

**The effect of burning frequency on invertebrate and indigenous flowering forb diversity
in a Drakensberg grassland ecosystem**

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Abstract

The KwaZulu-Natal Drakensberg, South Africa, is predominantly a grassland ecosystem maintained by fire. The effect of the current burning regime on invertebrate and flowering forb diversity in this ecosystem is poorly understood. The overall aim of this study was to contribute towards the development of an effective burning regime for the KwaZulu-Natal Drakensberg that will conserve invertebrates and indigenous forbs, two major components of biodiversity. The objectives were to examine the effect of fire and fire frequency on flowering forb and invertebrate species diversity, to determine whether fire frequency, time since last burn or locality were influencing species composition, and to identify potential biodiversity indicators that reflect overall species richness for use in monitoring of invertebrates and forbs.

Sampling took place in March, September and November of 2002 at Giants Castle Game Reserve. Invertebrates were sampled using sweep netting and targeted netting along transects, yellow pan traps and soil quadrats. Invertebrate taxa sampled were ants (Formicidae), butterflies (Lepidoptera), grasshoppers (Orthoptera), leafhoppers (Cicadellidae), bees (Apoidea), bee flies (Bombyliidae), hover flies (Syrphidae), robber flies (Asilidae), spiders (Araneae), earthworms (Oligochaeta) and millipedes (Diploda). These were identified to species level with the assistance of taxon experts. Flowering forbs were sampled using five replicates of five by five metre quadrats randomly placed in each site.

Overall flowering forb and invertebrate species diversity was higher in grasslands that were burnt for two consecutive years in 2001 and 2002 than in grasslands that were not burnt during those two years. Frequently (annual) and intermediately (biennial) burnt grasslands had

significantly higher invertebrate and flowering forb diversity than infrequently (five years without burning) burnt grasslands. This, together with the fact that grasslands burnt during the year of sampling had higher species richness than grasslands burnt two and five years previously suggests that invertebrates and forbs are generally resilient to fire and many forb species appear to be stimulated by fire. However, each burn frequency had its own suite of unique flowering forb and invertebrate species. Invertebrate communities were influenced mostly by locality and the length of time past since the last fire and flowering forb communities were influenced mostly by the length of time past since the last fire. Fire frequency had the least influence on both invertebrate and forb communities. Ecological succession occurred after each fire in the invertebrate communities but forb communities appear to need more than five years without fire for ecological succession to occur. The findings of this study therefore suggest that using a combination of three fire frequencies would result in patches of grassland in various stages of ecological succession, and would conserve species unique to each burning frequency, and would therefore conserve maximum diversity. Flowering forb species richness and certain invertebrate taxa (ants, leafhoppers, spiders and bees) have the potential to act as indicators of overall invertebrate species richness for use in monitoring programmes.

Preface

The experimental work described in this dissertation was carried out in the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg, from January 2002 to September 2004, under the supervision of Dr M. Hamer and co-supervision of Prof. R. Slotow.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

Signed: W. Arnott



Signed: Dr. M. Hamer (supervisor)



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CHAPTER 1

GENERAL INTRODUCTION

1.1. Biodiversity

1.1.1. The importance of conserving biodiversity

Biological diversity, otherwise known as biodiversity, encompasses all levels of natural variation from the molecular and genetic levels to the species level (Huston 1994), and also includes patterns in nature up to the landscape level. All these components of biodiversity are not independent but rather interact to maintain various ecosystems throughout the world. Some ecosystems are more diverse than others. This is evident in the increase in biodiversity from the poles towards the tropics (Myers 1979; Pullin 2002; Rosenzweig 1995; Samways 1994), a pattern that covers plant, animal and invertebrate assemblages in aquatic and terrestrial environments (Rosenzweig 1995). Biodiversity is vanishing before our eyes with a current annual extinction rate of 27 000 species (Purvis & Hector 2000; Wilson 2000). Man has caused the extinction rate to be 100 to 1000 times greater than the estimated natural rate of extinction (Wilson 2000).

Many biologists agree that we desperately need to conserve as much biodiversity as possible (Linden 2000; Margules & Pressey 2000; Purvis & Hector 2000; Wilson 2000) for several reasons. Aesthetically, species are important to many people around the world (Wilson 2000). In affluent nations many people will spend much time and money on television, films, and books about wildlife (Myers 1979). Many people appreciate the beauty of wildlife and find great pleasure in spending time in the natural environment. Large sums of money are also spent by people around the world who want to get a glimpse of rare species such as the Black

rhino (*Diceros bicornis* (Linnaeus, 1758)) in Africa, the Tiger (*Panthera tigris* Oken, 1816) in Asia, or the Tapir (*Tapirus terrestris* Brünnich, 1771) in South America (Myers 1979). The aesthetic reason for conserving biodiversity is closely linked with an ethical argument for conserving biodiversity which considers all life on earth as having a right to exist (Myers 1979; Spellerberg & Hargrove 1992).

Species conservation is of direct benefit to all humans and is therefore not purely for the idealistic preservationist (Myers 1979). Plant and animal communities maintain the integrity of the environment by regulating ecological cycles such as water, carbon and nitrogen (Spellerberg & Hargrove 1992). The more numerous an ecosystem's species the greater the ecosystem's stability (Myers 1979; Wilson 2000) and the more likely the ecosystem is to recover from natural disturbances such as fire, flood and drought. Some species contribute more to an ecosystem than others because of their numbers, biomass, capacity to exploit the sun's energy, and status in the food pyramid. Certain species can also act as "indicators" and signal the general ill health of a particular ecosystem that may contain other threatened species (Myers 1979).

From a utilitarian perspective biodiversity contributes to our material well-being in agriculture, medicine and industry (Myers 1979; Spellerberg & Hargrove 1992). There are many examples of under-exploited food plants with proven potential. Only 150 plants have been cultivated out of an estimated 80 000 edible plants world-wide and less than 20 plant species produce 90% of the world's food (Myers 1979; Wilson 2000). Animal species are also used as an important food source. The gene pools of plant and animal species that we use today are much reduced and declining rapidly. The wild relatives of species that we use for food should

provide genetic diversity responsible for characteristics offering defense against would-be pests (Spellerberg & Hardes 1992). Unfortunately wild relatives of major crop species are mostly found in the tropical regions which are being eroded at an alarming rate (Spellerberg & Hardes 1992).

Both plant and animal species contribute to our health by being present in a wide range of pharmaceuticals and there is still potential for further exploitation of plants and animals in this industry (Wilson 2000). Pain-killers, antibiotics, heart drugs, anti-leukemic agents and anti-coagulants are just a few drugs that are derived from a natural origin (Myers 1979). In South Africa traditional medicinal plants are important to rural and urban communities for physiological, psychological and religious purposes (Cunningham 1989). The use of medicinal plants is no longer restricted to African cultures but is widely used around the world with the growing value of medicinal plants in the United States being put at well over \$3 billion (Myers 1979).

A further reason for conserving biodiversity is that many plants and animals are used in industry. Industrial materials from plants include latex products, pectins, resins and cleoresins, gums and other exudates, essential oils for flavours, vegetable dyes and tannins, vegetable fats and waxes, insecticides, growth regulators (Myers 1979), cellulose, starch and hydrocarbons (Spellerberg & Hardes 1992). Trees provide timber which is important in the production of furniture, as fuel and as pulp for paper production (Spellerberg & Hardes 1992). Animal products such as skins, hides, tusks and horns are also used extensively in trade.

1.1.2. Threats to biodiversity

There are a number of human activities that are responsible for the decline in biodiversity. Habitat destruction is the single greatest threat to biodiversity throughout the world (Myers 1979; Spellerberg & Hargreaves 1992; Wilson 2000). This is inextricably linked to human population growth and the encroachment of man's activities into natural environments in almost every corner of the earth. Cultivation replaces natural vegetation with domestic crops and is a widespread practice throughout the world (Myers 1979). Livestock husbandry is another type of agriculture where domestic animals take over large areas of natural vegetation and use large amounts of water leaving very little for wild herbivores (Myers 1979). Possibly the most well known example of habitat destruction is deforestation of tropical forests (Purvis & Hector 2000; Spellerberg & Hargreaves 1992; Wilson 2000) with losses being estimated at about 76 000 km² per year (Spellerberg & Hargreaves 1992). This habitat loss results in the destruction of tropical forest populations and thousands of species (Purvis & Hector 2000). Conversely, afforestation of grasslands in South Africa has led to the extinction of some animals and plants and has resulted in others becoming threatened with extinction (Armstrong *et al.* 1998). Other species rich environments under threat from habitat destruction include coral reefs, salt marshes and mangrove swamps (Wilson 2000).

Overexploitation of animals in the form of hunting, fishing and international trade also results in destruction of species around the world. Hunting has resulted in the extinction of species such as the Bluebuck (*Hippotragus leucophaeus* (Pallas, 1766)) and the Quagga (*Equus quagga* Gmelin, 1788). The White rhino (*Ceratotherium simum* (Burchell, 1817)) and Black rhino populations have been reduced dramatically due to hunting and illegal poaching and are currently only found in fragmented populations in protected areas (Pullin 2002). Spellerberg & Hargreaves 1992 explain how hunting, fishing and international trade in wildlife is just as

prevalent in recent times as it was in the past. In Italy about 200 million native and migrating birds are shot annually for sport. Advanced technology in the fishing industry results in huge shoals of fish being caught as well as other marine animals such as turtles, dolphins, seals, whales and sealions. The international trade in wildlife is worth about \$5 billion annually and now threatens many species with extinction. The attractiveness of parrots has caused several species to be collected to the verge of extinction and dwindling numbers of these birds increase their price which encourages more intense hunting.

Two further threats to biodiversity are alien invasive species and pollution. Species introduced into countries can have a devastating effect on the endemic wildlife in the country. In Hawaii introduced domestic animals and predators such as cats, rats and mongooses have contributed to the extinction of 24 of the islands' 70 known endemic species and subspecies (Spellerberg & Hargrove 1992). Overpopulation results in excessive pollution which is toxic to wildlife and threatens its survival. A few examples of pollution are eutrophication, oil spills, pesticides and greenhouse gasses (Spellerberg & Hargrove 1992).

1.1.3. Conserving biodiversity

In order to conserve as much biodiversity as possible a number of strategic reserves around the world have been established and others are still needed, with the basic role of eliminating threats to biodiversity (Margules & Pressey 2000). Priority biodiversity areas that need conserving include areas of exceptional concentrations of endemic species that are experiencing exceptional loss of habitat, otherwise known as hotspots (Myers *et al.* 2000). In order to conserve the full array of biodiversity Margules and Pressey (2000) suggest that there are two objectives that need to be met. The first is that reserves around the world need to

represent the full variety of biodiversity, ideally at all levels of organisation. Secondly, once reserves are established they should promote the long-term survival of the species and other elements of biodiversity they contain by maintaining natural processes and viable populations and by excluding threats. This is done through maintaining the conditions within the reserve that are required for the key natural features to persist. Furthermore, monitoring of those features and adaptive management is also required (Margules & Pressey 2000).

1.1.4. Disturbance and biodiversity

A disturbance is a discrete event in time that disrupts ecosystem, community or population structure, changing the physical and biotic environment (Samways 1994). Natural disturbances have always occurred in ecosystems around the world in the form of storms, fires and floods, with many species of plants, insects and animals adapted to thrive on such disturbances (Pullin 2002).

Many scientists believe that highest species diversity will be maintained in an ecosystem with intermediate levels of disturbance, commonly referred to as the intermediate disturbance hypothesis (IDH) (Begon *et al.* 1996; Connell 1978). The frequency of intermediate disturbance for any community will be that frequency at which the community can be maintained as far from competitive equilibrium as possible, while allowing the greatest number of species to recover from the reduction that occurred during the disturbance (Huston 1979). Propagules of a few pioneer species arrive in the open space soon after a disturbance. If frequent disturbances occur, an area devoid of species as a result of disturbance will not progress beyond the pioneer stage, and the diversity of the community as a whole will be low. At intermediate levels of disturbance, the diversity will increase because time is available for

the invasion of more species. At very low frequencies of disturbance, most of the community for most of the time will reach and remain at the climax, with competitive exclusion resulting in reduced diversity.

The IDH has been tested mainly in tropical rain forests and coral reefs. Connell (1978) found that high diversity of trees and corals is maintained only in a nonequilibrium state. If disturbances within the communities do not occur, they will proceed towards a low-diversity equilibrium community. Tropical forests and coral reefs are, however, subject to severe disturbances often enough that equilibrium may never be attained. Other experiments supported the IDH in marine ecosystems (Sousa 1979) and forest ecosystems (Fox 1979).

However, the IDH may not necessarily hold true where fire is the disturbance (Huston 1994; Schwilk *et al.* 1997). In a fynbos community the plant species diversity was highest at the least frequently burnt sites (40 years between fires) and lowest at the sites of moderate frequency (15 to 26 years between fires) and high fire frequency (alternating four and six year fire cycle). Community heterogeneity was highest at the least frequently burned sites and lowest at the sites that experienced an intermediate fire frequency (Schwilk *et al.* 1997). In a vegetative study of North American tallgrass prairies Collins (1992) also found that the IDH did not hold true where fire was the disturbance. Heterogeneity or diversity of grasses within the grassland ecosystem was lowest at intermediate disturbance frequencies (biennial burning) rather than highest. Annual burning resulted in lower diversity than in unburnt grasslands because of the increase in C₄ grasses following fire.

In contrast to these findings, Huston (1994) supported the IDH where fire was the disturbance in North American tall-grass prairies. He suggested that annual fires led to a reduction in broadleaf forbs and a grassland with lower diversity of grasses dominated by warm season species. A lower frequency of burning (3-8 years) resulted in a community of high diversity with more forbs, woody plants and additional grass species. A grassland with the lowest frequency of burning resulted in lower species diversity due to thatch accumulation and eventually invasion and dominance by woody species.

1.1.5. Ecological succession and biodiversity

A disturbance in an ecosystem is usually followed by ecological succession, which is the change in community structure over time (Christensen 1997). Ecological succession results from the modification of the physical environment by the community, therefore succession is community controlled even though the physical environment determines the pattern, the rate of change and often sets limits as to how far development can go (Kikkawa & Anderson 1986). The result of succession is a stabilized ecosystem in which maximum biomass and symbiotic function between organisms are maintained per unit of energy flow. Ecological succession is critical in maintaining heterogeneity and complexity in the ecosystem (Christensen 1997).

Connell and Slatyer (1977) base their model of post-colonization succession on (1) the species' ability to prepare the ground for the advent of later successional species (facilitators); (2) the species' abilities to colonize open sites and maintain their captured space against all later would-be colonists (inhibitors); (3) a collective ability to exploit differentially low levels of resources (tolerators).

1.1.6. Biodiversity and ecosystem functioning

A disturbance can influence ecosystem processes, and biodiversity within an ecosystem can also impact the dynamics and functioning of populations, communities and ecosystems (Tilman 1999). The diversity-stability hypothesis suggests that the more diverse an ecosystem in terms of species richness the more stable it is as a whole (Tilman 1996a). Stability can refer to resistance to a disturbance, resilience (the rate of recovery after a disturbance), and constance (degree of temporal stability) (Tilman 1996b). The reasoning behind this diversity-stability concept is (1) an ecosystem with more species in the food web will be more complex, with greater redundancy among species in terms of their trophic roles; (2) diverse ecosystems may be less likely to be invaded by exotic species that could disrupt the ecosystem's structure and function; (3) in species-rich ecosystems diseases will spread more slowly because most species are relatively less abundant, thus increasing the average distance between individuals of the same species and disrupting disease transmission among individuals (Hunter 2002).

The diversity-stability theory was supported in a long-term study of 207 grassland plots in Minnesota (Tilman 1996a,b; Tilman & Downing 1994). It was found that biodiversity stabilized community and ecosystem processes, but not population processes. Over a 11-year period (including two years of drought) year-to-year variability in total above-ground plant community biomass was significantly lower in plots with greater plant species richness (Tilman 1996a). Specifically, drought resistance was greatest in species rich plots. However, year-to-year variability in species abundances was not stabilized by plant species richness. This difference between species vs. community biomass resulted from interspecific competition. When climatic variations harmed some species, unharmed competitors

increased. The compensatory increases stabilized total community biomass, but caused species' abundances to be more variable. Thus community above-ground production in more diverse grassland plots was more stable with normal year-to-year variations in climate as well as with a major disturbance such as drought.

1.2. Grasslands

1.2.1. Grasslands around the world

World Resources (2000) describe grassland ecosystems around the world as areas dominated by grassy vegetation and maintained by fire, grazing, and drought or freezing temperatures. Using this broad definition grasslands are found on every continent (predominantly in the interior of continents) and include non-woody grasslands, savannas, woodlands, shrublands and tundra (Figure 1.1). According to Russell *et al.* (1985) principal grasslands include the Great Plains of North America, stretching from Texas to mid-Canada; the Eurasian steppe extending from Hungary eastwards through the Soviet Union to Mongolia; Llanos of central and southern Brazil; Pampas of Argentina and Uruguay; Australian grasslands; and Africa's tree dotted savanna. Russell *et al.* (1985) suggest that climate is the most important factor for maintaining grasslands where 250 mm to 1016 mm of rainfall are required for grasslands to survive. The location of grassland is also affected by the character of the soil, the topography, and the altitude and latitude of the area.

Grasslands can be categorized and described by the climatic zone in which they lie *ie.* tropical, temperate and arctic (Russell *et al.* 1985). The hot tropical and sub-tropical regions are characterised by savanna, which are defined as grassland plains dotted with trees and shrubs. High rainfall is experienced in these regions where up to 1200 mm can be received within a

year. However rainfall is unpredictable and between three and seven months of the year experience no rain. The temperate zones generally receive more reliable and predictable rainfall with the climate generally being much harsher with a greater range in both annual and daily temperatures. In the arctic zone the tundra owes its special pattern of vegetation to the limited amount of moisture that is available. The tundra does receive much precipitation, however much of the moisture remains unavailable to plant life because the ground is frozen for most of the year.

Although grasslands cover 40 % of the world's land surface, 80 % of grasslands suffer from soil degradation (Linden 2000). The impact of humans on the world's grasslands is considered to have been more devastating than on any other of the world's biomes (Barnes 1998). Russell *et al.* (1985) suggest that overgrazing and overcultivation are the two greatest threats to grasslands around the world. This is especially apparent in the world's temperate zone grasslands which include the veld of southern Africa, the pampas of South America, and the steppes of Europe and Asia (the most extensive). Nearly all of these grassland areas have been converted from their natural state into grainfields or are being used to graze livestock (Russell *et al.* 1985). Overgrazing by livestock threatens most African grasslands and has resulted in extensive desertification. The process is slow and barely perceptible with decreasing ground cover, repeated drought, declining water table and increasing soil erosion eventually reducing a productive region into a desert (Russell *et al.* 1985).

According to World Resources (2000), the goods and services provided by the world's remaining grasslands have received far less attention than those supplied by, for example, tropical forests and coral reefs, although grasslands are arguably more important to a larger

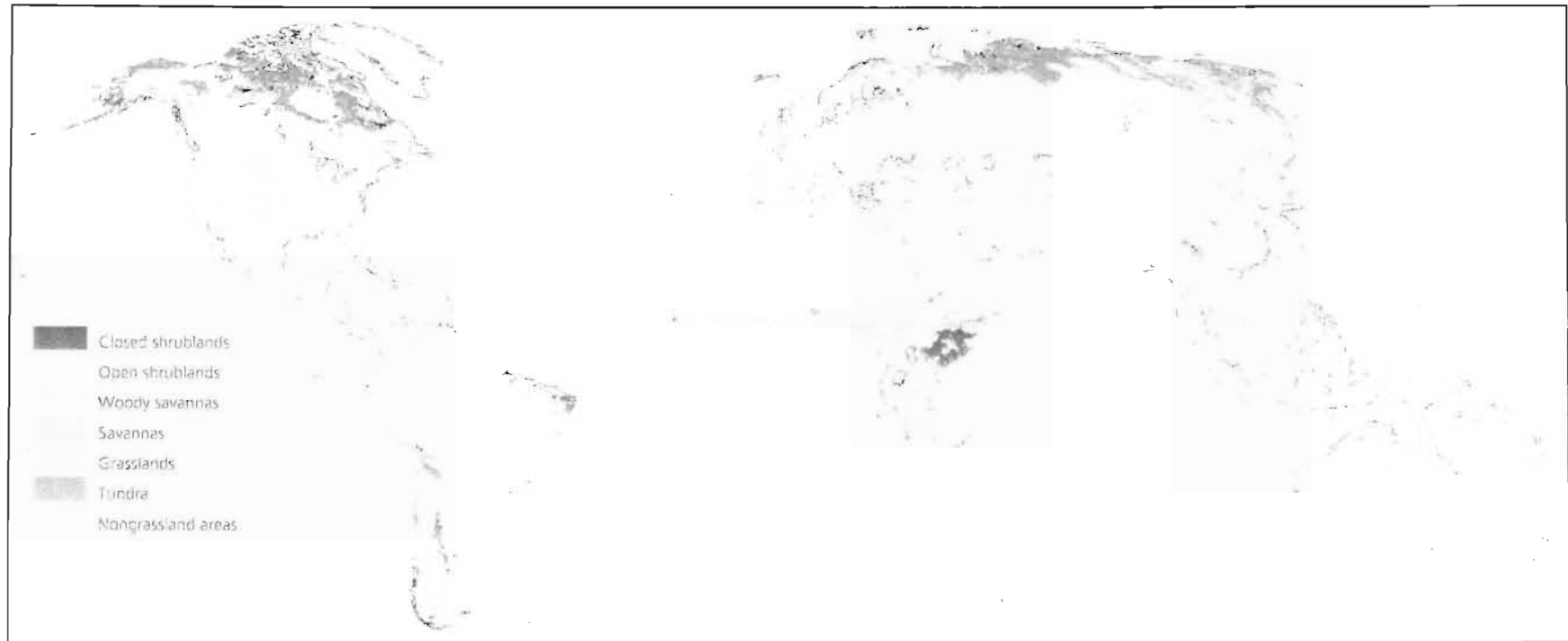


Figure 1.1: The extent of grasslands around the world (World Resources 2000).

percentage of people. All of the major foodgrains – corn, wheat, oats, rice, barley, millet, rye, and sorghum – originated in grasslands. Wild strains of grasses can provide genetic material to improve food crops and to help keep cultivated varieties resistant to disease. Other species of grasses eg. bamboo and giant reed grass, are used to make furniture, roof thatching, rope, hats and perfume essence (Russell *et al.* 1985). Indirectly, grasslands provide animal forage which in turn provides us with meat, dairy products, corn-fed poultry and eggs (Russell *et al.* 1985). Tourist attractions are provided by grasslands including hunting, game viewing and major migratory treks of Blue wildebeest (*Connochaetes taurinus* (Burchell 1823)) in Africa, Caribou (*Rangifer tarandus* Hamilton-Smith 1827) in North America and Tibetan antelope (*Pantholops hodgsoni* Hodgson 1834) in Asia. Furthermore as habitat for biologically important flora and fauna, grasslands make up 19 % of the Centers of Plant Diversity, 11 % of Endemic Bird Areas, and 29 % of ecoregions considered outstanding for biological distinctiveness (World Resources 2000). For these reasons it is critically important to conserve the little that we have left.

1.2.2. South African grasslands

South Africa is characterised by seven biomes, the savanna, grassland, nama karoo, succulent karoo, thicket, forest and fynbos (Figure 1.2). The grassland biome of South Africa is found predominantly on the high central plateau, and the inland areas of KwaZulu-Natal and the Eastern Cape (Low & Rebelo 1996) and covers 280 047 km² or 24.1% of the country's area (Huntley 1984). The topography is mainly flat and rolling, but includes the Drakensberg escarpment itself (Low & Rebelo 1996). The altitude varies from near sea level to 2 850 m above sea level (Low & Rebelo 1996). Grasslands in South Africa are those areas where the vegetation is dominated by grasses and in which woody plants are absent or rare (Huntley

1984) and geophytes are often well represented (Low & Rebelo 1996). Most grasslands occur within the summer rainfall area where the mean annual rainfall varies from less than 500 mm to well over 1000 mm. Winters are relatively dry, frosty to very cold with snow at the higher altitudes (Huntley 1984). Frost discourages forest vegetation which explains why parts of the high Drakensberg are dominated by extensive grasslands rather than forests (Meadows & Linder 1993). High summer rainfall, frequent fires, frost and grazing all help to maintain the grasslands and preclude the presence of shrubs and trees (Barnes 1998).

The grassland biome includes two categories, the sweet and sour grasslands. Sweet grasslands are found in low rainfall areas where the grasses are tall and have a low fibre content (Barnes 1998). Sour grasslands are found in high rainfall areas (> 625 mm p.a.) and have a short and dense grass sward with a high fibre content. The grasses of sour grasslands are largely unpalatable to stock during winter because they withdraw nutrients from their leaves to their roots (Barnes 1998; Killick 1963). Sour grasslands have also been referred to as “false” grasslands because the climate where these grasslands are found is suitable for the progression of succession beyond the grassland stage but grazing and fire have retained the grassland condition and prevented the development of a woody climax (Tainton & Mentis 1984). Fires have, however, never been excluded from these sour grasslands and have in the past been ignited by lightening, falling boulders and man (Edwards 1984), and fire should be considered an integral part of the grassland ecosystem.

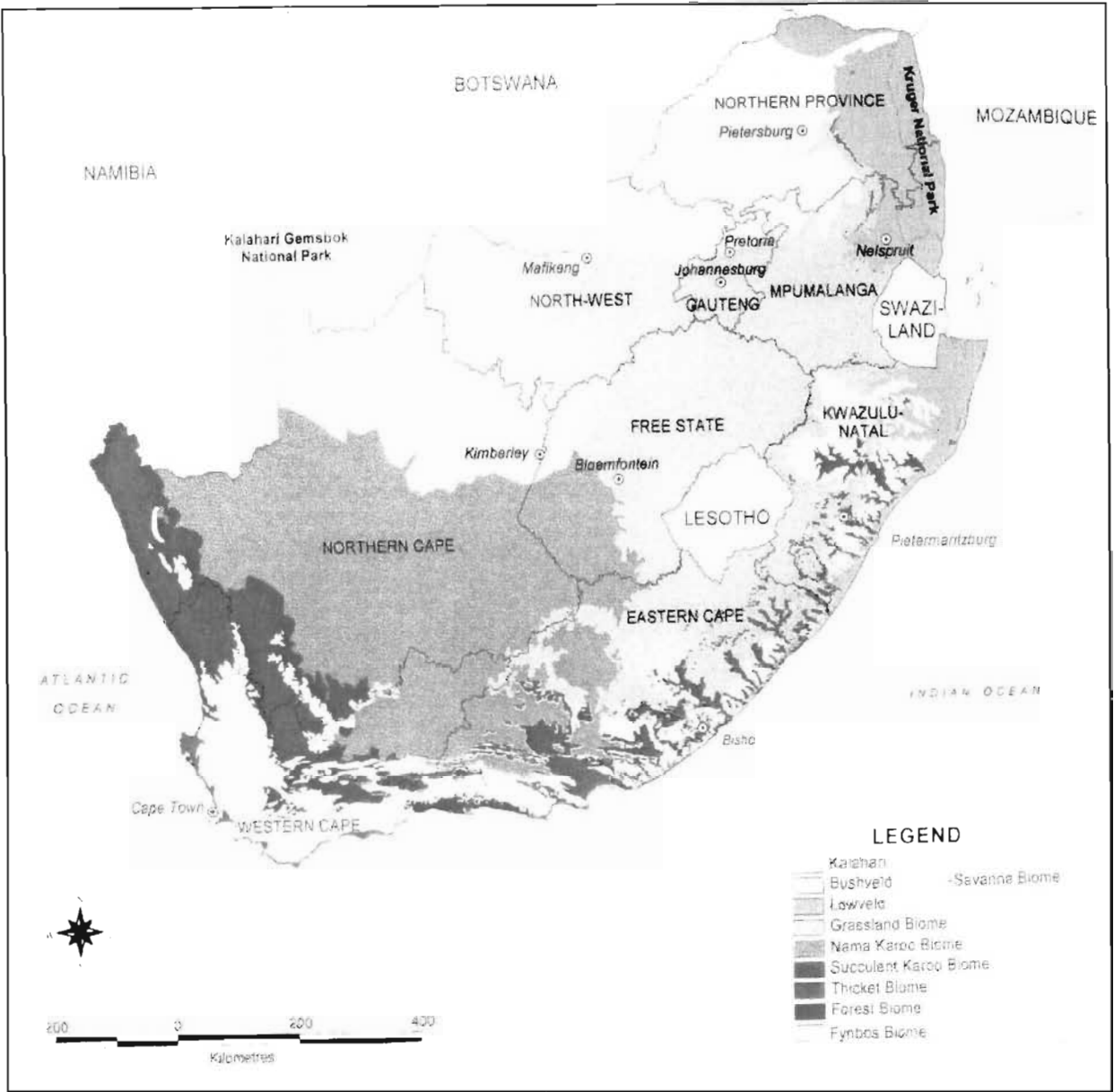


Figure 1.2: The biomes of South Africa (Knobel 1999).

An estimated 3 378 plant species are found in South African grasslands (Bredenkamp 1999). In terms of the total number of plant species per biome, the grassland biome lies third after the fynbos biome (with an estimated 7 316 species) and the savanna biome (with an estimated 5 788 species) (Bredenkamp 1999). However in terms of the number of plant species occurring in sample areas of 1 000 m², the grassland biome is even richer than the fynbos biome

(Bredenkamp 1999). The grassland biome is inhabited by a number of mammals, birds, reptiles, amphibians and invertebrates, many of which are endemic to South Africa (Table 1.1).

Table 1.1: Number of species found in South African grasslands and the number of South African endemics represented in grasslands (but not necessarily entirely restricted to them) (adapted from Bredenkamp 2002).

Taxonomic group	Number of species	Number of endemic species
Mammals	89	18
Birds	349	25
Reptiles	84	17
Amphibians	36	18
Invertebrates	Unknown	Unknown

The South African grassland biome has 10 bird species that are endemic to it (of a total of 35 South African endemic bird species) and 15 other endemic species that are associated with grassland but are not entirely restricted to it (Bredenkamp 1999). Eleven of 14 globally threatened bird species are found in South African grasslands and five of these are entirely restricted to grasslands (Barnes 1998). Grasslands support the highest number of bird species considered threatened in South Africa with many of them being in the highest category of threat (critically endangered) e.g. Blue swallow (*Hirundo atrocaerulea* Sundevall 1850), Bittern (*Botaurus stellaris* (Linnaeus 1758)), Whitewinged flufftail (*Sarothrura ayresi* (Gurney 1877)), Wattled crane (*Grus carunculatus* (Gmelin 1789)) and Rudd’s lark (*Heteromiraфра ruddi* (Grant 1908)) (Barnes 2000). Grasslands are also home to large

mammals such as Black wildebeest (*Connochaetus gnou* (Zimmerman 1780)), Burchell's zebra (*Equus burchelli* (Gray 1824)), Blesbok (*Damaliscus dorcas phillipsi* Harper 1939) and Springbok (*Antidorcas marsupialis* (Zimmerman 1780)) (Bredenkamp 1999). Smaller mammals such as the Rough-haired golden mole (*Chrysospalax villosus* (Smith 1833)) and Hottentot golden mole (*Amblysomus hottentotus* (A. Smith 1829)) are endemic to South African grassland (Bredenkamp 1999).

Despite its importance only two and a half percent of grasslands are formally conserved, which is extremely low in comparison to 69 % for forests and 10 % for savanna (Barnes 2000). The grassland biome is one of the most threatened in South Africa with an estimated 60 to 80 % already irreversibly transformed by agriculture, forestry, urban and industrial development and mining (Bredenkamp 1999). Commercial afforestation is probably the most critical threat to grasslands, with 1.4 million hectares under exotic plantations in 1998 and a further one million hectares expected in the next 25 years (Barnes 1998). Afforestation causes the grassland species composition to be totally altered as well as the structure of the vegetation from an open grassland ecosystem to a closed canopy plantation (Barnes 1998; Barnes 2000). Urbanization is another factor influencing the loss of natural grassland as Gauteng is centered in this biome as well as other cities such as Bloemfontein, Welkom, Klerksdorp, Witbank and Newcastle (O'Connor & Bredenkamp 1997). The mining of gold, coal and diamonds has also led to the natural vegetation of large tracts of grassland being virtually destroyed (O'Connor & Bredenkamp 1997).

1.2.3. Drakensberg escarpment

The Great escarpment is a continuous range of mountains and hills that separate the high-altitude interior plateau of South Africa from the narrow coastal plain. The escarpment extends from the Western Cape, through the Eastern Cape, KwaZulu-Natal, Lesotho, Swaziland, Mpumalanga and all the way up to the Limpopo Province, covering more than 1 000 km. It is characterised by majestic cliffs, rolling grasslands, patches of indigenous forest, mist and abundant rain in summer, frost and even snow in winter (Bredenkamp 1999). Pearse (1989) described the 95 km between Mont-aux-Sources and Giants Castle as being the most spectacular part of the Drakensberg range, with the highest peaks reaching 3 350 m.

The vegetation of the Drakensberg is characterised by three altitudinal zones; the montane zone (1 280 – 1 830 m.a.s.l.), the sub-alpine zone (1 830 – 2 865 m.a.s.l.) and the alpine zone (2 865 – 3 500 m.a.s.l.) (Johnson *et al.* 1998; Matthews & Bredenkamp 1999). The exact altitudinal limits of these three zones may vary with topography and latitude. The montane belt extends from the lowermost basalt cliffs to the valley floors (Johnson *et al.* 1998), where *Themeda triandra* Forssk. dominates and disappears very rapidly when fire is excluded from the grasslands (Killick 1963; Whelan 1995). *Protea caffra* Meisn. and *P. roupelliae* Meisn. are present on most spurs and crests and tall evergreen forests occur in moist valleys and kloofs where fire is excluded (Johnson *et al.* 1998). The low-altitude sub-alpine areas are dominated by grasslands whereas the high-altitude sub-alpine areas have a conspicuous presence of fynbos scrubland (Johnson *et al.* 1998; Matthews & Bredenkamp 1999). The alpine belt consists of climax heath, dominated by species from the genus *Erica* L. such as *E. dominans* Killick and *E. algida* Bolus, and interspersed with alpine grassland genera such as

Festuca L. (Johnson *et al.* 1998). Throughout all three zones woody communities flourish in rocky enclaves where *Cliffortia linearifolia* Eckl. & Zeyh, *Leucosidea sericea* Eckl. & Zeyh and *Buddleia salviifolia* (L.) Lam. dominate. A number of wetlands ranging from open waterbodies such as tarns, vleis, marshes and an intricate network of stream and river courses are also present (Johnson *et al.* 1998).

The high biodiversity and degree of endemism recorded from the Drakensberg grasslands is indicative of the age and uniqueness of the grassland (Matthews & Bredenkamp 1999). The Mpumalanga, Limpopo and KwaZulu-Natal Drakensberg areas are considered to be the richest floral regions of these provinces and have therefore been recognised as one of the most important conservation areas in southern Africa. According to van Wilgen *et al.* (1990) the KwaZulu-Natal Drakensberg supports a total of approximately 1 390 plant species of which 394 (29.5%) are endemic. Of the vertebrate fauna 232 birds, 49 mammals, 44 reptiles and 24 amphibians have been recorded, many of which are rare, endemic or have restricted distributions. A number of mammal, frog and bird species are endemic to the Drakensberg and the few studies on invertebrates suggest high invertebrate endemism (Derwent *et al.* 2001; Johnson *et al.* 1998) which may well exceed that of plants (Irwin & Irwin 1992). The extremely rare Mokhotlong blue (*Lepidochrysops loewensteini* Swanepoel 1951) and the widespread but habitat-restricted Bamboo Sylph (*Metisella syrinx* Trimen 1868) are present in the Drakensberg (Johnson *et al.* 1998). Furthermore the KwaZulu-Natal Drakensberg is also the most important mountain catchment in South Africa because of the high yield and quality of water that flows from it (Johnson *et al.* 1998).

The KwaZulu-Natal Drakensberg was declared a Wilderness Area in 1973 and has since been declared a World Heritage Site due to its spectacular scenery, geological history, rich fauna and flora and unique human culture (Barnes 2003). It has also been identified as a priority biogeographical region in the World Conservation Strategy (Irwin & Irwin 1992).

Furthermore there is also an initiative between South Africa and Lesotho to protect the exceptional biodiversity of the Drakensberg and Maloti mountains through the Maloti-Drakensberg Transfrontier Conservation and Development Area. The Drakensberg is therefore protected from large scale habitat destruction such as afforestation. However, the extensive grasslands still need appropriate management in the form of an effective fire regime in order to conserve important components of biodiversity *ie.* forbs and invertebrates.

1.3. Fire in grasslands

1.3.1. Fire as a disturbance in grasslands

Fire is a natural disturbance in most grassland ecosystems where natural fires, typically caused by lightening, are thought to occur about every one to three years in humid areas and every one to 20 years in dry areas (World Resources 2000). Fires play a major role in maintaining most grasslands, and eliminating trees and shrubs that would out compete and replace the grasses in the absence of fire (Huston 1994; Meadows & Linder 1993; Tainton & Mentis 1984). Fire also removes dry vegetation and recycles nutrients therefore keeping grasslands vigorous and productive (Turner & van Hoven 1997). Although fire does benefit grasslands, it can be harmful too, particularly when fires become much more frequent than is natural (World Resources 2000). Today, the number of natural fires is insignificant compared to the number of fires started by humans. Rather than trying to mimic the ‘natural’ fire regime of an area,

Whelan (1995) suggested that it would be more beneficial to place emphasis on understanding how organisms, populations and communities respond to experimentally imposed fire regimes.

Spatial and temporal heterogeneity are important elements in the functioning of ecosystems (Christensen 1997; Scholes & Walker 1993). Fire is an important tool used for producing and maintaining spatial heterogeneity in grassland ecosystems (Schwilk *et al.* 1997). Patchiness in resource availability provides opportunities for colonization and survival (Huston 1994), these in turn foster diversity and the mixture of patches forms the total resource base for biotic diversity (Parr *et al.* 2002). Spatial heterogeneity can be maintained by varying a number of fire parameters spatially and temporarily across the landscape (Brockett *et al.* 2001). These fire parameters are the time of year that the fires occur in (seasonality), the intensity of the fire and the frequency of fires (Scholes & Walker 1993; van Wilgen *et al.* 1990). The size of the area burnt is also important. Brockett *et al.* (2001) proposed a patch mosaic burning regime for South African savanna ecosystems as patchiness leads to higher biotic diversity. The principle goal of patch mosaic burning is to produce as much heterogeneity as possible by varying the fire parameters (frequency, seasonality, intensity and type of fire) throughout successive fire seasons. Fires are point-ignited under a range of fuel and weather conditions, and allowed to burn out by themselves. The patch mosaic burning regime used by Brockett *et al.* (2001) has also been successfully applied in Australia in Uluru National Park and in the Kakadu National Park.

In South Africa the effect of fire on the grass component of grasslands has been extensively studied (see Burgess 1991; Dillon 1980; Everson & Tainton 1984; Van Wilgen *et al.* 1990). The grassland fire regime is generally one of regular fires occurring during late autumn,

winter, and spring. Three years of protection from fire is usually sufficient to cause deterioration in structure and species composition of grasses (Edwards 1984). Fires are often applied in a fixed prescribed burning system where the area is divided into blocks of equal sizes and these are then burnt according to a schedule (eg. a two year interval in spring), and under prescribed weather conditions to create a relatively regular mosaic of post-fire ages (Brockett *et al.* 2001). As a result of these homogenous fire regimes a reduction in spatial heterogeneity could occur ultimately reducing diversity (Scholes & Walker 1993).

1.3.2. Burning regimes in the KwaZulu-Natal Drakensberg

Biennial burning in the KwaZulu-Natal Drakensberg has been practiced for many years and is largely responsible for the fine sward of *Themeda triandra* (Killick 1963), a highly palatable grass species. Everson and Tainton (1984) have extensively studied the effect of burning on grasses in the KwaZulu-Natal Drakensberg. After a 30 year period they found that annual and biennial burning resulted in no significant change in grassland condition, however after short periods of protection (5 years) a change in species composition occurred. The most noticeable change was the decrease in *T. triandra* and an increase in *Alloteropsis semialata* (R.Br.)

Hitchc. which resulted in a decrease in grassland condition. Bond (1999) stated that “*Past management of grassland and savanna areas was based on commercial rangeland principles and aimed at creating the most productive rangeland for animal production. Even the grasslands of the Drakensberg mountain catchment areas were burnt at seasons and frequencies to promote the optimum grass sward for beef production – in the absence of any beef herd*”. Mentis and Rowe-Rowe (1979) stated that the primary goal in management of the KwaZulu-Natal Drakensberg was to promote water production and second to that was to “perpetuate the native biota in abundance and variety”. Today the primary goal has shifted to

one that promotes biodiversity conservation above all else. Ezemvelo KwaZulu-Natal Wildlife's Mission is to 'ensure the conservation and wise use of the KZN's indigenous living resources (biodiversity), in partnerships with people'.

In the KwaZulu-Natal Drakensberg, the burning season is currently rotated between three periods: May (early winter); June – July (mid-winter); and August – mid-September (late winter to early spring) (Tainton 1999). Seasonal rotation ensures that any management compartment is only burnt in the same season once in every six years. Furthermore the grassland blocks are typically burned in a two-year cycle. This biennial rotational block burning induces rotational grazing by animals such as Eland (*Taurotragus oryx* (Pallas 1766)) (Edwards 1969). This controls the frequency of grazing and provides a recovery period for the grassland, ultimately resulting in a better quality grassland (Turner & van Hoven 1997).

Apart from maintaining the quality of the grassland for grazing, numerous studies in the KwaZulu-Natal Drakensberg have found that biennial burning promotes species diversity. Everson (1985) found that maximum grass species diversity in the KwaZulu-Natal Drakensberg was maintained by biennial burning. The biennial burning regime benefits the five most abundant antelope in the Drakensberg: Eland; Grey rhebuck (*Pelea capreolus* (Forster 1790)); Mountain reedbuck (*Redunca fulvorufula* (Afzelius 1815)); Oribi (*Ourebia ourebi* Laurillard 1842); and Blesbok (*Damaliscus pygargus* Sclater & Thomas 1894) (Rowe-Rowe 1982). Small mammals also benefit from biennial burning which in turn contributes to the abundance and species richness of avian and terrestrial predators (Rowe-Rowe & Lowry 1982). Mentis and Bigalke (1979) found that francolins did well in biennial burns and populations declined in the absence of fire.

Nanni (1969) suggested that an irregular fire regime would maintain species diversity, since no species or community would be favoured at the expense of others. Forbs would also favour an irregular burning regime because some depend on regular fires for their survival whilst others are fire sensitive (Bayer 1955; Scotcher 1982). No studies have included the effects of fire on invertebrates and very few include indigenous forbs even though both are a major component of biodiversity at a species level.

1.4. Invertebrates and forbs

The main goal of conservation in protected areas should be to maintain biotic diversity and ecosystem functioning (Parr & Brockett 1999). Invertebrates are the most important component of world fauna, both in numbers of species and biomass (New 1991) and may comprise 95% of all biodiversity (Myers *et al.* 2000). Invertebrates have a poor image among many people, however they play a significant ecological role in ecosystem functioning (Samways 1993). They feed on leaves, stems, flowers, seeds, roots and detritus and are certainly the dominant grazers in many grassland ecosystems (Picker *et al.* 2002; Samways 1993). Invertebrates pollinate flowers and disperse seeds and generally influence growth patterns of individual plants, plant populations and communities and influence plant succession (Samways 1993). They also play an important role in soil nutrient recycling, waste decomposition (Picker *et al.* 2002), pollution absorption, air and water renewal and purification, disease control and resource mobilization (Brown 1991). Invertebrates also have a wide range of utilitarian benefits, a few of these include pest and weed control, human food, industrial and medicinal products and they can be used in monitoring environmental quality (Kellert 1993). Despite their obvious importance they have not been taken into consideration

in the management of ecosystems (Myers *et al.* 2000). The distinct lack of information with regards to the total number of invertebrate species, their endemism and threatened status within grasslands, confirms that invertebrates are in need of further investigation.

Freeman (1998) describes forbs as non-graminoid herbs *ie.* herbs that are not grasses. They are an important and integral component of grasslands and contribute significantly to grassland diversity, however they have rarely been included in studies of disturbance effects in southern African grasslands (Uys *et al.* 2004). Throughout this introductory chapter the botanical studies that have been referred to are aimed specifically at grasses and have largely ignored the forb component found in grasslands. This indicates the need for more information on grassland forbs.

Invertebrates are abundant, have high species richness and higher taxon diversity in any assemblage or ecosystem (New 1999), hence the advantage of using them in conservation assessments. There are however, a number of limitations of using invertebrates in conservation assessments because for most of the higher taxa, (1) a high proportion of species is undescribed or undetected; (2) their distribution is unknown; (3) the number of specialists capable of identifying specimens is limited; (4) the protocols for comparative sampling are non-standardized and confusing; (5) knowledge of responses to environmental changes is generalized and limited; (6) there is little widespread sympathy for the problems or empathy with the animals themselves (New 1999).

Attempts to document all invertebrates in communities may not be useful for practical conservation (New 1999). Slotow and Hamer (2000) stated that there are too many

undescribed species and many taxa for which the expertise to identify species does not exist. They suggest that indicator species be used as an alternative to sampling the entire fauna of a site. However the ability of one taxon to reflect the diversity of other taxa has proved to be inaccurate. A number of focal groups should be carefully selected and these cannot include only easy to sample groups (New 1999; Slotow & Hamer 2000). This multi-taxa approach to biodiversity assessment is recommended (Kotze & Samways 1999) where the chosen taxa differ in their functional groups, body sizes, mobilities and life histories. Furthermore species-level identifications are of critical importance for understanding ecological interactions in an assemblage and most environmental questions can be more precisely answered using fine-level rather than coarse-level taxonomy (New 1998).

Apart from the necessity to select and sample only some taxa to measure invertebrate diversity, the ability of a single taxon to reflect the response of biodiversity in general to a disturbance is important for monitoring and management of a protected area. Carrying out a comprehensive sampling programme on a regular basis is time consuming and impractical. Determining plant diversity in an area is much easier and less time consuming than determining invertebrate diversity, even if only for one invertebrate taxon. Therefore the ability of plants to act as an indicator of invertebrate diversity is desirable for monitoring the impacts of management practices in protected areas.

1.5. Aims and objectives

Once an area of land is proclaimed as a reserve, it needs effective management and continual monitoring in order to ensure that biodiversity is maintained. Although current burning regimes in the KwaZulu-Natal Drakensberg are effective in maintaining good quality

grassland for grazing this may not be the most ideal burning regime for conserving invertebrates and forbs, the major components of biodiversity. The overall aim of this project was to contribute towards an effective burning regime for conserving biodiversity in the KwaZulu-Natal Drakensberg. This was achieved through a number of objectives, dealt with in chapters three, four, five and six.

The objective of the third and fourth chapters was to determine the effect of fire and fire frequency on invertebrate and flowering forb species diversity within a grassland ecosystem in the KwaZulu-Natal Drakensberg. The IDH was tested to determine whether intermediate burning frequency results in the highest invertebrate and flowering forb diversity, as predicted by the IDH. This will allow for recommendations to be made regarding fire frequency for management of invertebrate and flowering forb species diversity. The fifth chapter's objective was to determine whether fire frequency, time since the last fire, site locality, or a combination of all three environmental variables influenced invertebrate and flowering forb community structure in the grassland ecosystem. The objective of the sixth chapter was to determine whether flowering forb species richness acts as an indicator of invertebrate species richness and to determine whether certain invertebrate taxa act as indicators of overall invertebrate species richness. The use of indicator species in continual monitoring of grassland ecosystems would be useful for biodiversity management.

General site descriptions and materials and methods are dealt with in the second chapter in order to avoid repetition in subsequent chapters. The final chapter presents a summary and management recommendations for burning regimes in the KwaZulu-Natal Drakensberg.

CHAPTER 2

STUDY SITE AND GENERAL METHODS AND MATERIALS

2.1. Study Area

The Drakensberg is a World Heritage Site with rich invertebrate and forb diversity and many endemic species. In the conservation areas of the Drakensberg, burning is used as a management tool. The impact of fire on invertebrate species occurring in the area needed to be determined, and the invertebrate community and its response to fire may be distinct in the region. Giants Castle Game Reserve (Giants Castle) in the central KwaZulu-Natal Drakensberg, South Africa, provided an ideal opportunity for research because of accessibility of sites with different fire frequencies, and the presence of suitable sites in terms of standardized aspect, altitude and slope orientation with different fire frequencies.

The KwaZulu-Natal Drakensberg is currently managed by Ezemvelo KwaZulu-Natal Wildlife (EKZNW). The reserve covers an area of 36 000 ha and ranges in altitude from 1 500 m up to 3 000 m (Rowe –Rowe 1983). The three main geographic divisions in the Drakensberg include the Montane Belt, the Sub-alpine Belt and the Alpine Belt (Killick 1963). The Montane Belt below the sandstone cliffs covers 24 % of Giants Castle and is predominantly short (< 0.05 m), treeless, undulating *Themeda triandra* grassland, providing dense basal cover (Rowe-Rowe 1983). The Sub-alpine Belt covers 63% of Giants Castle (Rowe-Rowe 1983) and is also predominantly undulating *Themeda triandra* grassland (Killick 1963). Summers are mild to cool at night, while winters are very cold with frost, and snow at higher altitudes. The rainy season occurs from September to April and the mean annual rainfall is 1 092 mm (Rowe-Rowe 1983).

2.2. Study sites

An attempt was made to select sites with the same aspect, slope, altitude, the correct burning regime within close proximity to each other and which were accessible while carrying equipment. This ideal was achieved to a large extent where all grassland sites were situated in Highland Sourveld (Acocks 1988) on north-east facing slopes. All of the sites were dominated by *Themeda triandra* grassland and were below the basalt cliffs. Initially GIS maps provided by EKZNW were used to identify and locate grassland sites which differed in fire frequency between 1997 and 2001. After the first sampling period the burning records of Giants Castle dating back to 1994 were also consulted. The GIS maps did not correspond with what was shown in the burning records and this resulted in an uneven number of replicates for the three fire frequencies being sampled.

Sites were situated in three separate valleys that were unfortunately not at the same altitude (Table 2.1) but were found to be comparable. Analysis of variance (ANOVA) showed that there was no significant difference between all three valleys with respect to invertebrate species richness ($F_{2,15} = 3.72$, $P = 0.053$) suggesting that the altitudinal range sampled does not affect invertebrate species richness. However, the least squares difference test (LSD) revealed that valley two had significantly higher species richness than valley three (LSD value = 0.03), even though they were similar in altitude. Valley one and two were not significantly different in terms of species richness (LSD value = 0.69) even though they had the greatest difference in altitude (Figure 2.1). Therefore, for the selected study sites, there is no evidence that invertebrate species richness was influenced by altitude. Community structure may be influenced by locality and altitude, and this is investigated in Chapter 5.

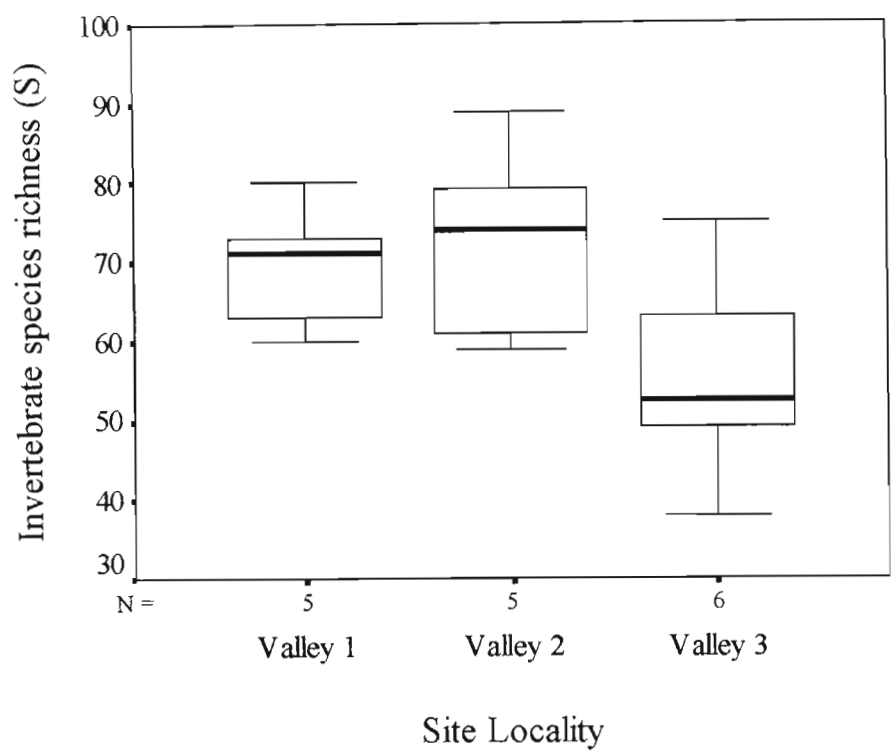


Figure 2.1: Invertebrate species richness in three separate valleys at Giants Castle. Valley 1 = Sites 1 – 5 (average altitude = 1862 m); Valley 2 = Sites 6 – 10 (average altitude = 1654 m); Valley 3 = Sites 11 – 16 (average altitude = 1711 m).

Three replicates of frequent burning (nine fires in nine years), eight replicates of intermediate burning (five fires in nine years) and five replicates of infrequent burning (three fires in nine years) were sampled (Table 2.1). Eight of the 16 sites had been burnt for two consecutive years in 2001 and 2002 (the year of sampling) and the other eight sites had not been burnt in 2001 and 2002.

The 16 sites were situated in three separate areas, however each of the three fire frequencies was not entirely confined to a single valley (Figure 2.2). Valley one and two were separated by the Mtshezana River and were approximately 2 800 m apart. Valley two and three were

separated by the Bushmans River and were approximately 1 500 m apart. Each sampling site was approximately one hectare in size, and was situated in a much larger block burn. Each site was situated on a separate north-east facing slope in order to ensure independence and avoid pseudoreplication.

Sites one to five were situated approximately three kilometers up the jeep track behind the Chimney Pot in valley 1 (Figure 2.2). This area was previously burnt biennially and burning was rotated between spring, autumn and winter (Table 2.1). However in recent years it has become a fire break and was burnt in 2001 and 2002 during autumn. Sites one to five were in a block burn of 445 ha which had been burnt five times in nine years which was considered an intermediate level of disturbance.

Sites six and seven were situated in valley two on the most north-eastern corner of Wilderbees Plateau (Figure 2.2). These two sites were on a permanent fire break that ran from the Mtshezana River up to World's View. They had been burnt nine times in nine years during autumn and were considered to have a high level of disturbance.

Sites eight to ten were also in valley two and ran along the north facing slope of Wildebees Plateau (Figure 2.2). These sites were in a block burn of 745 ha and had been burnt five times in nine years, an intermediate level of disturbance, and burning was rotated between autumn, winter and spring (Table 2.1). These sites were last burnt during winter two years before sampling (2000).




Sites 11 to 14 and 16 were situated in valley three between the road and the Bushmans River from north of Red Hill towards the rest camp. These sites were in a block burn of 375 ha and had been burnt three times in nine years in autumn and spring and the last fire had occurred in 1997, five years before sampling. These sites therefore had a low level of disturbance from fire. Site 12 was located between a rocky outcrop and a small stream with more woody vegetation than the other sites.

Site 15 was also situated in valley three but close to the picnic site at Giants Castle camp. This area was originally thought to be an infrequently burnt area however during the first sampling period it was discovered it was in fact a fire break. Later in the year this site was also mowed. Therefore this site became the third replicate for frequent levels of disturbance. While this site may not be directly comparable with the other two frequently burnt sites (sites six and seven), site 15 was still burnt every year, and had the additional disturbance of mowing in the year of sampling. Mowing occurred after sampling had started which meant that given the time frame of the study, another site could not be substituted. Removing the site from the analyses would have meant that only two frequently burnt sites were sampled, making any statistical analyses impossible. This site had a large sheet of rock to one side with scattered patches of bare soil and vegetation.

Table 2.1: Coordinates, altitude and pattern of burning in each site over a nine-year period. The season of burn varied between autumn (A), spring (S) and winter (W). Time since the last burn varied between sites where sites were burnt within the year of sampling (0), two years before sampling (2) or five years before sampling (5).

Site	Coordinates	Altitude	Year									Time since last burn
			1994	1995	1996	1997	1998	1999	2000	2001	2002	
1	29.20960°S 29.52111°E	1836 m	S		A		W			A	A	0
2	29.20943°S 29.51654°E	1851 m	S		A		W			A	A	0
3	29.20940°S 29.51454°E	1852 m	S		A		W			A	A	0
4	29.20811°S 29.51004°E	1866 m	S		A		W			A	A	0
5	29.20776°S 29.50337°E	1907 m	S		A		W			A	A	0
6	29.22461°S 29.54246°E	1657 m	A	A	A	A	A	A	A	A	A	0
7	29.22530°S 29.54007°E	1663 m	A	A	A	A	A	A	A	A	A	0
8	29.22600°S 29.53510°E	1649 m	A	W		S	W		W			2
9	29.22839°S 29.53145°E	1651 m	A	W		S	W		W			2
10	29.23035°S 29.52968°E	1649 m	A	W		S	W		W			2
11	29.24071°S 29.53791°E	1661 m	A	A		S						5
12	29.24283°S 29.53378°E	1654 m	A	A		S						5

Site	Coordinates	Altitude	Year									Time since last burn
			1994	1995	1996	1997	1998	1999	2000	2001	2002	
13	29.24803°S 29.53136°E	1707 m	A	A		S						5
14	29.25897°S 29.52604°E	1794 m	A	A		S						5
15	29.26401°S 29.52139°E	1770 m	A	A	A	A	A	A	A	A	A	0
16	29.24499°S 29.53098°E	1678 m	A	A		S						5

	Intermediate fire frequency – five fires in nine years
	High fire frequency – nine fires in nine years
	Low fire frequency – three fires in nine years

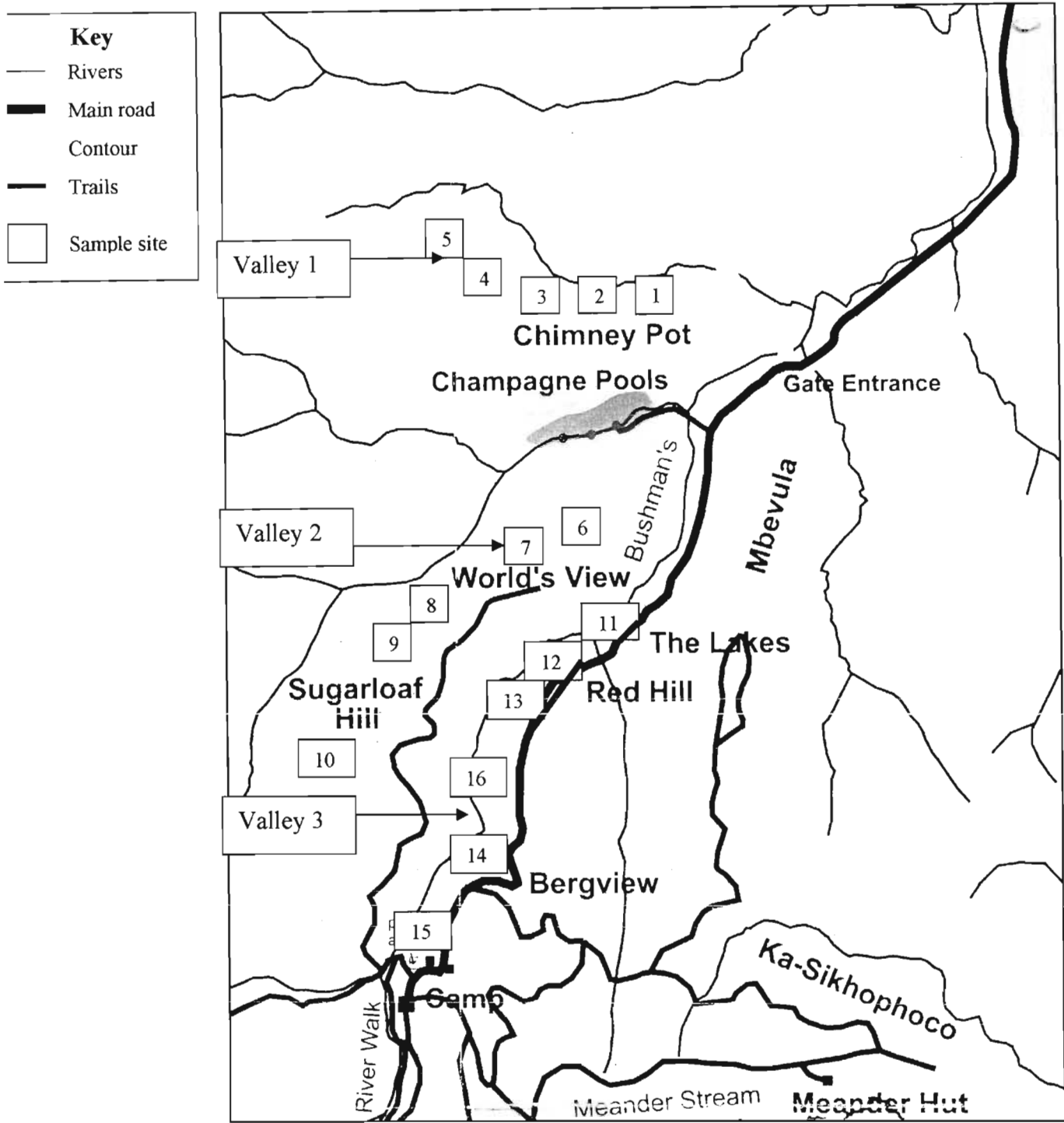


Figure 2.2: Location of sites sampled in Giants Castle. Sites 1-5 intermediately burnt and burnt during the year of sampling; Sites 6 and 7 frequently burnt and burnt during the year of sampling; Sites 8 – 10 intermediately burnt and last burnt two years before sampling; Sites 11 – 14 & 16 infrequently burnt and last burnt five years before sampling; Site 15 frequently burnt and burnt during the year of sampling.

2.3. Selected taxa

2.3.1. Invertebrates

A multi-taxa approach to assessing biodiversity is recommended (Kotze & Samways 1999) where the chosen taxa need to differ in their functional groups, body sizes, mobilities and life histories.

In terms of life history, insects can either be exopterygotes or endopterygotes. Picker *et al.* (2002) gives a description of these life histories as follows. Exopterygotes are the more primitive groups where the eggs hatch into nymphs, which resemble adults in both body form and habits, but are initially wingless. As they go through successive moults, the nymphs develop wing buds on the outside of their bodies which only become functional and expand to their full size after the last moult. The eggs of endopterygotes hatch into caterpillars or grub-like larvae, which are unlike the adults in habits and appearance. The larvae enter a separate immobile pupal stage, during which the entire body is reorganised into the adult form. The pupal stage of endopterygotes is totally immobile and could be more affected by fire than the nymphs of exopterygotes.

According to Lawrence (1987) millipedes lay several hundred small round eggs at a time. These eggs hatch into larvae with three pairs of legs. After their first moult they acquire more legs and body rings and this allows them to become more active. It takes more than a year to reach the size of a fully grown millipede. Each moult can last for three weeks, during which time the skin is soft and movement and feeding are impossible. Millipedes would be most severely affected by fire during this time.

Earthworms are hermaphrodites therefore all adult earthworms lay eggs into cocoons outside the body (Purves *et al.* 1995). The cocoon is shed and miniature worms emerge and live independently in the soil. Fire may not have as much of an effect on earthworms as above-ground invertebrates.

Spiders lay eggs into egg sacs and emerge looking the same as adults but smaller (Martin 1991). Spiders grow rapidly through a series of moulting which occurs from five to nine times before reaching adulthood (Leroy & Leroy 2000). Spiders generally only live for one year and would be most effected by fire during moulting.

The taxa chosen for this study not only differed in their life histories but also incorporated a range of different functional groups including herbivores, predators, pollinators and detritivores. They also varied in their mobility from highly mobile taxa such as butterflies to relatively immobile taxa such as earthworms. They were also known to be abundant in grasslands and had been relatively well studied by taxon experts and could therefore be identified to species level. The taxa chosen for study are described below. In subsequent chapters “total invertebrate species...” refers to all the species sampled in the following 11 taxa rather than to all invertebrate species.

Phylum Arthropoda

Supaclass Hexapoda

Class Insecta

Order Hymenoptera

Family Formicidae (Ants): Commonly found in grasslands; predators, decomposers, nectar feeders and seed predators; nests sedentary but adults fairly mobile; endopterygotes; good indicators of the extent of biodiversity in an

ecosystem (Robertson 2002, pers comm^{*}); act as indicators of ecosystem condition because their assemblages reflect the degree of habitat disturbance or successional state in a community (Parr *et. al.* 2002).

Superfamily Apoidea (Bees): Occur in all terrestrial habitats and biomes; pollinators and closely linked to the health and diversity of the flowering plant community within a grassland ecosystem; highly mobile; endopterygotes (Eardley 2002, pers comm.^{*}).

Order Orthoptera (Grasshoppers): Major primary consumers and account for a high percentage of the above-ground phytophagous insect biomass (Chambers & Samways 1998); found abundantly in grassland habitats, easily sampled and present throughout summer and autumn (Chambers & Samways 1998); mobile; exopterygotes.

Order Hemiptera

Family Cicadellidae (Leafhoppers): Commonly found in grassland; phytophagous; some highly migratory and others wingless therefore less mobile; can be effectively used as indicators of habitat destruction; exopterygotes (Stiller 2002, pers comm.^{*}).

Order Lepidoptera (Butterflies): Adults highly mobile; found in all vegetation types; many endemics found in grassland; nectarivores / flower feeders; charismatic group; endopterygotes.

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Order Diptera

Family Asilidae (Robber flies): Occur in all terrestrial habitats and biomes; predators; highly mobile; endopterygotes (Londt 2002, pers comm^{*}).

Family Bombyliidae (Bee flies): Highly mobile; important as pollinators; range of body sizes; endopterygotes (Picker *et al.* 2002).

Family Syrphidae (Hover flies): Highly mobile; feed on pollen and nectar; endopterygotes (Picker *et al.* 2002).

Class Arachnida

Order Araneae (Spiders): Abundant and diverse, taxonomically rich at species, genus and family levels and easily sampled (New 1999); predators; mobile; include grass-dwellers, flower dwellers and ground dwellers (Dippenaar-Schoeman 2002, pers comm^{*}).

Superclass Myriapoda

Class Diploda (Millipedes): Detritivores; fairly mobile; inhabit the soil and ground surface (Hamer 2002, pers comm^{*}).

Phylum Annelida

Class Oligochaeta (Earthworms): Detritivores; slow moving and low mobility; soil inhabitants of grasslands; high level of endemism in South Africa (Plisko 2002, pers comm^{*}).

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Fire could have more of a negative effect on wingless invertebrates (Table 2.2) than winged invertebrates because they are considerably less mobile. Certain invertebrate guilds (Table 2.2) may also be more affected by fire than others. Herbivores and pollinators are directly dependant on grass or forbs for their survival and could be more affected by frequent fires than predators that are not dependant on vegetation as a food source. For these reasons wingless invertebrates and invertebrate guilds have been considered in this study.

Table 2.2: Wingless invertebrate taxa and four different functional groups.

Wingless invertebrates	Functional groups (guilds)			
	Herbivores	Pollinators	Predators	Detritivores
Ants	Grasshoppers	Butterflies	Ants	Earthworms
Brachypterous grasshoppers	Leafhoppers	Bees	Robber flies	Millipedes
Brachypterous leafhoppers		Bee flies	Spiders	
Spiders		Hover flies		
Earthworms				
Millipedes				

2.3.2. *Plants*

Hemicryptophytes, geophytes and therophytes are three life forms that are found in grasslands (Rutherford & Westfall 1994). Hemicryptophytes are the most abundant life form followed by therophytes and then geophytes (Freeman 1998). These life forms are described by Rutherford and Westfall (1994) as follows. Hemicryptophytes are perennial herbaceous plants with their renewal buds at or close to ground level. They include perennial graminoids

(grasses), aphyllous restioids and perennial broad-leaved herbs (forbs). Geophytes are perennial plants with renewal buds below ground level and include plants with bulbs, corms, tubers, non-graminoid rhizomes and rootstocks. Therophytes include herbaceous graminoids and forbs that are annual or ephemeral and therefore complete their life cycle in one year or less. Freeman (1998) describes forbs as non-graminoid herbs *i.e* any broad-leaved herbs, geophytes and therophytes. As most studies have dealt with the diversity of grasses but largely excluded indigenous forbs, this study will only include indigenous forbs.

2.4. Sampling strategy

Sampling took place three times during 2002 in late summer (March), spring (September) and summer (November). The sampling strategy was replicated in all three sampling periods.

However soil quadrats looking specifically for earthworms were not dug in the first late summer sampling period because most earthworms were likely to have been in aestivation. In each sampling period two people carried out the active sampling (myself and one assistant) so that the sampling effort was standardized as far as possible. It would have been preferable to sample each site at the same time, on the same day but logistically this was not possible.

However each of the different valleys *ie.* sites 1-5, 6 –10 and 11–16 were sampled at the same time of day on different days. Replicating sites which were sampled on different days and limiting sampling to a week minimized temporal effects and the impact of slight variations in weather on the data collected.

2.4.1. Invertebrates

Quantified sampling of invertebrate diversity is extremely time consuming because of the range of sizes, behaviours and microhabitats dealt with (Slotow & Hamer 2000).

Nevertheless, quantified sampling is essential in invertebrate surveys in order to compare species diversity effectively. New (1998) suggested the use of a number of different sampling methods to help compensate for the bias of any individual method. However the suite of methods used must be feasible in terms of time and equipment required to do the sampling as well as the processing of material sampled. An additional consideration is the impact of the sampling on the habitat and invertebrate populations.

In most situations active sampling seems to be more effective than passive sampling. Passive sampling in the form of pitfall trapping has in the past been a popular method of sampling. However, the use of pitfall traps can result in large quantities of material being sampled and non-focal groups being discarded. Pitfall traps also result in less mobile taxa being inadequately sampled (Slotow & Hamer 2000), hence the use of active sampling rather than pitfall trapping in this study.

The sampling methods selected were active netting of target insects along transects, sweep netting, yellow pan traps and soil quadrats. At each site five 50 m transects spaced ten metres apart were walked up and down the slope alternately. An insect net was used to collect butterflies, robber flies, bee flies, hover flies and bees (Eardley 2002, pers. comm.*; New 1991; New 1998), along the transect. Any species from these taxa that were seen within one metre on either side of the transect were dry collected and pinned as soon as possible. Usually five metres on either side of the transect line are sampled when collecting butterflies (Pollard and Yates 1993) but the narrow width of the transects in this study was selected in order to overcome the different visibility in long, thick and short grass at the different sites. Any

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millipedes that were seen while walking the transect were also collected. Transects were walked between 09h00 and 15h00 on clear and warm days.

Sweep netting of the grass was used to sample leafhoppers, grasshoppers, robber flies, bee flies, hover flies, bees and spiders. This method was suggested for these taxa by various experts (Dippenaar-Schoeman 2002, pers. comm.*; Eardley 2002, pers. comm.; Stiller 2002, pers. comm.*) or in the literature (New 1991; New 1998; Samways 1990). At each site five 50 metre sweep netting transects, spaced 10 metres apart and 10 metres from the adjacent active netting transects, were walked at a steady pace alternately up and down the slopes with 60 sweeps sampled for each transect separated by one pace and on alternating sides of the transect. Grasshoppers were dry collected and any other taxa collected were preserved in 70 % ethyl alcohol. Samways and Moore (1991) do suggest visual counting of grasshoppers as the most effective sampling method but they also found that sweep netting gave good results. For the purpose of this study it was considered to be more accurate to use sweep sampling. To sample grasshoppers using visual counts would require the community structure at each site to be well known before the counting could be carried out, since to the untrained eye most of the grasshoppers look the same from a distance. This would not have been possible within the given time frame for this study.

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Yellow pan traps effectively catch bees, spiders, ants and leafhoppers (Dippenaar-Schoeman 2002, pers. comm.^{*}; Eardley 2002, pers. comm.^{*}; Robertson 2002, pers. comm.^{*}; Stiller 2002, pers. comm.^{*}). At each site six circular yellow pan traps (approximately 15 cm diameter) were placed 10 m apart in a line transect leading up the slope and these were left for 24 hours. Pan traps were filled with glycerol and water to which a small amount of liquid detergent was added to break the surface tension of the liquid. Any invertebrates collected were preserved in 70 % ethyl alcohol.

Soil sample quadrats were used to collect earthworms and millipedes at each site (Plisko 2002, pers. comm.^{*}). These soil samples were only dug in the spring and summer sampling periods and always after or during rain. Six randomly placed 30 cm x 30 cm soil quadrats were dug at each site to a depth of 30 cm. The quadrat size was purposely small because this is a labour intensive method of sampling and also because of the need to minimise the impact it has on the habitat. Earthworms were placed in four percent formalin and then preserved in 75 % alcohol.

All specimens were sorted to morphospecies and sent to relevant experts for identification. Spiders have been sent to the National Arachnid Collection of the Agricultural Research Council (ARC), bees and leafhoppers have been sent to the National Insect Collection (ARC) and robber flies have been sent to the Natal Museum. All other specimens are currently maintained as a reference collection at the School of Biological and Conservation Sciences,

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University of KwaZulu-Natal (Pietermaritzburg) and will eventually be accessioned into appropriate national institutions.

2.4.2. *Plants*

Previous examples of quantified sampling of forbs are limited. The frequency method, frequency-score method and the importance-score method all use a nested quadrat system and have been found to be accurate estimates of forb species richness in previous studies (see Morrison *et al.* 1995; Uys *et al.* 2004). Five metre by five metre quadrats have been found to be an optimal size for sampling plant cover and species richness in some vegetation types, determined by calculating a species-area curve (Dean & Milton 1995; Shimwell 1971). Using replicate samples of five metre by five metre quadrats would allow for accurate comparisons to be made between grassland plots with varying fire frequencies.

Within each of the 16 grassland sites, five quadrats of five by five metres were sampled. These plots were randomly placed within each site. Every new forb recorded was collected in order to build up a reference collection that is kept in the herbarium at the University of KwaZulu-Natal (Pietermaritzburg). Grasses were not sampled. Only forbs that were flowering at the time of sampling were taken into account as the flowers are a critical component used in the identification of the species. As many forbs are multi-stemmed and have more than one flower per plant, the abundance of each forb species in each quadrat was recorded where one forb was considered a single individual if it arose from a seemingly separate root from a neighbouring forb of the same species. The plant sampling method should be considered a relative measure allowing for comparison of sites, rather than an

absolute count of all species present which would require sampling continuously to record all flowering plants throughout the year.

2.5. Analysis

2.5.1. Diversity indices

Species diversity consists of both species richness (the number of species within the community) and species evenness (distribution of species abundance among the species) (Ludwig & Reynolds 1988). Species diversity is measured by using diversity indices which attempt to combine both richness indices and evenness indices. In the following chapters the term “species diversity...” incorporates the species diversity, richness and evenness indices as well as unique and endemic species.

Shannon’s diversity index (H') is a measure of the degree of uncertainty in predicting to what species an individual chosen at random from a collection of S species and N individuals will belong (Ludwig & Reynolds 1988). While the Shannon index is sensitive to sample size, and interpretation may be difficult, many long-term investigations have chosen it as their benchmark measure of biological diversity (Magurran 2004). For this reason, the Shannon index has been used in this study to ensure that the results are comparable to other similar ecological studies. Species diversity indices are often difficult to interpret therefore species richness and species evenness are often represented as separate values, as presented in this study. Species richness (S) is the total number of species in a sample, and does not consider abundance. Evenness incorporates abundance and gives more insight into the distribution of species within the community *ie.* species may be equally abundant or one species may be dominating in the community. The modified Hill’s ratio ($E5$) is the most appropriate evenness

index to use because it is relatively unaffected by species richness. This index approaches zero as a single species becomes more and more dominant in a community (Ludwig and Reynolds 1988).

$$H' = - \sum_{i=1}^{s^*} (p_i \ln p_i)$$

$$E5 = \frac{(1/\lambda) - 1}{e^{H'} - 1}$$

Where λ = Simpson's index

2.5.2. Statistical analysis

2.5.2.1. Calculation and comparison of species richness, diversity and evenness

Invertebrate and flowering forb species diversity (H'), richness (S) and evenness ($E5$) were calculated for each site using SPDIVERS (Ludwig & Reynolds 1988). All statistical analyses were performed using SPSS 11 (Norusis 1994). The Kolomogorov-Smirnov goodness of fit test showed that all data were normally distributed. Analysis of variance (ANOVA) determined whether two or more means were significantly different, and a post-hoc test determined which of the means being tested were significantly different. The post-hoc test used, least squares difference (LSD), is a robust test that is often used with small sample sizes.

ANOVA was used to compare invertebrate and flowering forb species diversity, richness and evenness between eight sites that had been burnt in 2001 and 2002 and eight sites that had not been burnt during those two years. ANOVA with a post-hoc LSD was used to compare total invertebrate and flowering forb species diversity, richness and evenness between frequent,

intermediate and infrequently burnt sites. The same analysis was used to compare wingless invertebrate species diversity, evenness and richness between the three fire frequencies. Invertebrate species richness of three guilds (pollinators, herbivores and predators) were compared between the three fire frequencies, also using ANOVA with a post-hoc LSD.

For infrequent burning, site 16 was not sampled in the first sampling period which resulted in exceptionally low species richness in this site, therefore it was not used as a replicate sample in Chapter three and four.

Boxplots are used in chapters three and four to show the median, interquartile range with 50% of the values, highest and lowest values as well as outliers (Figure 2.3). Because of the different number of replicates for each burn frequency, boxplots were used so that the variation within the samples could be clearly seen.

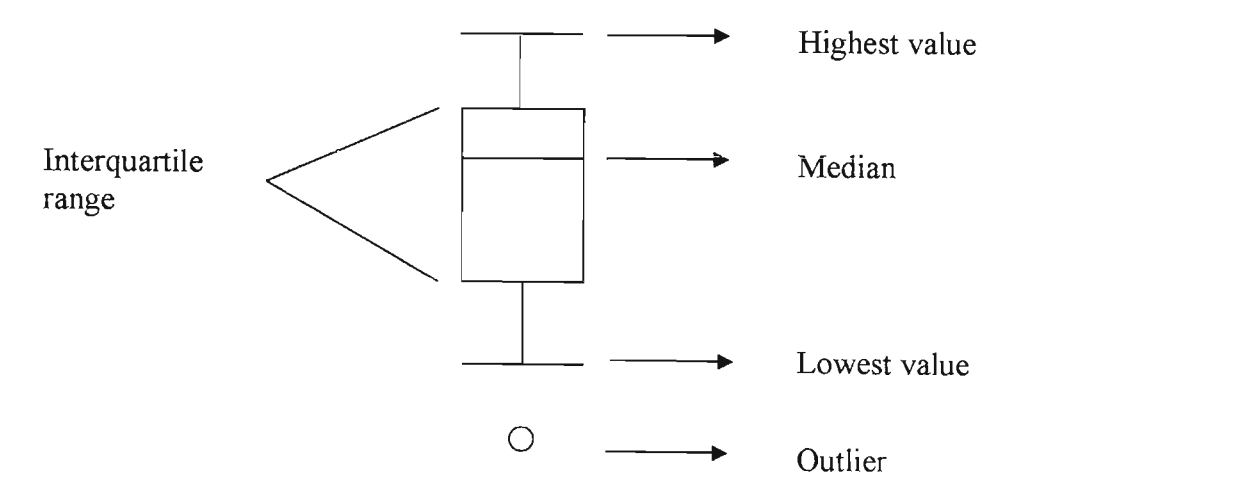


Figure 2.3: Boxplot with median, highest and lowest values, interquartile range and outliers.

2.5.2.2. *Unique species*

Unique species are those that were only found in either burnt or unburnt sites or in one specific burn frequency. The number of unique invertebrate and flowering forb species in burnt and unburnt sites and in each burn frequency was determined and compared.

Invertebrate and flowering forb species endemic to South Africa and KwaZulu-Natal and any new species found during sampling were compared between burnt and unburnt sites as well as between all three burn frequencies. For invertebrates, the number of unique species, South African endemics, KwaZulu-Natal endemics and new species in each burn frequency were compared with the Chi-square test to determine whether one burn frequency had significantly more unique, endemic or new species than the other two burn frequencies.

2.5.2.3. *Invertebrate and flowering forb community structure and environmental influences*

Ordination analysis clusters those communities that are similar in both species composition and relative abundance of each species. Ordination also determines the extent to which environmental variables are correlated with the species composition of clustered communities. Lepš & Šmilauer (2003) explained that ordination can be constrained (direct gradient analysis) or unconstrained (indirect gradient analysis). Constrained ordination is used to determine whether there is a relationship between multiple response variables (in this case invertebrate and flowering forb species composition) and the measured environmental variables.

Unconstrained ordination is used to determine the correlation between the multiple response variables but does not take environmental variables into consideration and is used when environmental variables have not been measured. In Chapter 5, constrained ordination with redundancy analysis (RDA) was used to determine the effect of three environmental variables (locality, fire frequency and time elapsed since the last fire) on invertebrate and flowering forb

species composition. RDA is the linear method of constrained ordination, used when species data is relatively homogenous resulting in shorter environmental gradients i.e. environmental gradient < 4 SD, determined by detrended canonical correspondence analysis (DCCA) (Lepš & Šmilauer (2003). The Monto Carlo permutation test tests the null hypothesis that the species composition is independent of the environmental variables (Lepš & Šmilauer 2003). The Monte Carlo analysis using 199 permutations was used to determine whether communities were significantly correlated with environmental variables. These analyses were performed in CANOCO 4.5 (ter Braak & Smilauer 2002). Site 15 was excluded from the analysis because it could have differed in species composition due to the site being mowed as well as burnt. Site 16 was also excluded from the analysis because it was not sampled during the first sampling period (late summer).

Plant species can be classified as facilitators, inhibitors and tolerators. Facilitators are species that move into an area after a disturbance to prepare the ground for later successional species. Once the facilitators have changed the environment sufficiently inhibitors arrive in the area and have the ability to maintain their captured space from later would-be colonists. Tolerators are those species which can survive with low levels of resources and out-compete other species (Kikkawa & Anderson 1986; Putman 1994). In Chapter 5, facilitators, inhibitors and tolerators were classified as flowering forb species that were only found in grasslands burnt within the year of burning (sites one to seven and 15), two years after burning (sites eight to ten) and five years after burning (11 to 14 and 16) respectively. Only species represented by more than five individuals were taken into consideration as this was the natural break-point in the abundance data.

Classification or cluster analysis assumes that communities consist of relatively discrete entities. It does not take environmental variables into consideration and simply groups similar species compositions together in subsets, and similar subsets may be further combined (Begon *et al.* 1996). In order to determine which grassland sites were similar in terms of invertebrate and flowering forb species composition, hierarchical cluster analysis was performed on flowering forb and invertebrate species data using SPSS11 (Norusis 1994). Dendrograms using average linkage between groups were produced of the invertebrate and indigenous flowering forb communities in each grassland site.

2.5.2.4. Identification of potential species richness indicators

Linear regression analysis was performed in Chapter 6 to determine whether flowering forb species richness is an indicator of invertebrate species richness and to determine whether certain individual invertebrate taxa are indicators of invertebrate species richness. Linear regression analysis with 95% confidence intervals was performed using SPSS 11 (Norusis 1994). Correlations between invertebrate and flowering forb species richness were determined using total invertebrate species richness, wingless species richness, herbivore, predator and pollinator species richness against total flowering forb species richness. Total invertebrate and flowering forb species richness refers to all the invertebrate and flowering forb species that were sampled in this study. Correlations between invertebrate and flowering forb species richness were also tested at different times of the year (March, September and November). Species richness of the most abundant flowering forb family, the Asteraceae, was compared to total invertebrate species richness and invertebrate species richness in each sampling period (March, September and November) to investigate any relationships. Correlations between the species richness of the richest individual invertebrate taxa and total invertebrate species

richness were compared to identify potential indicators of overall species richness. The numerical relationship between species richness in different taxa was extrapolated for several of the stronger correlations.

CHAPTER 3

THE INFLUENCE OF FIRE FREQUENCY ON INVERTEBRATE DIVERSITY IN A GRASSLAND ECOSYSTEM

3.1. Introduction

3.1.1. Fire and invertebrates

Fire has long been recognised as an important management tool used around the world to maintain grassland ecosystems. Alternating variables such as fire frequency, fire intensity, and the time of year that the grasslands are burnt promotes heterogeneity and patchiness which are important elements in ecosystem functioning (Christensen 1997). However most studies on heterogeneity and patchiness in the landscape have been botanical and the extent to which invertebrates are affected by fire remains unclear (Bigalke & Willan 1984; Parr *et al.* 2002; Zimmer & Parmenter 1998). Many entomologists criticize the use of fire in grasslands and recommend the reduction or elimination of burning as a management activity (Panzer 2002). This is often as a result of the high mortality of invertebrates directly after a fire, an area which has received more attention than the long term effects of current burning regimes in grassland ecosystems.

Tainton and Mentis (1984) described several immediate effects of fire on invertebrates in a tropical African savanna. Firstly, the strong flying groups disappear. Secondly, fire has a weak effect on the fauna of the soil surface, probably because of the relatively low temperatures at and below the soil surface. Thirdly, large invertebrates are more vulnerable to fires than small ones. Directly after fire, several strata are reduced to one, thus the immediate effect of fire on grassland invertebrates is to reduce the diversity of niches. Recorded mortality after a fire is not, in itself, an indication that the fire has had a significant impact on

the population (Whelan 1995). There are two reasons for this. Firstly, individuals that died in the fire were not necessarily those contributing to population dynamics. If fire kills only weakened, sick, old or injured individuals that were destined to die even without the fire, there may be an alteration in the timing of their deaths but little or no effect on population – level fecundity. Secondly, any mortality caused directly by fire may be compensated for after some time by increased immigration, fecundity or survivorship of the remaining organisms (Whelan 1995).

The few existing studies on invertebrate responses to fire indicate that plant dwelling species suffer high initial mortalities, but are replaced quickly from unburned nearby populations as the ecosystem recovers (Zimmer & Parmenter 1998). Panzer (2002) found that although invertebrate species declined initially after a fire the majority of species, even those that are fire sensitive, recovered within a year of burning and the rest within two years of the fire. Detritivores and other soil dwellers are initially affected very little by the fire, but subsequent changes in the environment brought about by the fire result in mortalities (Zimmer & Parmenter 1998). Morris (1975) showed that burning had a severe direct effect on numbers of Heteroptera and Auchenorrhyncha in carboniferous limestone grasslands in Britain with what he refers to as a long-lasting effect (at least six months). Mortality of invertebrates due to fire may be higher in those that are flightless (Bigalke & Willan 1984). However flightless species such as land snail communities in the Mediterranean initially decreased in diversity and abundance after a fire but proved to be resilient to fire perturbation as the community completely recovered one year after the fire (Kiss & Magnin 2003). It would appear that fires result in a temporary redistribution of faunal communities away from the burned patch initially, but later they tend to recolonize recently burned areas (Scholes & Walker 1993).

3.1.2. The effect of fire frequency on invertebrates

Fire frequency determines how often vegetation is returned to the beginning of the successional process (Chambers & Samways 1998). The time interval between successive disturbances is important as it may have a significant effect on the response of the community (Hobbs & Huenneke 1992). With the change in vegetation cover food supplies for various species are either diminished or improved and low cover availability may encourage some species but exclude others (Bigalke & Willan 1984). Certain phytophagous species such as grasshoppers benefit from frequently burnt grass due to the high crude protein, phosphate and calcium content of the burnt grass during the growing season (Chambers & Samways 1998), and other phytophagous invertebrates probably also respond in a similar way to frequently burnt grasslands. In Midwestern North American tallgrass prairie Panzer and Schwartz (2000) found that species richness and mean population densities of invertebrates were generally higher on frequently-burned sites when compared with invertebrate richness in grasslands excluded from fire.

Fire frequency is also related to fire intensity (Bigalke & Willan 1984). A reduced fire frequency results in a more intense fire because of the accumulation of moribund grass. However frequent fires are less intense because of a reduced grass load, this results in a more patchy burn providing refugia for invertebrates (Bigalke & Willan 1984). Studies of fire intensity in forests revealed that moderate and low intensity fires cause initial declines in species diversity however given a certain amount of time these communities recover (Abbott 1984; Neumann & Tolhurst 1991). In the Jarrah Forest of Western Australia invertebrate taxa took three years to recover in density after a moderate intensity fire (Abbott 1984). In dry

sclerophyll eucalypt forest of west-central Victoria epigeal arthropods took up to one year to recover and earthworms took up to three years to recover from low intensity fires (Neumann & Tolhurst 1991).

3.1.3. *Disturbance and grassland dynamics*

The intermediate disturbance hypothesis (IDH) is based on the argument that only a few species (ruderals) can persist when exposed to frequent disturbance; only a few species *ie.* the longest-lived, best competitors and those able to regenerate without disturbance, can persist in the absence of disturbance; but many species can survive at an intermediate level of disturbance in a region comprising patches in various stages of recovery (Hobbs & Huenneke 1992). However the IDH may not necessarily hold true in a grassland ecosystem where fire is the disturbance.

Other well known theories on grassland dynamics include the diversity-stability hypothesis and the diversity-productivity hypothesis as well as many other diversity related hypotheses. The diversity-stability hypothesis has largely been tested in plant communities and suggests that the more diverse an ecosystem in terms of plant species richness the greater the productivity which leads to greater nutrient retention in ecosystems and greater stability in the ecosystem as a whole (Tilman 2000). The same should be true for invertebrate communities. Stability can refer to resistance to disturbance, resilience (the rate of recovery after a disturbance), and constance (degree of temporal stability) (Tilman 1996b). These diversity theories have been supported in numerous studies focused specifically on grasses (Tilman *et al.* 1996; Tilman 1996a,b; Tilman & Downing 1994).

3.1.4. Burning regimes

Many areas of the KwaZulu-Natal Drakensberg are burnt annually as fire breaks in order to prevent hazardous run-away fires. The remaining grassland areas are divided into large blocks (sometimes over 400 ha) that are burnt predominantly in a biennial pattern but with the season of burn varying between autumn, winter and spring, otherwise known as rotational block burning. Burning also often takes place after rain thus creating a cooler, patchier burn.

Brockett *et al.* (2001) promote a patch mosaic burning regime in savanna ecosystems as it results in maximum spatial heterogeneity. However they warn that patch mosaic burning, created through point ignitions and left to burn out, may not be an effective burning regime for landscapes with diverse mixtures of forest, grassland and riparian valleys. Furthermore one of the main reasons for developing the patch mosaic burning regime was to conserve a number of large herbivores in the same confined area that require different habitats for their survival. Invertebrates were not taken into consideration when this burning regime was developed.

In the KwaZulu-Natal Drakensberg fire is the major disturbance factor within the grassland ecosystem. The biennial burning regime promoted in the Drakensberg is concerned primarily with maintaining a *Themeda triandra* grassland sward that is ideal for large grazing herbivores but is not necessarily the most ideal situation for promoting invertebrate diversity.

Invertebrates are an important component of biodiversity as they may contribute 95% of biodiversity at the species level and they are critical for ecosystem functioning (Myers *et al.* 2000). It is feared that current burning regimes may be having a negative impact on invertebrates, however there is a lack of data supporting a loss of invertebrate biodiversity as a result of current burning practices (Panzer & Schwartz 2000). The influence of fire frequency

on invertebrates specifically requires more investigation (Neumann & Tolhurst 1991; Parr *et al.* 2002).

3.1.5. Aims and objectives

Effective management of grasslands requires knowledge of the effects of fire on species richness on a large scale *ie.* greater than 100m², in order to simulate block burning that often takes place in grasslands (Chambers & Samways 1998; Cowling 1987). If realistic results are to be obtained large plots which mimic natural grasslands are required for sampling. The overall aim of this study was to determine the effect of fire and fire frequency on invertebrate diversity in order to contribute towards an effective burning regime in the KwaZulu-Natal Drakensberg that will promote and conserve maximum invertebrate diversity. This will be achieved through a number of objectives: (1) To compare invertebrate diversity in grasslands burnt for two consecutive years with grasslands left unburnt during those two years; (2) To determine whether grasslands burnt at an intermediate frequency have higher invertebrate diversity than grasslands burnt at a high or low level of frequency. This will ultimately result in the IDH being rejected or accepted in this montane grassland ecosystem where fire is the disturbance; (3) To test the IDH in montane grasslands in relation to wingless invertebrates; (4) To test the IDH in montane grasslands for invertebrate guilds (herbivores, predators and pollinators); (5) To determine the change in invertebrate diversity with increasing time since the last disturbance.

3.2. Materials and Methods

Refer to Chapter 2

3.3. Results

3.3.1. Total species richness and abundance

A total of 3 160 individuals, 225 species, 162 genera and 38 families of invertebrates were sampled over the three sampling periods (Appendix 1). The first sampling period in March produced 148 species, 27 additional species were found in September and a further 50 were found in November.

Species that are considered to have a high conservation value are those that are endemic to South Africa, KwaZulu-Natal or the Drakensberg. New or undescribed species are also important as they might be endemic to South Africa, KwaZulu-Natal or the Drakensberg. A total of 24 species sampled were endemic to South Africa, seven were endemic to KwaZulu-Natal, none were endemic to the Drakensberg and 14 new species were found (Appendix 1).

3.3.2. Comparison of invertebrates in burnt and unburnt grasslands

Burnt grasslands were those that had been burnt for two consecutive years in 2001 and 2002 and unburnt grasslands had not been burnt in those two years. Burnt grasslands produced more species (198) and individuals (1 800), than unburnt grasslands where 160 species and 1 401 individuals were found (Table 3.1). At a family level, burnt grasslands were represented by 36 families and unburnt grasslands by 32 families.

Species that are only found in either burnt or unburnt grasslands are considered to be unique. Burnt grasslands had more unique species (74) than unburnt grasslands (37) (Appendix 1). Of the unique species in burnt grassland 55 % were singletons (a single specimen collected) and in unburnt grasslands 59 % were singletons. Of the 45 endemic and new species sampled, 14

species were unique to burnt grasslands and three were unique to unburnt grasslands (Table 3.2 – see Appendix 1 for species names).

In comparing the average invertebrate species diversity (H') between burnt and unburnt grasslands, burnt grasslands had significantly higher species diversity than unburnt grasslands (ANOVA: $F_{1,13} = 4.65$, $P = 0.05$) (Figure 3.1a). Burnt and unburnt grasslands showed no significant difference in species evenness ($F_{1,13} = 0.63$, $P = 0.44$). The species evenness values for both communities were closer to one than zero thus indicating that there was a relatively even spread of species within both communities (Figure 3.1b). Species richness was significantly higher in burnt grasslands than in unburnt grasslands ($F_{1,13} = 7.65$, $P = 0.02$) (Figure 3.1c). For unburnt grassland Site 8 had exceptionally high species richness.

Table 3.1: The total number of invertebrate families, genera and species sampled at Giants Castle from different fire frequencies. 1 = frequent burning, 2 = intermediate burning and 3 = infrequent burning.

Taxa	Families with number of (genera, species)	Number of species (individuals) in burnt and unburnt grasslands and in three burn frequencies				
		Burnt	Unburnt	1	2	3
Ants	Formicidae (10, 16)	14 (240)	15 (111)	10 (50)	14 (240)	8 (17)
Grasshoppers	Acrididae (13, 15)	15 (147)	9 (166)	11 (68)	14 (167)	6 (78)
	Lentulidae (2, 2)	2 (6)	2 (6)	2 (4)	2 (10)	1 (2)
	Tetrigidae (2, 2)	2 (13)	2 (13)	2 (7)	2 (10)	1 (2)
	Thericleidae (1, 1)	1 (1)	1 (1)	1 (1)	0	1 (1)
	Pyrgomorphidae (1, 1)	1 (1)	1 (1)	1 (1)	1 (1)	0
	Cicadellidae (29, 47)	44 (329)	35 (518)	39 (160)	37 (315)	30 (358)
Butterflies	Hesperiidae (4, 5)	3 (6)	4 (7)	2 (3)	3 (4)	3 (6)
	Nymphalidae (6, 6)	6 (18)	3 (8)	4 (9)	5 (12)	3 (5)
	Pieridae (3, 3)	3 (6)	1 (1)	1 (1)	3 (6)	0
	Lycaenidae (2, 2)	2 (4)	0	0	2 (4)	0
	Papilionidae (1, 1)	1 (1)	0	0	1 (1)	0
	Halictidae (9, 17)	15 (122)	11 (33)	8 (31)	14 (91)	10 (13)
Bees	Apidae (5, 6)	4 (28)	3 (4)	1 (7)	3 (25)	2 (3)
	Collectidae (1, 1)	1 (7)	1 (5)	0	1 (8)	1 (3)
	Megachilidae (2, 2)	0	2 (2)	0	2 (2)	0
	Asilidae (8, 11)	11 (109)	7 (37)	5 (41)	11 (116)	6 (10)
Robber flies	Asilidae (8, 11)	11 (109)	7 (37)	5 (41)	11 (116)	6 (10)
Bee flies	Bombyliidae (3, 3)	3 (4)	0	3 (5)	0	0

Taxa	Families with number of (genera, species)	Number of species (individuals) in burnt and unburnt grasslands and in three burn frequencies				
		Burnt	Unburnt	1	2	3
Hover flies	Syrphidae (3, 3)	3 (2)	2 (5)	2 (11)	3 (3)	1 (1)
Spiders	Thomisidae (8, 18)	17 (326)	14 (122)	13 (70)	14 (248)	11 (55)
	Philodromidae (4, 4)	4 (15)	2 (6)	2 (23)	4 (12)	2 (2)
	Salticidae (8, 12)	10 (42)	8 (54)	8 (39)	12 (30)	5 (41)
	Linyphiidae (6, 6)	5 (13)	5 (11)	4 (32)	4 (9)	3 (8)
	Araneidae (5, 10)	8 (198)	10 (115)	8 (27)	7 (220)	10 (62)
	Theridiidae (7, 7)	3 (7)	5 (8)	2 (12)	5 (10)	2 (2)
	Dictynidae (2, 2)	1 (7)	2 (73)	1 (5)	2 (21)	2 (52)
	Clubionidae (1, 2)	2 (15)	2 (6)	2 (4)	2 (12)	2 (4)
	Oxyopidae (1, 1)	1 (2)	1 (2)	1 (2)	1 (1)	1 (1)
	Pisauridae (1, 1)	1 (3)	0	1 (1)	0	0
	Tetragnathidae (1, 2)	2 (23)	2 (13)	1 (1)	2 (24)	2 (7)
	Hahniidae (1, 1)	1 (1)	1 (2)	1 (1)	1 (1)	1 (1)
	Lycosidae (3, 4)	3 (21)	2 (10)	0	2 (22)	2 (6)
	Scytodidae (1, 1)	0	1 (1)	0	0	1 (1)
	Spirostreptidae (2, 2)	2 (21)	1 (1)	1 (8)	2 (21)	1 (1)
Millipedes	Gomphodesmidae (1, 1)	1 (1)	0	0	1 (1)	0
	Odontopygidae (1, 1)	1 (1)	0	0	1 (1)	0
	Michrochaetidae (2, 4)	3 (54)	4 (61)	3 (13)	3 (45)	4 (57)
Earthworms	Acanthodrilidae (2, 2)	2 (6)	2 (6)	1 (1)	1 (9)	0
Totals		198 (1800)	160 (1401)	141 (638)	182 (1702)	123 (820)

Table 3.2: The number of endemic and new species unique to burnt and unburnt grasslands.

	Burnt	Unburnt
South African endemic	6	2
KwaZulu-Natal endemic	3	0
New species	5	1

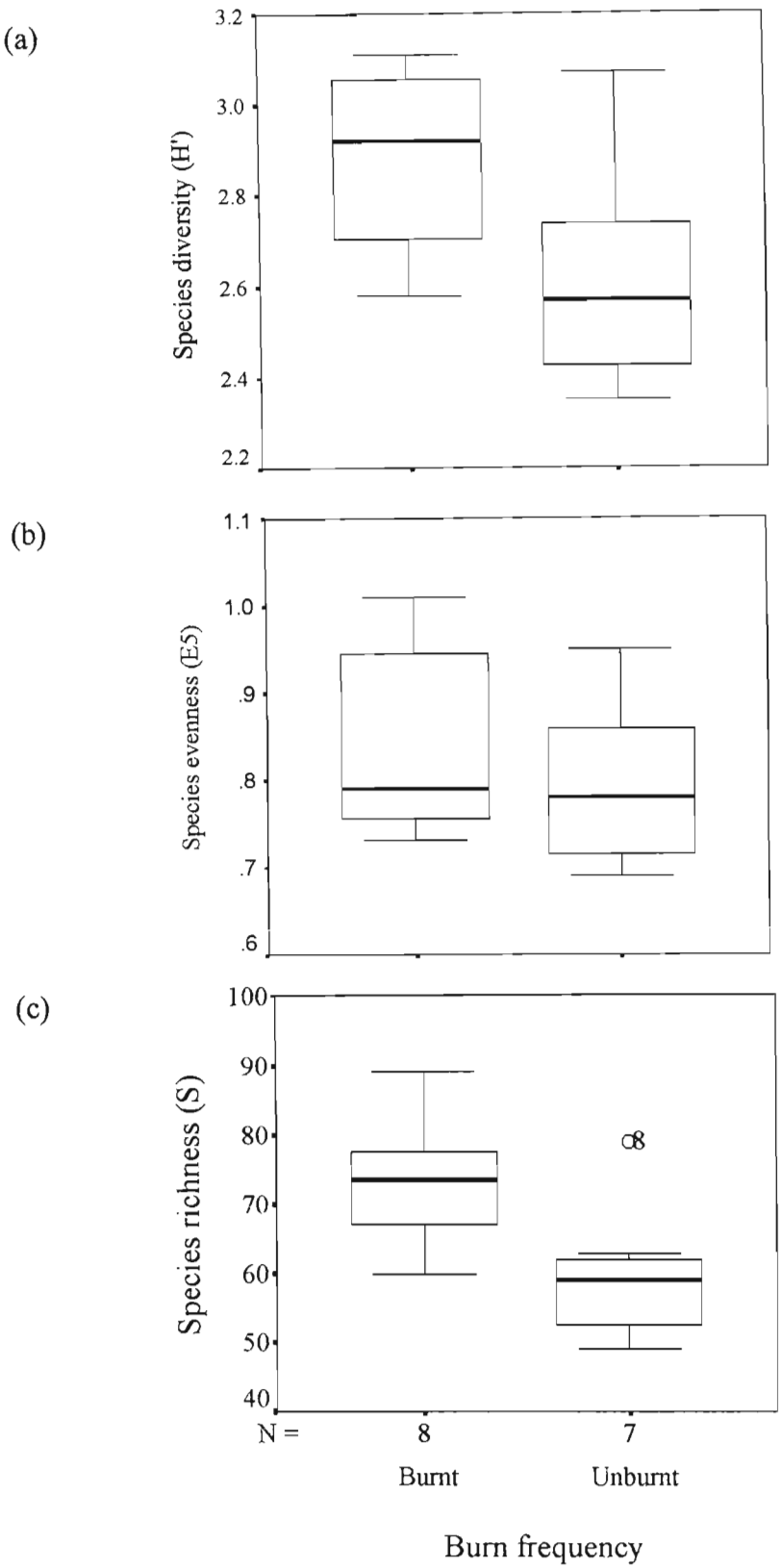


Figure 3.1: The effect of burning on invertebrate (a) diversity, (b) evenness and (c) richness. The median and interquartile range is presented as well as the highest and lowest values. N represents the number of sites in burnt and unburnt grasslands. For unburnt grasslands site 16 was not used as a replicate sample, hence only seven replicates were analysed.

3.3.3. Testing the IDH of all invertebrates sampled

a. Total species richness and abundance

Intermediate burning resulted in the highest number of invertebrate species (182) and individuals (1 702) (Table 3.1). Frequent burning resulted in more species (141) than infrequent burning (123), however infrequent burning resulted in more individuals (820) than frequently burnt sites (638). Intermediate burning was represented by the highest number of families (34), followed by frequent (30) and then infrequent (28) burning.

b. Unique taxa and endemic species

Each burn frequency has its own suite of unique species (Appendix 1). Intermediate burning resulted in 42 unique species (69% singletons), significantly more than frequent burning (27 unique species, 74% singletons) and infrequent burning (18 unique species, 53% singletons) (Table 3.3). In all three burn frequencies unique species contributed the least to overall species composition, followed by species shared with one other burn frequency. Most species were common to all three burning frequencies (Figure 3.2).

There was no significant difference in the cumulative number of South African endemics, KwaZulu-Natal endemics and new species between the three fire frequencies (Table 3.3). Of the 45 endemic and new species, 13 were unique to one burn frequency (Table 3.4 – see Appendix 1 for species names). Twelve of these unique species were single individuals.

Table 3.3: The effect of fire frequency on the cumulative number of endemic, unique and new invertebrate species.

	Frequent	Intermediate	Infrequent	χ^2 test
Endemic to KwaZulu-Natal	3	6	4	$\chi^2 = 1.08$; $P > 0.05$
Endemic to South Africa	17	21	14	$\chi^2 = 1.43$; $P > 0.05$
Unique to burn frequency	27	42	18	$\chi^2 = 10.14$; $P < 0.05$
New species	10	11	6	$\chi^2 = 1.55$; $P > 0.05$

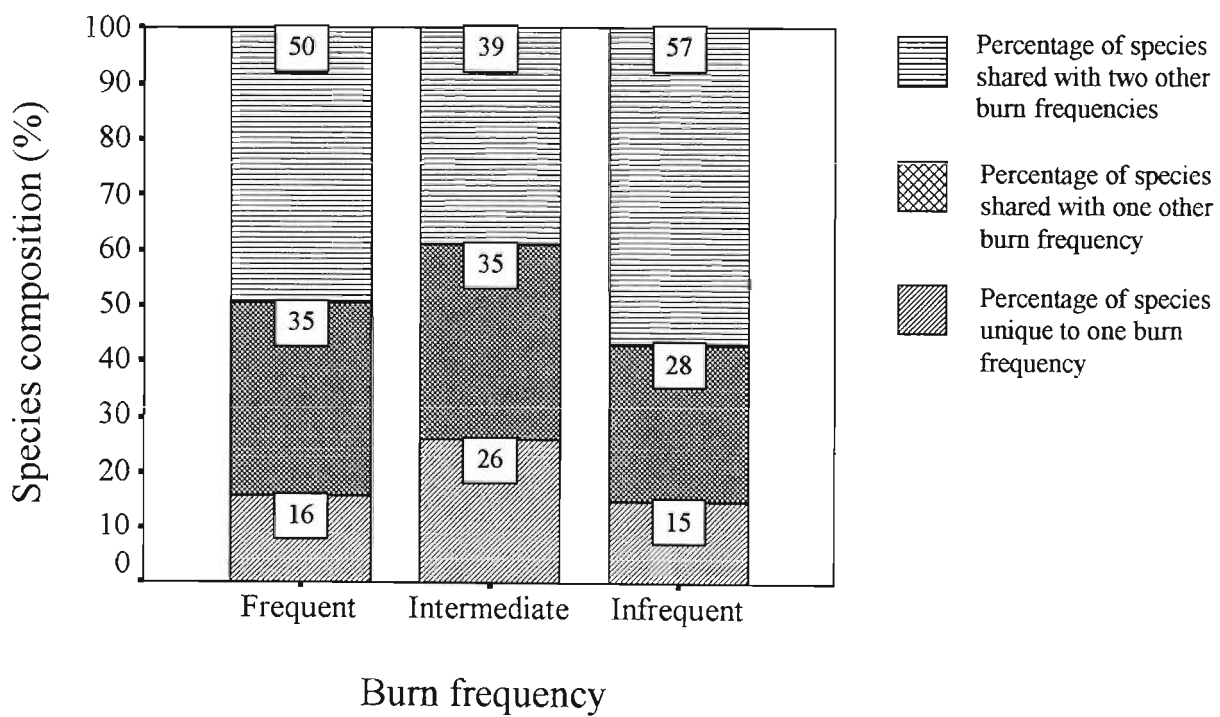


Figure 3.2: The effect of fire frequency on percentage of unique species, species shared with one other fire frequency and species shared with two other burn frequencies.

Table 3.4: The number of endemic and new invertebrate species unique to one burning frequency.

	Burn frequency		
	Frequent	Intermediate	Infrequent
South African endemic	3	2	1
KwaZulu-Natal endemic	0	2	0
New species	1	3	1

c. Species richness, evenness and diversity

Comparing the average total invertebrate diversity between all three burn frequencies revealed no significant difference between all three burn frequencies ($F_{2,12} = 3.61$, $P = 0.06$) (Figure 3.3a). Species evenness was not significantly different between frequent, intermediate and infrequent burning ($F_{2,12} = 0.99$, $P = 0.40$) (Figure 3.3b). All burn frequencies had an evenness index closer to one than zero suggesting that there is an even spread of species in all three communities, without a single species dominating. Frequent and intermediate burning had significantly higher species richness than infrequent burning ($F_{2,12} = 8.68$, $P = 0.01$; LSD values = 0.001 and 0.02 respectively), but species richness was not significantly different in frequent and intermediate burning (Figure 3.3c).

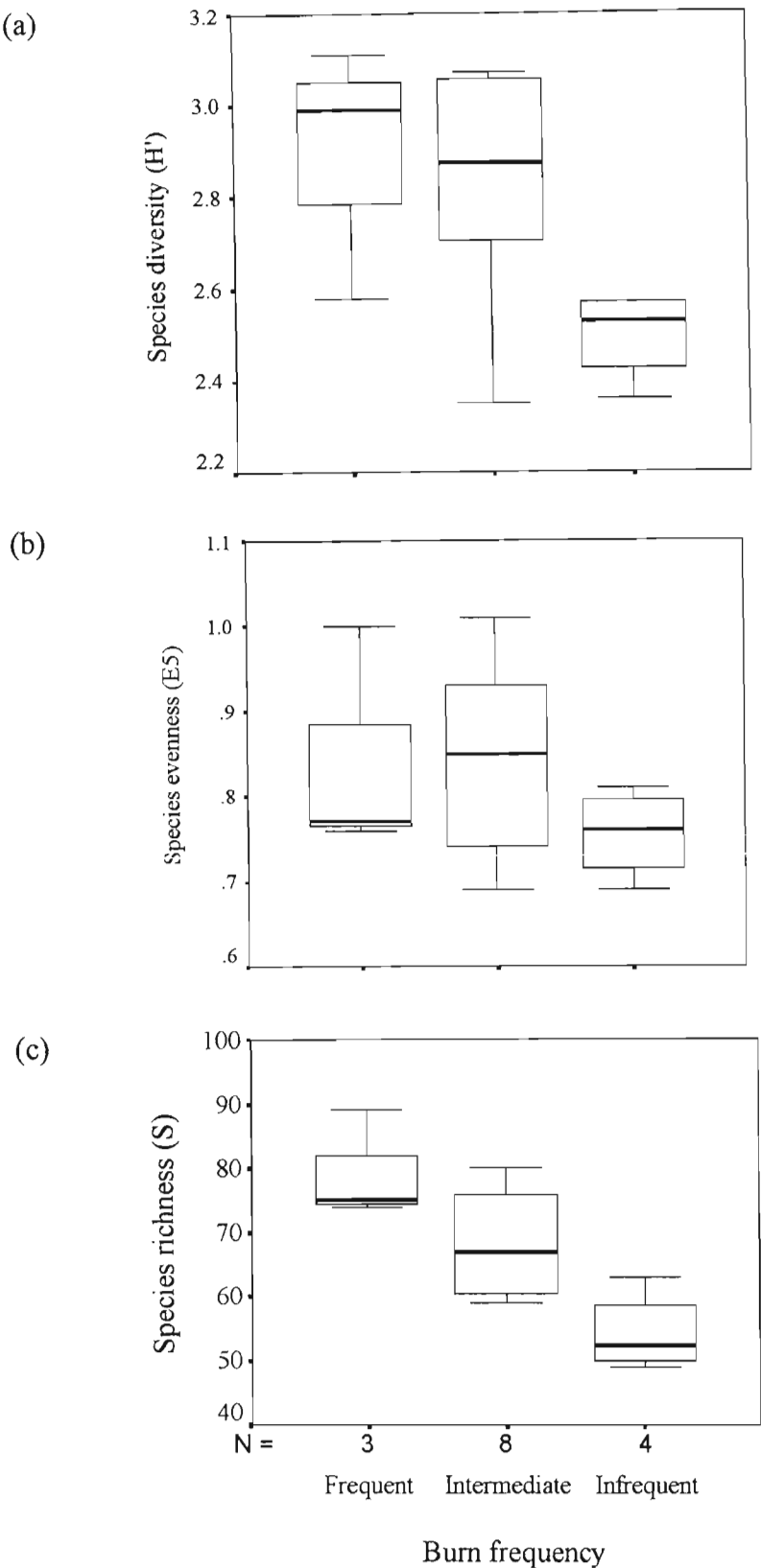


Figure 3.3: The effect of fire frequency on invertebrate (a) diversity, (b) evenness and (c) richness. The median and interquartile range is presented as well as the highest and lowest values. N represents the number of replicates for each fire frequency.

3.3.4. *Testing the IDH for wingless invertebrates*

Wingless invertebrates were assumed to be less mobile than winged invertebrates and therefore more vulnerable to burning. No significant difference in wingless invertebrate diversity was seen between frequent, intermediate and infrequent burning ($F_{2,12} = 1.23$, $P = 0.33$). Infrequent burning did result in significantly higher wingless invertebrate species evenness than frequent and intermediate burning ($F_{2,12} = 4.88$, $P = 0.03$; LSD values = 0.02 and 0.17 respectively) but frequent and intermediate were not significantly higher (Figure 3.4a). Contrary to what was expected, infrequent burning resulted in significantly lower species richness than frequent burning ($F_{2,12} = 4.25$, $P = 0.04$; LSD value = 0.01) (Figure 3.4b), but not intermediate burning. Therefore infrequent burning had fewer species but these were more evenly spread throughout the community than those in frequent and intermediate burning.

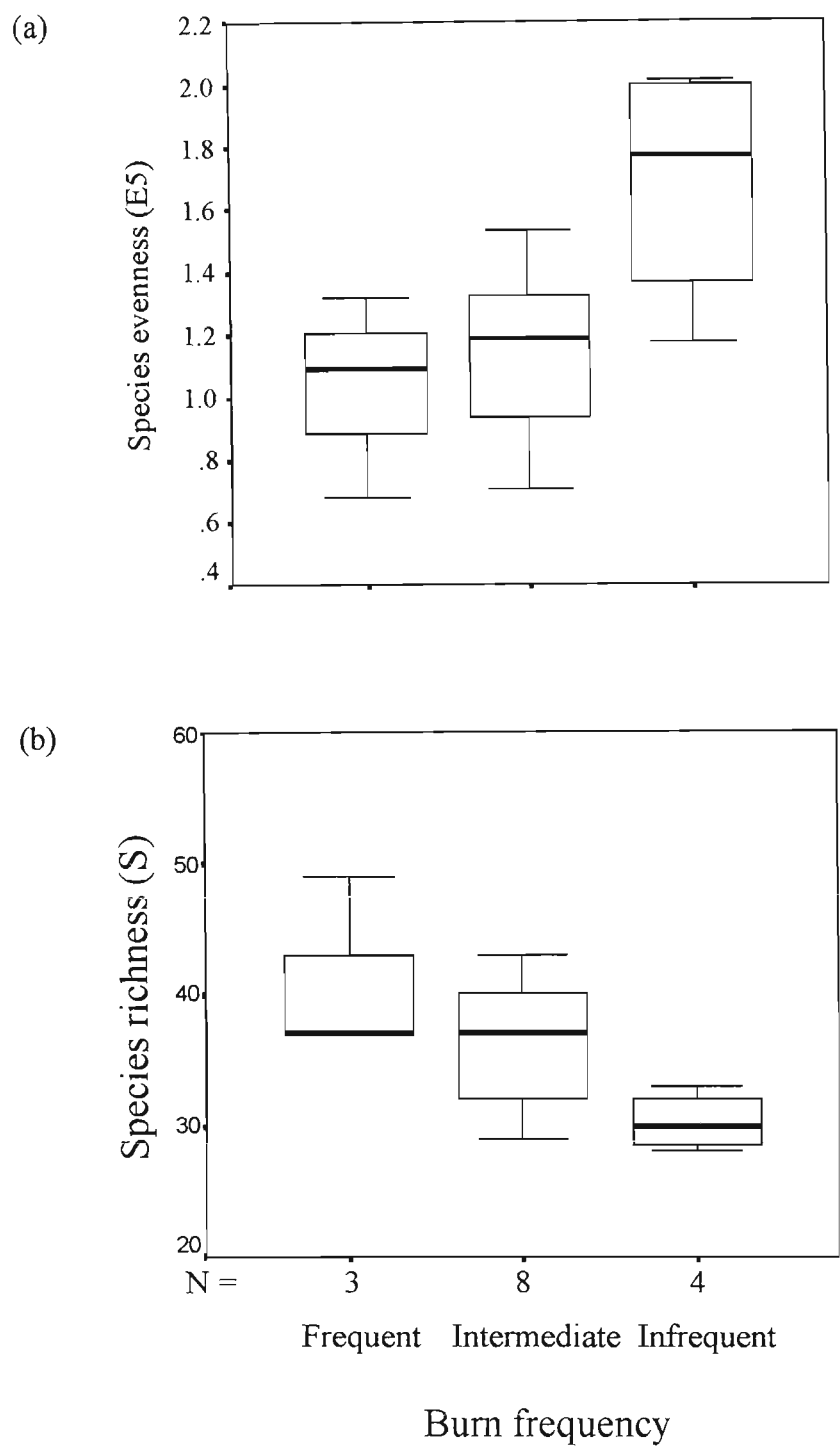


Figure 3.4: The effect of fire frequency on (a) species evenness and (b) richness of wingless invertebrates. The median and interquartile range is presented as well as the highest and lowest values. N represents the number of replicates of each burn frequency.

3.3.5. Testing the IDH for different invertebrate guilds

Herbivore species richness was significantly higher in frequently burnt grasslands than in intermediate and infrequently burnt grasslands ($F_{2,12} = 6.61$, $P = 0.01$; LSD values = 0.01 and 0.01 respectively). For predator species richness, frequent and intermediate burning had significantly higher species richness than infrequent burning ($F_{2,12} = 7.22$, $P = 0.01$; LSD values = 0.01 and 0.01), but predator species richness was not significantly different in frequent and intermediate burning. Pollinator species richness showed no significant difference between all three burn frequencies ($F_{2,12} = 1.81$, $P = 0.21$) (Figure 3.5).

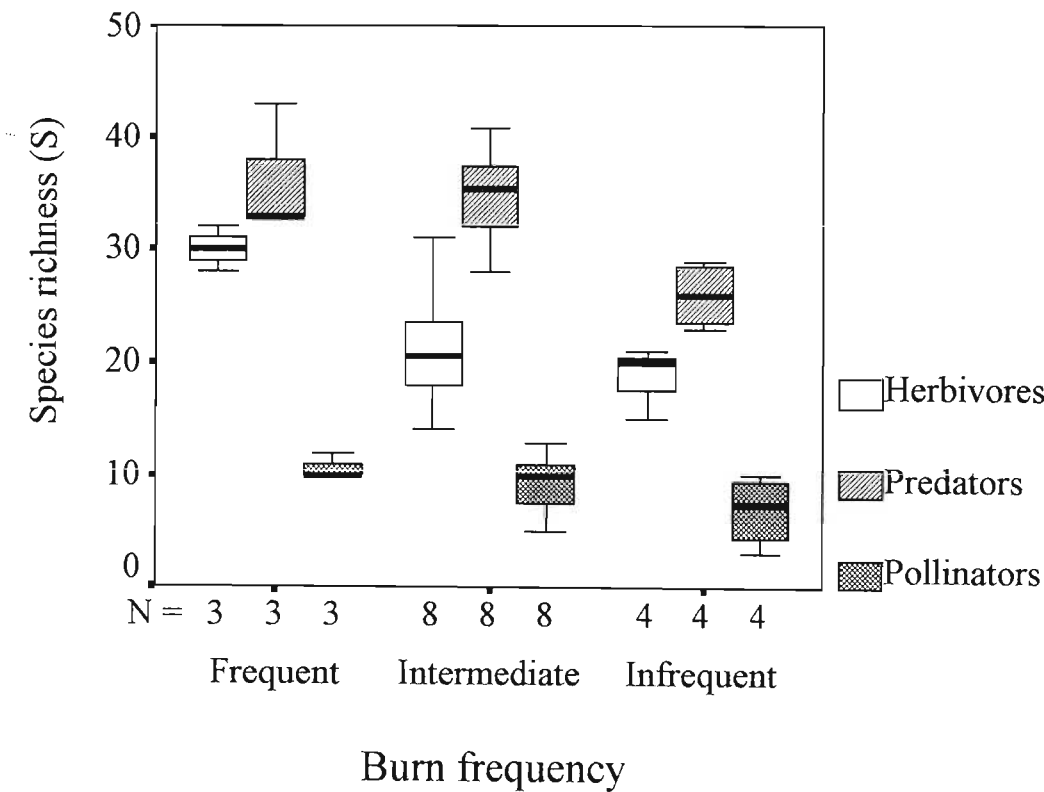


Figure 3.5: The effect of fire frequency on invertebrate herbivore richness, predator richness and pollinator richness. The median and interquartile range is presented as well as the highest and lowest values. N represents the number of replicates of each burn frequency.

3.3.6. *The change in diversity with time elapsed since the last fire*

Invertebrate diversity was significantly higher in grasslands that had been burnt during the year of sampling and five years before sampling ($F_{2,12} = 3.90$, $P = 0.05$; LSD value = 0.02). However the species diversity in grasslands burnt during the year of sampling and two years before sampling, and two years and five years before sampling were not significantly different (Figure 3.6a). There was no significant difference in species evenness between the three post-fire ages ($F_{2,12} = 1.00$, $P = 0.40$) (Figure 3.6b). Species richness was significantly higher in grasslands burnt during the year of sampling than those burnt five years before sampling ($F_{2,12} = 6.07$, $P = 0.02$; LSD = 0.01) but there was no significant difference between grasslands burnt during the year of sampling and two years before sampling or for grasslands burnt two years and five years before sampling (Figure 3.6c).

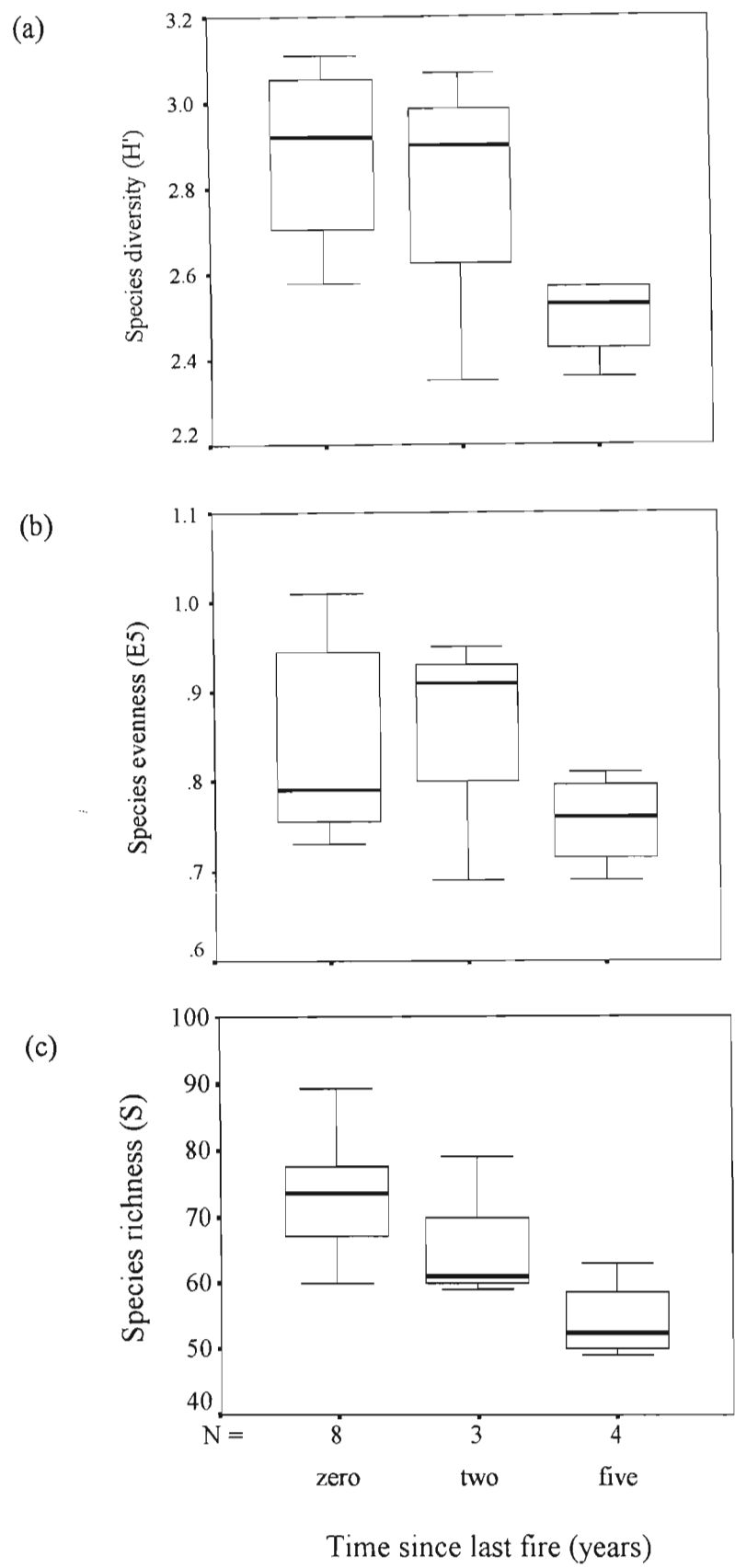


Figure 3.6: The effect of the length of time elapsed since the last fire on invertebrate (a) diversity, (b) evenness and (c) richness. N is the number of replicates of sites that were burnt in the year of sampling, two years before sampling and five years before sampling.

3.4. Discussion

The impact of fire on invertebrates is a contentious issue among entomologists with many fearing that fire results in high mortality of invertebrates. Fire does result in an immediate decrease in invertebrate species richness and abundance (Tainton & Mentis 1984; Uys *et al.* 2006; Zimmer & Parmenter 1998), but this effect may not be long-lasting in grassland ecosystems. The focus of the current study was not on the direct and immediate effect of fire on invertebrates, but rather on the longer-term effects of current burning regimes on invertebrate diversity in a grassland ecosystem.

Invertebrate species diversity was higher in grasslands that had been burnt for two consecutive years, including the year of sampling, than grasslands that had not been burnt during those two years. These findings support those of Panzer and Schwartz (2000) where species richness and mean population densities in tallgrass prairies were generally higher on frequently burned sites when compared with sites that had not been burnt. Within the unburnt sites, site 8 had exceptionally high species richness suggesting that species may have been using this site as a refuge and had accumulated here from the frequently burnt adjacent grassland site (site 7).

When comparing the total number of invertebrate species and their abundances in each burn frequency it appears that intermediate burning had more species than frequent and infrequent burning (Table 3.1). But more intermediately burnt grassland sites (eight) were sampled than frequently (three) and infrequently (five) burnt sites, therefore the number of species found in each burn frequency is not directly comparable. Even with fewer replicate samples, frequently burnt sites still had more species than infrequently burnt sites. To alleviate the problem of uneven replicates for each burn frequency, the average species diversity in each burn

frequency was compared between the three burn frequencies. The results did not support the IDH as intermediate burning did not result in the highest invertebrate diversity.

Each fire frequency had a high proportion of unique species and the conservation value of these needs to be taken into consideration. Many of the species collected were represented by only one specimen, otherwise known as singletons. This is a common occurrence in sampling invertebrates and does not suggest any bias in sampling if a standardized and quantified sampling method is used to sample all sites with equal sampling effort (Colwell and Coddington 1994; Gotelli and Colwell 2001). Intermediate burning produced the most unique species (Table 3.3) with a large proportion of them being singletons. Species recorded as singletons may also be rare as opposed to unique to individual burn frequencies. This may explain their limited distribution throughout the burn frequencies rather than the burn frequency affecting their distribution *per se*. Most of the endemic species were found in more than one burn frequency and those endemic species that were unique to one burn frequency were almost all single individuals, again making it difficult to determine whether fire frequency has a real impact on endemic species.

Wingless invertebrates were expected to be less mobile than winged invertebrates and more susceptible to burning. However, frequent and intermediate burning resulted in higher species richness of wingless invertebrates (Figure 3.4b). Therefore frequent fires do not appear to have a negative impact on less mobile species. Panzer (2002) found that although wingless species suffer initial losses after a fire they generally recover rapidly. Wingless species such as ants have in the past been found to be well adapted to fire (Zimmer & Parmenter 1998). Parr *et al.* (2002) found that frequent burning in grasslands resulted in higher species richness

of ants than less frequent burning thus frequent fires could be expected to maintain ant diversity at the local scale. Many ant species build underground nests (Picker *et al.* 2002) enabling ants to take refuge during a fire. If ant foragers are lost during a fire, the loss would only be temporary as nest-workers would assume foraging tasks and eventually replace the lost foragers (Zimmer & Parmenter 1998). Species such as spiders that are wingless are not necessarily immobile; New (1999) describes ballooning and air-borne spiders as being among the most vagile terrestrial invertebrates. Therefore many spiders not only have the ability to escape from fire effectively but also have good recolonization and dispersal mechanisms. Depending on the intensity of the fire, ground dwelling invertebrates such as earthworms and millipedes could be protected from fire. In past studies earthworms have been found to be vulnerable to ground fires and are often killed at high temperatures and are intolerant of low moisture levels in the soil as a result of fire (see Newman & Tolhurst 1991). But in the current study earthworms and millipedes were found in burnt and unburnt grasslands and did not appear to be adversely effected by fire (Table 3.1).

Herbivorous invertebrate richness was significantly higher in frequently burnt grasslands. Similar results to those in this study were found by Chambers and Samways (1998) where grasshopper species diversity was greatest in annually burnt grassland plots and decreased in biennially and triennially burnt plots in KwaZulu-Natal (South Africa). This was to be expected because frequently burnt vegetation is more palatable than unburnt vegetation (Chambers & Samways 1998). Collins and Steinauer (1998) also found that grasshopper species richness was greatest in frequently burnt grasslands in tallgrass prairies, and because of the high number of herbivores the predator species richness was also high in frequently burnt grasslands. A similar situation occurred in the Drakensberg grassland ecosystem.

Pollinator species richness did not differ significantly between the three burn frequencies. This may have been because of the overall low number of pollinators that were sampled.

The IDH states that intermediate disturbance in an ecosystem should result in the highest number of species. This was not the case in this study where total invertebrates, wingless invertebrates and individual guilds were tested with fire as the disturbance factor. In each situation frequent and intermediate burning were very similar in terms of species diversity and intermediate burning did not result in higher species diversity than infrequent burning. The frequent (annual) and intermediate (biennial) burning may have been too similar in terms of fire frequency which probably resulted in the similarity in their species richness. However, even if annual and biennial burning had been combined as frequent burning, grasslands burnt every five years had been sampled as intermediate burning, and grasslands left unburnt for 10 years or longer had been sampled as infrequent burning, the IDH would still not be true in this grassland ecosystem.

The diversity-stability theory states that the more diverse an ecosystem in terms of species richness the more stable it is as a whole and the more resilient the ecosystem is to disturbance (Tilman 1996a). This is possibly a better explanation for this grassland ecosystem because frequent and intermediate burning resulted in higher species richness than infrequent burning, suggesting that they are more stable and therefore more resilient to regular occurrences of fire. A community may be described as resilient if it is able to function as a viable ecosystem after a disturbance even though its composition and structure may have changed substantially (Putman 1994). These results are however inconclusive as species richness would ideally need to be sampled again after a fire has occurred in sites with low species richness *ie.* those

that have not been burnt for five years, in order to determine whether those grasslands are less resilient to fire than sites with high species richness.

Grasslands burnt within the year of sampling had higher species diversity and richness than those that were burnt five years before sampling. Uys *et al.* (2006) found that the invertebrate population at Giants Castle recovered within 12 weeks after a fire, although the recolonisation was in a much smaller area than the block size for burning. Panzer (2002) also found that the majority of invertebrate species studied recovered within one year of a fire and the remainder of the species recovered within two years of a fire. These results illustrate that invertebrates have a tendency to recover relatively quickly after a fire and are not adversely affected over a long-term period. Species richness does not take into account species composition therefore although species richness is higher in grasslands that were burnt during the year of sampling than those that were burnt five years before, two different communities may be represented in the different lengths of time past since the disturbance.

Sweep netting, one of the sampling techniques used in this study to sample invertebrates may have resulted in greater sampling efficiency in recently burnt grass because it is shorter and easier to sweep than grass that had become thick and moribund. No studies have been done comparing the efficiency of different sampling methods in different grass swards. Differences in effectiveness of sweep sampling in burnt and unburnt grass may have influenced the results in this study, but there is no direct evidence for this. However, future invertebrate studies in Drakensberg grasslands should take grass length and thickness into consideration when designing an effective sampling strategy.

One of the frequently burnt sites, site 15, was mown once during winter after the first sampling period had already taken place. Mowing could have affected invertebrate species diversity at this site but Chambers and Samways (1998) found that when annually burnt plots were compared with annually mown plots, grasshopper abundance and species richness were highest in the burnt plots. Therefore there would be greater cause for concern if site 15 had only been mown and not burnt at all, but this was not the case. There were no mowing records available for Giants Castle making it difficult to know if this site was mown annually. Future grassland studies in the Drakensberg should take the possibility of mowing into consideration before sampling.

Fire frequency is just one parameter of an effective burning regime. Other fire parameters such as the fire season, the fire intensity and the size of the block burn also need to be considered. The size of the block burn is important to consider because it will determine the speed of recolonisation of invertebrates after burning.

No general management recommendations can be given that benefit all species of conservation value at the same time and no single management practice should be given general priority in conservation programmes (Wettstein & Schmid 1999). Fire is an important management tool that can be used to create as much heterogeneity as possible. Frequent fires do not appear to have a long lasting detrimental effect on invertebrates which appear to be capable of recovering within a year of a fire. However it is important to consider that unique species were found within all three fire frequencies. Therefore all three fire frequencies should be used in combination in order to conserve and promote maximum invertebrate diversity in the KwaZulu-Natal Drakensberg.

CHAPTER 4

FIRE FREQUENCY AND ITS EFFECT ON INDIGENOUS FLOWERING FORB DIVERSITY IN A GRASSLAND ECOSYSTEM

4.1. Introduction

An annual or biennial burning regime is ideal for maintaining the grass diversity of the KwaZulu-Natal grasslands (van Wilgen *et al.* 1990), and this has been studied extensively. Fire stimulates vegetative reproduction in grasses and the absence of fire results in a decrease in the vigor of plants (Everson 1985). Grasslands left for a number of years become moribund, which leads to a decrease in light intensity at the base of the plant resulting in a reduced rate of tillering (van Wilgen *et al.* 1990). Thus grasslands that are not burnt regularly have a lower level of alpha diversity than those that are burnt regularly. However, grasses are only one vegetative component of a grassland ecosystem.

Forbs are perennial or annual broad leaved herbs and geophytes that contribute substantially to the diversity of the vegetative component in grasslands. There is a wide variety of perennial forbs associated with grasslands that are sensitive to fires. These fire sensitive species, also termed autumnal aspect plants, become conspicuous later in the season, flowering in January, February and March (Bayer 1955; Scotcher 1982). Many of the autumnal aspect plants possess perennial above ground stems, but some have perennial below ground stems that die in winter and are renewed in spring. They are not resistant to grass fires and are killed out by burning. Geophytes are plants with bulbs, corms, tubers, non-graminoid rhizomes and rootstocks. Many geophytic growth forms such as species belonging to the families Orchidaceae, Iridaceae, Liliaceae and Amaryllidaceae are stimulated by fire (Bond *et al.* 1996). These plant growth forms do not lose much material in fires and can rapidly marshal existing resources into reproduction.

According to Whelan (1995), there are five categories of flowering responses to fire in Africa:

- (1) immediate post-fire flowering but flowering very rare or completely absent if no fire;
- (2) immediate post-fire flowering with flowering less intense thereafter;
- (3) no flowering immediately after fire but flowering is intensified relative to unburned sites after 3 to 4 years;
- (4) flowering depressed after fire, returning to levels comparable to unburned sites after some years;
- (5) no apparent relationship of flowering to fire

Whelan (1995) further suggested that the causes of intense flowering may be closely related to increased productivity after fire, thus more vigorous plants may be able to support greater flowering. However, Pearse (1978) recognised that annual burning of grasslands in South Africa does sometimes have detrimental effects on flowering plants. In a piece of grassland that had not been burnt for 17 years, masses of *Erica woodii* Bolus flowers were produced annually while just over the fence where the grassland was burned every year not a single *E. woodii* plant could be found. Collins and Steinauer (1998) also found that annual burning in tallgrass prairie resulted in dominating C₄ grasses which are long-lived and highly competitive, but infrequently burnt sites had C₃ grasses, forbs and woody species as well as C₄ grasses thus having greater diversity and heterogeneity. According to Raven *et al.* (1992) C₃ and C₄ plants differ in their respiratory metabolic pathways. Photosynthesis in C₃ plants is always accompanied by photorespiration, a process that consumes oxygen and releases CO₂ in the presence of light, a wasteful process that limits their efficiency. C₄ plants are superior utilizers of available CO₂ therefore photosynthesis can be two to three times the rate of C₃

plants. C_4 plants are well adapted to high light intensities, high temperatures and dryness and grow well at temperatures that would eventually be lethal to many C_3 species.

Contrary to the results of Collins and Steinauer (1998), Vogl (1974) noticed that repeated burning in a native grassland prairie (North America) did not reduce the species diversity but rather increased the diversity by promoting growth of grasses, legumes and other forbs, including annual plants.

Intermediate disturbances have been known to promote highest diversity in a number of ecosystems but this may not necessarily be true in a grassland ecosystem where fire is the disturbance. Collins and Steinauer (1998) found that the tallgrass prairie grasslands did not conform to the IDH. Rather, plant species diversity decreased linearly with an increase in fire frequency. Uys *et al.* (2004) found that forb species richness showed no clear responses to fire frequency in South African grasslands.

Another theory in grassland dynamics is the diversity-stability theory which predicts that ecosystems with high diversity will be more stable than ecosystems with a low diversity and therefore more resilient to disturbance (Tilman & Downing 1994). Stable ecosystems are more likely to withstand environmental perturbations and are likely to recover quicker after a disturbance than less diverse ecosystems. This is because species-rich ecosystems are likely to have species with a wide array of responses to variable conditions such as drought. A species-rich ecosystem is also likely to have species with similar ecological functions, so that if a species is lost from an ecosystem, another species, probably a competitor, is likely to flourish and occupy its functional role (Hunter 2002). Support for this diversity-stability theory resulted from research on Minnesota grasslands (Tilman 1999; Tilman & Downing

2002; Tilman 1996a,b) which focused on diversity of grasses and the environmental perturbation was a drought.

In the KwaZulu-Natal Drakensberg the grassland is divided into large blocks (approximately 400 ha in size) and these are theoretically burnt biennially on a rotational basis. There are however many arson and runaway fires during winter which sometimes result in areas being burnt more often than the burning regime predicts. There are also numerous areas that are burnt annually as firebreaks and at the other extreme there are areas which have been left unburnt for five years or longer. The prescribed burning programme is mostly aimed at maintaining a *Themeda triandra* grassland sward that is ideal for large grazing herbivores (Killick 1963) but may not necessarily be the best for promoting indigenous forb diversity.

Forb diversity is extremely difficult to measure in a short-term project due to their different flowering responses to fire as described by Whelan (1995). However, the flowering phenology of indigenous forbs and their response to fire is important for promoting invertebrate diversity. These two components of biodiversity are inextricably linked as flowering forbs provide a source of food for invertebrates as well as important hunting, resting and mating sites for invertebrates.

The overall aim of this part of the study was to determine the effect of fire frequency and the time elapsed since the last burn on the flowering phenology of indigenous forbs in the KwaZulu-Natal Drakensberg grassland. One objective was to determine whether the diversity of flowering forbs is higher in burnt or unburnt grasslands. A second objective was to determine whether diversity of flowering forbs is higher in grasslands with an intermediate level of disturbance than in grasslands with a low or high level of disturbance where fire is the

disturbance. This will ultimately determine if the IDH holds true in this grassland ecosystem. A third objective was to determine whether species richness of forbs in flower differs according to the length of time elapsed since the last fire. The final objective was to identify certain species of flowering forbs that were sensitive to fire and specific fire frequencies. This study only focused on those forb species flowering at the time of sampling, and forb diversity here is therefore considered as the diversity of species flowering at the time of sampling. The influence of flowers on invertebrate diversity is investigated in Chapter five and six, in terms of patterns in community structure and environmental influences, and patterns in species richness respectively.

4.2. Materials and Methods

Refer to chapter two

4.3. Results

4.3.1. Total species richness and abundance of flowering forbs

A total of 3 628 individuals, 70 species (Appendix 2), 44 genera and 21 families of flowering forbs were sampled. The first sampling period in March produced 19 flowering forb species, an additional 13 species were recorded in September. November was the most productive sampling period with 38 additional species being recorded. The species of flowering forbs recorded were mostly perennial herbs (52 species), followed by geophytes in the form of bulbs, tubers, corms and rhizomes (16 species), and one perennial shrub and one annual herb were also recorded (Appendix 2).

4.3.2. Comparison of flowering forbs in burnt and unburnt grasslands

a. Total species richness and abundance of flowering forbs

Grasslands that were burnt for two consecutive years in 2001 and 2002 were represented by more families (19), species (61) and individuals (3211) of indigenous flowering forbs than grasslands that had not been burnt (Table 4.1). Of the individuals sampled in burnt grasslands 70% belonged to one species, *Helichrysum aureonitens* Sch. Bip, a perennial herb. This species was not found to be flowering in unburnt grasslands. Unburnt grasslands were represented by 16 families, 35 species and 472 individuals in flower (Table 4.1).

The Asteraceae was the most well represented family in terms of the number of species and abundance in burnt and unburnt grasslands. In burnt grasslands 48% of species were from the Asteraceae family and in unburnt grasslands 34% of species were from this family. Geophytic species belonging to Amaryllidaceae, Liliaceae, Iridaceae and Orchidaceae were found to be flowering in burnt and unburnt grasslands, while species from the family Commelineaceae were only found flowering in burnt grasslands (Table 4.1).

b. Unique taxa and endemic flowering forb species

Unique species are those that are only found flowering in burnt or unburnt grasslands. The majority of flowering forb species sampled were unique to burnt grasslands rather than unburnt grasslands. Burnt grasslands were represented by 37 unique species, of which 22% were single individuals (Appendix 2). Unburnt grasslands were represented by nine unique species with 44% of them being single individuals.

c. Species richness, evenness and diversity of flowering forbs

Grasslands that had been burnt for two consecutive years had significantly higher species diversity ($F_{1,13} = 7.42$, $P = 0.02$) (Figure 4.1a) and species richness ($F_{1,13} = 44.53$, $P = 0.000$) (Figure 4.1c) of flowering forbs than grasslands that had not been burnt for those two

consecutive years. Burnt and unburnt grasslands showed no significant difference in species evenness ($F_{1,13} = 0.05$, $P = 0.82$), and both burnt and unburnt grasslands had high evenness indices with a median of 0.87 and 1.00 respectively which suggests that there was an even spread of species (Figure 4.1b).

Table 4.1: The effect of fire on forb families and species flowering at Giants Castle. 1 = frequent burning, 2 = intermediate burning and 3 = infrequent burning. * Geophytes.

Families with the number of (genera and species)	The number of flowering forb species and (abundance) in burnt and unburnt grasslands and in various burn frequencies				
	Burnt	Unburnt	1	2	3
Asteraceae (14, 31)	29 (2575)	12 (331)	19 (499)	20 (2266)	10 (139)
Gentianaceae (1, 1)	1 (28)	1 (3)	1 (21)	1 (7)	1 (3)
Polygalaceae (1, 1)	1 (44)	1 (1)	1 (14)	1 (31)	0
Euphorbiaceae (2, 2)	1 (53)	2 (54)	1 (9)	1 (47)	2 (51)
*Amaryllidaceae (2, 5)	5 (335)	3 (28)	3 (6)	4 (334)	2 (17)
*Liliaceae (4, 4)	3 (9)	3 (5)	1 (6)	3 (4)	1 (1)
Campanulaceae (2, 5)	4 (36)	2 (11)	1 (5)	3 (33)	2 (9)
Rubiaceae (1, 1)	1 (19)	1 (7)	1 (4)	1 (18)	1 (4)
*Commelineaceae (2, 4)	4 (72)	0	1 (4)	3 (24)	0
Sterculiaceae (1, 1)	1 (3)	0	1 (3)	0	0
*Iridaceae (3, 4)	2 (5)	3 (6)	2 (3)	2 (5)	2 (3)
*Orchidaceae (2, 2)	2 (7)	1 (3)	1 (2)	2 (7)	1 (1)
Oxalidaceae (1, 1)	1 (3)	1 (2)	1 (2)	1 (3)	0
Thymelinaceae (1, 1)	1 (1)	1 (1)	1 (1)	0	1 (1)
Crassulaceae (1, 1)	1 (3)	1 (7)	0	1 (10)	0
Santalaceae (1, 1)	1 (10)	0	0	1 (10)	0
Asclepidaceae (1, 1)	1 (3)	1 (11)	0	1 (7)	1 (7)
Scrophulariaceae (1, 1)	1 (4)	0	0	1 (4)	0
Leguminosae (1,1)	0	1 (1)	0	1 (1)	0
Ranunculaceae (1, 1)	1 (1)	0	0	1 (1)	0
Labiatae (1, 1)	0	1 (1)	0	0	1 (1)
Total	61 (3211)	35 (472)	35 (579)	48 (2812)	25 (237)

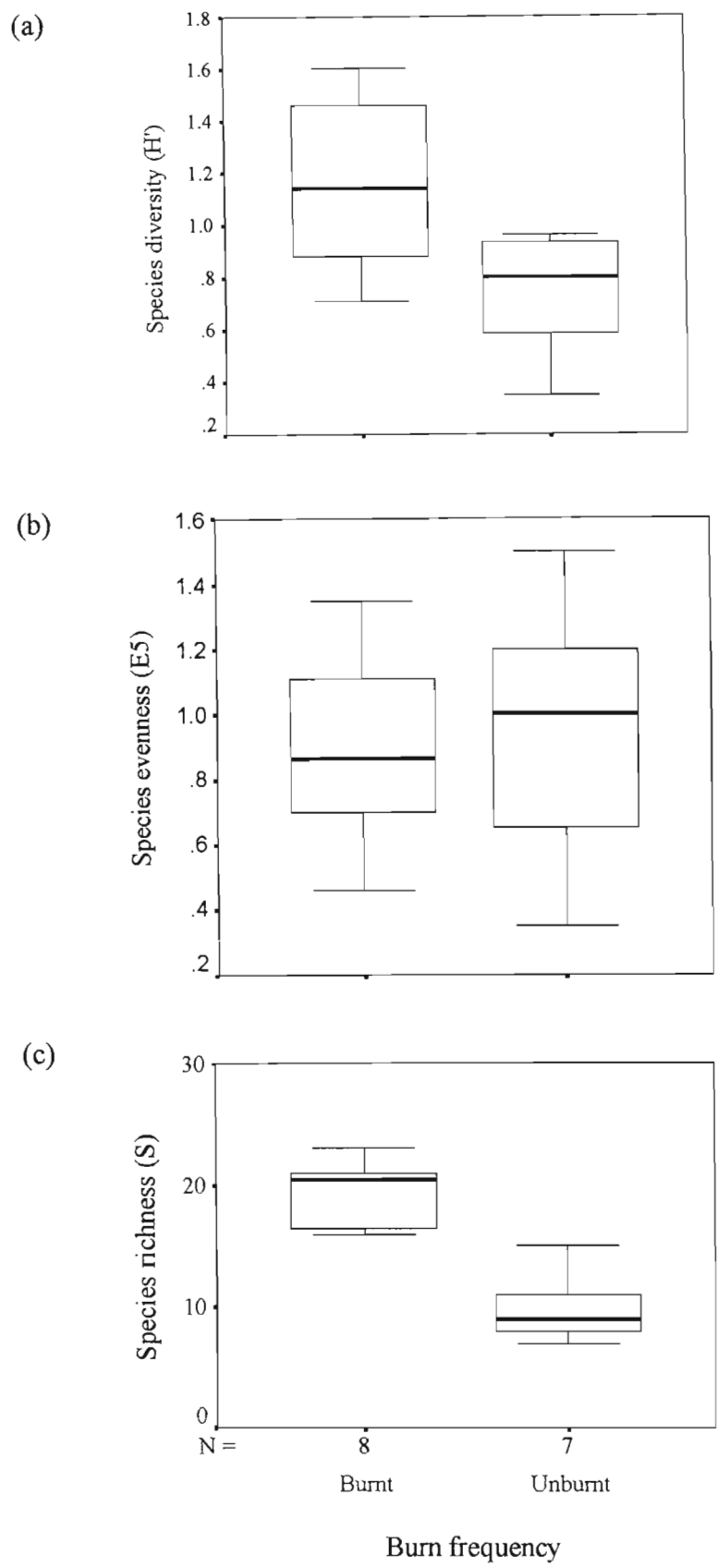


Figure 4.1: The effect of burning on flowering forb species (a) diversity, (b) evenness and (c) richness. The median and interquartile range is presented as well as the highest and lowest values. N represents the number of sites in burnt and unburnt grasslands.

4.3.3. The effect of fire frequency on forbs flowering in grasslands

a. Total species richness and abundance of forbs flowering in frequent, intermediate and infrequently burnt grasslands

When comparing indigenous flowering forbs between three fire frequencies, intermediate burning was represented by the highest number of families (18), species (48) and individuals (2 812) (Table 4.1). This was followed by frequent burning with 14 families, 35 species and 579 individuals. Infrequent burning was represented by the lowest number of families (12), species (24) and individuals (237). These data would, however, have been influenced by the unequal number of sites sampled for each burn frequency. The Asteraceae were the most well represented family in terms of the number of species and abundance in all three burn frequencies. Geophytic species belonging to Amaryllidaceae, Liliaceae, Iridaceae and Orchidaceae were found in all three burn frequencies (Table 4.1).

b. Unique taxa and endemic flowering forb species in frequent, intermediate and infrequently burnt grasslands

Each burn frequency had its own suite of unique forb species flowering at the time of sampling. Intermediate burning produced the highest proportion of unique species and the lowest proportion of species shared with two other burn frequencies (Figure 4.2), and a similar trend was seen in frequently burnt grasslands. Infrequent burning produced the lowest proportion of unique species and the highest proportion of species shared with two other burn frequencies. Again, this may have been the result of the unequal number of sites sampled for each burn frequency.

Helichrysum aureum (Houtt.) Merr. is an endangered species found in South Africa and according to the Southern African IUCN red data book for plants, it has a very small and restricted population (Golding 2002). This endangered species was found flowering in all three burn frequencies but was more abundant in intermediate burning. *Eulophia zeyheriana* Sond. (Orchidaceae) is classified as near threatened in South Africa by the IUCN red data list for plants (Golding 2002). This species was flowering in intermediate and infrequently burnt grasslands.

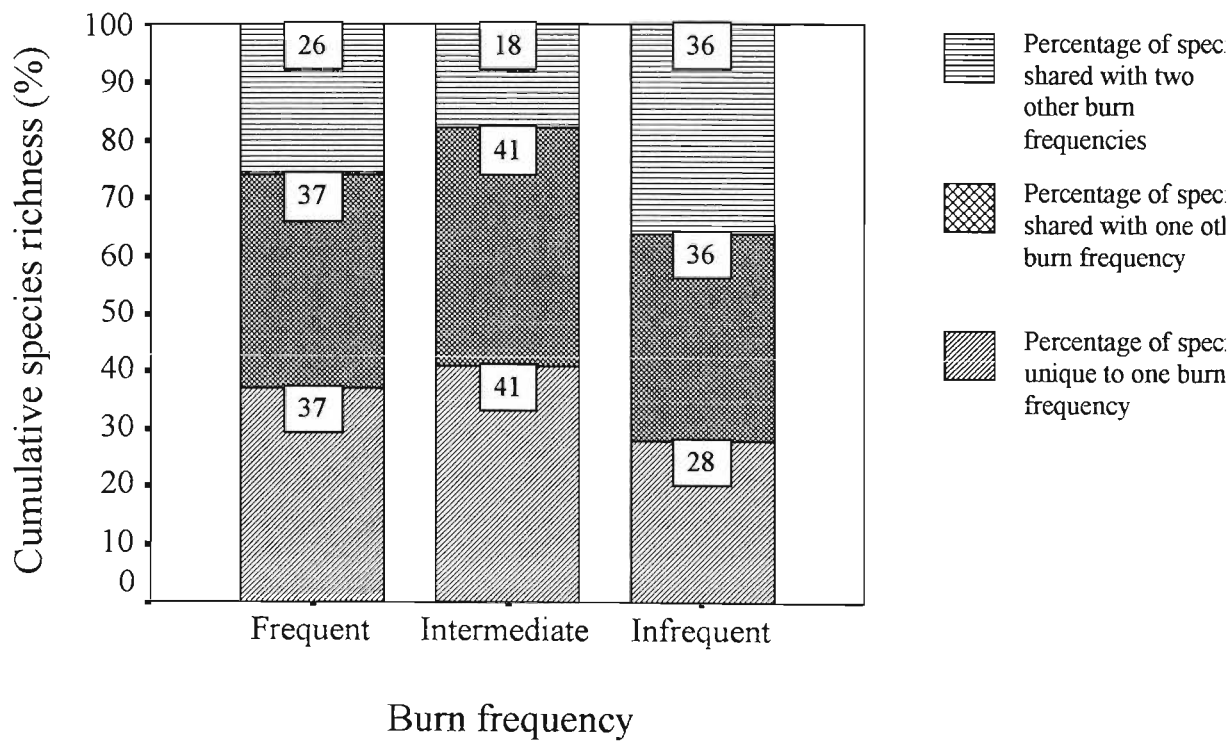


Figure 4.2: The effect of fire frequency on the proportion of flowering forb species that are unique, shared with one other burn frequency and shared with two other burn frequencies.

c. Species richness, evenness and diversity of forbs flowering in grasslands

Frequent burning resulted in significantly higher flowering forb diversity than intermediate and infrequent burning ($F_{2,12} = 4.77$, $P = 0.03$; LSD values = 0.02 and 0.01 respectively), and there was no significant difference in flowering forb diversity between intermediate and infrequent burning (Figure 4.3a). There was no significant difference in species evenness ($F_{2,12} = 0.01$, $P = 0.99$) between all three burning frequencies (Figure 4.3b). In comparing the species richness of flowering forbs between all three burning frequencies, species richness for frequent burning was significantly higher than infrequent burning ($F_{2,12} = 3.27$, $P = 0.07$; LSD value = 0.03) but there was no significant difference for frequent and intermediate burning and intermediate and infrequent burning (Figure 4.3c).

4.3.4. Effect of time since last burn on flowering forbs

The grasslands that were burnt during the year of sampling (2002) had significantly higher species richness of flowering forbs than sites that were burnt two years before sampling and five years before sampling ($F_{2,12} = 20.60$, $P = 0.00$; LSD values = 0.00 and 0.00 respectively) (Figure 4.4), but no difference between the sites that had been burnt two years and five years before sampling. There was no significant difference in flowering forb species diversity ($F_{2,12} = 3.45$, $P = 0.07$) and evenness ($F = 0.048$, $P = 0.95$) between the three different time periods since the last burn.

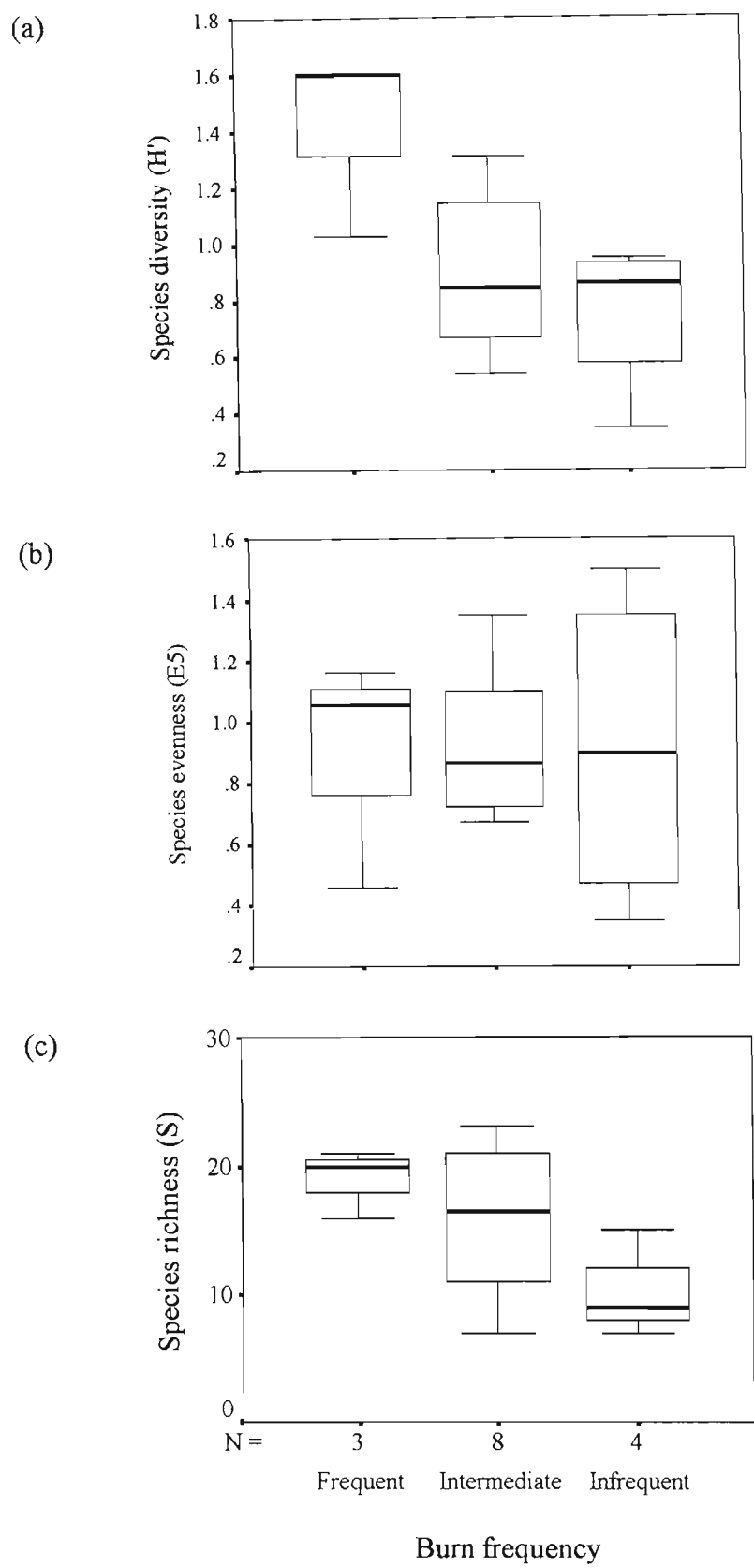


Figure 4.3: The effect of fire frequency on flowering forb species (a) diversity, (b) evenness and (c) richness. The median and interquartile range is presented as well as the highest and lowest values. N represents the number of sites in three burn frequencies.

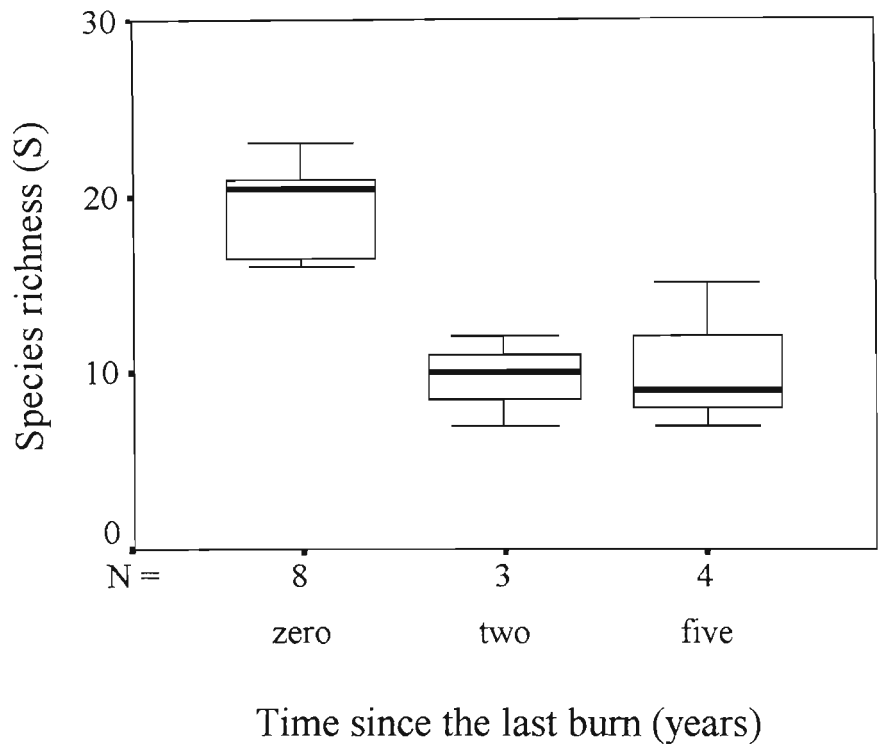


Figure 4.4: The effect of the length of time elapsed since the last fire on flowering forb species richness. N is the number of replicates of sites that were burnt in the year of sampling, two years before sampling and five years before sampling.

4.4. Discussion

Extensive studies of fire in the KwaZulu-Natal Drakensberg grasslands have shown that annual and biennial burning is ideal for maintaining grass diversity (Everson 1985; van Wilgen *et al.* 1990). Although grasses comprise most of the plant biomass in grasslands, it is the forb component that contributes to the grassland's diversity (Uys *et al.* 2004). The effect of current burning regimes in the KwaZulu-Natal Drakensberg on forb diversity is poorly known. In this Drakensberg grassland, flowering forbs appeared to follow a similar trend to that of grasses. Flowering forb diversity was higher in grasslands that were burnt for two consecutive years than those grasslands that had not been burnt over the same two years (Figure 4.1). Scholes and Walker's (1993) study on the effect of fire on savanna vegetation also found that the contribution of forbs to the herbaceous layer was higher on burnt than unburnt treatments. Of course, measurement of diversity as represented by forbs in flower may be misleading since species may be present in unburnt areas, but not in flower at the time of sampling.

The IDH predicts that diversity will be highest at intermediate levels of disturbance, but a number of grassland studies do not support the IDH where fire is the disturbance (Collins 1992; Collins & Steinauer 1998; Uys *et al.* 2004). In the current study intermediate levels of disturbance did not result in the highest flowering forb diversity and therefore did not conform to the IDH either. In contrast to these findings, Huston (1994) supports the IDH in North American tall-grass prairies. Direct comparisons between studies are extremely difficult because of the range of intermediate fire frequencies that have been used: four year intervals (Collins 1992; Uys *et al.* 2004), three to eight year intervals (Huston 1994) and two year intervals (current study).

Flowering forb diversity in the Drakensberg grassland ecosystem was highest in frequently burnt grasslands and decreased with a decrease in burn frequency. Similarly, Vogl (1974) found high plant diversity in frequently burnt grasslands and his study included forbs, grasses and woody vegetation. Both studies suggest that grasslands could be responding to the diversity-stability theory which predicts that ecosystems with high species diversity are more stable and therefore more resilient to disturbances than ecosystems with low species diversity. Collins (1992) and Collins and Steinauer (1998) found that plant diversity decreased with an increase in fire frequency and therefore did not support the diversity-stability theory. Collins (1992) focused only on grasses and Collins and Steinauer (1998) included forbs, grasses, and woody plants in their study. These conflicting results suggest that there is no common trend in the way that grassland plants respond to fire frequency. Perhaps this is because many different plants respond to fire in different ways (Whelan 1995).

Many plant species are well adapted to fire and can persist in fire-prone environments through avoidance in space, escape in time, tolerance and regeneration from seed (Frost 1984). Many plant species are stimulated by fire and this was seen by the high number of unique forb species flowering in the frequently burnt grasslands. Geophytes are particularly well adapted to fire because of their underground corm or bulb. The seed of geophytes germinates on the soil surface but the stem base of the seedling is drawn below the soil surface by contractile roots thus protecting it from fire. Although geophytes in flower were more abundant in burnt grasslands they did still occur in unburnt grasslands. The results showed that geophytes in flower were present in burnt and unburnt grasslands as well as in all three fire frequencies. Only one family of geophyte in flower (Commelineaceae) was not recorded in unburnt

grassland and another (Amarylladaceae) decreased in abundance in unburnt grasslands and in infrequently burnt grasslands. This may have been the result of fire stimulating flowering, rather than real abundance or absence. A number of plants such as *Schistostephium heptalobum*, *Senecio barbatus* and *Watsonia lepida* could be considered fire-sensitive species as they were only found flowering in unburnt or infrequently burnt grasslands. However each species unique to unburnt or infrequently burnt grasslands only occurred in very low abundance making it difficult to determine if these species are really fire-sensitive. There were many more flowering forb species unique to burnt grasslands than unburnt grasslands and intermediate burning also produced many unique forb species.

Species richness for forbs in flower was significantly higher in grasslands that had been burnt during the year of sampling than those that had been burnt two years and five years before. This together with the fact that the highest flowering forb diversity was found in grasslands burnt frequently suggests that fire stimulates flowering in a large number of species. Fire results in a change in the structure and functioning of the post-fire environment, including changes in the vegetation cover and rainfall infiltration which in turn leads to changes in microclimate, soil nutrient and soil moisture status (Frost 1984). These changes provide opportunities for enhanced reproduction which many plants exploit, especially geophytes. Some geophytes are totally dependent on fire and may remain dormant during periods between fires. Therefore, grassland areas in this study that had not been burnt for two or five years would have had a reduced flowering forb species diversity due to some species being dormant rather than completely absent. This has significant implications for grassland invertebrate species that are dependant on the flowering component of forbs for food, shelter, mating and resting sites.

The trends in invertebrate species diversity and their response to fire (Chapter 3) were very similar to those of flowering forbs. Invertebrates appear to be largely dependant on the flowering component of forbs where high species richness of flowering forbs in frequent and intermediately burnt sites reflected high invertebrate species richness. Burnt and unburnt grasslands and each burn frequency had its own suite of unique flowering species following the same trend as the invertebrates, therefore ideally a combination of all three burn frequencies needs to be used to create as much heterogeneity as possible.

Burn frequency is just one component of an effective burning regime. Other fire parameters also need to be taken into consideration such as fire intensity, the season of burn as well as the size of the patch burnt. Howe (1994) found that in order to maximise prairie plant species diversity, a variety of species abundance distributions should be promoted. To do this he suggested a mixture of fire intervals, seasonal burns, grazing frequencies, and grazing intensities by different animals should be promoted in order to produce the maximum species diversities within and between habitats. Therefore creating heterogeneity also involves manipulating grazing intensities and frequencies which can be done through prescribed burning.

CHAPTER 5

THE INFLUENCE OF ENVIRONMENTAL FACTORS ON INVERTEBRATE AND FLOWERING FORB COMMUNITY ASSEMBLAGES

5.1. Introduction

Communities are different species of plants and animals that interact with one another and together with their environment, form functional ecosystems (Anderson & Kikkawa 1986). These ecological communities vary in space and time and are distributed heterogeneously across the earth (Gaston 2000). Some ecological communities are more diverse than others with areas such as tropical forests and coral reefs being much more diverse than other areas such as deserts and polar regions which are virtually devoid of life (Gaston 2000). Species diversity varies on a local scale (within a site), on a mesoscale (among sites in a region) or on a regional scale (global or geographic scale) (Menge & Olson 1990). The general factors that affect species diversity spatially are latitudinal gradients, climate, habitat structure, disturbance and productivity (Rosenzweig 1995; Wettstein & Schmid 1999). Biogeographical factors such as habitat area and isolation also effect species diversity (MacArthur 1984).

The pattern in community composition on a local scale results from spatial variation in the physical habitat as well as from the activities of plants and animals that add further heterogeneity to the ecosystem (Greig-Smith 1986). Periodic disturbances occur within every landscape and also add to the heterogeneity of the ecosystem. Disturbances can be in the form of localised tree-fall to the widespread effect of volcanic eruption (Samways 1994) or in the case of grassland ecosystems disturbance occurs in the form of fire. These disturbances disrupt the ecosystem, community or population structure resulting in a change in the physical and biotic environment. As a result of these disturbances ecological succession occurs within the community resulting in temporal heterogeneity in the ecosystem. The species' succession

on a disturbed patch is influenced by the type of disturbance and also the seasonal timing of the disturbance, the size of it and neighbouring vegetation (Scholes & Walker 1993).

The gradual changes in environmental conditions which accompany succession could result in a number of different patterns of change in the organisms of a community (Putman 1994).

Ecological succession is defined as the non-seasonal, directional and continuous pattern of colonization and extinction on a site by species' populations (Begon *et al.* 1996). Post-colonisation succession in plant communities suggests that after a disturbance 'facilitator' species move into the area which prepares the ground for later successional species. Once the facilitators have changed the environment sufficiently the 'inhibitors' then arrive and have the ability to maintain their captured space from later would-be colonists. 'Tolerators' are those species which can survive with low levels of resources and out-compete other species (Kikkawa & Anderson 1986; Putman 1994). This results in a continual change in plant species composition in one area over time. Within a grassland ecosystem a variation of patches in different stages of ecological succession would promote species diversity rather than one uniform patch burnt at the same frequency.

The previous two chapters dealt with the influence of fire and fire frequency on invertebrate and flowering forb species diversity. However, measures of diversity do not take community structure into consideration. Fire frequency may affect species diversity, as seen in the previous two chapters, but may not be influencing species composition. Ecological succession after each fire may result in different community assemblages in grassland patches varying in the length of time since the last fire. Invertebrate and flowering forb species composition could also differ because of the spatial variation in the location of the grassland sites that were

sampled, where sites were situated in three separate valleys which were over a kilometer apart. Therefore the overall aim of this chapter was to determine the importance of fire in structuring communities. To achieve this, the objective was to determine whether the invertebrate and flowering forb species composition in each grassland site are most closely associated with locality, fire frequency or the time elapsed since the last fire.

5.2. Materials and Methods

Refer to Chapter Two

5.3. Results

5.3.1. Influence of environmental variables on invertebrate and flowering forb communities

In redundancy analysis (RDA) for invertebrates the first axes explained 28% of the variation in the invertebrate community assemblage and the second axes accounted for 13% of the variation. The Monte Carlo test of significance showed that the first canonical axis was statistically significant ($F = 3.96$; $P = 0.002$) as well as all the canonical axes together ($F = 3.38$; $P = 0.002$) confirming that the measured environmental variables (fire frequency, time since last fire and locality) explained a significant proportion of the variation in invertebrate species composition.

Invertebrate community composition was most closely associated with locality because sites in the same valley clustered close together (Figure 5.1). But invertebrate community composition was also associated with the time elapsed since the last fire. Sites that were burnt during the year of sampling (sites one to seven) fell along the same perpendicular bisector of the extended vector (time since last fire) suggesting similar species assemblages in those sites (Figure 5.1). Sites that were burnt two years before sampling (sites eight to ten) had similar

species assemblages and grouped together and those that were burnt five years before sampling (site 11-14) had similar species assemblages. These groups of sites that were burnt within the year of sampling, two years before sampling and five years before sampling fell along the 'time since last fire' vector in a sequential order.

Community composition was influenced least by fire frequency (Figure 5.1). Frequent and infrequent burning resulted in two different communities but sites that were burnt intermediately did not have the same species compositions as they did not fall along the same perpendicular bisector of the extended vector (fire frequency). All invertebrate species that were unique to frequently burnt and infrequently burnt grasslands (Appendix 1) had fewer than five individuals making it difficult to determine whether species are definitely fire tolerant or fire sensitive.

In RDA for forbs the first axes explained 47 % of the variation in flowering forb species composition and the second axes accounted for 10 % of the variation. The Monte Carlo test of significance showed that the first canonical axis was statistically significant ($F = 8.93$; $P = 0.002$) as well as all the canonical axes together ($F = 5.16$; $P = 0.002$) confirming that the measured environmental variables explained a significant proportion of the variation in flowering forb species composition (Figure 5.2).

Flowering phenology of forbs was influenced mostly by the time elapsed since the last fire (Figure 5.2). Species assemblages in sites that had been burnt two years before sampling (sites eight to ten) were very similar to those sites that had been burnt five years (sites 11 –14) before sampling, as they clustered close together. Sites that had been burnt during the year of

sampling (sites one to seven) fell along a similar perpendicular bisector of the extended vector (time since last fire) suggesting similar species composition. A number of potential facilitator species were identified (Table 5.1). No inhibitor or tolerator species could be identified in grasslands burnt two and five years before sampling.

Community assemblage of forbs in flower was also associated with fire frequency, although less so than time since the last fire (Figure 5.2). Sites that had been burnt frequently (six and seven) had a different species assemblage to those that had been burnt at an intermediate and infrequent level. However the three intermediately burnt sites (eight to ten) that were not burnt within the year of sampling clustered closer to infrequently burnt sites than the five intermediately burnt sites (one to five) that were burnt within the year of sampling, suggesting that the time since the last fire is more important in influencing flowering of forb species than fire frequency. All flowering forb species that were unique to infrequent burning (Appendix 2) could possibly be fire sensitive although none of these species were represented by more than five individuals.

Flowering phenology of forbs was influenced least by locality (Figure 5.2). Grassland sites in valley two were nearest to each other but site six and seven (frequently burnt and burnt within the year of sampling) had a very different flowering phenology to sites eight, nine and ten (intermediately burnt and burnt two years before sampling).

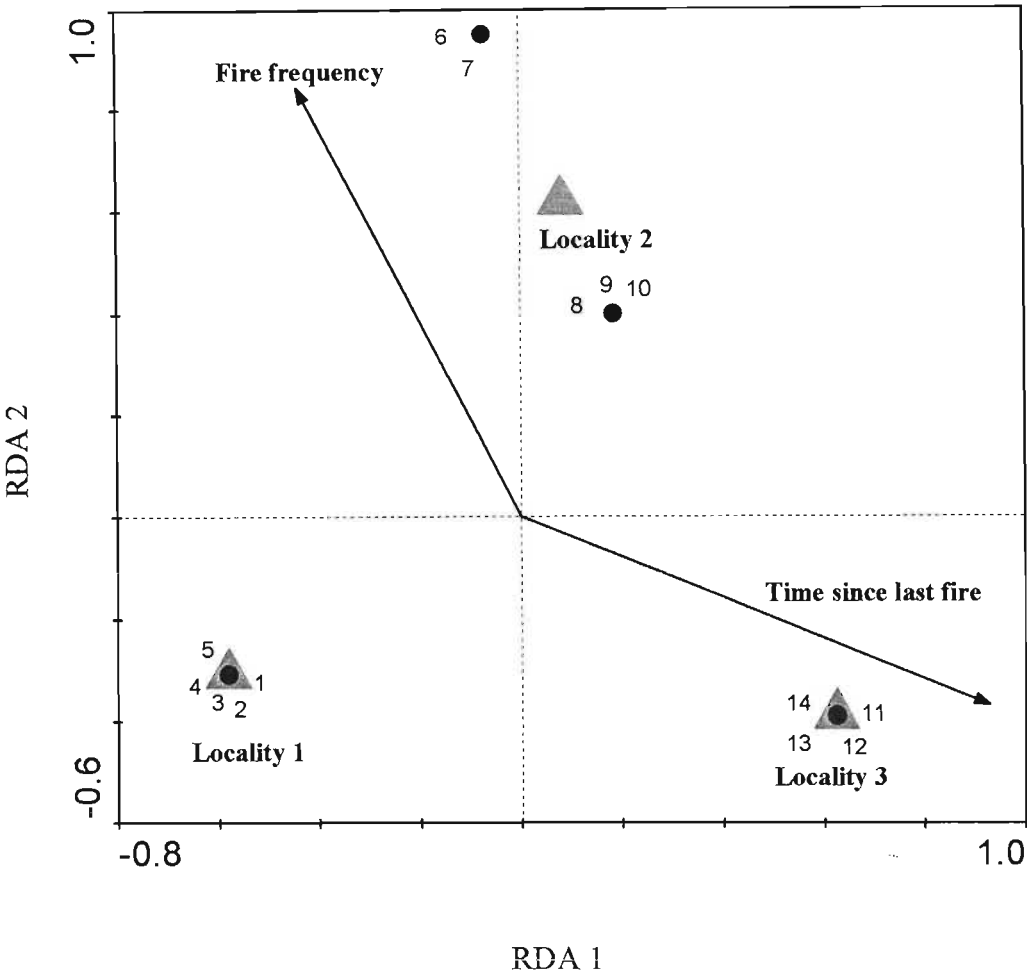


Figure 5.1: The effect of environmental variables on invertebrate community composition. Locality is a nominal variable (not quantitative) (▲) and fire frequency and the length of time since the last fire are non-nominal variables (quantitative) (→, the longer the line the greater the influence of the environmental variable on species composition). Locality 1 = Valley 1 (site (●) one to five); Locality 2 = Valley 2 (site six to ten); Locality 3 = Valley 3 (site 11 – 14). See chapter 2.5.2.3, pg 49 for an explanation of RDA.

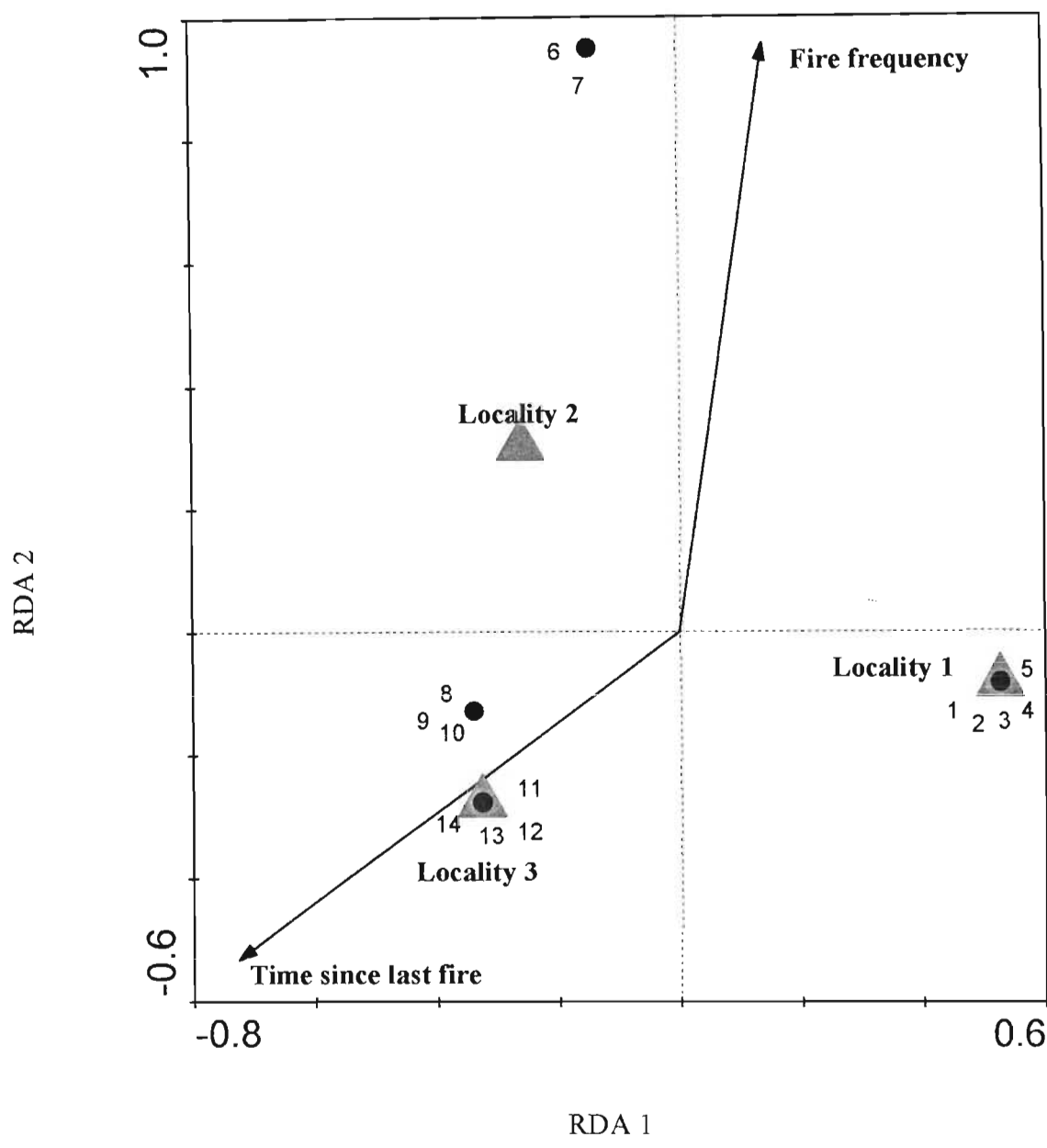


Figure 5.2: The effect of environmental variables on flowering forb phenology. Locality is a nominal variable (not quantitative) (▲) and fire frequency and the length of time since the last fire are non-nominal variables (quantitative) (→, the longer the line the greater the influence of the environmental variable on species composition). Locality 1 = Valley 1 (site (●) one to five); Locality 2 = Valley 2 (site six to ten); Locality 3 = Valley 3 (site 11 – 14) (see Chapter 2). See chapter 2.5.2.3, pg 49 for an explanation of RDA.

Table 5.1: Possible facilitator forb species found flowering in grasslands burnt within the year of sampling.

Family	Facilitator species
Amaryllidaceae	<i>Apodilirium buchananii</i>
Campanulaceae	<i>Lobelia flaccida</i>
Commelineaceae	<i>Commelina africana</i> <i>Ledebouria sandersonii</i> <i>Ledebouria cooperi</i>
Asteraceae	<i>Aster bakerianus</i> <i>Helichrysum aureonitens</i> <i>Helichrysum adenocarpum</i> <i>Helichrysum chionosphaerum</i> <i>Helichrysum coriaceum</i> <i>Helichrysum oreophilum</i> <i>Hirpicium armeroides</i>
Liliaceae	<i>Urginea tenella</i>
Polygalaceae	<i>Polygala gracilentia</i>
Santalaceae	<i>Thesium costatum</i>

5.3.2. Similarity of invertebrate and flowering forb species composition between sites

Cluster analysis of invertebrate species indicated three large clusters (Figure 5.3). The first cluster included sites 11 to 14; these sites were all infrequently burnt and had been burnt five years before sampling and were located in valley three. The second cluster included site one, two and five which were situated in valley one, had been burnt at an intermediate level of frequency and had been burnt during the year of sampling. The third cluster represented sites from valley one (sites three and four) and valley two (six to ten), intermediately (sites three, four, eight, nine and ten) and frequently burnt sites (six and seven) as well as sites burnt

during the year of sampling (three, four, six and seven) and two years before sampling (eight, nine and ten).

Similar species assemblages occurred within frequently and intermediately burnt grasslands, these species assemblages were different from those of infrequently burnt grasslands. Similar species assemblages were found in sites burnt within the year of sampling and sites burnt two years before sampling and these assemblages were different from those sites burnt five years before sampling. However, it is difficult to separate the effect of locality from the effects of fire in this analysis.

In the flowering forb community assemblages two main clusters were apparent (Figure 5.4). The first cluster consisted of sites that were burnt two and five years before sampling, except for site six and seven that were burnt during the year of sampling. This may be related to the effects of locality because all the other sites that were burnt within the year of sampling were situated in valley 1. Species assemblages of locality two and three were similar, and species in locality one differed from those in two and three as they were clustered separately.

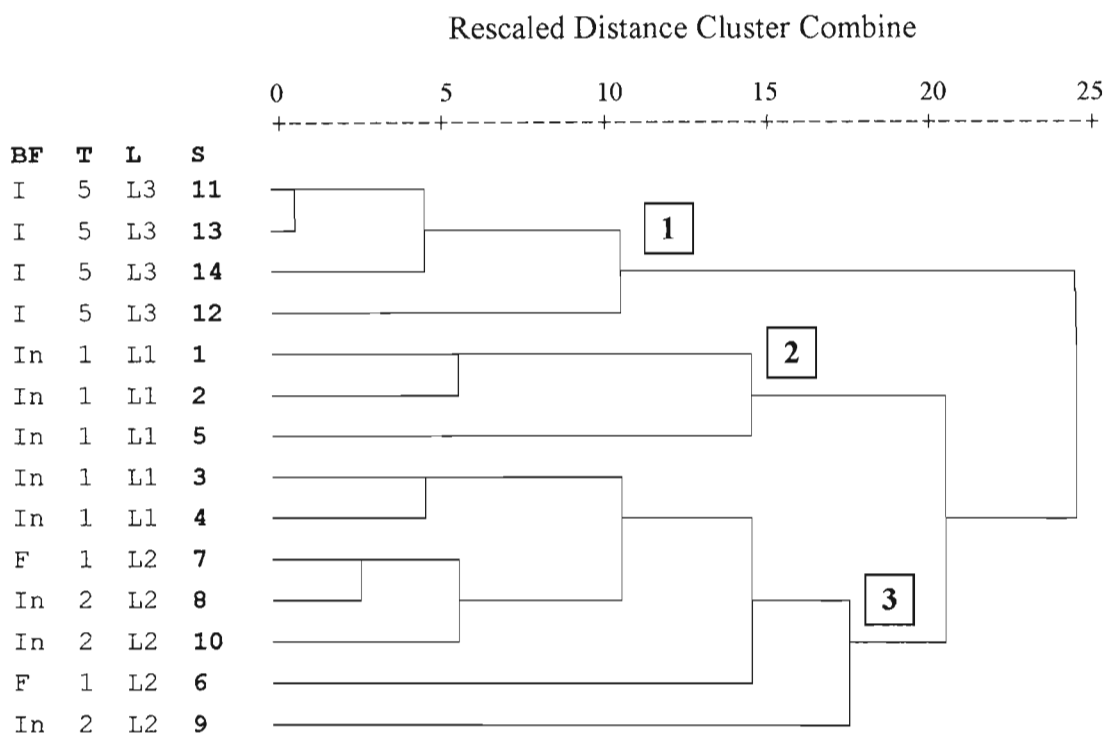


Figure 5.3: The effect of burn frequency (BF) (I = infrequent; In = intermediate; F = frequent), time since the last fire (T) (5 = last fire occurred five years ago; 2 = last fire occurred two years ago; 1 = burnt during the year of sampling) and locality (L) (L1 = Valley 1; L2 = Valley 2; L3 = Valley 3) on invertebrate community assemblages in various grassland sites (S). A dendrogram using average linkage between groups is presented.

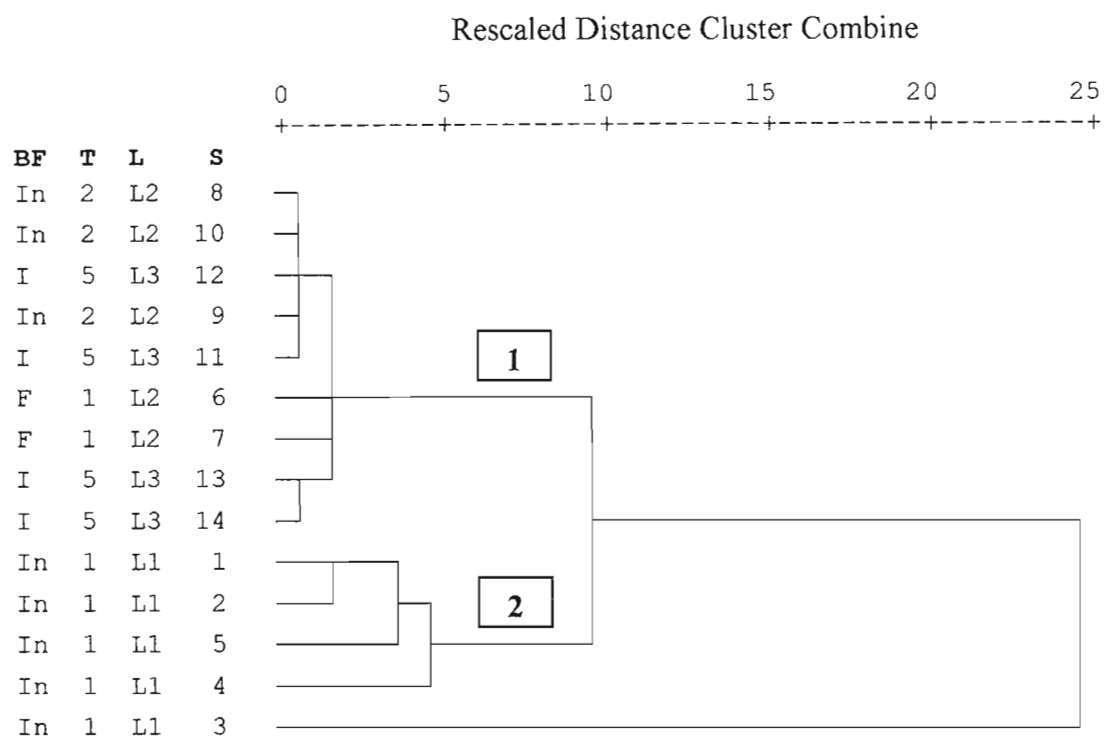


Figure 5.4: The effect of burn frequency (BF) (I = infrequent; In = intermediate; F = frequent), time since the last fire (T) (5 = last fire occurred five years ago; 2 = last fire occurred two years ago; 1 = burnt during the year of sampling) and locality (L) (L1 = Valley 1; L2 = Valley 2; L3 = Valley 3) on flowering forb community assemblages in grassland sites (S). A dendrogram using average linkage between groups is presented.

5.4. Discussion

5.4.1. Environmental variables influencing invertebrate communities

In any ecosystem there is considerable interaction between the effects of different environmental variables on species composition, therefore it is important not to consider any one abiotic factor in isolation (Putman 1994). An interaction of environmental variables was seen in this Drakensberg grassland ecosystem where a combination of all three environmental variables, locality, time since the last burn and fire frequency, appeared to be influencing invertebrate species composition. This was apparent in the cluster analysis where sites did not cluster out clearly in any one specific pattern indicating that invertebrate community assemblages are being influenced by more than one environmental variable.

However, invertebrate species composition appeared to be most strongly influenced by locality with species compositions being most similar in separate valleys suggesting that invertebrate communities are fairly localised and limited in their dispersal capabilities, especially when it comes to crossing valleys and mountain ranges. The specific factor/s of locality influencing species composition remains unclear from this study and needs further investigation. Armstrong and van Hensberg (1997) found a difference in grasshopper species composition within a 600 m difference in altitude in the Eastern Cape and a similar situation may have occurred in the current study where the slight altitudinal differences between localities may have influenced community structure. Other factors of locality that may have affected species composition include temperature, rainfall, geology, grass type and structure (length).

The species assemblages were also closely associated with the time elapsed since the last fire where different species assemblages were found in grasslands burnt within the year of sampling, two years before sampling and five years before sampling. This is a good indication that ecological succession is taking place after each burn.

Invertebrate species assemblages were associated least with fire frequency. Parr *et al.* (2002) found that ant communities were affected less by fire frequency than by the time since the last fire, however only species richness was taken into account and species composition was not considered. Although species composition of frequently burnt sites and infrequently burnt sites were quite different, all the intermediately burnt sites did not have the same community structure. The community structure of three intermediately burnt sites and two frequently burnt sites in the same valley were more similar than the intermediately burnt sites between valleys. Thus locality has a stronger influence on community composition than fire frequency.

Species in frequently burnt sites are likely to use unburnt sites nearby as refugia during and directly after a fire and colonization onto the burnt patch would occur from species in the unburnt patch. Therefore colonisation of frequently burnt sites is made possible through the presence of unburnt areas adjacent to the burnt areas. Small patch burns would allow for quicker invertebrate recolonisation following a fire. Uys *et al.* (2006) found that various invertebrate taxa rapidly recolonised a distance of 280 m after a burn. Invertebrate species composition in areas that are burnt annually will never go beyond that of the colonisers. Therefore greater patchiness throughout the landscape will promote more diverse invertebrate communities all in different stages of post-colonisation succession.

5.4.2. Environmental variables influencing flowering forb communities

Invertebrate communities should be dependant on post-fire habitat structure (Kiss & Magnin 2003) and as a result should have followed a similar trend in community structure to those of flowering forbs. Community structure of forbs in flower were most closely correlated with time since the last fire. But community assemblages of flowering forbs differed to those of invertebrates where sites that were burnt two and five years before sampling had similar community assemblages which differed from those burnt within the year of sampling. Therefore, invertebrate community structure does not appear to be directly dependent on the community structure of flowering forbs. A stronger association might have occurred if grasses were included in the plant analysis as many invertebrates are dependant on grass for their survival. However grass species may be less important than grass structure in terms of the invertebrate diversity related to grasses. Future studies could possibly include the grass length and structure (long, short, moribund) at the time of sampling. Forb flowering phenology was associated least with locality indicating that they have good dispersal capabilities or that they are influenced less by slight environmental differences such as altitude.

Forb flowering phenology was affected by fire frequency but to a lesser extent than time past since the last fire. This supports Uys *et al.* (2004) who found no difference in plant community structure in South African grasslands when comparing areas that had been burnt at different fire frequencies, but where all sites had been burnt the season before sampling, plant community structure was similar. In the current study the difference in community structure of flowering forbs between recently burnt grasslands and those that had not been burnt for two and five years suggests that there are forb communities that are either fire-tolerant or fire-intolerant or simply that the species flowering were mostly stimulated by recent fire. Forbs respond to fire in different ways. Some forbs are stimulated to flower directly after a fire and

others flower two or three years following a fire (Whelan 1995). Therefore forbs that were found in sites burnt within the year of sampling would probably still be present (but dormant) in sites that had not been burnt for two or five years. Uys *et al.* (2004) found that fire-tolerant species can be maintained by burning intervals of between one and five years.

Ecological succession in plant communities appears to be much slower than in invertebrate communities. Everson and Tainton (1984) noticed a change in grass species composition in South African grasslands after five years protection from fire. Uys *et al.* (2004) also found a distinct difference in plant communities between burnt grasslands and grasslands that were left unburnt for more than 10 years. Hobbs *et al.* (1984) found that plant succession did occur in Scottish heathland but this developed over a 39 year period with the first five years being dominated by colonizer forbs and grasses. In this Drakensberg grassland ecosystem a number of species were identified as possible facilitator species because they were found flowering in abundance only in grasslands burnt within the year of sampling. These facilitator species could well be present (but dormant) in grasslands that were burnt two and five years before sampling. Grasslands left unburnt for longer periods of time and sampling grasslands after they had been burnt following an unburnt period of two and five years, would have given more insight into the ecological succession of forb species in this ecosystem.

Due to the nature of forbs and the different way in which they respond to fire, a landscape with burnt and unburnt patches, of not more than five years, would provide maximum flowering forb diversity. Areas left unburnt for longer than ten years would also provide an opportunity for ecological succession to take place, maximizing forb diversity over the landscape.

CHAPTER 6

THE USE OF FLOWERING FORBS AND INDIVIDUAL INVERTEBRATE TAXA AS INDICATORS OF INVERTEBRATE DIVERSITY

6.1. Introduction

Once a reserve is established it should promote the long-term survival of species and other elements of biodiversity that it contains by maintaining natural processes and viable species populations and by excluding threats (Margules & Pressey 2000). This is achieved through maintaining the conditions within the reserve that are required in order for the key natural features to persist. Furthermore, continual monitoring of those features and adaptive management is also required.

The KwaZulu-Natal Drakensberg, South Africa, is predominantly a grassland ecosystem maintained largely by fire. The Drakensberg is a protected area that is managed and maintained by Ezemvelo KwaZulu-Natal Wildlife, whose primary goal is to promote biodiversity conservation above all else. Fire regimes have in the past focused on maintaining the quality of the grasses within the grassland but indigenous forbs and invertebrates, two major components of biodiversity, have largely been ignored. The effect of fire frequency and time since last fire on invertebrate and flowering forb species diversity has been established in chapters three and four.

The ability of flowering forbs or one invertebrate taxon to act as an indicator of overall invertebrate diversity would be a useful monitoring tool in order to obtain a relatively quick and easy assessment of the overall biodiversity in grasslands under different burning regimes. Monitoring refers to “intermittent surveillance carried out in order to determine the extent of

compliance with a predetermined standard or the degree of deviation from an expected norm” (McGeoch 1998). Chapter three and four showed that various fire frequencies result in different levels of invertebrate and flowering forb species richness. Continual monitoring of the invertebrates and flowering forbs in each of those fire frequencies on an annual basis would determine the “health” of the grassland ecosystem in terms of change in species richness and management practices could alter accordingly.

McGeoch (1998) reviewed the use of terrestrial insects as bioindicators and found that bioindication has been used in a broad range of contexts, including the indication of habitat alteration, destruction, contamination and rehabilitation, vegetation succession, climate change and species diversity. From these, three categories corresponding to the three main applications of bioindicators have developed. These are environmental indicators, ecological indicators and biodiversity indicators. Biodiversity indicators are a particular taxon or functional group that is used to estimate the species richness of other taxa (McGeoch 1998). In biodiversity assessments species-level identification of many invertebrates is labour intensive, time-consuming and costly (Pik *et al.* 1999; Williams & Gaston 1994). Therefore biodiversity indicators are often used as an alternative to sampling the entire fauna of an area (Slotow & Hamer 2000). There is much controversy in the literature as to whether biodiversity indicators are reliable and accurate in reflecting general patterns of species biodiversity especially in the context of conservation planning (see Balmford *et al.* 1996; Fagan & Kareiva 1997; Faith & Walker 1996 for a few examples).

Sutton and Collins (1991) suggest that indicator taxa should be taxa that have already attracted a lot of attention, taxonomically straightforward, easy to collect and reasonably diverse but

with a fair degree of endemism. Indicator taxa also need to be relatively sedentary and functionally important in the ecosystem (Brown 1991). Invertebrate taxa that are migratory, poorly differentiated, highly erratic in time, eurytopic or easily adaptable to anthropic habitats should not be used as indicator taxa (Brown 1991). Most authors concede that a small “shopping basket” of indicator taxa need to be used in measuring diversity (Panzer & Schwartz 1998). This involves using more than one taxon and the species richness of these taxa should reflect the overall diversity within the area sampled. But even this approach can prove time-consuming, costly and labour intensive.

Some of the invertebrate taxa found to be good indicators of overall species diversity include Lepidoptera (butterflies), Odonata (dragonflies and damselflies), Tettigonidae (bush crickets) Scarabaeidae (dung beetles) (Sutton & Collins 1991), Collembola (springtails), Isoptera (termites), Formicidae (ants), Apoidea (bees) and Asilidae (Robber flies) (Brown 1991). Cicindelidae (tiger beetles) have also been found to be effective indicators (Pearson & Carroll 1998; Pearson & Cassola 1992). Pearson and Carroll (1998) found that although some species appear to be good indicators of other taxa the same indicator taxa may not be used from continent to continent.

Plants have often been used as indicators of invertebrate diversity in the past (Panzer & Schwartz 1998). The invertebrate-plant interaction is highly significant in maintaining the earth's biocycles (Samways 1993). Invertebrates assist plants in pollination, seed dispersal and protection from pest outbreaks through biological control (Kellert 1993). Plants are an important food source for many invertebrates and also provide important refuges to invertebrates seeking shelter from the elements and protection from predators. Some

invertebrate functional groups, such as herbivores as opposed to predators, may be more closely associated with flowering forb species richness. Despite the close association between plants and invertebrates the use of plants as indicators of invertebrate diversity is being questioned because plants only comprise a fraction of the species in most ecosystems (Panzer & Schwartz 1998). Despite this fact plants have been found to be good surrogates for overall biodiversity (Noss & Cooperrider 1994; Panzer & Schwartz 1998; Sauberer *et al.* 2004; Scott *et al.* 1993). Flowering forbs are easily identified and an expert taxonomist is not necessarily required for identification purposes therefore the whole process of measuring plant diversity is easier, less time consuming and more cost effective than measuring invertebrate diversity.

MacArthur and MacArthur (1961) found that bird species diversity was directly correlated with the amount of vertical complexity in different kinds of plant communities. This idea has been applied successfully to even very simple communities such as grasslands (Murdoch *et al.* 1972). Therefore the more structurally diverse the plant community the more diverse the invertebrate community should be. A greater variety of plants should lead to a greater variety of herbivorous invertebrates as well as a greater variety of pollinators (Murdoch *et al.* 1972). The greater availability of herbivore and pollinator prey should result in greater predator diversity too. Therefore plant species diversity is important for ensuring insect diversity (Huston 1979; Murdoch *et al.* 1972).

The overall aim of this part of the Drakensberg study was to identify potential indicators for biodiversity monitoring. The first objective was to determine whether richness of flowering forb species and flowering Asteraceae, the largest family of forbs sampled in this study, act as indicators of total invertebrate species richness. Total invertebrate species richness refers to

the eleven taxa from various functional groups that were sampled in this study (see Chapter 2). The second objective was to determine whether the relationship between flowering forb species richness and total invertebrate species richness changes with the time of year (late summer, spring and summer), which would influence monitoring procedures. The third objective was to determine whether species richness of individual invertebrate taxa (leafhoppers, spiders, ants and bees) is correlated with total invertebrate species richness, and whether any of these taxa could act as an indicator for monitoring.

6.2. Materials and Methods

Refer to Chapter two

6.3. Results

Most of the correlations between richness of flowering forb species and species richness of different categories of invertebrates were significant (Table 6.1) proving that flowering forbs do act as indicators of invertebrate species richness in this grassland ecosystem. A strong correlation was seen with flowering forbs acting as an indicator of total invertebrate species richness (Figure 6.1). Through extrapolation it is evident that for every 10 forb species found flowering in a grassland patch, an average of 59 invertebrate species (53 and 65, lower and upper confidence intervals respectively) of the focus taxa would occur in that habitat. An even stronger correlation was seen with Asteraceae acting as an indicator of invertebrate species richness where every 10 species of flowering Asteraceae would represent an average of 72 invertebrate species (65 and 79, lower and upper confidence intervals respectively) of the focus taxa (Figure 6.2).

In correlating different invertebrate guilds with number of flowering forb species it was found that wingless invertebrates (Figure 6.3a), predators (Figure 6.3b) and pollinators (Figure 6.3c) were significantly positively related to flowering forbs but herbivores were not (Table 6.1). The predators had the strongest and most significant correlation with flowering forbs but this was only slightly stronger than pollinators and wingless invertebrates.

With the individual sampling seasons, March (Figure 6.4) and November (Figure 6.5) produced significant results where there was a positive correlation between species richness of forbs in flower and invertebrate species richness. The stronger of the two correlations occurred in November where for every 10 forb species in flower, an average of 32 invertebrate species could be found (28 and 36, lower and upper confidence intervals respectively). During March and November, species richness of one family of forb, the Asteraceae, resulted in significant positive correlations with invertebrates with a slightly stronger correlation than for total flowering forbs during March (Figure 6.6) but not in November (Figure 6.7). September did not produce significant correlations between flowering forb and invertebrate species richness.

Certain individual invertebrate taxa appear to be good indicators of invertebrate species richness (Table 6.1). Species richness of bees (Figure 6.8), ants (Figure 6.10), leafhoppers (Figure 6.11) and spiders (Figure 6.12) all had significant positive correlations with total invertebrate species richness. An individual family of bees (Halictidae) also had a significant positive correlation with total invertebrate species richness (Figure 6.9). The Halictid bees displayed the weakest significant correlation with total invertebrate species richness.

Species richness of spiders had the strongest and most significant correlation with total invertebrate species richness and for every 20 species of spider, an average of 59 species of invertebrates (54 and 64, lower and upper confidence intervals respectively) would be found in that grassland habitat (Figure 6.12). Of the two largest spider families sampled during this study, Salticidae species richness did not have a significant correlation with total invertebrate species richness (Table 6.1) but Thomisidae did have a strong significant correlation with total invertebrate species richness where only six species of the Thomisidae would be equivalent to an average of 59 invertebrate species in total (53 and 65, lower and upper confidence intervals respectively) (Figure 6.13).

Table 6.1: Correlations between species richness of different taxa of invertebrates and flowering forbs. **P < 0.05** is a significant correlation and the closer the R-square value is to 1 the stronger the correlation.

Taxon / Category	Taxon	Significance		
		R-squared	F-value	P-value
Total invertebrates	Forbs	0.47	$F_{1,14} = 12.63$	P = 0.003
Total invertebrates	Asteraceae	0.50	$F_{1,14} = 14.15$	P = 0.002
Wingless invertebrates	Forbs	0.33	$F_{1,14} = 6.89$	P = 0.02
Herbivores	Forbs	0.20	$F_{1,14} = 3.38$	P = 0.09
Predators	Forbs	0.39	$F_{1,14} = 9.00$	P = 0.01
Pollinators	Forbs	0.37	$F_{1,14} = 8.07$	P = 0.01
Invertebrates (March)	Forbs (March)	0.28	$F_{1,14} = 5.05$	P = 0.04
Invertebrates (September)	Forbs (September)	0.10	$F_{1,14} = 1.58$	P = 0.23
Invertebrates (November)	Forbs (November)	0.45	$F_{1,14} = 11.57$	P = 0.004
Invertebrates (March)	Asteraceae (March)	0.37	$F_{1,14} = 8.09$	P = 0.01
Invertebrates (November)	Asteraceae (November)	0.39	$F_{1,14} = 8.99$	P = 0.01
Leafhoppers	Invertebrates	0.54	$F_{1,14} = 16.33$	P = 0.001
Bees	Invertebrates	0.34	$F_{1,14} = 7.10$	P = 0.02
Halictidae	Invertebrates	0.28	$F_{1,14} = 5.44$	P = 0.04
Ants	Invertebrates	0.55	$F_{1,14} = 16.97$	P = 0.001
Spiders	Invertebrates	0.67	$F_{1,14} = 28.65$	P = 0.00
Salticidae	Invertebrates	0.19	$F_{1,14} = 3.37$	P = 0.09
Thomisidae	Invertebrates	0.58	$F_{1,14} = 19.54$	P = 0.001

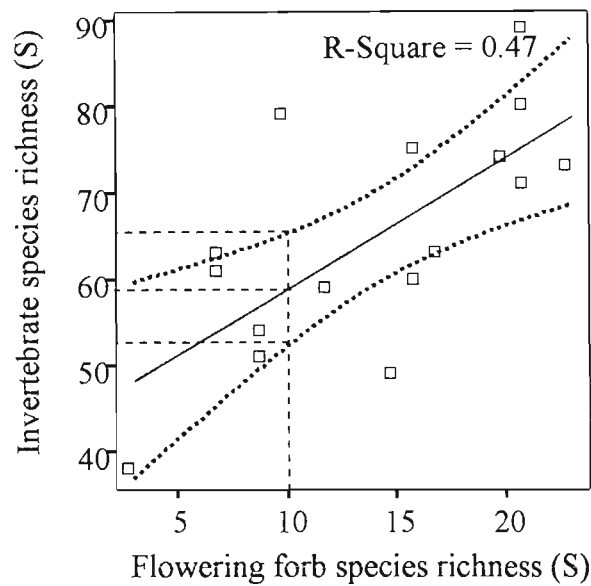


Figure 6.1: Flowering forb species richness as an indicator of invertebrate species richness with 95% confidence intervals (---) and the mean number of invertebrates predicted from 10 flowering forb species with lower and upper confidence limits (---).

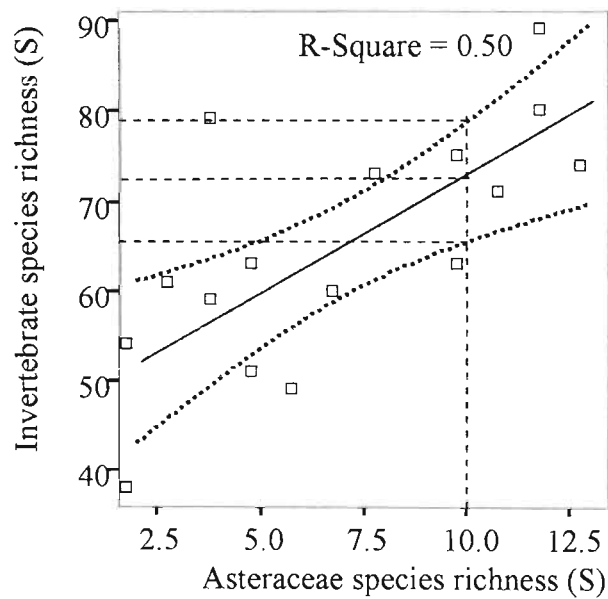


Figure 6.2: Flowering Asteraceae species richness as an indicator of invertebrate species richness with 95% confidence intervals (---) and the mean number of invertebrates predicted from 10 flowering Asteraceae species with lower and upper confidence limits (---).

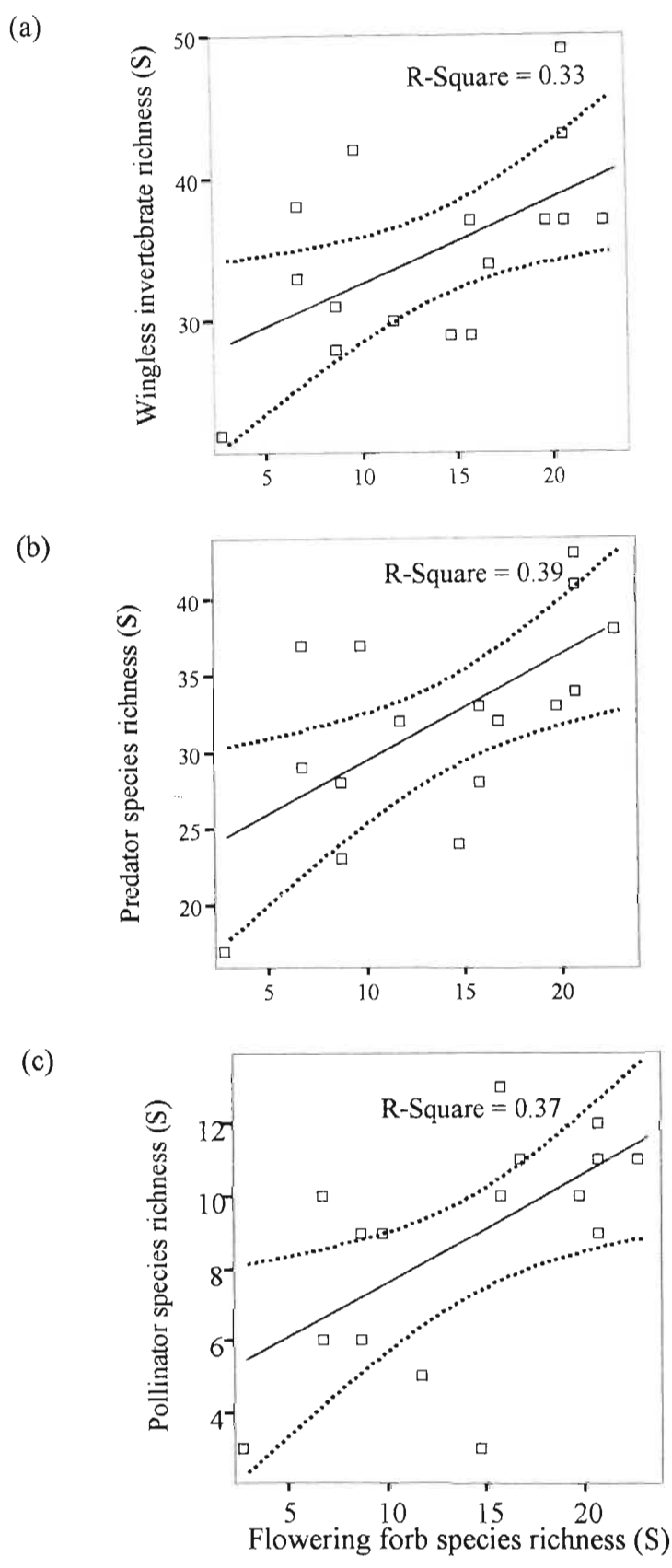


Figure 6.3: Flowering forb species richness as an indicator of different invertebrate guilds: (a) wingless invertebrates, (b) predators and (c) pollinators, with 95% confidence intervals (...).

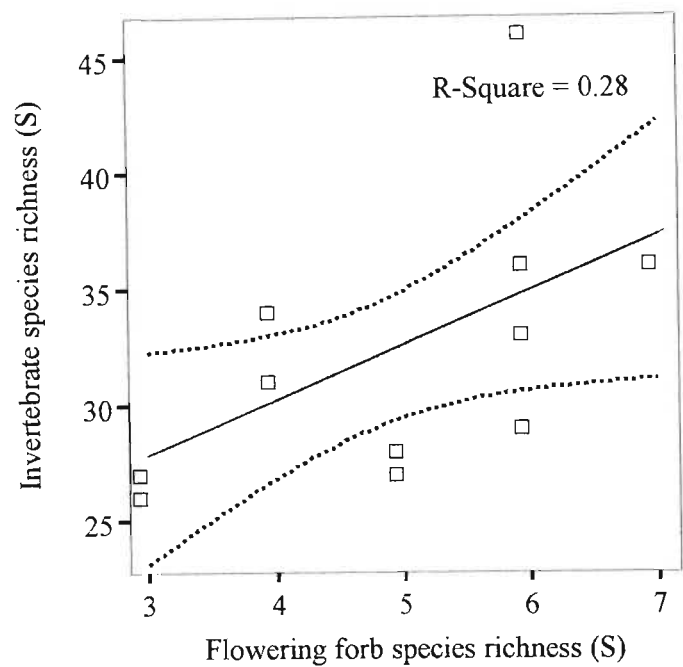


Figure 6.4: Flowering forb species richness as an indicator of invertebrate species richness during March with 95% confidence intervals (...).

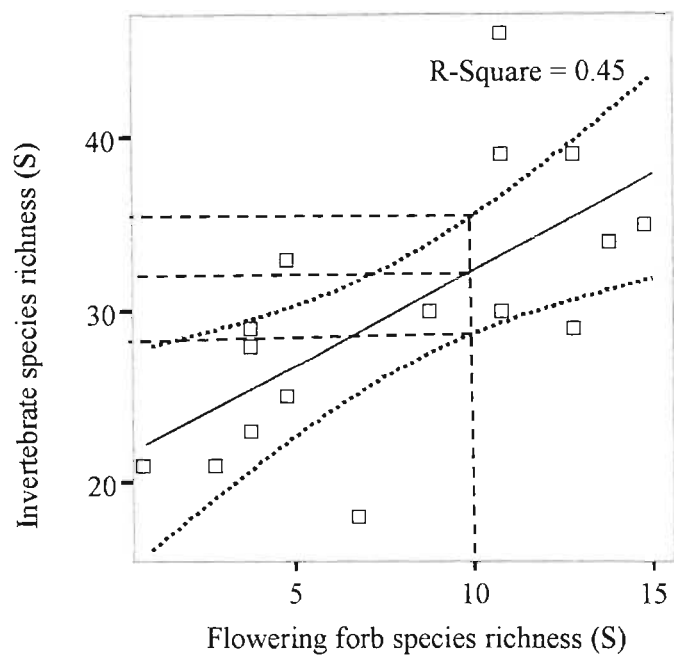


Figure 6.5: Flowering forb species richness as an indicator of invertebrate species richness during November with 95% confidence intervals (...) and the mean number of invertebrates predicted from 10 flowering forb species with lower and upper confidence limits (---).

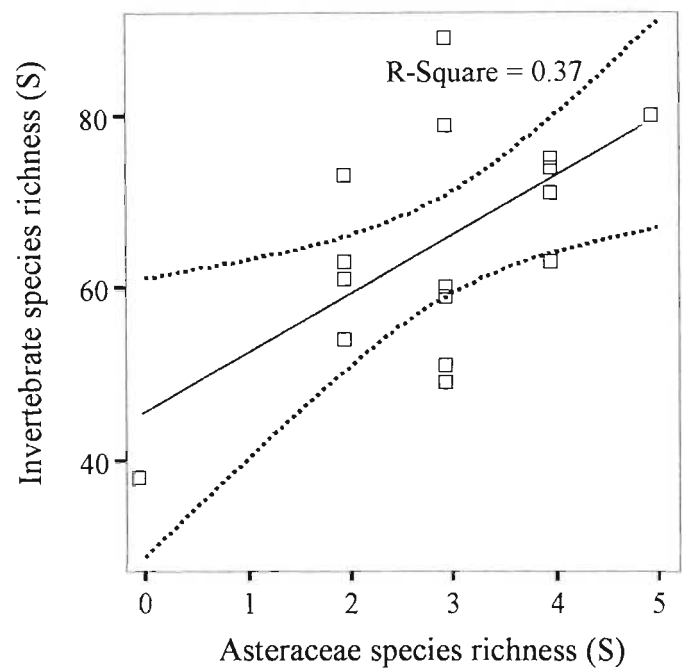


Figure 6.6: Flowering Asteraceae species richness acting as an indicator of invertebrate species richness during March with 95% confidence intervals (...).

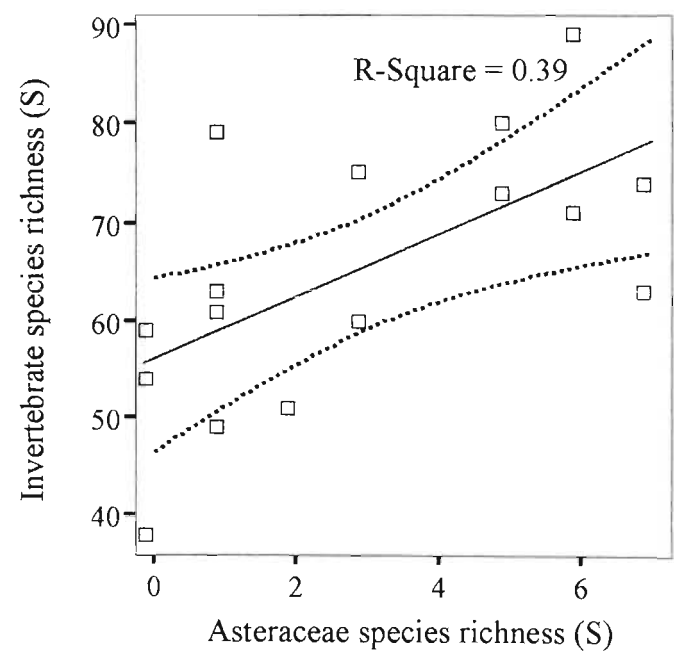


Figure 6.7: Flowering Asteraceae species richness acting as an indicator of invertebrate species richness during November with 95% confidence intervals (...).

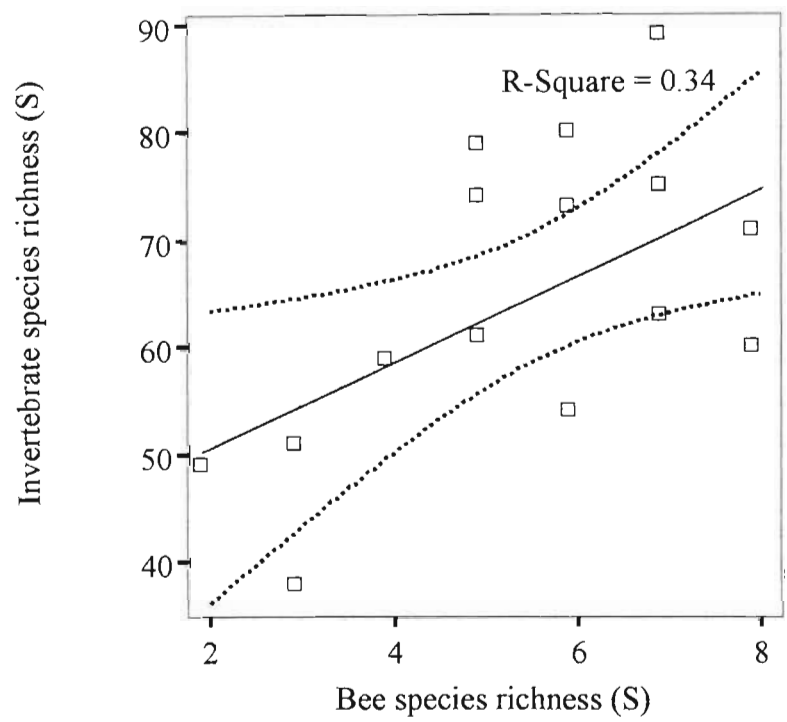


Figure 6.8: Species richness of bees as an indicator of invertebrate species richness with 95% confidence intervals (...).

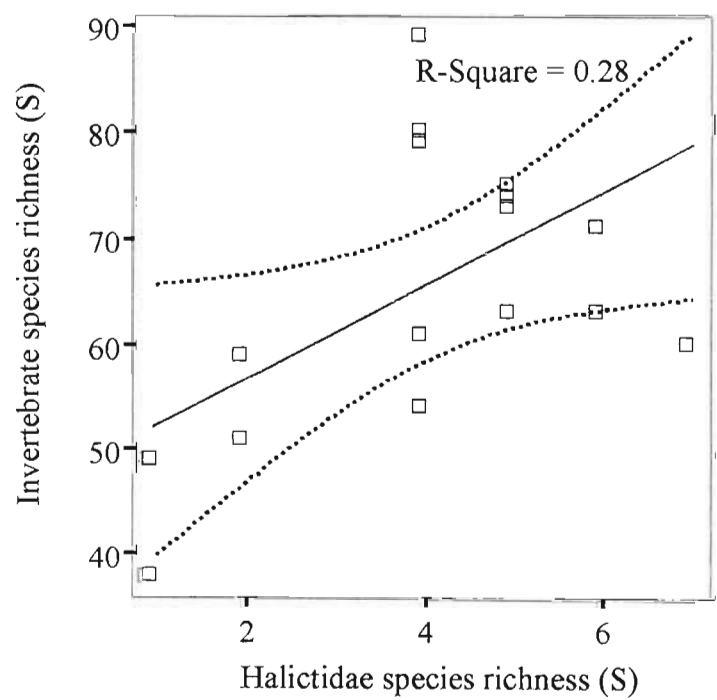


Figure 6.9: Species richness of a family of bees (Halictidae) as an indicator of invertebrate species richness with 95% confidence intervals (...).

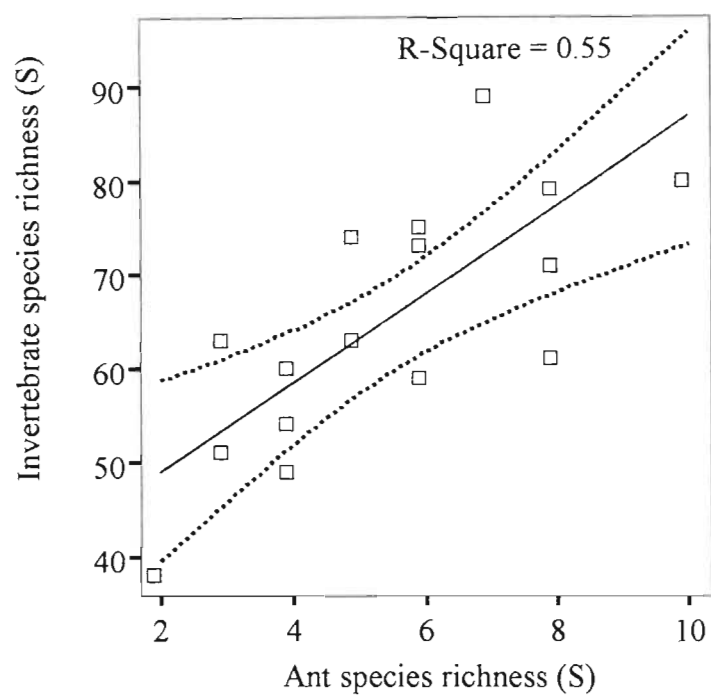


Figure 6.10: Species richness of ants as an indicator of invertebrate species richness with 95% confidence intervals (---).

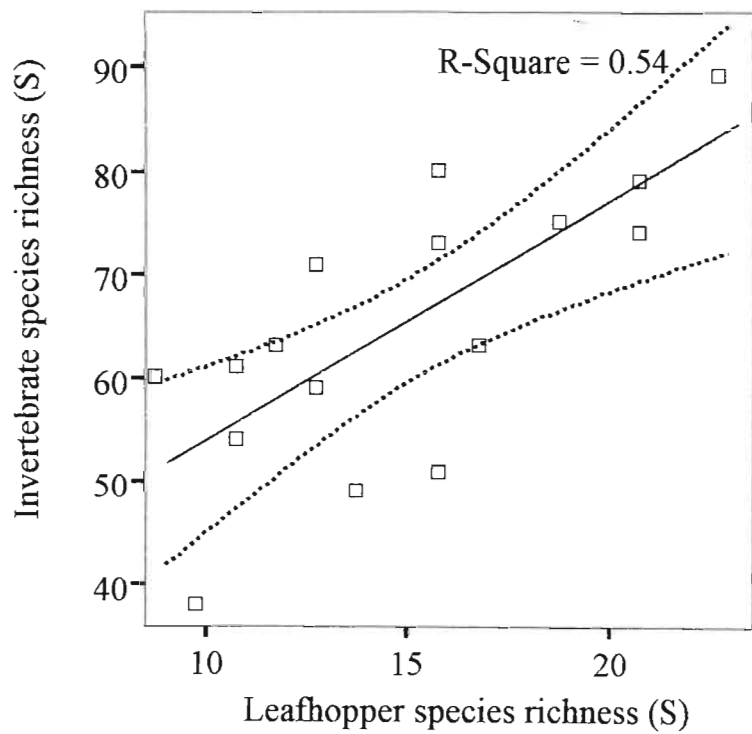


Figure 6.11: Species richness of leafhoppers as an indicator of invertebrate species richness with 95% confidence intervals (---).

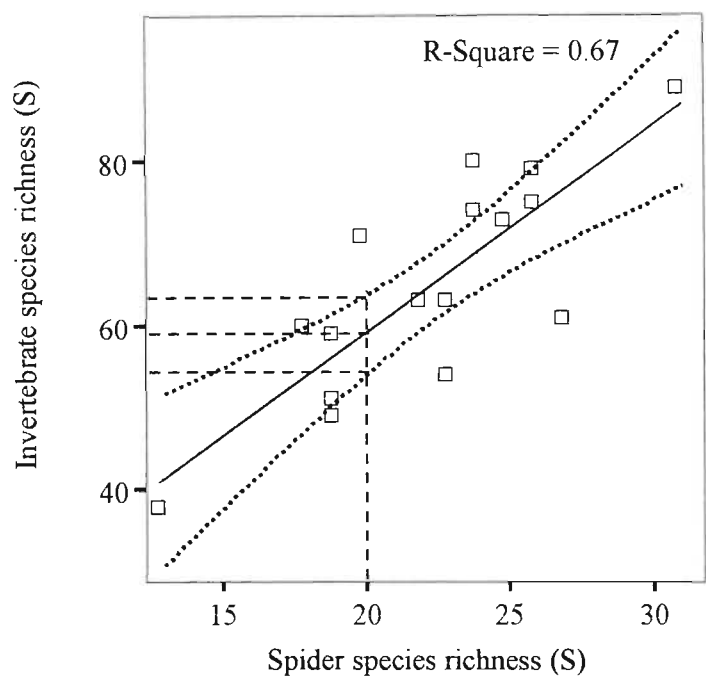


Figure 6.12: Species richness of spiders as an indicator of invertebrate species richness with 95% confidence intervals (---) and the mean number of invertebrates predicted from 20 spider species with lower and upper confidence limits (---).

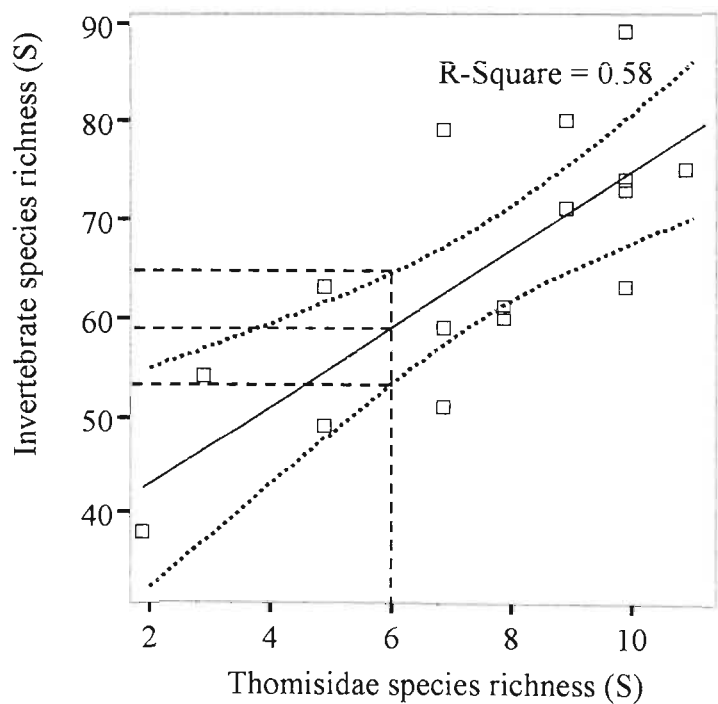


Figure 6.13: Species richness of the spider family Thomisidae as an indicator of invertebrate diversity with 95% confidence intervals (---) and the mean number of invertebrates predicted from 6 Thomisidae species with lower and upper confidence limits (---).

6.4. Discussion

Animals and plants are inextricably interrelated in all communities; any process that affects one will influence the other (Putman 1994). Past studies have shown that an increase in structural heterogeneity of plants creates a wider diversity of available niches (MacArthur & MacArthur 1961; Putman 1994). Therefore animals are found to be most closely correlated with structural diversity of plants rather than plant species richness. However the results from this study suggest that flowering forbs and invertebrates are closely interrelated at a species richness level as flowering forb species richness did act as an indicator of invertebrate species richness. Similarly, a number of other studies have found that plant species richness is a good indicator of invertebrate species richness (see Murdoch *et al.* 1972; Panzer & Schwartz 1998; Saetersdal *et al.* 2003; Sauberer *et al.* 2004). Flowering forbs also acted as indicators of certain individual invertebrate guilds, specifically wingless invertebrates, pollinators and predators, as has been previously suggested by Murdoch *et al.* (1972). A greater variety of flowering forbs would result in a greater variety of pollinators which would in turn result in a greater variety of predators too. Flowering forbs were surprisingly not an indicator for herbivores. A possible explanation for this could be attributed to the fact that grasses were not taken into account for plant species richness during sampling, and herbivores may be more dependant on grass, which is the main component of vegetation in terms of biomass, than forbs.

Although flowering forbs in general were a good indicator of total invertebrate species richness, Asteraceae was an even better indicator having stronger correlations with total invertebrate species richness. Sampling only one family of flowering forb is easier and less time consuming than sampling flowering forbs in general and it appears that Asteraceae could be a good family to use as an indicator taxon. However, Asteraceae were less effective as an

indicator when used in individual sampling periods at different times of the year. Of the individual sampling periods November had the strongest correlation between flowering forbs and invertebrates suggesting that this would be the most appropriate time of year to sample grasslands for monitoring purposes. Sampling at one time during the year would be useful for monitoring because it would be less time consuming and more cost effective.

Four individual invertebrate taxa (ants, leafhoppers, spiders and bees) were strongly correlated with total invertebrate species richness, with spiders showing the strongest correlation. One of the larger spider families, Thomisidae, proved to be a good indicator of overall invertebrate species richness but the Salticidae, another large spider family were not. Whitemore (2000) found that spiders were good indicators of invertebrate diversity however as soon as the spiders were divided into guilds their correlation with total invertebrate species richness was not as strong. Spiders are abundant and diverse in terrestrial ecosystems; taxonomically rich at species, genus and family levels; have a variety of life styles and ecological specialization and they are also easily sampled (New 1999). This makes them an ideal possible surrogate group for sampling biodiversity in an ecosystem.

Ants have been used previously as indicators of ecosystem condition as they often reflect the degree of habitat disturbance or successional state in a community (Parr *et al.* 2002). Parr *et al.* (2002) cautions that in using them as indicators of ecosystem health they may not necessarily be surrogates for overall biodiversity, but they may reflect patterns of loss of biodiversity of other species.

Although bees have been found to be good indicators of total invertebrate diversity in the past (Brown 1991), the positive correlation between bees and total species richness in this study was unexpected. The correlation did not appear to be that strong however and was even weaker when one family of bee, the Halictidae, which were the most common bees, were correlated with invertebrates.

In this study leafhoppers proved to be good indicators of invertebrate species richness even though they are highly host-specific, feeding on trees, shrubs and grasses (Picker *et al.* 2002). They could also be good indicators of ecosystem health because of their host specificity and could be correlated with plant species richness.

Monitoring is important to ensure that diversity does not decline over time in response to specific and repetitive fire frequencies. In using biodiversity indicators, a baseline species richness of the indicator needs to be established using quantified methods of sampling. Grassland sites could then be monitored on an annual basis and the change in species richness of that indicator taxon would provide insight into the “health” of the grassland biodiversity. However, it should be stressed that these indicator taxa are not necessarily species that are sensitive to environmental stresses, pollution or disturbance such as fire. Ideally sensitivity levels of specific taxa or species to fire would be more useful for monitoring impacts of fire and this is an area that needs further investigation. These disturbance indicators could be used in combination with biodiversity indicators. Identification of indicators of sensitivity is, however, a complex process (McGeogh 1998). In this study identification of fire sensitive species was difficult because of the high number of singletons but species that were only

found in sites not burnt for two or five years, and in infrequently burnt sites could be a starting point for further studies.

CHAPTER 7

SUMMARY AND MANAGEMENT RECOMMENDATIONS

Fire frequency is one component of a burning regime and was the primary focus of this study. Invertebrate and flowering forb species diversity was highest in grasslands that had been burnt for two consecutive years as opposed to those that had not been burnt for those two years. Fire appears to promote invertebrate and flowering forb diversity. The intermediate disturbance hypothesis did not hold true in this grassland ecosystem. This was apparent with total flowering forb and invertebrate diversity as well as with wingless invertebrates and three guilds of invertebrates (herbivores, predators and pollinators). The same trend was seen in all these components of biodiversity where frequent (annual) and intermediate (biennial) burning were not significantly different in terms of species diversity but both had significantly higher species diversity than infrequent burning.

Each burn frequency had its own suite of unique invertebrate and flowering forb species. However on average frequent burning resulted in more unique invertebrate species (9) than intermediate (5.25) and infrequent burning (4.5). Flowering forbs followed the same trend with frequent burning resulting in more unique species (4.33) than intermediate (2.38) and infrequent burning (1.75). Most of these unique species were single individuals. Therefore these species could be simply rare rather than entirely unique to individual fire frequencies. However whether they are rare or unique to one burn frequency they still need to be conserved because of their potentially high conservation value. Most endemic invertebrate species were found in more than one burn frequency and those endemic species that were unique to one burn frequency were almost all single individuals, making it difficult to determine whether fire frequency has a real impact on endemic invertebrate species.

Invertebrate species richness was significantly higher in grasslands burnt during the year of sampling and two years before sampling than those that were burnt five years before sampling. Fire does not appear to affect the majority of species in the long-term with most species recovering within two years of the last fire. Although species richness probably declines directly after a fire, communities seem to recover relatively quickly. A similar pattern was seen with species richness of flowering forbs, however flowering forb species richness in grasslands burnt during the year of sampling was significantly higher than in grasslands burnt two and five years before sampling. The results from this study suggest that fire promotes flowering in forbs. Forbs in grasslands burnt two and five years before sampling may only be dormant and not necessarily absent. A resting period may promote more vigorous growth of forbs, an area that needs further investigation.

Invertebrate communities were closely correlated with locality and time since last burn. It is apparent that ecological succession of invertebrates is taking place after each fire because different species compositions were found in grasslands burnt during the year of sampling, two years before sampling and five years before sampling. Similarity of species assemblages in grasslands nearest each other suggests that invertebrates are fairly localized. Unburnt areas in the same valley as burnt areas act as refugia for invertebrates during a fire and species from these unburnt refuges may be first to colonize those areas that have recently been burnt. Maximum species diversity will be achieved by having various patches of grassland in different stages of ecological succession.

Flowering in forb communities is closely correlated with the time elapsed since the last fire. Species composition of flowering forbs in grasslands burnt two and five years before sampling were very similar and both were different from those areas burnt within the year of sampling. This suggests that certain forbs are stimulated by fire and others are not. Ecological succession does not appear to be taking place in this grassland ecosystem. A five year period without burning is not quite long enough for ecological succession to take place. Plants need more than five years without fire to change composition within the grassland ecosystem. Flowering forb communities were not strongly correlated with fire frequency and locality.

Total species richness of forbs in flower and in the family Asteraceae did act as good indicators of invertebrate species richness. Richness of flowering forb species and of flowering species in the Family Asteraceae were also correlated with invertebrate species richness during the individual March and November sampling periods but not the September sampling period. Four invertebrate taxa (ants, leafhoppers, spiders and bees) representing predators, herbivores and pollinators were significantly correlated with total invertebrate richness therefore these taxa have the potential to be used as indicators of overall invertebrate species richness for monitoring purposes. Spiders showed the strongest correlation with total invertebrate species richness. The species richness of one of the larger spider families, the Thomisidae, was also strongly correlated with invertebrate species richness but that of the Family Salticidae was not.

Once an area is proclaimed a reserve continual monitoring is needed in order to ensure that biodiversity is being maintained. The ability of flowering forbs and individual invertebrate taxa to act as biodiversity indicators of overall invertebrate species richness could be a useful

tool in monitoring biodiversity within the grasslands of Giants Castle. Although various fire frequencies have different levels of species richness, monitoring that diversity on an annual basis will provide insight into the “health” of the grassland so that management practices can be altered accordingly. The effect of various fire frequencies on biodiversity can be quickly and effectively monitored by using flowering forb species richness as an indicator of invertebrate species richness or species richness of individual invertebrate taxa (spiders, ants, leafhoppers and bees) as an indicator of total invertebrate species richness. It would appear that spiders would be the most reliable and effective indicator of invertebrate species richness. These biodiversity indicators are not necessarily indicators of ecosystem health, further investigation of this is needed.

In the KwaZulu-Natal Drakensberg current burning regimes are based predominantly on a rotational biennial block burning system. Each of the fire frequencies sampled had a number of unique species therefore a combination of at least all three fire frequencies investigated should be used in order to promote maximum invertebrate and forb species diversity. Using different fire frequencies would result in patches of grassland in various stages of ecological succession. It is important to continually monitor the invertebrate and forb species richness in each fire frequency in order to determine the long-term effects of one specific fire frequency. Monitoring these grasslands will give an indication of whether the maximum diversity is being maintained for that specific fire frequency. Other components of an effective burning regime need to be taken into consideration as well, such as season of burn, fire intensity and the size of individual block burns. These are aspects that need further investigation, especially the size of individual block burns. Patch mosaic burning has been used successfully in savanna

ecosystems to create optimum levels of patchiness and also needs to be explored in this Drakensberg grassland ecosystem.

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Appendix 1: Invertebrates at Giants Castle Game Reserve, South Africa. Unique species found in Burnt (B), Unburnt (UnB), frequently (1), intermediately (2) and infrequently (3) burnt grasslands are presented as well as endemic species to South Africa and KwaZulu-Natal and any new species. The sample sites where each species was found is presented as well as species recorded as a singleton (Single).

Ref. No.	(Taxa) Family	Genus and Species	Author	Sites	Unique					Endemic			Single
					B	UnB	1	2	3	SA	KZN	New	
	(Araneae)												
S11	Araneidae	<i>Araneus nigroquadratus</i>	Lawrence, 1937	S1, S4, S5, S12						X			
S28	Araneidae	<i>Araneus sp.A</i>		S6, S7, S9, S10, S12, S14, S15, S16					X				
S2	Araneidae	<i>Araneus sp.B</i>		S1, S8, S13, S16									
S38	Araneidae	<i>Larinia sp.A</i>		S11, S14		X			X				
S62	Araneidae	<i>Larinia sp.B</i>		S1, S4, S5, S6, S8, S11, S13								X	
S45	Araneidae	<i>Lipocrea longissima</i>	(Simon, 1881)	S15	X		X						X
S4	Araneidae	<i>Neoscona alberti</i>	(Strand, 1913)	S1, S2, S3, S4, S5, S6, S7, S8, S9, S10, S12, S14, S15									
S36	Araneidae	<i>Neoscona moreli</i>	(Vinson, 1863)	S11		X			X				X
S17	Araneidae	<i>Neoscona subfusca</i>	(C.L. Koch, 1837)	S1, S2, S3, S4, S5, S6, S7, S8, S9, S10, S11, S12, S13, S14, S15, S16									
S98	Araneidae	<i>Singa lawrencei</i>	(Lessert, 1930)	S3, S8, S11, S16									
S1	Clubionidae	<i>Clubiona sp.A</i>		S1, S2, S3, S5, S6, S7, S9, S10, S12, S14									
S55	Clubionidae	<i>Clubiona sp.B</i>		S3, S5, S11, S13									
S27	Dictynidae	<i>Devade sp.A</i>		S6, S7, S8, S9, S10, S11, S12, S13, S14, S16									
S34	Dictynidae	<i>Dictyna sp.A</i>		S9, S10, S11, S12, S14		X							
S50	Hahniidae	<i>Hahnia tabulicola</i>	Simon, 1898	S8, S13, S15									
S26	Linyphiidae	<i>Eperigone sp.A</i>		S6	X		X						X
S52	Linyphiidae	<i>Limoneta sp.A</i>		S10, S15									
S89	Linyphiidae	<i>Mecynides sp.A</i>		S3, S10, S12, S14, S16									
S39	Linyphiidae	<i>Meioneta natalensis</i>	Jocque	S12, S15						X			
S100	Linyphiidae	<i>Metaleptyphantes sp.A</i>		S10		X		X					X
S23	Linyphiidae	<i>Microlinyphia sp.A</i>		S5, S6, S7, S12, S14, S15									
S88	Lycosidae	<i>Pardosa sp.A</i>		S12, S14		X			X				

Ref. No.	(Taxa) Family	Genus and species	Author	Sites	Unique					Endemic			Single
					B	UnB	1	2	3	SA	KZN	New	
S53	Lycosidae	<i>Proevippa sp.A</i>		S1, S2, S3, S4	X			X					
S10	Lycosidae	<i>Trabea purcelli</i>	Roewer, 1951	S1, S2, S3, S5, S6, S8, S10, S12, S13, S14									
S58	Lycosidae	<i>Trabea sp.B</i>		S15	X		X						X
S49	Oxyopidae	<i>Oxyopes sp.A</i>		S15	X		X						
SP3S13	Philodromidae	<i>Gephyra sp.A</i>		S4, S5, S6, S7, S8, S9, S10, S16									
S113	Philodromidae	<i>Philodromus sp.A</i>		S2, S3, S6, S7	X								
SP3S20	Philodromidae	<i>Suemus sp.A</i>		S12		X			X				X
S119	Philodromidae	<i>Tibellus sp.A</i>		S2	X			X					X
S44	Pisauridae	<i>Perenethis sp.A</i>		S6, S15	X		X						
S22	Salticidae	<i>Brancus sp.A</i>		S4, S6, S8, S10, S12, S13, S14, S15									
S77	Salticidae	<i>Brancus sp.B</i>		S10		X							X
S112	Salticidae	<i>Euophrys sp.A</i>		S4, S6, S7	X								
S69	Salticidae	<i>Heliophanes hastatus</i>	Wesolowska, 1986	S3, S7, S8, S10						X			
S80	Salticidae	<i>Heliophanes sp.A</i>		S4	X			X				X	X
S40	Salticidae	<i>Hyllus sp.A</i>		S12, S14		X			X				
S101	Salticidae	<i>Hyllus sp.B</i>		S10		X		X					X
S7	Salticidae	<i>Myrmarachne sp.A</i>		S1, S3, S5, S6, S7, S8, S9, S10, S11, S12, S13, S14, S15, S16									
S6	Salticidae	<i>Rhene sp.A</i>		S1	X			X					
S118	Salticidae	<i>Rhene sp.B</i>		S2	X			X					
S56	Salticidae	<i>Stenaelurillus sp.A</i>		S4, S5, S6, S15	X								
S37	Salticidae	<i>Thyene sp.A</i>		S5, S6, S7, S8, S9, S11, S13, S14, S16									
S106	Scytodidae	<i>Scytodes sp.A</i>		S14		X			X				X
S5	Tetragnathidae	<i>Leucage auronotum</i>	Strand, 1907	S1, S2, S3, S4, S5, S9, S10, S11, S12, S13, S14							X		
S63	Tetragnathidae	<i>Leucage sp.A</i>		S2, S3, S5, S6, S7, S10, S14									
S21	Theridiidae	<i>Enoplognatha sp.A</i>		S3, S5, S8				X					
S104	Theridiidae	<i>Euryopsis sp.A</i>		S7, S14									
S32	Theridiidae	<i>Latrodectus renivulvatus</i>	Dahl, 1902	S8		X		X					X

Ref. No.	(Taxa) Family	Genus and species	Author	Sites	Unique					Endemic			Single
					B	UnB	1	2	3	SA	KZN	New	
R4	Asilidae	<i>Dasophrys nigroflavipes</i>	(Hobby, 1933)	S2, S3, S4, S5, S6, S7, S9									
R7	Asilidae	<i>Dikowmyia mediorus</i>	Londt, 2002	S4	X			X					
R8	Asilidae	<i>Gonioscelis sp.A</i>		S4	X			X					X
SP3R6	Asilidae	<i>Gonioscelis truncatus</i>	Oldroyd, 1974	S1, S2, S3, S6, S7	X								
SP3R3	Asilidae	<i>Microstylum sp.A</i>		S2, S6, S7	X								
R3	Asilidae	<i>Neolophonotus sp.A</i>		S3, S4, S5, S9, S11									
SP3R2	Asilidae	<i>Neolophonotus variabilis</i>	Londt, 1986	S1, S2, S3, S5, S6, S9, S12									
R5	Asilidae	<i>Neolophonotus wroughtoni</i>	(Ricardo, 1920)	S1, S5, S8, S9, S10, S12									
R6	Asilidae	<i>Rhabdogaster sp.A</i>		S3, S4, S5, S9, S13									
D68	Bombyliidae	<i>Anthrax sp.A</i>		S7	X		X						X
SP2R1	Bombyliidae	Bombyliidae sp.A		S6			X						
SP2R2	Bombyliidae	<i>Systoechus sp.A</i>		S6	X		X						X
D66	Syrphidae	Syrphidae sp.A		S8, S14		X							
SP3BB2	Syrphidae	Syrphidae sp.B		S5	X			X					X
Bee3	Syrphidae	Syrphidae sp.C		S14, S16		X			X				
	(Hemiptera)												
Leaf 9	Cicadellidae	<i>Afroideus sp.A.</i>	Linnavuori, 1961	S5, S6, S7, S8								X	
Leaf 42	Cicadellidae	<i>Afrorubria vitticollis</i>	(Stal, 1855)	S12		X			X				X
Leaf 29	Cicadellidae	<i>Austroagallia sp.A</i>	Evans, 1935	S15	X		X						X
Leaf 14	Cicadellidae	<i>Balclutha rosea</i>	(Scott, 1876)	S6, S7, S8, S9, S10, S11, S12, S13, S15, S16									
Leaf 28	Cicadellidae	<i>Balclutha rubrocincta</i>	(Melichar, 1905)	S15	X		X						X
SP2Leaf6	Cicadellidae	<i>Balclutha sp.A</i>	Kirkaldy, 1900	S4, S5, S6, S7, S12									
Leaf 24	Cicadellidae	<i>Bhooria theroni</i>	Young, 1986	S5, S14, S15									
SP3Leaf32	Cicadellidae	<i>Caplopa sp.A</i>	Evans, 1947	S8, S9, S11, S12, S14, S15									
SP3Leaf22	Cicadellidae	Gen. nov sp.A		S7	X		X					X	X
SP2Leaf31	Cicadellidae	<i>Dagama sp.A</i>	Distant, 1910	S7	X		X						X
SP2Leaf12	Cicadellidae	<i>Drakensbergena fuscovittata</i>	Linnavuori, 1961	S3, S5, S6, S7, S8, S13, S16						X			
SP2Leaf4	Cicadellidae	<i>Drakensbergena ochraceae</i>	Linnavuori, 1961	S1, S2, S3, S4, S5, S6, S7	X					X			

Ref. No.	(Taxa) Family	Genus and species	Author	Sites	Unique					Endemic			Single
					B	UnB	1	2	3	SA	KZN	New	
Leaf 15	Cicadellidae	<i>Elginus sp.A.</i>	(Naude, 1926)	S1, S2, S3, S4, S5, S7, S8, S9, S10, S15, S16								x	
SP2Leaf27	Cicadellidae	<i>Empoascanara ethiopica</i>	Dworakowska, 1972	S1, S5, S6, S7, S8, S10, S11, S12, S13, S16						x			
Leaf 26	Cicadellidae	<i>Exititanus distanti</i>	Ross, 1968	S15	x		x						
Leaf 25	Cicadellidae	<i>Exititanus natalensis</i>	Ross, 1968	S4, S11, S12, S15, S16									
SP2Leaf26	Cicadellidae	<i>Goniagnathus obesus</i>	Jacobi, 1910	S5	x			x					x
SP2Leaf29	Cicadellidae	<i>Hecalus macilentus</i>	Linnavuori, 1975	S7, S8, S15									
Leaf 1	Cicadellidae	<i>Hecalus sp.A</i>	Stal, 1864	S2, S3, S6, S7, S8, S9, S10, S11, S12									
SP3Leaf15	Cicadellidae	<i>Issidae sp.A</i>		S4, S6, S13							x		
SP3Leaf7	Cicadellidae	<i>Issidae sp.B</i>		S2, S6	x						x		
Leaf 4	Cicadellidae	<i>Kosasia typica</i>	Distant, 1910	S7, S8, S9, S15									
Leaf 32	Cicadellidae	<i>Ladya longipennis</i>	Theron, 1982	S1, S2, S4, S6, S7, S8, S12, S13						x			
Leaf 34	Cicadellidae	<i>Lualabanus near affinis</i>	Linnavuori, 1975	S8, S9, S15									
Leaf 5	Cicadellidae	<i>Mapochia collaris</i>	Distant, 1910	S13		x							x
Leaf 41	Cicadellidae	<i>Gen.nov. sp.A.</i>		S1, S4, S5, S6, S8, S9, S10, S11, S12, S13, S14, S15, S16								x	
Leaf 43	Cicadellidae	<i>Naudeus bivittatus</i>	(Naude, 1926)	S3, S15	x								
Leaf 2	Cicadellidae	<i>Paradorydium sp.A.</i>	Kirkaldy, 1901	S1, S2, S3, S4, S5, S6, S7, S8, S9, S10, S11, S12, S13								x	
SP3Leaf9	Cicadellidae	<i>Pravistylus sp.A</i>	(Naude, 1926)	S3, S6, S8, S15								x	
Leaf 31	Cicadellidae	<i>Pravistylus sp.B.</i>	(Naude, 1926)	S1, S3, S4, S5, S6, S7, S8, S9, S10, S11, S12, S13, S14, S15, S16									
SP3Leaf10	Cicadellidae	<i>Pravistylus sp.C</i>	(Naude, 1926)	S3	x			x				x	x
Leaf 39	Cicadellidae	<i>Recilia rugulans</i>	(Naude, 1926)	S1, S6, S7, S8, S10, S11, S12, S13, S14, S16									
Leaf 12	Cicadellidae	<i>Stirellus sp.A</i>	(Stal, 1866)	S6, S7, S11									
Leaf 13	Cicadellidae	<i>Stirellus sp.B</i>	(Stal, 1866)	S7, S8, S9, S10, S12, S13									
SP3Leaf12	Cicadellidae	<i>Stirellus sp.C</i>	(Stal, 1866)	S3, S4, S5, S6, S11									
Leaf 7	Cicadellidae	<i>Tetartostylus sp.A</i>	Wagner, 1951	S1, S2, S3, S4, S5, S6, S8, S9, S11, S13, S14, S15									
Leaf 36	Cicadellidae	<i>Tortotettix dispar</i>	Theron, 1982	S3, S6, S7, S8, S9, S10, S11						x			

Ref. No.	(Taxa) Family	Genus and species	Author	Sites	Unique					Endemic			Single
					B	UnB	1	2	3	SA	KZN	New	
Leaf 33	Cicadellidae	<i>Typhlocybinae sp.A</i>		S6, S8, S10, S12, S14									
Leaf 27	Cicadellidae	<i>Typhlocybinae sp.B</i>		S15	X		X						
Leaf 22	Cicadellidae	<i>Typhlocybinae sp.C</i>		S13		X			X				X
SP2Leaf24	Cicadellidae	<i>Typhlocybinae sp.D</i>		S3	X			X					X
SP2Leaf9	Cicadellidae	<i>Typhlocybinae sp.E</i>		S2, S3, S5, S6	X								
SP3Leaf31	Cicadellidae	<i>Typhlocybinae sp.F</i>		S13, S14		X			X				
SP3Leaf38	Cicadellidae	<i>Typhlocybinae sp.G</i>		S5, S14									
SP3Leaf37	Cicadellidae	<i>Typhlocybinae sp.H</i>		S1, S4	X			X					
Leaf 30	Cicadellidae	<i>Tzitzikamaia irrorata</i>	Linnavuori, 1961	S1, S3, S6, S7, S13, S14						X			
Leaf 40	Cicadellidae	<i>Tzitzikamaia sp.A</i>	Linnavuori, 1961	S1, S11, S12, S15						X			
	Hymenoptera												
Ant4	Formicidae	<i>Anoplolepis custodiens</i>		S6	X		X						X
H2	Formicidae	<i>Camponotus sp. A</i>		S1, S2, S3, S4, S5, S6, S7, S8, S10, S15									
H47	Formicidae	<i>Camponotus sp. B</i>		S1, S2, S3, S4, S5, S8, S15									
H50	Formicidae	<i>Camponotus sp.C</i>		S2, S3, S5, S6, S7, S8, S9, S10, S11, S12, S13, S14, S15									
Ant5	Formicidae	<i>Camponotus sp.D</i>		S1, S3, S4, S6, S7, S9, S10, S15									
H58	Formicidae	Myrmicinae sp.A		S4, S5, S6, S8, S9, S10, S11, S14									
SP2H3	Formicidae	<i>Pheidole sp. A</i>		S3, S7, S9, S10, S15									
H49	Formicidae	<i>Ponerine sp.A</i>		S1, S2, S3, S4, S5, S7, S8, S9, S10, S13, S14, S16									
H6	Formicidae	Formicinae sp. A		S3	X			X					X
H17	Formicidae	Formicinae sp. B		S6, S13, S14									
H31	Formicidae	<i>Crematogaster sp.A</i>		S3, S4, S8, S10, S11, S12, S15									
Ant14	Formicidae	<i>Lepisiota sp. A</i>		S8		X		X					X
Ant3	Formicidae	<i>Lepisiota sp. B</i>		S1, S3, S4, S5, S6, S9, S10									
H9	Formicidae	<i>Lepisiota sp. C</i>		S3, S4, S12									
H73	Formicidae	<i>Lepisiota sp. D</i>		S11		X			X				X
H64	Formicidae	<i>Leptogenys nitida</i>		S8, S16		X							

[illegible]

Ref. No.	(Taxa) Family	Genus and species	Author	Sites	Unique					Endemic			Single
					B	UnB	1	2	3	SA	KZN	New	
SP2L3	Pieridae	Pieridae sp. A		S5	X			X					X
L24	Hesperiidae	Hesperiidae sp.A		S11, S14		X			X				
L10	Hesperiidae	<i>Kedestes mohozutza</i>	Wallengren, 1857	S6	X		X						X
SP2L6	Hesperiidae	<i>Kedestes sp.A</i>		S8				X					X
L21	Lycaenidae	<i>Anthene sp.A</i>		S1, S2	X			X					
SP3L2	Lycaenidae	<i>Orachrysops subravus</i>	G.A. & S.F. Henning, 1994	S1	X		X			X			X
L2	Nymphalidae	<i>Danaus chrysippus aegyptius</i>	Linnaeus, 1758	S2, S7, S8, S14									
L23	Nymphalidae	<i>Hyalites anacreon</i>	(Trimon, 1868)	S3	X			X					X
L8	Nymphalidae	<i>Junonia octavia sesamus</i>	Trimen, 1883	S2, S5, S6, S7, S8, S12, S13, S15									
SP2L1	Nymphalidae	<i>Pseudonympha poetula</i>	Trimen, 1891	S6	X		X						X
SP3L1	Nymphalidae	<i>Serradinga clarki drakomontana</i>	G.A. & S.F. Henning, 1996	S2, S5	X		X			X			
L6	Nymphalidae	<i>Stygionympha wichgrafi</i>	VanSon, 1955	S4, S7, S9, S12, S15						X			
SP3L3	Papilionidae	<i>Papilio nireus</i>	Doubleday, 1845	S1	X			X					X
SP3L5	Pieridae	<i>Belenois aurota</i>	Fabricus, 1793	S2, S3	X			X					
L13	Pieridae	<i>Colias electo electo</i>	Linnaeus, 1763	S10, S15									
	(Oligochaetes)												
SP3Earth3	Acanthodrilidae	<i>Dichogaster sp.A</i>		S2, S4, S8			X						
SP3Earth30	Acanthodrilidae	<i>Acanthodrilidae sp.A</i>		S15	X								X
Earth1	Michrochetidae	<i>Proandricus sp.A</i>		S1, S2, S3, S4, S5, S6, S9, S12, S13, S14, S15, S16									
Earth3	Michrochetidae	<i>Proandricus sp.B</i>		S2, S4, S5, S6, S11, S12, S14, S15, S16								X	
SP3Earth8	Michrochetidae	<i>Proandricus sp.C</i>		S4, S5, S7, S8, S11, S12, S15, S16								X	
Earth16	Michrochetidae	<i>Tritogenia sp.D</i>		S13		X			X			X	X
O14	Acrididae	<i>Acrida bicolor</i>	(Thunberg 1815)	S4, S15	X								
	(Orthoptera)												
O13	Acrididae	<i>Acorypha nigrovariegata</i>	(I.Bolivar 1889)	S3, S4, S7, S15	X								
O6	Acrididae	<i>Anablepia dregei</i>	(Ramme 1929)	S3	X			X		X			X

Appendix 2: Indigenous flowering forb species found at Giants Castle. Unique species found in burnt (B), unburnt (UnB), frequently (1), intermediately (2) and infrequently (3) burnt grasslands are presented as well as the sites where each species was found, species with single individuals (S) and their various life forms.

Ref. no.	Family	Genus and species	Author	Sites	Unique species					S	Life form
					B	UnB	1	2	3		
SP31	Amaryllidaceae	<i>Apodolirium buchananii</i>	Baker	S2, S3, S4, S5	x			x			Geophyte - Bulb
SP35	Amaryllidaceae	<i>Hypoxis acuminata</i>	Baker	S2, S14							Geophyte - tuber
SP26	Amaryllidaceae	<i>Hypoxis angustifolia</i>	Lam.	S7	x		x				Geophyte - tuber
SP36	Amaryllidaceae	<i>Hypoxis gerrardi</i>	Baker	S1, S2, S3, S4, S5, S6, S7, S8							Geophyte - tuber
SP43	Amaryllidaceae	<i>Hypoxis rigidula</i>	Baker	S9, S11, S14, S15							Geophyte – tuber
SP37	Asclepiadaceae	<i>Asclepias cucullata</i>	(Schltr.) Schltr.	S2, S5, S8, S9, S10, S11, S14							Hemicryptophyte – perennial herb
SP55	Asteraceae	<i>Aster bakerianus</i>	Burt Davy ex C.A. Sm.	S1, S3, S6, S7	x						Hemicryptophyte – perennial herb
SP28	Asteraceae	<i>Aster confertifolius</i>	Hilliard & B.L. Burt	S6, S7	x		x				Hemicryptophyte – perennial herb
SP71	Asteraceae	<i>Berkheya setifera</i>	DC.	S7	x		x				Hemicryptophyte – perennial herb
SP67	Asteraceae	<i>Callilepis laureola</i>	DC.	S6, S7	x		x				Hemicryptophyte – perennial herb
SP11	Asteraceae	<i>Dicoma anomala</i>	Sond.	S3, S6, S7, S8, S9, S10, S11, S13, S14, S15							Hemicryptophyte – perennial herb
SP9	Asteraceae	<i>Europs laxus</i>	(Harv.) Burt Davy	S2	x			x			Hemicryptophyte – perennial herb
SP24	Asteraceae	<i>Gazania krebsiana</i>	Less.	S2, S3, S4, S9				x			Hemicryptophyte – perennial herb
SP23	Asteraceae	<i>Gazania linearis</i>	(Thunb.) Druce	S1, S15	x						Hemicryptophyte – perennial herb
SP49	Asteraceae	<i>Gerbera piloselloides</i>	(L.) Cass.	S4	x			x			Hemicryptophyte – perennial herb
SP73	Asteraceae	<i>Haplocarpha scaposa</i>	Harv.	S2, S3	x			x			Hemicryptophyte – perennial herb
SP8	Asteraceae	<i>Helichrysum adenocarpum</i>	Hilliard	S1, S2, S3, S4, S15	x						Hemicryptophyte – perennial herb

Ref. no.	Family	Genus and species	Author	Sites	Unique species					S	Life form
					B	UnB	1	2	3		
SP38	Asteraceae	<i>Helichrysum aureonitens</i>	Sch.Bip	S1, S2, S3, S4, S5, S6, S15	x						Hemicryptophyte – perenial herb
SP20	Asteraceae	<i>Helichrysum aureum</i>	(Hout.) Merr.	S4, S5, S6, S7, S11, S13, S16						x	Hemicryptophyte – perenial herb
SP1	Asteraceae	<i>Helichrysum auriceps</i>	Hilliard	S3, S5, S12, S13							Hemicryptophyte – perenial herb
SP63	Asteraceae	<i>Helichrysum chionosphaerum</i>	DC.	S15	x		x				Hemicryptophyte – perenial herb
SP39	Asteraceae	<i>Helichrysum coriaceum</i>	Harv.	S1, S3, S5, S6, S7, S13							Hemicryptophyte – perenial herb
SP5	Asteraceae	<i>Helichrysum glomeratum</i>	Klatt	S1, S3, S4, S5, S6, S7, S8, S9, S10, S11, S12, S13, S15							Hemicryptophyte – perenial herb
SP10	Asteraceae	<i>Helichrysum herbaceum</i>	(Andrews) Sweet	S2, S3, S4, S6, S7, S8, S9, S10, S11, S12, S14, S15							Hemicryptophyte – perenial herb
SP70	Asteraceae	<i>Helichrysum miconiifolium</i>	DC.	S7	x		x				Hemicryptophyte – perenial herb
SP18	Asteraceae	<i>Helichrysum odoratissimum</i>	Sweet.	S15	x		x				Hemicryptophyte – perenial herb
SP13	Asteraceae	<i>Helichrysum oreophilum</i>	Klatt	S4, S5, S6, S7	x						Hemicryptophyte – perenial herb
SP48	Asteraceae	<i>Helichrysum pilosellum</i>	(L.F.) Less.	S4	x			x			Hemicryptophyte – perenial herb
SP12	Asteraceae	<i>Helichrysum umbraculigerum</i>	Less.	S4	x			x			Hemicryptophyte – perenial herb
SP27	Asteraceae	<i>Hirpicium armeroides</i>	(DC.) Roessler	S6, S7	x		x				Hemicryptophyte – perenial herb
SP16	Asteraceae	<i>Schistostephium heptalobum</i>	(DC.) Oliv. & Hiern	S12		x			x		Hemicryptophyte – perenial herb
SP21	Asteraceae	<i>Senecio barbatus</i>	DC.	S11, S16		x			x		Hemicryptophyte – perenial herb
SP56	Asteraceae	<i>Senecio coronatus</i>	(Thunb.) Harv.	S1	x						Hemicryptophyte – perenial herb
SP22	Asteraceae	<i>Senecio macrocephalus</i>	DC.	S15	x		x			X	Hemicryptophyte – perenial herb
SP34	Asteraceae	<i>Senecio scitus</i>	Hutch & Burt Davy	S1, S2, S3, S4, S5, S6, S7, S8, S15							Hemicryptophyte – perenial herb

Ref. no.	Family	Genus and species	Author	Sites	Unique species					S	Life form
					B	UnB	1	2	3		
SP32	Asteraceae	<i>Ursinia tenuiloba</i>	DC.	S1, S3, S5, S11							Hemicryptophyte – perenial herb
SP54	Asteraceae	<i>Vernonia natalensis</i>	Oliv. & Hiern	S1, S10, S12							Hemicryptophyte – perenial herb
SP6	Campanulaceae	<i>Lobelia flaccida</i>	(C.Presl) A.DC.	S4, S5	x						Therophyte – annual herb
SP57	Campanulaceae	<i>Wahlenbergia capillata</i>	Brehmer	S1, S3	x			x			Hemicryptophyte – perenial herb
SP19	Campanulaceae	<i>Wahlenbergia fasciculata</i>	Brehmer	S15	x		x				Hemicryptophyte – perenial herb
SP15	Campanulaceae	<i>Wahlenbergia huttonii</i>	(Sond.) Thulin	S11, S13		x			x		Hemicryptophyte – perenial herb
SP3	Campanulaceae	<i>Wahlenbergia paucidentata</i>	Schinz	S5, S9, S11, S14							Hemicryptophyte – perenial herb
SP72	Commelinaceae	<i>Commelina africana</i>	C.B.Clarke	S2, S3, S7	x			x			Hemicryptophyte – perenial herb
SP41	Commelinaceae	<i>Ledebouria cooperi</i>	(Hook.f.) Jessop	S2, S4, S5	x			x			Geophyte - bulb
SP42	Commelinaceae	<i>Ledebouria sandersonii</i>		S1, S2, S3, S4, S5	x			x			Geophyte - bulb
SP29	Commelinaceae	<i>Ledebouria revoluta</i>	(L.f) Jessop	S6	x		x				Geophyte - bulb
SP7	Crassulaceae	<i>Crassula alba</i>	Forssk.	S1, S3, S9, S10				x			Hemicryptophyte – perenial herb
SP45	Euphorbiaceae	<i>Acalypha schinzii</i>	Pax	S4, S5, S7, S10, S11, S12, S14, S15, S16							Hemicryptophyte – perenial herb
SP65	Euphorbiaceae	<i>Euphorbia ericoides</i>	Lam.	S15		x			x	x	Hemicryptophyte – perenial herb
SP2	Gentianaceae	<i>Sebaea sedoides</i>	Gilg.	S4, S5, S6, S7, S13							Hemicryptophyte – perenial herb
SP59	Iridaceae	<i>Aristea cognata</i>	N.E. Br ex Weim	S11		x			x	x	Geophyte - rhizome
SP25	Iridaceae	<i>Moraea stricta</i>	Baker	S1, S6, S8, S9							Geophyte - corm
SP51	Iridaceae	<i>Moraea trifida</i>	R.C. Foster	S4, S7	x						Geophyte - corm
SP60	Iridaceae	<i>Watsonia lepida</i>	N.E.Br.	S11, S12		x			x		Geophyte - corm
SP17	Labiatae	<i>Stachys kuntzei</i>	Gurke	S14		x			x	x	Hemicryptophyte – perenial herb
SP14	Leguminosae	<i>Rhynchosia totta</i>	(Thunb.) DC.	S8		x		x		x	Hemicryptophyte – perenial herb

Ref. no.	Family	Genus and species	Author	Sites	Unique species					S	Life form
SP66	Liliaceae	<i>Albuca setosa</i>	Jacq.	S9, S13		x					Geophyte - bulb
SP46	Liliaceae	<i>Anthericum cooperi</i>	Baker	S5	x			x			Hemicryptophyte – perenial herb
SP53	Liliaceae	<i>Scilla nervosa</i>	(Burch.) Jessop	S1	x			x			Geophyte - bulb
SP62	Liliaceae	<i>Urginea tenella</i>	Baker	S15	x		x				Geophyte - bulb
SP4	Orchidaceae	<i>Habenaria dregeana</i>	Lindl.	S3, S5, S9, S11							Hemicryptophyte – perenial herb
SP52	Orchidaceae	<i>Eulophia zeyheriana</i>	Sond.	S1, S6, S7	x						Geophyte - tubers
SP68	Oxalidaceae	<i>Oxalis obliquifolia</i>	Steud. ex Rich	S2, S7, S8							Hemicryptophyte – perenial herb
SP33	Polygalaceae	<i>Polygala gracilentia</i>	Burt Davy	S1, S2, S4, S5, S6, S7, S8							Hemicryptophyte – perenial herb
SP74	Ranunculaceae	<i>Ranunculus multifidus</i>	Forssk.	S3	x			x			Hemicryptophyte – perenial herb
SP40	Rubiaceae	<i>Pentanisia angustifolia</i>	(A.Rich. ex DC.) Verdc.	S3, S4, S5, S6, S9, S10, S14, S15							Hemicryptophyte – perenial herb
SP44	Santalaceae	<i>Thesium costatum</i>	A.W. Hill	S5	x			x			Hemicryptophyte – perenial herb
SP47	Scrophulariaceae	<i>Hebenstretia dura</i>	Choisy	S5	x			x			Chamaephytes – perenial shrub
SP64	Sterculiaceae	<i>Hermannia woodii</i>	Schinz	S6, S15	x		x				Hemicryptophyte – perenial herb
SP30	Thymelaeaceae	<i>Gnidia kraussiana</i>	Meisn	S6, S11							Hemicryptophyte – perenial herb