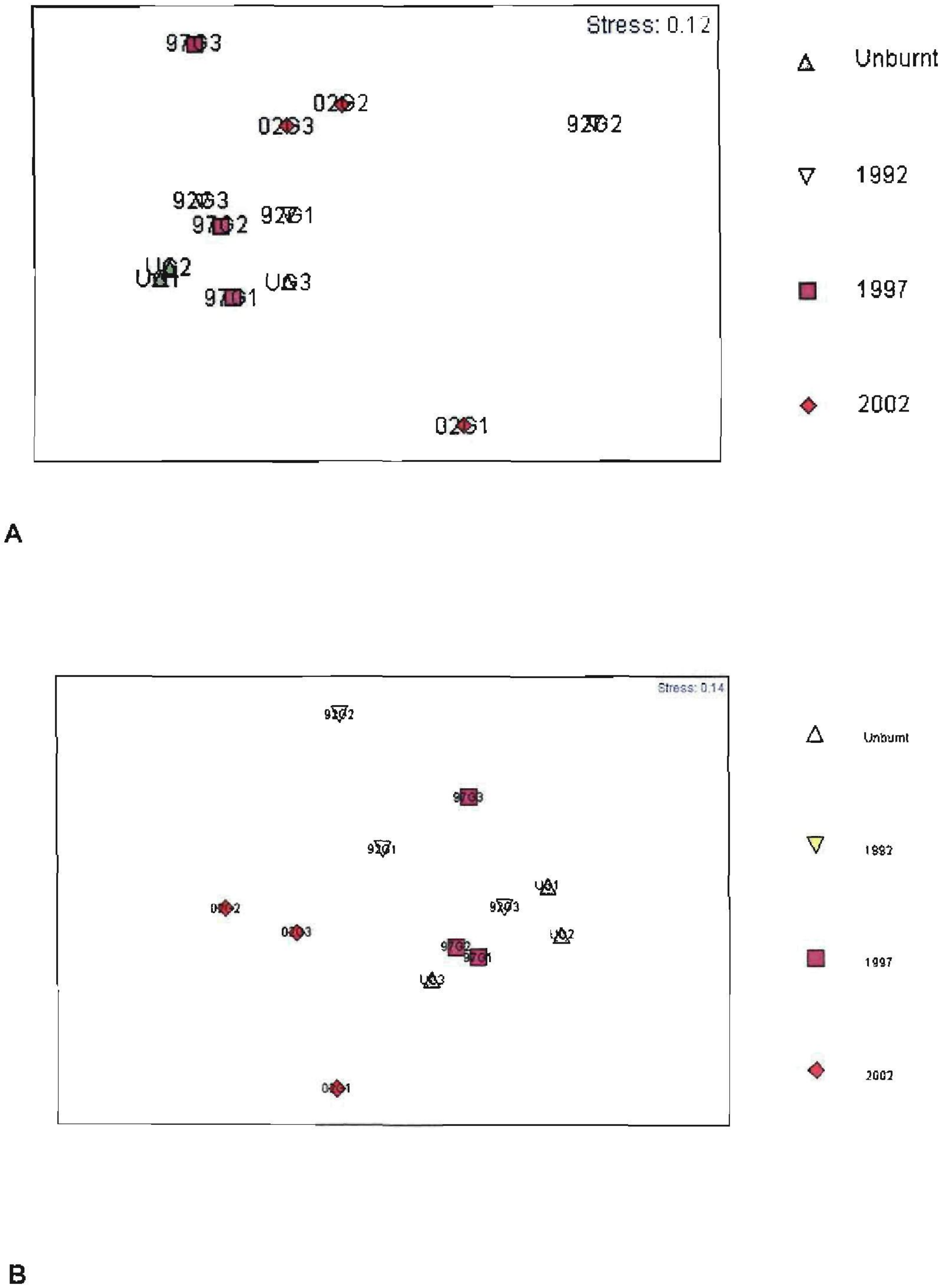


Figure 3.9. MDS (Multi-Dimensional Scaling) of the number of species per beetle family within each replicate of the different burn treatments (A: February and B: April).

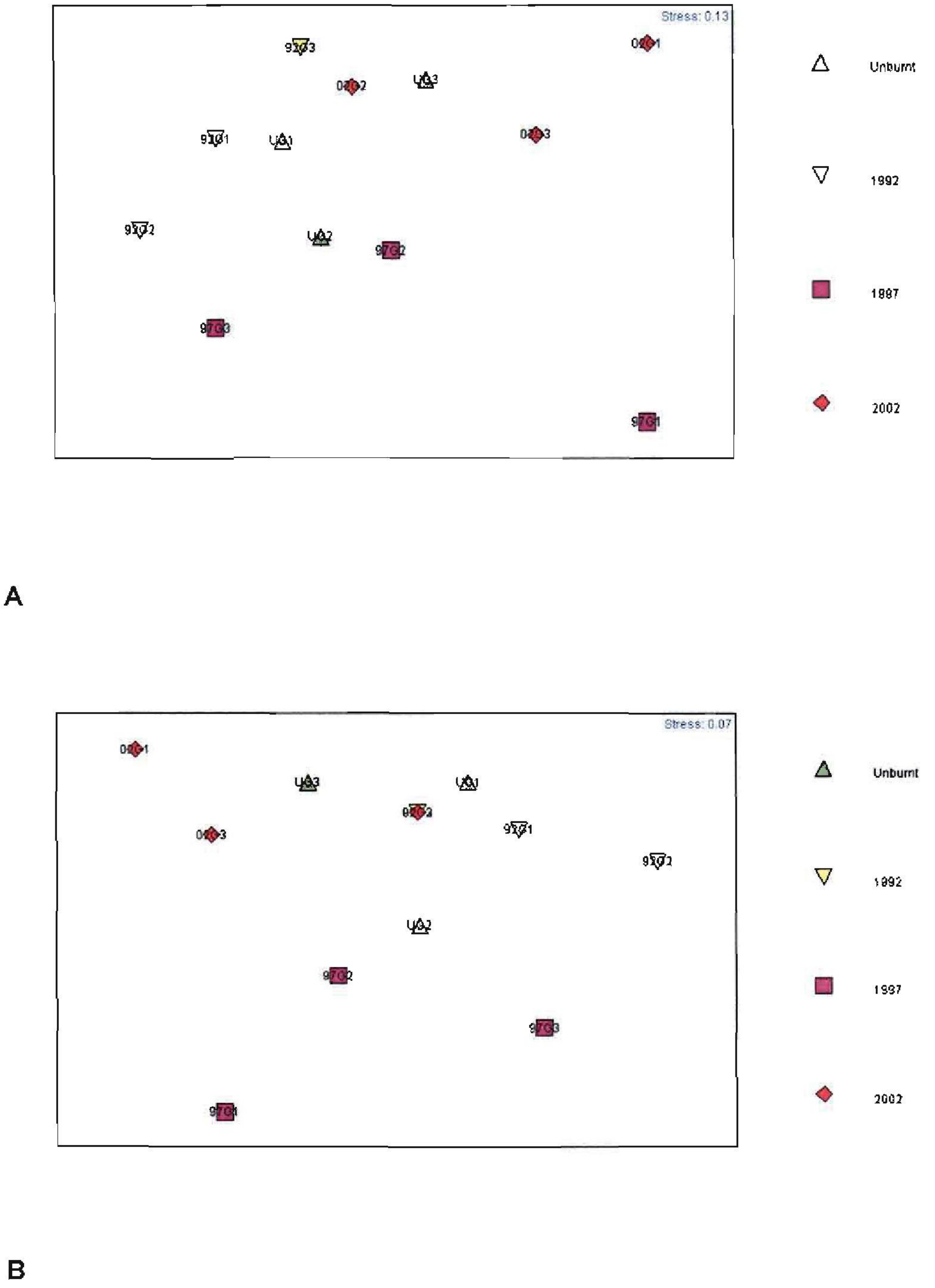


Figure 3.10. MDS (Multi-Dimensional Scaling) of the abundance per beetle family within each replicate of the different burn treatments (A: February and B: April).

As in the case of the ants, all beetle data was put through the Anosim and Simper procedures, described previously, to determine whether the beetle diversity indices indicate any between treatment dissimilarities, as well as the species that account for those dissimilarities. The Anosim and Simper results are summarised in Table 3.13 Table 3.14.

Table 3.13. Anosim and Simper results indicating the greatest species contributions for absolute abundance of beetles in the open grassland areas during the February survey. (Values listed in bold in each column correspond with the first site, values in normal print correspond with the second site.)

Anosim Global R Statistic: 0.407

Simper % dissimilarities between groups

	Unburnt	1992	1997	2002
Unburnt	-	50.96	37.59	55.71
1992	50.96	-	49.23	54.09
1997	37.59	49.23	-	50.67
2002	55.71	54.09	50.67	-

% Species Contributions	Unburnt/1992	Unburnt/1997	Unburnt/2002	1992/ 1997	1992/ 2002	1997/ 2002
Mon ind	**11.13**	**10.9**	-	-	-	-
Pas for	-	-	-	8.12	-	**5.95**
Pri bin	-	-	14.86	-	17.69	16.37
Sca fla	-	-	7.78	-	-	7
Sil ind	**11.77**	**15.84**	**10.22**	**9.36**	**7.98**	-
Zop boe	-	11.99	8.7	-	9.41	-
Zop bur	**7.92**	**8.83**	-	7.52	**6.92**	**6.02**
Zop sub	**16.47**	5.39	**10.35**	**16**	**7.94**	**10.39**

Table 3.14. Simper results indicating the greatest species contributions for absolute abundance of beetles in the open grassland areas during the April survey. (Values listed in bold in each column correspond with the first site, values in normal print correspond with the second site.)

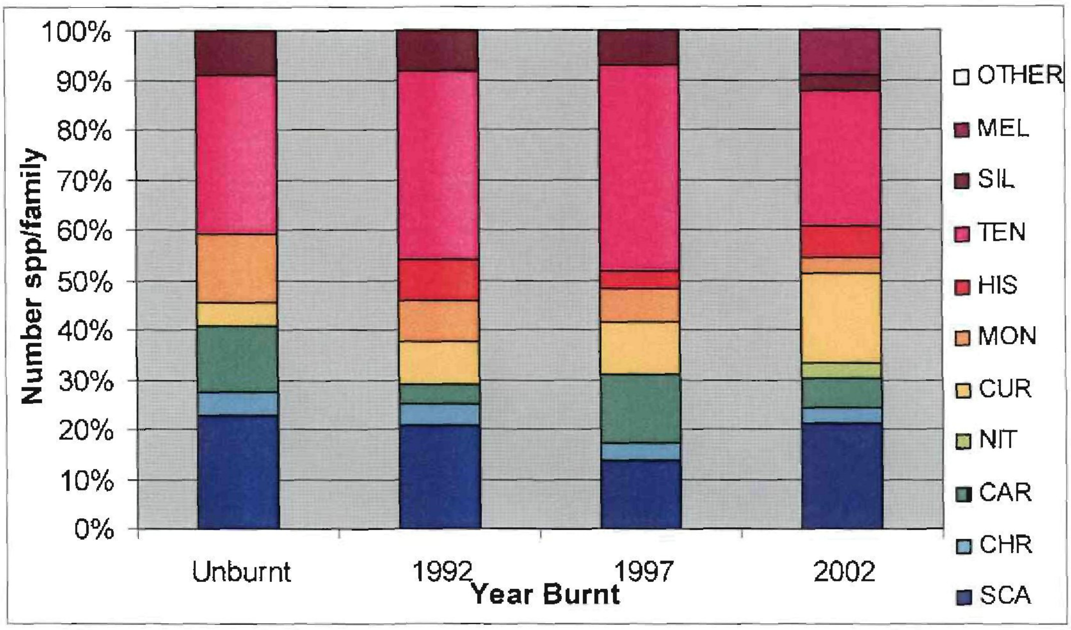
Anosim Global R Statistic: 0.417

Simper % dissimilarities between groups

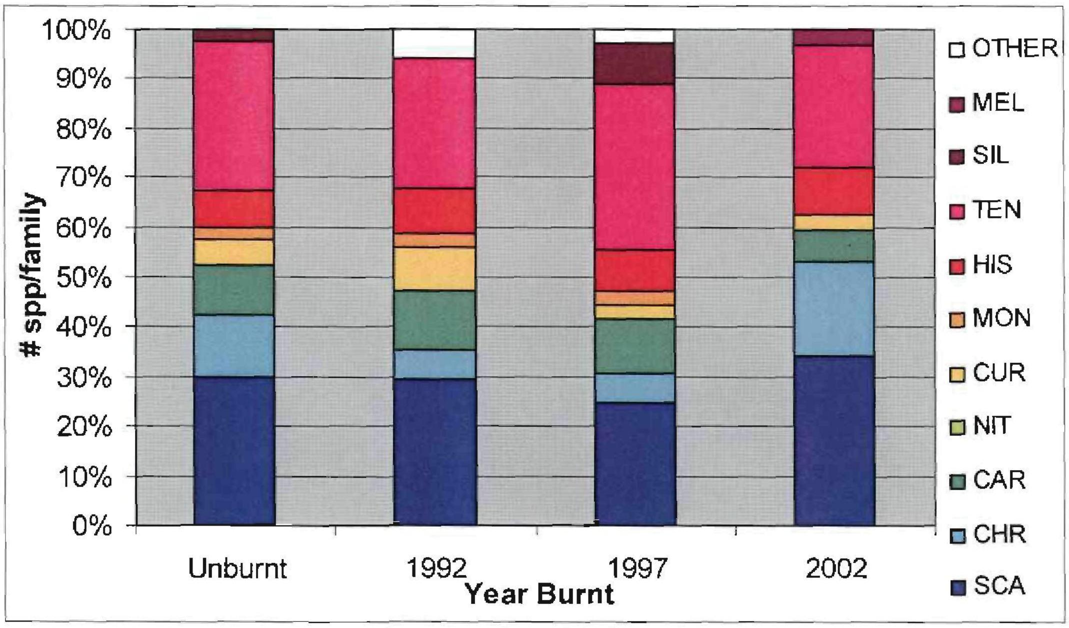
	Unburnt	1992	1997	2002
Unburnt	-	50.91	61	51.5
1992	50.91	-	66.51	65.38
1997	61	66.51	-	67.28
2002	51.5	65.38	67.28	-

% Species Contributions	**Unburnt/1992**	**Unburnt/1997**	**Unburnt/2002**	**1992/ 1997**	**1992/ 2002**	**1997/ 2002**
Mon ind	-	-	-	**5.92**	**6.36**	-
Ont sp	**18.03**	**14.64**	**17.29**	**3.83**	8.09	8.41
Pas for	11.72	-	6.98	**12.59**	14.54	-
Pri bin	-	-	-	-	-	-
Sca fla	13.63	11.46	23.17	-	24.46	20.42
Sil ind	-	20.65	-	21.19	-	19.35
Zop boe	-	**5.34**	-	5.64	5.55	-
Zop bur	**9.16**	**6.24**	11.56	**5.85**	-	11.32
Zop sub	**5.24**	-	-	-	**5.57**	**4.33**

Figures 3.11 and 3.12 are stacked bar graphs which provide a percentage breakdown of the beetle family compositions occurring at each site, specifically the percentage number of species per family for February and April, Figure 3.11, as well as the percentage total abundance per family for February and April, Figure 3.12. There is little indication of significant patterns on overall beetle diversity and distribution and thus it is futile to apply the Anosim and Simper procedures to the beetle data. There is however some indication that the 1997 treatment exhibits some effect on lower Scarab richness and abundance. The 2002 burn treatment showed a greater occurrence of Meloidae species in the February survey.

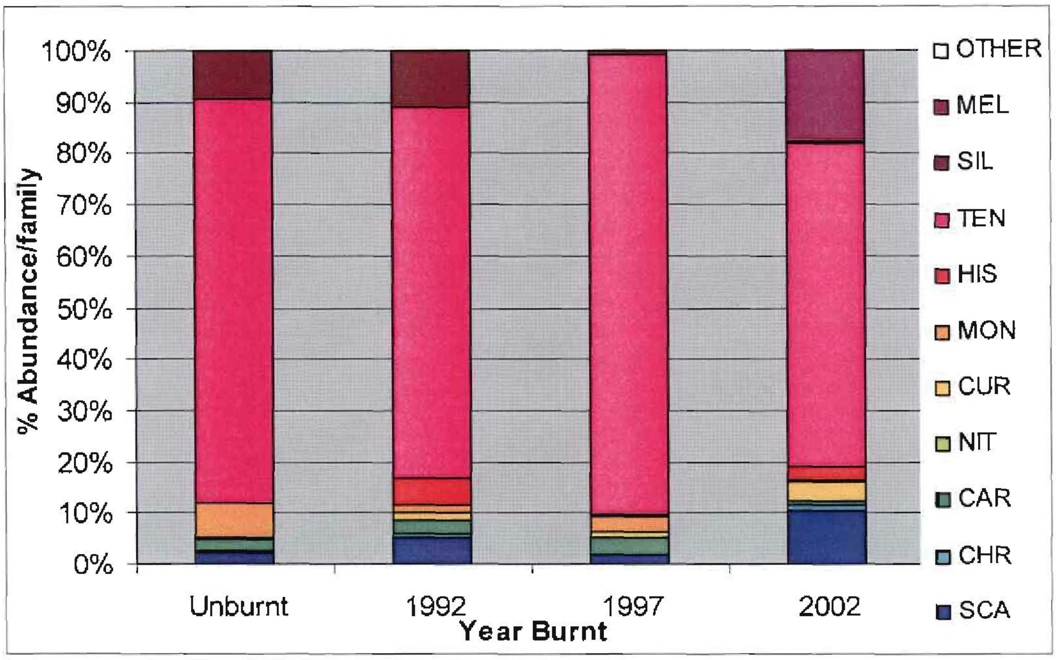


A

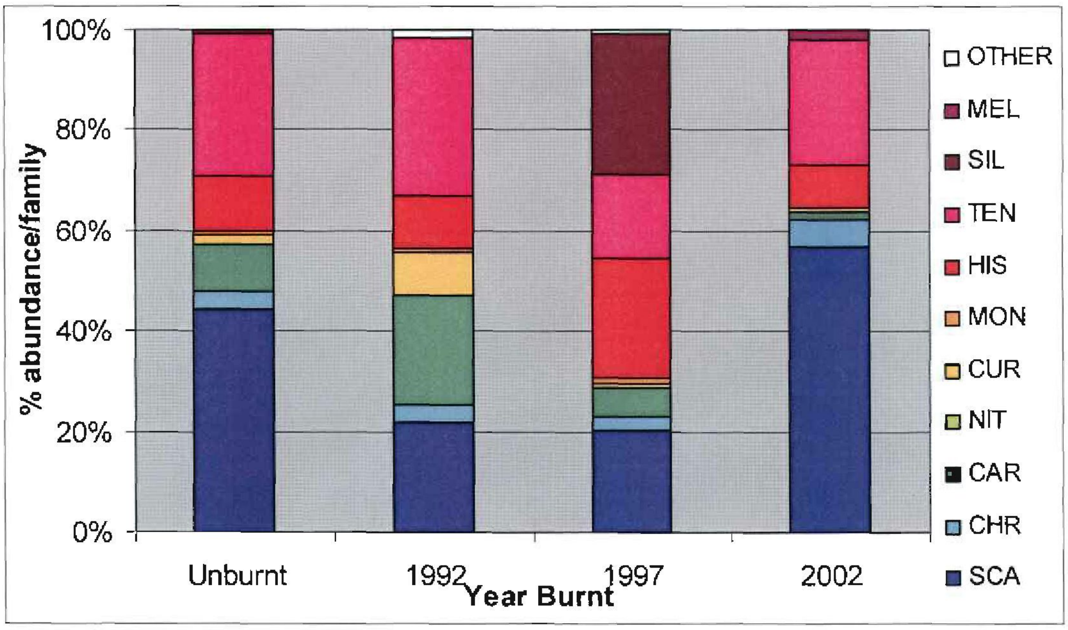


B

Figure 3.11. Histogram representing the number of species per beetle family present in the open grassland areas of each of the burn treatments (A: February and B: April)



A



B

Figure 3.12. Histogram representing the abundance per beetle family present in the open grassland areas of each of the burn treatments (A: February and B: April).

3.2 Habitat characterization at the various burn treatments

In order to attempt associating the changes in ant and beetle assemblages as being in response to changes in their habitats possibly brought on by fire treatments, it is necessary to first describe and define the habitats from which the organisms were sampled. For this reason, vegetation and soil analyses were conducted, the findings of which will be discussed in the sections to follow.

3.2.1 Vegetation

Rélevés of each of the burn treatment replicates were conducted making use of the Braun Blanquett method as described in the Materials and Methods. These rélevés were conducted within the perimeters of the sampling grids to determine the vegetation composition and structure and were selected in what appeared to be more grassland type areas. The species and their relative abundances for each burn treatment are reflected in Table 3.15. The absolute abundances can be referenced in Appendix A. Most of the species shown were present in most of the burn treatments and their replicates, but when considering the particularly high relative abundance values in some of the cases, it seems that grass and bare patches were more dominant in the 1997 burn treatment, shrubs more dominant in the unburnt replicates, trees in 1992 and forbes in 2002. This is, however, a very superficial look at vegetation structure in a given burn treatment, and it is necessary to investigate this in more detail. The first consideration in this regard was to apply Anosim and Simper procedures to the vegetation data to determine the greatest species contributions to vegetation composition and the greatest plant structural group contributions.

Table 3.15. Percentage relative abundance of each of the vegetation species occurring within each of the burn treatments.

Group	Abbreviation	Full name	Unburnt	1992	1997	2002
	BP	Bare patches	5.23	1.21	7.13	5.05
GRASSES	Ant pub	*Anthephora pubescens*	0.09	0	0	0.17
	Ari jun	*Aristida junciformes*	2.35	2.05	4.32	0
	Ari sti	*Aristida stipitata*	0	0.04	0.08	0
	Era pal	*Eragrostis pallens*	0.26	0.12	0.25	0.17
	Mel rep	*Melinis repens*	0.17	0.04	0	0.17
	Sch kal	*Schmidtia kalahariensis*	0.26	0.04	0.25	0.17
	Sch pap	*Schmidtia pappophoroides*	6.67	30.22	62.95	42.12
	Set sph	*Setaria sphacelata*	0.09	0.04	0.08	0
	Sti uni	*Stipagrostis uniplumis*	0.26	0.12	0.25	0.17
	Ura pan	*Urachloa panicoides*	0.17	0	0	0
SHRUBS	Aca eri	*Acacia erioloba*	0	0	0	0
	Aca mel	*Acacia mellifera*	0.09	30.22	2.31	0.17
	Asp spp.1	*Asparagus spp.1*	2.35	0.12	0.08	0
	Asp spp.2	*Asparagus spp.2*	0	0.04	0	0
	Asp tra	*Asparagus spp. 3*	0	0	0.17	0
	Bos alb	*Boscia albitrunca*	0	0	0	4.21
	Eie ret	*Elephantorrhiza elphantina*	0.09	0.04	0	0
	Eie rig	*Eriocephalus pubescens*	0	0.04	0.17	0.17
	Gre fla	*Grewia flava*	45.79	3.08	6.29	42.12
	Gym bux	*Gymnosporia buxifolia*	21.98	0.04	4.28	0.17
	Rhus spp	*Rhus spp*	0	0	0	0.17
	Rhus ten	*Rhus tenuinervis*	0	0	2.1	0

TREES	Ziz muc	*Zizyphus musculata*	0	0	0	0.17
	Aca eri	*Acacia erioloba*	2.27	12.11	0.08	0.17
	Aca rob	*Acacia robusta*	0.09	0.04	0	0
	Aca sp1	*Acacia sp1*	4.8	0	2.22	0
	Aca sp2	*Acacia sp2*	0	0.04	0.17	0.17
	Aca tor	*Acacia tortillus*	4.45	0.04	2.22	0
	Bos alb	*Boscia albitrunca*	2.27	20.19	4.32	0.17
FORBES	Tri ter	*Tribulus terrestris*	0.26	0.12	0.25	4.3

The percentage dissimilarities of each burn treatments' specific species and their percentage contributions were determined using the Anosim and Simper procedures, the results of which are summarized in Table 3.16 for the species contributions, and Table 3.17 for the plant structural group contributions.

Table 3.16. Anosim and Simper results indicating the greatest species contributions of vegetation composition within each of the burn treatments. (Values listed in bold in each column correspond with the first site, values in normal print correspond with the second site.

Anosim Global R Statistic: 0.744						
Simper % dissimilarities between groups						
	Unburnt	**1992**	**1997**	**2002**		
Unburnt	-	63.05	50.97	53.48		
1992	63.05	-	42.07	48.78		
1997	50.97	42.07	-	44.4		
2002	53.48	48.78	44.4	-		
% Species Contributions	**Unburnt/1992**	**Unburnt/1997**	**Unburnt/2002**	**1992/ 1997**	**1992/ 2002**	**1997/ 2002**
Aca eri	10.38	-	-	**19.7**	**15.58**	-
Aca mel	22.47	-	-	**28.72**	**20.26**	-
Ari jun	-	-	-	-	**5.97**	-
Bos alb	13.88	-	-	**18.89**	**18.13**	**9.46**
Gym bux	**7.84**	**13.78**	**10.48**	-	-	**9.45**

Gre fla	**9.25**	**13.88**	6.27	-	16.81	22.21
Sch pap	13.87	20.75	18.55	-	-	-
Tri ter	-	-	10.92	-	9.89	12.97

Table 3.17. Anosim and Simper results indicating the greatest Plant Structural group contributions of vegetation composition within each of the burn treatments. (Values listed in bold in each column correspond with the first site, values in normal print correspond with the second site.)

Anosim Global R Statistic: 1.0						
Simper % dissimilarities between groups						
	Unburnt	**1992**	**1997**	**2002**		
Unburnt	**-**	**16.87**	**17.67**	**24.66**		
1992	**16.87**	**-**	**17.97**	**27.57**		
1997	**17.67**	**17.97**	**-**	**22.96**		
2002	**24.66**	**27.57**	**22.96**	**-**		
% Group Contributions	**Unburnt/1992**	**Unburnt/1997**	**Unburnt/2002**	**1992/ 1997**	**1992/ 2002**	**1997/ 2002**
Grass	4.23	45.24	24.76	17.43	-	-
Shrubs	-	**36.37**	-	**18.29**	-	-
Trees	-	**10.59**	**41.99**	**30.01**	**50.46**	**36.66**
Forbes	-	-	24.72	-	24.77	27.4
Bare patches	-	-	-	31.53	15.06	-

Figure 3.13 shows an MDS on the basis of the plant species compositions at the various burn treatments, indicating clear groupings between the burn treatments. An additional MDS, Figure 3.14, was constructed considering the vegetation on the basis of plant structural types, namely grasses, shrubs, trees, and forbes, as well as bare patches. This was done in order to determine whether the burn treatments may be differentiated on the basis of vegetation structure. Figure 3.14 illustrates very clear clustering of the replicates within their representative burn treatments, especially the 2002 and unburnt treatments. To illustrate which burn treatment is dominated by which plant structural type, a bar graph was constructed, Figure 3.15 representing the percentage cover per vegetation type for each of the burn treatment replicates, with the variance being very little.

Figure 3.13. MDS (Multi-Dimensional Scaling) of the plant species composition within each of the burn treatment replicates.

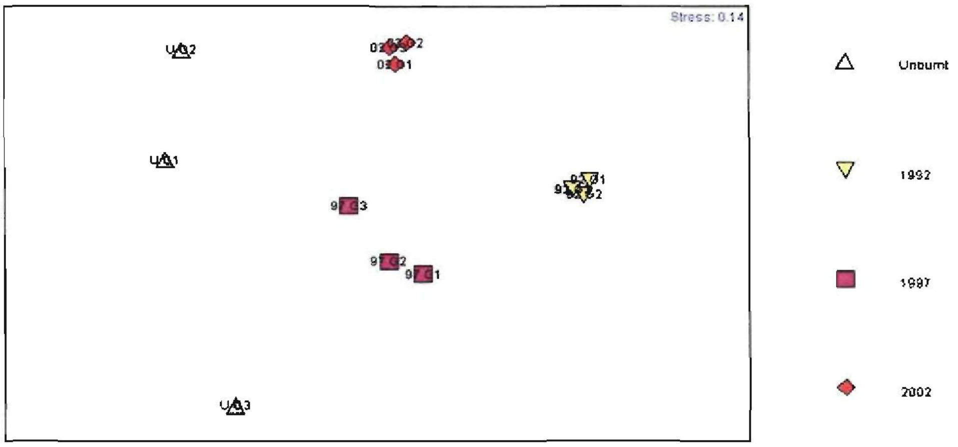


Figure 3.14. MDS (Multi-Dimensional Scaling) of the plant structural groups within each of the burn treatment replicates.

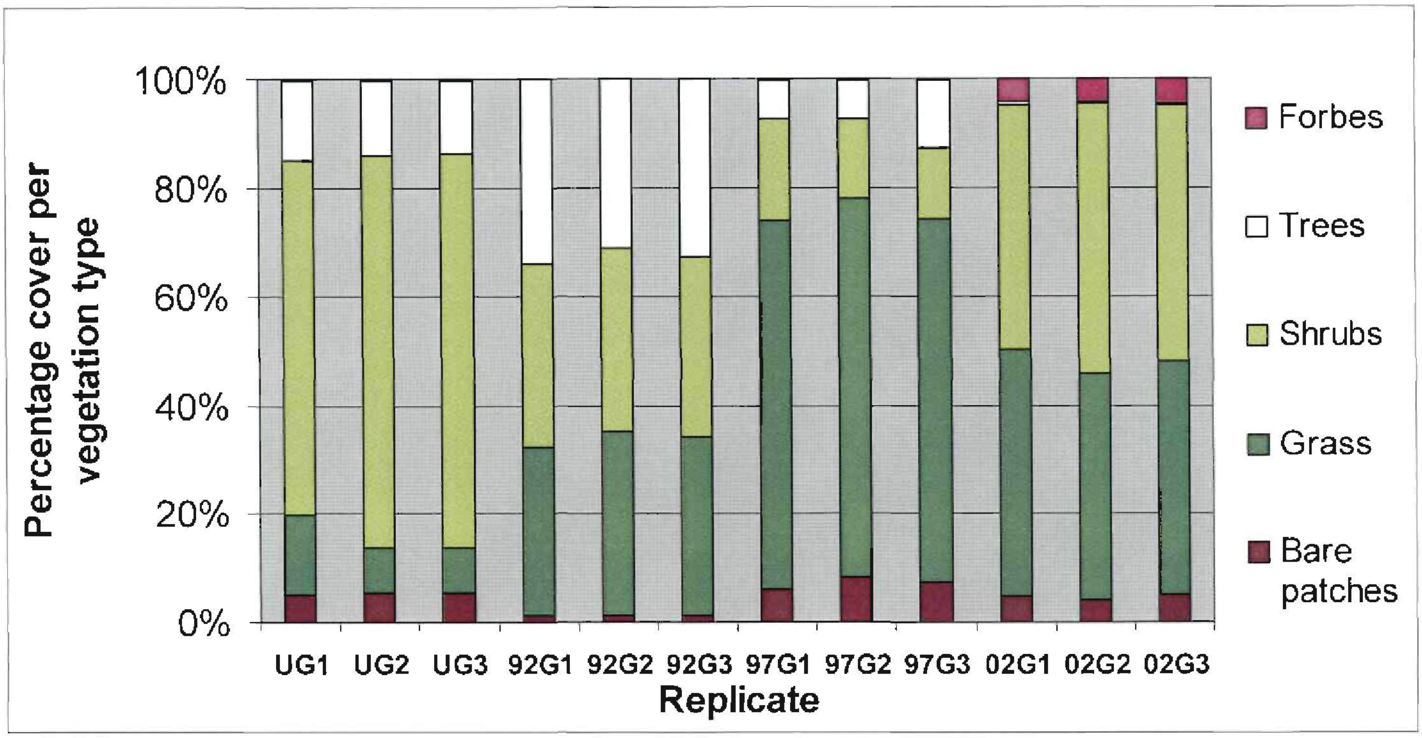


Figure 3.15. Histogram representing the percentage cover per plant structural group in each burn treatment replicate.

Analyses of variance (ANOVA) were carried out to compare the densities of each of the plant structural groups at each replicate trap site at each burn treatment, and Tukey HSD tests were done to determine statistically significant differences between the mean density of the vegetation structural types and bare patches (Tables 3.18-3.22). Box and whisker graphs were drawn to illustrate these differences in Figures 3.16-3.20.

Table 3.18. Tukey HSD results indicating the significant marked difference for bare patch density at each burn treatment. The probability values are given in red. F-value =52.5782

	Tukey HSD test; Variable= Bare Patches. Marked differences are significant at P<0.05000			
Year Burned	**(1) M= 5.2333**	**(2) M= 1.2067**	**(3) M=7.1733**	**(4) M=4.6833**
Unburnt (1)		0.000348	0.016756	0.680478
1992 (2)	0.000348		0.000232	0.000612
1997 (3)	0.016756	0.000232		0.004061
2002 (4)	0.680478	0.000612	0.004061	

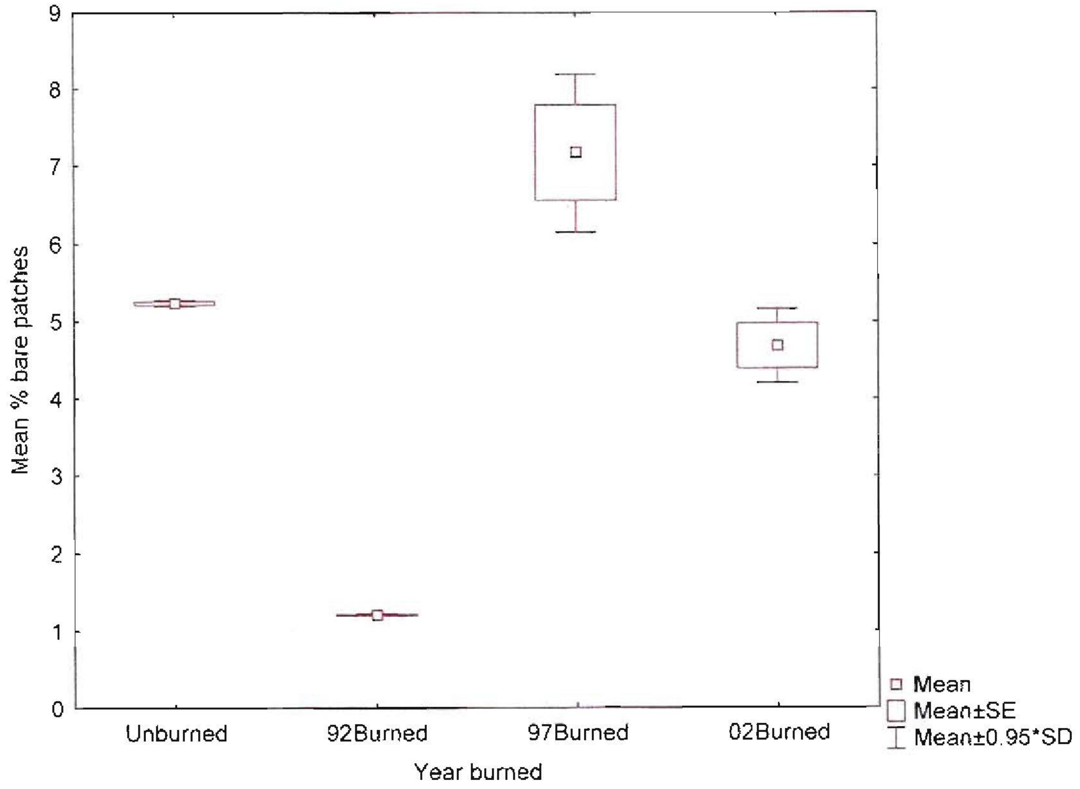


Figure 3.16. Box and whisker plot representing the mean % density of bare patches occurring at the replicate sites in each of the burn treatments.

Table 3.19. Tukey HSD results indicating the significant difference for grass density at each burn treatment. The probability values are given in red. F-value= 347.2097.

	Tukey HSD test; Variable= Grass Density. Marked differences are significant at p<0.05000			
Year Burned	**(1) M= 10.343**	**(2) M= 32.677**	**(3) M=68.253**	**(4) M=43.337**
Unburnt (1)		0.000232	0.000231	0.000231
1992 (2)	0.000232		0.000231	0.001891
1997 (3)	0.000231	0.000231		0.000231
2002 (4)	0.000231	0.001891	0.000231	

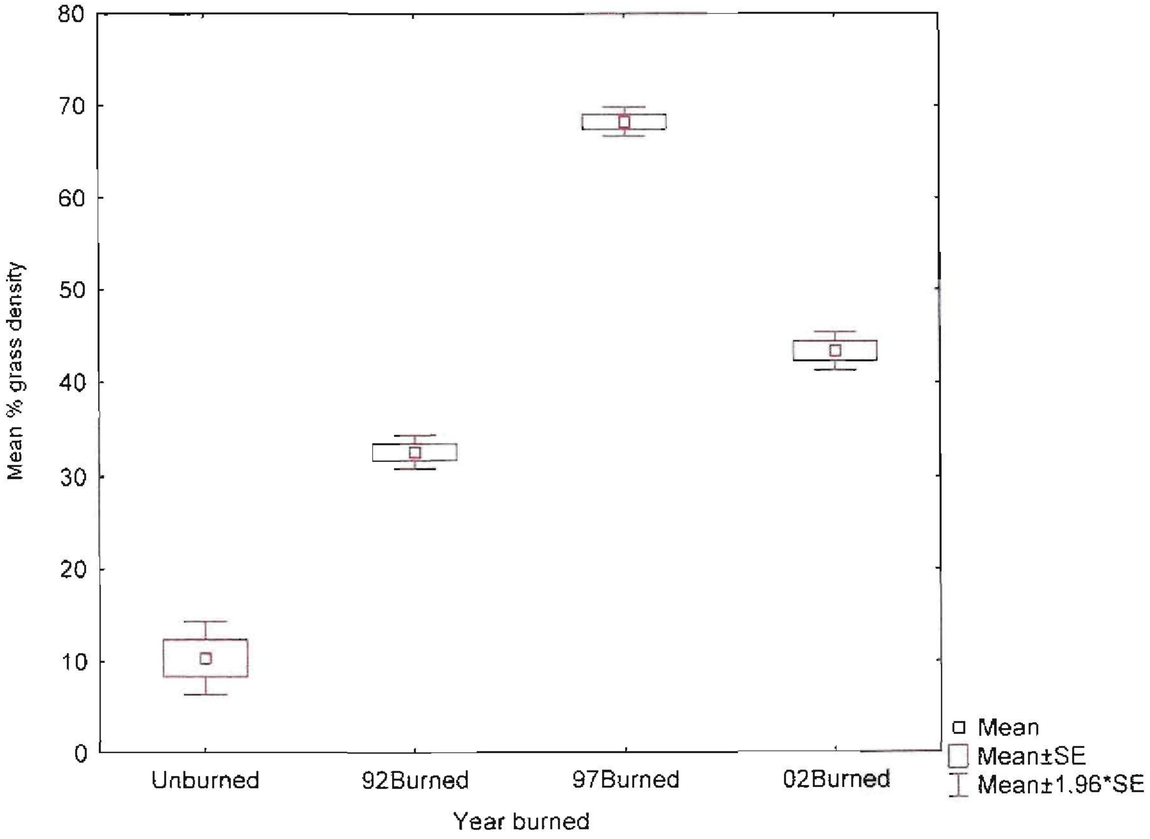


Figure 3.17. Box and whisker plot representing the mean % density of grasses occurring at replicate sites in each of the burn treatments.

Table 3.20. Tukey HSD results indicating the significant marked difference for shrub density at each burn treatment. The probability values are given in red. F-value= 209.2077.

	Tukey HSD test; Variable= Shrub Density. Marked differences are significant at p<0.05000			
Year Burned	**(1) M= 70.323**	**(2) M= 33.587**	**(3) M=15.383**	**(4) M=47.373**
Unburnt (1)		0.000231	0.000231	0.000246
1992 (2)	0.000231		0.000384	0.001483
1997 (3)	0.000231	0.000384		0.000231
2002 (4)	0.000246	0.001483	0.000231	

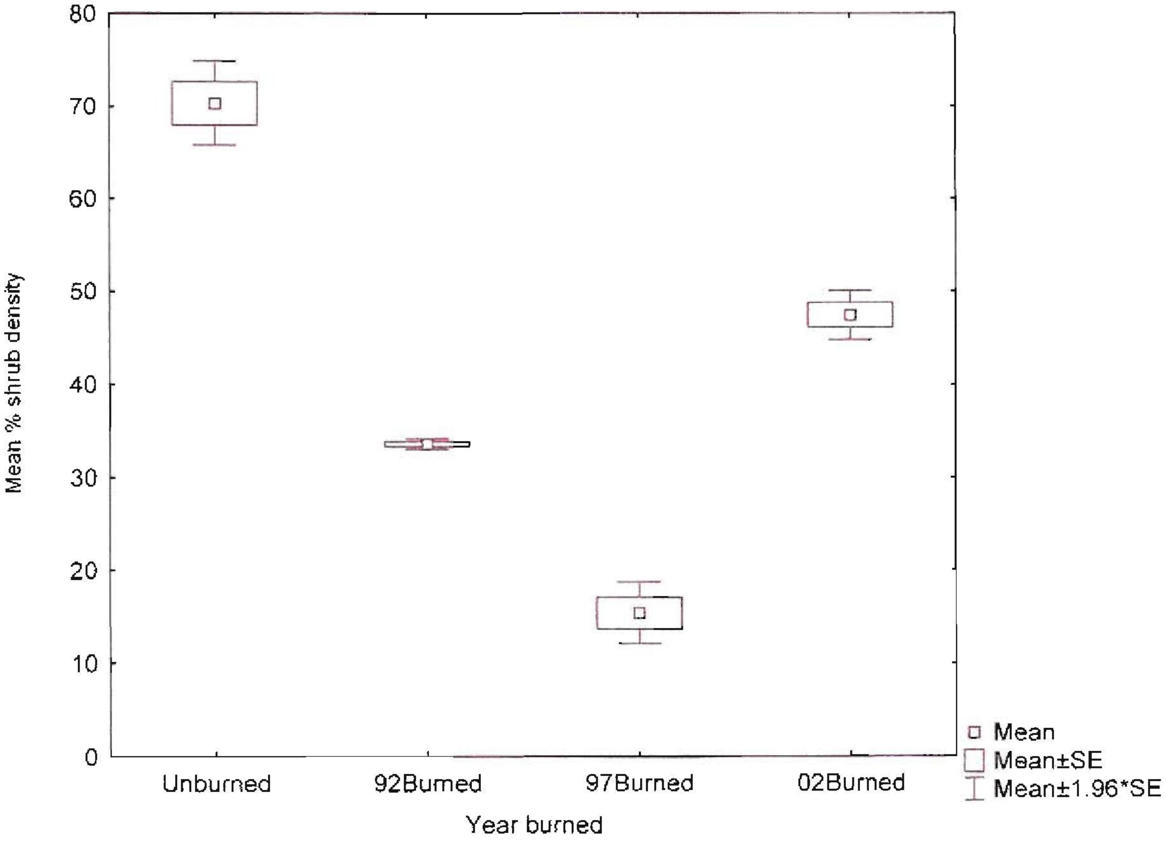


Figure 3.18. Box and whisker plot representing the mean % density of shrubs occurring at replicate sites in each of the burn treatments.

Table 3.21. Tukey HSD results indicating the degree of marked difference significance for tree density at each burn treatment. The probability values are given in red. F-value= 8408.5350.

	Tukey HSD test; Variable= Tree Density. Marked differences are significant at p<0.05000			
Year Burned	**(1) M= 13.863**	**(2) M= 32.410**	**(3) M=8.9367**	**(4) M=0.38667**
Unburnt (1)		0.000231	0.034051	0.000261
1992 (2)	0.000231		0.000231	0.000231
1997 (3)	0.034051	0.000231		0.001553
2002 (4)	0.000261	0.000231	0.001553	

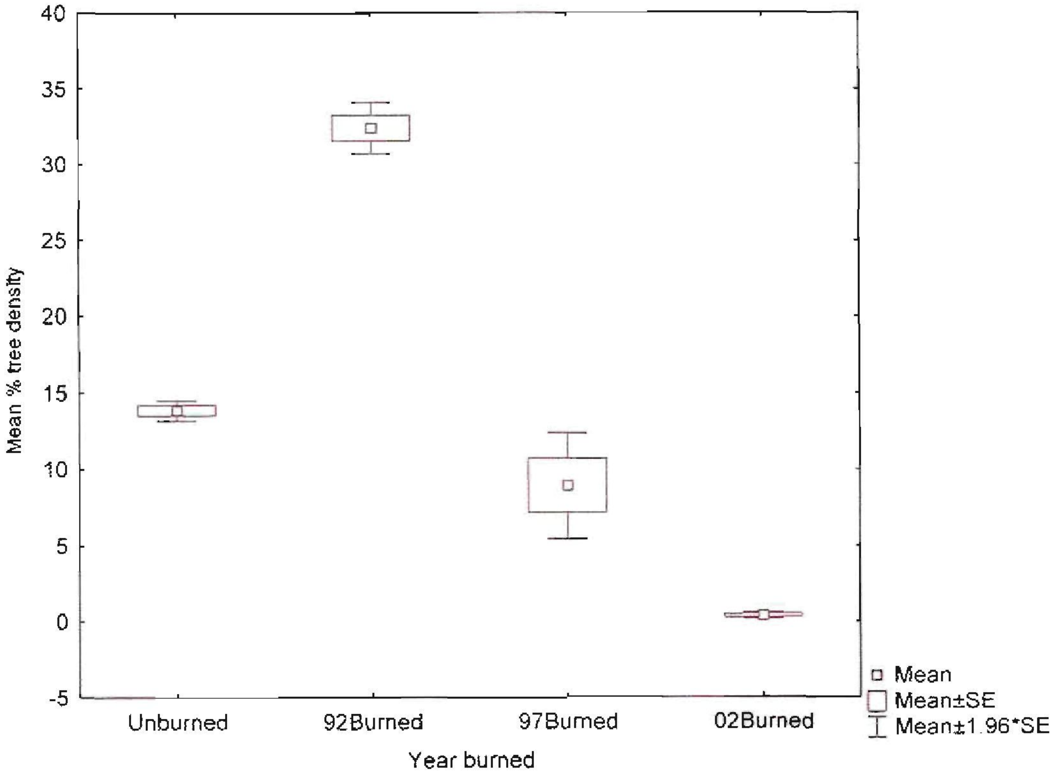


Figure 3.19. Box and whisker plot representing the mean % density of trees occurring at replicate sites in each of the burn treatments.

Table 3.22. Tukey HSD results indicating the significant marked difference for forbe density at each burn treament. The probability values are given in red. F-value= 182.8119.

	Tukey HSD test; Variable= Forbes Density. Marked differences are significant at p<0.05000			
Year Burned	**(1) M= 13.863**	**(2) M= 32.410**	**(3) M=8.9367**	**(4) M=0.38667**
Unburnt (1)		0.000231	0.034051	0.000261
1992 (2)	0.000231		0.000231	0.000231
1997 (3)	0.034051	0.000231		0.001553
2002 (4)	0.000261	0.000231	0.001553	

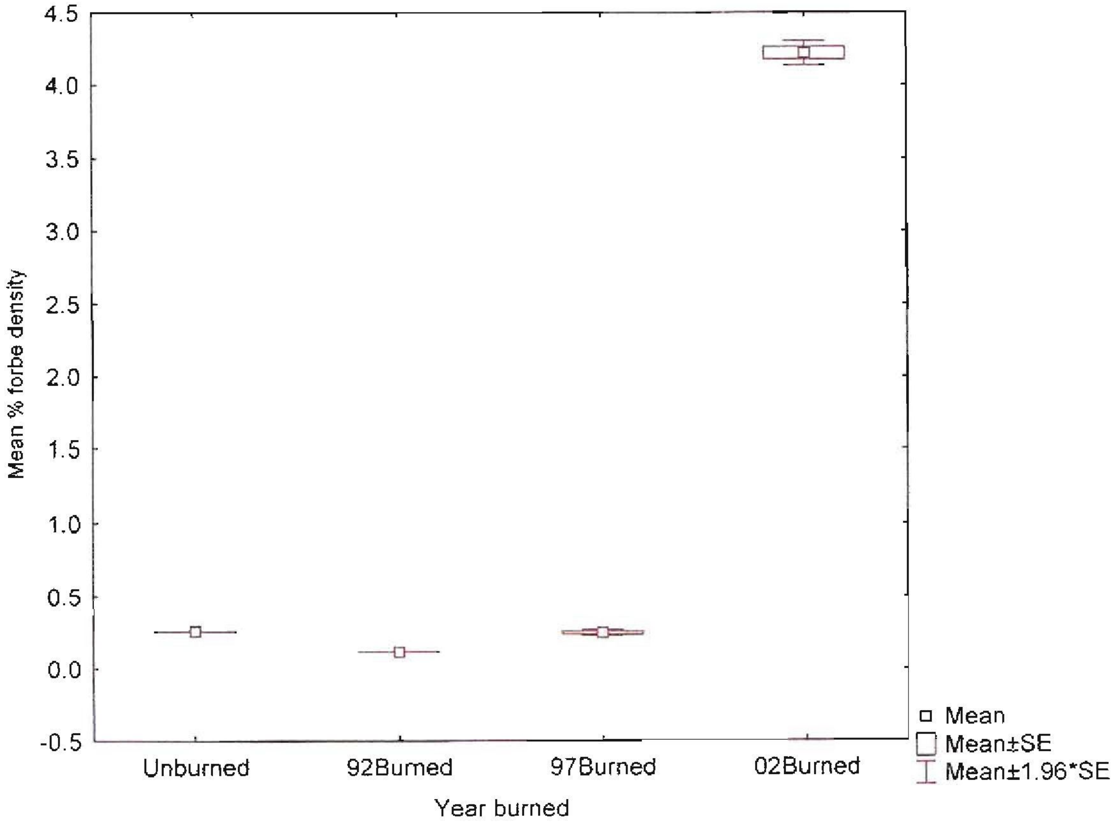


Figure 3.20. Box and whisker plot representing the mean % density of forbes occurring at replicate sites in each of the burn treatments.

The results shown in Figures 3.16-3.20 and the associated Tukey test Tables provide evidence for the differences in plant group structures between the four burn treatments around the three grid replicates.

The F-value for the bare patches is 52.5782, and the comparisons drawn between each of the sites are represented in Table 3.18, probabilities in red being lower than 0.05, and thus baring a significant statistical difference, whilst values in black indicate that no significant difference exists. The values in this Table reflect the pattern illustrated in Figure 3.16. With regards to the density of bare patches, the most notable difference is between burn treatments 1992 and 1997. Figure 3.16 illustrates the mean density of the bare patches at each of the burn treatments, unburnt and 2002 showing the same density, treatment 1997 the highest density, and 1992 showing the lowest density.

Table 3.19 and Figure 3.17 reflect the pattern and values for the density of grass within each of the burn treatments. The F-value is 347.2097. Grass density is greatest at burn treatment 1997, and lowest at the unburned treatment, and all Tukey test values differ significantly in terms of the grass densities for each of the burn treatments.

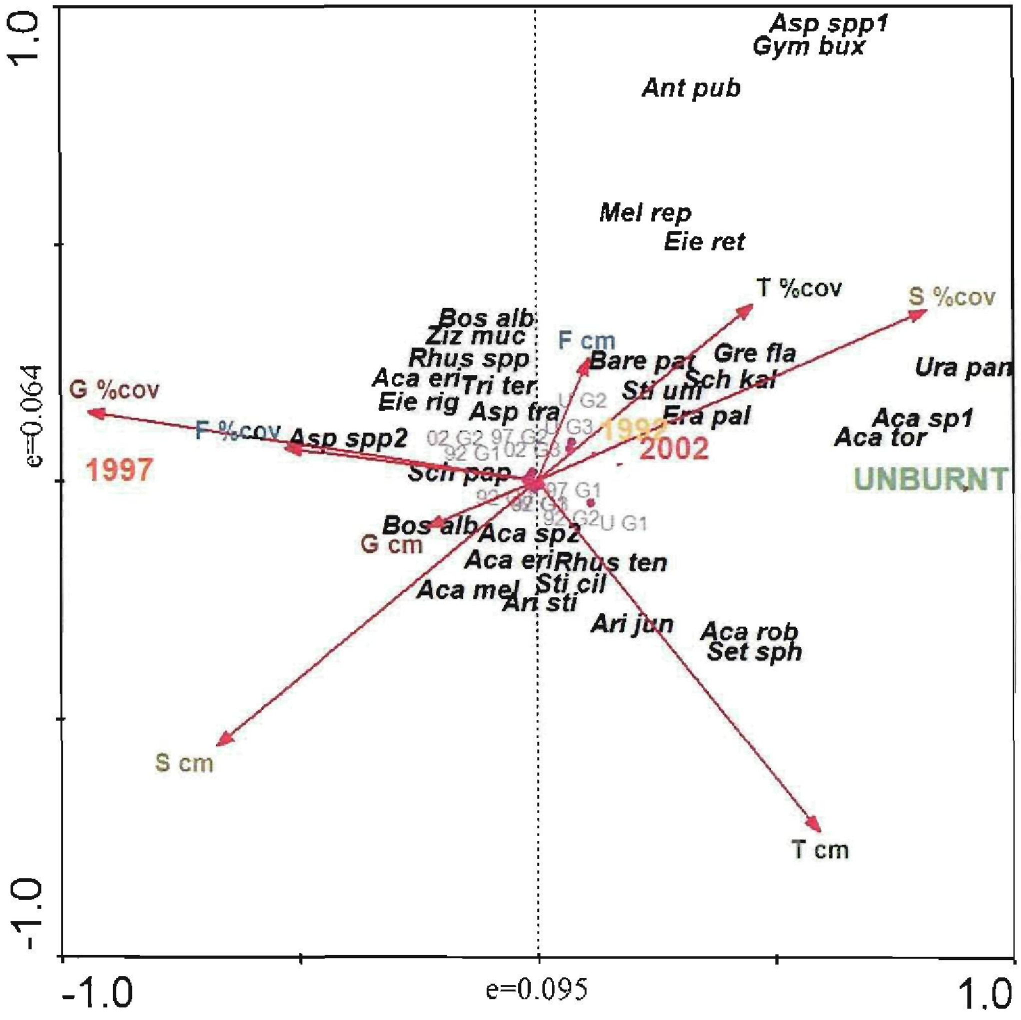
The F-value of the mean shrub density at the burn treatments is 209.2077, and is represented in Table 3.20 and Figure 3.18. The trend is completely opposite to that of the grass density seen in the previous Figure and Table. Shrub density appears to be greatest at the unburnt treatment, declining through 1992 and more so to 1997, and then increasing again at 2002. The Tukey test values indicate significant differences between all the means.

The mean tree density, shown in Figure 3.19, paints a different picture as compared to that of the grasses and shrubs. Here the greatest density occurs at burn treatment 1992, preceded by an intermediate density at the unburnt treatment, and followed by a lower density at the 1997 burn treatment, and an even lower density at burn treatment 2002. The Tukey results, reflected in Table 3.21, are all statistically significant for between site differences, with an F-value of 8408.5350.

Lastly, Table 3.22 and Figure 3.20 illustrate the density of the forbes found at each of the replicates within the burn treatments, their abundance being highly evident at burn treatment 2002, but being comparatively lower at the remaining burn treatments, with no notable differences between the three. The F-value is 182.8119. The Tukey test results emphasise this very clearly, with between site comparisons in which burn treatment

2002 are compared with another burn treatment, showing highly statistically significant differences. Comparisons between burn treatments unburnt, 1992 and 1997 are less significantly different from each other, with the black value of 0.034051 at unburnt and 1997 being statistically insignificant. The high forbe percentage in 2002 could be a result of the 2002 fires, providing a gap for Tribulus terrestris to establish and increase their density significantly.

Physiognomy possibly reflects general vegetation structure in a highly effective way because it considers the height at which each plant structure occurs, and the estimated percentage cover within the rélevéd area. The Canonical Correspondence Analysis, CCA, illustrated in Figure 3.21, is a final representation of the vegetation species and the sites with which they associate the most, as well as with which physiognomy aspects they are most associated. The results reflect that the vegetation structure at each of the burn treatments show differences believed to be brought on by the fire treatments, differences which may cause changes in ant and beetle community assemblages.



Key

Abbreviation	Meaning
G cm	Grass height in cm
S cm	Shrub height in cm
T cm	Tree height in cm
F cm	Forbe height in cm
G % cov	Percentage grass cover
S % cov	Percentage shrub cover
T % cov	Percentage tree cover
F % cov	Percentage forbe cover

Figure 3.21. CCA of the plant species and their main associations with each of the burn treatments.

3.2.2 Soil

Soil analyses were performed in order to determine if soil could have been a factor in the vegetation differences between the burn treatments. Anosim procedures were run on the soil data, the global R statistic being of no statistically significant value. The between site dissimilarity percentage values depicted in Table 3.23 clearly indicate that no significant differences exist between the sites in terms of their soil characteristics, the largest difference being a mere 7.4 %.

Table 3.23. Anosim results indicating the global R-statistic and Simper results indicating the percentage dissimilarity between the burn treatments in terms of soil composition.

Anosim Global R Statistic: 0.416

Simper % dissimilarities between groups

	Unburnt	1992	1997	2002
Unburnt	-	7.74	6.79	6.4
1992	7.4	-	6.35	8.22
1997	6.79	6.35	-	6.89
2002	6.4	8.22	6.89	-

A CCA was done on the soil data, as given in Figure 3.22 to illustrate the close clustering of the soil characteristics in context of the burn treatments, with the eigen values on the first and second axes being very small. None of the soil characteristics satisfactorily segregate towards a specific site. This finding is illustrated in Figure 3.23, a Principle Components Analysis (PCA), showing each burn treatments' replicates grouped and subsequently each soil characteristic grafted over the site perimeters, in order to illustrate whether the burn treatment replicates segregate sufficiently in terms of the analysed soil characteristics. Too much overlap of the four burn treatment groups occurs, indicating that the burn treatments cannot be separated based on soil characteristics.

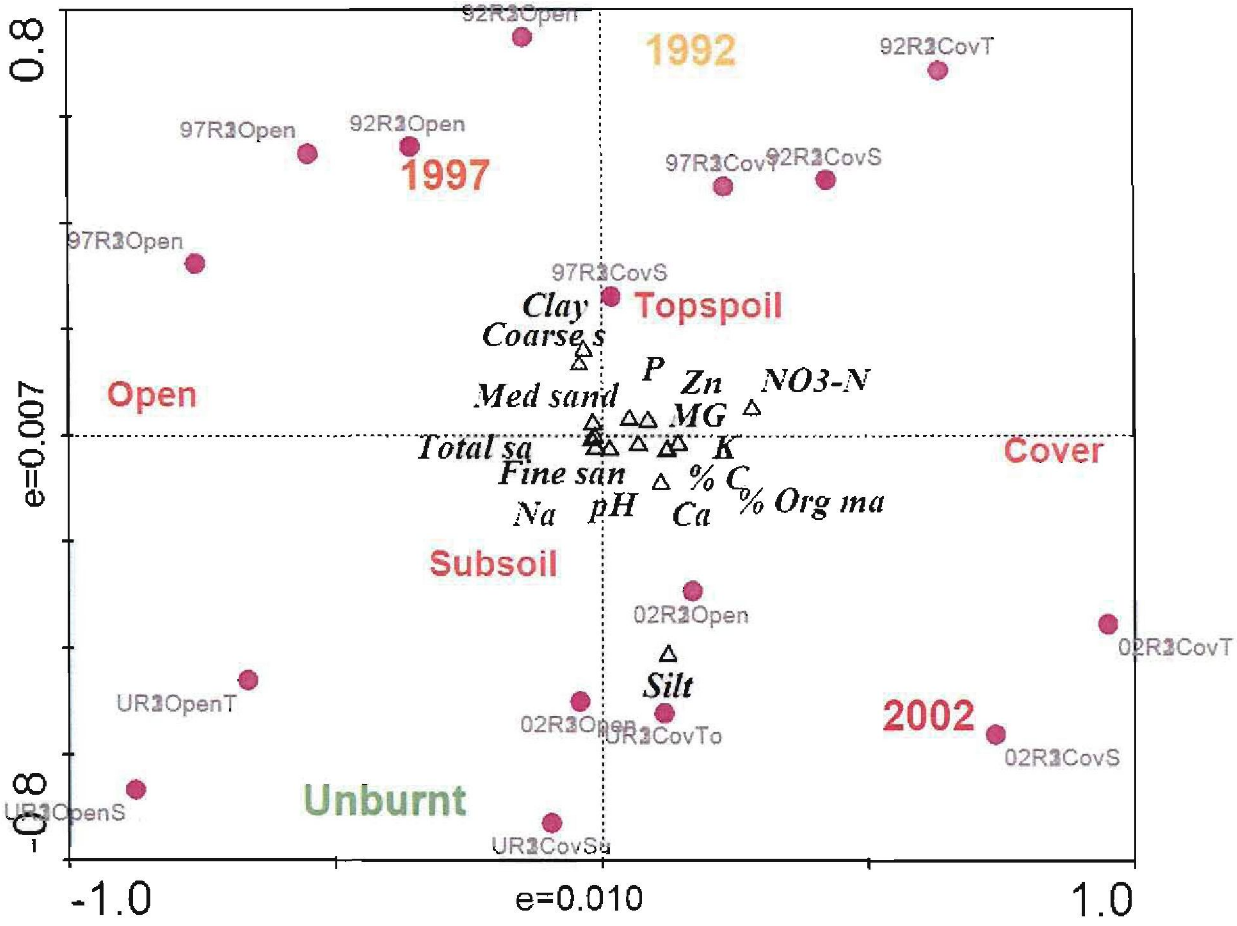


Figure 3.22. CCA of the soil characteristics and their main associations with each of the burn treatments.

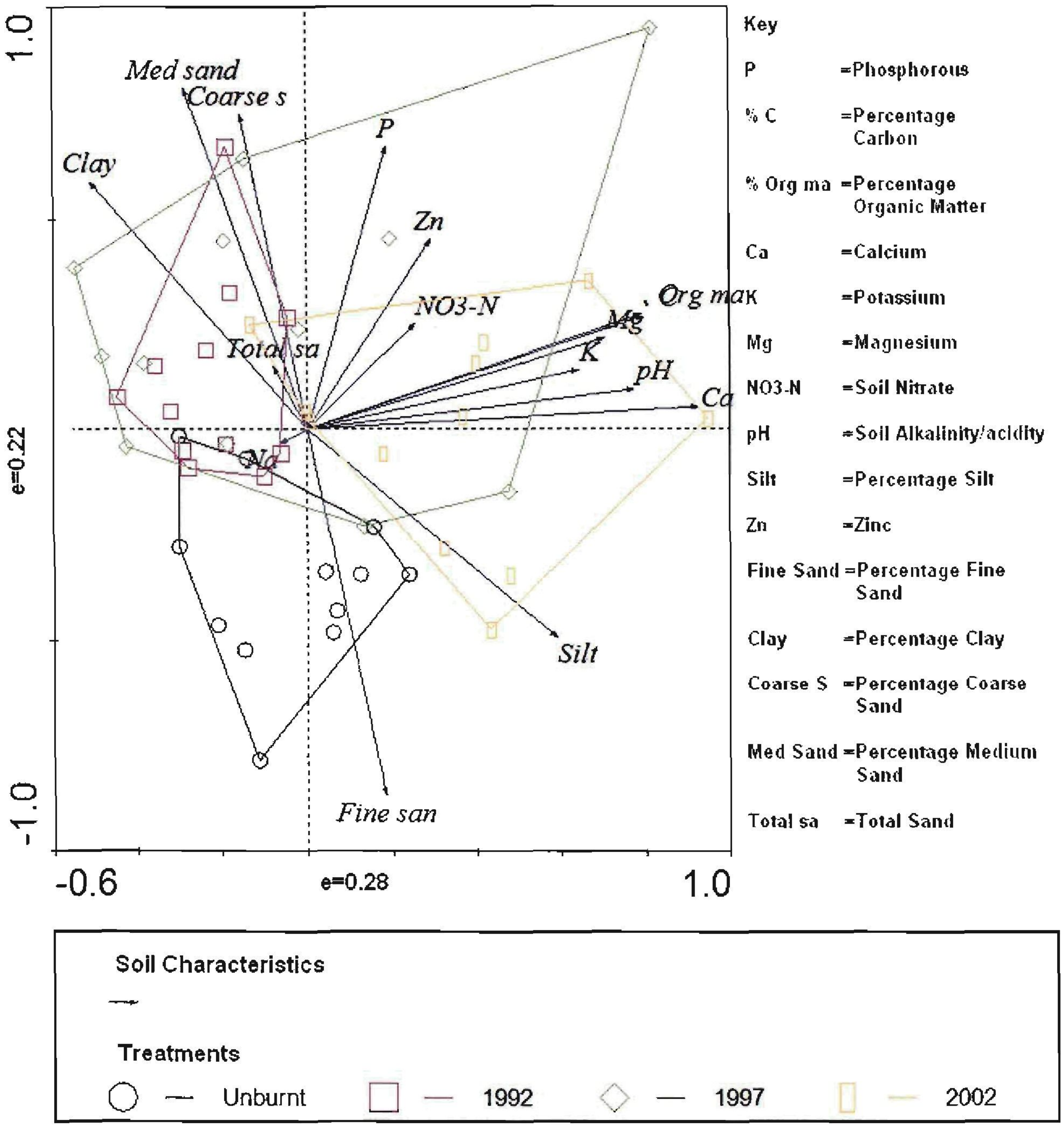


Figure 3.23. PCA of the soil characteristics and their main associations with each of the burn treatments.

3.3 Ordinations of ants, beetles and vegetation

As formerly stated, it would seem appropriate to represent all the ant and beetle data collected in context of the vegetation data. These representations are provided in CCA's so that the invertebrate data may be viewed superimposed with the vegetation data for both the ants and beetles.

The CCA's provide a summarized illustration of the results discussed in former sections, but they do so in context of the vegetation cover, allowing one to determine the degree of association between the environmental parameter in question, and the proposed invertebrate indicator.

The placement of a given species within a particular spatial framework does not mean it is limited to that association, but rather that it is mostly associated with that situated closest to it graphically. Each of the species thus observed do occur elsewhere, but having run the CCA procedures, they were found to be statistically more associated with one given item as opposed to another, the degree of which is reflected by the eigen value.

3.3.1 Soil and vegetation associations

CCA's of the soil data and the vegetation were constructed, each time making use of the specific region of the soil sample; open-top, open-sub, cover-top, or cover-sub. Figure 3.24 represents the results of the soil data and vegetation data combined using the open-sub soil data. The remaining soil sample groups showed almost identical results and are thus not included. Once again, it is very apparent that the vegetation shows a greater inclination towards segregating in the direction of specific burn treatments, whilst the soil characteristics, despite certain types of vegetation being favoured by specific soil characteristic combinations, do not show enough segregation to consider it as a determining factor for the differences in the vegetation compositions at each of the burn treatments.

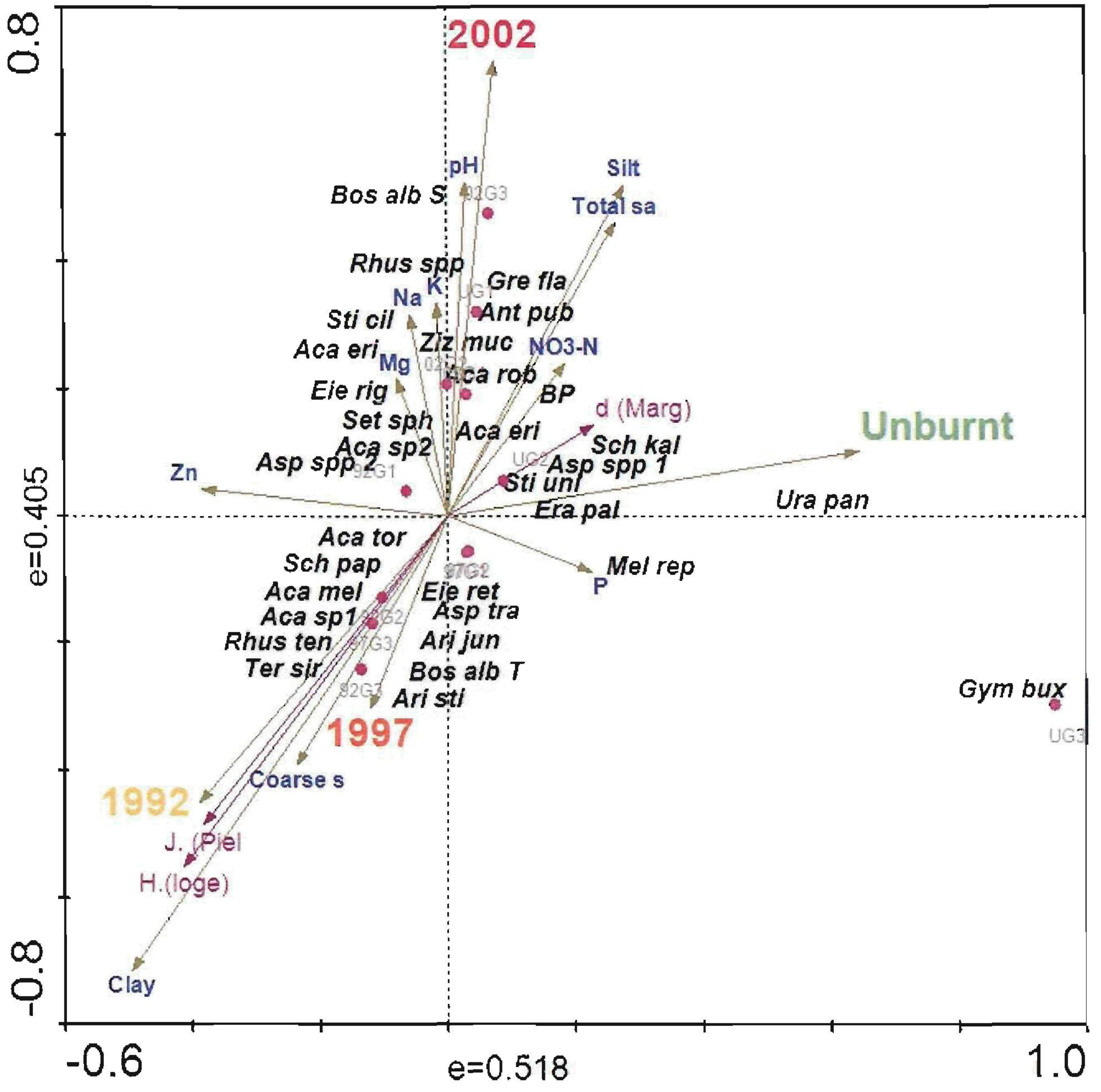


Figure 3.24. CCA of the soil characteristics and the vegetation composition and the manner in which these associate within each of the burn treatments.

3.3.2 Ant and beetle responses to habitat change

In order to link changes in ant and beetle assemblages as being in response to habitat change brought on by fire, it seems essential to represent the ant and beetle assemblage structures in relation to that of the habitat structure as indicated by the vegetation assemblages. This was achieved by constructing CCA's where ant or beetle data were combined with the vegetation data, firstly making use of the total abundance of ants or beetles per species, and secondly, the total abundance of ants or beetles per functional group/ family. Each CCA represented reflects the February sample data on the left, and the April sample data on the right.

3.3.2.1 Ants Response

Figure 3.25 illustrates the vegetation types and the burn treatments with which the various ant species are associated in terms of overall species composition. Despite the addition of ant species into the CCA procedure, the vegetation associations remain reasonably consistent, save a few minor deviations.

Figure 3.26 illustrates the abundance of ants per functional group in relation to the various plant species and the different burn treatments.

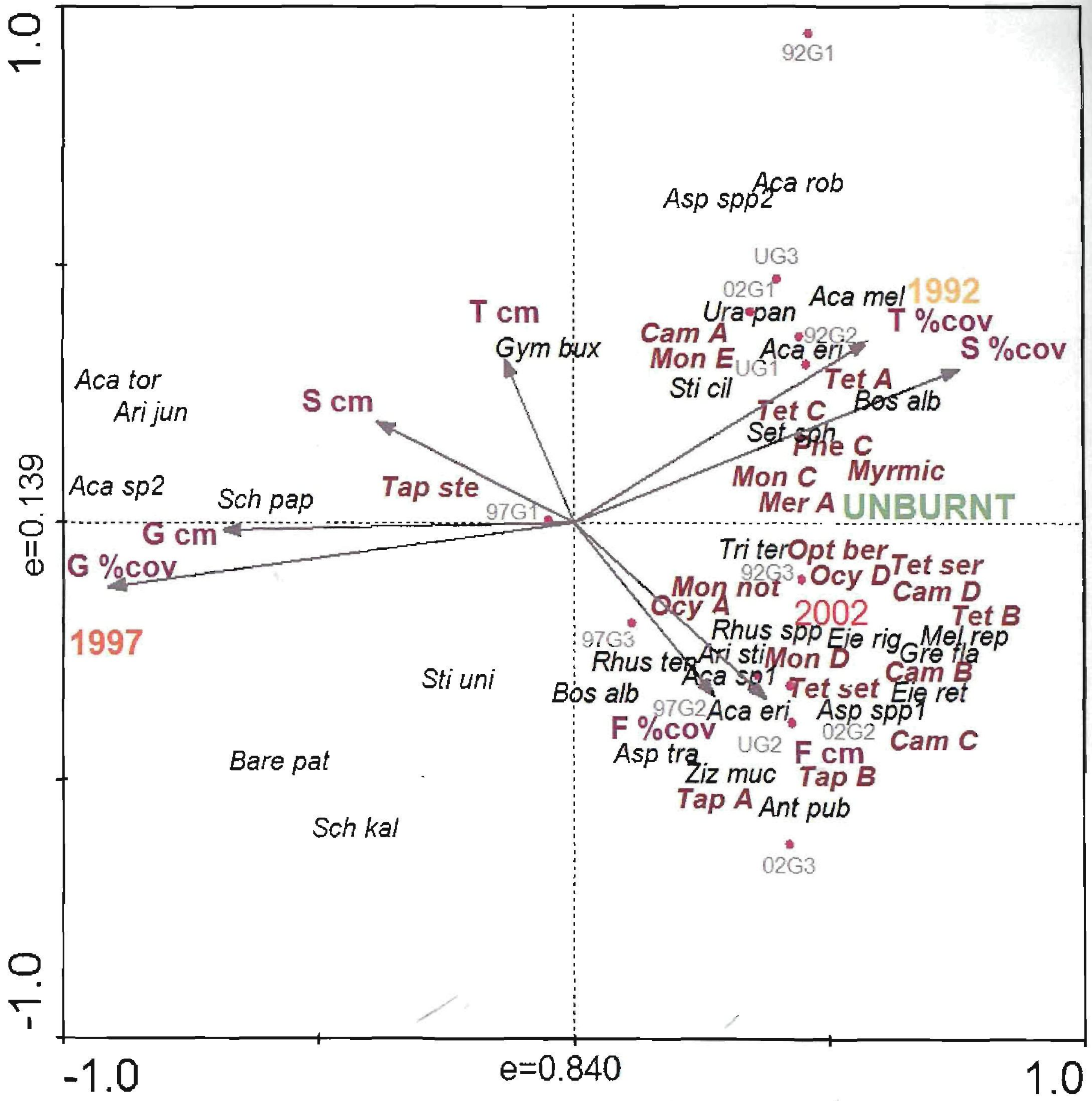
Rain was eliminated as a contributory separating environmental factor in the Molopo Nature Reserve in personal communication with Richard Newberry of the North West National Parks, who stated that rain fall has been consistent from year to year for an extended period of time and does not fall in significantly different volumes over the identified burn treatments. Soil characteristics were also eliminated as a significant determining factor. Trampling is another possible contributing source, but no sufficient evidence that this exists in the replicate sites could be established and although it is a very important factor estimating trampling densities would be merely speculative. Management practice also plays a major role in habitat change, but with the reserve being in existence for the past 24 years, such practice has also been reasonably consistent. The areas which have burned and the times which they burned were documented since the reserve's inception, and thus it does suggest the plausible and possibly exclusive role that fire played in this regions' environmental dynamics.

3.3.2.2 Beetles Response

Section 3.1.2 reflected the results for the beetle data, with the general outcome being that no convincing influence of fire treatments could be identified. In this section, the beetle data is considered one last time in conjunction with the vegetation data in CCA representations. The aim is to determine whether any grouping may still be identified in combination with the patterns exhibited by the vegetation.

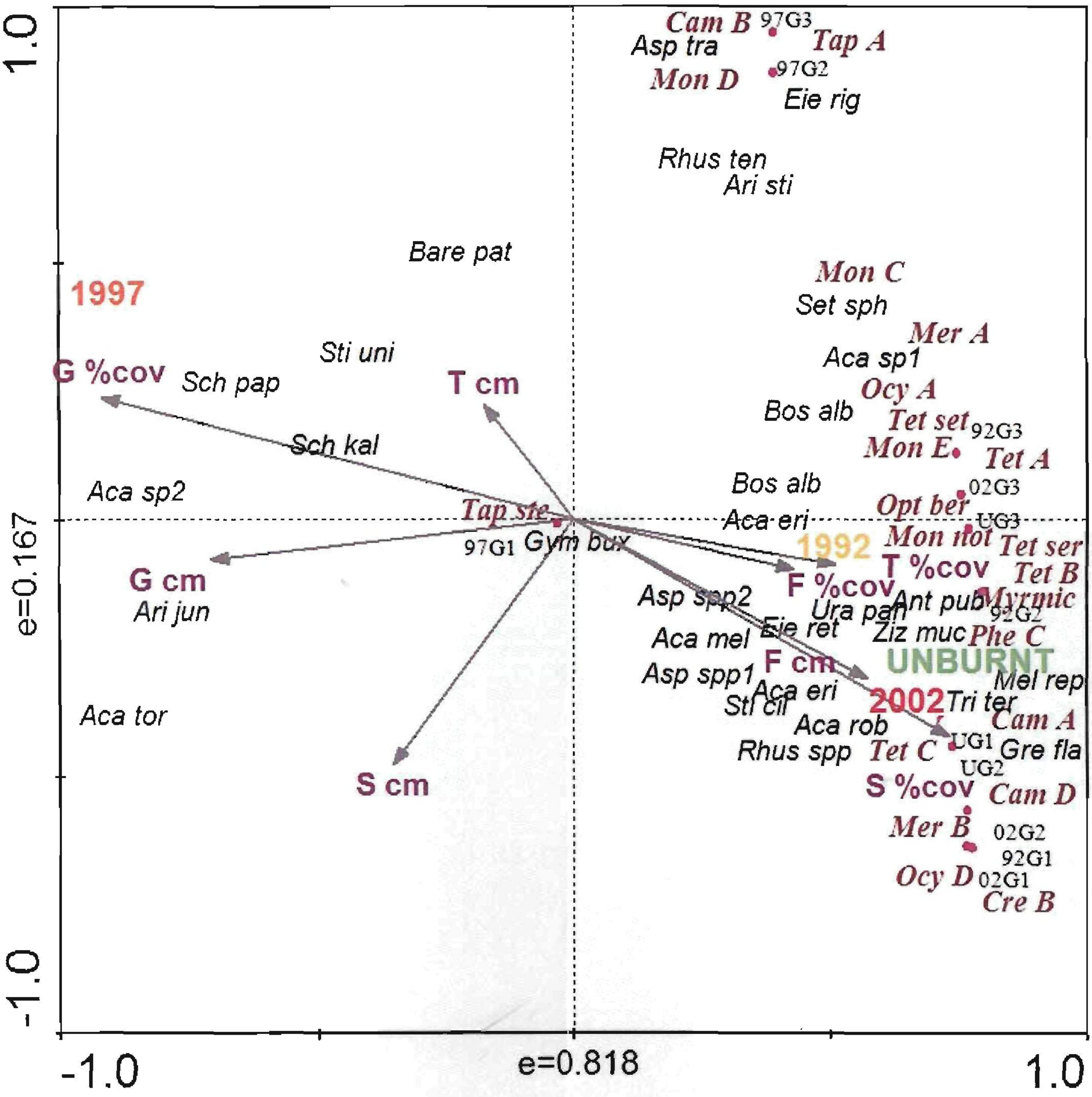
Figure 3.27 represents the beetle species composition CCA in their association with the vegetation in respect to each burn treatment. Abundance of beetle families were used to establish possible groupings with plant species, the results of which are depicted in Figure 3.28.

The groupings indicated by the ants showed similarities for the February and April surveys in the segregation of the 1997 burn treatment, for both the ant species composition and the functional groups. The beetles however don't show any significant groupings.



February

Figure 3.25: CCA of the ant and plant species composition associations along the burn treatment g



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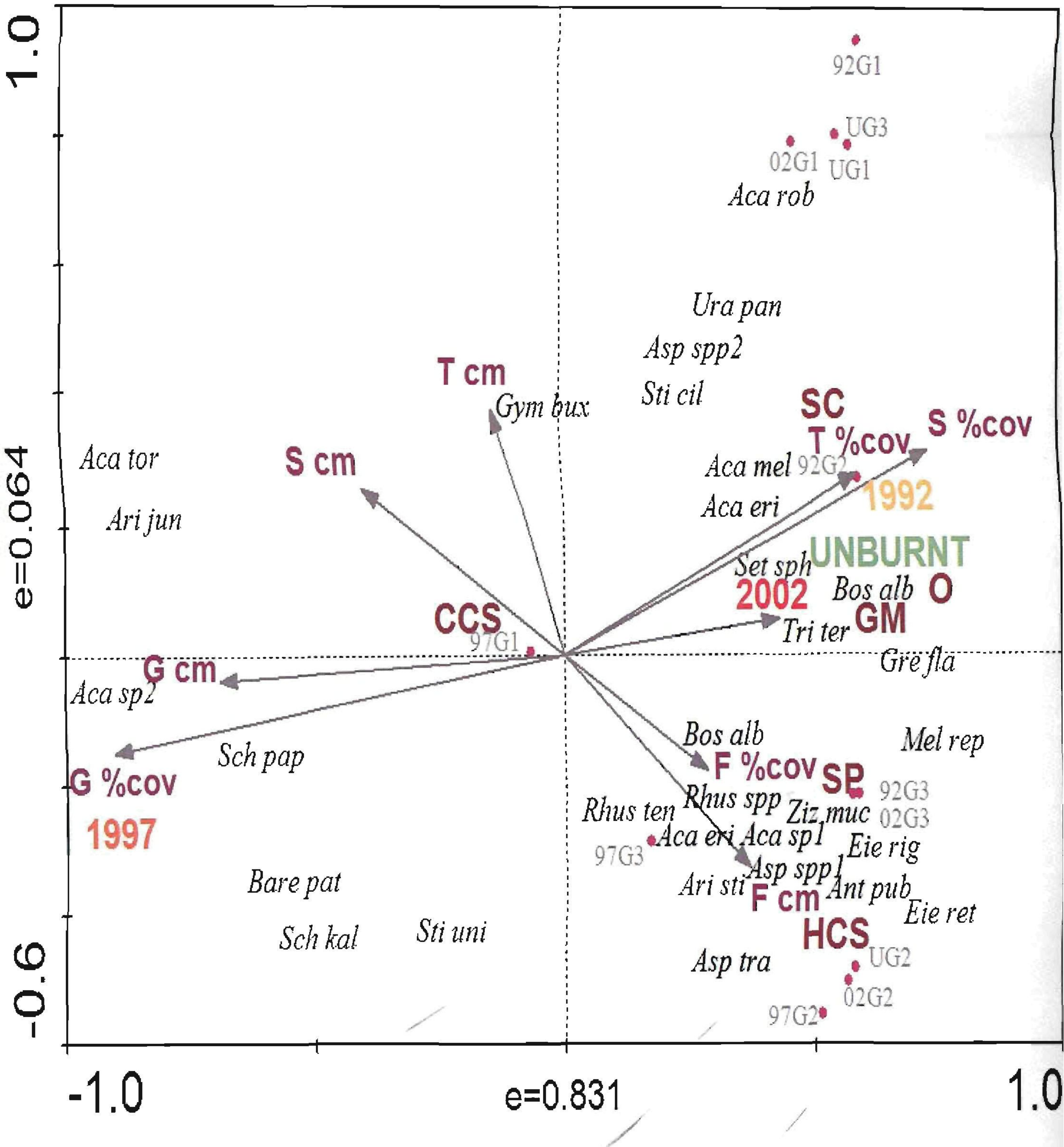

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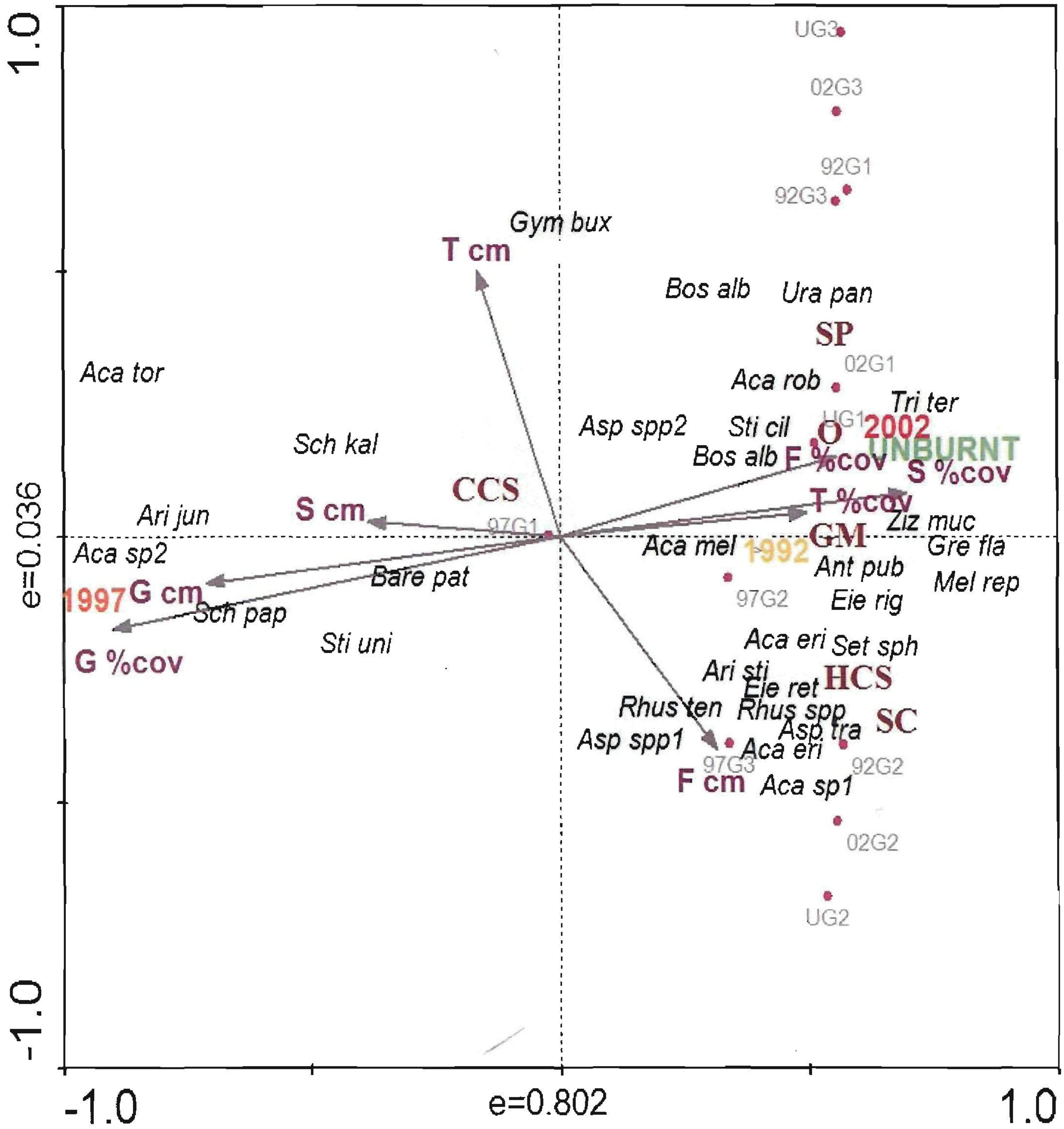
Figure 3.26: CCA of the abundance of ants per functional group and plant species composition as



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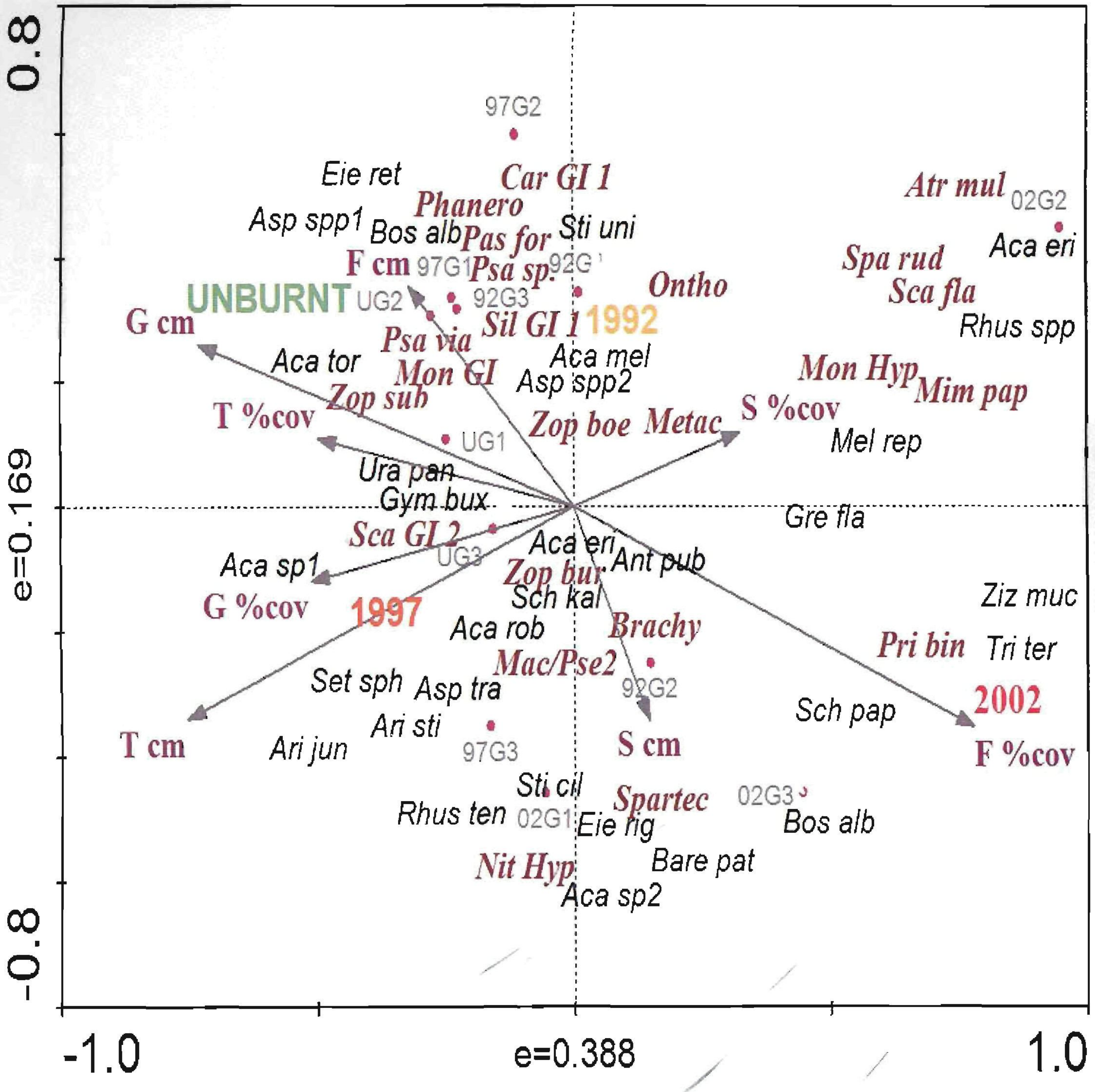
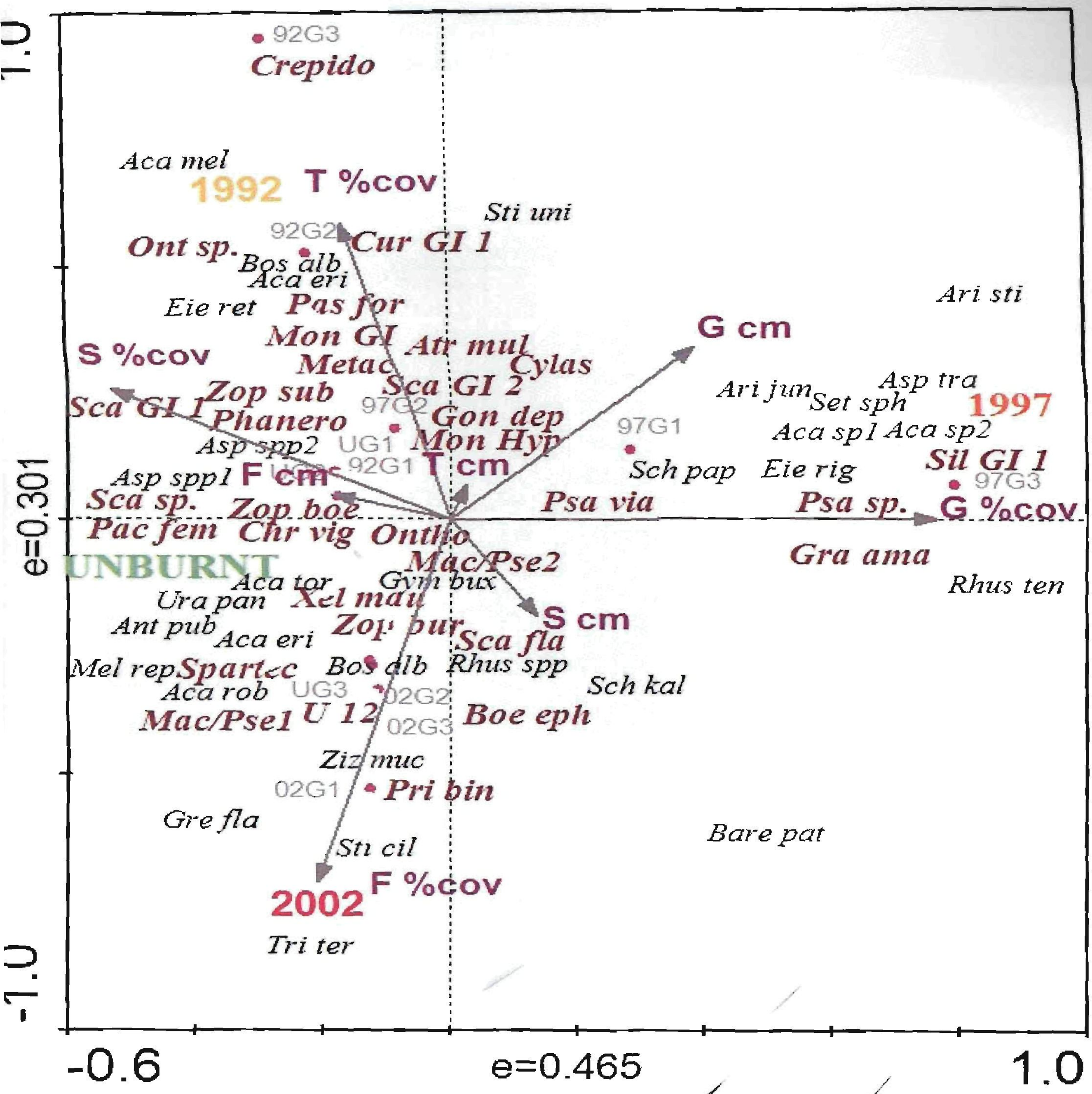


February

Figure 3.27: CCA's of the beetle and plant species composition associations along the burn treatme

ators of ecosystem change due to veld fires.



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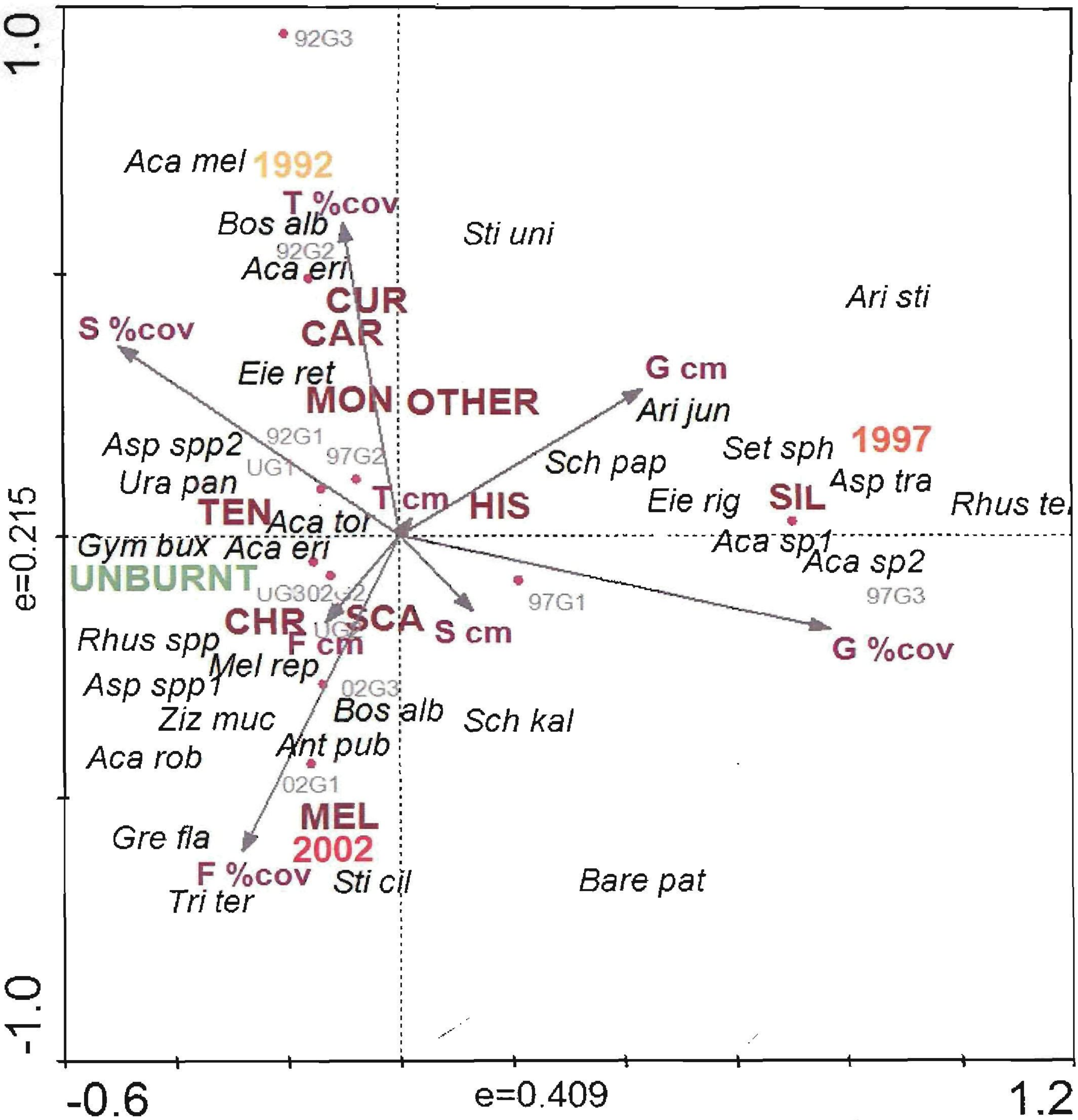

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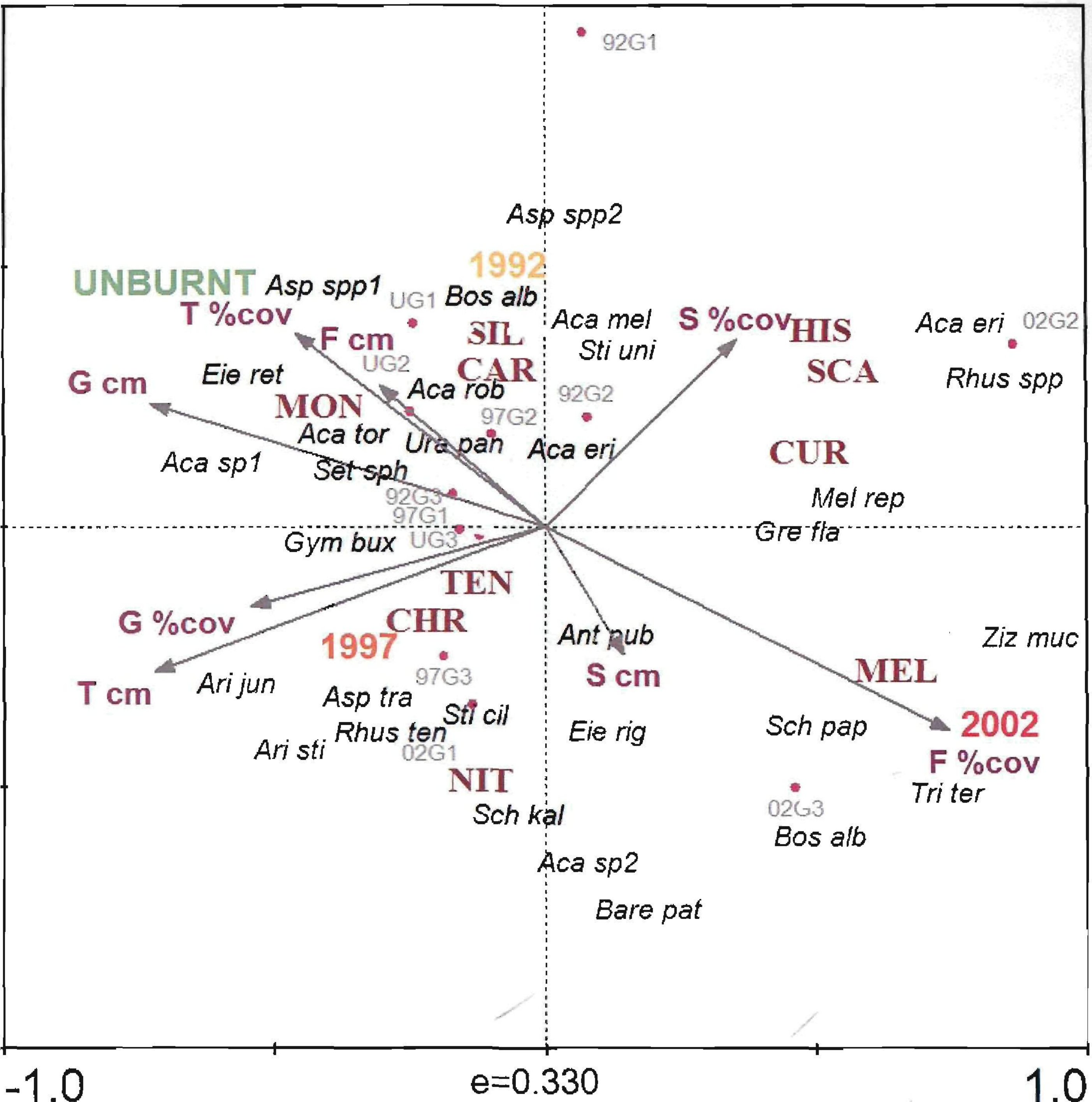
Figure 3.28: CCA of the abundance of beetles per family and plant species composition associatic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3.4 The Influence of Acacia mellifera bushes on ant and beetle assemblages

In this final section, the results for the determination of the effect of bush density on ant and beetle abundances is presented. The aim was to establish ant and beetle composition along a gradient away from A. mellifera bushes.

Figure 3.29 and 3.30 are MDS representations of the presence/absence of ants and beetles, respectively, caught at each of the pitfall distances as placed in the Acacia mellifera dense regions of the study site during the October survey (see 2.2.3). The purpose of this particular survey was to establish a gradient away from A. mellifera bush density from the shrub base, to 3 x 1m intervals away from the shrub base, and to determine what type of effect, if any, this may have had on the ants and beetles. The aim of testing this is to determine whether these invertebrates exhibit any kind of response to bush density, especially regarding the fact that the Acacia mellifera shrub has been identified as an invader species, responsible for bush encroachment.

3.4.1 Ants

In consideration of the effect of A. mellifera bushes on ant assemblages, the diversity and richness indices for the ants were determined, as presented in Table 3.24. The results do not appear to provide an indication of significant gradient patterns in terms of any of the indices.

Table 3.24. Diversity indices for the October ant surveys along a distance gradient from Acacia mellifera bushes in each fire treatment. Indices are indicated for each distance as described in the materials and methods. (S- number of species; N- total abundance; d- Margalef; J'- Pielou's eveness.)

			S	N	d	J'
October	Unburnt	**0m**	14	692.0	2.0	0.6
		1m	10	872.0	1.3	0.7
		2m	11	868.0	1.5	0.6
		3m	11	820.0	1.5	0.6

	1992	**0m**	12	676.0	1.7	0.6
		1m	8	174.0	1.4	0.7
		2m	12	200.0	2.1	0.7
		3m	9	150.0	1.6	0.6
	1997	**0m**	3	2 820.0	0.3	0.7
		1m	5	1 396.0	0.6	0.5
		2m	6	982.0	0.7	0.5
		3m	4	1 456.0	0.4	0.6
	2002	**0m**	13	150.0	2.4	0.7
		1m	13	296.0	2.1	0.6
		2m	12	178.0	2.1	0.6
		3m	12	208.0	2.1	0.7

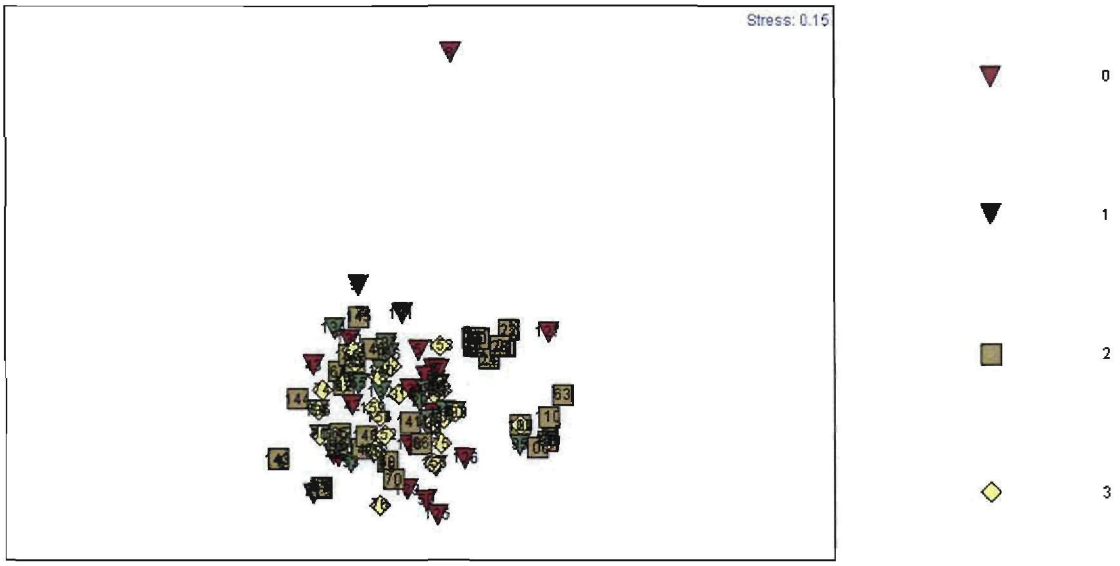

Figure 3.29. MDS representation of the presence/absence of ants at each of the pitfall distances placed in the survey areas along a distance gradient from Acacia mellifera bushes in each fire treatment for the October survey.

3.4.2 Beetles

In consideration of the effect of A. mellifera bushes on beetle assemblages, the diversity and richness indices for the beetles were determined, as presented in Table 3.25. As seen with the ant data, no significant patterns arise from this survey.

Table 3.25. Diversity indices for the October beetle surveys along a distance gradient from Acacia mellifera bushes in each fire treatment. Indices are indicated for each distance as described in the materials and methods. (S- number of species; N- total abundance; d- Margalef; J'- Pielou's eveness.)

			S	N	d	J'
October	**Unburnt**	**0m**	9	122	1.665	0.499
		1m	7	106	1.287	0.523
		2m	5	114	0.845	0.532
		3m	7	132	1.229	0.471
	1992	**0m**	4	30	0.882	0.675
		1m	4	46	0.784	0.628
		2m	5	38	1.100	0.659
		3m	3	10	0.869	0.859
	1997	**0m**	10	84	2.031	0.638
		1m	4	160	0.591	0.582
		2m	4	294	0.528	0.643
		3m	5	304	0.700	0.528
	2002	**0m**	6	26	1.535	0.751
		1m	6	34	1.418	0.699
		2m	5	44	1.057	0.664
		3m	4	26	0.921	0.693

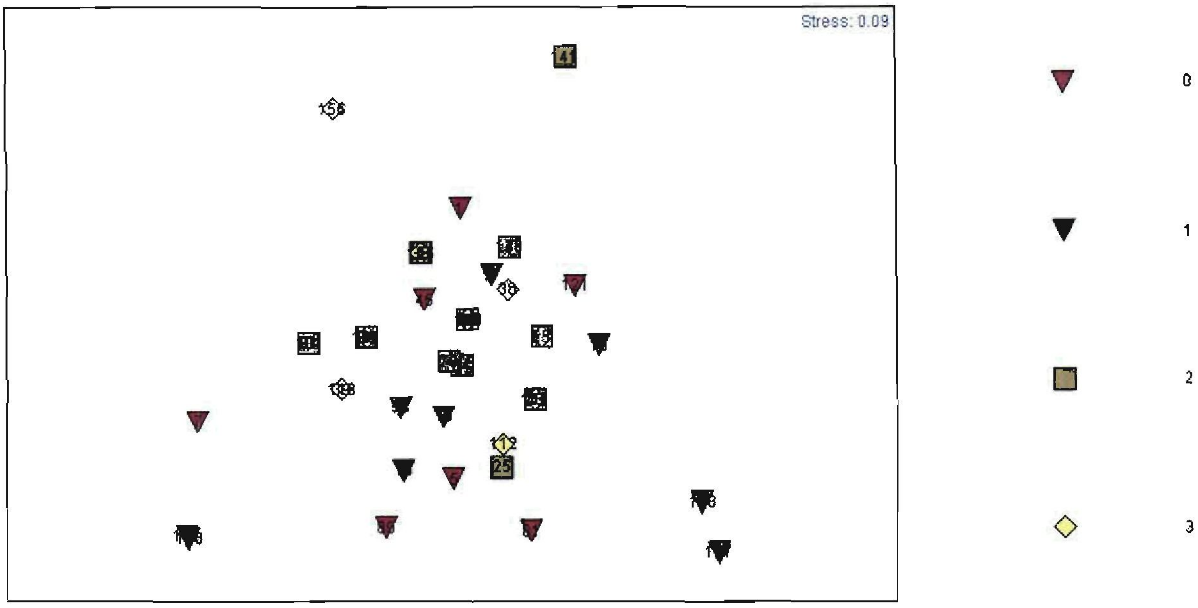

Figure 3.30. MDS representation of the presence/absence of beetles at each of the pitfall distances placed in the survey areas along a distance gradient from Acacia mellifera bushes in each fire treatment for the October survey.

The discussions for each of the results represented in this chapter follow in the next section.

CHAPTER 4: DISCUSSION

4.1 Indicators of ecosystem change brought on by fire

The research question of this study was to determine whether ant and beetle assemblages are affected by habitat changes as a result of veld fire and if these assemblages could be used as indicators of the changes in habitat. This was attempted investigating the effect of burning specific to the Molopo conditions, and sampling data under extended periods of recovery after burning.

4.1.1 Ants as indicators

When considering the distribution of ants in context of their absolute abundance within each of the burn treatments and their replicates for the two surveys in 2004, the replicates for the 1997 burn treatments always segregate to a greater extent than the rest of the burn treatments (Fig.3.2). In general the 1997 treatment presented the lowest species diversity and evenness and highest total abundance of all the treatments by far. The unburnt and 2002 burn treatments showed little difference in ant assemblages whereas the 1992 treatment seemed to return to a more diverse ant assemblage. This does not necessarily imply causation but it could indicate a trend with little effect on ants shortly after fire (2 years) but with large longer term habitat effects caused by the fire treatment with the biggest impact on habitat around 7 years after burning (1997 burn treatment), impacting on ant diversity and composition The high ant dominance (*Anoplolepis steingroeveri*) and high ant abundance in this treatment could be indicative of disturbed veld condition or at least habitat change. The increased ant diversity 12 years after the fire (1992 burn treatment) could be indicative of a return of the habitat to the before burn situation.

Before being able to link ant assemblage composition to habitat change, it is important to describe the burn treatment habitats in terms of vegetation diversity and structure, as well as soil, and finally to establish what relationships, if any, exist between all these factors.

The diversity data and ant assemblage data presented thus far seem to greatly echo these findings. Once again, in order to verify the stated hypothesis, these data need to be considered in context of environmental data, particularly that of habitat structure as defined by the vegetation and soil.

4.1.2 Beetles as indicators

The **beetle assemblage** data showed no significant pattern according to fire treatments but large differences between the seasonal surveys. These variations could probably be attributed to seasonal activity or the availability of required resources. More research is necessary to investigate the reasons for seasonal variation. The MDS graphs (Fig. 3.17 and 3.18) also indicate little consistent clustering along the burn treatments across the seasonal surveys and it is evident that the February and April surveys differ from each other on the community level.

The beetles, although exhibiting interesting trends in their data, and apart from their trends shown in contrast to the trends of the ants, don't seem to indicate convincing patterns that would validate them as useful indicators of ecosystem change in the context of this study and the research question. This is even more so when considering that the February and April beetle data don't correlate with one another to any noticeable extent.

The ant data for the unburnt treatment and the 2002 treatment often reflected similar results, save a few minor differences. It was for the 1997 burn treatment that the ant community assemblages were markedly different, especially in terms of their abundances as seen in the species composition context and the functional group context. As the recovery time moved in the direction of the 1992 burn treatment, it was seen that the ant community assemblages were again very different from that of 1997, but leaned towards the patterns reflected in the unburnt treatment. The observation is thus that ants do not exhibit an immediate response to fire, but rather that their responses become more apparent over time, as the habitat adapted to disturbances brought on by fire.

The observation stated above is supported by similar findings in previous studies, in which a variety of explanations were offered and verified. During a fire, ants are mostly protected from direct mortality due to their colonial structure and associated nesting behaviour, with their sensitivity increasing in the wake of fire-induced modifications to the habitat structure and micro climate (Andersen 1991a; Andersen *et al.* 2003), as well as decreases in food resources and the commencement of interspecific competition by other organisms, be they ants or other taxa (Andersen 1991a). The abundance of highly active thermophilic savanna ant species is known to be promoted by the reduced tree and shrub cover that typically results from frequent fire (Andersen *et al.*, 2007; Andersen, 1991b).

Ants have shown to benefit initially from fire because of the preference for high temperatures and open spaces (Greenslade 1997), and an increase in activity of certain ant species following burning may hold advantages in terms of their foraging rate for seeds and seed dispersal (Hosking & Turner 1997). Vanderwoude *et al.* (1997) discovered that burning frequency may affect the dominance of specific functional groups because of the functional group differences to habitat requirements and their competitive interactions. Burning leads to the establishment of new habitats that are preferred, for example, by opportunistic and hot climate specialists (Jackson & Fox 1996). Most specialist ant species are not favoured by burning because of their requirement of high vegetation cover, precise food and habitat requirements, and competition for resources by other ant species that have a greater competitive edge.

The ant data also appeared to repeat similar trends for both the February and April sampling efforts, serving as an indication of their consistency in behavioural response. Apart from some community assemblage rearrangement, or species absence due to the seasonal differences, the ant species richness and overall abundance, as well as species eveness (Table 3.3 and Figure 3.1) are represented with much similarity. Even when placing the ant data in context with the vegetation data in the CCA representations, for the species composition, number of species per functional group and abundance of ants per functional group for both the February and April surveys, it is clear that the ants display definite and comparable patterns.

The beetles however, did not seem to reflect this long-term response, and no satisfactorily discernable trends were observed. When considering the beetle data at species composition level, family level and finally in conjunction with the plant data in the CCA representations, the outcome is cluttered, making it difficult to ascertain any viable tendencies and grouping along the fire gradient. The beetle species richness, abundance and eveness for both the February and April sampling surveys also do not reflect similarities, whilst the rank abundance graphs illustrated in Figure 3.7 show in their shallow curves that any differences existing between the burn treatments are too random and slight, and can not be described in terms of beetle community assemblages.

4.2 Habitat characterization at the various burn treatments

4.2.1 Vegetation

The results depicted in Table 3.16 and Table 3.17 and in Figure 3.13 and Figure 3.14 reiterate the diversity indices presented. In terms of species composition, the unburnt and 1992 treatments were most dissimilar at 63.05%, and the least difference occurred between treatments 1992 and 1997 at 42.07%. The species that contributed the most towards these differences are Gymnosporia buxifolia, with higher percentage occurrence at the unburnt replicates, Acacia erioloba, Acacia mellifera, Boscia albitrunca with higher percentage occurrences at 1992, Schmidtia pappopheroides being most prevalent at 1997, and relatively prevalent at 2002, and Tribulus terrestris (an annual pioneer forb) being almost exclusive to the 2002 replicates.

Regarding the plant structural types, the unburnt and 1997 differed to the smallest degree at 17.67%, and the greatest difference of 24.66% being between unburnt and 2002. Shrubs appeared to be most prevalent at the unburnt sites, Grasses at the 1997 sites, trees at the unburnt and 1992 sites, forbes at 2002, and bare patches being most apparent at 2002, and to some degree at 1997. This does not mean that these structural groups did not occur at other sites, it does however provide statistical information as to the extent and type of cover of each of these groups at each of the grid replicates in the different burn treatments.

The CCA illustrated in Figure 3.21 shows various plant structural types also added in terms of their height in cm and their percentage cover to provide an overall picture of the vegetation spread found at the various burn treatment replicates. Once again, 1997 had greater grass cover, whereas the trees and shrubs are shown to group more extensively around the unburnt and 1992 treatments, whilst the forbes, specifically Tribulus terrestris, despite not appearing exclusively at 2002, certainly is highly associated with it. The eigen values however are very low, serving as a reminder that most of the species are not exclusive to a given site, and that it is still in their percentage contribution that they reflect specific differences. Figure 3.21 thus neatly summarizes the findings reflected in Tables 3.18-3.22 and Figures 3.16-3.20.

Vegetation in any given ecosystem is always subjected to the effects of an array of factors, and the manner in which these factors behave together will ultimately determine the specific outcome for the vegetation community assemblage in question. Fire has been identified as a major contributing factor in a variety of biomes, and the Kalahari thornveld is no exception. The manner in which the vegetation in a said habitat will be affected by a fire is highly dependent on the components of fire behaviour; fire type, fire intensity, season of burning and frequency of burning (Tainton, 1999). The components of fire behaviour are in turn influenced by moisture levels, biomass density and wind. The effect of fire on habitat structure is diverse and highly varied. As discussed in the introduction, trees are favoured by the absence of fire to which they are sensitive during the early stages of establishment (Stocks *et al.*. 1997, Van de Vijver 1999). Grasses, on the other hand, are favoured by the presence of fire which stimulates new growth. In moist savannas, fire can be used to control bush encroachment but in arid savannas it has the role of maintaining trees and shrubs at an available height and in acceptable state to browsers (Trollope 1980). The differences in the height and percentage cover of the trees, shrubs, grasses and forbes in each of the burn treatments is very apparent. Fire thus has a very important effect on vegetation structure, as it is a factor attributed to the origins of savannas and the maintenance of the balance between trees and grasses in these ecosystems (Tainton 1981, Werger 1983, Singh *et al.* 1985, Menaut *et al.*. 1985). Modern range managers and researchers have realised the importance of fire in savanna management as it can readily be manipulated. Researchers in fire ecology have revealed that fire is important and usually beneficial in maintaining the diversity, structure and functioning of savanna ecosystems (Frost 1984, 1985, Van de Vijver 1999; Parr & Andersen, 2006). Fire therefore also has a great influence on general habitat structure.

4.2.2 Soil

The between site dissimilarity percentage values depicted in Table 3.23 clearly indicate that no significant differences exist between the sites in terms of their soil characteristics, the largest difference being a mere 7.4 %.

It is with these findings of soil not appearing to have any significant contributions towards the state of the given burn treatment environment in terms of the research question, that soil is eliminated as a contributing factor, and with this, receives no further attention, apart from one final illustration in section 3.3.1.

4.3 Responses of Ant Assemblages to Habitat Change

The results shown by the ants and the beetles indicate different trends; the ants suggest that they may be effective indicators of ecosystem change, whereas the beetles do not, and with this will not be discussed further.

The 1997 burn treatment has been identified as grouping separately according to ant diversity and abundance for both surveys. Grasses appear to be strongly associated with the 1997 treatment, with a small tree component, relatively high percentage of bare patches and virtually no forbes (Fig. 3.25), whilst the taller vegetation structures, with their accompanying densities, are more correlated to the unburnt sites and 1992. *Anaplolepis steingroeveri* was highly associated with the 1997 burn treatment, dominating to a great extent, whilst all other species indicate a greater association with the unburnt, 1992 and 1997 burn treatments. The grasses remain closely correlated with 1997, with the tree and shrub structure densities exhibiting closer associations at 1992 and unburnt, and the forbe Tribulus terrestris being highly correlated with 2002.

Thus, as vegetation has a significant effect on ant communities, any changes in plant composition and structure are likely to be reflected by changes in ant species and community composition (Parr *et al.*, 2002; Andersen 1983). Frequent fires may result in a more open plant community with higher day temperatures and low moisture levels at the surface (Parr *et al.*, 2002; Greenslade 1997), which will influence ant species composition since some ant species are particularly sensitive to moisture levels and soil temperatures. Fire acts to modify vegetation structure, litter cover and phytomass (Parr *et al.*, 2002; Chambers & Samways 1998) as indicated by different foliage densities, which influences foraging routes and ant behaviour (Parr *et al.*, 2002; Zimmer & Parmenter 1998). It has been shown by Parr *et al.* (2002) that there is a clear relationship between habitat structure and species richness. Differences in vegetation structure significantly affect ants It is likely that it is the effect of habitat changes, especially structure and cover, rather than fire directly, that may account for the differences observed in the study by Parr *et al.*, as well as in this study.

Although increased vegetation diversity such as increased bush component affects ant diversity, this is not confirmed by the Acacia mellifera sampling and no increased ant or beetle diversity along a gradient towards bushes was found. This suggests that ant and beetle communities do not differ markedly from one another within the very immediate area surrounding dense shrubbery. This particular observation may however show different results should a greater variety of sampling methods be applied, which may provide more tangible results in terms of species turnover, and thus possible differences along a gradient from dense shrubbery.

Figure 3.26 considers the manner in which the ant functional groups are related to the vegetation structure, and the cold climate specialists show a strong correlation with 1997, whilst the hot climate specialists and specialist predators correlate more with 2002 and unburnt, and the subordinate camponotinii exhibiting greater numbers at 1992. The opportunists and generalised myrmicinae exhibit a correlation with unburnt and 1992, as well as with 1997 and 2002, although in lesser degrees. This observation is interesting when considering the conclusions drawn in former studies that the abundant presence of opportunists and generalised myrmicinae is an indication of disturbance (Andersen, 1999).

In context of the research question, the pattern which has been observed up to this point is that the ants show the lowest diversity, accompanied with dominance at 1997, slowly increasing in diversity as recovery years go by. Initial species richness values at 2002, are greater than at 1997, and seem to be on a par with the unburnt treatment species details, suggesting, and in accordance with other studies (Parr *et al.*, 2004; Andersen *et al.*, 2006) that the ants do not respond to environmental changes immediately, but rather over time. The study by Parr *et al.* (2002) in which the effect of various fire characteristics on ant assemblages was investigated, demonstrated that fire plays a role in determining ant community composition, despite relatively subtle differences in the appearance of different grassland sites. Time since fire (age), and also the combined effects of age and frequency (overall fire influence) appear to be the main determinants influencing ant diversity.

The data patterns for the April survey of the ants closely resemble those of the February survey, in that the remaining functional types are more closely correlated with unburnt, 1992 and 2002, albeit minor deviations, which are to be expected in the natural environment.

When considering these findings in terms of the research question, it does suggest that ant communities, in accordance with their environmental function, respond to structural changes. As there are a variety of factors involved in causing habitat change, attributing a specific local occurrence as the main contributing factor is very subjective, hence the need to eliminate as many additional factors as possible. An additional concept to consider with regard to how ants may respond to habitat change is that of specific species biogeographical histories, especially ecologically dominant species, as investigated by Andersen *et al.* (2007), Their findings indicated that two species demonstrated opposing fire-related resilience due to the different ecological niches they inhabit.

As described in chapter 2, the study area is driven by rain and fire, and the area is prone to trampling. Rain was eliminated as a contributory factor in the Molopo Nature Reserve in personal communication with Richard Newberry of the North West National Parks, who stated that rain fall has been consistent from year to year for an extended period of time and does not fall in substantially different volumes over the identified burn treatments. Soil characteristics were also eliminated as a determining factor. Trampling is another possible contributing source, but no sufficient evidence that this exists in the replicate sites could be established. Management practice could also play a major role in habitat change, but with the reserve being in existence for the past 24 years, such practice has also been reasonably consistent. The areas which have burned and the times which they burned was documented since the reserve's inception, and thus it does suggest the plausible and possibly exclusive role that fire played in this regions' environmental dynamics. Pre-reserve management strategies may have had effects which have not been recorded. This is suggested by the findings of Parr *et al.* (2002) in a study to determine the importance of different fire variables in promoting ant diversity. Here, ants were studied in savanna grassland patches of different post-fire fuel age, and fire frequency, where there was pronounced dominance by a few species on young and infrequently burnt plots; ant diversity thus appeared to be influenced more by post-fire fuel age than frequency of burning, The Pilanesberg study considered a maximum age of six years recovery after fire, whereas the study in the Molopo Nature Reserve looked at considering what might happen beyond this. In considering the different conclusions which may be drawn from these two studies, and others, it emphasises the need for repetition of such research in diverse environments and under diverse burn treatments in order to have a wider base of information from which to ascertain more general trends.

The aspect of the research question pertaining to the determination of the effect of bush density on ant and beetle abundances provided no satisfactorily significant results, and is thus not covered in the discussion. The effect of bush density on ant and beetle abundances could however be investigated more thouroughly through improved methodologies and expanding this research may prove to provide very interesting results. A more robust knowledge of fire and other habitat modifying factor histories in any given study area is thus more helpful in assuring the correct data collection methods and the interpretation of results.

CHAPTER 5: CONCLUSIONS AND RECCOMENDATIONS

5.1 Conclusions

Answering the question as to what the immediate, short-term and long-term effects of fire on habitat structure are, and how this affects ant and beetle assemblage structures in context of absolute abundance, species richness, species diversity, functional groups and families, is not so simple, and requires more extensive investigation.

While the beetles did not indicate satisfactory results, the ant community assemblages showed that there appears to be a delay in response to fire induced habitat modifications in the short term, with diversity declining in the mid-term, and increasing towards a plateau in the long-term with habitat recovery after fire. The short-term findings of this study agrees to some extent with the research of Parr *et al* (2002) in that ant diversity increased after fire recovery. While the Pilanesberg ant diversity continued to increase towards the oldest surveyed recovery age of six years, the Molopo study found that ant diversity began to decrease beyond this recovery time (at seven years), before increasing again towards a recovery time of twelve years. This observation raised the possibility of ant diversity being affected in the medium to long-term, before being able to increase and stabilise within the long-term. This extended study of recovery time after fire may be indicative of more complex relationships in the response of biotic components to abiotic influences within a given habitat, and should be investigated more extensively to gain more knowledge on the matter.

In establishing whether ant and beetle assemblages respond to any effect that a gradient of bush density may pose, no satisfactory trends could be identified, and while bush encroachment is regarded as a very serious environmental concern, neither the ant or beetle assemblages provided any useful information in this regard. Research methodology in this regard needs to be improved and implemented in order to gather very valuable information for application in future best-use practice strategies.

In considering the initial research question, the results from this study indicate that the ants could serve as indicators of habitat change brought on by fire in the Molopo Nature Reserve, whereas the beetles do not. However, replication of the study is essential under different conditions and within a variety of environments to verify the outcome of this study.

5.2 Recommendations

Given the limited amount of information available with regard to invertebrate community dynamics and fire behaviour and its effects on South African landscapes, it is crucial that more research efforts are conducted to gather data. Such research will not only support current scientific knowledge but holds the potential to provide valuable insight into more effective fire management strategies.

Means of improving studies such as this one:

- The present experiment should be replicated to determine longer term habitat effects as a result of fire.
- The present experiment should be replicated in different types of habitats in order to identify the effect of different fire behaviour factors which are common in different habitats and eliminate those which are not.
- More grid replicates need to be established in different survey areas in order to accommodate patchy species distributions, and lessen the possibility of pseudo-replication.
- The study period needs to be extended to allow for more data to be obtained regarding the change of ant or other invertebrate communities over time.
- Surveys should ideally be conducted seasonally in order to eliminate seasonal effects.

- Although pitfall trapping was effective in this particular study based on the grassland habitats, additional collection methods such as tree beating, hand collecting and sweep-netting may be employed to ensure that scarcer, cryptic and nocturnal species are also represented in samples.
- The art of identifying and classifying these tiny organisms requires more time and attention to working at the species level when assessing the role of invertebrates in ecology. Their great diversity and the accompanying limited information on their biology hampers effective interpretations to observed responses.
- The consideration and inclusion of species' biogeographical history, especially for those species found to be ecologically dominant in a given study, may provide clearer answers.
- Fire behaviour and its components need to be recorded more effectively over extended periods of time for a given area in order to establish fire history and related patterns, which will be useful in interpreting habitat change more conclusively.

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IN MEMORIUM

Jauné-Pierré Smith

6 September 1981- 11 October 2004

1 God is our refuge and strength, a very present help in trouble.

2 **Therefore will not we fear, though the earth be removed, and though the mountains be carried into the midst of the sea;**

3 though the waters thereof roar and be troubled, though the mountains shake with the swelling thereof.

4 There is a river, the streams whereof shall make glad the city of God, the holy place of the tabernacles of the Most High.

5 God is in the midst of her; she shall not be moved: God shall help her and that right early.

6 The heathen raged, the kingdoms were moved: he uttered his voice, the earth melted.

7 The LORD of hosts is with us; the God of Jacob is our refuge.

8 Come; behold the works of the LORD, what desolations he hath made in the earth.

9 He maketh wars to cease unto the end of the earth; he breaketh the bow, and cutteth the spear in sunder; he burneth the chariot in the fire.

10 "**Be still, and know that I am God**: I will be exalted among the heathen,
I will be exalted in the earth."

11 The LORD of hosts is with us; the God of Jacob is our refuge.

The Holy Bible: King James Version. 2000.
The Psalms: Psalm 46 "God Is Our Refuge and Strength"

This Master's dissertation is compiled in loving memory of Jauné-Pierré Smith, JP, a man for all seasons. A loving son, brother and friend with an indescribable passion for life and a heart larger than life. His absence is greatly felt but the pleasure and the privilege of having known him is a priceless blessing. JP is sorely missed by his family and friends and his memory will live on within us all.

APPENDIX

Appendix A: Ant abbreviations

Functional Group	Abbreviation	Species Name
Cold Climate Specialists	Tap ste	*Anaplolepis steingroeveri*
Generalised Myrmicinae	Cre A	*Crematogaster* sp. A
	Cre B	*Crematogaster* sp. B
	Mon not	*Monomorium notulum*
	Mon ruf	*Monomorium rufulum*
	Mon C	*Monomorium* sp. C
	Mon D	*Monomorium* sp. D
	Mon E	*Monomorium* sp. E
	Phe A	*Pheidole* sp. A
	Phe B	*Pheidole* sp. B
	Phe C	*Pheidole* sp. C
Hot Climate Specialists	Tap A	*Anaplolepis* sp. A
	Tap B	*Anaplolepis* sp. B
	Mer A	*Meranoplus* sp. A
	Mer B	*Meranoplus* sp. B
	Ocy A	*Ocymyrmex* sp. A
	Ocy B	*Ocymyrmex* sp. B
	Ocy D	*Ocymyrmex* sp. D
Opportunists	Lep A	*Lepisiota* sp. A
	Lep C	*Lepisiota* sp. C
	Myrmic	*Myrmicaria*
	Tet bau	*Tetramorium baufra*
	Tet ser	*Tetramorium sericeiventre*
	Tet set	*Tetramorium setuliferum*
	Tet A	*Tetramorium* sp. A
	Tet B	*Tetramorium* sp. B
	Tet C	*Tetramorium* sp. C
Subordinate Camponotini	Cam A	*Camponotus* sp. A (fulvopilosus group)
	Cam B	*Camponotus* sp. B
	Cam C	*Camponotus* sp. C
	Cam D	*Camponotus* sp. D
Specialist Predators	Opt ber	*Opthalmopane berthoudi*
	Ple man	*Plectroctena mandibularis*

Appendix B: Beetle abbreviations

Group	Family	Abbreviation	Species Name
Athicidae		Not bru	*Notoxus brutoni*
Brentidae	Cycladinae	Cylas	*Cylassp.*
Carabidae	Graphipterini	Graphi	*Graphipterus sp.*
		Gra ama	*Graphipterus amabilis*
	Scaritini	Pas for	*Passalidius fortipes*
	Bradybaenina	Boe eph	*Boeomimetes ephippium*
	Crepidogastrini	Crepido	*Crepidogaster*
	Anthiini	Atr mul	*Atractonotus mulsanti*
		Car Gl 1	Anthiini Gen. et spec. indet
		Ant hom	*Anthia homoplata*
Chrysomelidae	Eumolpinae	Mac/Pse1	*Macrocoma/ Pseudocolaspis* sp. 1
		Mac/Pse2	*Macrocoma/ Pseudocolaspis* sp. 2
		Mac/Pse3	*Macrocoma pseudocalaspis* sp. 3
	Chrysomelinae	Chr vig	*Chrysolina vigintiquatuorsignata*
Curculionidae	Entiminae	Cur Gl 1	Entiminae Gen. et spec. indet
		Mim pap	*Mimaulus papulosus*
		Spa rud	*Spartecerus cf. rudis*
		Spartec	*Spartecerus sp.*
	Brachycerini	Brachy	*Brachycerus*
		Erirhin	*Erirhininae sp.*
		Baris	*Baris sp.*
Histeridae	Saprininae	Mon Hyp	Saprininae *Hypocacculus sp.*
Meloidae		Pri bin	*Prionolytta binotata*
		Cer ang	*Ceroctis near angolensis*
Monommatidae		Mon Gl	*Monom Indeterminate*
Nitidulidae		Nit Hyp	Anthiini *Hypocacculus sp.*
Scarabaeidae	Scarabaeini	Sca fla	*Scarabaeus flavicomis*
		Sca sp.	*Scarabaeus sp.*
		Pac fem	*Pachylomerus femoralis*
	Canthonini	Sca Gl 1	Canthonini Gen. et spec. indet
	Aphodiinae	Sca Gl 2	Aphodiinae Gen. et spec. indet
	Cetoniini	Xel mau	*Xeloma maura*
	Onthophagini	Ontho	*Onthophagus*
		Ont sp.	*Onthophagus sp.*
	Coprini	Metac	*Metacatharsius*
Silvinidae		Sil Gl 1	Silvanidae sp. indeterminate
		Mas sp 1	*Mastigus sp.*
Tenebrionidae	Zophosini	Zop bur	*Zophosis burkei*
		Zop boe	*Zophosis boei*
		Zop sub	*Zophosis subaenea*

	Platynotini	Gon dep	*Gonopus deplanatus*
	Molurini	Phanero	*Phanerotomea*
	Pimeliinae	Psa via	*Psammodes vialis*
		Psa sp.	*Psammodes sp.*
		Ten Gl 2	*Tenebrionidae* sp. indeterminate
		Ten Gl 1	Molurini Gen. et spec. indet
		Cas sp.	*Cassida sp.*

Appendix C: Plant abbreviations

Group	Abbreviation	Full name
Grass	Ant pub	*Anthephora pubescens*
	Ari jun	*Aristida junciformes*
	Ari sti	*Aristida stipitata*
	Era bip	*Eragrostis biphlora*
	Era pal	*Eragrostis pallens*
	Mel rep	*Melinis repens*
	Sch kal	*Schmidtia kalahariensis*
	Sch pap	*Schmidtia pappophoroides*
	Set sph	*Setaria sphacelata*
	Sti cil	*Stipagrostis ciliata*
	Sti uni	*Stipagrostis uniplumis*
	Ura pan	*Urachloa panicoides*
Shrubs	Aca eri	*Acacia erioloba*
	Aca mel	*Acacia mellifera*
	Asp spp.1	*Asparagus* spp.1
	Asp spp.2	*Asparagus* spp.2
	Asp tra	*Asparagus* spp. 3
	Bos alb	*Boscia albitrunca*
	Eie ret	*Elephantorrhiza elphantina*
	Eie rig	*Eriocephalus pubescens*
	Gre fla	*Grewia flava*
	Gym bux	*Gymnosporia buxifolia*
	Rhus spp	*Rhus spp*
	Rhus ten	*Rhus tenuinervis*
	Ziz muc	*Zizyphus musculata*
Trees	Aca eri	*Acacia erioloba*
	Aca rob	*Acacia robusta*
	Aca sp1	*Acacia* sp1
	Aca sp2	*Acacia* sp2
	Aca tor	*Acacia tortillus*
	Bos alb	*Boscia albitrunca*
Forbes	Tri ter	*Tribulus terrestris*

Appendix D: Absolute Ant Abundances from grid surveys

Species	February				April			
	Unburnt	**1992**	**1997**	**2002**	**Unburnt**	**1992**	**1997**	**2002**
Anaplolepis sp. A	1	2	6	5	0	0	2	0
Anaplolepis sp. B	0	0	0	3	0	0	0	0
Anaplolepis steingroeveri	24	0	20266	43	17	1	29669	5
Camponotus sp. A (fulvopilosus group)	1	4	0	10	1	1	0	1
Camponotus sp. B	2	2	0	1	0	0	1	0
Camponotus sp. C	0	0	1	0	0	0	0	0
Camponotus sp. D	6	0	5	9	7	6	0	6
Crematogaster sp. A	0	0	0	0	0	0	0	0
Crematogaster sp. B	0	0	0	0	0	1	0	0
Lepisiota sp. A	0	0	0	0	0	0	0	0
Lepisiota sp. C	0	0	0	0	0	0	0	0
Meranoplus sp. A	20	7	9	2	1	10	9	3
Meranoplus sp. B	0	0	0	0	6	0	0	14
Monomorium notulum	84	83	124	97	50	34	54	49
Monomorium rufulum	0	0	0	0	0	0	0	0
Monomorium sp. C	69	42	151	42	40	9	187	43
Monomorium sp. D	28	1	24	0	0	0	40	0
Monomorium sp. E	80	160	122	92	51	40	81	43
Myrmicaria	3	21	0	13	13	11	0	10
Ocymyrmex sp. A	78	89	184	72	13	11	36	13
Ocymyrmex sp. B	0	0	0	0	0	0	0	0
Ocymyrmex sp. D	2	3	0	0	0	1	0	0
Opthalmopane berthoudi	3	1	3	4	10	5	7	10
Pheidole sp. A	0	0	0	0	0	0	0	0
Pheidole sp. B	0	0	0	0	0	0	0	0
Pheidole sp. C	227	266	34	86	146	35	52	127
Plectroctena mandibularis	0	0	0	0	0	0	0	0
Tetramorium buafra	0	0	0	0	0	0	0	0
Tetramorium sericeiventre	0	1	0	2	1	0	0	0
Tetramorium setuliferum	16	2	9	19	12	3	17	12
Tetramorium sp. A	2	1	0	4	0	4	0	0
Tetramorium sp. B	0	2	0	0	0	13	0	0
Tetramorium sp. C	16	16	23	10	21	8	11	40

Appendix E: Absolute Beetle Abundances from grid surveys

Species	February				April			
	Unburnt	1992	1997	2002	Unburnt	1992	1997	2002
Scarabaeus flavicomis	1	2	1	12	70	18	53	157
Scarabaeus sp.	0	0	0	0	3	1	0	3
Pachylomerus femoralis	0	0	0	0	6	0	0	3
Canthonini Gen. et spec. indet	0	0	0	0	6	1	5	9
Aphodiinae Gen. et spec. indet	0	0	0	0	8	1	8	0
Xeloma maura	0	0	0	0	3	0	0	9
Onthophagus	0	4	0	1	79	13	8	52
Metacatharsius	2	0	1	2	0	0	3	0
Macrocoma/Pseudocolaspis sp. 1	0	0	0	0	3	0	0	9
Macrocoma/Pseudocolaspis sp. 2	0	1	0	2	3	0	5	3
Chrysolina vigintiquatuorsignata	0	0	0	0	8	6	5	12
Graphipterus amabilis	0	0	0	0	0	0	5	0
Passalidius fortipes	3	3	3	0	31	36	13	3
Boeomimetes ephippium	0	0	0	0	6	0	0	3
Crepidogaster	0	0	0	0	0	1	0	0
Atractonotus mulsanti	0	0	0	0	0	0	5	0
Anthiini Gen. et spec. indet	0	0	1	0	0	0	0	0
Anthiini Hypocacculus sp.	0	0	0	0	0	0	0	0
Entiminae Gen. et spec. indet	0	0	0	0	8	15	3	0
Brachycerus	0	1	0	0	0	0	0	0
Spartecerus cf. rudis	0	0	1	2	0	0	0	0
Spartecerus sp.	0	0	0	0	0	0	0	3
Monom Indeterminate	9	2	5	0	3	1	5	0
Saprininae Hypocacculus sp.	0	6	0	4	42	18	89	35
Zophosis burkei	79	58	103	79	42	18	20	81
Zophosis boei	5	3	5	8	31	16	5	9
Zophosis subaenea	28	20	23	3	31	15	23	3
Gonopus deplanatus	0	0	0	0	3	3	3	6
Phanerotomea	0	1	0	0	3	1	3	0
Psammodes vialis	0	1	3	0	3	0	8	3
Psammodes sp.	0	0	0	0	0	0	3	0
Silvanidae sp. indeterminate	14	12	1	0	3	0	106	0
Prionolytta binotata	0	0	0	25	0	0	0	9
Mimaulus papulosus	0	1	0	3	0	0	0	0

Onthophagus sp.	0	0	0	0	0	1	0	0
Cylas sp.	0	0	0	0	0	3	3	0
Unknown 12	0	0	0	0	6	0	0	0